AMPHIBIAN DIVERSITY CONSERVATION IN A CHANGING WORLD: A VIEW FROM MEXICO

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ABSTRACT

Amphibians are the most abundant terrestrial vertebrates on Earth. They are crucial in maintaining the transfer of energy and matter from freshwater to terrestrial systems and are also indicators of ecosystem health. Mexico hosts great amphibian diversity with high levels of endemism. Nevertheless, the knowledge of amphibian ecology in the country is at an early stage. This thesis aspires to contribute to the knowledge of Mexican amphibian ecology and to the understanding of the processes underlying amphibian responses to environmental changes.

To do so the thesis includes: 1) analyses from fine scales (at landscape level) based on data from two consecutive rainy seasons of fieldwork (nocturnal sampling), in two protected areas in southern Mexico, La Pera and Nahá; 2) at regional scales, analyses based on spatial databases of conservation instruments (i.e. environmental services, governmental, private, and community protected areas, etc.) generated specifically for Mexico; 3) to coarse scales (the whole country), analyses based on ecological niche modelling using the most complete database for Mexican amphibian records and climate layers developed purposely for the country. Thus, the thesis involves different time-scale processes, from ecological to biogeographical. In addition this thesis contains an analysis of the media representation of amphibian biodiversity threats and issues, specifically climate change, based on literature research. I was involved in the process of generating most of the databases used in this thesis.

Whilst the main theme of this thesis is amphibian conservation, it also encompasses a wide range of specific subjects. Firstly, foundational knowledge about amphibian conservation is established in Chapter I. Also, the region, Chiapas in southern Mexico, where the fieldwork was carried out for two consecutive years (2009-2010) is described within a historical context and a glossary of terms is presented. In Chapter II, based on one year of fieldwork in two fragmented protected areas (PAs) of different management category, one state and one biosphere reserve, I examine how community structure is related to key features of the environment. The possible effects of governance issues in protected areas and their relationship with the drivers of amphibian metacommunities are also explored. A total of 144 transects were sampled from 33 patches in La Pera and 140 transects from 36 patches in Nahá. In each transect environmental variables were recorded. Partial Canonical Correspondence Analyses (partial CCA) indicated that the drivers of metacommunity patterns vary between the sampled landscapes. Habitat structure explained more of the community variation than either space or weather conditions: > 50% for La Pera and 30% Nahá; but the relationship to geographical space and local climate varied greatly. The differences in relationships among the environmental variables and between them and the amphibian metacommunities finds expression also in the pattern of human exploitation of these areas, which has latterly at least also found expression through differing governance.

In Chapter III, the effects of environmental variation on metacommunities structure are explored. Metacommunity theory assumes that emergent properties can be determined that characterise a set of linked communities within a landscape. It follows that change in environmental conditions should generate changes in the metacommunity structure. In La Pera a total of 30 patches were sampled, with a total of 120 transects in 2009, and 133 transects in 2010. In Nahá 31 patches were sampled, with a total of 111 transects in 2009 and 122 transects in 2010. In the analyses of this chapter only transects sampled in both years are included. The total number of individuals increased greatly from 2009 to 2010, but the most abundant species between surveyed years varied slightly, in both areas. In La Pera metacommunity the structure changed from quasi-Clementsian to quasi-Gleasonian, while in Nahá it changed from Clementsian to Gleasonian. CCA show that the variance explained between years was similar. Re-arrangements in the metacommunity structures linked to environmental changes are observed. Results show that amphibian metacommunity structure can change with short environmental changes or disturbances, mainly weather variations from one year to another. This would suggest that metacommunity structures are a dynamic property in fluctuating systems.

The aim of Chapter IV is to assess patterns of beta diversity for Mexican terrestrial vertebrates, and explore their relationships with environmental heterogeneity metrics at different spatial scales, identifying the most important surrogates at each spatial scale. The analyses in this chapter are based on the most complete database of Mexican terrestrial vertebrates, comprising distribution maps of 2513 species: 883 resident birds, 344 mammals, 364 amphibians and 811 reptiles. Higher β-diversity values are found along mountain ranges for amphibians, reptiles and mammals, whereas for birds high values are also found on the Mexican Plateau. Results demonstrate that the relationships between β-diversity and the environmental heterogeneity surrogates vary in form and strength across scale and between vertebrate groups.

In Chapter V, I set out to characterize at fine scale, alpha and beta diversity patterns for Mexican amphibians and analyze how these patterns might change under a moderate climate-change scenario, and to highlight the overall consequences for amphibian diversity at the country level. The analyses are performed with a climatic envelope modelling approach using MaxEnt and a set of climatic layers developed specifically for Mexico. Models of future scenarios for Mexican amphibian alpha and beta diversity for 2020, 2050, 2080, show that high levels of species extinctions follow if low dispersal capability and high presence thresholds are used, but the overall geographic pattern of beta diversity remains *stable.* Zones of high beta diversity are associated with topographic formations, whilst the values of beta diversity initially increase, then decline over time under a moderate climate scenario. Extinctions (complete loss of range within country boundaries) are particularly intense during

the period 2020–2050. The results imply that heterogeneous zones associated with mountain ranges will remain particularly important for amphibian diversity and thus such areas should be targeted for continued conservation prioritization in the face of climate change scenario.

There is an inevitable degree of uncertainty associated with future climate projections and the possible ecological and biogeographical responses. Nevertheless, the climate change projections are typically translated in the media as certain. Chapter VI illustrates the interplay of these competing communication goals, through a review of the representations of the golden toad (*Incilius* [*Bufo*] *periglenes*) in print media and in peer-reviewed literature. The concept of “distanciation”, which means placing a distance between two connected issues (cause and effect), is introduced in this chapter, along with the potential issues that this process may generate in the implementation of conservation strategies. Distanciation is a perception created in the members of the audience of the media, but does not imply a total separation regarding an issue. For example, the audience is interested in the news about climate change effects, but they feel distant because the effects of climate change might be evident within a large time period (i.e. 2050); and although the causes are occurring now, the audience does not see the urgent need to act.

Chapter VII represents the first attempt to analyze the status of conservation of some microendemic amphibians in Latin America when some social initiatives (e.g. private and community reserves) are included in the assessment. The efficiency of the existing set of governmental protected areas (PA), and the contribution of social initiatives for land protection of amphibians are evaluated. The chapter shows how the role of land conservation, through social initiatives, is fast becoming a crucial element for the survival of a substantial number of species not protected by state-designated PA.

Given the current speed of land use change, we cannot expect to save all species from extinction, and so it must be decided, rather quickly, how to focus the limited resources available to prevent the greatest number of extinctions. In Chapter VIII, a simple conservation triage method is proposed. Using this triage method, the threat status for 145 micro-endemic Mexican amphibian species is evaluated, alongside potential threat abatement responses derived from existing policy instruments and social initiatives. Both indicators are combined to provide broad-scale conservation strategies that would best suit amphibian micro-endemic buffered areas (AMBAs) in Mexico. Results show that almost 25% of the species analysed urgently need field-base verification to confirm their persistence; for the rest, a conservation strategy is developed based on existing conservation instruments. Monitoring populations is essential in order to understand temporal patterns of community change and to better comprehend the underlying processes that shape and maintain biodiversity. These aspects, along with a general discussion focused mainly on the distanciation problem are addressed in Chapter IX.

Anotheca spinosa, La Pera 2009. Mother taking care of her tadpoles.

“UNA SOCIEDAD JERÁRQUICA SÓLO ES POSIBLE

GENERANDO IGNORANCIA Y POBREZA”

(A HIERARCHICAL SOCIETY IS ONLY POSSIBLE

BY CREATING IGNORANCE AND POVERTY)

PANCHO VILLA IN TAIBO II, 2006

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Morning walk exploring the biosphere reserve of Nahá, 2009.

PREFACE

(OR A WARNING TO THE READER)

This thesis is composed of seven main chapters, an introduction and a general discussion. Each chapter is self-contained and has been submitted, or will be submitted, for review and publication. While the format and section numbering of the main text has been unified for the thesis, the citation and referring style varies as required by the individual journals. At the beginning of each chapter, I specify the journal to which it has been submitted and the current status of the manuscript. This information is summarized in a list below. The main chapters are not very long *per se*, but each of them has at least one appendix. I hope you enjoy any bit of this thesis you choose to read as much as I've enjoyed writing it.

An anecdote seems appropriate to exemplify my fascination for amphibians and inexhaustible desire to understand almost everything pertaining to them. When I started my master degree in 2004 there were 6,035 described species of amphibians: by 2012 the figure was 6,936 species. More than 900 species in eight years! Isn't it enthralling?

This thesis is submitted under departmental guidelines, prescribing that the thesis comprise an introduction and discussion along with at least four empirical chapters submitted for publication to refereed journals.

Ochoa-Ochoa, L.M. & R.J. Whittaker. Amphibian metacommunity structure drivers vary between two protected areas in Chiapas, Mexico. ***Conservation Biology*** (in preparation).

Ochoa-Ochoa, L.M. & R.J. Whittaker. Variability of amphibian metacommunities in fluctuating environments: key-factor for long-term persistence? ***Journal of Animal Ecology*** (in preparation).

Ochoa-Ochoa, L.M., M. Munguía-Carrara, A.G. Navarro-Sigüenza, O.A. Flores-Villela, V.

Sánchez-Cordero & P. Rodríguez. Multi-scale effects of environmental heterogeneity on β-diversity patterns of Mexican terrestrial vertebrates. ***Journal of Biogeography*** (Submitted 20th February, 2012).

Ochoa-Ochoa, L.M., P. Rodríguez, F. Mora, O. Flores-Villela, & R.J. Whittaker. Climate change and amphibian diversity patterns in México. ***Biological Conservation*** (Accepted 8th March, 2012).

Ochoa-Ochoa, L.M., R.J. Whittaker & R.J. Ladle. The demise of the golden toad and the creation of a climate change icon species. ***Conservation and Society*** (Submitted 15th February 2012).

Ochoa-Ochoa, L.M., J.N. Urbina-Cardona, L.B. Vázquez, O. Flores-Villela & J. Bezaury-Creel. **2009.** The Effects of Governmental Protected Areas and Social Initiatives for Land Protection on the Conservation of Mexican Amphibians. ***PlosOne*** **4**: e6878.

Ochoa-Ochoa, L.M., J. Bezaury-Creel, L.B. Vázquez & O. Flores-Villela. **2011.** Choosing the survivors? A GIS-based triage support tool for micro-endemics: application to data for Mexican amphibians. ***Biological Conservation*** **144:** 2710–2718.

Canseco-Márquez L., J.L. Aguilar-López, R. Luría-Manzano, E. Pineda & **L.M. Ochoa-Ochoa**. A new species of treefrog of the genus *Duellmanohyla* (Anura: Hylidae) from southern Mexico. ***Copeia*** (Submitted 10th August, 2010; resubmission was encouraged and new genetic analyses were required).

Canseco-Márquez et al. submitted was not primarily my work. The manuscript is presented (in Appendix A) just as an illustration of the still unknown amphibian diversity of Mexico. Journal authorship statements for all co-authored papers are attached at Appendix B.

to Rafa

because every morning you make me want to sing

funny songs of love,

every time I’m in your arms you make me smile,

and listening to you I feel confident:

there is hope for this World.

Male of *Agalychnis callidryas* calling, Nahá 2010

I. GENERAL INTRODUCTION

Our brain, about of a cauliflower size,
inside fits the heaven, sky, earth, sun, and stars,
in it fits Plato's ideas, Beethoven's music, French Revolution, Tolstoy’s novel,
and the desert and the oceans, even the dinosaurs and the marine monsters,
the hope of humanity, the desires, errors and fantasies,
there is space for everything...
Amos Oz, 2006

SECTION 1. A BRIEF REVIEW OF AMPHIBIAN CONSERVATION

> "All species encounter stochastic disasters now and again."
>
> Rosenzweig 2003, p. 197

Humans, like any other species, can affect their environment. But since the Neolithic Revolution around 10,000 BC, human populations have increasingly modified the ecosystems in which they live. For example, some authors argue that, in the course of prehistory, humans were the final factor leading to the extinction of mammoths in Europe (Nogués-Bravo *et al.*, 2008), large mammals in North America (Barnosky *et al.*, 2004), and megafauna in Australia, Tasmania, and New Zealand (Turney *et al.*, 2008). Anthropogenic activities have had more widespread and diverse effects on biodiversity, particularly after the Industrial Revolution in the 19th Century. Moreover, the over-use of all kinds of fossil fuels – coal, oil, and its derivates – has resulted in anthropogenic climate change. Expansions of domesticated ungulates (cattle, sheep, and goats) and agricultural frontiers, thanks to technological advances, have transformed the world's ecosystems into fragmented semi-natural landscapes (Dirzo & Raven, 2003; Ehrlich & Pringle, 2008; Dornelas, 2010). Moreover, the increase in use of chemicals on farmlands (pesticides and agrochemicals), the production of solid wastes, overfishing, the introduction of invasive non-native species and air pollution have significantly modified almost every place on Earth. According to the current mainstream environmental scientific orthodoxy, when these various forms of environmental changes are combined with the implications of global warming, the outcome could be the next mass extinction on Earth (e.g. Myers *et al.*, 2000; Thomas *et al.*, 2004; Wake & Vredenburg, 2008).

Amphibians are mostly rather small poikilothermic animals, with just a few exceptions, such as the giant salamanders of the genus *Andrias,* which can measure up to

1.8m. The class is divided into three orders: Anura (frogs and toads), Caudata (salamanders), and Gymnophiona (caecilians or limbless amphibians). The amphibian orders have different diversity patterns (Fig. I-1). Amphibians have a huge variety of breeding strategies and some species provide parental care. Most of their respiration is done through the skin. The life span is known for perhaps around 100 species and only for individuals in captivity. For example, the life span of *Xenopus laevis* on this basis is known to be ~15 years. Similarly, the dispersal capability, ranging to more than 15km/per year in the case of *Rhinella marina* (e.g. Marsh & Trenham, 2001), is also known only for a handful of species.

Amphibians are one of the most abundant groups of vertebrates in tropical environments (Stebbins & Cohen, 1997). They play integral roles in connecting aquatic and terrestrial systems, influencing primary production, and transferring energy and organic matter along food webs as herbivores, predators, and prey (Whiles *et al.*, 2006). This taxonomic group has been on the Earth for over 350 million years, and has survived great environmental changes. They can be found in almost every major terrestrial environment on Earth (Fig. I-1), but the tolerances of individual species to shifts in climatic and ecological factors are in general narrow, thus they are very susceptible to environmental changes (Duellman & Trueb, 1994; Jiang & Morin, 2004). Hence amphibians are considered to be a key indicator group of an ecosystem's health (Welsh & Ollivier, 1998).

Over the last two decades, amphibians have come to be regarded as one of the most threatened taxonomic groups. Widespread concern gathered momentum at the first World Conference of Herpetology in 1989 (Sarkar, 1996), where several scientists agreed that there was an apparent general "declining" trend among amphibian populations in different parts of the world (Blaustein & Wake, 1990; Blaustein & Dobson, 2006). Six principal threats have been identified for amphibian diversity (Alford & Richards, 1999; Gibbon *et al.*, 2000; Collins, 2003; Alford *et al.*, 2007): 1) introduction of alien species (e.g. Kats & Ferrer, 2003);

2) over-exploitation and the pet trade (e.g. Altherr *et al.*, 2011); 3) emerging diseases, including fungal infections (e.g. chytrids), and viruses (Lips, 1998, 1999; La Marca *et al.*, 2005; Lips *et al.*, 2005; Crawford *et al.*, 2010); 4) global climate change (e.g. Donnelly & Crump, 1998; Beebee, 2002; Araújo *et al.*, 2006; Pounds *et al.*, 2007; Wake, 2007) and ultraviolet radiation (Blaustein *et al.*, 1996, 1999; Bruner *et al.*, 2002; Weyrauch & Grubb, 2006; Alton *et al.*, 2010); 5) pollution including DDT, heavy metals (Lefcort *et al.*, 1998), and pesticides (e.g. Krest *et al.*, 2003; Rohr *et al.*, 2003, 2008; Rohr & Palmer, 2005; Solomon *et al.*, 2008); and finally 6) land use change representing landscape modifications, habitat fragmentation, and habitat loss through deforestation (e.g. Bell & Donnelly, 2006; Cushman, 2006; Hillers *et al.*, 2008). Land use change has been identified as the major threat for amphibian diversity loss by some authors (e.g. Alford & Richards, 1999; Alford *et al.*, 2007; Fischer & Lindenmayer, 2007).

General assumptions about amphibian community ecology are commonly made from very few studies compared to the number of species of amphibian in the world, 6,771 according to Frost (2011) or 6,936 according to AmphibiaWeb (2012). There is therefore a lack of solid data in order to properly judge the level of threat to the survival of the vast majority of species (Whittaker *et al.*, 2005). This thesis aspires to contribute to the knowledge of Mexican amphibian ecology and to the understanding of the processes underlying amphibian responses to environmental changes. Ultimately, this thesis aims to make a contribution that will help amphibian conservation in the long-term.

Mexico is considered to be one of the mega-diverse countries of the world (Myers *et al.*, 2000). It has 375 species of amphibians, of which more than 60% are endemic (Frías-Alvarez *et al.*, 2010). However, in Mexico not only is the knowledge of amphibian ecology at an early stage but so too is the status of the taxonomic records. For example, in the decade between 1993 and 2003, 26 frog species and 31 salamanders were described as new taxa (Flores-Villela & Canseco-Márquez, 2004; and see Appendix A of the thesis).

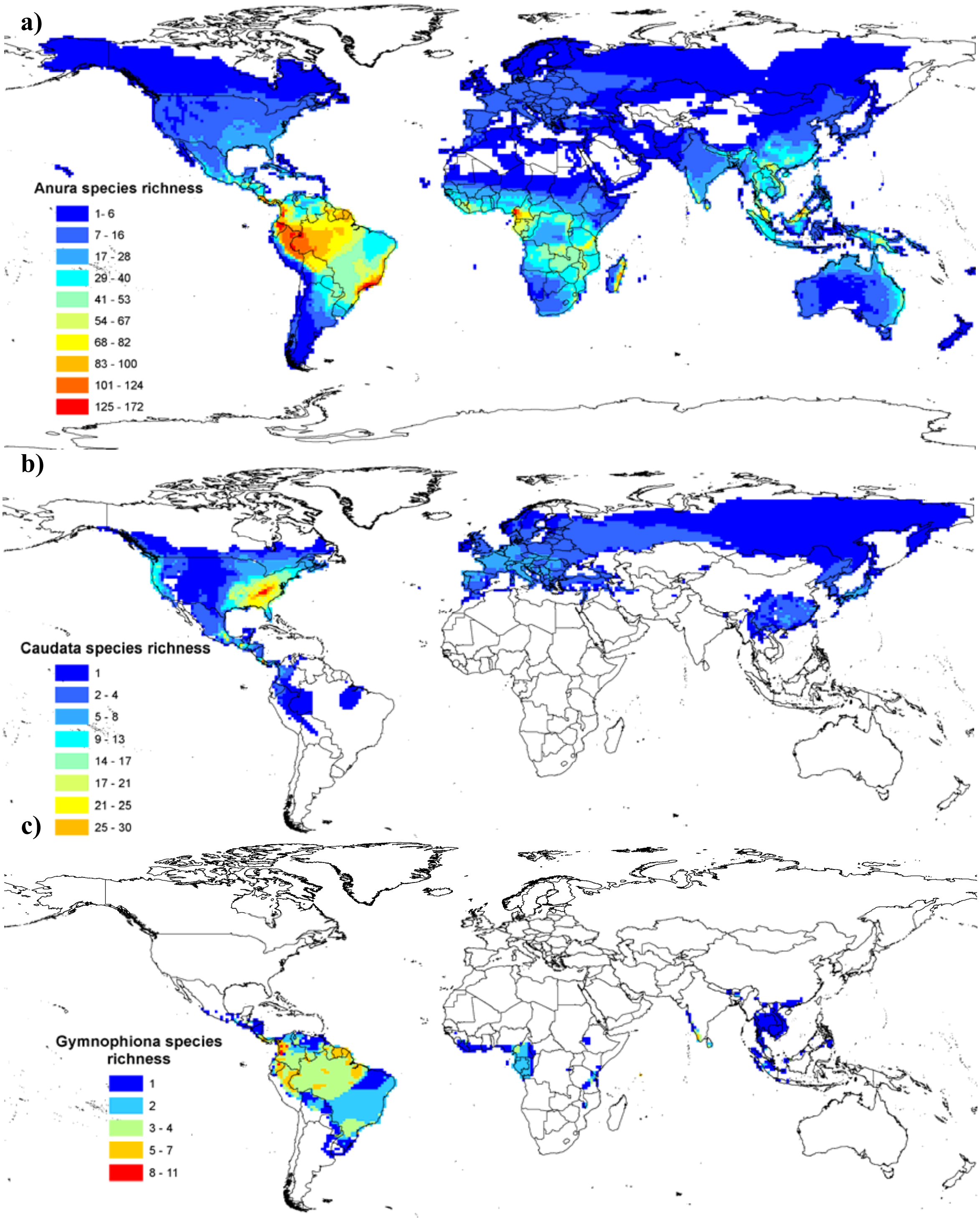


Figure I-1. Amphibian species richness in the world. a) Anura, b) Caudata, and c) Gymnophiona. **Source data: IUCN Spatial Data (IUCN, 2010). Maps generated with ArcGIS 9.3.1 (ESRI, 2009).**

It is expected that more amphibian taxa will be described in the next few years, despite the signs of threats such as the presence of chytridiomycosis in wild and captive populations (Frías-Alvarez *et al.*, 2008).

Nowadays, Neotropical amphibians are considered highly threatened by deforestation (Fig. I-2), for example, recent data from Mexico and Guatemala show the critical situation of many plethodontids (Rovito *et al.*, 2009). These declines have been linked to the deforestation of lowlands and pre-montane zones, which has been linked to an increase in the elevation of the cloud base (Lawton *et al.*, 2001; Nair *et al.*, 2003; Ray *et al.*, 2006), reducing humidity in the forest floor, and thus severely affecting some terrestrial amphibians.

Mexico ranks 4th in the world for amphibian diversity in terms of number of species (AmphibiaWeb, 2012), or 5th according to the Global Amphibian Assessment (IUCN, 2011). Of the 250 endemic species, 80% are micro-endemics, i.e. they are species with very restricted distribution range (Johnson *et al.*, 2001; Ochoa-Ochoa & Flores-Villela, 2006; Frías-Alvarez *et al.*, 2010). Endemics and/or highly rare species are expected on grounds of parsimony to be more prone to extinction due to habitat loss and other drivers (Lehtinen *et al.*, 2003; Urbina-Cardona *et al.*, 2006). Given the foregoing, it is perhaps unsurprising that only Colombia (with more than 700 species) has more endangered amphibian species according to IUCN assessments (IUCN, 2011, Fig. I-2).

It has been estimated that fragmentation threatens 89% of Neotropical amphibians (Young *et al.*, 2004) through population isolation, inbreeding, and edge effects. Another important point is the increasing disconnection between aquatic and terrestrial environments, both of which are essential for amphibian reproduction and persistence (Stuart *et al.*, 2004; Becker *et al.*, 2007, 2010). Transformation of tropical forests has had a long, shattering history, which over recent centuries has been driven by imperialism and colonialism, and often entangled in different culture senses of ownership of the world (K. Buckingham et al. *in* *prep*). As a consequence, most tropical areas have become complex systems that contain zones of different degrees of transformation. Mexico is no exception to this.

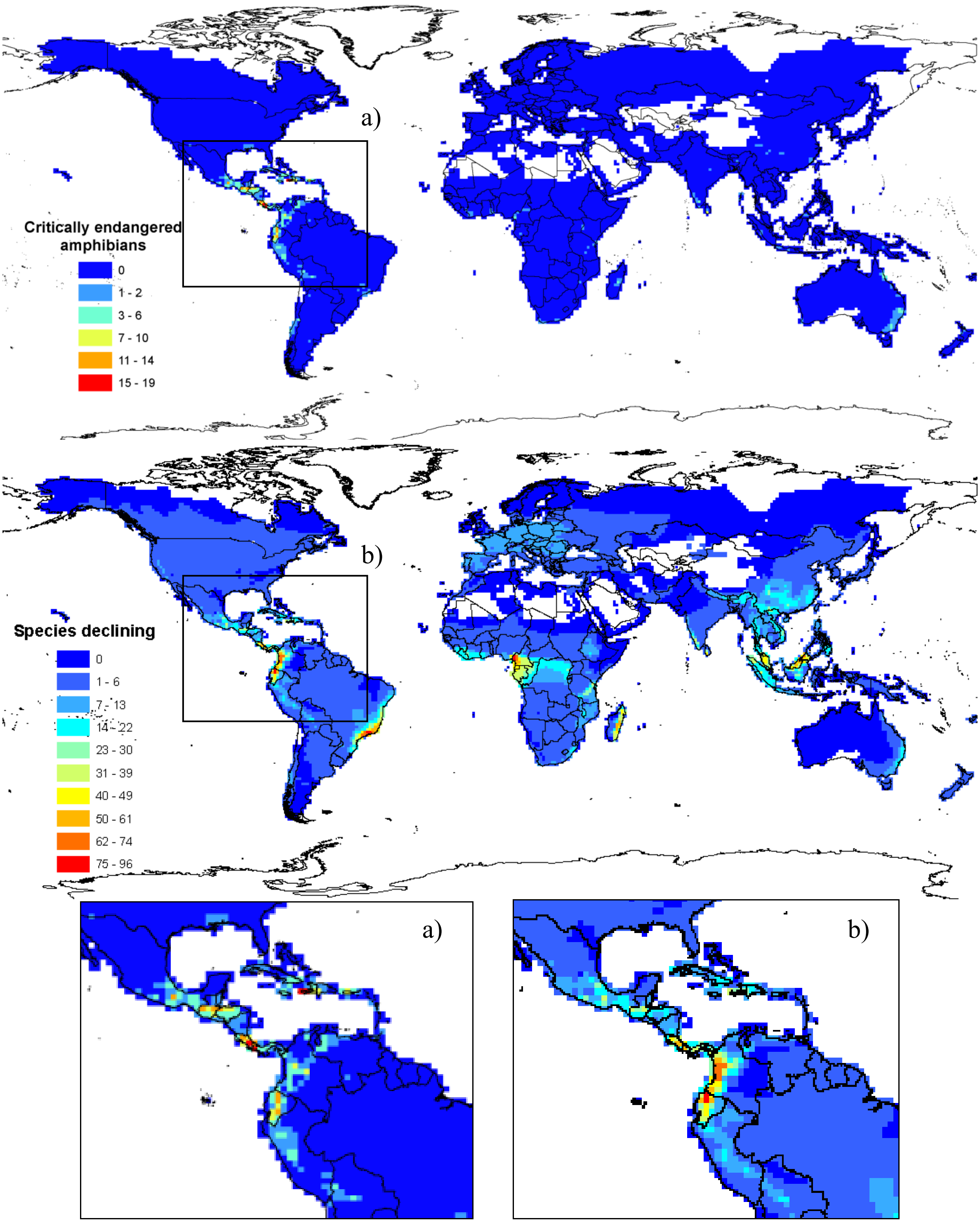


Figure I-2. Distribution of critically endangered (top), and 'declining' (bottom) amphibians. Zoom-in to the Mesoamerican Transition zone and surrounding areas, a) critically endangered, and b) 'declining' amphibians. Source data: species distribution of IUCN Spatial Data (IUCN, 2010). Maps generated with ArcGIS 9.3.1 (ESRI, 2009).

The fieldwork for this thesis was carried out in two protected areas (PA) under different categories of protection, La Pera, a state PA, and Nahá, a biosphere reserve. Both are located in the state of Chiapas in southern Mexico. It has been pinpointed as a key area for conservation, both at a national and global level, because of its vast ecological and cultural richness. Chiapas has a complex topography and high species diversity, including more than 100 species of amphibians, as well as an ancient and complex history of human civilizations.

Therefore, ecosystems within this region have a huge biological and social value (Dirzo & Raven, 2003). The recent history of the region of Chiapas is heartbreaking. Three historical facts tightly related to fragmentation and conservation status must be highlighted. 1) **Uprooted people:** in 1972, in order to accomplish the agreements of the "Reforma Agraria 1853", several groups of people were displaced from their places of origin. Others were encouraged to settle in the region by land grants (50 ha for "mestizos or ladinos", 20 ha for indigenous people). This kind of land redistribution caused two main persisting conflicts: i) land ownership conflicts (Castillo, 2000) and ii) settlers lacking *traditional ecological knowledge* about the surrounding environment. 2) **Land conversion subsidy:** in the same decade (1970s) the use of subsidies promoting the conversion of tropical rain forest to cattle-land was initiated. For this purpose a National Commission of Clearing was created. And it oversaw the most significant period of deforestation of tropical rain forest in the history of the country, alongside the promotion of new settlements. 3) **Exploitation of Precious woods:** selective cutting has brought about changes in tree communities. In addition, several clearing concessions were granted, e.g. from 1954 to 1963 the timber company "Maderera Maya" (with US capital) exploited 437,334 ha (de Vos, 2002), and from 1974 to 1988 just one of the companies, "COFOLASA", got the concession to clear 1,308,312 ha (Castillo, 2000). On top of that, a huge wildfire affected most of the highlands in 1998. As a result, the region is a complex and dynamic matrix of cattle pasture, abandoned pasture, primary forest and exploited forest.

It has been proposed that in fragmented landscapes, populations of plants and animals can behave as metapopulations (e.g. Opdam, 1991; Bascompte & Sole, 1996; Marsh & Trenham, 2001; Fortuna *et al.*, 2006), and communities (sets of populations) as metacommunities (Leibold & Mikkelson, 2002; Leibold *et al.*, 2004; Holyoak *et al.*, 2005). Nevertheless, a question arises, should all the metacommunities (those of the same or similar composition of species) respond in similar ways to environmental factors? Or should it be expected that different combinations of environmental factors characterise different landscapes, thereby generating different arrangements of metacommunities? These questions are addressed in Chapter II based on four months of fieldwork in Chiapas. This Chapter also compares how key features of protected areas, in terms of resources, governance, people's awareness, etc. may lead to changes in habitat structure, influencing the characteristics of the metacommunities.

Environmental changes are in many ways the norm: they have occurred, are occurring and will occur at different intensities, in every place, all the time. Therefore, the environmental structure of landscapes will change either by human intervention, climate (initially via weather variability) or both. Environmental changes can be long lasting ("permanent" in ecological time scales i.e. within the life span of a frog), or temporary: the former could be called *stress* and the latter *disturbance* (but see Lorrillière *et al.*, 2012). Chapter III addresses how communities respond to temporary changes in the form of responses to local weather conditions.

Mexico has a privileged geographic location. Situated between two geographical realms, namely the Nearctic and Neotropic, most of the country lies in a transition zone: the Mesoamerican Transition Zone (Fig. I-3; and see Johnson *et al.*, 2001). As a result, it is probably one of the most fascinating places on earth for biogeographical studies. It has an extremely complex topography, relatively modest α-diversity but notoriously high β-diversity. Biogeographers typically associate increased β-diversity with increased environmental heterogeneity, but the particular relationships between β-diversity and different facets of environmental heterogeneity remain relatively unexplored. This is particular the case for Neotropical amphibians. Thus, the relationship between β-diversity and environmental heterogeneity is the topic of Chapter IV.

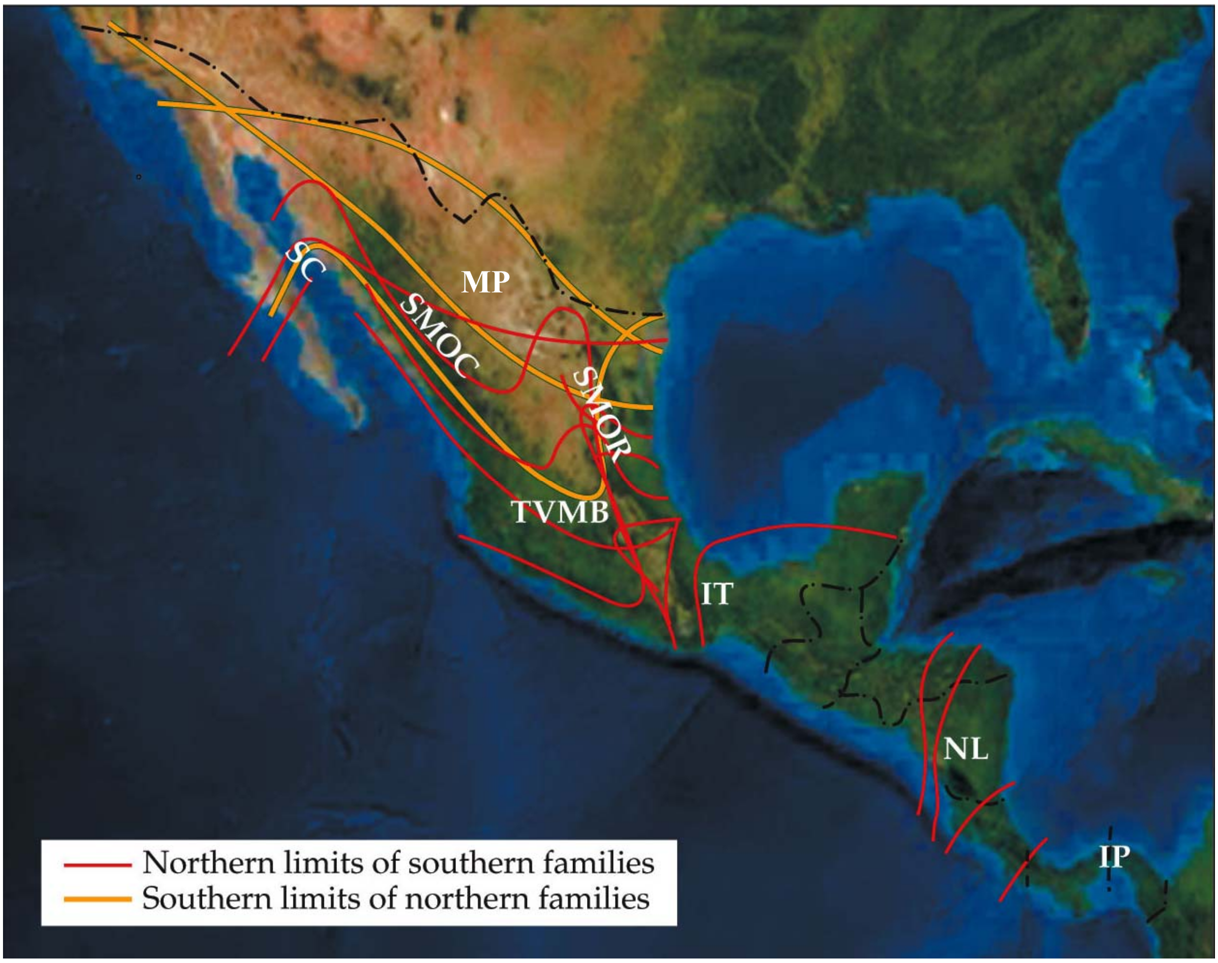


Figure I-3. Mesoamerican Transition Zone (MTZ). Northern limits of ranges of Neotropical mammal families (red lines) and southern limits of the range of Neartic families (yellow lines). Similarly complex patterns occur in nearly all taxa. A prominent feature of this transition zone is the remarkably complex topography, including the Central American-South American transition across the Isthmus of Panama (IP), the Nicaragua lowlands (NL), the Isthmus of Tehuantepec (IT), the Trans-Mexican Volcanic Belt (TMVB), the Sierra Madre Occidental (SMOC), the Sierra Madre Oriental (SMOR), the Mexican Plateau (MP), and the Sea of Cortés (SC). This figure and the legend have been modified from Lomolino *et al.* (2010, p. 382).

As mentioned before, habitat fragmentation has been recognized as probably the principal cause of diversity loss at global scale (Cushman, 2006; Gallant *et al.*, 2007). However, many scientists argue that climate change will become a greater threat for biodiversity in the next few decades (Malcolm *et al.*, 2006; Pounds *et al.*, 2007; Calosi *et al.*, 2008; Bickford *et al.*, 2010). Climate is a major controlling factor for species distribution (e.g. Woodward, 1987; Hawkins *et al.*, 2003; Pearson & Dawson, 2003). Recent evidence shows a direct effect of contemporary climate change on shifts in species distributions (Walther *et al.*, 2002; D'Amen & Bombi, 2009). By simple extension, we should expect changes in biodiversity patterns whenever climate or other major controlling environmental variables change significantly (Whittaker *et al.*, 2001; O'Brien, 2006). In Chapter V, I explore how amphibian diversity patterns might change under a climate change scenario, emphasizing β-diversity patterns, which are important aspects of diversity patterning that have been little studied in this context.

The period 1987 to 1992 witnessed something of a shift in the United Nation's focus, from "poverty reduction in developed countries" to "biodiversity crisis", including climate change, biodiversity and forests (McManus, 2000). Climate change became one of the main issues during the United Nations Conference on Environment and Development (UNCED) in 1992 – also known as the "Rio summit" – and the following gatherings of the Conference of the Parties (COP) were the focus of close media attention globally. As climate change increasingly became established as a major priority among the UN members in the late 1990s, it became, for conservationists, like a train with no brakes and the only option for conservationists was to jump on board or risk being left on the platform. Some non-governmental organizations (NGOs) embraced the climate change priority enthusiastically, e.g. Jennifer Morgan, director of the World Wide Fund for Nature's climate change's campaign said: "Global warming means a horrifying future for nature" (*The Times*, London, August 31, 2000). But climate change has proven to be a very complex subject, and all future climate models, even if based on the most accurate data, feature numerous sources of uncertainty. I explored these aspects in Chapter VI, which focuses on the first species claimed to be have driven to extinction by contemporary climate change: the golden toad (*Incilius* [*Bufo*] *periglenes*). It reflects on the potential implications for public perceptions of uncertainty in relation to the rather fatalistic statements of many commentators.

A key strategy for protecting biodiversity from human-exploitation pressures has been the establishment and maintenance of protected areas (PAs). However, typically PAs are, to varying degrees, isolated from one another, while often the natural biological pathways for plant and animal dispersal have become increasingly disrupted by anthropogenic barriers (Becker *et al.*, 2007, 2010). In this sense, isolated PAs managed by either federal or local governments alone are not effective in maintaining biodiversity; thus, the necessity of developing representative and interconnected conservation area networks to preserve biodiversity is becoming more important (e.g. Rodrigues *et al.*, 2004). Recently, several calls have been made to recognise local participation as a core element of conservation strategies (Zimmerer *et al.*, 2004; Vermeulen & Sheil, 2007). Social initiatives for land conservation therefore play a crucial role in increasing not just the range of instruments of protection, but also the area under protection. They also raise awareness of the threatened and endemic species, leading to efforts to ensure their persistence. These social initiatives are based on cooperative schemes where strong social participation is used to implement conservation actions. In Chapter VII, I explore the possible benefits of implementing social initiatives for Mexican amphibians.

Given the current speed of land use change, we cannot expect to save all species from extinction, and so it must be decided how to best focus the limited resources to prevent the greatest number of extinctions. The aim of Chapter VIII is to support prioritization of conservation strategies within the context of often rapidly changing patterns of land use, such as those currently found in Mexico. This includes the adoption of a wide range of conservation instruments to build up more efficient strategies.

Finally, in the general discussion (Chapter IX) the key findings of the thesis are discussed within a wider context. In particular, I provide further discussion of the problem of *distanciation* in conservation. *Distanciation* occurs when the media are involved in a process of separating cause and effect through the construction of space and time (McManus, 2000; Rantanen, 2005). I argue that d*istanciation* a key societal problem that must be solved if we want to halt the biodiversity crisis.

SECTION 2. GLOSSARY OF TERMS AND CONCEPTS

My research pays frequent reference to the following concepts: β-diversity, *distanciation*, ecological space, environmental change, habitat, metacommunity, and niche. These and other terms that occur in several places within the thesis are briefly defined.

β-diversity has been calculated in innumerable ways (for reviews see Koleff *et al.*, 2003; Tuomisto, 2010). Within the present thesis I mostly use R.H. Whittaker's β-diversity, $\beta=\gamma/\alpha_{average}$ (Whittaker, 1972). However, in Chapter IV, I use a different but not uncommon way of calculating the same measure of β-diversity. This form is based on the proportion of a region occupied by each species. When using this approach it is necessary to know the distribution range size of each species in the region or at least to have a very good approximation (the full derivation is presented in Appendix 1 of Chapter IV).

β-diversity has often been calculated as the ratio among two scales of species richness values and it is called "scaling β-diversity" (Fig. I-4a). The small scale has been conventionally called "locality" and the coarse scale "region", although there have been several papers discussing the geographical extents over which each term may be applied (e.g. Whittaker *et al.*, 2001; Tews *et al.*, 2004). There are three possible iterative procedures to calculate the scaling of β-diversity at *continuous* scales, as shown in Figure I-4.

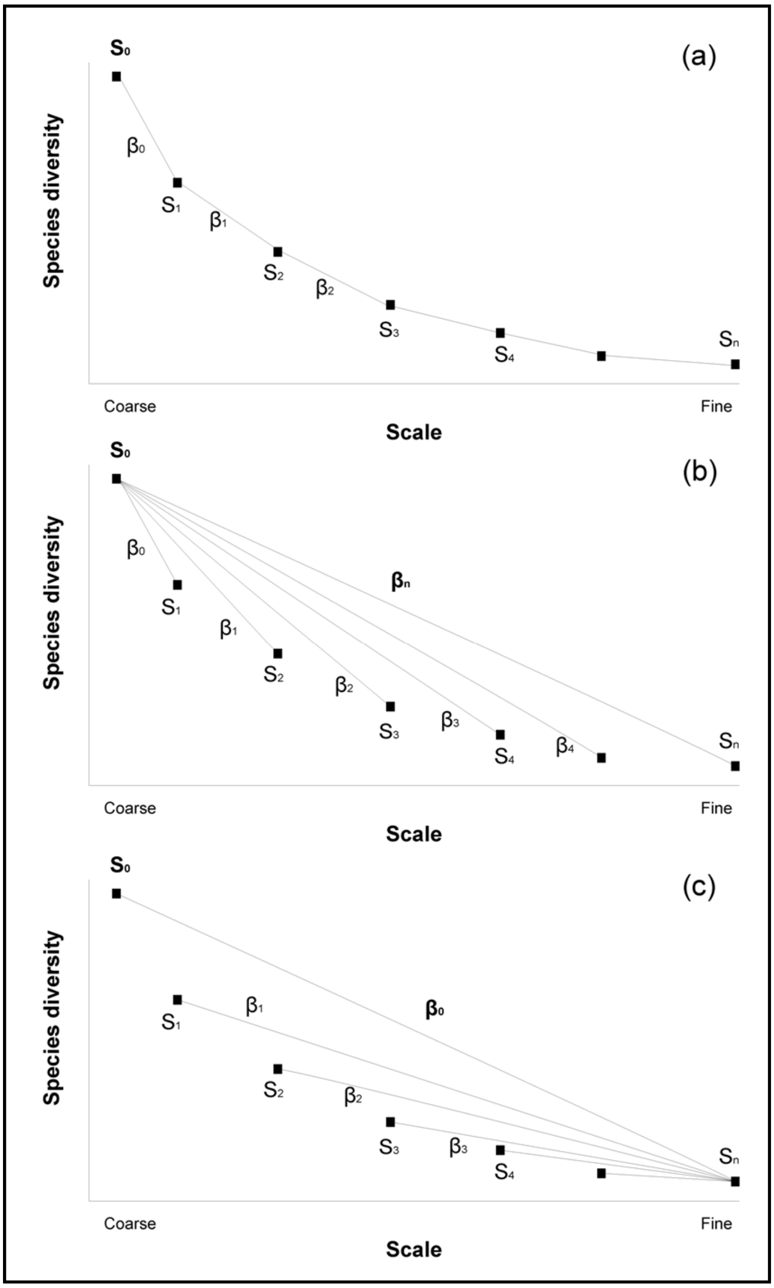
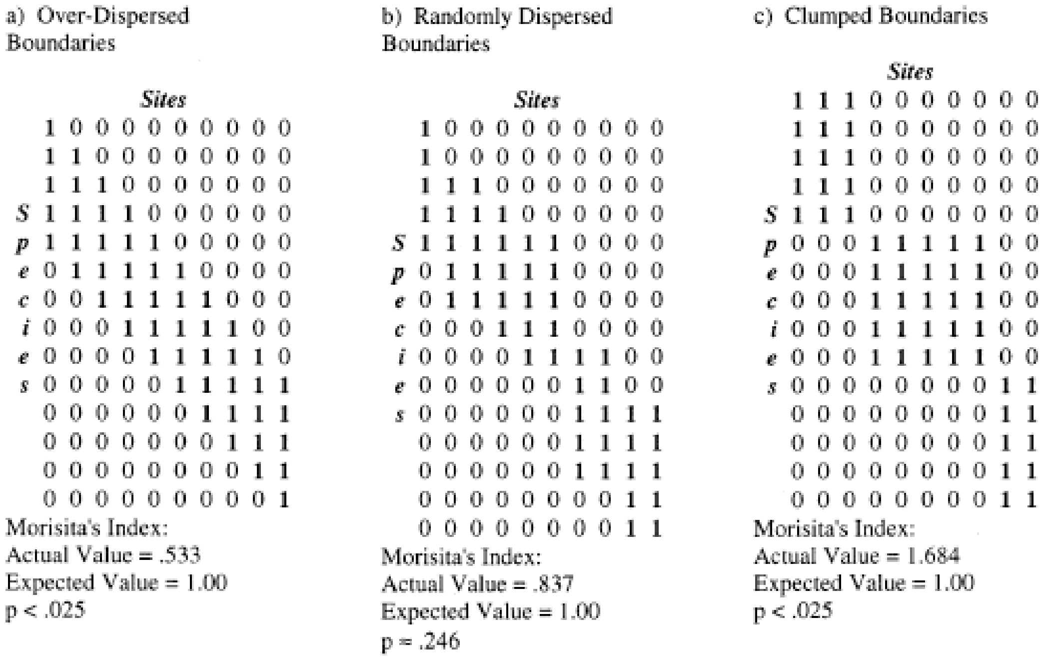


Figure I-4. The three possible iterating procedures to calculate the scaling of β-diversity; in a) different sizes of locality and regions are used in each iteration, in b) the same region size but different locality sizes are used, and finally in c) different region sizes but a consistent locality size is used. “$S_{0....n}$” represents the scale, n will increase towards finer scales, β is the value of the slope.

Possibly the most common procedure used to calculate the scaling of β-diversity is that shown in Figure I-4a (e.g. Arita & Rodriguez, 2002), whereas in Chapter IV I use the approach shown in Figure I-4c. That means that β-diversity was calculated using the same fine scale but with different region sizes. In this case β-diversity can be equated to the slope between two scales (Harte *et al.*, 1999; Arita & Rodriguez, 2002). In nested areas (localities within the region), unless self-similarity is fully accomplished, the slope will vary between scales. The slope will be steeper (higher β-diversity) as the differences between "locality" and "region" increase. To the best of my knowledge the scaling of β-diversity has not hitherto been assessed as set out in Figure I-4b, or I-4c.

Boundary clumping (within the metacommunity framework) is the degree to which the boundaries of different species' ranges are clustered together along a gradient (Leibold & Mikkelson, 2002). In other words, it indicates how the replacement along the major environmental gradient is taking place, i.e. by groups or individually (Willig *et al.*, 2011; Fig. I-5). Within the framework of Leibold *et al.* (2004), the Morisita index (I) is used to evaluate the degree of clumping of community boundaries, and of individual species distributional boundaries. This is calculated along the dominant axis of variation, evaluating how the results differ from a simple null model (Leibold & Mikkelson, 2002). When the range boundaries are placed randomly, I takes a value of 1; $I > 1$ means that range boundaries are more clumped than expected; and $I < 1$ indicates less clumped or over-dispersed range boundaries. A Chi-square test is used to evaluate if the Morisita Index is significantly different from 1 (higher or lower). Crucial to this procedure is that embedded absences are first replaced with presence values.



a) Over-Dispersed Boundaries

	Sites									
	1	0	0	0	0	0	0	0	0	0
	1	1	0	0	0	0	0	0	0	0
	1	1	1	0	0	0	0	0	0	0
S	1	1	1	1	0	0	0	0	0	0
p	1	1	1	1	1	0	0	0	0	0
e	0	1	1	1	1	1	0	0	0	0
c	0	0	1	1	1	1	1	0	0	0
i	0	0	0	1	1	1	1	1	0	0
e	0	0	0	0	1	1	1	1	1	0
s	0	0	0	0	0	1	1	1	1	1
	0	0	0	0	0	0	1	1	1	1
	0	0	0	0	0	0	0	1	1	1
	0	0	0	0	0	0	0	0	1	1
	0	0	0	0	0	0	0	0	0	1

Morisita's Index:
Actual Value = .533
Expected Value = 1.00
p < .025

b) Randomly Dispersed Boundaries

	Sites									
	1	0	0	0	0	0	0	0	0	0
	1	0	0	0	0	0	0	0	0	0
	1	1	1	0	0	0	0	0	0	0
	1	1	1	1	0	0	0	0	0	0
S	1	1	1	1	1	1	0	0	0	0
p	0	1	1	1	1	1	0	0	0	0
e	0	1	1	1	1	1	0	0	0	0
c	0	0	0	1	1	1	0	0	0	0
i	0	0	0	0	1	1	1	1	0	0
e	0	0	0	0	0	0	1	1	0	0
s	0	0	0	0	0	0	1	1	1	1
	0	0	0	0	0	0	1	1	1	1
	0	0	0	0	0	0	1	1	1	1
	0	0	0	0	0	0	0	0	1	1
	0	0	0	0	0	0	0	0	1	1

Morisita's Index:
Actual Value = .837
Expected Value = 1.00
p = .246

c) Clumped Boundaries

	Sites									
	1	1	1	0	0	0	0	0	0	0
	1	1	1	0	0	0	0	0	0	0
	1	1	1	0	0	0	0	0	0	0
	1	1	1	0	0	0	0	0	0	0
S	1	1	1	0	0	0	0	0	0	0
p	0	0	0	1	1	1	1	1	0	0
e	0	0	0	1	1	1	1	1	0	0
c	0	0	0	1	1	1	1	1	0	0
i	0	0	0	1	1	1	1	1	0	0
e	0	0	0	1	1	1	1	1	0	0
s	0	0	0	0	0	0	0	0	1	1
	0	0	0	0	0	0	0	0	1	1
	0	0	0	0	0	0	0	0	1	1
	0	0	0	0	0	0	0	0	1	1
	0	0	0	0	0	0	0	0	1	1

Morisita's Index:
Actual Value = 1.684
Expected Value = 1.00
p < .025

Figure I-5. Boundary clumping as indicated by Morisita's Index. Entries denote the presence (1) or absence (0) of species (rows) at sites (columns). Diagram and legend extracted from Leibold and Mikkelson (2002) to exemplify.

Coherence (within the metacommunity framework) occurs when species/communities are distributed more or less continuously along an environmental gradient. They appear at a certain point, and although varying in abundance, continue appearing, until again declining to zero incidence at some point along the same gradient (Figs I-6 and I-7). This general humped response to an environmental gradient is long-established at the species level and is known as the 'Gaussian response curve'. Coherence measures the distribution of species along the gradient, through the number of embedded absences found. Most communities exhibit significant coherence (Leibold *et al.*, 2004). In the process of analysing metacommunity parameters, the first step is to identify the dominant compositional gradient by indirect gradient analyses (reciprocal averaging). The second step is to test for coherence and assuming the communities are coherent, then the next step is to replace embedded absences with presences prior to calculating boundary clumping and turnover.

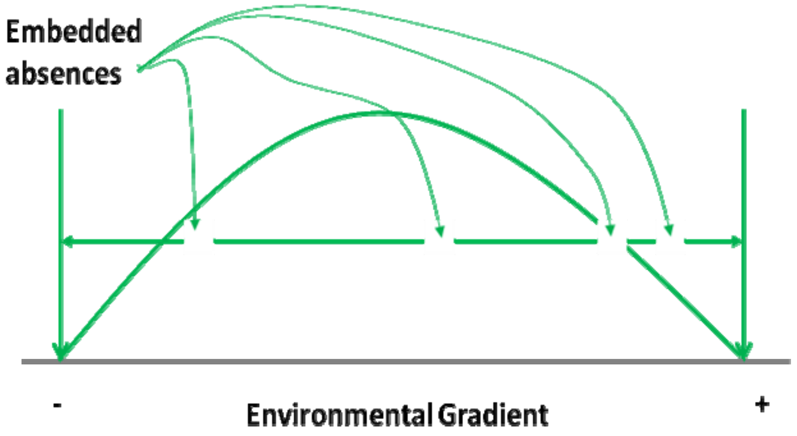
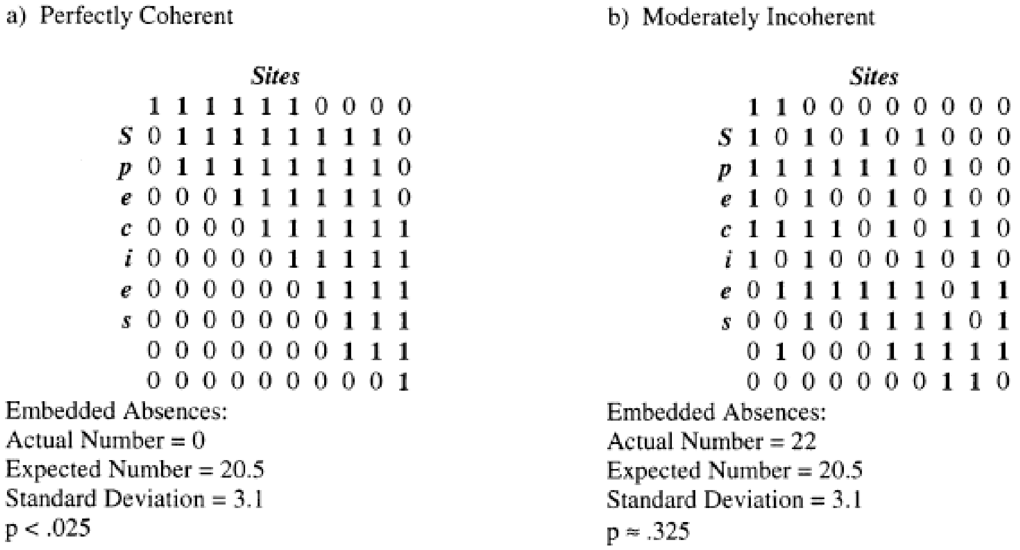


Figure I-6. Graphic description of the species/communities distribution along an environmental gradient; and the representation of embedded absences (original diagram).


a) Perfectly Coherent

Sites

	1	1	1	1	1	1	0	0	0	0
S	0	1	1	1	1	1	1	1	1	0
p	0	1	1	1	1	1	1	1	1	0
e	0	0	0	1	1	1	1	1	1	0
c	0	0	0	0	1	1	1	1	1	1
i	0	0	0	0	0	1	1	1	1	1
e	0	0	0	0	0	0	1	1	1	1
s	0	0	0	0	0	0	0	1	1	1
	0	0	0	0	0	0	0	1	1	1
	0	0	0	0	0	0	0	0	0	1

Embedded Absences:
Actual Number = 0
Expected Number = 20.5
Standard Deviation = 3.1
$p < .025$

b) Moderately Incoherent

Sites

	1	1	0	0	0	0	0	0	0	0
S	1	0	1	0	1	0	1	0	0	0
p	1	1	1	1	1	1	0	1	0	0
e	1	0	1	0	0	1	0	1	0	0
c	1	1	1	1	0	1	0	1	1	0
i	1	0	1	0	0	0	1	0	1	0
e	0	1	1	1	1	1	1	0	1	1
s	0	0	1	0	1	1	1	1	0	1
	0	1	0	0	0	1	1	1	1	1
	0	0	0	0	0	0	0	1	1	0

Embedded Absences:
Actual Number = 22
Expected Number = 20.5
Standard Deviation = 3.1
$p \approx .325$

Figure I-7. Coherence as indicated by the occurrence of embedded absences in ordinated matrices. Entries denote the presence (1) or absence (0) of species (rows) at sites (columns). Diagram and legend extracted from Leibold and Mikkelson (2002) to exemplify.

Deforestation can be defined as the conversion of forest to another land use, or the long-term (over ecological time scales) reduction of the tree canopy cover below the minimum 10 percent threshold (FAO, 2005). For some species of forest dwellers this could imply their habitat loss, but for other species it could only mean a degradation of their habitat, which may or may not affect their long term survival.

Distanciation "means placing a distance between", but does not imply a total separation, a disconnection, or a standing outside. "We remove ourselves from the immediate vicinity, but we are still within the general realm of concern" (Gould, 1983 p. 381). Here I use the term with a slightly different meaning, closely following McManus (2000, p. 306), who defines 'distanciation' as the 'separation of cause and effect in regard to an issue'. One way in which distanciation occurs is when the media are involved in a process of separating cause and effect through the construction of space and time (McManus, 2000; Rantanen, 2005). For example, consider the statement that "several species are going to be extinct by 2050 as a result of climate change". In this case the cause is occurring in the present moment, but the consequences will be far reaching, probably far greater than the life expectancy of many of the public of the same media. When distanciation takes places people become interested because it is news, but not truly involved, and so distance is constructed and maintained.

Ecological space (*ES*) is the space with n-dimensions that represent all of the possibilities in which life can occur in a determined geographic place and time. It depends on all of the characteristics of the place, biotic and abiotic. The *ES* will be changing as the place changes –it is dynamic. Unlike habitat, *ES* is not species specific. The dynamics of the *ES* depend entirely on environmental changes.

Environmental Change is any movement from one *steady* state to another in any aspect that contributes to the structure of the environment, such as climate, sea level, vegetation belts, soils, landforms, organism populations, etc. (Anderson *et al.*, 2007).

Habitat can be defined as the range of resources (biotic and abiotic) suitable for a particular species (Fisher & Lindermayer, 2007). Habitat, like niche, cannot be separated from a particular species (Fisher & Lindermayer, 2007). It is also part of the species niche (Elton, 1927; Hutchinson, 1957). Habitat only has meaning in relationship with the range and needs of a particular species. While, we frequently refer to habitat as a place, without referring to any species in particular, in a strict sense there is no “general habitat”. Consequently habitat modifications are species specific.

Habitat loss has been used as a general term and can incorporate a range of different phenomena, such as deforestation (Brooks *et al.,* 2002; Fahrig, 2002; Hoekstra *et al.*, 2005), habitat fragmentation (Andrén, 1994), and habitat degradation (Harrison & Bruna, 1999). Some authors use the term to cover a mix of such phenomena (e.g. Owens & Bennett, 2000). It is perhaps rarely use in a strict sense to mean habitat loss, the final point in the spectrum of habitat degradation (Fisher & Lindermayer, 2007). This means that the place has been transformed (habitat modification) in such a way that it becomes unsuitable for a particular species. As a result there is no more habitat and the specific species becomes extinct in that place. To summarize, any extinction occurs (locally, regionally or globally), because there was a strong or repeated modification to the habitat, and finally, habitat loss for the extinct species.

Habitat modifications occur all the time since the *ES* is dynamic and constantly changing. This means that any change in the *ES*, could affect the habitat of a particular species. Habitat modifications are not necessarily about structure, but can be a result of exotic species immigration/introduction, diseases, and even new predators (including human hunting). Habitat modifications can be permanent or temporary depending on the strength and duration of the environmental changes. Long-lasting changes could be called 'stress', and temporary changes can be called 'disturbances' (modified from Lorrillière *et al.*, 2012). Modifications can result in different outcomes for different species, for example negative habitat alterations may occur such as *fragmentation, degradation*, or even the complete *habitat loss* for some species, which at the same time could imply an expansion of habitat for another species.

Metapopulations are local populations connected through the dispersal of individuals (Hanski & Gilpin, 1991), involving population colonization–extinction processes. Richter-Boix *et al.* (2007) are around several recent authors who have extrapolated this approach to communities, assuming that communities are sets (or collections) of populations. However, the metapopulation approach focuses only on factors that affect the population dynamics, while the metacommunity approach focuses on the mechanisms that preserve species richness at local and regional level.

A **metacommunity** is a set of local communities, comprising local populations that use resources at the same patch scale connected by dispersal (Leibold & Mikkelson, 2002; Leibold *et al.*, 2004). The framework of metacommunity ecology emerged as an attempt to explain the dynamics of entire communities in spatially structured habitats (e.g. collections of patches). It is a multi-scale approach that allows the establishment of different hypotheses about the structure and the processes that explain patterns of diversity, in terms of richness and abundance (Leibold *et al.*, 2004; Holyoak *et al.*, 2005; Elliott & Brook, 2007). Within the metacommunity framework, Leibold and Mikkelson (2002), proposed three parameters to evaluate the structure of the metacommunity: coherence, turnover and boundary clumping. These terms are based on the response of the putative metacommunity to the dominant axis of variation (calculated by reciprocal averaging or correspondence analysis) and each is separately defined.

Niche has been defined in many ways (e.g. Peterson *et al.*, 2011); the most commonly used definition is the Grinnellian Niche (Grinnell, 1917), at least for modelling species ranges or ecological niche modelling (Losos *et al.*, 2003). Soberón (2007, p. 1117) interpreted the Grinnellian Niche as '*subsets of scenopoetic* (non-interactive or scenery) *variable space corresponding to geographic areas defined by actual or potential properties of species*'. The Grinnellian Niche has sometimes been referred as habitat, but I regard it as distinct from habitat as the latter must involve interacting biotic and abiotic variables.

Turnover, within the framework of metacommunity structure, refers to the replacement of species between sites following a) rearrangement in to an intrinsic compositional gradient and b) in-filling of all embedded absences. Presley *et al.* (2010, p. 910) defined turnover in this context "as the number of times one species replaces another between two sites (i.e. number of replacements) for each possible pair of species and for each possible pair of sites. A replacement between two species (A and B) occurs when the range of A extends beyond that of B at one end of the gradient and the range of B extends beyond that of A at the other end of the gradient" (Figs I-8a and I-9c).

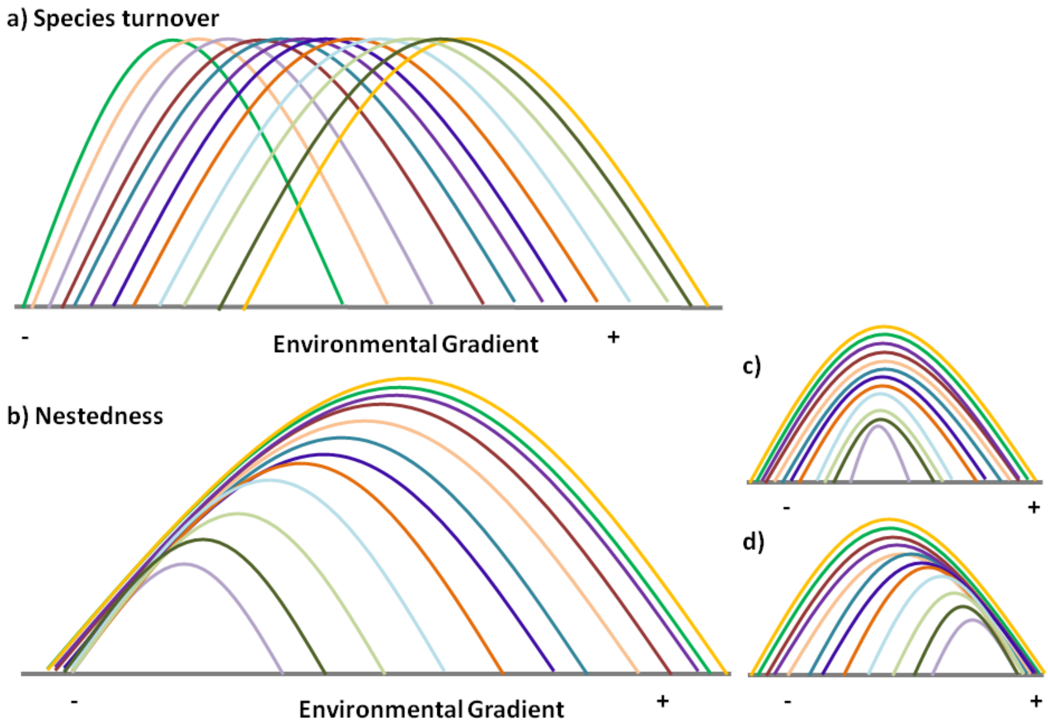
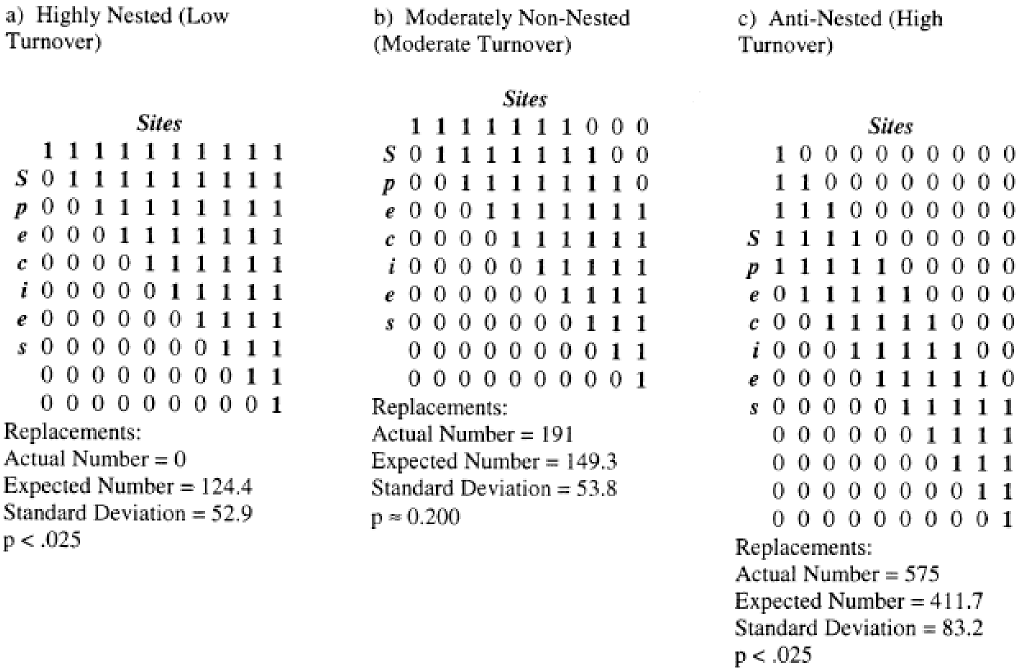


Figure I-8. Graphic representation of turnover (a), and the non-existence of turnover or nestedness (b, c, d). The graphic just represents cases to illustrate the concept; it does not pretend to be accurate to a specific ecological scenario (original diagram).

In this context 'species range' refers to the distribution along the environmental gradient, thus it differs from the biogeographical concept of 'distribution range'. Where species are not replaced along a gradient, but rather drop out in sequence (in any direction), this may generate distributions that tend to exhibit nestedness (Figs I-8b,c,d and I-9a,b). Within this method, the assumption is that embedded absences are essentially erroneous, and thus to measure true turnover, each species distribution is 'filled in' prior to the turnover analysis. Then, the number of replacements is compared to a null model that shifts the entire species distribution along the gradient.



a) Highly Nested (Low Turnover)

	Sites									
	1	1	1	1	1	1	1	1	1	1
S	0	1	1	1	1	1	1	1	1	1
p	0	0	1	1	1	1	1	1	1	1
e	0	0	0	1	1	1	1	1	1	1
c	0	0	0	0	1	1	1	1	1	1
i	0	0	0	0	0	1	1	1	1	1
e	0	0	0	0	0	0	1	1	1	1
s	0	0	0	0	0	0	0	1	1	1
	0	0	0	0	0	0	0	0	1	1
	0	0	0	0	0	0	0	0	0	1

Replacements:
Actual Number = 0
Expected Number = 124.4
Standard Deviation = 52.9
p < .025

b) Moderately Non-Nested (Moderate Turnover)

	Sites									
	1	1	1	1	1	1	1	0	0	0
S	0	1	1	1	1	1	1	1	0	0
p	0	0	1	1	1	1	1	1	1	0
e	0	0	0	1	1	1	1	1	1	1
c	0	0	0	0	1	1	1	1	1	1
i	0	0	0	0	0	1	1	1	1	1
e	0	0	0	0	0	0	1	1	1	1
s	0	0	0	0	0	0	0	1	1	1
	0	0	0	0	0	0	0	0	1	1
	0	0	0	0	0	0	0	0	0	1

Replacements:
Actual Number = 191
Expected Number = 149.3
Standard Deviation = 53.8
p ≈ 0.200

c) Anti-Nested (High Turnover)

	Sites									
	1	0	0	0	0	0	0	0	0	0
	1	1	0	0	0	0	0	0	0	0
	1	1	1	0	0	0	0	0	0	0
S	1	1	1	1	0	0	0	0	0	0
p	1	1	1	1	1	0	0	0	0	0
e	0	1	1	1	1	1	0	0	0	0
c	0	0	1	1	1	1	1	0	0	0
i	0	0	0	1	1	1	1	1	0	0
e	0	0	0	0	1	1	1	1	1	0
s	0	0	0	0	0	1	1	1	1	1
	0	0	0	0	0	0	1	1	1	1
	0	0	0	0	0	0	0	1	1	1
	0	0	0	0	0	0	0	0	1	1
	0	0	0	0	0	0	0	0	0	1

Replacements:
Actual Number = 575
Expected Number = 411.7
Standard Deviation = 83.2
p < .025

Figure I-9. Species turnover as indicated by the number of times one species replaces another between two sites. Entries denote the presence (1) or absence (0) of species (rows) at sites (columns). Diagram and legend extracted from Leibold and Mikkelson (2002) to exemplify.

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Craugastor sp. Nahá 2010

II. AMPHIBIAN METACOMMUNITY STRUCTURE DRIVERS VARY BETWEEN TWO PROTECTED AREAS IN CHIAPAS, MEXICO

“Frogs have it easy, they can eat what bugs them”

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ABSTRACT

Species distributions are limited by several direct and indirect factors in a given landscape. In fragmented landscapes those factors include human activities, even in protected areas (PAs). Well-defined, clumped, metacommunities can be expected when fragmentation occurs. Thus we analyzed how amphibian metacommunities were structured in two fragmented PAs with different environmental characteristics: La Pera and Nahá. We also examined how community structure was related to key features of the environment (habitat, space and local climatic conditions) within each PA. We sampled amphibians in transects at night during the rainy season of 2010 and we recorded environmental data also at transect level. We employed a recently proposed method based on community coherence, turnover and boundary clumping within a reciprocal averaging ordination to evaluate metacommunity structure, in combination with community–environment analyses based on partial canonical correspondence analyses (CCA). The results revealed that the amphibian metacommunity of La Pera has a quasi-Gleasonian structure and that Nahá exhibits a Gleasonian structure. Partial CCA analyses showed that a substantial proportion of community variation could be explained by habitat structure, > 50% and almost 30% for La Pera and Nahá respectively. The relationships between community compositional gradients, geographical space and local weather conditions at the time of sampling varied between the two systems. The variation may reflect underlying processes connected with human use and governance, which affect the spatial structure of the habitat. Understanding how metacommunity structure and dynamics vary between landscapes could result in more efficient management of protected areas to conserve biodiversity in the long term.

Keywords: Amphibians, boundary clumping, canonical correspondence analyses, coherence, landscape management, metacommunity structure, Mexico, protected areas, turnover.

INTRODUCTION

In a landscape there are several factors (biotic and abiotic) that limit, directly or indirectly, species distribution. The limits are primarily shaped by factors that regulate permanency of species within the patch or site, and the level of permeability for dispersion among the different patches embedded within the landscape. In the same way, those factors shape the metacommunity structure within the landscape. A metacommunity is a set of communities potentially conceived of as being linked by periodic dispersal (Leibold & Mikkelson 2002; Resetarits et al. 2005). A community is a set of species occupying a particular habitat (or locality) that have, theoretically, the same opportunity to interact (Holyoak et al. 2005). Although there are several caveats defining the limits of a community, here we follow the definition of Resetarits et al. (2005): “a collection of individuals occurring in a discrete habitat patch”. Patches are defined by environmental characteristics that differentiate them from the surrounding landscape (Pickett & Cadenasso 1995). Thus, a patch can be forest, a secondary forest, or even an open area, i.e. crops, pastures, village, etc., here termed as matrix habitat. Where the characteristics change from one state to another, we may identify ecotonal or ‘edge’ habitats, sometimes featuring their own dynamics and set of species. In sum, the communities inhabiting a set of adjoining patches, if linked by occasional dispersal or migration, form a metacommunity.

The idealized patterns of community structures were summarized by Liebold and co-authors (Leibold & Mikkelson 2002; Leibold et al. 2004) and are classified as: checkerboards, nested subsets, Clementsian, Gleasonian, evenly spaced gradients, and random. Subsequently, Presley et al. (2010) recognized that there are communities that do not fit with the previous classification and which may be deemed quasi-states. Equally important is to recognize that the classification outcome will depend on the scales (spatial and temporal) at which the sites are selected and sampled (Leibold & Mikkelson 2002; Leibold et al. 2004).

Nowadays it is very difficult to find a landscape that has not been modified by human hands (Chown 2010), and it is known that Neotropical forests are highly fragmented (Dirzo & Raven 2003). Mexico, considered one of the megadiverse countries in the World, is no exception to these generalizations (Mittermeier et al. 1999). Within Mexico's borders live more than 375 species of amphibians, and more than 60% of Mexican amphibians are endemic (Frías-Alvarez et al. 2010; O. Flores-Villela *pers. com*.). Mexico has the second largest proportion (>50%) of endangered amphibians globally (IUCN 2011). Located in the south of the country, Chiapas is a region of complex topography, and an ancient and complex history of human civilizations. It has been repeatedly pinpointed as a key area for conservation, at national and global level, because of its vast ecological richness and social value (Mittermeier et al. 1999; Dirzo & Raven 2003). Chiapas has at least 120 public protected areas (PAs), 32 federal PAs, 26 state PAs and 62 Municipal PAs, plus around 50 community conserved areas (Bezaury-Creel et al., 2008a,b, 2009, 2010). Each category receives different levels of investment and has different degrees of permanence (Ochoa-Ochoa et al. 2011). Therefore there is a huge variation in terms of programs and resource allocation in each of them. Consequently the governance effectiveness also varies. This in turn may cause differences in diversity structuring and dynamics.

Although species vary in their tolerance, it is commonly known that amphibians, as a group, have narrow environmental tolerances (Duellman & Trueb 1994). We would predict that in fragmented landscapes of forest and disturbed, open areas, we should find well-defined, clumped, amphibian communities, with mixtures of species in the ecotones (e.g. Urbina-Cardona et al. 2006). We would also expect that the constituent communities will be found to respond to different properties of the environment, and that the metacommunity structure would be clearly distinct from a random pattern. We also expect that differences in the governance of protected areas would be reflected in the structure of the forest in the landscape, thus in the drivers that structure the metacommunity. In areas with resources, we assume good management, i.e. the structure of the community will be more related to local weather conditions because sampling was undertaken during the rainy season. Conversely, in areas with low or no resources, habitat will be directly influenced by human activities.

In this paper our aims are: (1) to test the foregoing predictions as to how amphibian communities are structured in two fragmented PA with different environmental characteristics during the rainy season; (2) to examine how community structure is related to key features of the environment (habitat, space and local climatic conditions); and (3) to test if there are differences among the factors driving metacommunity patterns between the landscapes.

METHODS

Study Area. The fieldwork was carried out in two natural protected areas (PAs) in Chiapas: “La Pera” (most common known as “El Pozo”), and the biosphere reserve “Nahá” (~ 17ºN, Fig. II-1). La Pera, a pre-montane zone, belongs to a zone historically known for its remarkable herpetofauna and interesting biogeography (Johnson & Savage 1995). Located in the North East of the Chiapas State, this state PA is of very recent creation (15/Nov/2006). The decree followed an exploratory excavation in search of petroleum performed by Petroleos Mexicanos (PEMEX). Actually, the exploratory area was popularized as “El Pozo” (*Pozo* means excavation hole for water or oil). An endemic frog was named after the ‘excavations’, *Craugastor pozo* described by Johnson and Savage (1995). The PA covers 7,506 ha and includes 49 established communities, with a total of 1,054 inhabitants. The topography is complex and the elevation range is from 500 m to 1,200 m. The predominant agricultural system is “slash-and-burn”, but due to the soil characteristics (very shallow), the rate of land transformation is very high. There are two types of vegetation according to INEGI (2005): tropical rain forest and evergreen seasonal forest, both, pristine and disturbed.

The predominant agricultural system is the same but in this case the soil is very poor, thus the rate of land transformation is also very high (e.g. Ochoa-Gaona et al. 2007).

Nahá was established in 2000 by agreement between the *Lacandons* and the government. It was recently transferred in status from a federal PA to a biosphere reserve. It is located in the northwest of the Lacandona region. Nahá has 3,847 ha, and a total population of 216 inhabitants (INEGI 2009). The vegetation types are tropical rain forest, cloud mountain forest, pine-oak forest and disturbed vegetation commonly known as "acahuales" (Willuhn & Comisión Nacional de Áreas Naturales Protegidas (México) 2006).

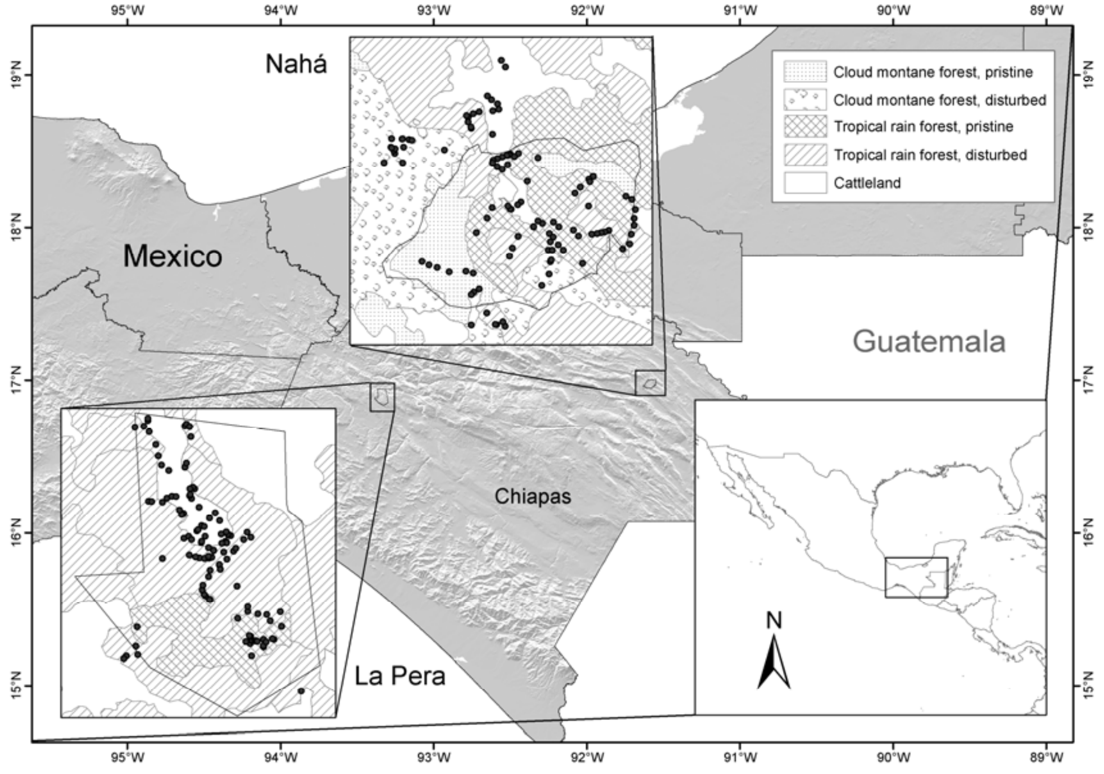

Figure II-1. Location of the protected areas sampled during the rainy season of 2010, La Pera to the west and Nahá towards the east, highlighted with a surrounding square. Source: geographic database of Mexican protected areas (Bezaury et al. 2009). Maps generated with ArcGIS 9.3.1 (ESRI, 2009).

Field-sampling. The sampling was performed at night during the rainy season, June-September, of 2010. Three types of areas were sampled: interior (forested), edge and matrix (transformed/disturbed areas). Sampling was conducted primarily with transects (50m x 2m) although where the characteristics of the site did not permit use of transects, sampling was done in plots (10m x 10m). Time was not controlled during sampling. A total of 144 transects/plots were sampled from 33 patches in La Pera and 140 transects from 36 patches in Nahá (4-5 transects on each patch depending on patch size). Sampling effort varied from 2 to 4 people sampling and involved thorough searching by torchlight of water bodies, ground surface, leaf litter and low level vegetation. All amphibians within the sampling units were recorded. Defining where the edge effects end or begin depends on the vegetation type and the age of the patch. For example, young or recent patches will present more variation in some micro-environmental variables, such as temperature and humidity (Williams-Linera et al. 1998). Also, it is possible that the edge influence can vary in range between seasons, especially regarding humidity and temperature; these two variables are very important to the amphibian life cycle (Stebbins & Cohen 1997). During sampling the edge was defined as the outer 20m of a forested patch and the rest of the patch was defined as interior habitat (following Urbina-Cardona et al. 2006).

The environmental variables measured were classified into three groups: space (Svar), habitat (Hvar) and local climatic conditions or weather (L-Cvar). Space (Svar) included latitude (Y), longitude (X), elevation in meters above level sea (m.a.s.l.) and a second grade polynomial of lat–long (XY, X^2, Y^2, X^2Y, XY^2). Local climatic conditions (L-Cvar) were rain intensity: no rain (0), rain the same day (1), and at the moment of sampling light rain or drizzle (2); rain (3), and heavy rain (4), local temperature (in ºC) measured with data loggers (LogTag HAXO-8), atmospheric pressure (in hPa, measured with Casio PAG40-7V), and the interaction among pairs; and habitat variables (Hvar): forest status (no forest (0), very disturbed (1), disturbed (2), managed (3) and conserved (4)), forest location (matrix, edge or interior), canopy coverage (the mean of three measures of the coverage in percentage), litter (the mean of three measures of litter depth in cm, taken with a metal rule); grass (mean of three measures of the grass height in meters), and presence of water bodies (temporary ponds

(TP), temporary streams with less than 2m width (TS), permanent streams (PS), permanent pond and lakes (PP), permanent river with more than 2m width (PR)). Environmental variables were measured for each transect. We obtained the values for each patch as the mean of transects within it.

Sampling effort and expected richness. Sampling efficiency on the PAs was assessed by examining species accumulation curves (Coleman and Mau Tau) and associated statistics employing EstimateS ver 8.2 (Colwell 2011). Four different estimators were used, reflecting distinct features of the sampled dataset (uniques, *singletons*, duplicates, *doubletons*, occurrences, proportions, etc.). These non-parametric estimators based on unseen species are appropriate when the aim is to assess richness of samples that are suspected to be under-sampled or that contain many rare species (Chao et al. 2005).

Community structure and association. We used a pattern based approach to evaluate whether the pattern presented by the analyzed metacommunities is statistically different from random (Leibold & Mikkelson 2002; Presley & Willig 2010). The structure of the community was explored following Presley et al. (2010). This method is based on an ordinated sites/species presence/absence matrix (by reciprocal averaging/ correspondence analysis) along the major compositional gradient (in this case the first axis). It evaluates three different attributes by contrasting them with a null model: coherence, species turnover and boundary clumping among the sampled sites. Coherence measures the distribution of species along the gradient, through the number of embedded absences found; the test is done under the assumption that species should have a continuous distribution along the gradient (Leibold & Mikkelson 2002). Positive coherence (fewer embedded absences than the null model) means that the metacommunity is structured; negative coherence implies random metacommunities. The following two aspects are tested after all embedded absences are replaced by presences (i.e. assuming that all embedded absences are essentially measurement errors). Turnover indicates how the replacement happens site by site; the number of replacements is compared to a null model that shifts the entire ranges along the gradient (Presley et al. 2010). Boundary clumping indicates how the replacement along the environmental gradient is taking place, i.e. by groups or individually (Willig et al. 2011). It is measured with Morisita's Index and compared to the null model with a chi-square test. Based on the assumption that sampling effort was adequate, we chose a null model that constrained simulated species richness of each patch to equal observed richness, with equiprobable occurrences for each species. These analyses were performed in Matlab 7.7.0 using the script "Metacommunity" (Higgins 2008). The parameters used were: 1 = reciprocal averaging, 3 = species richness per site is fixed & species occurrence is equiprobable, 0 = range perspective, 1000 = number of iterations, 1 = axis of correspondence to use in ordination.

The relationship between amphibian community structure and environment was analyzed based on the original species abundance data using normal and partial Canonical Correspondence Analyses (pCCA) following Olano & Luzuriaga (2008). Canonical correspondence analysis (CCA) is a multivariate method designed to reveal the relationships between biological assemblages and the environment (ter Braak & Verdonschot 1995). CCA extract succinct environmental gradients from ecological data sets. Within environmental data sets such as those used there is usually a lot of redundancy, thus partialling-out the variance explained for each of the three groups of variables space (Svar), habitat (Hvar) and local-climatic conditions (L-Cvar) was desirable. All CCA were performed in CANOCO (ter Braak & Šmilauer 2002). CANOCO detects the presence of perfectly correlated pairs of environmental variables and in such cases eliminates one of the variables. One of each pair of significantly correlated variables was also manually eliminated. Reduced models were computed that include only variables with inflation factors significantly different from zero. Significant variables were selected using stepwise forward selection. With stepwise selection (forwards or backwards) the effect of the variable (or the set) under examination will depend on the variables (or set) already selected (Legendre & Legendre 1998); thus we used Monte Carlo permutation tests that reduce the error of selecting a non-significant variable. We performed 999 permutations with a reduced model, for both specific variables and sets of variables. The test is based on the null hypothesis of the independence of the species data matrix and the environmental data matrix (Lepš & Šmilauer 2003). It starts randomly permuting the samples in the environmental data matrix, and in every permutation an F-like statistic is calculated. Only when the value of the test statistics from the real data (with no permutation) is highly improbable compared to the distribution of the values obtained during the permutation process is the null hypothesis rejected (Lepš & Šmilauer 2003). In order to partial-out the variance of each matrix, additional CCA were performed with the chosen environmental variable set (e.g. habitat) as explanatory variables and another variable set (e.g. local climatic conditions) as co-variables, and so on. The significance of the sets of variables in pCCA was tested through eigenvalues. This can be done because it is possible to formulate a null hypothesis about the relationship between the sets of variables, i.e. species distribution is not related to habitat, and/or habitat is not related to climate (Legendre & Legendre 1998). The variance explained by a set of variables can be obtained by dividing the total variation (total inertia) of the species' matrix by the sum of all canonical eigenvalues. This gives the proportion of the variation of the species matrix explained by a set of variables, as the r-square in a multiple regression (Legendre & Legendre 1998).

RESULTS

A total of 2,394 individuals of 22 species were recorded in La Pera, and 2,176 individuals of 30 species in Nahá. The species found within La Pera are nearly all also found within Nahá (see Appendix 1 from the Supporting Information for the complete list of species and specific abundances in Table SI II-1). In La Pera the most abundant species was *Smilisca baudini*

(22% of the individuals recorded), followed by *Agalychnis moreleti* (~17%) and *Craugastor pipilans* (~13%). Four of the estimators of species richness, both rarefaction (Cole and Coleman) curves and the two Chao indices, indicate that the landscape is well surveyed (see Appendix 1 Fig. SI II-1). The Jack1 and Jack2 estimators indicate that two or three additional species may have gone unsampled. In Nahá the three top species in abundance were *Tlalocohyla picta* (~16%), *S. baudini* (~13%) and *Rhinophrynus dorsalis* (~9%). For this region, three of the species richness estimators, rarefaction curves and Chao 1, indicate that the sampling effort was sufficient, but Chao2 indicated that another species might be found, while both Jack1 and Jack2 indices suggest the possibility of finding a few more species, reflecting the large numbers of singletons and doubletons recorded in the samples (see Appendix 1, Fig. SI II-2).

Metacommunity structure

Both metacommunities have significantly fewer embedded absences than the null model, and thus show significant positive coherence (see Table II-1). In La Pera, turnover was greater than the mean produced by the null model and non-significant, consistent with a non-nested quasi-structure. In the case of Nahá, turnover was significantly greater than the mean produced by the null model. As a consequence, the Naha metacommunity presents one of the idealized patterns of distribution, i.e. it does not show a quasi-state (following Presley et al. 2010). In the context of transient dynamics driven by vagaries of weather, where the patches boundaries are practically non-existent, boundary clumping values should be low and non-significant. In our 2010 data for both PA, boundary clumping was non-significant and around one (i.e. stochastic). In sum, according to the classification matrix of Prestley et al. (2010) the metacommunity of La Pera has a quasi-Gleasonian structure and that for Nahá a Gleasonian structure (see Appendix 1 Figs SI II-3 and SI II-4).

Table II-1. Summary of the metacommunity structure analyses (coherence, species turnover and boundary clumping) for amphibians of La Pera and Nahá.

		La Pera	**Nahá**
Coherence	Number of embedded absences	277	308
	p-value	3.15E-06	2.05E-22
	Mean	352.992	546.394
	SD	16.3042	24.4776
Species Turnover	Number of replacements	6798	18484
	p-value	0.0707	0.0165
	Mean	4537.8	13011
	SD	1250.4	2283.5
Boundary clumping	Morisita's index	0.9899	1.0408
	p-value	0.5167	0.3751
Structure		**quasi-Gleasonian**	**Gleasonian**

Canonical Correspondence Analyses

In both landscapes CCAs showed that forest status was the most important variable explaining community structure (see Table II-2). The next most important variables, in Nahá were rain intensity and amount of litter, while the presence of temporary ponds and temperature were more important in La Pera. Partial CCAs confirmed that Hvar was the foremost set of factors in explaining community variation in both PAs more than 50% and almost 30% for La Pera and Nahá, respectively. These analyses also showed that interaction among the three sets of variables explaining the community structure differed among landscapes. While in La Pera habitat alone (Hvar) explained over half of the variance that could be explained (36% of the total 63% explained) (Fig. II-2a), in Nahá this set of variables explains only ~26% and local climatic conditions explains another ~24% from the total of ~65% variation explained, with very little variance attributable to their common effect (Fig. II-2b). The role of the spatial variables (S-var) also varied, while in La Pera it does not contribute to the explanation of the variance at all, in Nahá it explains a small percent, ~12% (see Table II-2).

Table II-2. Summary of the CCA and partial CCA analyses. Lambda is a measure of the total variance explained from each variable, Fr is the F ratio and p is the probability based on Monte Carlo tests (999 permutations). VE is the variance explained. CCA first block: just the three most significant variables for the amphibian community structure in La Pera and Nahá from each group: geographical space (*n* = 8), habitat (*n* = 11) and local climatic conditions (*n* = 6); *n* is the number of variables in each matrix of explanatory variables. Second block, also CCA: total variance explained by each of the models as reduced models including only variables with inflation factors different from cero. Third block, partial CCA: common variance explained by the different sets of environmental variables tested as covariables (see main text). Fourth block, partial CCA: variance explained by each of the matrices. At the bottom: combined total variance explained by the three matrices of environmental variables.

	La Pera			**Nahá**		
Space	**Lambda**	**Fr**	**P**	**Lambda**	**Fr**	**P**
Elevation	0.21	2.26	**0.006**	0.25	2.04	**0.012**
Longitude	0.1	1.16	0.306	0.13	1.02	0.381
Latitude*Longitude	0.08	0.84	0.552	0.11	0.91	0.441
Local climatic conditions						
Rain intensity	0.29	3.33	**0.002**	0.27	2.22	**0.014**
Temperature*Pressure	0.15	1.67	0.112	0.21	1.71	0.052
Temperature	0.1	1.24	0.228	0.14	1.23	0.226
Habitat						
Forest type	0.39	4.58	**0.001**	0.42	3.52	**0.001**
Permanent pond incidence	0.36	4.75	**0.001**	0.17	1.47	0.122
Permanent river incidence	0.2	2.79	**0.012**	0.14	1.28	0.199
Reduced models	**VE**	**Fr**	**P**	**VE**	**Fr**	**P**
Space	12.80%	1.417	0.089	12.74%	1.131	0.245
Local climatic conditions	19.01%	1.642	0.025	26.83%	1.758	0.001
Habitat	52.05%	2.772	0.001	29.70%	1.426	0.007
Common variance						
Local climatic conditions - Space	4.82%	1.304	0.091	0.00%	1.769	0.002
Habitat - Space	12.80%	2.163	0.001	1.11%	1.324	0.038
Habitat - Local climatic conditions	7.97%	2.519	0.001	2.95%	1.507	0.007
Variance explained only by						
Space	0.00%	1.251	0.183	11.63%	1.119	0.249
Local climatic conditions	11.04%	1.278	0.149	23.73%	1.782	0.001
Habitat	36.01%		0.001	25.64%		0.007
Total variance explained	**63.10%**			**65.04%**		

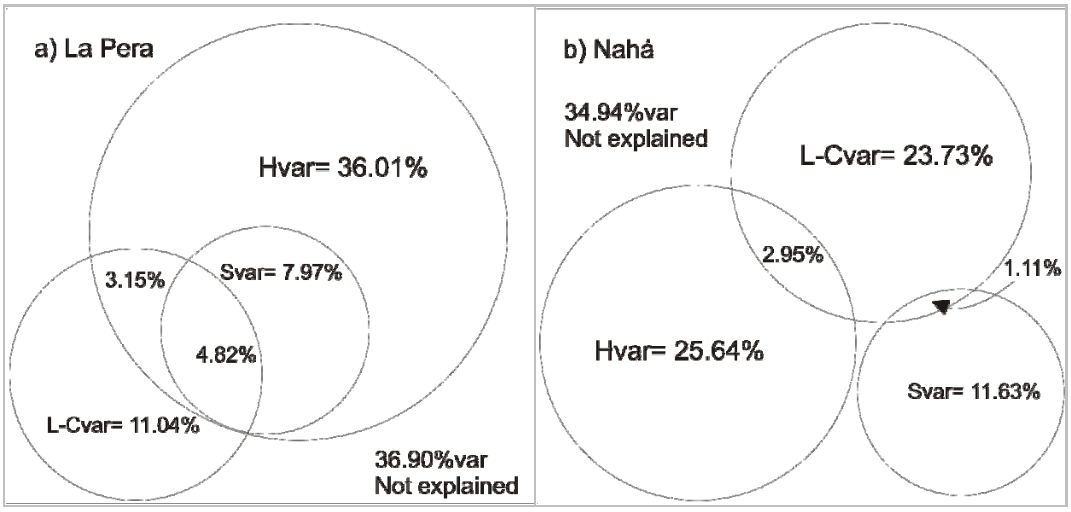

Figure II-2. Graphical view of the partial canonical correspondence analyses to represent the variance explained; and how the different environmental matrices, habitat (Hvar), local climate (L-Cvar), and space (Svar), interact to explain the metacommunity structure. a) La Pera, and b) Nahá.

DISCUSSION

It is commonly appreciated that both historical and local current environmental conditions shape metacommunity structure. Nevertheless, at the landscape level, the latter is the main driving force of metacommunity structure (Tuomisto & Ruokolainen 1997). Our data from two protected areas in Chiapas show that amphibian metacommunity structures were not random in either landscape and that they were determined by latent environmental gradients (positive coherence). Structure in these systems is based on individualistic responses, although, to varying degrees. In La Pera, a quasi-Gleasonian structure was found. Biologically this means that amphibians, as a group, are responding to the same environmental gradient (i.e. positive coherence), but that although turnover occurs, it is not very pronounced (i.e. high but not significant). This may occur because: a) the environmental gradients during the rainy season shorten (i.e. all patches are extremely humid, solar radiation decreases, etc., which makes contrasting patches, such as forest interior, edge, and matrix, more similar). Therefore, the environmental gradient in the landscape becomes smaller in comparison with the niche breadths of the species. Alternatively, b) the sampled area may have been insufficient to cover the whole environmental gradient. The results of the metacommunity analyses also show that limits of the species boundaries or distribution are individualistic (i.e. values of Morisita's index near to one and not significant). The boundaries depend entirely on the characteristics of each species (i.e. dispersal capability, environmental tolerance, and even defences), in agreement with Gleason's individualistic concept of the association (Gleason 1926; Leibold et al. 2004; Presley et al. 2010). The metacommunity of Nahá only differed from La Pera in the significance of the turnover. In biological terms, there is strong dissimilarity among the sets of patches sampled, notwithstanding the individualistic responses of the species within the Nahá metacommunity (see Table II-1). It is very likely that the strength of structuring mechanisms could be indicated by the level of significance associated with turnover (Presley et al. 2010). In the case of quasi-structures (i.e. La Pera) it is possible to assume weaker structuring forces than those in which turnover is significant (i.e. Nahá).

We think it likely that the Gleasonian metacommunity structure is strongly influenced by patterns of breeding boom and bust among the species. During the rainy season individuals will look for good breeding sites, where mates are present, responding especially after a heavy rain event to conspecific calls (Gottsberger & Gruber 2004). It is also known that some amphibians prefer warm and shallow ponds to reproduce because these factors contribute to rapid larval development (Richter-Boix et al. 2006), and generally these ponds are located in naturally open or disturbed areas, so that some species of amphibians only use open areas for reproduction purposes while the rest of the year they are restricted to the forests, i.e. allopatry for reproduction. Moreover, it has been documented that juveniles of some species present high dispersion rates (Sinsch 1997; but see Smith & Green 2005), although this depends on the permeability of patches boundaries (Stevens et al. 2006). It is not known how many times these particular amphibian species reproduce during the rainy season, or if they have variations in their mating patterns (e.g. Olson et al. 1986), how many species present philopatry (e.g. Sinsch 1990), or given the case of more than one mating, whether the individual moves to other ponds/places for the following mating.

The CCA and partial CCA showed that environmental drivers of the metacommunity structure differed between the two PAs (Table II-2). In La Pera, habitat variables are spatially structured, such that forest status was related to elevation, latitude and longitude. It is interesting that conserved forest seems to be located more in the highlands, probably because these areas are more difficult to access, whether for logging or agriculture. The gradient of conserved forest to open areas runs from south to north and from east to west (Fig. II-1). Thus the spatial parameters did not explain any unique variance, because they were confounded with the habitat structure (Fig. II-2). One of the possible reasons that local weather conditions alone barely explain 11% of the variance in the metacommunity structure of La Pera is that a strong air current from the Gulf of Mexico enters through the north of La Pera and ascends the mountains in the south, where lifting generates condensation and a cloud or mist belt forms. So the landscape is usually covered by clouds (Johnson & Savage 1995) in the morning and in the evening most of the year: thus it is very humid. Therefore, almost half of the variance explained by local weather conditions is also explained by habitat structure (Fig. II-2a). In Nahá the story is quite different; first the total variance explained is divided principally between local weather conditions and habitat structure, each explaining around 25%. Second, there is practically no overlap between habitat and local climatic conditions in terms of the common variance explained. And third, there is practically no overlap between the space and habitat structure and no relation at all between space and local climate (Fig. II-2b). As a result of these factors, the differences in relationships among the environmental variables and between them and the amphibian metacommunities finds expression also in the pattern of human exploitation of these areas, which has latterly at least also found expression through differing governance.

Governance in Protected Areas

As previously mentioned, Nahá PA, which is now a biosphere reserve, was established at the request, and by common agreement, between the Lacandons (local indigenous people) and the government. In the village of Nahá, the National Commission of Natural Protected Areas (CONANP) established a field base with constant visits of biologists employed by CONANP. Furthermore, the CONANP has established a program that involves the Lacandons as paid rangers, who have to rotate every year. CONANP has also established a huge reforestation program and organic coffee plantations involving Nahá's surrounding communities, including other indigenous groups such as Tzetals. This is just to mention a few of the programs currently running in the PA. The constant presence of CONANP personal ensures the success of environmental projects because it allows the follow-up of any given program or project, and therefore the zone has been granted financial resources continuously since its establishment. This is reflected in the conservation status within the PA.

In La Pera, although all communities living within the park received a formal letter mentioning the establishment of the protected area, most of the people are unaware that they live in a protected area. There was one initiative for environmental services in the area, but there are few people that can demonstrate land ownership, thus very few people got into the program. As far as we know there hasn't been any environmental education program in this PA. Another important aspect for conservation is that even though La Pera is nearly two times bigger, it has five times more population than Nahá, and this is divided into 49 communities. This may give clues as why to well-preserved forests in La Pera remain mostly in high and inaccessible areas. These forested areas will remain only as long as the communities do not need them for agriculture or pasture (e.g. Ochoa-Gaona et al. 2007). On top of this La Pera has a huge problem with litter extraction (sold as organic fertilizer) and illegal selected logging of precious wood. Litter extraction may have already had some impacts on litter frogs: one possible example is the endemic *Craugastor pozo* (Ochoa-Ochoa et al. 2009), which has not been found recently in the area. The selected logging may already have had impacts on the metacommunity of La Pera, but because we lack any sort of a monitoring programme prior to the present study we may only speculate on this point.

This study shows that the drivers of metacommunities vary among protected landscapes. The variation may occur because of differences in the structure of the environment (i.e. topography), or other underlying processes connected with human use and governance, which affect the spatial structure of the habitat. Understanding such drivers could result in a more efficient management of protected areas to conserve biodiversity in the long term.

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APPENDIX II-1

Additional results. A total number of 22 species was recorded in La Pera and 30 species in Nahá, the assemblage from the former is almost completely nested in the latter as can be observed in Table SI II-1. The list of environmental variables recorded within each transect is shown in Table SI II-2. Estimators of species richness are shown in figures SI II-1 and SI II-2. Ordinated matrices are illustrated in figures SI II-3 and SI II-4.

Table SI II-1. List of the species sampled during the rainy season of 2010 in the two landscapes sampled: La Pera and Nahá. Total number of individuals sampled, average and standard deviation are shown.

Species	La Pera	Nahá
Agalychnis callidryas	31 (0.94 ± 4.37)	93 (2.58 ± 6.62)
Agalychnis moreleti	404 (12.24 ± 41.65)	172 (4.78 ± 13.8)
Anotheca spinosa	19 (0.58 ± 1.44)	
Bolitoglossa mexicana		16 (0.44 ± 2.34)
Bolitoglossa rufescens	20 (0.61 ± 1.2)	19 (0.53 ± 1.11)
Craugastor alfredi	177 (5.36 ± 8.29)	16 (0.44 ± 1.21)
Craugastor brocchi	41 (1.24 ± 1.82)	2 (0.06 ± 0.23)
Craugastor rhodopis	3 (0.09 ± 0.29)	8 (0.22 ± 0.64)
Eleutherodactylus pipilans	318 (9.64 ± 12.57)	
Craugastor spI	36 (1.09 ± 3.49)	4 (0.11 ± 0.52)
Craugastor spII	8 (0.24 ± 0.61)	
Craugastor spIII	102 (3.09 ± 5.68)	38 (1.06 ± 2.4)
Craugastor spIV		9 (0.25 ± 0.65)
Craugastor laticeps		35 (0.97 ± 1.96)
Dendrosophus ebraccata		19 (0.53 ± 2.29)
Dendrosophus microcephala		133 (3.69 ± 7.85)
Duellmanohyla zoque	48 (1.45 ± 4.65)	5 (0.14 ± 0.59)
Hyalinobatrachium fleishmani	13 (0.39 ± 2.26)	107 (2.97 ± 8.24)
Hypopachus variolosus	66 (2 ± 5.57)	
Incilius macrocristatus		9 (0.25 ± 0.81)
Incilius valliceps	282 (8.55 ± 16.1)	150 (4.17 ± 9.12)
Gastrophryne elegans		61 (1.69 ± 6.33)
Leptodactylus labialis		15 (0.42 ± 1.48)
Lithobates brownorum	147 (4.45 ± 12.37)	119 (3.31 ± 5.01)
Lithobates vaillanti	48 (1.45 ± 4.47)	66 (1.83 ± 3.43)
Plectrohyla matudai		8 (0.22 ± 1.33)
Ptychohyla macrotympanum	3 (0.09 ± 0.52)	6 (0.17 ± 1)
Rhinella marina	33 (1 ± 1.9)	1 (0.03 ± 0.17)
Rhinophrynus dorsalis		204 (5.67 ± 19.76)
Scinax staufferi		77 (2.14 ± 6.35)
Smilisca baudini	517 (15.67 ± 31.98)	283 (7.86 ± 16.94)
Smilisca cyanosticta	71 (2.15 ± 3.67)	2 (0.06 ± 0.33)
Tlalocohyla loquax	7 (0.21 ± 1.05)	145 (4.03 ± 11.39)
Tlalocohyla picta		354 (9.83 ± 18.22)

Several richness estimators were calculated using EstimateS (Colwell 2005). The indices shown here, Chao1, Chao2, Jack1 and Jack2, are based on the probability that two randomly chosen individuals, one from each of two samples (*e.g.* patches), belong to species shared by both samples, but not necessarily to the same shared species (Colwell 2011). The estimators for these indexes take into account the contribution to the true value of this probability made by species actually present at both sites, but not detected in one or both samples (Chao et al. 2005). Two individuals-based rarefaction curves were calculated: the Coleman curve, which is based on random replacement (Gotelli & Colwell 2001); and Sobs (MaoTau), which reproduces the curve expected from the data, i.e. the equivalent of sampling without replacement. The rarefaction curves are not species richness estimators, rather they represent the *behaviour* of the sample under a randomization process; whereas other estimators such as Chao2 and Jack1, estimate the *total* species richness including those species that were not found in any sample (Chao et al. 2005).

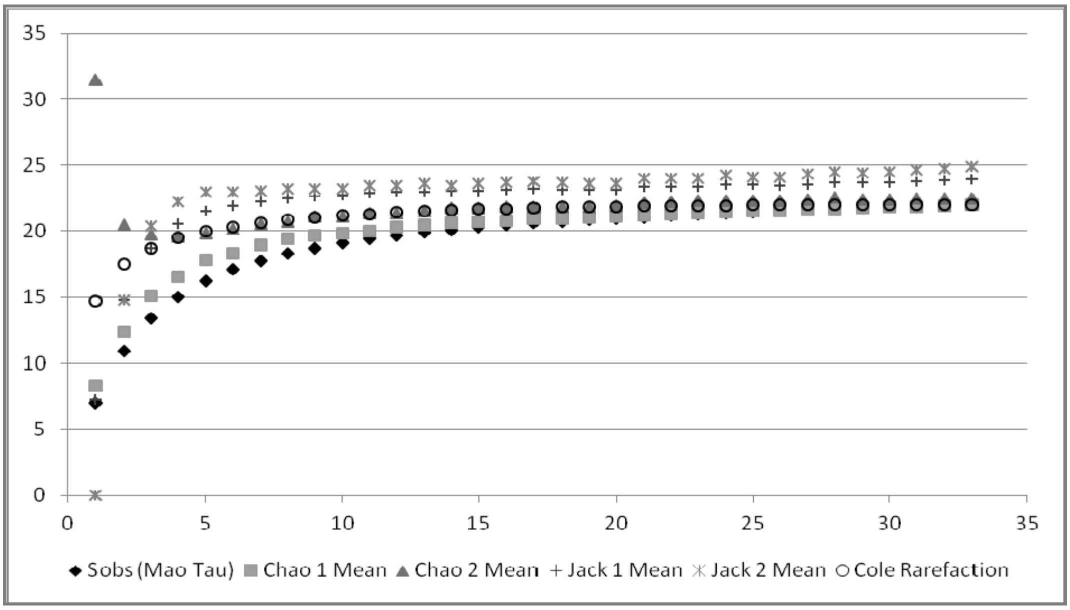

Figure SI II-1. La Pera estimators of total species richness: Chao1, Chao2, Jack1 and Jack2; and two rarefaction curves: Coleman (Cole) and Sobs (Mau Tau). Number of patches sampled (X axis) *versus* number of species estimated (Y axis). Four of the estimators, both rarefaction curves and the Chao's, indicate that the landscape is well surveyed, and the Jack's estimators, based on unseen or rare species, point to the possibility of finding two or three species more (Jack1 and Jack 2, respectively).

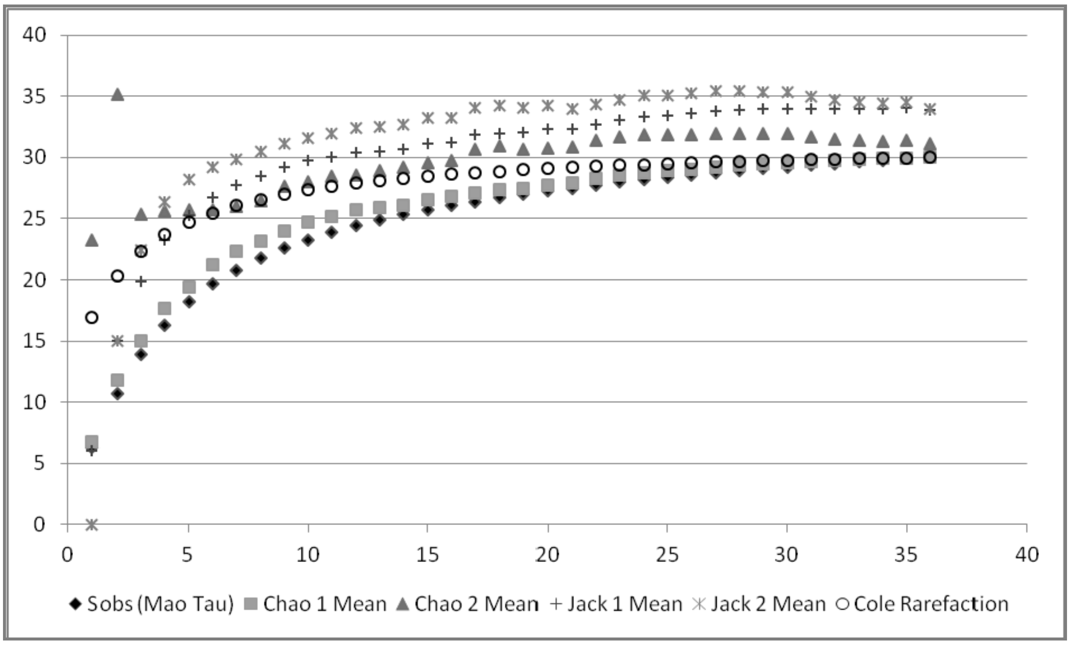

Figure SI II-2. Nahá estimators of total species richness: Chao1, Chao2, Jack1 and Jack2; and two rarefaction curves: Coleman (Cole) and Sobs (Mau Tau). Number of patches sampled (X axis) *versus* number of species estimated (Y axis). Three of the species richness estimators, rarefaction curves and Chao 1, indicate that the sampling effort was sufficient, but Chao2 indicated the possibility of finding another species and, both Jack's estimators indicated the possibility of finding four more species.

Figure SI II-3. Ordinated matrix of La Pera based on the first axis of a Correspondence Analysis (i.e. Reciprocal Averaging). Species names are on the left and forest conservation status for the patch is given along the top. Forest status was recorded for each of the transects sampled within the patch, divided into: no forest (0), very disturbed (1), disturbed (2), managed forest (3) and conserved forest (4), afterwards a simple average of the transect's forest status was performed. Thus, on one side of the spectrum, a patch with an average of 4 indicates a conserved forest without clearings; on the other side a patch with an average of zero indicates a very disturbed patch without forest at all. Ordination was performed in Matlab using the scripts of Leibold & Mikkelson (2002) updated by Higgins (2004: http://www.tarleton.edu/Faculty/higgins/EMS.htm). The gradient of forest status was included after the analyses to illustrate the importance of habitat structure for the metacommunity arrangement.

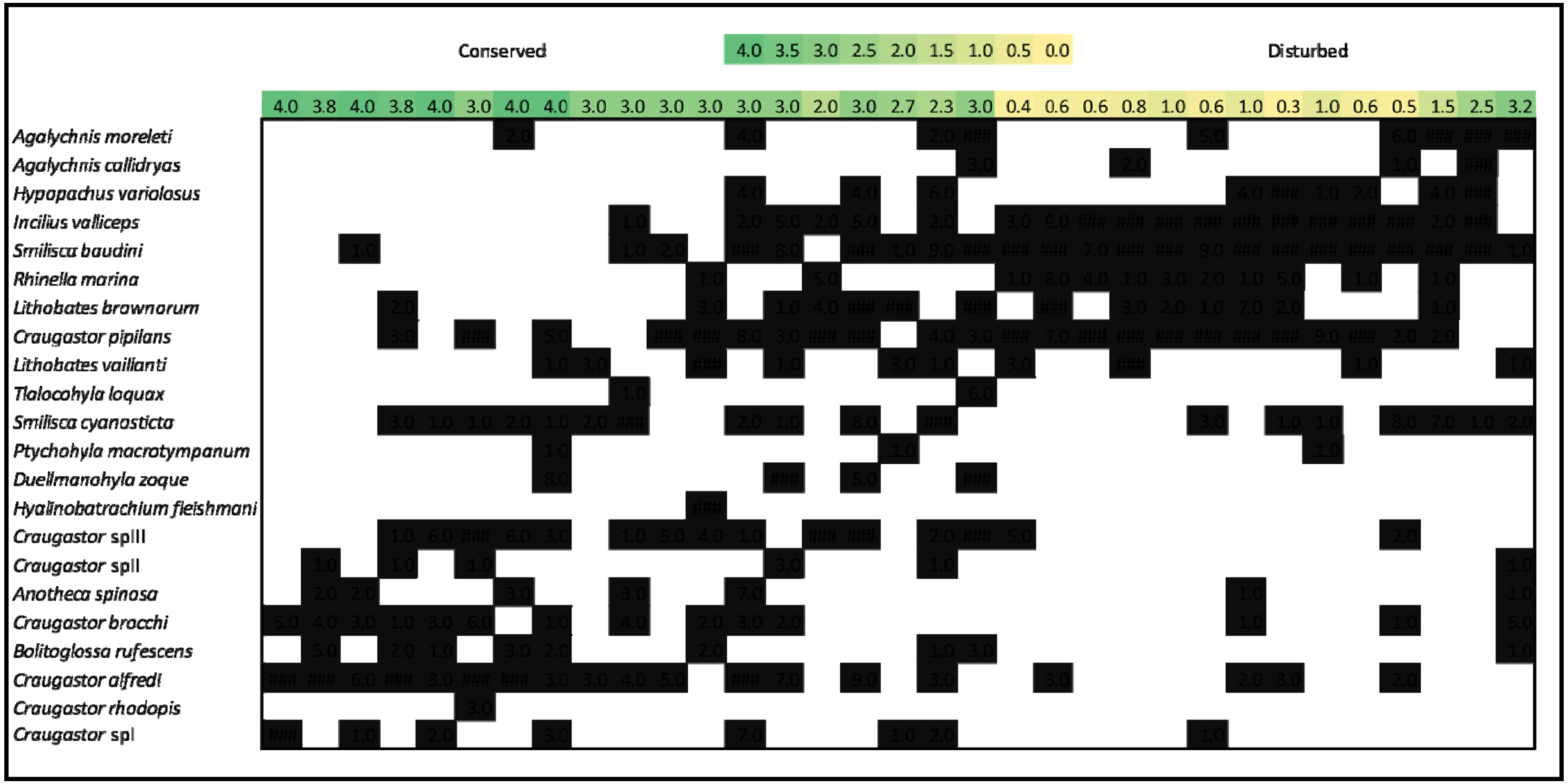

Figure SI II-4. Ordinated matrix of Nahá based on the first axis of a Correspondence Analysis (i.e. Reciprocal Averaging). Species names are in the left and forest conservation status for the patch is located at the top. Forest status was recorded for each of the transects sampled within the patch, divided into: no forest (0), very disturbed (1), disturbed (2), managed forest (3) and conserved forest (4), afterwards a simple average of the transects forest status was performed. Thus, on one side of the spectrum, a patch with an average of 4 indicates a conserved forest without clearings; on the other side a patch with an average of zero indicates a very disturbed patch without forest at all. Ordination was performed in Matlab using Higgins' (2004) script. The gradient of forest status was included after the analyses to illustrate the importance of habitat structure for the metacommunity arrangement.

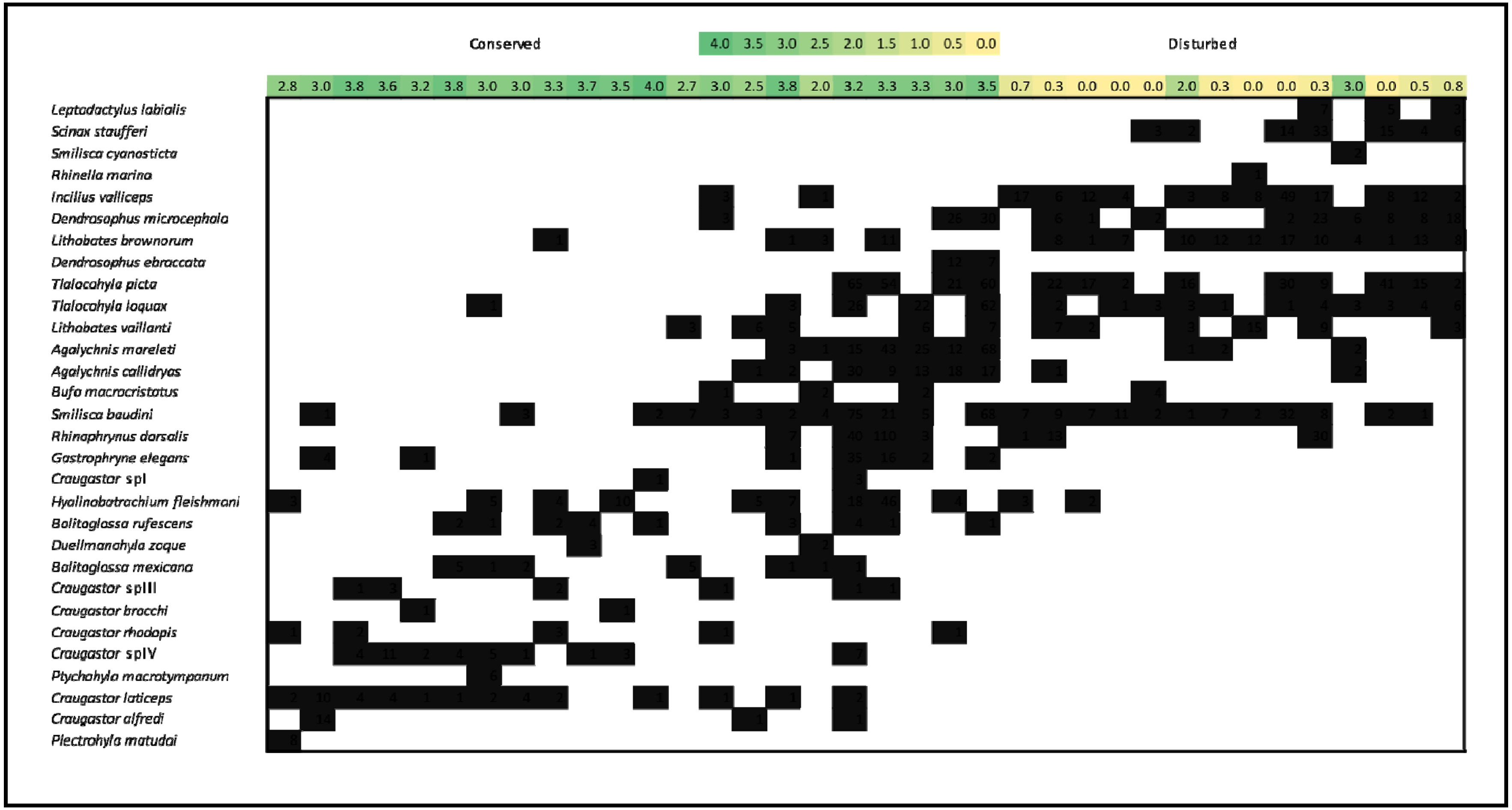

Table SI II-2. List of the variables recorded during the rainy season of 2010 in the two landscapes sampled: La Pera and Nahá. Range, mean and standard deviation of each variable within each landscape. In bold are the original variables.

	La Pera	Nahá
Space		
Latitude (decimal degrees)	16.85 - 16.95 (16.89 ± 0.02)	16.95 - 17.05 (16.98 ± 0.02)
Longitude (decimal degrees)	-93.37 - -93.31 (-93.34 ± 0.01)	-91.63 - 45.8 (-83.53 ± 26.44)
Altitude (metres above sea level)	465.25 - 1187.2 (880.26 ± 187.16)	685 - 1179 (942.19 ± 103.14)
Latitude*Longitude	-1581.58 - -1572.18 (-1576.49 ± 2.42)	-1560.57 - 776.72 (-1418.9 ± 448.99)
Latitude*Latitude	8706.33 - 8716.56 (8711.49 ± 2.65)	931.67 - 8395.67 (7657.5 ± 2105.15)
Longitude*Longitude	283.91 - 286.99 (285.29 ± 0.82)	287.07 - 290.38 (288.45 ± 0.75)
Latitude*Latitude*Longitude	146696.01 - 147655.92 (147141.83 ± 241.64)	15813.37 - 142918.4 (130,067.11 ± 35769.33)
Latitude*Longitude*Longitude	-26792.79 - -26490.16 (-26627.76 ± 79.16)	-26592.59 - 13173.77 (-24101.2 ± 7625.52)
Habitat		
Forest status: 0 = no forest, 1 = very disturbed, 2 = disturbed, 3= managed, and 4 = conserved	0.34 - 4 (2.31 ± 1.31)	0 - 4 (2.18 ± 1.47)
Interior: presence/absence (dummy variable)	0 - 1 (0.24 ± 0.44)	0 - 1 (0.39 ± 0.49)
Edge: presence/absence (dummy variable)	0 - 1 (0.39 ± 0.5)	0 - 1 (0.28 ± 0.45)
Matrix: presence/absence (dummy variable)	0 - 1 (0.36 ± 0.49)	0 - 1 (0.33 ± 0.48)
Canopy cover: in percentage	0 - 98 (49.85 ± 29.83)	0 - 100 (55.23 ± 36.41)
Litter: in centimetres	0 - 4 (1.25 ± 1.18)	0 - 7.25 (2.08 ± 1.99)
Grass: in metres	0 - 90 (11.05 ± 18.97)	0 - 1.2 (0.13 ± 0.23)
Temporary ponds: frequency of incidence in the patch from 0 to 1	0 - 0.8 (0.29 ± 0.28)	0 - 1 (0.33 ± 0.334)
Temporary streams: frequency of incidence in the patch from 0 to 1	0 - 0.4 (0.07 ± 0.13)	0 - 1 (0.09 ± 0.21)
Permanent ponds: frequency of incidence in the patch from 0 to 1	0 - 0.6 (0.13 ± 0.19)	0 - 0.5 (0.12 ± 0.18)
Permanent rivers: frequency of incidence in the patch from 0 to 1	0 - 1 (0.15 ± 0.26)	0 - 0.75 (0.07 ± 0.16)
Local weather conditions		
Rain intensity: 0 = no rain, 1 = rain the same day. During sampling: 2 = light rain or drizzle, 3 = rain, 4 = heavy rain	0 - 3 (1.28 ± 0.97)	0 - 3 (1.04 ± 1.02)
Temperature: in Celsius degrees	19.2 - 25.78 (23.51 ± 1.32)	20.74 - 25.35 (23.39 ± 1.03)
Atmospheric pressure: in hectopascals (hPa)	748.8 - 954 (902.7 ± 43.15)	890.34 - 929 (909.37 ± 10.32)
Temperature*Atmospheric pressure	14376.96 - 24250.68 (21271.85 ± 2012.8)	18840.22 - 23201.78 (21270.14 ± 1022.29)
Temperature*Rain Intenstity	0 - 76.26 (30.23 ± 23.29)	0 - 74.93 (24.15 ± 23.97)
Rain Intensity*Pressure	0 - 2862 (1159.77 ± 889.86)	0 - 2757 (951.37 ± 937.14)

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Bolitoglossa rufescens, La Pera 2009

III. VARIABILITY OF AMPHIBIAN METACOMMUNITIES IN FLUCTUATING ENVIRONMENTS: A KEY FACTOR FOR LONG-TERM PERSISTENCE?

“Curiosity takes courage.
The most important promises are the ones you make to yourself.
Pay Attention.
Appreciate. Listen. Imagine”.
Mary Anne Radmacher

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Main text: 4,434

ABSTRACT

1. Amphibians are known to be very sensitive to environmental changes. Thus, we expect changes in the structure of metacommunities in response to short term environmental change and variability. We employed the framework of metacommunity analysis to test for variation in community properties and environmental relationships across different sites and habitat types within two protected and fragmented areas in Chiapas, south Mexico: La Pera and Nahá.
2. Amphibians were sampled in transects, only at night, for two consecutive years (2009–2010) during the rainy seasons. For each transect, we also recorded relevant environmental data combining all data to patch level for analysis. Metrics for coherence, turnover and boundary clumping were used to evaluate metacommunity structure while canonical correspondence analyses (CCA) were used to explore how the association of metacommunities and environment changed between years.
3. Fewer individuals were recorded in 2009 than in the second wet season 2010, but the most abundant species in each landscape were consistent. In La Pera the metacommunity structure changed from quasi-Clementsian to quasi-Gleasonian, and in Nahá it changed from Clementsian to Gleasonian.
4. The most important environmental variables were those related to habitat structure in both years but in 2010 variables related to rain were also important. Total variance explained was similar between years but re-arrangements in the metacommunity structures occurred between years.

5. These Mexican amphibian metacommunities occupy dynamic and fluctuating environments and they respond dynamically, such that their emergent metacommunities properties are variable between protected areas and within each protected area from one year to the next.

Key-words boundary permeability, Clementsian pattern, metacommunity dynamics, environmental fluctuations, fragmented landscapes, Gleasonian patterns, Mexican amphibians.

INTRODUCTION

> "Time is a stream in which there is no turning back; if conditions change, individuals must cope, move, or die"
>
> J.A. Wiens (2000, p. 11)

For a long time, probably since the early 19th Century, there was a pervasive thought among ecologists: natural ecosystems would, through succession, reach a mature state or climax, and stay there if nothing perturbed them (e.g. Clements 1936). Nowadays, it is well known that ecosystems change continuously from one state to another (Anderson, Goudie, & Parker 2007; Magurran & Dornelas 2010), and are highly dynamic. Thus, communities live in fluctuating environments (Yachi & Loreau 1999). The effects of temporal variations in environmental quality have been studied for single species at the population and metapopulation level (e.g. Andrén 1996; Bosch & Martínez-Solano 2003; Buckley & Beebee 2004; Hare, Hoare, & Hitchmough 2007; Prugh *et al.* 2008). There have, in contrast, been relatively few attempts to explore the effects of fluctuating environment in community and metacommunity terms, in part because they are more difficult to comprehend, frame and analyse (but see Magurran & Henderson 2010; Varughese 2011; Presley, Higgins & Willlig 2010). This is especially for tropical amphibian communities, for which we have very little knowledge of temporal dynamics based on systematic, standardized sampling. Here we set out to address this knowledge gap by the analysis of two years of transect data from two protected areas in Chiapas, Mexico, a frog diversity hotspot region.

Within a landscape, local communities are restricted to certain habitats, defined by environmental boundaries, reflecting for example, local hydrology, microclimate, soils, geology, topography, etc. In the case of a fragmented landscape comprising patches of different characteristics (e.g. forests, edges, and open areas), the interior of the forest is normally cooler and more humid than the edge, as a result of the dense canopy (e.g. Welsh, Hodgson & Lind 2005), and open areas are known to have more extreme temperatures. The relationships are multidirectional: plants shaping microclimates, animals using them, other plants growing around, etc., often resulting in well-defined units with well-characterized boundaries, the patches. These patch boundaries act as a multilevel filter for species and consequently have direct implications for both dispersion and permanency of populations. Nevertheless, because the environment changes continuously in such seasonally variable landscapes, the boundaries are dynamic and may become thicker or thinner through the seasons, modifying their permeability. Boundary permeability, as defined by Stevens *et al.* (2004, p. 830), “is the probability of stepping over the boundary [border] between two different components [or patches] of the landscape”. The changes in boundary permeability may result in transient community dynamics in which populations and densities are not at equilibrium and have varying trajectories (Ovaskainen & Hanski 2002). Therefore, we may posit that transient dynamics are ubiquitous in natural systems, and crucial to an understanding of multispecies persistence and coexistence, even if rarely studied as such.

Herein we explore how amphibian metacommunities respond to fluctuating environments through the evaluation of their structure within the landscape. The concept of metacommunity is a direct extension of the idea of the metapopulation and thus refers to sets of communities occupying different sites within a landscape, close enough together that they may be linked by occasional dispersal of individuals (e.g. Leibold & Mikkelson 2002; Presley *et al.* 2010). Changes in the emergent properties of the metacommunities can be quantified by means of a recently developed analytical framework and may provide insight into the trajectory of the communities and their constituent populations. Moreover, in places where seasons are clearly defined, i.e. dry *vs.* rainy season, local climatic boundaries can change drastically, affecting the species dispersion across the landscape. Seasonality affects everything, from simply humidity and solar radiation, to the distribution of predators (García & Cabrera-Reves 2008). It is also well known that most amphibians respond to rain for mating (Duellman & Trueb 1994; Stebbins & Cohen 1997), so it is reasonable to expect that in a strongly seasonal tropical environment, the structure of amphibian communities will shift from clumped to over-dispersed to a clumped structure again within, an annual cycle. Specifically, we would expect the metacommunities to be over-dispersed (*sensu* Leibold & Mikkelson 2002) during the wet season and to see differences between years if they feature strongly contrasting precipitation levels.

Our hypothesis is that if the conditions of the environment change, species distributions will change within the landscapes and this will in turn generate changes in metacommunity patterns, such that either (i) the organisational structure and relationships with environment remain constant but the communities shifts around spatially, or (ii) the constituent communities demonstrate change in structural properties and relationships with environment, or (iii) some combination of change and flux. Which condition applies may provide insight into the amphibian community properties and dynamics. Thus, in this paper we evaluated: 1) how the metacommunities change year to year in two landscapes in the south of Mexico; 2) how metacommunity patterns respond to temporally variable factors, such as rainfall and temperature; and 3) the potential implications of these responses for amphibian conservation.

MATERIALS AND METHODS

Study Area. The fieldwork was carried out in two natural protected areas (PAs) of Chiapas (~ 17ºN), south Mexico (Fig. III-1): “La Pera”, a state PA, and the biosphere reserve of “Nahá”. The topography of both regions is complex. “La Pera” is an area of around 7,506 ha containing pristine and disturbed patches of two natural vegetation formations: tropical rain forest and evergreen seasonal forest (INEGI 2005). The area is placed in two climatic zones: warm–humid (Am(f)), with the rainy season in the summer and a percentage of winter rain >10.2% annual; and warm–sub humid (Aw20), in which the summer rains represent >55.3% of the annual rain, and winter rain of 5% to 10.2% of the annual total (García 1988). Nahá is located in the northwest of the Lacandona region and has an area of 3,847 ha. The vegetation types are tropical rain forest, cloud montane forest, pine-oak forest and disturbed vegetation commonly known as “acahuales” (INEGI 2005). The area has a hot sub-humid climate with rains in the summer (Aw2(w)(i’)g) and a humid period from May to December (García 1988). In order to sample approximately the same area in both landscapes, some areas outside the Nahá PA were also sampled.

Field-sampling. The sampling was performed mostly with transects (50m x 2m) although where the characteristics of the site did not permit use of transects, sampling was done in plots (10m x 10m); during the rainy seasons, June–September, of 2009 and 2010, only at night. The sampling was performed in forested (interior), edge (as the outer 20m of a forested patch) and transformed/disturbed areas (matrix). Time was not controlled during sampling. In La Pera a total of 30 patches were sampled, with a total of 120 transects in 2009, and 133 transects in 2010. In Nahá 31 patches were sampled, with a total of 111 transects in 2009 and 122 transects in 2010. Four to five transects were sampled per patch depending on the size of the patch. Sampling effort varied from 2 to 5 people in 2009 and 2 to 4 people in 2010: to compensate more transects were sampled in 2010. All amphibians within transects were registered. All the analyses herein were based on the patches sampled in both years, and all data were aggregated to patch level prior to analysis, resulting in 30 sites in La Pera and 31 sites in Nahá in all analyses.

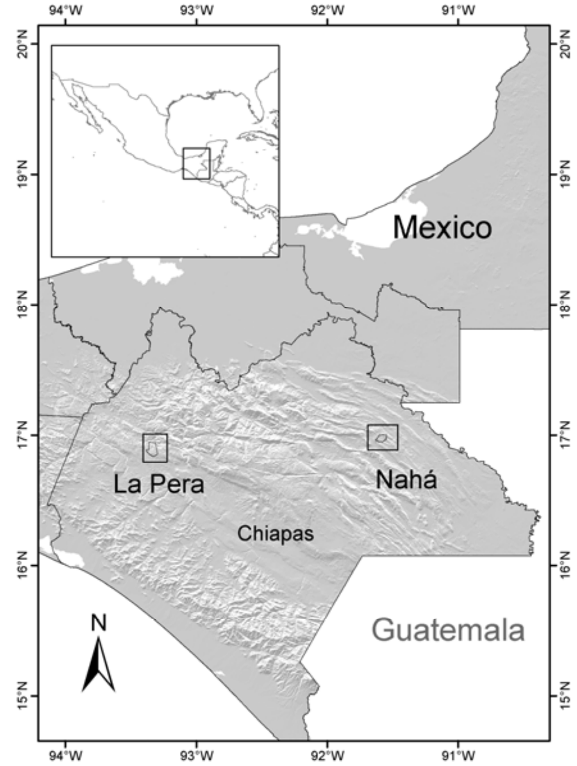

Figure III-1. Location of the landscapes sampled, La Pera to the west and Nahá towards the east.

The environmental variables measured were: latitude (Y); longitude (X); elevation in metres above level sea (m.a.s.l.); rain intensity divided into: no rain (0), rain the same day (1), light rain or drizzle (2), rain (3), heavy rain (4); local temperature (in ºC, measured with data loggers LogTag HAXO-8); forest status divided into: no forest (0), very disturbed (1), disturbed (2), managed (3) conserved (4); patch location: matrix, edge or interior; canopy coverage, as the mean of three measures of the coverage in percentage; litter as the mean of three measures of litter depth in cm; grass height, the mean of three measures of the grass height in metres; water body presence divided into six categories: temporary ponds (TP), temporary streams with less than 2m width (TS), permanent streams (PS), permanent ponds and lakes (PP), permanent river of > 2m width (PR). Environmental measures of each patch were obtained as the mean from all transects within each patch in the year in question. In total 16 environmental variables were used for the following analyses (see Table SI III-3, Appentix III-1).

Sampling efficiency was assessed by examining species accumulation curves (Coleman and Mau Tau) and associated statistics (Chao1, Chao2, Jack1 and Jack2) employing EstimateS ver 8.2 (Colwell 2011). The structure of the metacommunity and its variation between years was analysed following Presley *et al.* (2010). First, the presence/absence matrices are arranged along the major compositional gradient by correspondence analysis (CA i.e. reciprocal averaging). Next, the structure of the metacommunity is evaluated through three different parameters: coherence, species turnover and boundary clumping among the sampled sites by comparing each parameter with a null model (for derivation and methods see: Leibold & Mikkelson 2002; Presley *et al.* 2010; Presley & Willig 2010). The first assumption in this framework is that species should be distributed continuously along an environmental gradient (identified by indirect gradient analysis using CA) between the extreme points at which they occur. Coherence is evaluated through the number of embedded absences within the distribution along the axis (Leibold & Mikkelson 2002). The next step is to replace embedded absences with presences. Turnover then measures the extent of species replacement along the gradient. Boundary clumping measures the regularity of this process of turnover, i.e. the degree to which the end points of multiple species distributions coincide along the gradient once embedded absences are filled in with dummy presences (Leibold & Mikkelson 2002). To evaluate boundary clumping, Morisita's index (I) is used and compared to a null model. When range boundaries are random $I = 1$, when range boundaries are more clumped than expected $I > 1$, and $I < 1$when they are less clumped than expected or are over-dispersed. A Chi-square test is used to evaluate if I is significantly different from 1 (higher or lower). Although null models can vary in their susceptibility to type I and type errors II, the framework developed by Presley *et al.* (2010), allows the operator to choose from a selection of highly random to more constrained null models. In these analyses the null model that maintains the observed richness per site (prior to the filling, Leibold & Mikkelson 2002) and assigns equal probability to the occurrence of each species was chosen, because we could reasonably assume that the area was well sampled. These analyses were performed in Matlab 7.7.0 using the script "Metacommunity" (Higgins 2008). The parameters used were: 1 = reciprocal averaging, 3 = species richness per site is fixed & species occurrence is equiprobable, 0 = range perspective, 1000 = number of iterations, 1 = axis to use in ordination.

Canonical correspondence analyses, CCA (ter Braak & Verdonschot 1995; Legendre & Legendre 1998) using the raw species abundance data were performed for each area to explore if the associations between the metacommunities and environment changed between years. Environmental factors varied between years, therefore we decided to compute analyses separately for each year rather than summarizing the presences in a single matrix (cf. Werner *et al.* 2007). We conducted the CCA analyses in R (R Development Core Team 2009), using "vegan" 1.17-00 (Oksanen *et al.* 2011). In order to represent the species' responses to the environment from one year to another, we plotted the CCAs together maintaining the identity of the species and variables of each year, as they were separated sets of species/variables. Significant variables were selected using Monte Carlo permutation tests, with 999 permutations in CANOCO (Lepš & Šmilauer 2003).

RESULTS

The total number of individuals varied considerably between years in both landscapes. In La Pera, 667 individuals were recorded for 2009 and 2,188 individuals for 2010, with 18 and 22 species found respectively (Table SI III-1, Appendix III-1). For La Pera in 2009 five of the estimators indicate that the landscape is well surveyed, but the Jack 2 index points point to the possibility of finding one further species. The estimations for 2010 were similar, although both Jack's estimators point to the possibility of finding two or three species more (see Fig. SI III-1a,b, Appendix III-1). In Nahá, a total of 1,218 individuals were recorded for 2009 and 1,941 individuals for 2010, with 24 and 29 species found respectively. In addition, *Plectrohyla matudai* was found in some additional 2010 transects in Nahá that were omitted from the statistical analyses because these patches lacked 2009 samples (see full species list in Table SI III-2, Appendix III-1). The estimations for Nahá in 2009 indicated that up to 11 species went unsampled whereas for 2010 four of the estimators indicate that the landscape is well surveyed, and Jack's estimators point to the possibility of finding three species more (see Figs SI III-2a,b, Appendix III-1). Because the number of individuals sampled varied enormously between years we calculated the proportional abundance for each species. The most abundant three species in La Pera varied slightly between years (Fig. III-2a). For 2009 they were *Smilisca baudini* (almost 20% of the total of individuals sampled), followed by *Craugastor pipilans* (~16.5%) and *Incilius valliceps* (~15.3%). In 2010 they were

Smilisca baudini (~19%), *Agalychnis moreleti* (~17%) and *Craugastor pipilans* (~12% see also Fig. SI III-3a, Appendix III-1).

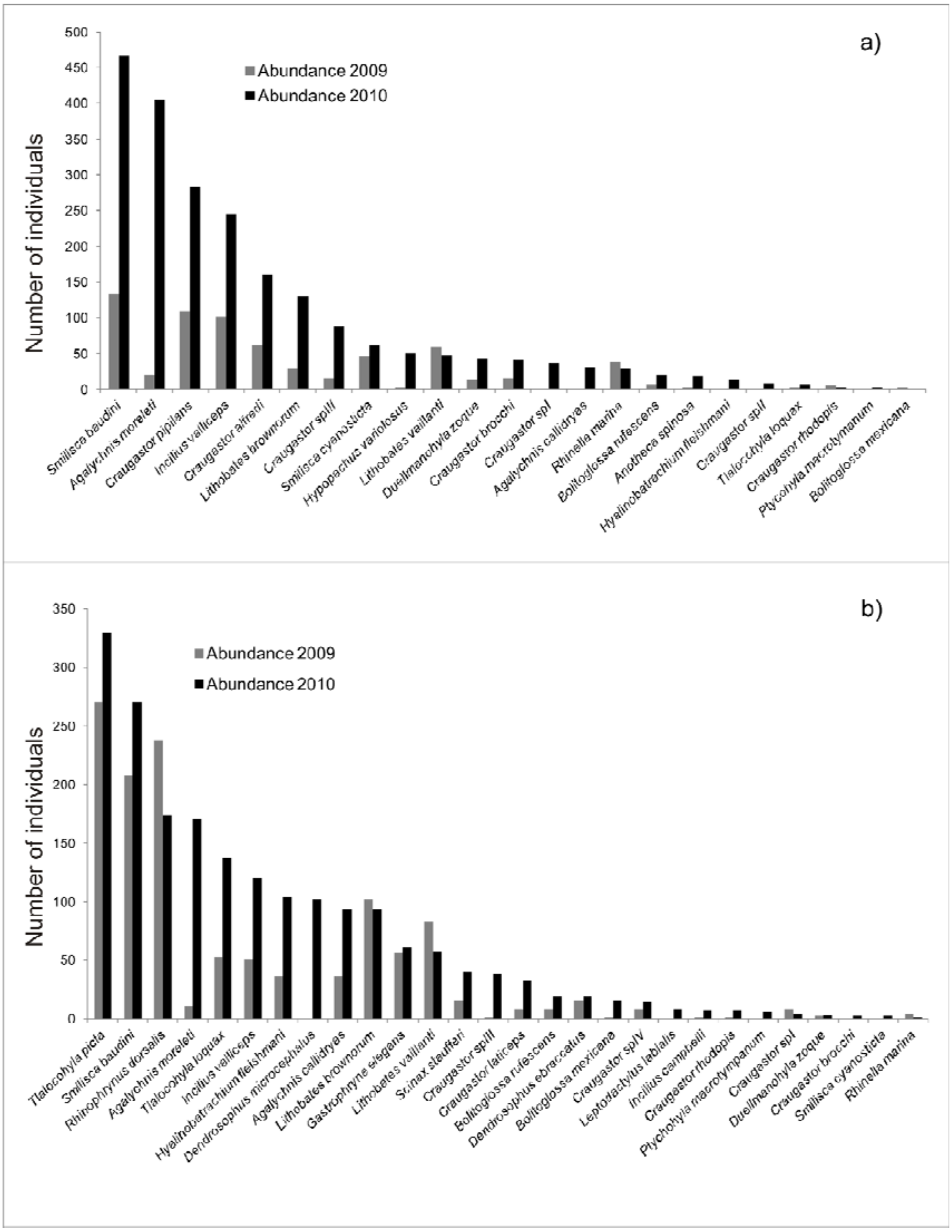

Figure III-2. Variation of species abundance of (a) La Pera and (b) Nahá between the sampling seasons of 2009 (in grey) and 2010 (in black). Abundance is represented as the total number of individuals sampled in the transects without extrapolation. Variation in proportion of the total individuals can be observed in Figs SI III-1 and SI III-2.

In Nahá the three most abundant species were the same in both years: *Tlalocohyla picta* (~22% and ~16% in 2009 and 2010, respectively), *Rhinophrynus dorsalis* (19.5% and ~9%) and finally *S. baudini* (~17% and ~14%)(Figs III-2b and SI III-3b, Appendix III-1).

The metacommunity structure changed in both landscapes between years (Table III-1). Both metacommunities, in both years, presented significant positive coherence (i.e. have fewer embedded absences than the mean of the null model). This suggests that species distributions in both landscapes are molded by latent environmental gradients.

Table III-1. Summary of the metacommunity structure analyses (coherence, species turnover and boundary clumping with the first axis of a correspondence analysis of presence/absence data) for amphibians of La Pera and Nahá between sampling seasons of 2009 and 2010. The null model equals the observed richness and assigns equal probability to the occurrence of each species. *We took the p-value as significant because Morisita's Index was almost 1.5.

		La Pera		**Nahá**	
		2009	**2010**	**2009**	**2010**
Coherence	Number of embedded absences	184	245	170	256
	p-value	0.0027	7.182E-06	0.0066	1.065E-16
	Mean	229	315	258.158	449.271
	SD	15.0005	15.5046	32.4546	23.2933
Species Turnover	Number of replacements	4800	6043	5907	13266
	p-value	0.0821	0.0518	0.0474	0.0283
	Mean	3333.4	3985.2	4306.1	9488.9
	SD	843.435	1058	807.4398	1722.3
Boundary clumping	Morisita's index	1.4815	0.7529	1.5676	1.0435
	p-value	0.051	0.1159	0.0096	0.3675
Structure		**quasi-Clementsian***	**quasi-Gleasonian**	**Clementsian**	**Gleasonian**

In La Pera, in both years, turnover was greater than the mean produced by the null model and non-significant in both cases, suggesting that the metacommunities present a non-nested quasi-structure. In the case of Nahá, turnover was greater than the mean produced by the null model and the difference was significant in both years. As a consequence, the Nahá metacommunity present idealized patterns of distribution, i.e. non-quasi structures (*sensu* Presley *et al.* 2010). Both landscapes present a similar behaviour for boundary clumping between years. Boundary clumping was significant in 2009 and greater than 1, indicating a delineation of compartments, and non-significant (around 1) in 2010, indicating that boundary clumping was stochastic. Given these results, the metacommunity of La Pera in 2009 presents a quasi-Clementsian structure that changed in 2010 to a quasi-Gleasonian structure. The Nahá metacommunity presents a Clementsian structure in 2009 and a Gleasonian structure in 2010.

The proportion of the total variance explained by the La Pera CCA in 2009 was 62.92%. The first three eigenvalues explained 31.5% of the variation. The most important variables were amount of litter, forest status, and incidence of temporary streams in the patch. In 2010 the total variance explained was 74.32%. The first three eigenvalues explained 34.3% of the variation. The most important variables were coverage, and the incidence of temporary streams and ponds (Table III-2).

The CCA for Nahá in 2009 explained 68.20% of the variance in the species-site matrix. The first three eigenvalues explained 28.1% of the variation. The most important variables in 2009 were coverage, incidence of permanent rivers, and temporary streams. In 2010 total variance explained was 61.98%. The first three eigenvalues explained 25.3% of the variation. The most important variables included canopy coverage, incidence of permanent rivers, and rain intensity (Table III-2).

Figure III-3 demonstrates the ephemeral nature of both emergent community structure and emergent species–environment relationships in La Pera and Nahá from 2009 to 2010.

Table III-2. Summary of the canonical correspondence analyses for La Pera and Nahá in 2009 and 2010. Selected significant variables (with forward selection). Lambda it is a measure of the total variance explained by the variable. F is the *F*-ratio statistic for the test on the trace. The p is the p-value in a Monte Carlo test with 999 permutations. Analyses performed with CANOCO (Lepš & Šmilauer 2003).

		2009				**2010**	
La Pera							
Sum of all canonical eigenvalues	6.44	**Inertia**	4.053	**Sum of all canonical eigenvalues**	4.084	**Inertia**	5.495
	Lambda	F	p		Lambda	F	p
Amount of litter	0.8	2.71	0.001	Canopy coverage	0.73	2.52	0.002
Forests status	0.78	2.8	0.001	Temporary streams	0.64	2.29	0.02
Temporary streams	0.72	2.76	0.016	Temporary ponds	0.49	1.79	0.016
Nahá							
Sum of all canonical eigenvalues	6.378	**Inertia**	9.353	**Sum of all canonical eigenvalues**	5.691	**Inertia**	9.181
	Lambda	F	p		Lambda	F	p
Canopy coverage	0.64	3.11	0.002	Canopy coverage	0.54	3.04	0.002
Permanent rivers	0.45	2.26	0.006	Permanent rivers	0.53	3.23	0.002
Temporary streams	0.42	2.21	0.024	Rain intensity	0.4	2.58	0.002

DISCUSSION

Rainfall patterns are of huge importance for amphibian metacommunity dynamics because most amphibians depend entirely upon rainfall to reproduce (Duellman & Trueb 1994; Beebee 2002) and require environmental humidity to survive (e.g. Rovito *et al.* 2009). Therefore changes in rainfall patterns can be directly linked to amphibian ecology and persistence of populations (e.g. Pounds & Crump 1994). Many amphibians have low recruitment rates (at least much of the time) and –

together with environmental stochasticity (deviation of rivers, pond desiccation, differences in rainfall patterns year to year, and others) – this can result in negative rates of population growth for a great part of the time. Such natural phenomena are often misunderstood as indicating population declines (e.g. Alford & Richards 1999; Gardner 2002; Gardner, Barlow, & Peres 2007a), when in fact only much longer data series can reasonably be used as the basis for such judgements (e.g. Salvidio 2009).

There was a great difference in the number of individuals recorded from one year to another, in both landscapes, but especially in La Pera. Both metacommunities follow the hollow curve in the frequency of abundance typically reported for assemblages of species at all scales (Gaston & Blackburn 2000). Although the total abundance varied greatly, it is interesting that in both landscapes the most abundant species in 2009 continued being the most abundant species in 2010. Nevertheless for the rest of the communities the proportional abundance did vary (Fig. SI III-3). Biologically, this may mean that the most abundant species are also the most plastic, while others need specific conditions and exhibit more extreme patterns of boom-breeding. Our data indicate that such a pattern of behaviour may be exemplified by *A. moreleti*, *A. callidryas*, *Hypopachus variolosus* and *Dendrosophus microcephalus* (Figs III-2), although two years of sampling is not sufficient evidence to be confident of this. Other amphibian communities show similar fluctuations in population sizes, e.g. leaf-litter frogs in Tanzania (Gardner *et al.* 2007b); communities in Italy (Vignoli, Bologna, & Luiselli 2007); and in Brazil (Vasconcelos *et al.* 2011. This implies that when conditions change, frequency in abundance (net or proportional) and habitat use from amphibians will change. Such expansions in abundance (inflation) may be crucial to the persistence of many species within fragmented landscapes (e.g. Gonzalez & Holt 2002).

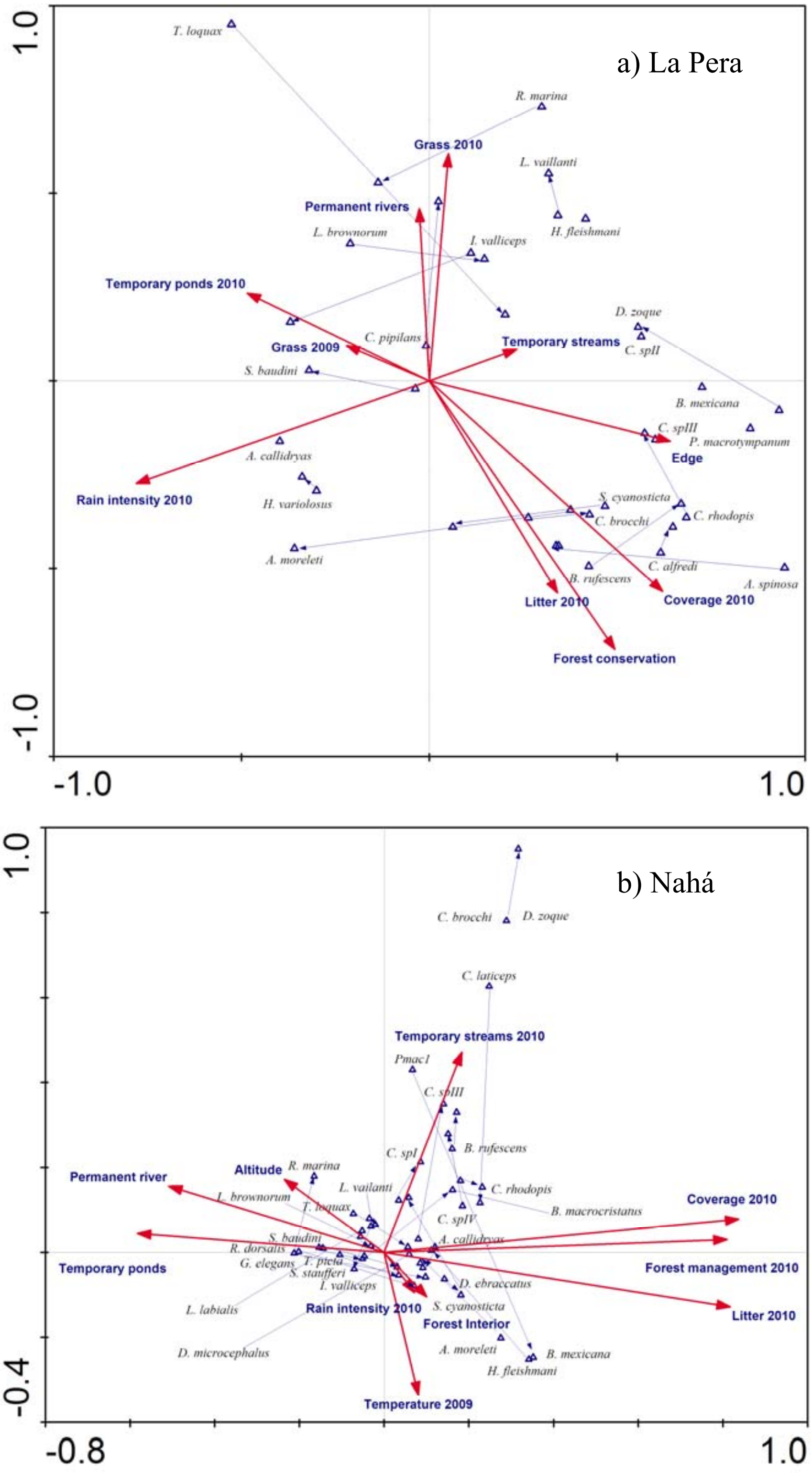

Figure III-3. Variation in the ordination scores, using Canonical Correspondence Analyses, a) La Pera and b) Nahá, from the sampling season of 2009 and 2010, with arrows indicating the direction and magnitude of the displacement involved. In each panel the main environmental loadings are also represented for each year. Not all the environmental factors are represented for the sake of clarity.

The changes in the metacommunities from a Clementsian (or quasi-Clementsian) to Gleasonian (or quasi) structure, between years, support the suggestion that amphibians are very sensitive to environmental changes (Duellman & Trueb 1994; Stebbins & Cohen 1997; Gardner *et al.* 2007a). But, these ‘adjustments’ may also imply that the amphibians comprising these particular metacommunities (La Pera and Nahá) have the capacity to acclimatize or relocate in response to the local weather disturbances. In Clementsian metacommunity structures species boundaries are highly coincidental. In biological terms this means that the sets of species that inhabit each patch are well defined, i.e. forest species such as leaf-litter frog are limited to the high-coverage forests, a genus like *Lithobathes* is limited to open areas, streams-hylids are limited to patches with forest and streams, etc. It also means that the boundary permeability among patches decreased because the difference in environmental characteristics increased. For Mexico, especially in the south, the 2009 rainy season was particularly dry; indeed, in several places seasonal crops were lost due to the lack of rain. Thus, the climatic disparity between open areas, and forested areas was huge in 2009, allowing more differentiation in amphibian communities inhabiting those areas. Conversely, 2010 was a year with plenty of rain, and as a result patch boundary permeability increased. Therefore, each species, instead of being limited to a certain patch, could move freely across the landscapes, limited only by its physiological constraints. So this may be the reason that metacommunities of 2009 were more Clementsian and in 2010 they were Gleasonian. The quasi-structures emerge in two cases: when the niche breath of the species is greater than the environmental gradient existent, or when only a part of an empirical gradient is sampled (Presley *et al.* 2010). In the case of La Pera, which presented a quasi-structure in both years, the only way to evaluate which of the two processes is the cause would be to sample more of the environmental gradient, i.e. more area.

Canonical correspondence analyses results showed very little difference in the variance explained between years, but very different community–environment configurations (Fig. III-3). In La Pera in 2010 two of the most important variables were related to rain (temporary streams and ponds). While in Nahá in each year the third most important variables was related to rain (temporary streams and rain intensity). The CCA analyses also indicate patterns of displacement of species along environmental factors (Figs III-3a, b). Frogs from the genus *Craugastor*, leaf-litter frogs with direct development, and *Bolitoglossa* (a salamander genus), move towards forested areas, explosive breeders like *Lithobathes*, *Incilius*, *Smilisca*, *Hypopachus*, move towards warm open ponds. *C. pipilans* likes open areas too. These aspects of specific responses are very important to understand because environmental variables are associated with abundance and distribution in the long-term (e.g. Brodman 2009).

Variation in abundance or structure between years does not necessarily mean population decline is prevalent (Salvidio 2009). Therefore studies that compare amphibian data between periods need to take account of environmental variation, sampling effort (not just a few days e.g. Lips *et al.* 2004), and the period of activity (e.g. Ron *et al.* 2003), if they are to produce meaningful assessments of the population status. Amphibian populations respond to varying weather, and principally to the distribution of the rainfall within and between years (Stewart 1995), rather than the total, monthly or annual, precipitation (Alexander & Eischeid 2001). This taxonomic group has been on the earth for over 350 million years, and as a group has survived huge environmental changes. They can be found in almost every major terrestrial environment on earth, but their tolerances to shifts in climatic and ecological factors are in general held to be narrow (Duellman & Trueb 1994; Jiang & Morin 2004). Our results show that amphibian metacommunity structure is highly labile in response to short term environmental variation, mainly in weather conditions, although it will require longer term data to determine what such dynamics mean for the long term sustainability of the constituent species populations in these regions. The apparent 2010 response of outbreaks, even if only of one year, could be crucial to our understanding of species persistence in the landscape (e.g. Holt *et al*. 2003). If so, this undoubtedly complicates the problem of determining the implications of long-term shifts in environmental conditions such as are associated with climate change and habitat fragmentation.

In landscapes inhabited by human communities, environmental variability will be increased by human activities, e.g. agriculture, building, construction, etc. When habitats are modified (e.g. fragmented by deforestation) distribution patterns of species change, therefore the structure of the communities living there change. We have seen that the metacommunity structure may also vary significantly from year to year in respect to varying weather. It is imperative that we learn to distinguish between environmental fluctuations that communities can cope with and those that they cannot and that we should manage to avoid or mitigate (Magurran & Dornelas 2010) –or even accept as lost causes (e.g. Ochoa-Ochoa *et al.* 2011).

Either the community and metacomunity structures are transient properties as individual species respond individualistically to environmental space, or the structure of metacommunities is a stable emergent property. Our results pointed to the first option. However, it has been long kown that sampling size affects the outcomes of biodiversity studies (Preston 1960), and of community analyses (Lande *et al*. 2003). Although we compared the same number of sites, the number of individuals varied between the two years, reflecting environmental variation driving the community dynamics (Guo *et al*., 2002; Grøtan *et al*., 2012). We cannot be certain to what extent the changing metacommunity properties revealed in our analyses reflect variation in number of invididuals sampled as opposed to changing distributions of individuals within the landscape. As both may be involved, a longer period of sampling is necessary to make further statements.

Although the data presented here are for just two years, being based on a standardized protocol and extensive plot-based sampling, they provide a base-line of evidence and insights into how metacommunities respond to environmental change and variability. These variations in the metacommunity structure will be mainly caused by the individual responses of each species, as members of each population search for places to reproduce. Therefore, it is of absolute importance to monitor the changes of metacommunities, environments and species, especially, in fluctuating environments such as the seasonal tropics (e.g. Whiteman & Wissinger 2005).

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APPENDIX III-1

Additional results. List of species found in La Pera during each field season is presented in Table SI III-1, species list of Nahá is showed in Table SI III-2. Estimators for La Pera and Nahá are presented in Figure SI III-1 and SI III-2 respectively. Variation of proportional species abundance for each species is shown in Figure SI III-3.

Table SI III-1. Species found in "La Pera" during two field seasons (2009-2010), in comparison with the locality records database. The database was compiled from all the museums in the World which had an electronic catalogue or database, up to 2004, and complemented in 2006 with the catalogue of the National Collection of Amphibians and Reptiles (CNAR, UNAM), financed projects from the National Commission of Knowledge and Use of Biodiversity (CONABIO), and the Faculty of Science Museum of Zoology (MZFC, UNAM). The records in the database were georeferenced by L. Ochoa-Ochoa and checked with Mexican experts in Herpetology (for further details see Ochoa-Ochoa *et al.* 2006). New species (+); we did not collect any specimen so the species assignation could be mistaken (*).

Field work 2009	Field work 2010	World Data base
	Agalychnis callidryas	
Agalychnis moreleti	*Agalychnis moreleti*	*Agalychnis moreleti*
Anotheca spinosa	*Anotheca spinosa*	*Anotheca spinosa*
Bolitoglossa mexicana		*Bolitoglossa mexicana*
Bolitoglossa rufescens	*Bolitoglossa rufescens*	
		Bufo bocourti
Rhinella marina	*Rhinella marina*	
Bufo valliceps	*Bufo valliceps*	*Bufo valliceps*
Duellmanohyla zoque+	*Duellmanohyla zoque+*	
Cragugastor alfredi	*Craugastor alfredi*	
Cragugastor brocchi	*Craugastor brocchi*	
	Craugastor spIII*	*Cragugastor lineatus*
Eleutherodactylus pipilans	*Eleutherodactylus pipilans*	
		Cragugastor pozo
	Craugastor spI*	*Cragugastor pygmaeus*
Cragugastor rhodopis	*Craugastor rhodopis*	*Cragugastor rhodopis*
	Craugastor spII*	*Cragugastor rugulosus*
		Cragugastor stuarti
		Exerodonta sumichrasti
	Hyalinobatrachium fleishmani	
		Hyla walkeri
Hypopachus variolosus	*Hypopachus variolosus*	
		Ixalotriton niger
	Ptycohyla macrotymanum	*Ptychohyla macrotympanum*

Field work 2009	Field work 2010	World Data base
Lithobates brownorum	*Lithobates brownorum*	
Lithobates vaillanti	*Lithobates vaillanti*	
Smilisca baudini	*Smilisca baudini*	*Smilisca baudini*
Smilisca cyanosticta	*Smilisca cyanosticta*	*Smilisca cyanosticta*
Tlalocohyla loquax	*Tlalocohyla loquax*	*Tlalocohyla loquax*

Table SI III-2. Species found in "Naha" during two field seasons (2009-2010), in comparison with the locality records database. The database was compiled from all the museums in the World, as per the previous table.

Field work 2009	Field work 2010	World Data base
Agalychnis callidryas	*Agalychnis callidryas*	
Agalychnis moreleti	*Agalychnis moreleti*	
Bolitoglossa mexicana	*Bolitoglossa mexicana*	
Bolitoglossa rufescens	*Bolitoglossa rufescens*	
	Bufo macrocristatus	
Rhinella marina	*Rhinella marina*	
Bufo valliceps	*Bufo valliceps*	*Bufo valliceps*
Dendropsophus ebraccatus	*Dendropsophus ebraccatus*	
	Dendropsophus microcephalus	
	Craugastor brocchi	
Craugastor laticeps	*Craugastor laticeps*	*Craugastor laticeps*
Craugastor rhodopis	*Craugastor rhodopis*	
	Craugastor spI	
Craugastor spIII	*Craugastor* spIII	
Craugastor spIV	*Craugastor* spIV	
		Craugastor alfredi
Duellmanohyla zoque	*Duellmanohyla zoque*	
Gastrophryne elegans	*Gastrophryne elegans*	
Hyalinobatrachium fleischmanni	*Hyalinobatrachium fleishmani*	
Leptodactylus labialis	*Leptodactylus labialis*	
Lithobates brownorum	*Lithobates brownorum*	
Lithobates vaillanti	*Lithobates vaillanti*	*Lithobates vaillanti*
	Plectrohyla matudai	
	Ptychohyla macrotympanum	
Rhinophrynus dorsalis	*Rhinophrynus dorsalis*	
Scinax staufferi	*Scinax staufferi*	
Smilisca baudini	*Smilisca baudini*	
	Smilisca cyanosticta	
Tlalocohyla loquax	*Tlalocohyla loquax*	*Tlalocohyla loquax*
Tlalocohyla picta	*Tlalocohyla picta*	

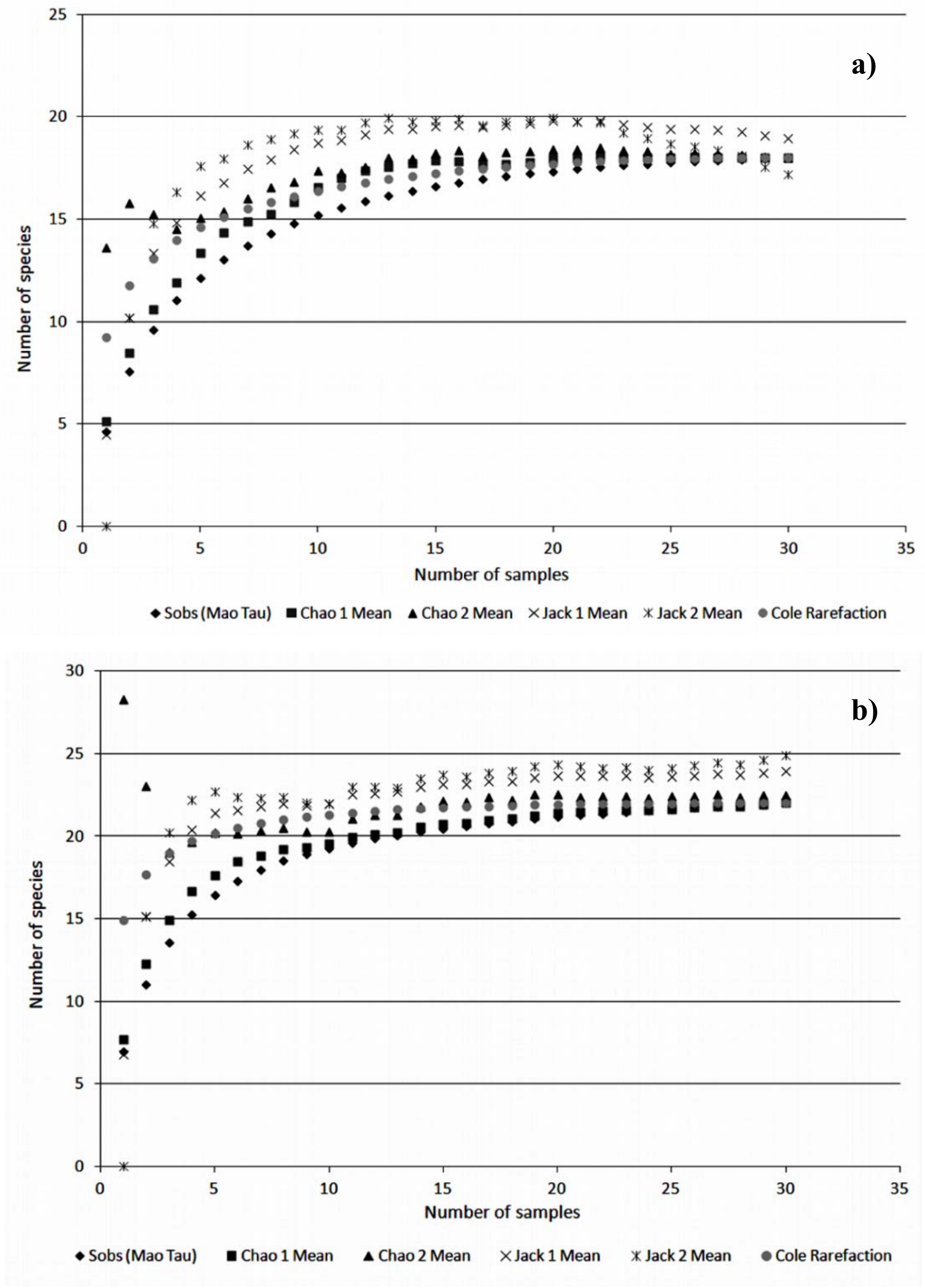

Figure SI III-1. La Pera estimators of total species richness: Chao1, Chao2, Jack1 and Jack2, and two rarefaction curves: Coleman (Cole) and Sobs (Mau Tau). a) In 2009, five of the estimators indicate that the landscape is well surveyed, and Jack2 points to the possibility of finding one species more. b) In 2010, four of the estimators indicate that the landscape is well surveyed, and Jack's estimators point to the possibility of finding two or three species more (Jack1 and Jack 2, respectively).

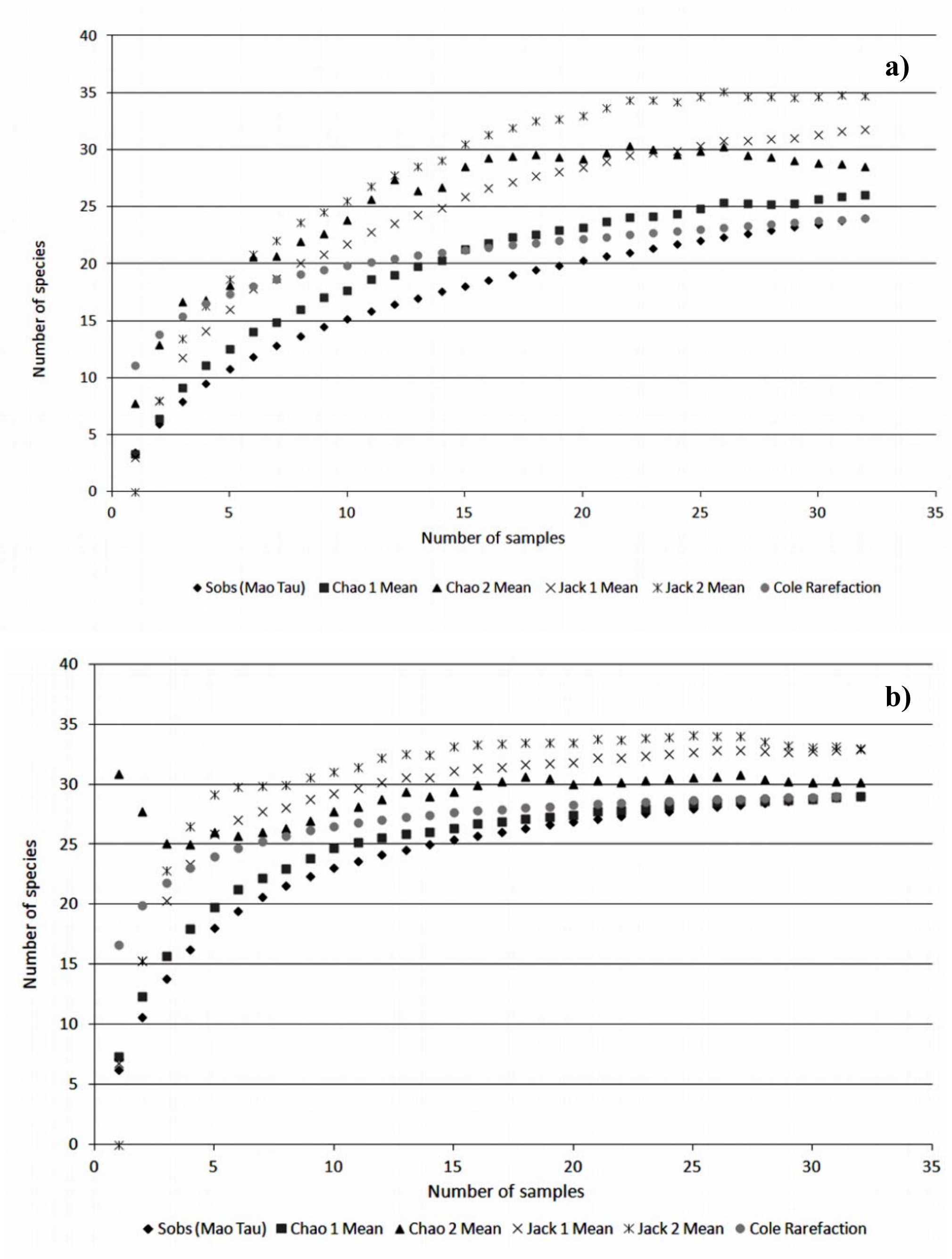

Figure SI III-2. Nahá estimators of total species richness: Chao1, Chao2, Jack1 and Jack2, and two rarefaction curves: Coleman (Cole) and Sobs (Mau Tau). a) In 2009, all the estimators point to the possibility of finding up to 11 species more. b) In 2010, four of the estimators indicate that the landscape is well surveyed, and Jack's estimators point to the possibility of finding three species more.

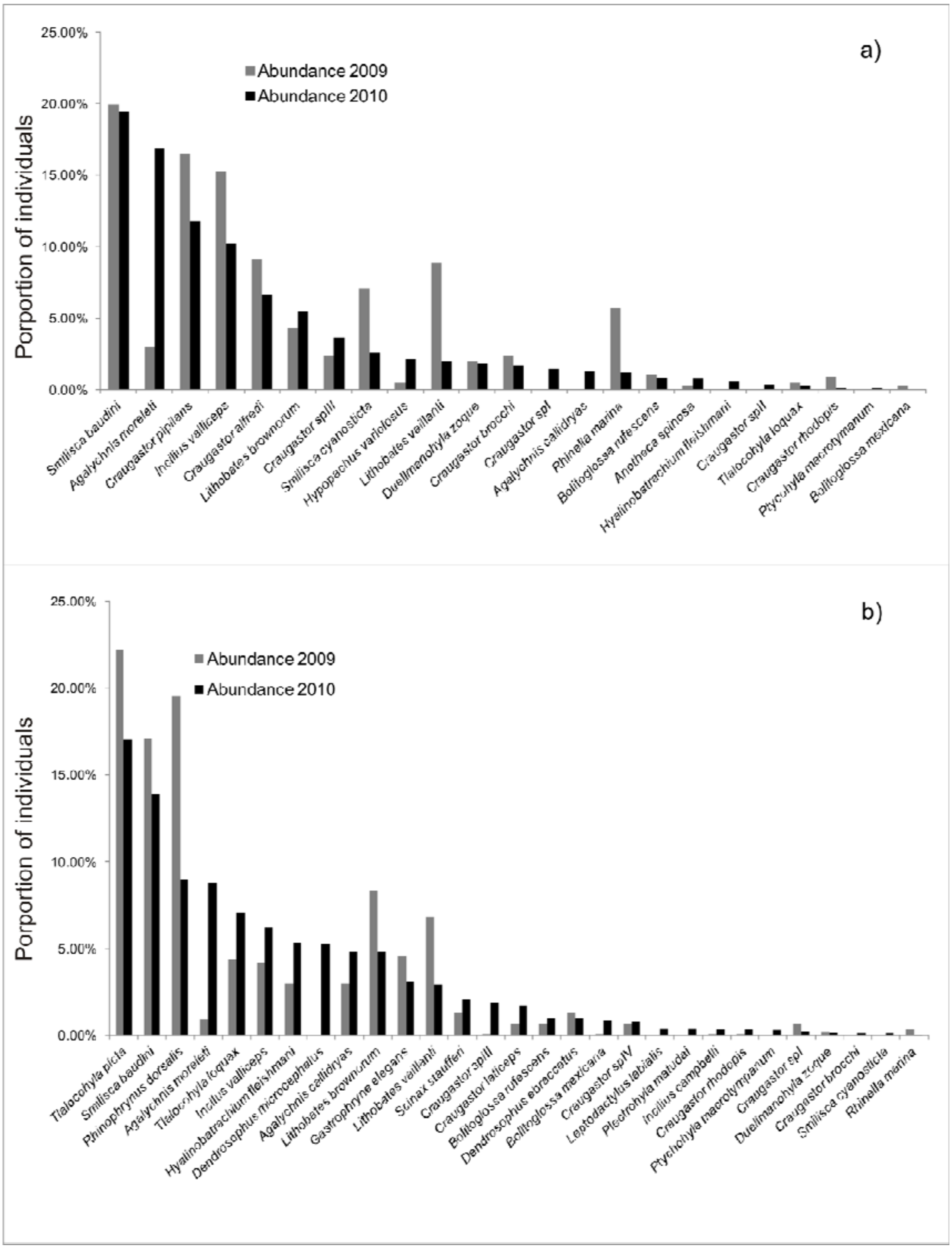

Figure SI III-3. Variation of species abundance of a) La Pera, b) Nahá, between the sampling seasons of 2009 (in grey) and 2010 (in black). Abundance for each species is represented as the proportion of the total number of individuals sampled in the transects without extrapolation.

Table SI III-3. List of the variables recorded during the rainy seasons of 2009 and 2010 in the two landscapes sampled: La Pera and Nahá. The range, mean and standard deviation of each variable within each landscape per year are shown.

	La Pera		**Nahá**	
Environmental variable	**2009**	**2010**	**2009**	**2010**
Latitude: in decimal degrees	16.85 - 16.95 (16.9 ± 0.03)	16.86 - 16.95 (16.9 ± 0.03)	16.85 - 16.95 (16.99 ± 0.03)	16.95 - 17.03 (16.99 ± 0.03)
Longitude: in decimal degrees	-93.37 - -93.31 (-93.34 ± 0.02)	-93.37 - -93.32 (-93.34 ± 0.02)	-93.37 - -93.31 (-86.83 ± 15.24)	-91.63 - -30.53 (-86.83 ± 15.24)
Altitude: in metres above sea level	465.25 - 1187.2 (864.82 ± 186.88)	465.25 - 1139 (860.96 ± 181.08)	465.25 - 1187.2 (947.85 ± 98.51)	784.25 - 1179 (947.85 ± 98.51)
Forest status: 0 = no forest, 1 = very disturbed, 2 = disturbed, 3= managed, and 4 = conserved	0.34 - 3.8 (2.21 ± 1.07)	0.34 - 4 (2.21 ± 1.33)	0.34 - 3.8 (2.44 ± 1.39)	0 - 4 (2.26 ± 1.48)
Matrix: presence/absence (dummy variable)	0 - 1 (0.44 ± 0.51)	0 - 1 (0.4 ± 0.5)	0 - 1 (0.35 ± 0.49)	0 - 1 (0.32 ± 0.48)
Edge: presence/absence (dummy variable)	0 - 1 (0.37 ± 0.5)	0 - 1 (0.37 ± 0.5)	0 - 1 (0.29 ± 0.46)	0 - 1 (0.29 ± 0.46)
Interior: presence/absence (dummy variable)	0 - 1 (0.2 ± 0.41)	0 - 1 (0.24 ± 0.44)	0 - 1 (0.38 ± 0.5)	0 - 1 (0.41 ± 0.5)
Canopy cover: in percentage	3.34 - 93.75 (54.33 ± 28.67)	0 - 93.75 (48.09 ± 29.98)	3.34 - 93.75 (54.08 ± 30.55)	0 - 100 (58.12 ± 35.59)
Litter: in centimetres	0 - 10.25 (3.63 ± 2.94)	0 - 3.63 (1.17 ± 1.12)	0 - 10.25 (4.5 ± 3.53)	0 - 7.25 (2.25 ± 2.02)
Grass: in metres	0 - 0.75 (0.13 ± 0.21)	0 - 0.9 (0.12 ± 0.19)	0 - 0.75 (0.1 ± 0.16)	0 - 1.2 (0.13 ± 0.24)
Temporary ponds: frequency of incidence in the patch from 0 to 1	0 - 1 (0.1 ± 0.22)	0 - 0.8 (0.32 ± 0.28)	0 - 1 (0.22 ± 0.26)	0 - 1 (0.3 ± 0.33)

	La Pera		Nahá	
Environmental variable	**2009**	**2010**	**2009**	**2010**
Temporary streams: frequency of incidence in the patch from 0 to 1	0 - 0.5 (0.04 ± 0.13)	0 - 0.4 (0.08 ± 0.13)	0 - 0.5 (0.02 ± 0.07)	0 - 1 (0.1 ± 0.22)
Permanent ponds: frequency of incidence in the patch from 0 to 1	0 - 0.67 (0.15 ± 0.21)	0 - 0.6 (0.13 ± 0.19)	0 - 0.67 (0.16 ± 0.26)	0 - 0.5 (0.12 ± 0.18)
Permanent rivers: frequency of incidence in the patch from 0 to 1	0 - 0.75 (0.16 ± 0.24)	0 - 1 (0.17 ± 0.28)	0 - 0.75 (0.07 ± 0.14)	0 - 0.34 (0.06 ± 0.12)
Rain intensity: 0 = no rain, 1 = rain the same day. During sampling: 2 = light rain or drizzle, 3 = rain, 4 = heavy rain	0 - 2.25 (1.2 ± 0.66)	0 - 3 (1.25 ± 0.96)	0 - 2.25 (1.49 ± 0.81)	0 - 3 (1.13 ± 1.04)
Temperature: in Celsius degrees	21.02 - 25.7 (22.98 ± 1.28)	19.2 - 25.78 (23.47 ± 1.37)	21.02 - 25.7 (25.01 ± 3.22)	20.74 - 25.13 (23.3 ± 0.99)

REFERENCES APPENDIX III-1

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Bolitoglossa mexicana, Nahá 2009

IV. B-DIVERSITY AND ENVIRONMENTAL HETEROGENEITY RELATIONSHIP VARIES WITH SCALE AND TAXON FOR MEXICAN TERRESTRIAL VERTEBRATES

“There never were in the world two opinions alike, no more than two hairs or two grains; the most universal quality is diversity”

Michel de Montaigne

This chapter was finished in January 2012, and submitted for review and publication in February of the same year to *Journal of Biogeography* (see Appendix B). The co-authors that contributed to this work were (in authorship order): Leticia M. Ochoa Ochoa, Mariana Munguía, Adolfo G. Navarro-Sigüenza, Oscar A. Flores-Villela, Víctor Sánchez-Cordero, and Pilar Rodríguez who kindly gave consent to include this article in the thesis.

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ABSTRACT

Aim: To assess patterns of β-diversity for Mexican terrestrial vertebrates and explore their relationships with environmental heterogeneity metrics at different spatial scales, identifying the most important surrogates at each spatial scale.

Location: Mexico.

Methods: We used distribution ranges predicted by ecological niche models (ENMs) of 2513 species of birds, mammals, amphibians and reptiles occurring in Mexico, and estimated their β-diversity using the properties of R.H. Whittaker's multiplicative formula. Surrogates of environmental heterogeneity (EH) were derived from data for the range and variation of temperature, precipitation, and elevation, and from data for vegetation and soil types. Both β-diversity and EH metrics were calculated at different spatial scales (2, 1, 0.5, 0.25 and 0.125 degrees lat-long). We performed regression trees, linear models (LM), simultaneous (SAR) and conditional (CAR) autoregressive models to explore the relationship between β-diversity and EH for each spatial scale and each group of vertebrates.

Results: For amphibians, reptiles and mammals we found higher β-diversity values along mountain ranges, whereas for birds high values were also found in the Mexican Plateau. Models (LM, SAR and CAR) showed best fits at coarser scales, except for birds, where half-degree models increased performance. Regression trees showed congruent results with the previous models at coarse scales but differed at finer scales. β-diversity patterns of amphibians and reptiles were best related to coefficient of variation of temperature, while for birds, the most important variables were range of temperature and coefficient of variation of precipitation. In mammals, a different variable emerged at each scale.

Main conclusions: The relationships between β-diversity and the environmental heterogeneity surrogates varied in form and strength across scale and between vertebrate groups.

Keywords: amphibians, β-diversity, birds, conditional autoregressive models, distribution ranges, heterogeneity surrogates, mammals, Mexico, reptiles, scale effects.

INTRODUCTION

> "In a very real sense, 'heterogeneity' has become the ecologist's mantra"
>
> J.A. Wiens (2000, p.11)

Although formalised only in the second half of the 20th Century, the concept of β-diversity has long fascinated biologists, as evident for example in the work of Alfred Russel Wallace and Alexander von Humboldt. Despite recent attempts to define β-diversity, for example, as dissimilarity, turnover, and as a scaling factor, among others (Vellend, 2001; Koleff *et al.*, 2003; Moreno & Rodríguez, 2010; Tuomisto, 2010), varying concepts and usages persist. Here, we used the concept as originally defined (Whittaker, 1960) where β-diversity is the variation in species composition across communities within a landscape. This concept is problematic to interpret, as communities, ecosystems and landscapes are arbitrarily defined. For example, a landscape unit from the human perspective may be defined from 30 to 300 km^2 (Fischer & Lindenmayer, 2007), but for a beetle a landscape unit can be a few metres wide (Wiens & Milne, 1989). Thus, the spatial scales at which these terms best apply will vary depending on the biological attributes of the different taxa and the scales at which the organisms involved interact with their environment (Whittaker *et al.*, 2001; Tews *et al.*, 2004).

β-diversity is a key concept for understanding the spatial patterns of biodiversity (Hillebrand, 2004; Legendre *et al.*, 2005; Drakare *et al.*, 2006; Soininen *et al.*, 2007), how these patterns vary as a function of scale (Loreau, 2000; Crawley & Harral, 2001; Whittaker *et al.*, 2001) and habitat fragmentation (Noss, 1983; Pineda & Halffter, 2004). It is also closely related to the concept of rarity-complementarity proposed by Sánchez-Cordero *et al.* (2005); consequently is relevant to conservation (Gaston *et al.*, 2001). Analysis of β-diversity is a useful approach for understanding the dynamics of patterns of species richness, as it is mathematically equivalent to the inverse of species average range size within a system (Routledge, 1977; Arita & Rodríguez, 2002). The larger, more continuous, and the more overlapped the individual ranges are, the more homogeneous the pattern of α-diversity will be and the lower the values of β-diversity. In contrast, small and disjointed individual ranges generate heterogeneous patterns of α-diversity with high β-diversity values.

Spatial patterns of β-diversity have been mapped for different taxonomic groups, regions and scales, using an extensive variety of measures and indices (see Koleff *et al.*, 2003; Tuomisto, 2010 for reviews). However, most commonly, β-diversity patterns have been analysed using turnover metrics applied at coarse scales and to systems of large extent, encompassing sub-continental regions or entire continents (e.g. McKnight *et al.*, 2007; He & Zhang, 2009; Quian, 2009; Powney *et al.*, 2010). Variation in β-diversity has been analysed in relation to a variety of environmental and geographical variables, with several studies highlighting the potential explanatory value of measures of environmental heterogeneity (e.g. Balvanera *et al.*, 2002; Balvanera & Aguirre, 2006; Declerck *et al.*, 2011).

The definition of environmental heterogeneity remains ambiguous, i.e. it is a general term that encompasses very different phenomena (Wiens & Milne, 1989; Milne, 1991; Stuefer, 1996; Wiens, 2000). There are two broad types of heterogeneity: temporal and spatial, which may each be interlinked and scale-dependent (Wiens, 2000). In more detail, environmental heterogeneity includes the entire range of variability of the different aspects in a region, including climate variables, landscape complexity, and – depending on definitions of environment –

the interactions with other organisms. Therefore, to measure heterogeneity is a complex task with no single 'perfect index' (Wiens, 2000). In the present study we focus on the explanatory power of variability in a set of environmental properties representing climate, topography, vegetation, and soils for describing spatial patterns in β-diversity of four groups of vertebrates.

Mexico contains around 10% of global species diversity of several taxonomic groups, in just 2% of the world's land surface area (CONABIO, 2008). The high rate of endemism is exemplified by figures of >60% for amphibians, >40% for mammals, and >55% for reptiles (Koleff *et al.*, 2008). Although the percentage of endemism in birds is much lower (< 10%, CONABIO, 2008), this is compensated by the high total number of species for the country. Arita & León-Paniagua (1993) highlighted that underpinning the megadiversity of Mexican mammals is a pattern of unremarkable α-diversity but high β-diversity, associated, in turn, with the high number of range restricted mammals existing in the country. This comment may also be applied to other taxonomic groups (i.e. amphibians and reptiles). A first effort to evaluate the β-diversity component of the birds, amphibians, reptiles and mammals of Mexico was undertaken by Koleff *et al.* (2008) based on the proportion of the average range size in each grid cell, using 0.5 degrees (lat–long) of cell-size. Their analysis revealed profound differences in the patterns of diversity between different taxonomic groups, but was carried out at just one scale of analysis. In addition, other studies have proposed that the high overall species richness and high endemism of the country is explained as result of the complex geological history and/or the high environmental heterogeneity, often reflected in high β-diversity (e.g. Balvanera *et al.*, 2002; Rodríguez *et al.*, 2003).

We based our approach on the proposition that β-diversity patterns may vary between different major taxa and with varying grain of analysis (cf. Whittaker *et al.,* 2001), and analyzed the relationship between β-diversity and a range of specific environmental heterogeneity (EH) metrics, to assess the hypothesis that variation in β-diversity within Mexico is explained by environmental heterogeneity.

Specifically, we address the following questions: (i) which EH metrics have greatest relevance to explaining variation in β-diversity? (ii) how do they vary between the four major taxa of Mexican vertebrates? (iii) how do these relationships vary with changing grain of analysis? Finally (iv), at what scale do the models correlating β-diversity and EH have the best fits?

MATERIALS AND METHODS

Terrestrial Vertebrates Distribution Range Maps

We use the most complete database of Mexican terrestrial vertebrates, comprising distribution maps of 2513 species: 883 resident birds (Navarro-Sigüenza *et al.*, 2003; Navarro-Sigüenza & Peterson, 2007), 344 mammals (of 451; Ceballos *et al.*, 2002), 364 amphibians and 811 reptiles (of 372 and 830 respectively; Ochoa-Ochoa *et al.*, 2006). There has been a long debate about which algorithm(s) are the best to model species distributions (Liu *et al.*, 2005; Araújo & New, 2006; Pearson *et al.*, 2006, 2007; Lozier *et al.,* 2009; Phillips *et al.*, 2009; Hirzel & Lay 2008; Pineda & Lobo, 2009; Soberón & Nakamura 2009; Peterson *et al.*, 2012), and no single algorithm has been found to be superior in all circumstances. However, it has been found that the General Algorithm for Rule Productions (GARP) method (Stockwell & Peters, 1999) overpredicts or performs better in predicting more unknown areas (e.g. for invasive species). Therefore in Mexico, where there are vast unsampled areas, GARP is a reasonable choice for modelling distribution ranges. Species distributions were modelled in two sets: species with fewer than 10 occurrences were classified as rare in one set, and species with more than 10 were classed as common in another set. For the former set, all records were used to create the models and the ‘soft’ option for threshold of presence was selected (GARP generates all the models and then selects the best), in the latter 30% of the occurrences for each species were used to evaluate the models and the ‘hard’ option for threshold of presence was selected (each model is evaluated after being created; if it fulfil the requirements of the ‘best models’ then it is kept; the program stops generating models as soon as it has accomplished the proportion of best models specified). Five best models were obtained for the rare species and 10 for the common ones. The selection of the best models was based on automatic omission–commission thresholds. After that a consensus was generated from the best models to determine presence. Further details for each group can be found in Appendix IV-1. These exactly same maps have been considered a good approximation to the real distributional areas for Mexican species and have been widely used for biogeography and conservation issues (*e.g.* Sánchez-Cordero *et al.*, 2005; Lira-Noriega *et al.*, 2007; Pronatura-Mexico & The Nature Conservancy, 2007; CONABIO-CONANP-TNC-Pronatura-FCF & UANL, 2007; Munguía *et al.*, 2008; CONABIO, 2008). Details of the methods used are also to be found in these publications. The maps represent between 70 and 97% of the total species of terrestrial vertebrates occurring in Mexico.

β-diversity

β-diversity was calculated using the same fine scale (1km^2) but different region sizes: two degrees (~40,000km^2), one degree (~10,000km^2), 0.5 degrees (~2,500km^2), 0.25

degrees (~625km^2), and 0.125 degrees (~156.25km^2). To estimate β-diversity, we used the derivation of the multiplicative formula proposed by Whittaker (1960) to calculate β-diversity, $\beta_W=\gamma\alpha_{mean}^{-1}$ as it allows comparison between taxonomic groups and sites with different overall species richness values (Srivastava, 1999). We follow the procedure proposed by Schluter and Ricklefs (1993) to obtain β-diversity. They suggested that β-diversity should be expressed exclusively in terms of the distribution of species, defining β-diversity as the inverse of the occupancy: that is, the average number of sites occupied by species (Ney-Nifle & Mangel, 1999). As this procedure is based on the occupancy, we calculated the proportion of the average range size in each grid cell (Arita & Rodríguez, 2002; Arita *et al.,* 2008), and obtained the inverse of the proportion. This value is β-diversity for each grid cell (for a full derivation see Appendix IV-1).

Environmental heterogeneity metrics

Five variables were selected as surrogates of EH (herein EH metrics), extracted from different sources: temperature and annual precipitation (Worldclim Project: Hijmans *et al.,* 2005); elevation (digital elevation model, USGS, 1998); vegetation types (potential primary vegetation map, INEGI, 2004); and soil types (INIFAP-CONABIO, 1995). To obtain the values of heterogeneity, we calculated the range of values (ROV), maximum minus minimum, for temperature, precipitation and elevation (e.g. Kerr & Parker, 1997; Veech & Crist, 2007). We also calculated the coefficient of variation for the same environmental variables (CV; e.g. Davidar *et al.*, 2007). CV represents the frequency of the values along their range within the unit of analysis. High CV is expected when most of the values are far from the mean, low CV when most of the values are near the mean, and medium CV when the distribution of the values is balanced (some near some far). CV can take high or low values regardless of the minimum or maximum values of the variable (range).

To represent the heterogeneity of vegetation (Veg_{H}) and soils (Soil_{H}), we calculated the Shannon diversity or equity index $H= -\Sigma(p_i \ln p_i)$, where p_i is the proportion of the grid occupied by the species *i*. The abundance parameter of the index was substituted by the extension in km^2 of each type (vegetation or soil); meanwhile S was the number of categories in every grid cell analyzed. All the environmental surrogates were calculated for each scale separately.

EH & β-diversity relationships

To test if the relationship among different EH metrics and β-diversity patterns varied with scale, we first performed regression trees as suggested by Hawkins (2011). As our data presented autocorrelation at most scales (from 1 to 0.125 degrees lat-long) we carried out simultaneous and autoregressive models (following, e.g. Meynard *et al.*, 2011). Spatial autocorrelation is a property of diversity patterns and environmental variables and represents a problem for classical statistics (Legendre & Legendre, 1998). Although there is no consensus as to how to deal with the problem of spatial autocorrelation in such data, simultaneous and conditional autoregressive models (SAR and CAR respectively) have been promoted by some authors (e.g. Dorman *et al.*, 2007; Lichstein *et al.*, 2002; Meynard *et al.*, 2011). Autoregressive models, in general, assume that the response variable is a function of the explanatory variables and their spatial structure within the neighbourhood of interest.

The concept of multivariate spatial correlation focuses on the extent to which values for one variable observed at a given location show a systematic association with another variable observed at the neighbouring locations. To take into account the influence of neighbouring sites, it is possible to use weights estimated as function of the distance between the focal and surrounding sites (Legendre & Legendre, 1998). Therefore, we generated correlograms for each dependent variable (β-diversity for each group) at every scale of analysis in order to construct a weight matrix for each taxon based on the neighbourhood at which autocorrelation reaches zero (Table SI IV-1 Appendix IV-1).

To be able to test the relative importance of each EH metric, we standardized the values of the ranges of each metric to proportional values from 0 to 1. We took the maximum value of the range then divided the rest with that maximum. This also standardizes the values for the coefficient of variation derived from these data. Before running the models, climatic variables were tested for co-linearity, and then we eliminated one of each pair of co-variables as suggested by Legendre & Legendre (1998). In order to eliminate the less meaningful EH metric from the co-linear pair, we ran simple regression trees, first with all the variables, then eliminating one of the co-linear pair, retaining the better performing member of the pair. We then ran classical linear models for all scales (Table SI IV-2 Supporting Information). From the scales of one to 0.125 degrees the residuals were not normally distributed. Although some researchers argue that if sample size is over 100 then normality assumptions should not be of much concern (e.g. Lumley *et al.*, 2002), we ran GLM from the Gaussian and Gamma families to test how much influence non-normality of the residuals might have on the models and whether the significant variables or their level of importance might change (e.g. Lichstein *et al.*, 2002). We performed linear models (LM) when Moran's *I* was not significant for the dependent variable and CAR and SAR if it was. To eliminate the non-significant EH metrics we used the function step implemented in R (Hastie & Pregibon, 1993), and then we ran the model again checking the AIC, Log likelihood and Lambda, to verify the performance. Given the current limitation on running large matrices of data in R for CAR and SAR and knowing that the results from LM were qualitatively similar to the autoregressive models in the previous scales (one to 0.25 degrees) we ran a LM at the 0.125 degree scale.

The average of the distribution ranges size was calculated for each group using a planar projection (North America Lambert Conformal Conic WGS84) in km^2 in ArcMap10 (ESRI, 2011). Frontier and coastal grid-cells were eliminated when more than 50% of the unit area fell beyond the national border or over the sea. The weighted matrix for the CAR and SAR models was created using GEODA (Anselin *et al.*, 2006), and all regressions were calculated in R using spgrass6 (R Development Core Team, 2008; Bivand, 2011).

RESULTS

Overall, the spatial patterns of β-diversity showed similarities among the four vertebrate groups (Fig. IV-1), with birds the least similar to the others (see also Fig. SI IV-1, Appendix IV-2). For example, birds showed surprisingly high values of β-diversity in the Mexican Plateau, but the highest β-diverse zones were found in the northwest, and across the entire extent of the Sierra Madre Oriental. The β-diversity patterns between the other three taxonomic groups (amphibians, mammals and reptiles) are very similar to each other. These groups showed higher β-diversity values mainly in cells containing mountain ranges, i.e. along the Sierra Madre Occidental, Sierra Madre Oriental, Sierra Madre de Chiapas, and eastern Transvolcanic Belt.

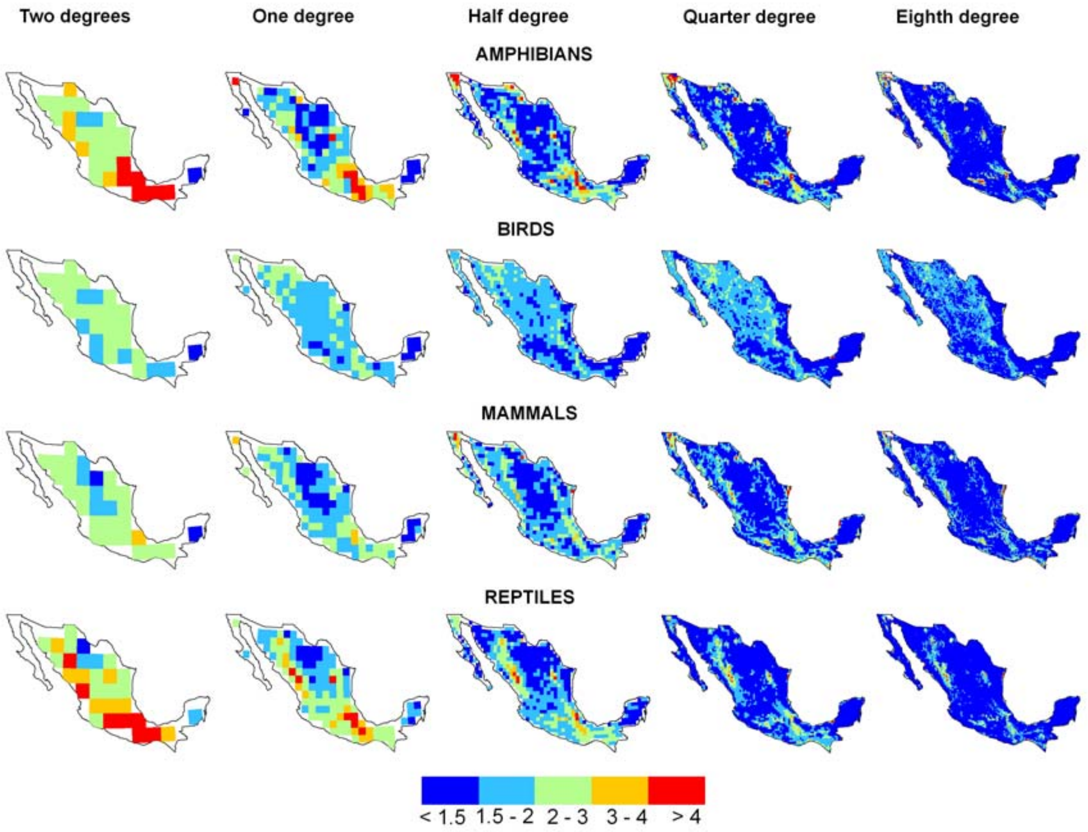

Figure IV-1. β-diversity patterns of Mexican terrestrial vertebrates at different scales. β-diversity was calculated for each grid cell using the procedure proposed by Schluter and Ricklefs (1993) where β-diversity is be expressed in terms of the distribution of species, as the inverse of the average of the distribution ranges sizes of the species within that cell. In order to compare the patterns we used the same scale of values across the scales (see also Fig. SI IV-1, Appendix IV-2). See Materials and Methods for details of data derivation.

Results from regression trees, LM, SAR and CAR were qualitatively very similar. Therefore, we will just describe the CAR results (but see Appendix IV-2, Table SI IV-3 for LM, Table SI IV-4 for CAR with all the variables, and Table SI IV-5 for SAR results). The models increased in explanatory power from the finer to coarse scales in most cases (amphibians, mammals and reptiles), but in birds the highest amount of variance explained was at the 0.5 degrees grain size. The number of significant variables decreased roughly in the same order (Table IV-1). Results from regression trees (see Appendix IV-2, Figs SI IV-2–21) coincide with the spatial autoregressive models at coarser scales (2, 1, and 0.5 degrees). More differences can be observed at finer scales (0.25 and 0.125), principally in the order of importance of the EH metrics. The most complex trees were found at 0.5 degrees in all groups.

Most of the variables correlated positively with β-diversity. In general, for amphibians and reptiles, CV of temperature was the foremost explanatory variable for β-diversity (Fig. IV-3, ROV of Elev is collinear with CV of Tm). For mammals, a different EH metric emerged at each scale, while in birds, ROV of temperature and CV of precipitation seem to be the most important variables (Table IV-1). Soil never emerged as the most important variable in any scale or group.

DISCUSSION

Searching for ecological drivers of diversity patterns has been one the major aims of biogeography (e.g., Andrewartha & Birch, 1954; Pianka, 1966b; Lomolino *et al.*, 2004). Recent research has demonstrated that the relationship among climate and coarse scale patterns of species richness is strong (e.g., Hawkins *et al.*, 2003; O'Brien *et al.*, 2006; Whittaker *et al.*, 2007), that explanatory variables best accounting for statistical variation in species richness vary with scale (Rahbek & Graves, 2001; Rahbek, 2005), and that limiting factors of species distribution vary between taxa of differing biological characteristics (e.g. Wiens, 2000).

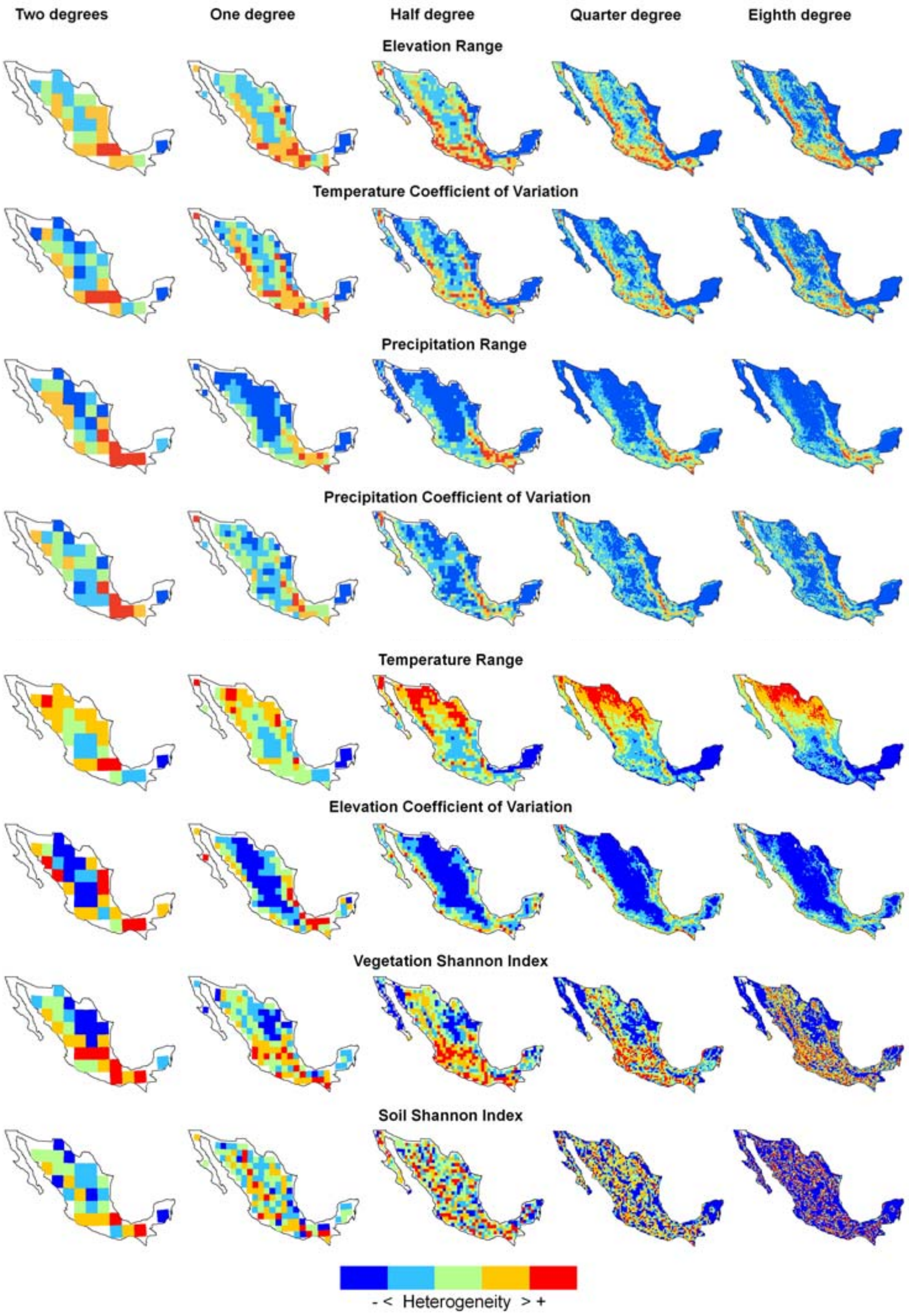

Figure IV-2. Patterns of environmental heterogeneity (EH) of the different surrogates used to explain β-diversity of terrestrial vertebrates in Mexico at different scales. Range was calculated, maximum minus minimum, within each cell. Coefficient of variation was calculated as the ratio of the standard deviation to the mean. The scale of values was determined by Jenks natural breaks classification. This classification minimizes the variance within the class and maximizes it among classes.

Table IV-1. Conditional autoregressive models performed to explain the patterns of β-diversity of terrestrial vertebrates in Mexico. The surrogates of environmental heterogeneity included in the models are: range of elevation (ROV of Elev), range of precipitation (ROV of Pp), range of temperature (ROV of Tm), coefficient of variation of elevation (CV of Elev), coefficient of variation of precipitation (CV of Pp) coefficient of variation of temperature (CV of Tm), Shannon diversity index of vegetation (Veg$_H$) and soil (Soil$_H$). This table shows the models with only significant elements; complete models are presented in Appendix IV-2. All models were performed in R (2008). At the scale of two degrees neither the variables nor the residuals presented significant spatial autocorrelation, thus a simple linear model was performed. At the scale of one-eighth degree the number of grid cells exceeds the computational capability of R. Because of the qualitatively similar results among the linear models and the autoregressive models we presented the results from the former at one-eighth degree. The regression coefficient presented is the adjusted R^2 for linear models and the Nagelkerke pseudo-R-squared for the autoregressive models (Nagelkerke, 1991; Liang & Zhou, 2010). Levels of significance are as follow: ’ < 0.1, * < 0.05, ** < 0.01, *** < 0.001.

Group	Scale	N	Model	R^2	F	AIC	Log Likelihood	Lambda	ROV of Elev	ROV of Pp	ROV of Tm	CV of Elev	CV of Pp	CV of Tm	Veg (H)	Soil (H)
Amphibians	2º	30	LM	0.79	37.82	-22.02	-	-	2.15*	4.22***	-	-1.03*	-	-	-	-
	1º	127	CAR	0.59	-	32.28	-9.14	-0.16	-	-	-0.44**	-	1.87***	4.10***	-	-0.27***
	0.5º	594	CAR(ln)	0.36	-	-151.37	-69.68	-0.67*	-	-	-	-	1.97***	2.24***	-	-0.11 **
	0.25º	2770	CAR(ln)	0.49	-	2408.3	-1194.5	-0.06	-	-0.30***	0.06*	2.69***	0.09**	-0.57***	2.37***	-
	0.125º	10932	LM	0.14	292.6	18902.3	-	-	-	-	0.08***	0.28***	1.25***	4.38***	-0.17***	-0.05***
	2º	30	LM	0.53	17.18	-76.57	-	-	-	0.92***	1.03**	-	-	-	-	-
	1º	127	CAR(ln)	0.49	-	-68.05	42.03	-0.13	0.37*	0.41**	0.39**	0.14*	-	-	-	-0.09*

Group	Scale	N	Model	R^2	F	AIC	Log Likelihood	Lambda	ROV of Elev	ROV of Pp	ROV of Tm	CV of Elev	CV of Pp	CV of Tm	Veg (H)	Soil (H)
Mammals	0.5º	594	CAR	0.28	-	649.98	-317.99	-0.25	-	-	0.54***	0.29***	2.20***	1.32**	-	-
	0.25º	2770	CAR(ln)	0.46	-	1214.9	-598.45	-0.11	-	-	-0.05**	1.71***	0.38***	-0.42***	1.35***	0.01***
	0.125º	10932	LM	0.22	625.8	23691.96	-	-	-	-	0.13***	0.53***	1.59***	2.49***	0.10***	-
Reptiles	2º	30	LM	0.68	32.03	31.37	-	-	2.91***	1.50**	-	-	-	-	-	-
	1º	127	CAR	0.61	-	-33.44	21.72	-0.62*	0.97***	0.72***	-	-	-	-	-	-
	0.5º	594	CAR	0.44	-	654.3	-320.15	-0.53*	-	-	-0.17*	-	1.52***	6.37***	-	-0.12*
	0.25º	2770	CAR	0.47	-	-4184.4	2101.22	-0.06	-	-	-0.03**	0.63***	0.14***	-0.15***	0.58***	0.002***
	0.125º	10932	LM	0.27	811.3	27612.9	-	-	-	0.41***	-	0.18***	-1.07**	5.07***	-0.06***	-
Birds	2º	30	LM	0.23	9.51	-81.91	-	-	-	-	0.94**	-	-	-	-	-
	1º	127	CAR	0.42	-	9.50	2.25	-0.19	-0.43*	0.58**	1.51***	-0.18*	-	-	-	-
	0.5º	594	CAR	0.48	-	-256.92	135.46	0.00	-	-	0.95***	-0.08***	1.20***	-0.91***	-	-
	0.25º	2770	CAR(ln)	0.42	-	418.32	219.16	0.05	-	0.64***	-0.06***	0.31***	-0.05**	-1.30***	3.29***	0.01***
	0.125º	10932	LM	0.41	1076	-34428.88	-	-	-	-0.76***	0.46***	0.08***	3.87***	1.96***	0.03***	0.03***

In addition, some authors have found a positive relationship between heterogeneity (habitat diversity, resource diversity, etc.) and species diversity (e.g. Kerr & Parker, 1997; Kerr, 2001). It is also known that changes in species composition are related to environmental heterogeneity directly or indirectly (e.g. Williams-Linera & Lorea, 2009). Moreover, Wiens (2000) highlighted that different forms of heterogeneity have different properties and may have different ecological consequences, and some groups may be more sensitive than others to different environmental conditions (Buckley & Jetz, 2008). Therefore, it is unsurprising that our results showed that the correlates of β-diversity varied among groups and scales; but it was unexpected that some EH metrics were not positively related to β-diversity (Table IV-1). It was also interesting that, in general, EH metrics related with temperature emerged as important variables in all groups, albeit at varying scales of analysis.

The range of annual precipitation was the most important variable in the model at two degrees for amphibians; this means that in regions of around 40,000km^2 incorporating places varying from very wet to very dry there will be large variation in amphibian community composition within the unit of analysis. This is ecologically intelligible, since it is known that precipitation is of crucial importance for amphibian reproduction and can be a limiting factor for their distribution (Duellman & Trueb, 1994). CV of temperature was the most important in the next two scales and at the smallest one (1, 0.5 and 0.125 degrees), followed by CV of precipitation. Thus, high β-diversity, at those scales, is located in grid cells with few places possessing extreme temperature and precipitation regimes in comparison to the rest of the grid cell. Therefore, communities living in such different and restricted environmental conditions are very likely also to be geographically constrained from the rest of the grid cell. Thus the average of the distribution range decreases, thereby causing high β-diversity.

For reptiles, the range of elevation was the most important EH metric at the two coarsest scales, followed in both cases by range in precipitation. This means that the larger the range of elevation and precipitation the higher the β-diversity for reptiles. The pattern of β-diversity of reptiles is shared with amphibians at the three smallest scales; thus the same causal processes might apply. It is worth noting that CV of temperature is collinear with range in elevation, therefore when one was included in the models the other was excluded. This supports the idea that temperature may be important in limiting species distributions of amphibians and reptiles. This has been widely recognised and it is of relevance with respect to future climate change (e.g. Sinervo *et al.*, 2010).

β-diversity patterns were most distinctive for birds, being clearly related to ROV of temperature (Figs IV-1 & IV-2). Although the model at the coarsest scale did not perform very well (<25% of the variation explained), temperature was the only significant EH metric. At the next finest scale (1 degree lat–long cells), temperature was followed in importance by ROV of precipitation and the model improved; we may consider this the best model performance, as it had the lowest AIC, although not the highest R^2. At half degrees, and at 0.125 degrees, CV of precipitation was the most important variable, followed by different EH temperature metrics. This implies that grids with few places with extreme values of precipitation have more β-diversity. Previous analyses of β-diversity for birds in France using 50-km windows (~ 0.5 degrees) have generated similar conclusions, where spatial structured factors can explain large proportion of the variation of diversity, especially for phylogenetic diversity (Meynard *et al.,* 2011).

It is difficult to generalize about β-diversity for mammals as a different EH metric was important at each scale. In such a heterogeneous group as mammals, with a wide range of body sizes, functional groups and distribution range sizes, it is possible that at each scale different subgroups emerge as dominants in the pattern β-diversity. It is very likely that their β-diversity patterns at finer scales were mostly influenced by non-volant mammals of restricted distribution. The range restricted mammals tend to be of small body size. At coarser scales the pattern was more influence by subgroups such as carnivores and volant mammals showing greater dispersal abilities (Munguía *et al.*, 2008) and larger geographical ranges (Arita *et al.*, 1997).

At the scale of 0.25 degrees (~600km^2), the pattern was shared among amphibians, mammals and reptiles: high β-diversity occurs in units with high CV of elevation and high vegetation diversity (Veg$_H$), e.g. cells that might contain a mountain or a valley possessing vegetation distinct from the remainder of the grid cell. For birds Veg$_H$ was the most important variable explaining β-diversity. Mountain ranges play a key role for diversity because they have high diversification rates, and have acted as environmental refuges in the long term (Smith *et al.*, 2007; Wiens *et al.*, 2007; Araújo *et al.*, 2008). It is known that for reptiles, at least in the south of Mexico, mid-elevation habitats, which are characterised by pine-oak and montane cloud forest systems, play a crucial role for biodiversity, in terms of species number and also in number of endemics (Flores-Villela & Goyenechea, 2002; Urbina-Cardona & Flores-Villela, 2010). Moreover, most of the endemic birds and mammals are observed in Central Mexico (Transvolcanic Belt), and along Sierra Madre Oriental, where they occupy mainly highlands, with lowland areas representing geographical barriers to species movements (Koleff *et al.*, 2008). Mountain ranges, specifically the zones showing high β-diversity such as Sierra Madre Occidental, Sierra Madre Oriental (mainly south), and Transvolcanic Belt, have complex historical patterns for vertebrates. These mountain ranges not only are the transitional or dispersal routes for Neartic and Neotropical flora and fauna but present evidence of different phylogenetic historic events within them. To give an example, in the Transvolcanic Belt three zones have been identified based on the distribution of mammals: the western, central and eastern regions. Each of these regions can be clearly differentiated due to the endemic fauna existing in each part, and very few mammals exist in all three zones (Sánchez-Cordero *et al.,* 2005; Escalante *et al.*, 2007; Navarro-Sigüenza *et al.*, 2007).

It is clear that in order to talk about “heterogeneity” we must also be referring to a specific group at a specific scale (Wiens, 2000). The last part of the aims of this work was to explore if there was an optimal scale to get the best fits of the models to describe β-diversity given the data used. Based on our results, we might conclude that for amphibians and reptiles coarse scales of analysis might be most informative (2 and 1 degrees), while for birds and mammals intermediate scales (from 1 to 0.5 degrees) would be satisfactory. Nevertheless there are some methodological aspects that we must consider.

Scale domain for predictor and response variables. Following the definition and recommendation of some authors (Whittaker *et al.*, 2001; Willis & Whittaker, 2002; Pearson & Dawson, 2003) it is sensible not to go beyond the regional scale when using interpolated climate to explore drivers of diversity, in this case β-diversity, because it would be out of the scale domain of the variables. It is important to highlight that our smallest scale of analysis falls within this range. Scale domain represents the range of scales (spatial and temporal) over which a predictor variable has *measurable* influence over the response variable. This scale domain is defined by the process and raw data from which the variable was created. Thus, we recognised two kinds of EH variables with different scale domains: first, the climatic set, temperature and precipitation, have coarser scale domains, while second, vegetation and soil diversity have finer scale domains. Therefore, the latter may have been unimportant at coarse scales simply because these scales are out of their scale domain.

Statistical issues using larger datasets. It is known that the significance of a correlation/regression coefficient of a particular magnitude will vary depending on the size of the sample from which it was estimated. Given a large enough dataset almost any relation or even “no relation” at all can be statistically significant (Legendre & Legendre, 1998). This may explain the increase in the number of significant variables at finer scales of the analysis. At the finest scales we had more than 11,000 sample grid cells, thus almost all EH metrics were significant for all the groups. Similarities among the results from regression trees, linear multiple regression and CAR/SAR seem to point to the supposition that space (lat/long) does not influence patterns of β-diversity or that the EH metrics are spatially structured such that we are including the spatial structure in each analysis. Another important aspect of the analyses is that the models used (LM, CAR and SAR) are based on linear functions, and the form of the relationships among β diversity and EH metrics may also vary with scale, thus some non-linear form of model might be more appropriate (Dormann *et al.*, 2007): but investigation of this possibility was beyond the scope the scope of the present study.

CONCLUDING REMARKS

High β-diversity zones for amphibians, reptiles and mammals, occurred along mountain ranges, although not exactly in the same regions; while birds followed a strikingly different pattern, showing high values in the Mexican Plateau. Obvious different responses to environmental gradients between the taxa caused differences in the relative importance of the various environmental heterogeneity variables used in our analyses. In general, for amphibians and reptiles, heterogeneity of temperature (CV) was the single best variable explaining β-diversity. For mammals, a different EH metric emerged at each scale, while in birds, range of temperature and coefficient of variation in precipitation seem to be the most important variables.

Not all EH metrics are positively related to β-diversity, probably because different forms of heterogeneity have different properties at different scales. Therefore, selection of scale for studies of β-diversity should be done very carefully according to the data properties of the taxon and environmental variables under analysis, because the fit of the models will depend on these choices.

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APPENDIX IV-1

Additional details of MATERIALS AND METHODS.

1. Modelling distribution ranges through an ecological niche approach

a. ***Amphibians and reptiles*** (source: Ochoa-Ochoa *et al.,* 2006). We used the most complete database of locality records of Mexican herpetofauna in the World with more than 390,000 records, and more than 80,000 unique species-localities. We used climate layers (precipitation, maximum and minimum temperature) developed for Mexico, with a spatial resolution of 0.008' ~1 km^2 (Téllez, 2004) to generate 19 climate variables using Hijmans' script (2006, same as mammals see below). We used GARP to model the ecological niche under the best subsets option (Anderson *et al*., 2003). As mentioned in the main text species distributions were modelled in two sets: species with fewer than 10 occurrences were classified as rare in one set, and species with more than 10 were classed as common in another set. The limit of the presence threshold, for the rare species, was where the presence of three or more best models coincided; for the common ones eight or more best models had to coincide. The resulting consensus model was evaluated for each species individually based on expert knowledge (herpetologists from the Zoology Museum Faculty of Sciences, UNAM) and available literature; the species models that did not conform to previous distributional information were eliminated from these analyses. For those models deemed reasonable, we accepted the model but eliminated over-predictions (places where it is known that the species does not occur), through a trimming process, to derive a moderately conservative distributional model.

b. ***Birds.*** Details of the niche modelling can be found in Lira-Noriega *et al.* (2007).

c. ***Mammals.*** Details of the niche modelling can be found in Munguía *et al.* (2008).

2. Derivation of β-diversity from species' distribution range sizes

The procedure is the following: imagine a region divided in different sites *j*=1, 2, 3, … *H*. These particular sites are smaller enough (finest scale) that the sum of the presences in the presence–absence matrix is the same as the distribution range size of each species. The total number of species can be conceptualized from two different perspectives. One, the number of sites that contains *i = 1, 2, 3, ... S* species could be denoted by *Hp(i),* where *p(i)* represents the proportion of sites that contains exactly *i* species. Summarizing, total diversity (gamma) can be obtained (eq. 1):

$$H\sum_{i=1}^{S} ip(i) \qquad (1)$$

Please note that in the former formula *p(i)* represents the mean species per site, alpha diversity. Second, species records can be also expressed in terms of the number of species occupying exactly *j = 1,2,3,…H* sites, denoted by *Sq(j)*, where *q(j)* is the proportion of species that inhabit precisely *j* sites. The sum represents the occupancy, actually a measure of the distribution range (Ney-Nifle & Mangel, 1999).

$$S\sum_{j=1}^{H} jq(j) \qquad (2)$$

When both equations expressed the record of species (gamma):

$$H\sum_{i=1}^{S} ip(i) = S\sum_{j=1}^{H} jq(j) \qquad (3)$$

We may derive *S as follows:*

$$S = \frac{H\sum_{i=1}^{S} ip(i)}{\sum_{j=1}^{H} jq(j)} \qquad (4)$$

Because the sum in the numerator is the species average per site (average of alpha), Whittaker's (1972) relationship can be recovered defining *H* as β (Schluter & Ricklefs, 1993):

$$S = \overline{\alpha}\beta = \overline{\alpha} / \beta^{-1} \tag{5}$$

Therefore, β is the result of the average number of sites occupied by species divided by the total number of sites in the region (Schluter & Ricklefs, 1993), i.e. the inverse of the average range size. This measure of β can take values from a minimum of one, when all species are present in all *H* sites, to *H* when each species is present in only one site. β-diversity is the reciprocal of the proportion of sites occupied on average by all the species (Routledge, 1977).

3. Distances used for the construction of the weight matrix for each taxa, based on the neighbourhood at which autocorrelation reaches zero.

Table SI IV-1. Number of neighbours (grid cells) at which autocorrelation reaches zero obtained from correlograms of β-diversity for each taxon. At two degrees there was no spatial autocorrelation.

	1º	**1/2º**	**1/4º**	**1/8º**
Amphibians	5	9	13	32
Birds	5	30	42	96
Mammals	4	7	16	40
Reptiles	5	7	14	28

Table SI IV-2. Pair-wise correlations to test co-linearity among climatic environmental heterogeneity metrics: range of elevation (ROV of Elev), range of (ROV of Pp) range of temperature (ROV of Tm), coefficient of variation of elevation (CV of Elev), coefficient of variation of (CV of Pp) coefficient of variation of (CV of Tm). High correlation values are highlighted in grey.

Two degrees	ROV of Elev	ROV of Pp	ROV of Tm	CV of Pp	CV of Elev	CV of Tm
ROV of Pp	0.55	1.00				
ROV of Tm	0.59	-0.05	1.00			
CV of Pp	0.52	0.84	0.12	1.00		
CV of Elev	0.35	0.47	0.04	0.31	1.00	

CV of Tm	0.85	0.48	0.51	0.45	0.21	1.00
One degree	ROV of Elev	ROV of Pp	ROV of Tm	CV of Pp	CV of Elev	CV of Tm
ROV of Pp	0.57	1.00				
ROV of Tm	0.55	-0.01	1.00			
CV of Pp	0.61	0.67	0.32	1.00		
CV of Elev	0.19	0.55	-0.09	0.24	1.00	
CV of Tm	0.86	0.49	0.46	0.54	0.07	1.00
Half degree	ROV of Elev	ROV of Pp	ROV of Tm	CV of Pp	CV of Elev	CV of Tm
ROV of Pp	0.46	1.00				
ROV of Tm	0.53	-0.09	1.00			
CV of Pp	0.47	0.64	0.21	1.00		
CV of Elev	0.08	0.24	-0.17	0.18	1.00	
CV of Tm	0.92	0.46	0.42	0.49	0.02	1.00
Quarter degree	ROV of Elev	ROV of Pp	ROV of Tm	CV of Elev	CV of Pp	CV of Tm
ROV of Pp	0.47	1.00				
ROV of Tm	0.40	-0.15	1.00			
CV of Elev	0.02	0.23	-0.20	1.00		
CV of Pp	0.49	0.58	0.22	0.17	1.00	
CV of Tm	0.93	0.48	0.32	-0.03	0.51	1.00
Eighth degree	ROV of Elev	ROV of Tm	ROV of Pp	CV of Elev	CV of Pp	CV of Tm
ROV of Tm	0.24	1.00				
ROV of Pp	0.54	-0.19	1.00			
CV of Elev	0.09	-0.19	0.21	1.00		
CV of Pp	0.59	0.23	0.55	0.17	1.00	
CV of Tm	0.93	0.18	0.56	0.03	0.61	1.00

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APPENDIX IV-2

Additional results. Linear Models with all the variables are shown in Table SI IV-3, the complete Conditional Autoregressive models (CAR) in Table SI IV-4, and of the complete Simultaneous Autoregressive models (SAR) in Table SI IV-5. β-diversity patterns of Mexican terrestrial vertebrates at different scales using the Jenks rank classification are shown in Figure SI IV-1. Additional figures included in this appendix (Fig. SI IV-2–21) provide Classification and Regression Trees for each taxon at each separate scale of analysis.

Table SI IV-3. Linear Models performed to describe the patterns of β-diversity of terrestrial vertebrates in Mexico. The surrogates of environmental heterogeneity included in the models are: range of elevation (**ROV of Elev**), range of precipitation (**ROV of Pp**), range of temperature (**ROV of Tm**), coefficient of variation of elevation (CV of Elev), coefficient of variation of precipitation (**CV of Pp**) coefficient of variation of temperature (**CV of Tm**), Shannon diversity index of vegetation (**Veg *H***) and soil (**Soil *H***). Levels of significance are as follows: ’ < 0.1, * < 0.05, ** < 0.01, *** < 0.001.

Group	Scale	N	R^2	F	AIC	ROV of Elev	ROV of Pp	ROV of Tm	CV of Elev	CV of Pp	CV of Tm	Veg (H)	Soil (H)
Amphibians	2º	30	0.79	19.36	-19.63	2.17’	4.81***	0.46	-0.98*	-	-	-0.13	-0.71
	1º(ln)	127	0.58	30.44	-333.52	-	-	-0.45*	-0.10	1.80***	4.29***	-0.05	-0.24***
	1/2º(ln)	594	0.35	54.4	-1540.08	-	-	0.08	0.02	1.74***	2.34***	-0.03	-0.12 **
	1/4º(ln)	2770	0.19	92.85	-7512.77	-	-0.25**	0.16*	0.17***	0.60***	1.75**	-0.001	0.06***
	1/8º	10932	0.14	250.8	18900.37	-	-0.01	0.08**	0.28***	1.27***	4.39***	-0.17***	-0.05***
	2º	30	0.20 ns	2.25	-77.01	-0.60	0.35	1.44**	-0.15	-	-	-0.01	-0.11

Birds	1º	127	0.54	25.87	-389.14	-	-	1.26***	-0.18**	1.36***	-2.4***	0.13*	0.00
	1/2º	594	0.48	91.3	-1956.98	-	-	0.95***	-0.08***	1.18***	-0.93***	-0.03	0.02
	1/4º(ln)	2770	0.49	376.7	-11126.27	-	-0.44***	0.40***	0.02*	-1.57***	0.91***	0.01***	-0.02***
	1/8º	10932	0.41	1076	-34428.88	-	-0.76***	0.46***	0.08***	3.87***	1.96***	0.03***	0.03***
Mammals	2º	30	0.55	6.82	-74.61	-0.02	0.49	1.02’	0.24	-	-	0.22	0.07
	1º (ln)	127	0.47	20.11	-435.81	0.33*	0.33**	0.41**	0.15*	-	-	0.07	-0.10*
	1/2º	594	0.27	38.19	-1044.92	-	-	0.49***	0.27***	2.20***	1.52***	0.00	-0.01
	1/4º(ln)	2770	0.29	156.4	-8755.15	-	0.13**	0.16***	0.30***	0.51***	1.47***	0.001**	-0.02’
	1/8º	10932	0.22	447.2	23689.63	-	0.04	0.14***	0.53***	1.59***	2.43***	0.10***	0.01
Reptiles	2º	30	0.70	12.2	-29.83	3.49**	1.29*	-0.71	-0.44	-	-	0.42	-0.33
	1º(ln)	127	0.60	32.7	-397	1.39***	0.45***	-0.39*	-0.06	-	-	-0.01	-0.07
	1/2º	594	0.43	76.09	-1040.27	-	-	-0.34**	-0.05	1.55***	7.05***	0.04	-0.09
	1/4º	2770	0.35	210.3	-6486.68	-	0.68***	-0.01	0.17***	-0.71***	4.67	-0.00	0.04’
	1/8º	10932	0.27	579.9	27611.67	-	0.42***	0.01	0.17***	-1.08**	5.07***	-0.06***	-0.01

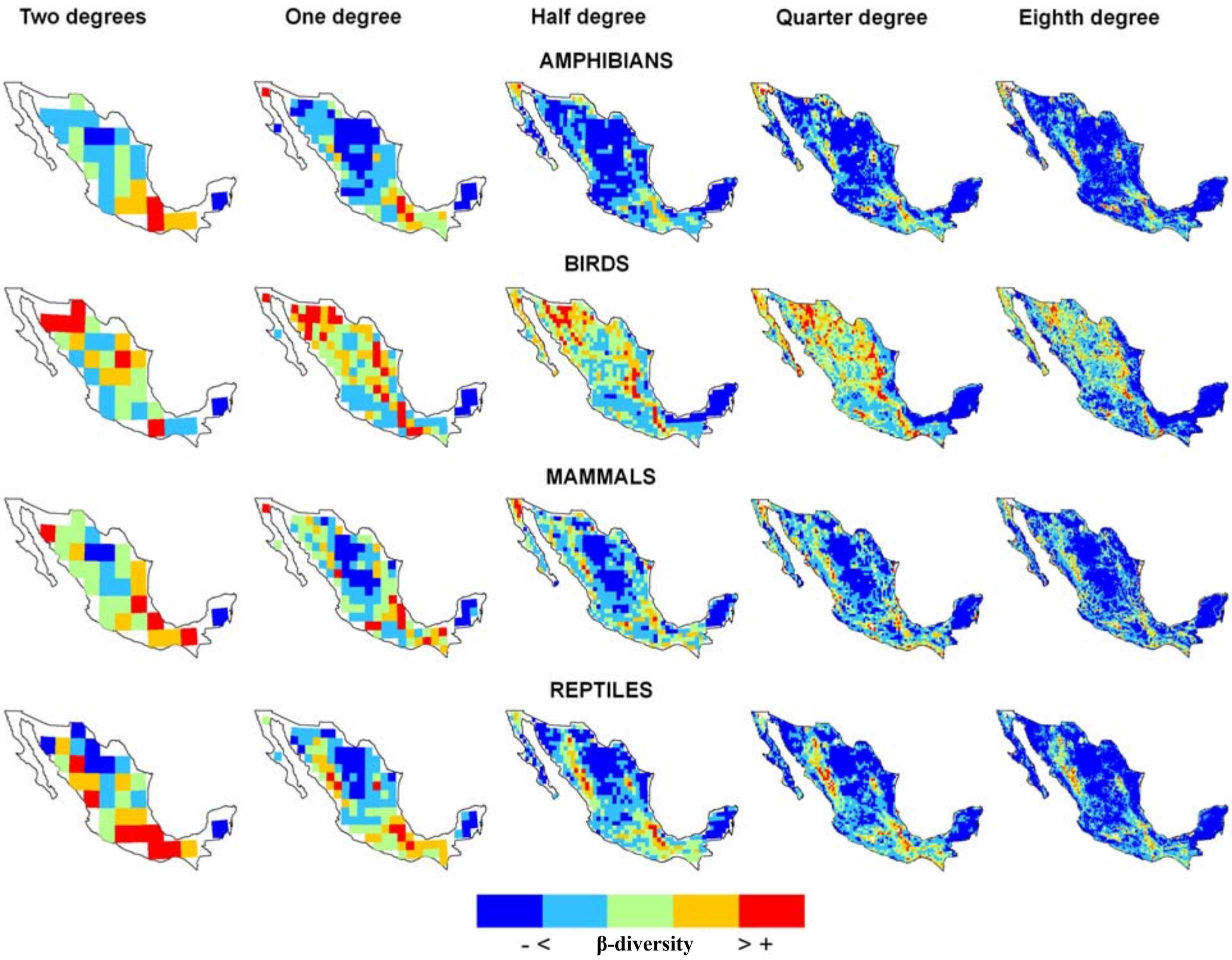
Table SI IV-4. Conditional Autoregressive models (CAR) with all the variables **to explain the patterns of beta diversity of terrestrial vertebrates in Mexico.** The surrogates of environmental heterogeneity included in the models are: range of elevation (**ROV of Elev**), range of precipitation (**ROV of Pp**), range of temperature (**ROV of Tm**), coefficient of variation of elevation (**CV of Elev**), coefficient of variation of precipitation (**CV of Pp**) coefficient of variation of temperature (**CV of Tm**), Shannon diversity index of vegetation (**Veg *H***) and soil (**Soil *H***). Levels of significance are as follow: ’ < 0.1, * < 0.05, ** < 0.01, *** < 0.001.

Group	Scale	N	Model	R^2	AIC	Log Likelihood	Lambda	ROV of Elev	ROV of Pp	ROV of Tm	CV of Elev	CV of Pp	CV of Tm	Veg (H)	Soil (H)
Amphibians	1º	127	CAR(ln)	0.60	33.47	-7.73	-0.18	-	-	-0.44*	0.12	1.79***	4.29***	-0.05	-0.24**
	1/2º	594	CAR(ln)	0.36	-156.68	-69.33	-0.52*	-	-	0.10	0.06*	1.83***	2.19***	-0.02	-0.12 **
	1/4º	2770	CAR(ln)	0.49	2408.3	-1194.15	-0.06	-	-0.30***	0.05*	2.69***	0.09***	-0.57***	-2.37***	-0.001
Birds	1º	127	CAR	0.43	10.83	3.59	-0.17	-0.51*	0.44**	1.55***	-0.15*	-	-	0.12’	-0.02
	1/2º	594	CAR	0.48	-255.23	136.61	0.00	-	-	0.94***	-0.08***	1.18***	-0.93***	-0.03	0.02
	1/4º	2770	CAR(ln)	0.42	418.32	219.16	0.05	-	0.64***	-0.06***	0.31***	-0.05**	-1.30***	3.29***	0.01***
Mammals	1º	127	CAR(ln)	0.50	-68.67	43.33	-0.10	0.31’	0.34*	0.43**	0.16**	-	-	0.07	-0.10*
	1/2º	594	CAR	0.28	654	-318	-0.24	-	-	0.54***	0.29***	2.20***	1.35**	-0.00	-0.03
	1/4º	2770	CAR(ln)	0.46	1216.8	-598.39	-0.11	-	0.01	-0.05**	1.70***	0.38***	-0.43***	1.34***	0.01***
Reptiles	1º	127	CAR(ln)	0.63	-32.77	25.39	-0.41*	1.21***	0.63***	-0.23	-0.05	-	-	-0.02	-0.07
	1/2º	594	CAR	0.44	659.04	-320.52	-0.21	-	-	-0.24*	0.01	1.55***	6.77***	0.04	-0.10'
	1/4º	2770	CAR	0.47	-4184.9	2102.43	-0.06	-	0.03	-0.02***	0.62***	0.14***	-0.16***	-0.54***	0.002***

Table SI IV-5. Simultaneous Autoregressive models (SAR) with only significant variables, performed to explain the patterns of β-diversity of terrestrial vertebrates in Mexico. The surrogates of environmental heterogeneity included in the models are: range of elevation (**ROV of Elev**), range of precipitation (**ROV of Pp**), range of temperature (**ROV of Tm**), coefficient of variation of elevation (**CV of Elev**), coefficient of variation of precipitation (**CV of Pp**) coefficient of variation of temperature (**CV of Tm**), Shannon diversity index of vegetation (**Veg *H***) and soil (**Soil *H***). Levels of significance are as follow: ' < 0.1, * < 0.05, ** < 0.01, *** < 0.001.

Group	Scale	N	Model	R2	AIC	Log Likelihood	Lambda	ROV of Elev	ROV of Pp	ROV of T	CV of Elev	CV of Pp	CV of Tm	Veg (H)	Soil (H)
Amphibians	1º	127	SAR	0.59	32.26	-9.13	-0.09	-	-	-0.47 **	-	1.86 ***	4.15 ***	-	-0.27 ***
	1/2º	594	SAR(ln)	0.36	153.06	-70.53	-0.25 '	-	-	-	-	1.88 ***	2.35***	-	-0.11 **
	1/4º	2770	SAR(ln)	0.49	2406.5	-1194.24	0.03		-0.30 ***	0.05 *	2.70 ***	0.08 **	-0.56 ***	2.34 ***	-
Birds	1º	127	SAR	0.48	-3.55	8.77	-0.76***	-0.35 '	0.63 ***	1.39 ***	-0.27 ***	-	-	-	-
	1/2º	594	SAR	0.48	-257.42	135.71	0.1	-	-	0.95 ***	-0.08 ***	1.13 ***	-0.91 ***	-	-
	1/4º	2770	SAR(ln)	0.42	-420.35	220.18	0.13		0.65 ***	-0.06 ***	0.28 ***	-0.04 **	-1.30 ***	3.31***	0.01 ***
Mammals	1º	127	SAR	0.49	-68.43	42.22	-0.19	0.40 **	0.40 **	0.35 **	0.13 *	-	-	-	-0.10 *
	1/2º	594	SAR(ln)	0.33	-188.95	101.48	-0.42 '	-	-	0.25 ***	0.15 ***	1.15 ***	0.86 ***	-	-
	1/4º	2770	SAR(ln)	0.40	1506	-743.99	-0.06	0.14 ***	-0.19 ***	-0.05 *	1.77 ***	-	-	1.25 ***	0.003 **
Reptiles	1º	127	SAR(ln)	0.66	-45.39	30.7	-0.87 ***	1.48 ***	0.56 ***	-0.47 ***	-0.13 *	-	-	-0.13 *	-
	1/2º	594	SAR(ln)	0.48	-270.32	141.16	0.18 '	-	-	-0.26 ***	-	0.61 ***	3.63 ***	-	-
	1/4º	2770	SAR	0.47	-4184.6	2101.30	0.06	-	-	-0.02 ***	0.63 ***	0.14 ***	-0.15 ***	0.58 ***	0.002 ***

Figure SI IV-1. β-diversity patterns of Mexican terrestrial vertebrates at different spatial scales. β-diversity was calculated for each grid cell using the properties of the multiplicative approach proposed by R.H. Whittaker (1960), as the inverse of the average of the distribution ranges sizes of the species within that cell. The scale of values was determined by Jenks natural breaks classification. This classification minimizes the variance within the class and maximizes it among classes.



Classification and Regression Trees

Classification and regression trees (CART) were performed as extra analyses following the suggestion of Hawkings (2011) to compare the resulting trees with the linear and autoregressive models, used to explore the relationships of the patterns of β-diversity of terrestrial vertebrates in Mexico with environmental surrogates (sEH). The sEH included in the trees are: range of elevation (**ROV of Elev**), range of precipitation (**ROV of Pp**), range of temperature (**ROV of Tm**), coefficient of variation of elevation (**CV of Elev**), coefficient of variation of precipitation (**CV of Pp**) coefficient of variation of temperature (**CV of Tm**), Shannon diversity index of vegetation (**Veg *H***) and soil (**Soil *H***). One of each pair of collinear variables was excluded. The analyses were performed in R (v. 2.12.2) using the libraries vegan, mgcv, and tree.

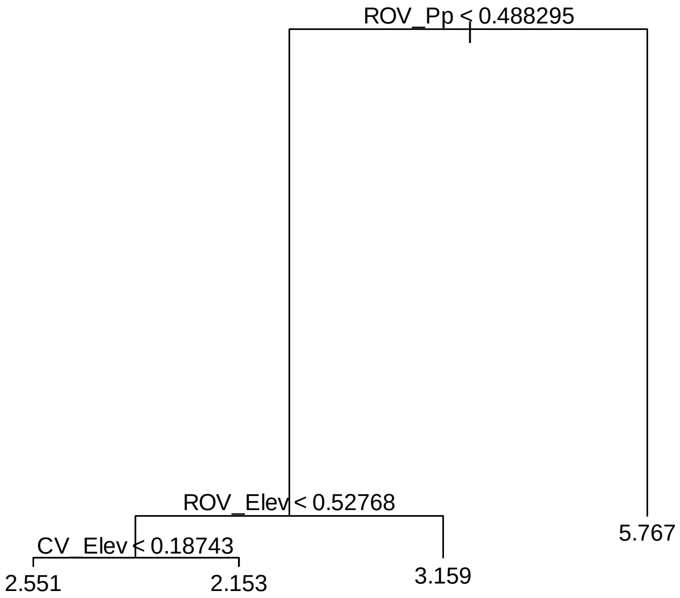


Figure SI IV-2. Amphibian data: regression tree at two degrees. The figure shows coincidence with the results of the LM, in other words the order and importance of the variables is the same (see Table SI IV-3 in this appendix).

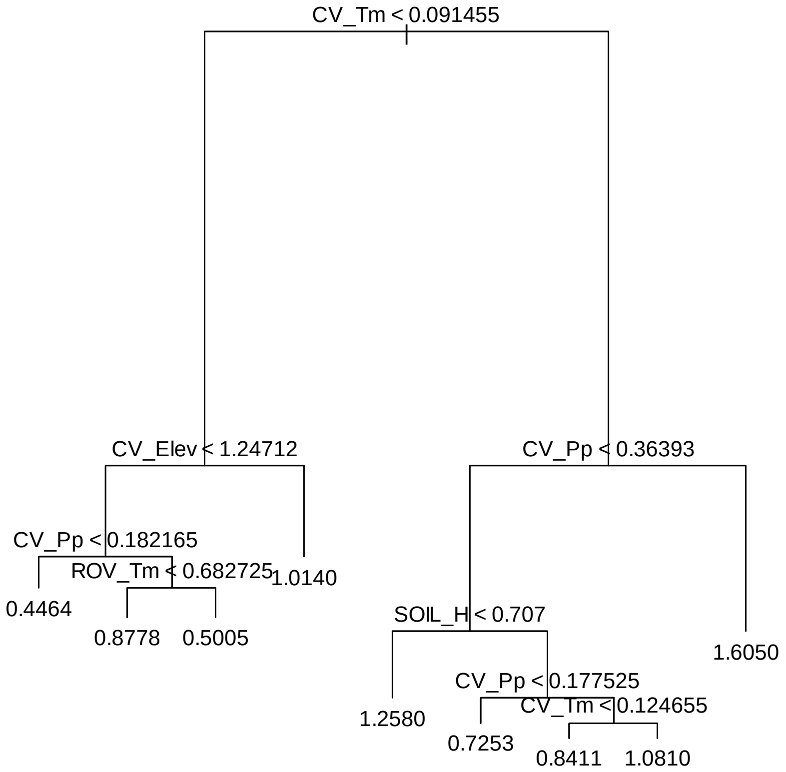


Figure SI IV-3. Amphibian data: regression tree at one degree. The figure shows coincidence with the results of the CAR, in other words all the significant variables in the autoregressive model are present, and non-significant variables in the models are at the bottom (see Table SI IV-4 in this appendix).

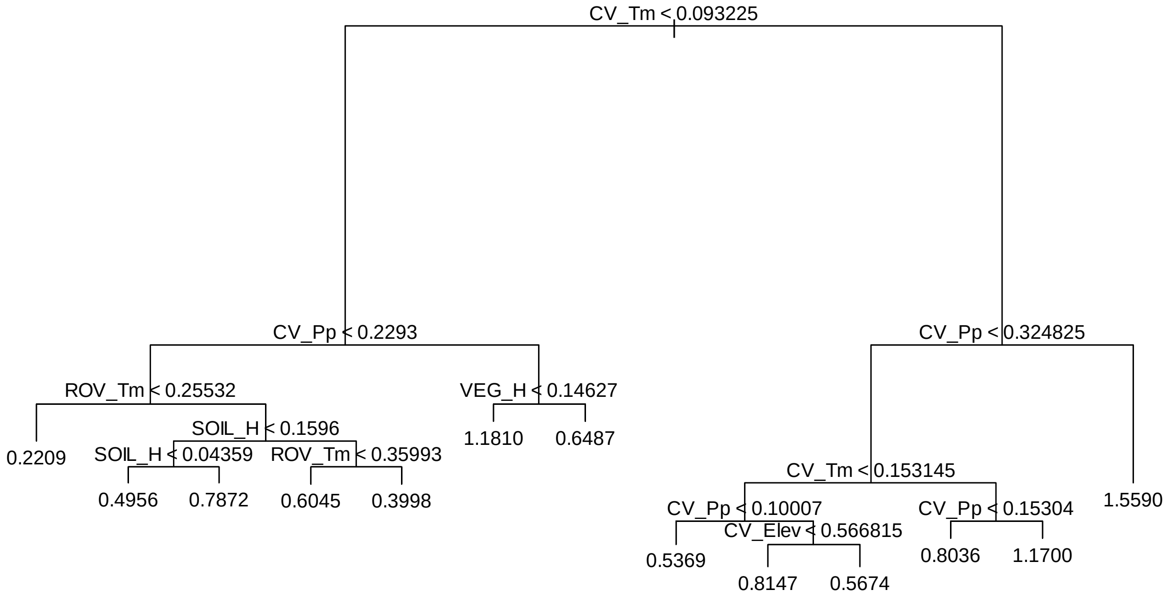


Figure SI IV-4. Amphibian data: regression tree at 0.5 degrees. The figure shows coincidence with the results of the CAR, non-significant variables in the models are at the bottom (Table SI IV-4).

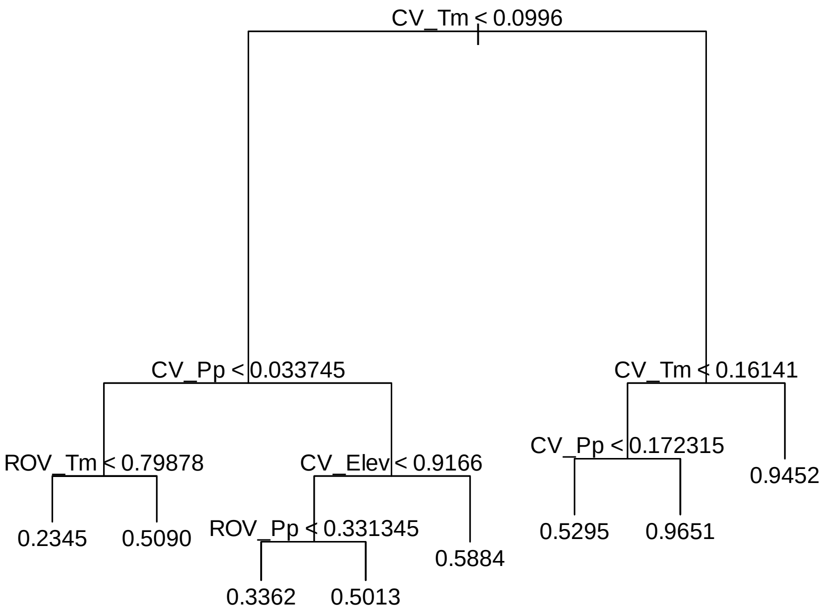


Figure SI IV-5. Amphibian data: regression tree at 0.25 degrees. The figure shows overall coincidence with the results of the CAR model but in this the most important variable was CV of Elevation (see Table SI IV-4 in this appendix).

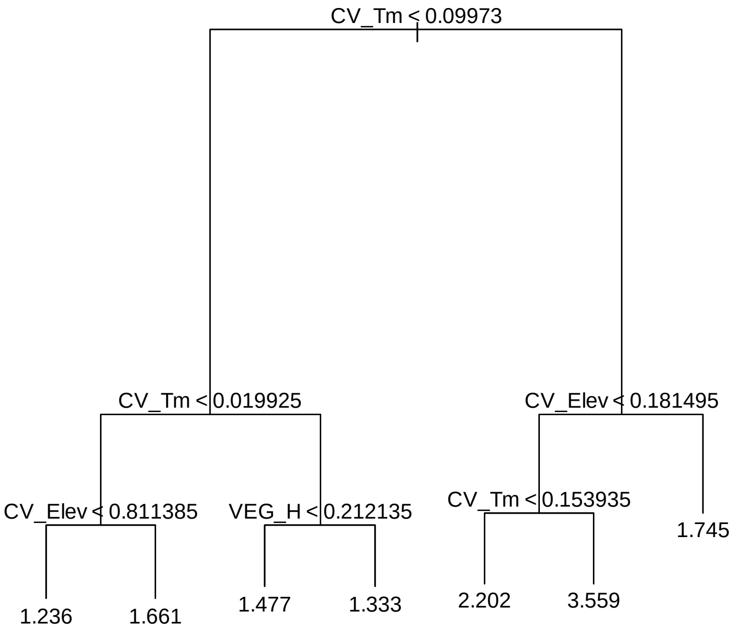


Figure SI IV-6. Amphibian data: regression tree at 0.125 degrees. The figure shows overall coincidence with the results of the CAR, but in contrast to the outcome observed in the autoregresive models CV of Pp was not present in the tree (see Table SI IV-4 in this appendix).

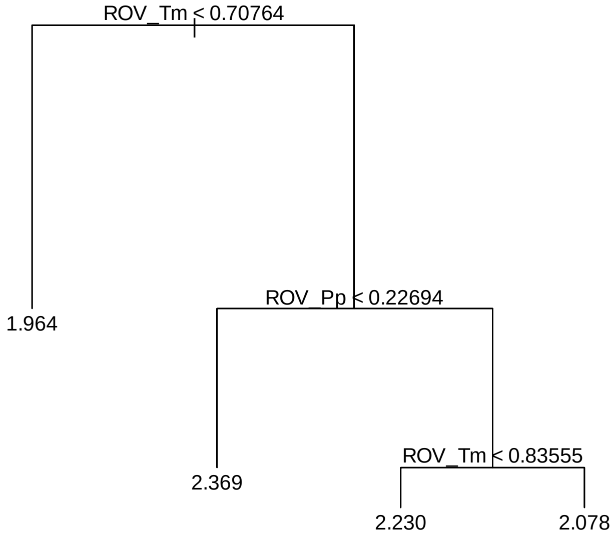


Figure SI IV-7. Bird data: regression tree at two degrees. The figure shows coincidence with the results of the LM (see Table SI IV-3 in this appendix).

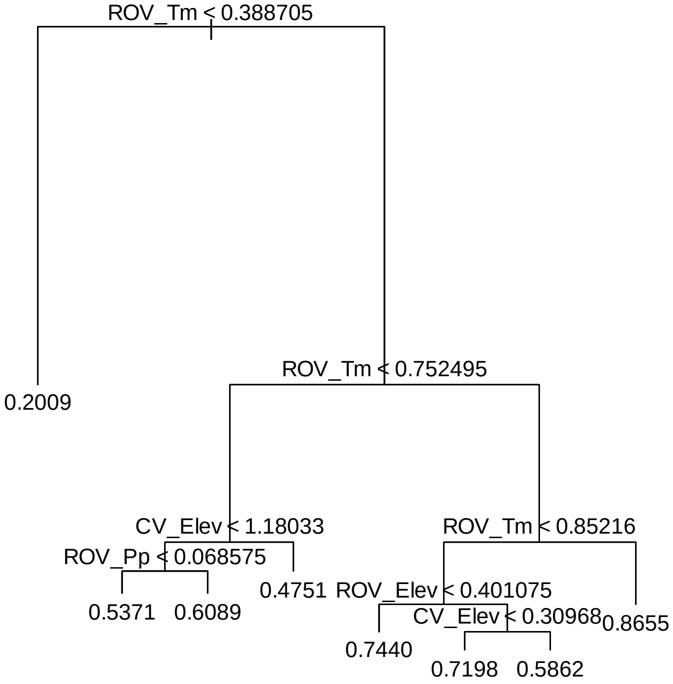


Figure SI IV-8. Bird data: regression tree at one degree. The figure shows coincidence with the results of the CAR (see Table SI IV-4 in this appendix).

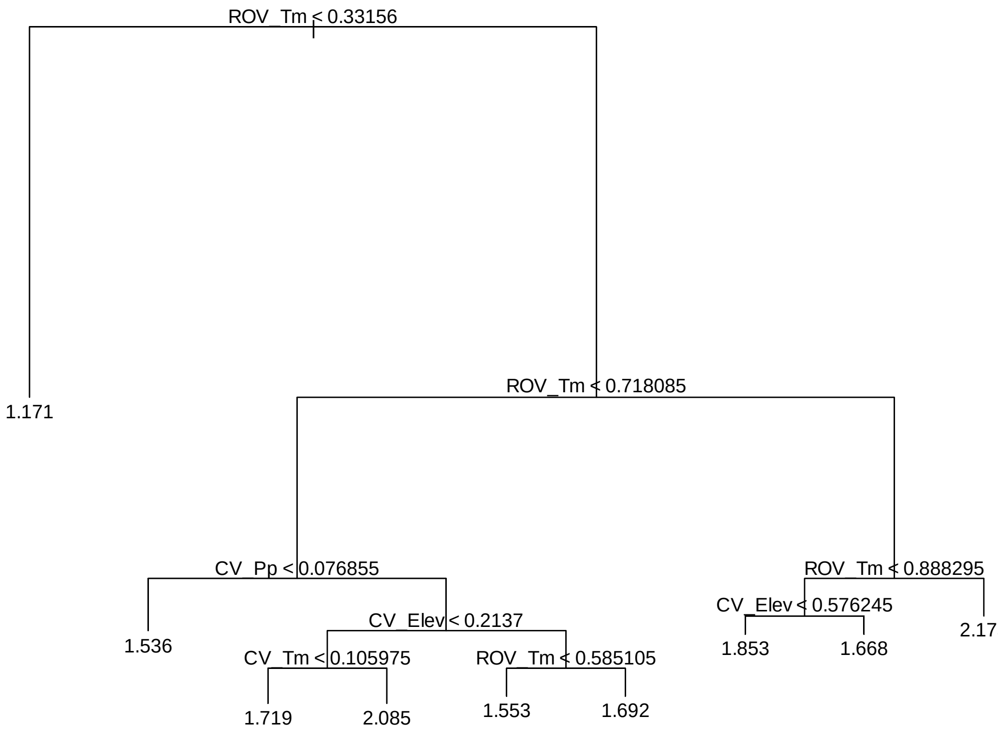


Figure SI IV-9. Bird data: regression tree at 0.5 degrees. The figure shows coincidence with the results of the CAR although the most important variable in this last one was CV of Pp and here appears in the second place (see Table SI IV-4 in this appendix).

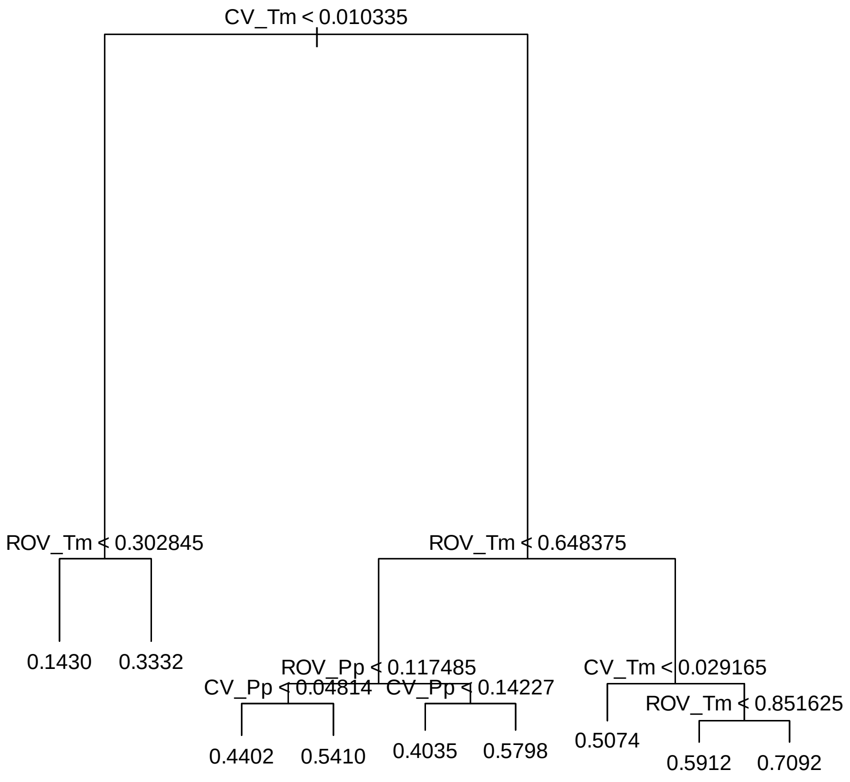


Figure SI IV-10. Bird data: regression tree at 0.25 degrees. The figure differs with the results of the CAR, in which diversity of vegetation (VEG *H*) was the most important variable, followed by CV of Tm (see Table SI IV-4 in this appendix).

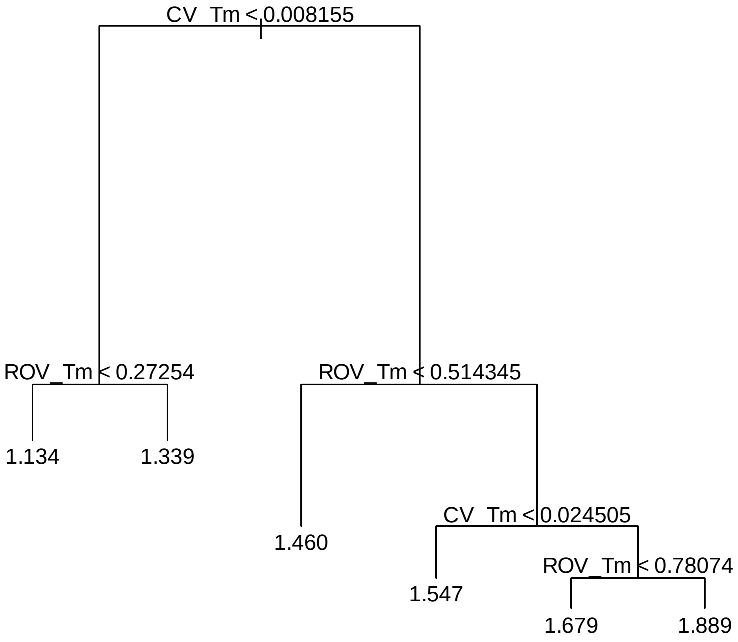


Figure SI IV-11. Bird data: regression tree at 0.125 degrees. The figure differs from the results of the CAR, where CV of precipitation was the most important variable, followed by CV of Tm, while in the former tree CV of Pp did not appear (see Table SI IV-4 in this appendix).

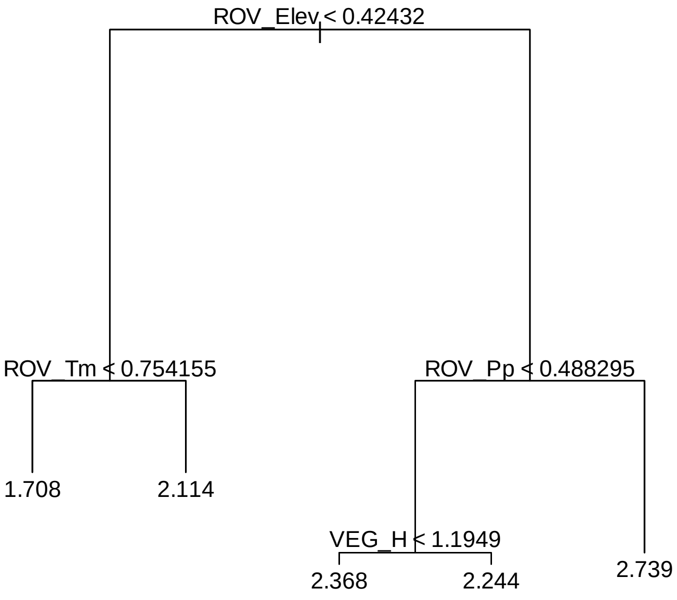


Figure SI IV-12. Mammal data: regression tree at two degrees. The figure shows coincidence, but not completely with the results of the LM, in other words the place and importance of the variables varied, i.e. in the LM ROV of Elevation did not figure as sn important sEH while in the tree above, it is the most important (see Table SI IV-3 in this appendix).

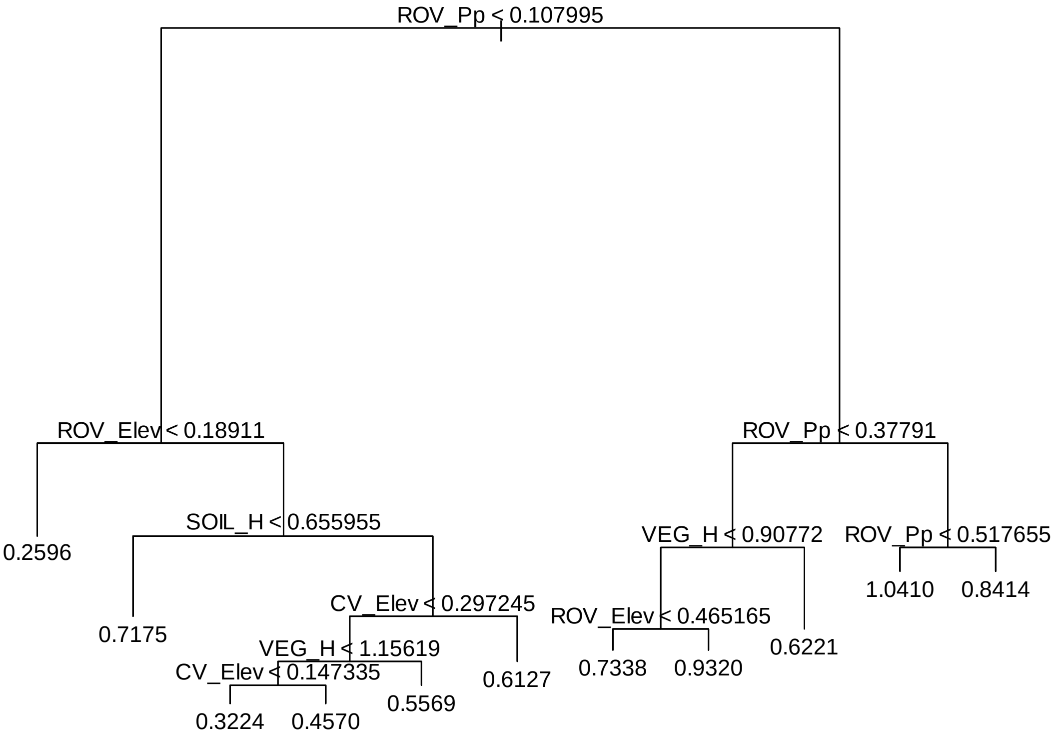


Figure SI IV-13. Mammal data: regression tree at one degree. The figure shows differences from the results of the CAR, in which ROV of Tm was the most important she; in the tree, this variable did not appear (see Table SI IV-4 in this appendix).

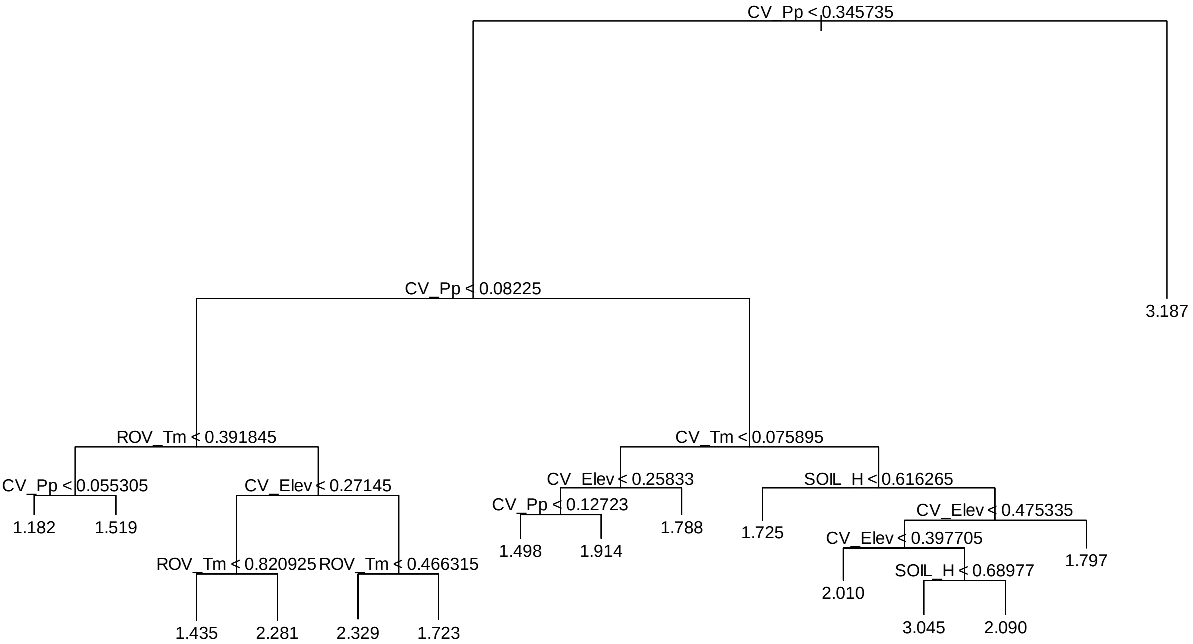


Figure SI IV-14. Mammal data: regression tree at 0.5 degrees. The figure shows coincidence with the results of the CAR (see Table SI IV-4 in this appendix).

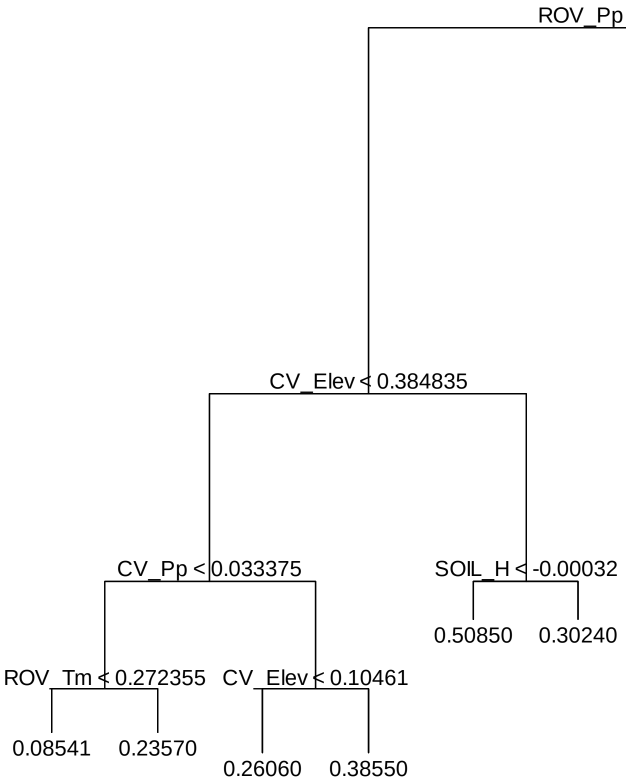


Figure SI IV-15. Mammal data: regression tree at 0.25 degrees. The figure differs from the results of the CAR, in which CV of Elev was the most important variable, followed by diversity of vegetation (VEG *H*). The latter metric did not appear in the tree (see Table SI IV-4).

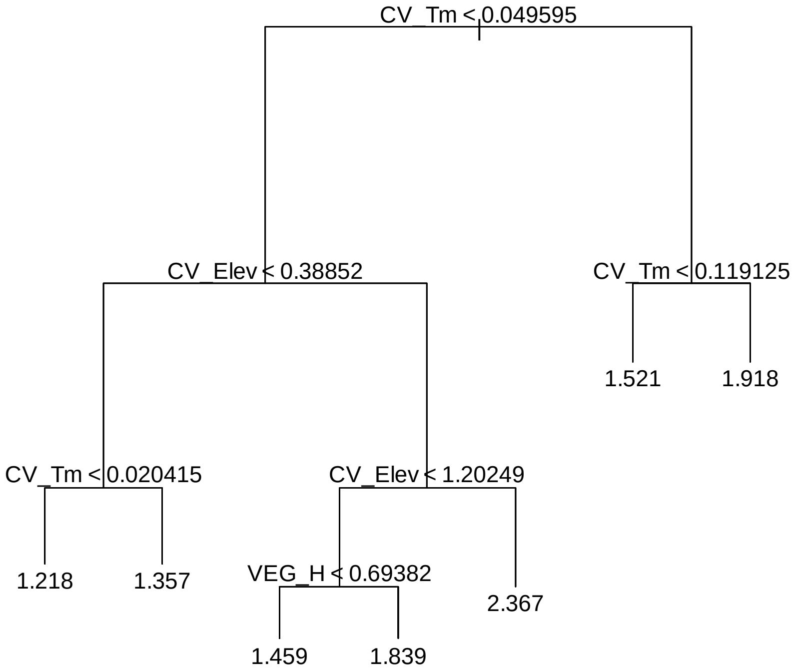


Figure SI IV-16. Mammal data: regression tree at 0.125 degrees. The figure shows general coincidence with the results of the CAR, except for CV of Pp, which is the second most important variable in the model, but did not appear in the tree (see Table SI IV-4).

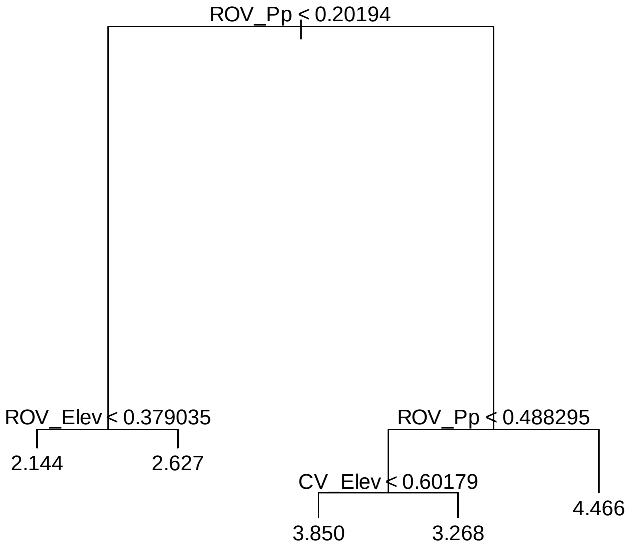


Figure SI IV-17. Reptile data: regression tree at two degrees. The figure shows partial coincidence with the results of the LM where ROV of Elev was the most important followed by ROV of Pp, while here the former variable seems to be of little importance (see Table SI IV-3 in this appendix).

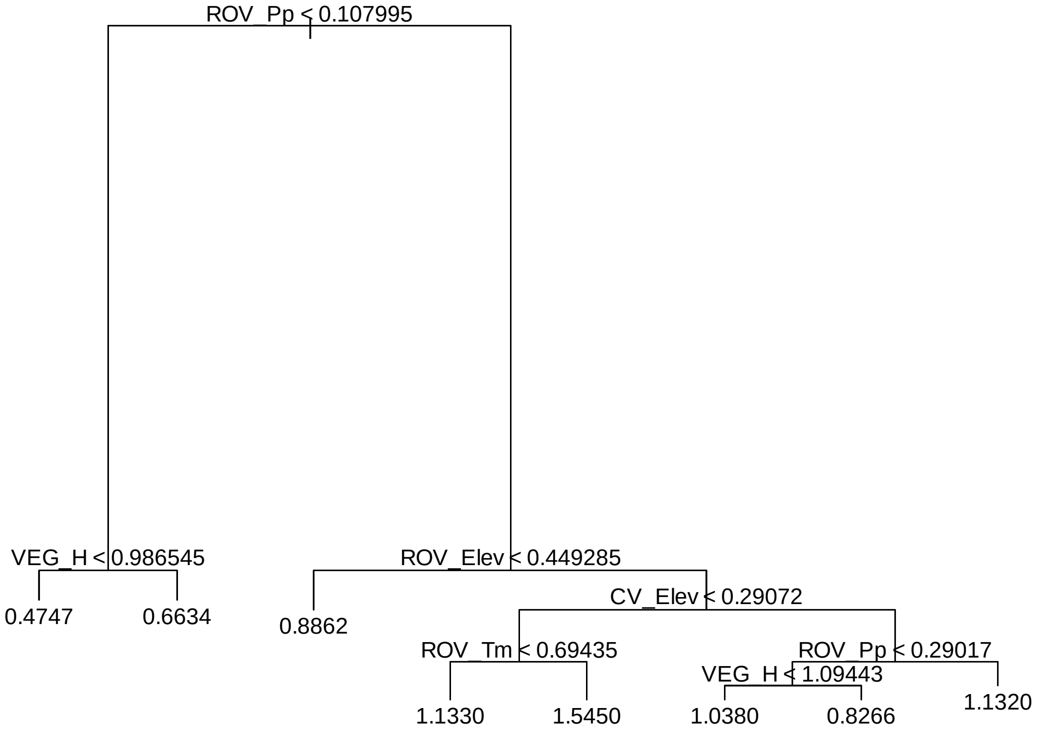


Figure SI IV-18. Reptile data: regression tree at one degree. The figure shows coincidence with the results of the CAR, but in the autoregressive model ROV of Elevation was the most important sEH (view Table SI IV-4 in this appendix).

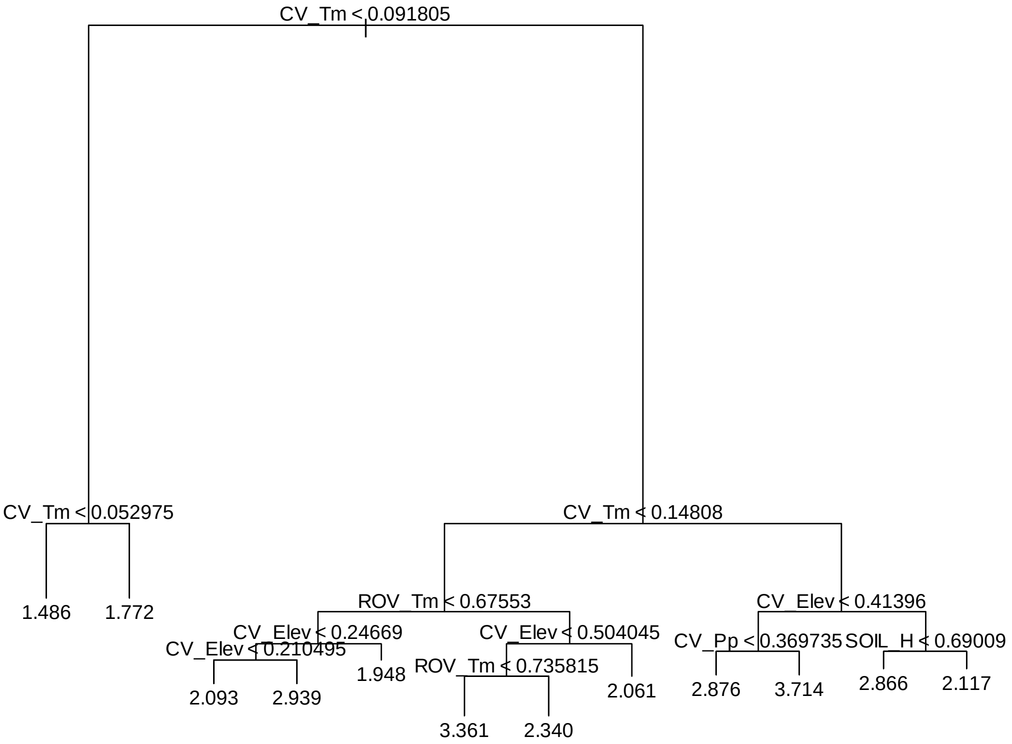


Figure SI IV-19. Reptile data: regression tree at 0.5 degrees. The figure shows coincidence with the results of the CAR (see Table SI IV-4).

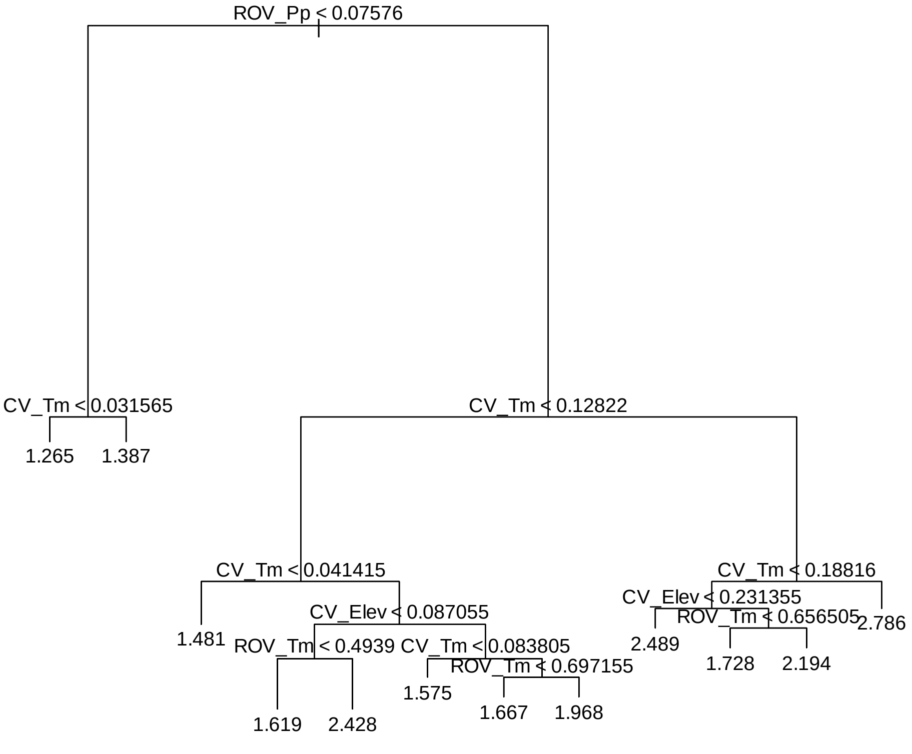


Figure SI IV-20. Reptile data: regression tree at 0.25 degrees. The figure shows little coincidence with the results of the CAR, in which CV of Elev was the most important variable, followed by Veg *H,* while here the former metric seems to be of little importance and the latter did not appear (Table SI IV-4).

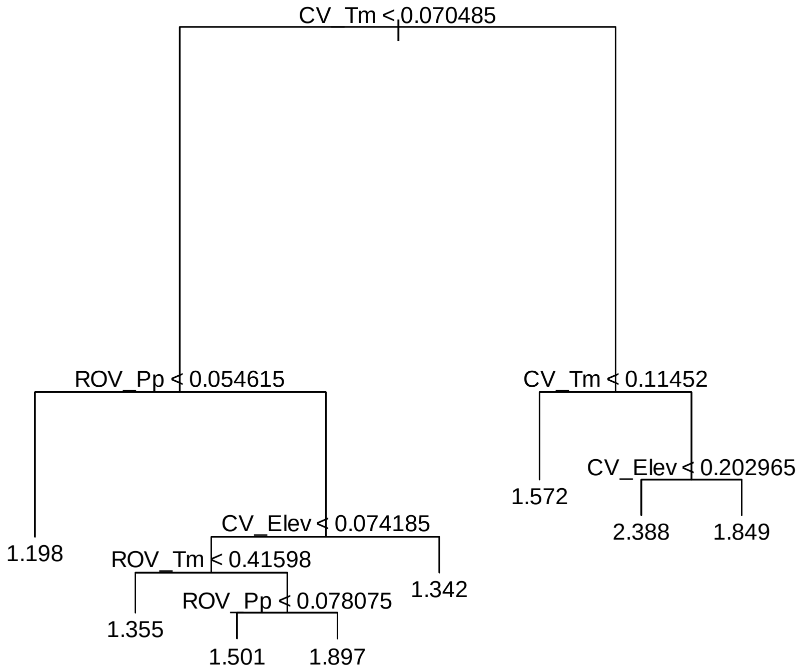


Figure SI IV-21. Reptile data: regression tree at 0.125 degrees. The figure shows coincidence with the results of the CAR, except for CV of Pp, which did not appear in the tree but is the second most important variable in the model (Table SI IV-4).

REFERENCES APPENDIX IV-2

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V. CLIMATE CHANGE AND AMPHIBIAN DIVERSITY PATTERNS IN MEXICO

“Humans are amphibians - half spirit and half animal. As spirits they belong to the eternal world, but as animals they inhabit time”.

C.S. Lewis

This chapter was finished in May 2010, and submitted for review and publication in November 2011 and accepted in March 2012 in *Biological Conservation* (see Appendix B). The co-authors that contributed to this work were (in authorship order): Leticia M. Ochoa Ochoa, Pilar Rodríguez, Franz Mora, Oscar A. Flores-Villela, and Robert J. Whittaker who kindly gave consent to include this article in the thesis.

Chapter word count including references, tables and appendices: 11,104

Main text: 4,854

ABSTRACT

The aim of this article is to characterize at fine scale alpha and beta diversity patterns for Mexican amphibians and analyze how these patterns might change under a moderate climate-change scenario, highlighting the overall consequences for amphibian diversity at the country level. We used a geo-referenced database gathered from museums worldwide as a basis for climatic envelope models, assuming we can accurately model the ecological niche, niche conservatism, and that the future climate scenario is realistic. We generated six sets of models with different parameters (thresholds of presence and dispersal capability) in the modelling processes. We simulated the base line (2000) and future scenarios for Mexican amphibian diversity (2020, 2050, 2080), using climate data layers constructed for Mexico. Using moving-window analyses of different sizes (9, 25, 100, 225 and 400 km^2) we calculated beta diversity with R.H. Whittaker's formula $\beta=\gamma/\alpha_{\text{mean}}$. We analyzed the changes of alpha- and beta- diversity spatial patterns during these periods, and performed an analysis of sensitivity for the beta-diversity patterns. We found that setting low dispersal capability generates high levels of species extinctions, but the overall geographic pattern of beta-diversity remained *stable.* Zones of high beta diversity resulted that were associated with topographic formations, while the values of beta diversity initially increased, and then declined over time. Extinctions (complete loss of range within country boundaries) were particularly intense during the period 2020–2050. The results implied that heterogeneous zones associated with mountain ranges will remain particularly important for amphibian diversity and thus constitute areas for continued conservation prioritization in the face of climate change.

Key words: Amphibians, alpha diversity, beta diversity, climate change, conservation biogeography, Mexico.

INTRODUCTION

We live in an era of accelerating global environmental changes. One of the most important global change processes is habitat fragmentation, which has been recognized as the principal cause of terrestrial diversity loss (Cushman, 2006). However, many scientists argue that climate change may become a greater threat in the next few decades (Malcolm et al., 2006).

It has long been recognized that climate is a major controlling factor for species distribution (e.g. Currie, 1991; Hawkins et al., 2003; Pearson and Dawson, 2003). Recent evidence shows a direct effect of climate change on shifts in species distributions, including the expansion, reduction, and disappearance of individual species ranges (Hughes, 2000; Walther et al., 2002; Perry et al., 2005). Climate change effects on complete assemblages have been less studied and those studies have been focused on coarse-scale datasets (e.g. Araújo et al., 2006; Jetz et al., 2007; but see Peterson et al., 2002). Based on modelled species range shifts, studies have shown general changes in projected patterns of diversity. A common emergent finding is that the location of hotspots and areas with high numbers of endemic or endangered species will change and some may disappear (e.g. Malcolm et al., 2006).

Amphibians have been identified as one of the most threatened groups in the world (Young et al., 2001; Rohr et al., 2008) and there is concern that global climate change may greatly increase threats to many amphibian populations (Blaustein et al., 2001; Corn, 2005). Mexico is home to more than 372 species and possesses one of the highest levels of endemism worldwide (>65%). Mexican amphibians may be anticipated to be severely threatened by climate change (García, 2006) because around 80% of the endemics are actually micro-endemics (Ochoa-Ochoa et al., 2011), with the highest concentration in the south of the country. Mexican amphibians exhibit both a latitudinal gradient in species richness (Ochoa-Ochoa and Flores-Villela, 2006), and high beta diversity at fine (e.g. Pineda and Halffter, 2004) and coarse scales, with higher values towards southern latitudes (Flores-Villela et al., 2005). Surprisingly, despite the high species richness and endemism, there have been no fine-scale analyses of the effects of climate change on the biodiversity patterns of this group of vertebrates for Mexico (e.g. Hof et al., 2011).

Alpha (species richness within a community), gamma (species richness in a landscape) and beta diversity (variation in species composition across communities within a landscape) are important concepts to understand the patterns and the processes of communities. Geographical gradients of species richness (alpha and/or gamma) have long been studied (e.g. Pianka, 1966; Hawkins et al., 2003) and while a single global model of spatial variation in species richness remains elusive, a high proportion of variance in regional and global biodiversity models is attributable to climate, especially to the dynamics of water and energy regimes (e.g. Whittaker et al., 2001; Hawkins et al., 2003; O'Brien, 2006).

Beta diversity metrics provides insight into the spatial pattern dynamics of species (Drakare et al., 2006; Soininen et al., 2007) and are relevant in conservation planning (Gaston et al., 2001). For example, the high beta diversity of Mexican mammals reflects the existence of a large number of range restricted species within the country (Arita and León-Paniagua, 1993). Similar characteristics in spatial variations of beta diversity for amphibians can be observed across Mexico as there are many micro-endemic species, a high proportion of which are associated with specific mountain ranges, featuring strong environmental gradients. From a conservation biogeography perspective (Whittaker et al., 2005) diversity patterns of amphibians for the country would thus be better characterized by the variations in beta than alpha diversity.

Until now no consensus about the form of the relationship between beta diversity and latitude have emerged (Rodríguez and Arita, 2004; McKnight et al., 2007), as it depends on the method and scale of analysis selected (Koleff et al., 2003). Notwithstanding that environment seems to play a crucial role in the structure and patterns of beta diversity (Legendre et al., 2005), we may expect a latitudinal gradient due to the location of micro-endemics, but we currently lack a clear basis for predicting the form of the pattern and how it may change as a function of changing climate in the study region.

In principle, under a climate change scenario, spatial patterns in local ‘alpha’ and regional ‘gamma’ diversity could, to some extent, be decoupled during a period of species distributional resorting (cf. Whittaker et al., 2001). As beta diversity registers the re-arrangements of species distribution ranges across space, following the patterns of beta diversity may thus provide early indication of how ongoing local changes in distribution impact the biodiversity patterns. Following this, there are three possible outcomes in terms of beta diversity pattern at the scale of Mexico as a whole: no change, homogenization, or increased differentiation. The first scenario, of unchanging beta diversity pattern, can be defined as the ***stable beta hypothesis***. For this scenario, the mean of distribution range sizes has to remain more or less the same, and any increase or decrease in alpha and gamma diversity has to be proportional across the study system, e.g. if gamma decreases alpha decreases at the same rate. A second scenario, in which decreasing values of beta diversity occur, can be termed the ***homogenization hypothesis***. In this case the mean size of the distribution ranges would increase, either through the extinction of micro-endemics, or due to the expansion of species ranges. The third case, whereby beta diversity increases, could be termed the ***heterogenization hypothesis*** and would correspond with a decrease in the mean of the distribution range sizes, either through the incursion of micro-endemic species into the study area, or through the net contraction of species ranges. These projections of course take no account of any gains from migration into Mexico of non-native species. These three scenarios outline a set of hypothetical responses to climate change in biodiversity measures that are based on differing abilities of species to accommodate environmental change locally (i.e. broad-narrow fundamental niches), resulting in changing local patterns of species richness, and in turn altering patterns of beta diversity. We suggest that these hypotheses can theoretically be applied to any group and place.

In this paper we used Mexican amphibians as an assemblage and climate change scenarios as the only driver to explore the changes of diversity patterns from a baseline to three future points in the 21st century, with an emphasis on the patterns in beta diversity, focussing on the three possible scenarios described above. In addition, to explore sensitivity of our analyses to input values, we evaluated the effects of altering parameters for presence–absence threshold, dispersal capability and window size.

MATERIALS AND METHODS

Distribution ranges in the baseline

We used a database containing around 418,500 data points of amphibians and reptiles, with 27,419 unique collecting localities, corresponding to 363 of the 372 species of amphibians that inhabit Mexico (Museums and projects that contributed data are listed in Appendix V-1). The database consists of geo-referenced species' presence records, gathered from various museums worldwide, and was geographically and taxonomically verified by experts (for further details, see Ochoa-Ochoa and Flores-Villela, 2006). These records were used to model the range distribution of each species through a climatic envelope modelling approach (CEM). This modelling approach assumes that climate is a major contributing factor for species distributions (Pearson and Dawson, 2003). Thirty micro-endemic species from 145 inhabiting the country (Ochoa-Ochoa et al., 2011) were found to have too few data points to generate an accurate model for the baseline. The remaining analyses reported below are thus based on models for the remaining 115 micro-endemic species, as well as all the non-micro-endemic (218 species). In total 333 species were analyzed.

There are several papers that discuss CEM caveats, ranging from the concepts (e.g. Hirzel and Lay 2008; Soberón and Nakamura 2009) to the methods (e.g. Pearson et al., 2006, 2007). In general, limitations of databases, sampling bias, decisions made on choice of modelling method, the climate change scenarios adopted, and parameters such as threshold of presence and dispersal rate allowed in the modelling are each important in determining model outputs (Whittaker et al., 2005; Lozier et al., 2009; Phillips et al., 2009; Pineda and Lobo, 2009). The spatial representation of the resulting ecological niche model in CEM analyses is therefore best regarded as a *proxy* of the range distribution of the species (potential distribution) in the context of a particular set of assumptions about future climate and species response capabilities.

For the CEM process we used climate layers (monthly precipitation, maximum and minimum temperature) developed for Mexico, with a spatial resolution of 0.008' or ~1 km^2 (Téllez, 2004) to generate 19 climate variables using Hijmans' script (2006). Several of these data layers capture the interactions between temperature and precipitation, reflecting key aspects of climatic seasonality (Table SI V-1 in Appendix V-1). We used a Maximum Entropy modelling approach (MaxEnt; Phillips et al., 2004, 2006) to model the species distribution ranges based on climate data for Mexico. We selected 2000 as the baseline. We used climate data averaged across the 30 year time period up to 2000 as such period is necessary to provide robust estimates of climate means. We also evaluated other sources of variability such as threshold of presence, dispersion and window size. To assess the importance of the chosen threshold, four levels were tested, following precedents established in previous work: these were 50% probability of presence, 70% probability of presence, the 10th percentile training presence of the logistic threshold of the distribution model, and the lowest presence threshold (see Liu et al., 2005; Pearson et al., 2007; Urbina-Cardona and Loyola, 2008; Pineda and Lobo, 2009).

Distribution ranges in the future

The use of models to generate future scenarios has been widely expanded in recent years and may provide valuable insights into the biodiversity implications of global change processes (e.g. Peterson et al., 2002; Pearson and Dawson, 2003; Araújo et al., 2004, 2006; Pearson et al., 2006; Jetz et al., 2007; Lawler et al., 2009; Carvalho et al., 2011; Hof et al., 2011). In the present analysis, we used the model obtained for the baseline date of 2000 to predict the future distribution of each species. This approach relies on the following key assumptions. First, it is assumed that the ecological niche has been accurately determined in the first place. Second that fundamental niche evolves slowly so it is likely that it remains stable over the period of time analyzed (Holt, 1996; Peterson et al., 1999; Wiens and Graham, 2005; Araújo and New, 2006). Third, it is assumed that the future climate scenario is realistic. Fourth, assumptions have to be made about the dispersal capabilities of the species as they respond individualistically to changing patterns of climate across the country (e.g. Hughes, 2000; Peterson et al., 2002; Whittaker et al*.,* 2005; Carvalho et al., 2011; Ladle and Whittaker, 2011). A critical decision in the process of generating the hypothetical future distributions of amphibians was determining the *dispersion* allowed for the species projections of the niche modelling in future periods. In this context, dispersion was defined as the capacity of a species to shift from the distribution of the previous date to a new one by the following date. Therefore different scenarios of "dispersion" were also tested: zero dispersion, total dispersion and moderate dispersion. The latter was set at 1 km per year and was based on empirical evidence of the dispersion capability and available literature data (Stebbins and Cohen, 1995; Marsh and Trenham, 2001). As species geographic distributions are also limited by ecological and historical factors (Peterson et al*.,* 2002) another scenario was simulated, whereby each model was trimmed in the baseline model based on expert evaluation. In this simulation, we used the moderate dispersion rate setting (further details of these procedures can be found in Appendix V-2).

The future climatic scenarios for Mexico were constructed based on a single climatic scenario: the SRES-B2 of the Second Generation Coupled Global Climate Model (CGCM2) of the Canadian Centre for Climate Modelling and Analysis (CCCma), because it is a good predictor for North America including Mexico (e.g. Sawada et al., 2004). These climate layers have a coarse resolution (3.75° x 3.75°). To downscale the variables we use the simplest available statistical method, the 'delta-change' approach (Fowler et al., 2007). This involves applying coarse GCM-scale projections in the form of change factors (CFs), to fine-scale climate baseline layers (Wilby and Wigley, 1997). It is the most straightforward approach according to Wilby et al. (2004) and has the advantage of providing point-scale climatic variables from

GCM-scale output. In addition, it can be used to derive variables not available from regional climate models. All downscaling methods involve caveats, in this case the high uncertainties involved in downscaling to very fine scales and the assumption that any bias is constant through time (Fowler et al., 2007). Further sensitivity analyses could be undertaken using alternative climate change scenarios but were outside the scope of the present study.

Information corresponding to each of the 12 monthly values for each variable (precipitation, maximum and minimum temperature), was downloaded from the IPCC website (http://www.ipcc-data.org, accessed January 2007). We calculated a 30-yr mean of the variables for each period. Based on those layers we generated the same 19 climatic variables as for the baseline (Table SI V-1), for the periods 2020, 2050 and 2080, using Hijmans' script (2006). Further details are given in Appendix V-1.

Patterns of alpha and beta diversity

Species richness values per cell, hereafter alpha diversity, were obtained through spatial assembling of all species for each period for each 1 km^2 pixel. Beta diversity values were calculated by means of a moving window analysis (MWA) performed using different window sizes, 3, 5, 10, 15 and 20-pixels to a side (~9, 25, 100, 225 and 400 km^2 respectively). The purpose of applying a MWA at different resolutions was to identify zones of marked change, and/or local complexity of the patterns. Beta diversity was calculated using the classic formula of R.H. Whittaker (1960), which relates gamma and the average alpha diversity in a multiplicative way, $\beta_W = \gamma/\alpha_{mean}$, where: γ is the number of species whose distribution range intersected the window; and α_{mean} is the arithmetic mean of species richness of all the pixels within the window (number of pixels depend on the size of the windows, varying from nine to 400 pixels). We used Whittaker's metric of beta diversity because it is not sensitive to contrasting values of gamma diversity (Srivastava, 1999) and because of its straightforward interpretation. In this context, beta may vary from a minimum of 1 when $\alpha_{mean}= \gamma$; to a maximum of gamma, when $\alpha_{mean} = 1$.

The spatial patterns of alpha and beta diversity were mapped for each period separately (2000, 2020, 2050, and 2080). We then obtained the spatial representation of the changes in alpha and beta diversity between each period; we called these variables 'Δ alpha diversity' and 'Δ beta diversity', respectively. Unlike spatial explicit approaches, MWA concentrates on local pattern description of beta, rather than testing the effects of similarity due to distance.

RESULTS

Sensitivity analyses

The diversity patterns resulting from the variation of the different sources of uncertainty: threshold of presence, dispersion capability and window size, are provided in Appendix V-2 (Figs. SI V-1–26 Appendix V-2, Supporting information). Both diversity patterns, alpha and beta, can change depending on the thresholds selected. Nevertheless while the changes can be abrupt in alpha diversity, beta is more stable and remains concentrated within the mountain ranges in all simulations. Larger window sizes generate higher values of beta diversity than do smaller windows; higher presence thresholds generate higher values of beta than lower ones, but also higher numbers of extinctions and therefore substantial changes in alpha (and country-level) diversity patterns; and finally, lower dispersion values lead to higher numbers of extinctions, although not necessarily higher values of beta, unless combined with a higher presence threshold (i.e. 70%).

Bearing in mind these sensitivity tests, we choose to focus on one simulation in order to describe the patterns in depth. This scenario was selected as being, in our view, the most realistic of those modelled with regard to the scale at which amphibians appear to interact with their environment. This model was based on the 10th percentile training presence of the logistic threshold of the distribution model (following Urbina-Cardona and Loyola, 2008), a 100 km^2 window size, moderate dispersion rate (1 km $year^{-1}$), with trimming of baseline models based on expert evaluation. Given the scale at which amphibians interact with and move through their environment, we regard this window size as ecologically appropriate (Gardner et al., 2007). This window size allows detection of areas of rapid change or complexity (Burrough and McDonnell, 1998); in this case this means significant changes in the species communities (beta diversity).

Alpha diversity and climate

Alpha diversity (species richness in each $1km^2$ cell) in the baseline analysis ranged from 0 to 38 species (8.13 mean ± 5.05 Stdv, n = 2,003,150 cells; Fig. V-1a). In some places in the north, particularly in dry areas, there are no records of amphibians. The alpha diversity pattern at the baseline (2000) showed a general decrease in species richness with latitude, and also presented particularly high values for some mountain ranges. Differences in alpha diversity values between 2000 and 2020 largely consisted of decreases (net decline in species number) in the north, northern Pacific coast, southern coast of the Gulf of Mexico and in most parts of the Yucatan peninsula; while, increments in species number occur along the Sierra Madre Oriental and within the south (Fig. V-2a). In 2020, the alpha diversity pattern remains similar to that estimated for 2000 (Fig. V-1b), with a highest value of 40 species (6.73 mean ± 5.31 Stdv, n = 1,616,321 cells). The greatest decreases, of up to 30 species per $1km^2$ cell, occur between 2020 and 2050, for the coastal region of the Gulf of Mexico and the Yucatan peninsula. Increments of species numbers were mainly observed towards the southern Pacific coast (Fig. V-2b).

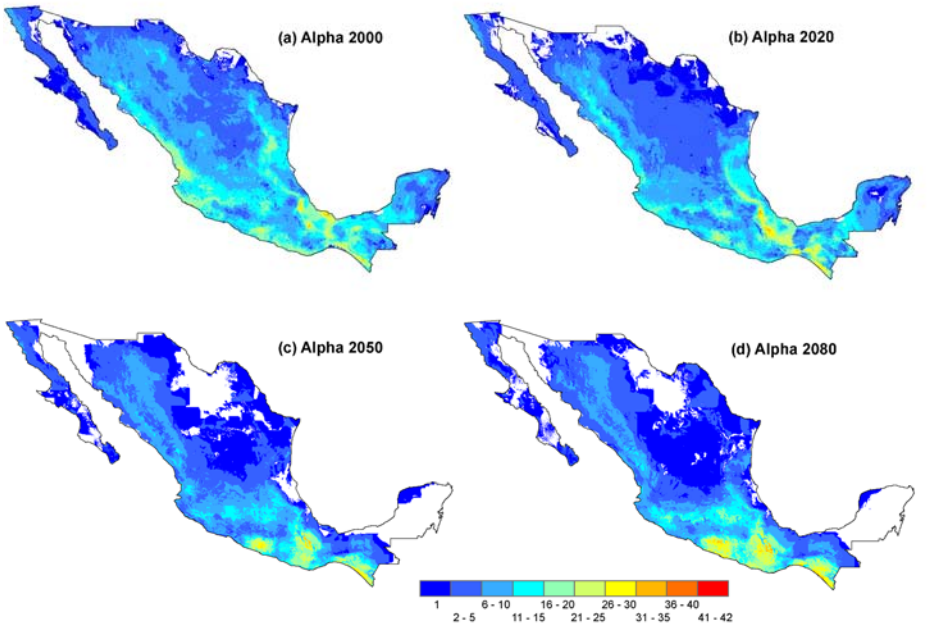

Figure V-1. Spatial patterns of alpha diversity using grid cells of ~1 km^2 for Mexican amphibians in: a) the baseline year 2000; b) 2020; c) 2050; and d) 2080. White spaces within the country limits mean zero species.

By 2050 species richness is concentrated in the south (Fig. V-1c), with a highest alpha value of 37 species (5.11 mean ± 4.92 Stdv, *n* = 1,373,403 cells). The main changes in the pattern of alpha diversity are the substantial extinctions in the north and Yucatan Peninsula. Between 2050 and 2080, reductions in species numbers are projected to be focused in the northwest, while increases occur in the south (Fig. V-2c). Finally, in 2080, the latitudinal pattern is slightly more pronounced than in 2050 (Fig. V-1d). Although alpha diversity is projected to be reduced in a large proportion of the country, the highest values increase to 42 species (5.49 mean ± 5.97 Stdv, *n* = 1,412,527 cells). The species are concentrated in the south-Pacific slope. According to the models, the total number of amphibian species in Mexico decreases from 333 species in the baseline year, to 300 in 2020 (29 endemics extinct), to 258 (14 endemics extinct) in 2050 and finally to 254 (2 endemics extinct) species at 2080.

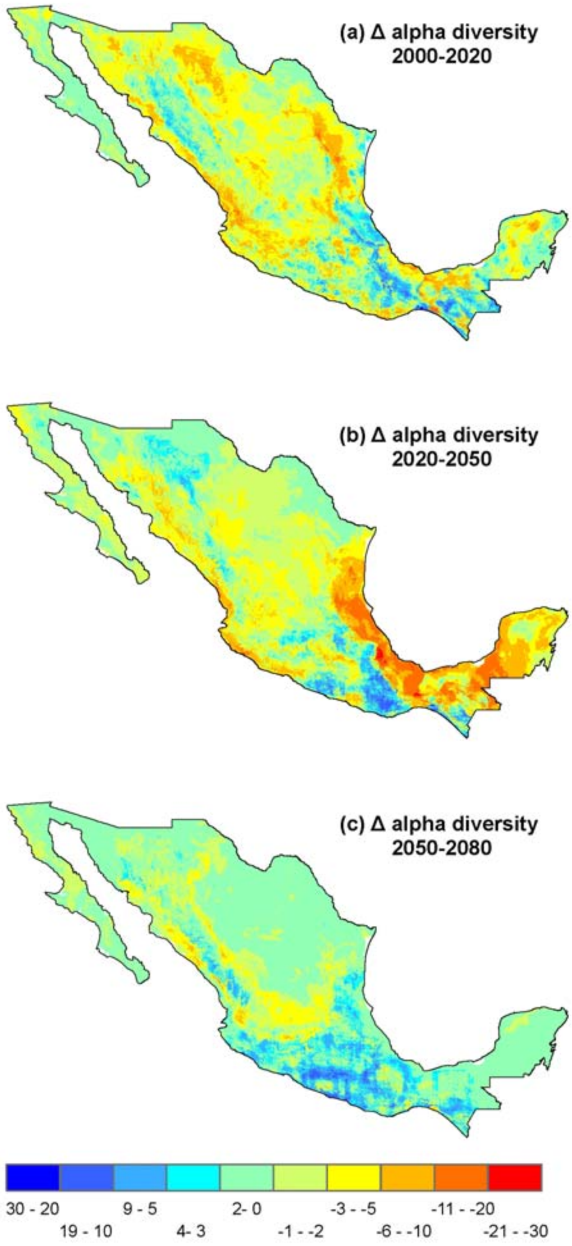

Figure V-2. Spatial patterns of changes in alpha diversity. Δ alpha diversity: α_1=2000–2020, α_2=2020–2050 and α_3=2050–2080. Positive values imply increments in species richness (blue), negative values imply decrements (red). White spaces within the country limits mean zero species.

Beta diversity and distribution ranges

In the baseline analysis, beta diversity is spatially heterogeneous, ranging from 1 to 12 (1.39 mean ± 0.42 Stdv, n= 1,985,340 cells), but with prevailing low values, from 1 to 3, in most parts of the country (Fig. V-3a). Contrary to our initial expectations the analyses depict no latitudinal pattern of beta diversity. The highest values are mainly observed in the foothills and slopes of mountain ranges.

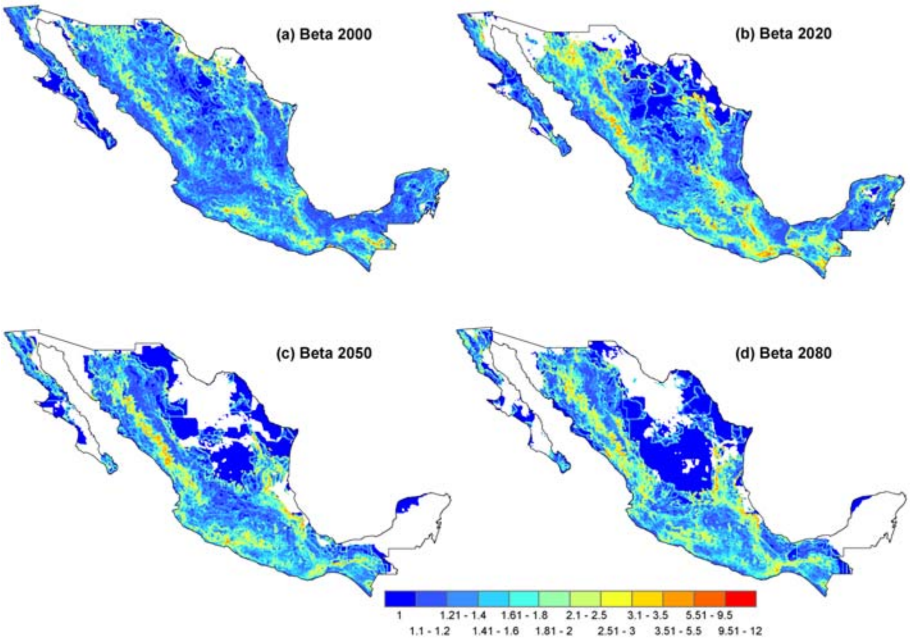

Figure V-3. Spatial patterns of beta diversity in: a) the baseline year, 2000; b) 2020; c) 2050; and d) 2080. White spaces within the country limits mean zero species.

Between 2000 and 2020, beta diversity increases in most parts of the country, with decreases concentrated in the north (Fig. V-4a). For 2020 beta diversity displays a similar spatial pattern as in 2000, but with higher values and slightly shifted to the west (Fig. V-3b). The highest value being 10.98 (1.53 mean ± 0.56 Stdv, *n* = 1,585,887). From 2020 to 2050, the pattern of change in beta diversity becomes largely inverted from that of the previous period, with most parts showing a decrease (Fig. V-4b).

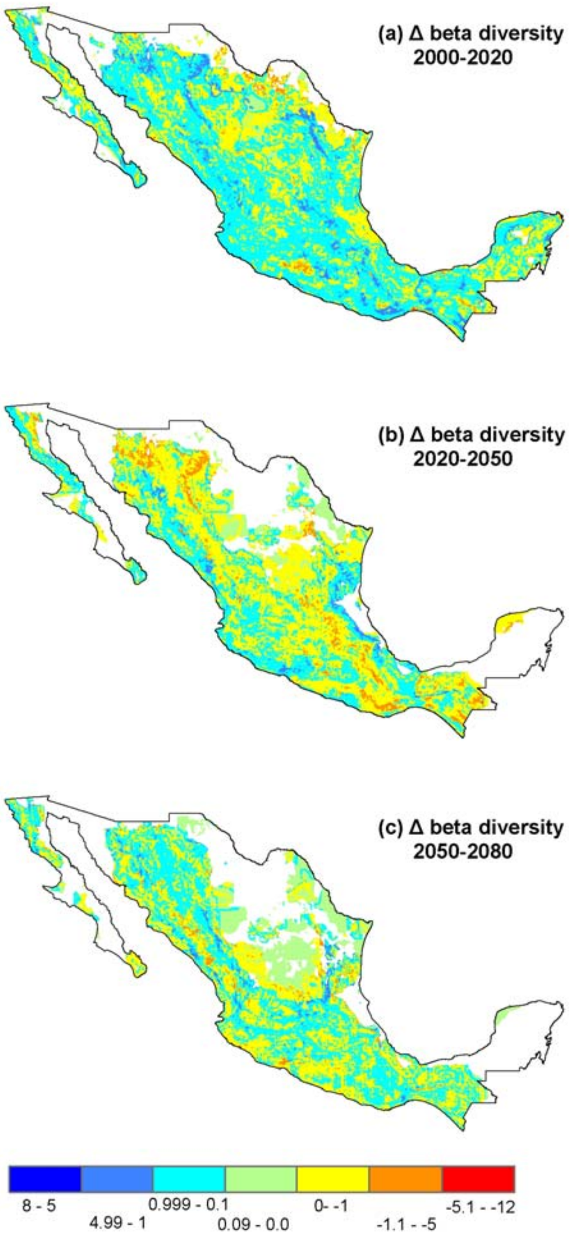

Figure V-4. Spatial patterns of the changes in beta diversity. Δ beta diversity: β_1=2000–2020, β_2 =2020–2050 and β_3=2050–2080. Positive values imply increments in beta (blue), negatives values imply decrements (red). White spaces within the country limits mean zero species.

By 2050 modelled beta has decreased principally in the southern part of the Pacific coast (Fig. V-3c, V-5b), the maximum value generated being 8.57 (1.44 mean ± 0.51 Stdv, n = 1,304,464). From 2050 to 2080 the simulations show approximately half of the country having increased and half decreased values of beta diversity (Fig.

V-4c). In 2080 beta diversity shows an increase in its maximum value 9.52 (1.45 mean ± 0.51 Stdv, n = 1,336,563). High decreases occur mainly on the peripheries (see Fig. V-4c).

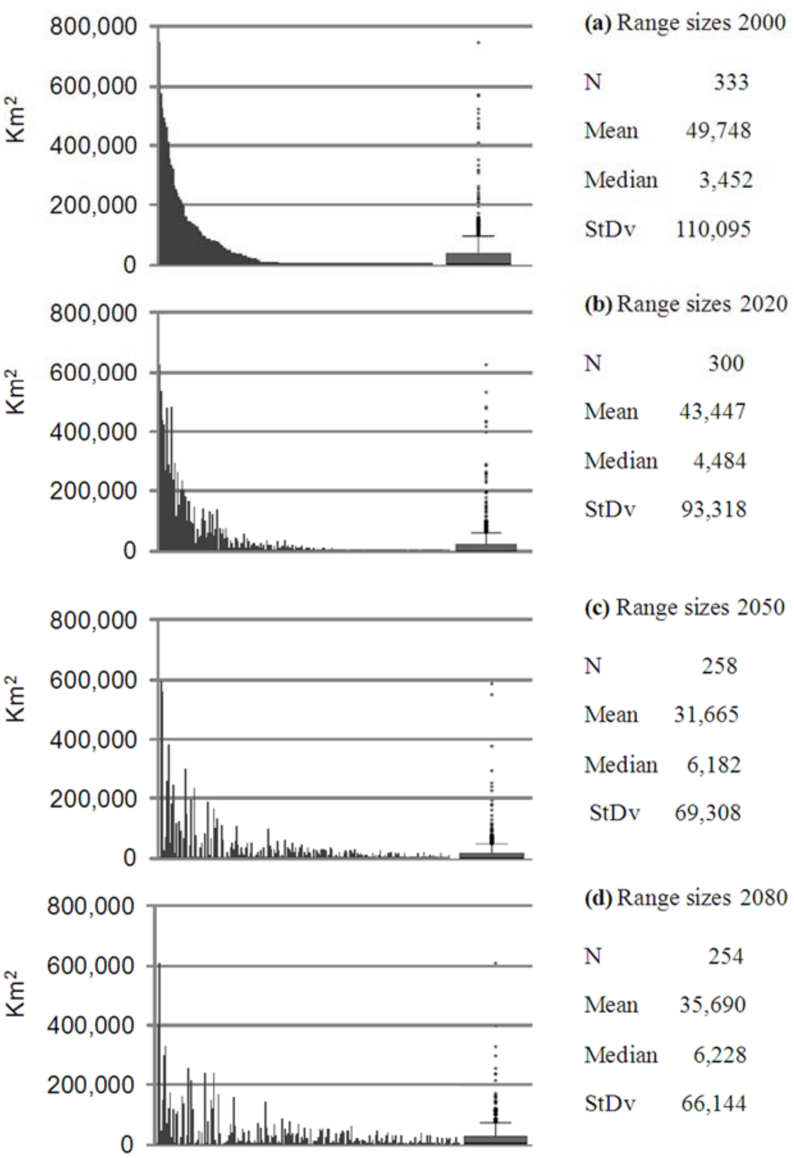

Figure V-5. Histogram of range sizes of Mexican amphibians in km^2, arranged according to declining range size of the species in the baseline year, 2000 AD, showing the distribution in each period: (a) 2000; (b) 2020; (c) 2050; and (d) 2080. The box-plots to the right show the mean and median (thick bar at base), the upper standard deviation (line) and the outliers.

The distribution ranges of the modelled species within the bounds of Mexico at the baseline varied highly from 2 km^2 to 750,000 km^2, with a mean range size of 49,748 km^2 (± 110,095 Stdv, n = 333, Fig. V-5a). Between 2000 and 2020 the mean size of the distribution ranges decreased to 43,447km^2 (± 93,748 Stdv, n = 300, Fig. V-5b). By 2050 the average of the distribution ranges again decreases, to 31,665 km^2 (± 69,302 Stdv, n = 258, Fig. V-5c), as a result of a general pattern of range contractions and high number of species extinctions. Finally, by 2080 the mean distribution range size increases to 35,690 km^2 (± 66,144 Stdv, n = 254, Fig. V-5d). It is interesting to observe that while mean range size decreases from 2020 to 2050 and increases in 2080, the median increases constantly (from 3,452 to 6,228 km^2), reflecting the extinction of micro-endemic species.

DISCUSSION

The presence of a strong relationship between climatic variables and species richness has been appreciated ever since the late 18th century, e.g. through the writings of Johann Reinhold Forster, and Alexander von Humboldt (Currie, 1991; Hawkins et al., 2003; Lomolino et al., 2010). If climate is the principal determinant of biodiversity patterns, then we should expect changes in the biodiversity patterns whenever significant changes in climate regimes occur (Whittaker and Field, 2000; O'Brien, 2006). Consistent with this line of reasoning, this study depicts changes in species richness patterns under a moderate climate change scenario. The behaviour of the spatial patterns of beta diversity does not appear to have been analyzed in this way in previous work and our findings indicate some unexpected but not totally counter-intuitive results. We first discuss our favoured scenario then the implications of the sensitivity analyses reported in Appendix V-2.

Alpha diversity

Our finding of a weak and discontinuous latitudinal gradient from north to south in the baseline, differs from patterns observed at coarser scales (Ochoa-Ochoa and Flores-Villela, 2006), but is consistent with the analyses reported by Pineda and Lobo (2009) at a similar spatial scale (10 km^2). The spatial pattern in alpha diversity changed through time, resulting in richer zones in the south. The implications of such changes in amphibian richness patterns through time could be of enormous importance for amphibian conservation. For example, future alpha diversity could be concentrated in the south of the country, Oaxaca and Chiapas states, where there are few protected areas (Ochoa-Ochoa et al*.,* 2009). Even if more protected areas were to be declared, the survival of many species would still be compromised if our simulations were to be borne out (e.g. Araújo et al*.,* 2004).

The zones with high alpha diversity for 2050 and 2080 are located in the centre and south of the country, in the most populated areas, with the largest urban zones. A key obstacle for the survival of many amphibians in the region is likely to be the lack of connectivity between putatively suitable habitats. Without the possibility of dispersion the probability of extinction due to climate change becomes higher. These results not only imply that the zones of maximal species richness could change but that amphibian communities may experience rearrangements in composition, transforming relationships among species, with unknown effects for communities (Walther et al*.,* 2002; Botkin et al., 2007).

Beta diversity

Estimating the beta diversity pattern for the whole country at such a fine scale is to the best of our knowledge a novel approach and so close comparisons with other studies are not possible (but see: Lennon et al*.,* 2001; McKnight et al*.,* 2007; Buckley and Jetz, 2008; using different similarity indices). Within our analyses the zones with high beta diversity were concentrated in the slopes and foothills of the mountains ranges, where many micro-endemics are concentrated. Most of the lowland parts of the country showed low values of beta diversity (~1 to 3). Some places within Baja California and the Yucatan Peninsula show anomalously high beta diversity, as an artefact resulting from the great number of places without species, the same occurred with the peripheries from 2050 to 2080. The distribution ranges of the modelled species followed the typical hollow curve reported for assemblages of species at large scales (Gaston and Blackburn, 2000), i.e., most species have small distribution ranges. The beta diversity results, in our favoured simulation, showed an apparent overall stability of pattern, i.e. conforming to the ***stable beta hypothesis*** (Fig. V-3). However, the analyses of Δ beta diversity showed substantial changes given that >95% of the study area has initial values < 3 (Fig. V-4). In the first period, increases of ~1 in the values of beta diversity represent heterogenization across the country, driven by a general shrinking of distribution ranges and some species extinctions. From 2020 to 2050 the trend switches to a general pattern of homogenization (decreases of ~1 in beta diversity values), driven in fact by the same causes. In the final period (2050–2080), a mix of increases and decreases occur, together with an increase in the mean distribution range size and a low number of overall extinctions. The increase of the mean distribution range occurs due to the extinction of micro-endemics and the expansion of the generalists.

Sensitivity analyses

Although the alpha diversity patterns varied widely in our sensitivity analyses, depending entirely of the parameters used, bigger window higher alpha, high presence threshold and low dispersion allowed causes more extinctions (Figs. SI V-1 to V-4 Appendix V-2), the rearrangement of alpha diversity driven by climate change was not mirrored in the patterns of beta diversity (Figs. SI V-4 to SI V-20 Appendix V-2). This means that while rich zones may move greatly, the *transition* or *beta diverse* zones, while they varied depending on the settings, appear to remain coupled with topographic formations. Mountain ranges are environmentally heterogeneous areas that could function as 'biogeographic crossroads" (Hortal and Lobo, 2006) and as natural corridors that would permit metapopulation persistence and allow migration to new habitats under conditions of changing climate. Preserving those areas, perhaps as open management reserves (Sutherland, 2002), could provide the pathway for many species to survive episodes of regional/global climate change, especially if aligned across elevational or latitudinal gradients.

It is noteworthy that not all of the changes in the distribution ranges shown by the modelled patterns were negative: some zones were re-populated when moderate dispersal was allowed. However, the reality of landscape fragmentation may prevent or limit this in practice. Nevertheless, if conservation planners can provide pathways (e.g. corridors, stepping stones) in order to connect natural landscapes, some species may be better able to access their niche space and thus have improved chances of persistence in the landscape.

The number of extinctions by 2080 can vary widely, from 12 to 114 species, depending on the presence–absence threshold and the dispersion allowed. In our favoured simulation the models showed that ~24% of Mexican amphibian (79 of 333) species are at risk of extinction (complete loss of range within country boundaries) by 2080. Nonetheless, we should not forget that first, this is only a simulation exercise using climate envelope modelling with several critical assumptions, for example that species exhibit strong niche conservatism so that there is limited or no adaptation to new conditions outside the fundamental niche (Skelly et al., 2007), and that it is possible to obtain a good proxy of the fundamental niche with just climatic variables. Second, our results are also based on one moderate climate scenario (B2). Should climate change be closer to what is predicted by an A2 scenario, we would expect more dramatic changes in alpha diversity pattern and a higher rate of extinction. For example, Saenz-Romero et al. (2009) found that by 2090, the reduction in precipitation for Mexico under an A scenario (-22%) is projected to be nearly twice that of the B scenario (-12.2%). Third, 30 micro-endemic species were excluded from our analyses because of inadequate data: if models were available for these 30 species, we may anticipate that many of them would also be simulated to join the list of extinctions. Fourth, Mexico has other threats to her biodiversity that must be evaluated, e.g. the current socio-economic pressures resulting from natural resource management, especially in the south of the country. Therefore, climate change coupled with pollution, diseases, deforestation (including associated land use change), and habitat loss, all being threats not considered in the projections performed here, could generate an even worse scenario for amphibian biodiversity, especially if habitat connectivity is allowed to decrease further. The development and implementation of monitoring programmes is essential to evaluate how amphibian communities and species distributions actually respond to environmental changes, especially in zones that are forecast to suffer the most drastic decreases (Figs. V-3 and V-5).

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APPENDIX V-1

Climatic variables for projections of the distribution ranges.

Table SI V-1. Climatic variables from the WorldClim data set (Hijmans et al., 2005).

1. Annual Mean Temperature
2. Mean Diurnal Range (Mean of monthly (max temp – min temp))
3. Isothermality (Mean Diurnal Range / Temperature Annual Range) (* 100)
4. Temperature Seasonality (monthly standard deviation *100)
5. Max Temperature of Warmest Month
6. Min Temperature of Coldest Month
7. Temperature Annual Range (Max Temperature of Warmest Month - Min Temperature of Coldest Month)
8. Mean Temperature of Wettest Quarter
9. Mean Temperature of Driest Quarter
10. Mean Temperature of Warmest Quarter
11. Mean Temperature of Coldest Quarter
12. Annual Precipitation
13. Precipitation of Wettest Month
14. Precipitation of Driest Month
15. Precipitation Seasonality (Coefficient of Variation)
16. Precipitation of Wettest Quarter
17. Precipitation of Driest Quarter
18. Precipitation of Warmest Quarter
19. Precipitation of Coldest Quarter

Downscaling

The future climatic scenarios for Mexico were constructed based on the B2 series of the Second Generation Coupled Global Climate Model (CGCM2) of the Canadian Centre for Climate Modelling and Analysis (CCCma) due to proximity and availability. The B2 series predicts a non-uniform increase in temperatures over the next 100 years, which will be more pronounced in the northern latitudes of Mexico. The model also predicts increasing aridity in northern and western latitudes within Mexico. The detailed process of downscaling variables for future projections followed these steps:

1) We obtained the change factors (CF) (increases or decreases) for monthly precipitation and for temperature (maxima and minima) for around 90 years from the IPCC website (http://www.ipcc-data.org, accessed January 2007). All layers were analysed in the form of raster datasets.

2) With these data we calculated the 30-yr mean for each monthly variable to obtain the CF_{mean} for each period (2020, 2050 and 2080), e.g. for the 2020 period we obtained 36 layers (12 monthly precipitation, 12 monthly temperature maxima and 12 monthly temperature minima). The resolution of those layers was 3.75° x 3.75°.

3) These layers were re-sampled to match the resolution of the climatic data used for the baseline, year 2000 ($\sim 1\ \text{km}^2$).

4) With a GIS system we generated future precipitation and temperature (maxima and minima) layers, by simply adding the corresponding mean climatic CF to each current fine resolution layer previously constructed for Mexico (Tellez, 2004) (eq. 1).

$$\text{Variable } A_{Tx} = \text{variable } A_{T0} + CF_{mean} \text{ Variable } A \qquad \text{(eq. 1)}$$

Where variable A_{Tx} is the climatic layer in the future periods of time, variable A_{T0} is the layer in the year 2000 and the CF_{mean} is the value obtained in step 2.

5) With each set of 36 layers obtained from step 4 we generated three new sets of 19 climatic variables each, for the periods 2020, 2050 and 2080, using Hijmans' script (2006). Those new sets contain the same climate variables as for the baseline (Table SI V-1).

Museums and projects that contributed data

Museums and projects that contributed data, in alphabetical order were: American Museum of Natural History; Arizona State University; Auburn University Museum; Brigham Young University; British Museum; California Academy of Sciences; Cambridge Museum; Carnegie Museum; Clemson University; Colección Nacional de Anfibios y Reptiles, IB-UNAM; Comisión Nacional para el Conocimiento y uso de la Biodiversidad (CONABIO) projects: A014, A027, B002, B043, B099, B144, G015, H103, H104, H127, H245, H250, H330, J002, J112, K038, L003, L103, L283, M099, P028, P060, P132, Q049, R045, R067, R232;Cornell University; Field Museum of Natural History, Chicago; Florida Museum of Natural History; Instituto de Historia Natural, Chiapas; James Ford Bell Museum of Natural History, University of Minnesota; Kansas University, Collection of Herpetology; Los Angeles County Museum; Louisiana State University Museum of Zoology; Harvard University Museum of Comparative Zoology; Milwaukee Public Museum of Vertebrate Zoology; Museo Civico Di Storia Naturale Di Genova 'Giacomo Doria'; Museo de Zoología "Alfonso L. Herrera", UNAM; University of California at Berkeley Museum of Vertebrate Zoology; National Museum of Natural History, Smithsonian Institution (Natural History Building), Washington; Northeast Louisiana University Museum of Zoology; New Brunswick Museum; Royal Ontario Museum; Southern Illinois University (Carbondale) University Museum; Strecker Museum Baylor University; Saint Mary's University; San Diego Natural History Museum; Soul Ross

State University,; Texas Cooperative Wildlife Collection; Texas A & M University, Collection of Herpetology; Texas Natural History Collection, Texas Memorial Museum; University of Arizona Museum of Natural History; University of Colorado Museum; University of Michigan Museum of Zoology; University of Illinois Museum of Natural History; University of Oregon, Museum of Zoology; University of Oklahoma Stovall Museum of Zoology; University of Texas at Arlington; University of Texas at El Paso; Yale University Peabody Museum; and Zoologische Staatssammlung Collection, Munich.

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APPENDIX V-2

Sensitivity Analyses

Uncertainty can be defined as how the variation in the output of a mathematical model can be apportioned, qualitatively or quantitatively, to different sources of variation in the input of the model (Wikipedia, accessed May 2011).

Since the start of computer-based modelling of species distributional ranges in the 1990s concerns have been raised as to the reliability of these methods, both in estimating present and future distributions (e.g. Pearson and Dawson, 2003; Whittaker et al., 2005; Pearson et al., 2006, 2007; Botkin et al., 2007; Hirzel and Lay, 2008; Lozier et al., 2009; Soberón and Nakamura, 2009). There have been several articles discussing these sources of uncertainty in modelling the current distribution ranges. Key issues include the following:

1) **Spatial and temporal bias in data collection** (e.g. locality records generally near to roads (Phillips et al. 2009; Pineda and Lobo, 2009) and a general lack of information on the role of ecological interactions in shaping range limits (Hirzel and Lay, 2008).
2) Resolution and accuracy of "current" environmental **information for modelling** (e.g. number of years of climate data from field stations to generate the average climate, type of interpolation, etc.).
3) **Algorithm used** to model the distribution range sizes.
4) **Threshold of presence** (i.e. 'objective' vs. 'subjective', trimming, etc.; Liu et al., 2005).

Other sources of uncertainty can be added at the moment of projecting the niche model to generate a distribution range in the future:

5) **Variation in climatic projections and scenarios** (i.e. Hadley vs. CSIRO Vs CCCma).

6) **Downscaling** of the climate models (i.e. straightforward methods vs. interpolations).

7) **Dispersion "allowed"** for each species (i.e. total, zero, moderate, etc.).

In this particular article there is another source of variation. Here, our aim is to analyze beta diversity pattern under a climate change scenario using R.H. Whittaker's formula (1960). In order to do so, we have to define the size of a landscape, which we did by imposing a window of a particular standardized area, the size of which can be varied in different runs of the analysis. Hence, an additional factor is:

8) **Window size** of analysis.

To evaluate all these sources of uncertainty would be unmanageable, so we fix some of the aspects and vary others. Because our main interest is in the patterns of diversity, and specifically of beta diversity, and as other aspects have been evaluated elsewhere (e.g. variation in climatic projections and algorithm used), we varied the presence threshold, the dispersion allowed and window size.

To evaluate these sources of variation we assigned them different parameters:

A) For the **Threshold of presence** we choose four different thresholds (following previous work by Liu et al*.,* 2005):

a. The 10th percentile training presence of the logistic threshold of the distribution model (following Urbina-Cardona and Loyola, 2008).

b. The lowest presence threshold. The second approach consists of identifying pixels predicted as being at least as suitable as those where a species' presence has been recorded (Pearson *et al.*, 2007). For the resulting patterns in alpha diversity see figures SI V-1 and SI V-2, respectively.

c. We used the 50% of the probability of presence of the output model, the *heads or tails* threshold.

d. Finally we used 70% of the probability of presence, following the suggestion of Pineda and Lobo (2009). For the resulting patterns in alpha diversity see figures SI V-3 for 50% and SI V-4 for 70%.

B) Dispersion allowed:

a. Total dispersion.

b. Zero.

c. Moderate (1 km per year).

d. Moderate (1 km per year), commencing with trimmed models at time zero (the trimming process involved expert scrutiny of the modelled distribution of each species, with areas considered to be unrealistic trimmed out before further analysis).

C) Window size:

a. 3 x 3 pixel window (9 km^2)

b. 5 x 5 pixel window (25 km^2)

c. 10 x 10 pixel window (100 km^2)

d. 15 x 15 pixel window (225 km^2)

e. 20 x 20 pixel window (400 km^2)

The diversity patterns that resulted from the variation of the different sources of uncertainty are presented here. A qualitative appreciation of the similarities and difference can be gained from scrutiny of figures SI V-5 to SI V-20. In figures SI V-5 to SI V-8 we show the differences resulting from changing dispersion and window sizes, fixing the threshold to the 10th percentile training presence of the logistic threshold of the distribution model. In figures SI V-9 to SI V-12 we show the differences resulting from changing dispersion and window sizes, fixing the threshold to the lowest presence threshold. Figures SI V-13 to SI V-16 show the same but based on the 50% of presence probability threshold. Figures SI V-17 to SI V-20 show the same but based on the 70% of presence probability threshold.

Figure SI V-1. Alpha diversity patterns of Mexican amphibians with different dispersion parameters. Threshold used: **10th percentile training presence of the logistic threshold of the distribution model.** Two versions of the maps are presented, (a) using the same scaling of values in each map and (b) stretched colours using two standard deviations.

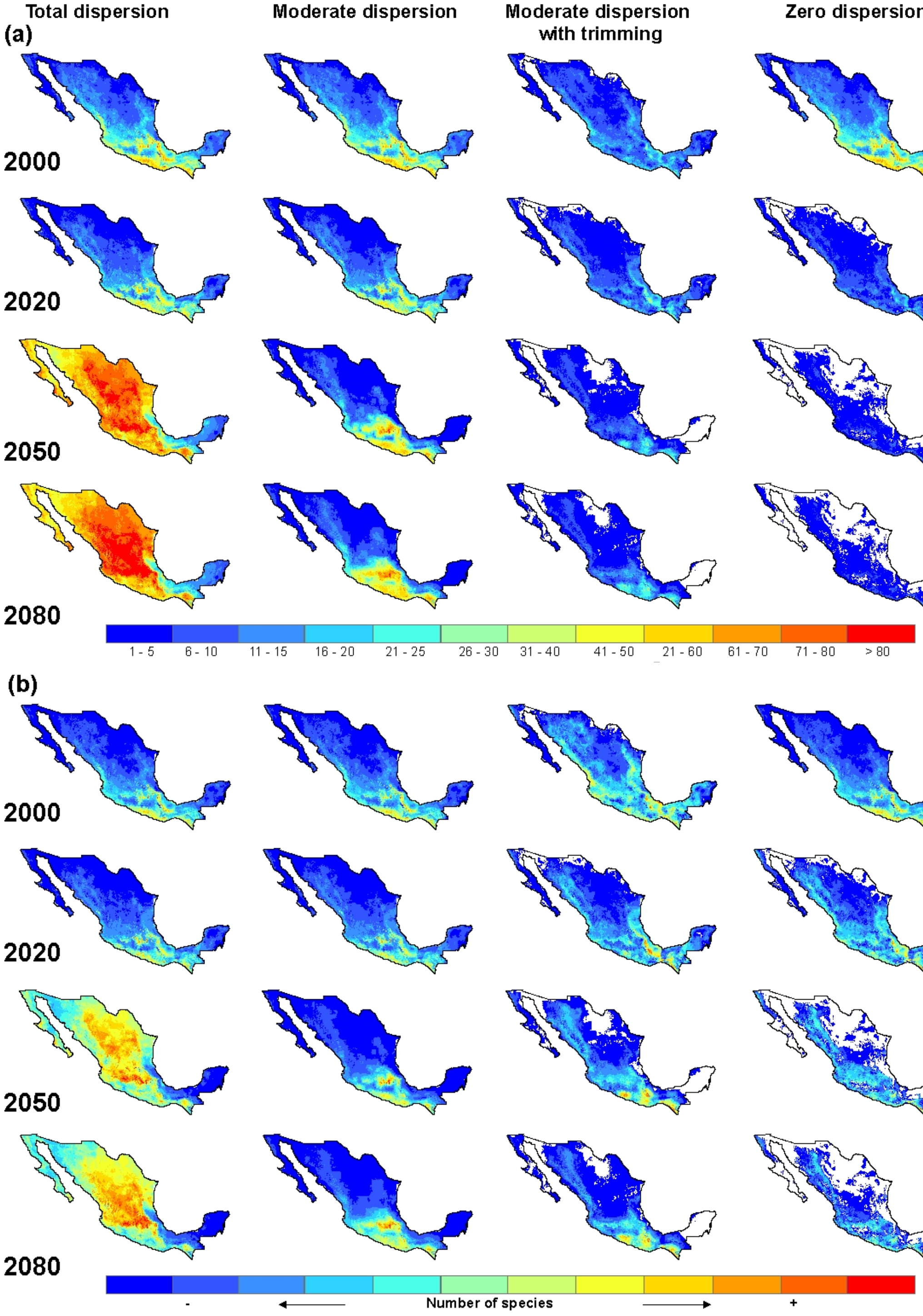


Figure SI V-2. Alpha diversity patterns of Mexican amphibians with different dispersion parameters. Threshold used: **lowest presence threshold.** Two versions of the maps are presented, (a) using the same scaling of values in each map and (b) stretched colours using two standard deviations.

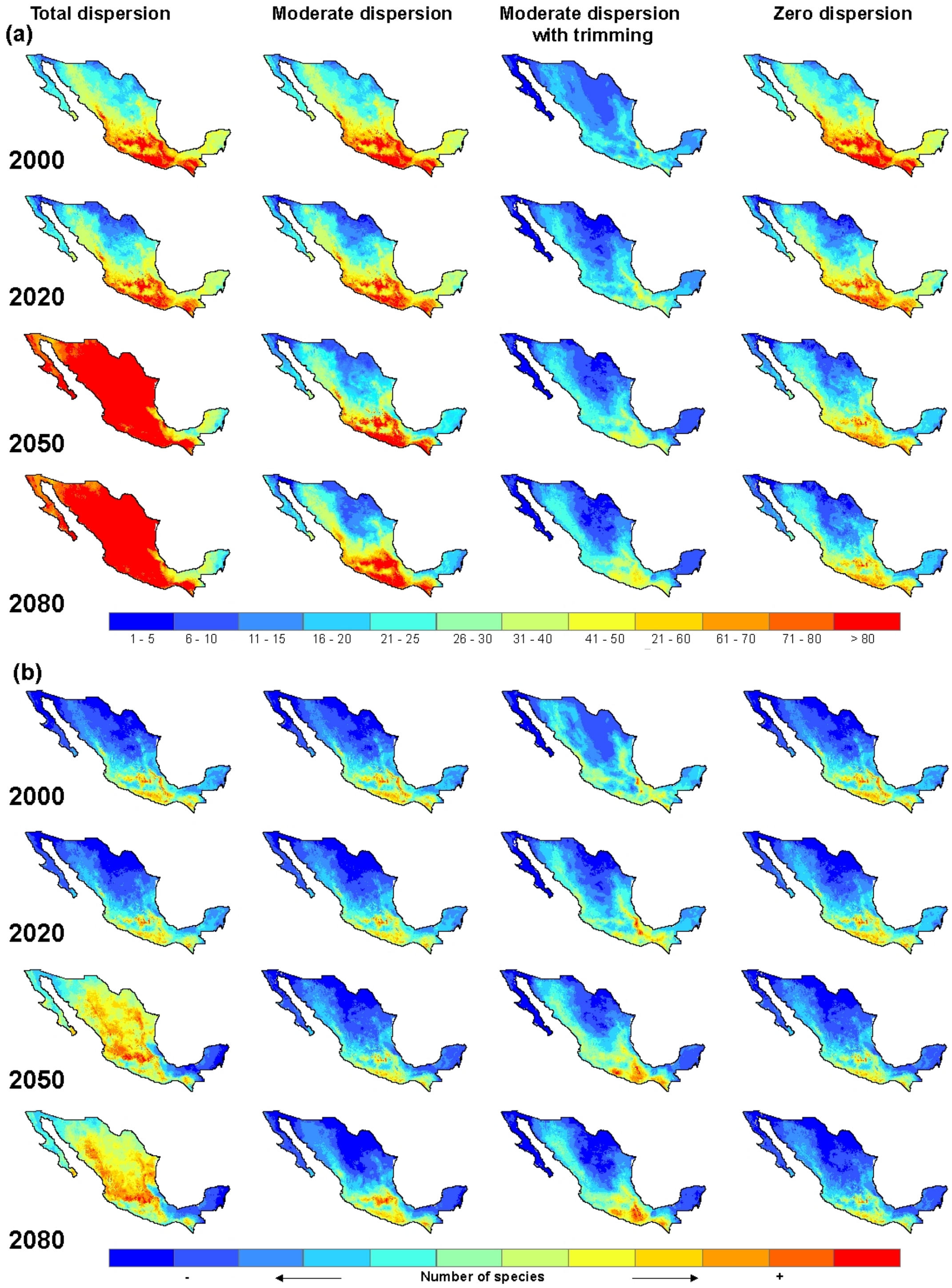


Figure SI V-3. Alpha diversity patterns of Mexican amphibians with different dispersion parameters. Threshold used: **50% probability of presence threshold.** Two versions of the maps are presented, (a) using the same scaling of values in each map and (b) stretched colours using two standard deviations.

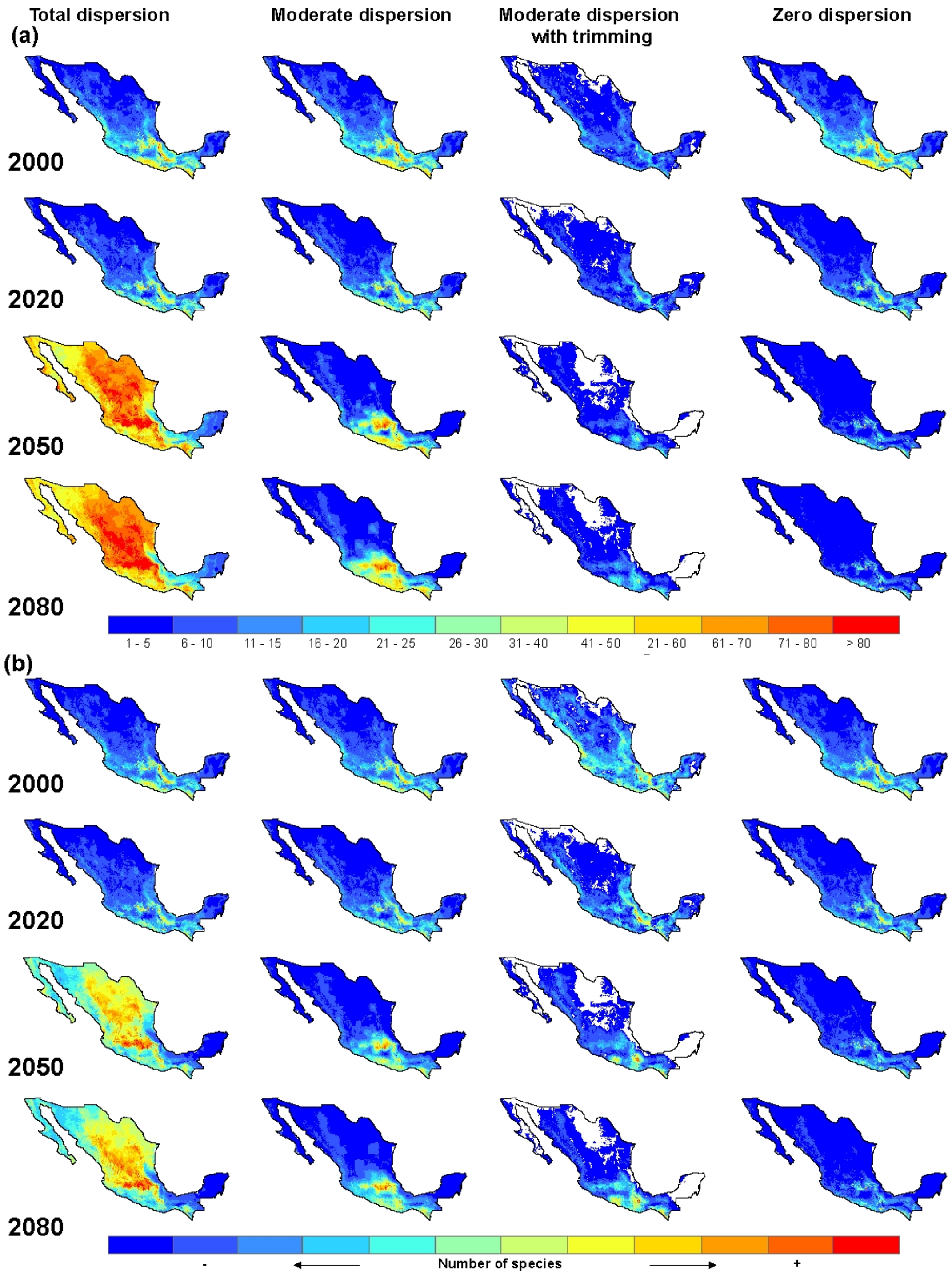


Figure SI V-4. Alpha diversity patterns of Mexican amphibians with different dispersion parameters. Threshold used: **70% probability of presence threshold.** Two versions of the maps are presented, (a) using the same scaling of values in each map and (b) stretched colours using two standard deviations.

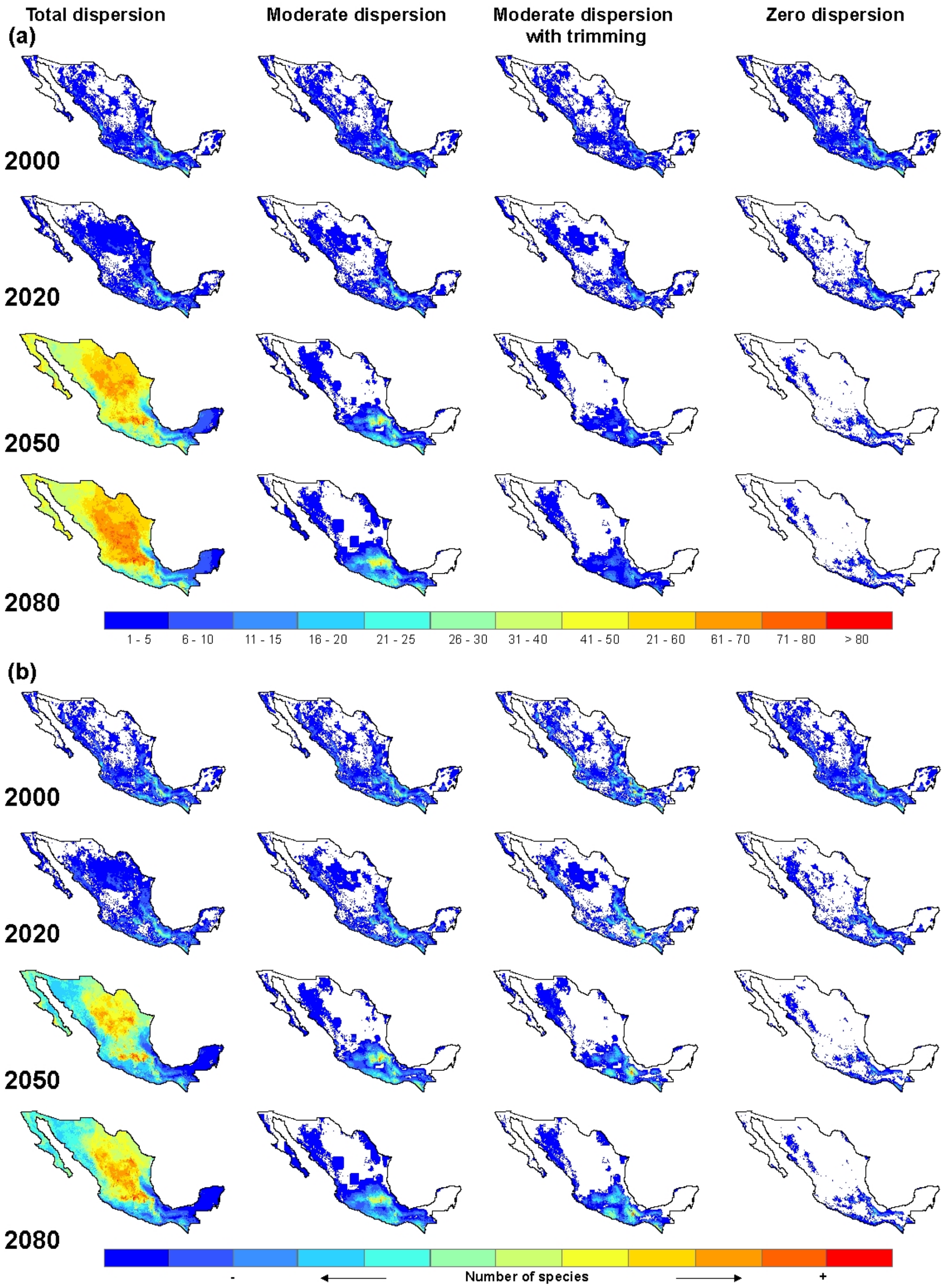


Figure SI V-5. Beta diversity patterns of Mexican amphibians using the 10th percentile training presence of the logistic threshold of the distribution model with different window sizes and <u>total dispersion</u> parameter. Two versions of the maps are presented, (a) using the same scaling of values in each map and (b) stretched colours using two standard deviations.

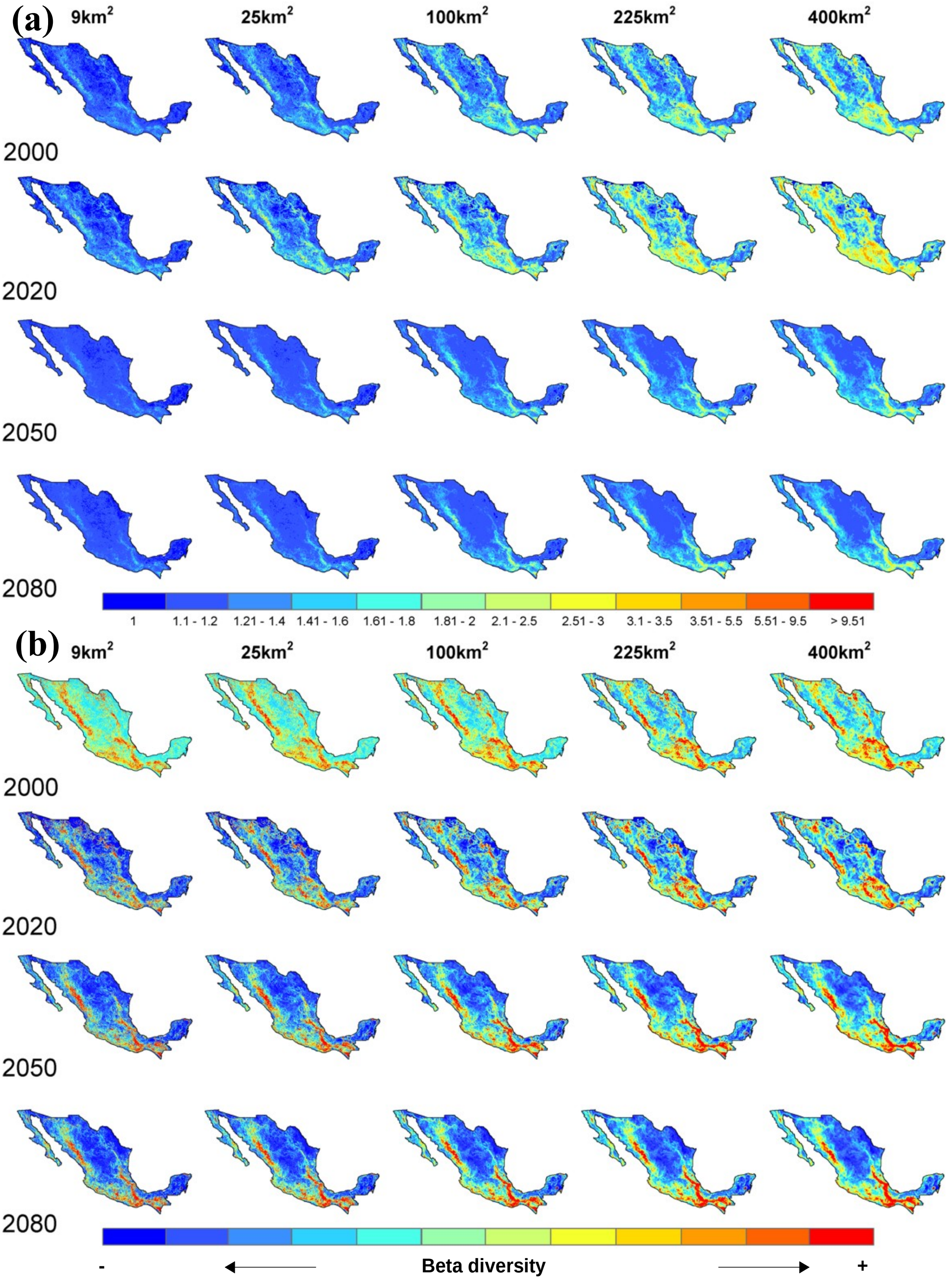


Figure SI V-6. Beta diversity patterns of Mexican amphibians using the 10th percentile training presence of the logistic threshold of the distribution model with different window sizes and zero dispersion parameter. Two versions of the maps are presented, (a) using the same scaling of values in each map and (b) stretched colours using two standard deviations.

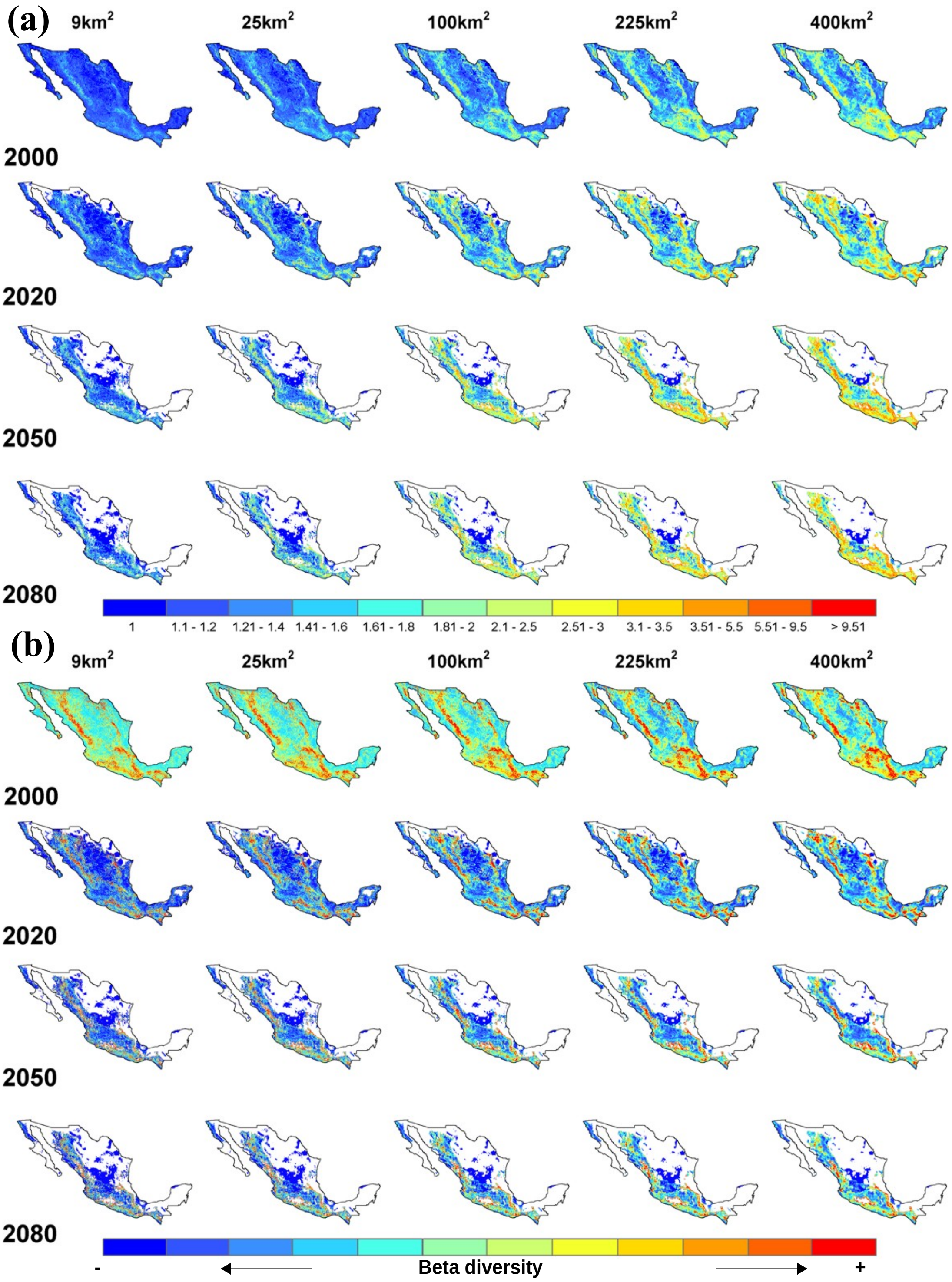


Figure SI V-7. Beta diversity patterns of Mexican amphibians using the 10th percentile training presence of the logistic threshold of the distribution model with different window sizes and moderate dispersion parameter. Two versions of the maps are presented, (a) using the same scaling of values in each map and (b) stretched colours using two standard deviations.

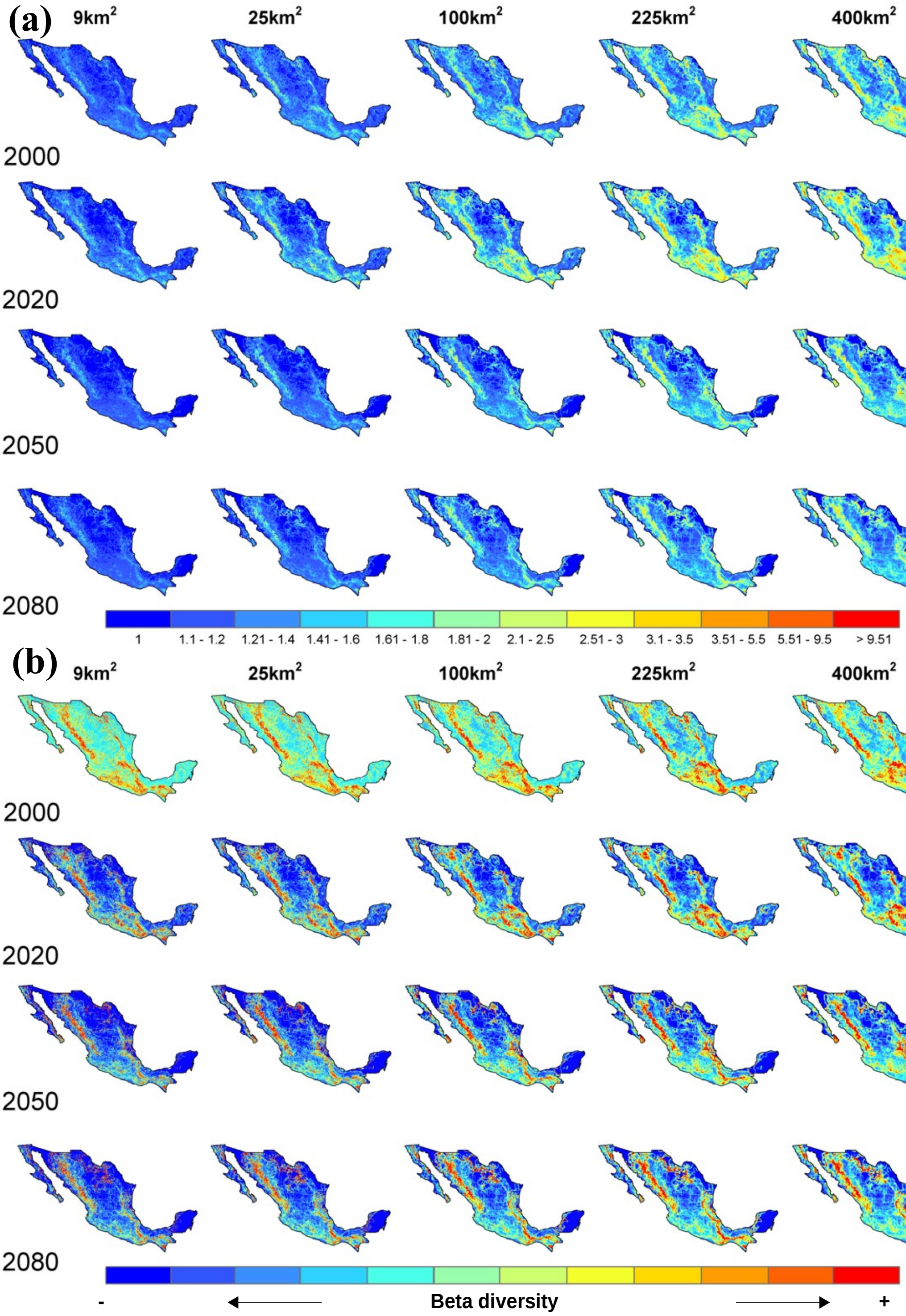


Figure SI V-8. Beta diversity patterns of Mexican amphibians using the 10th percentile training presence of the logistic threshold of the distribution model with different window sizes and <u>moderate dispersion with trimming</u> parameter. Two versions of the maps are presented, (a) using the same scaling of values in each map and (b) stretched colours using two standard deviations.

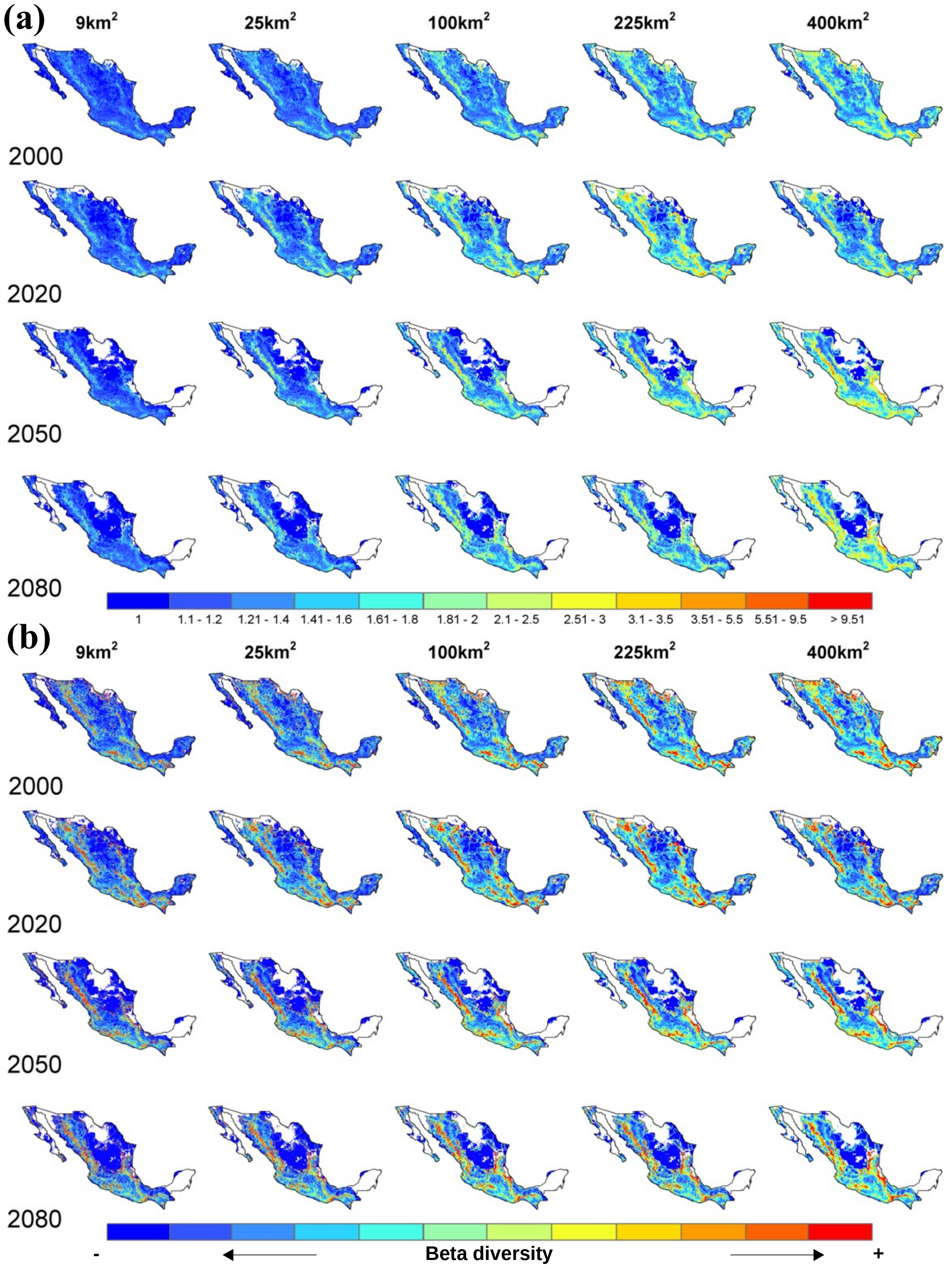


Figure SI V-9. Beta diversity patterns of Mexican amphibians using the lowest presence threshold with different window sizes and <u>total dispersion</u> parameter. Two versions of the maps are presented, (a) using the same scaling of values in each map and (b) stretched colours using two standard deviations.

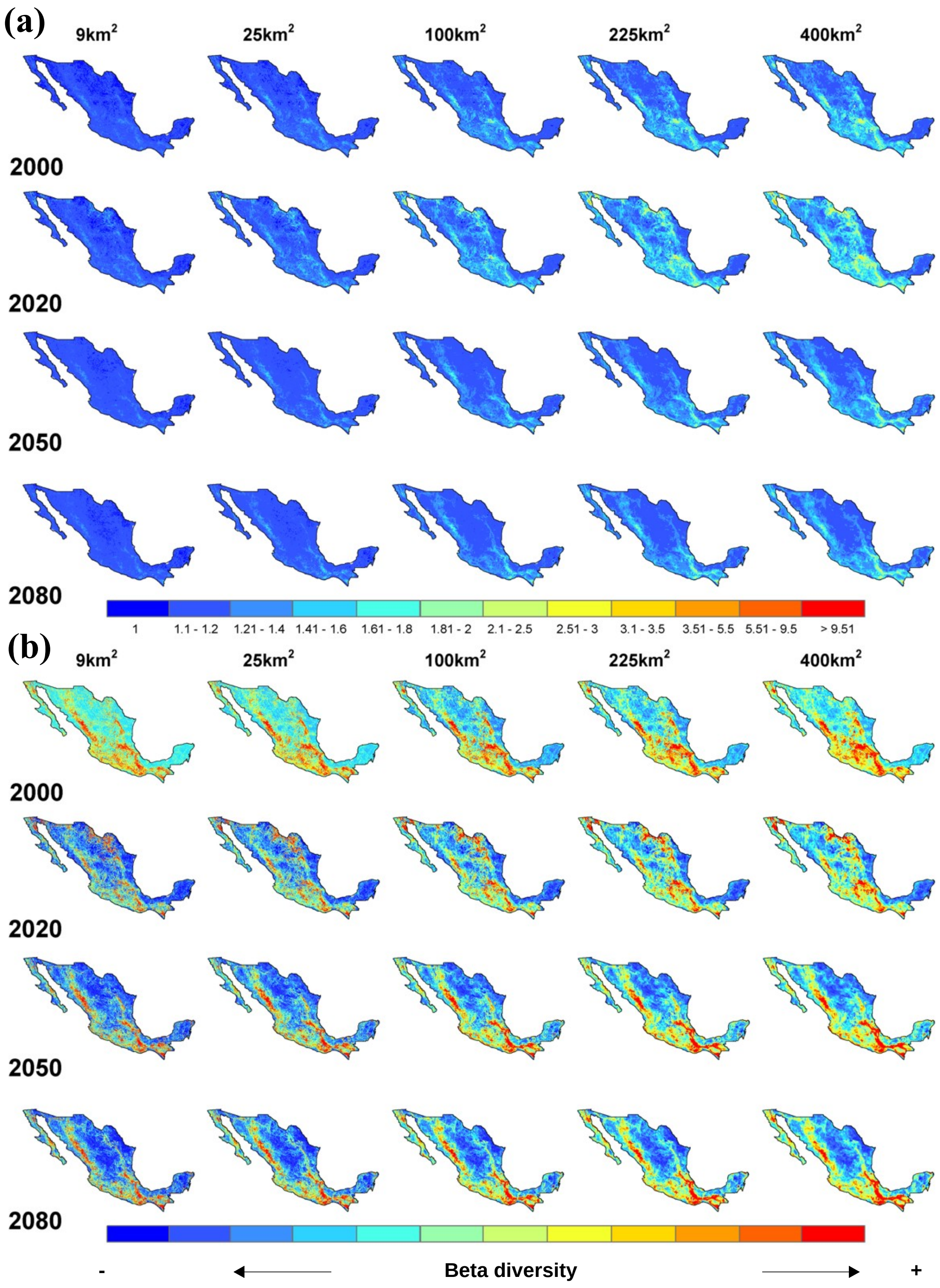


Figure SI V-10. Beta diversity patterns of Mexican amphibians using the lowest presence threshold with different window sizes and zero dispersion parameter. Two versions of the maps are presented, (a) using the same scaling of values in each map and (b) stretched colours using two standard deviations.

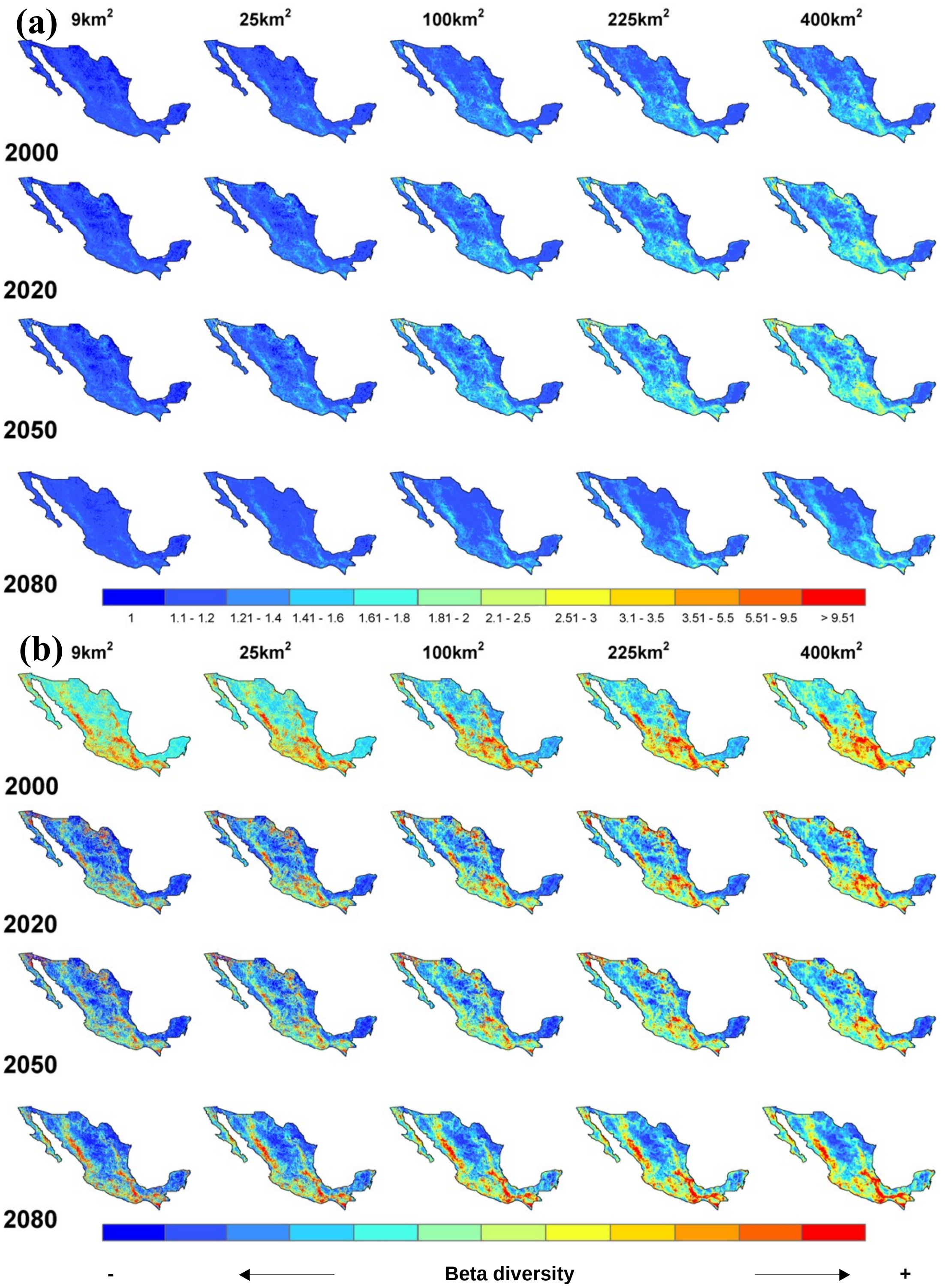


Figure SI V-11. Beta diversity patterns of Mexican amphibians using the lowest presence threshold with different window sizes and moderate dispersion parameter. Two versions of the maps are presented, (a) using the same scaling of values in each map and (b) stretched colours using two standard deviations.

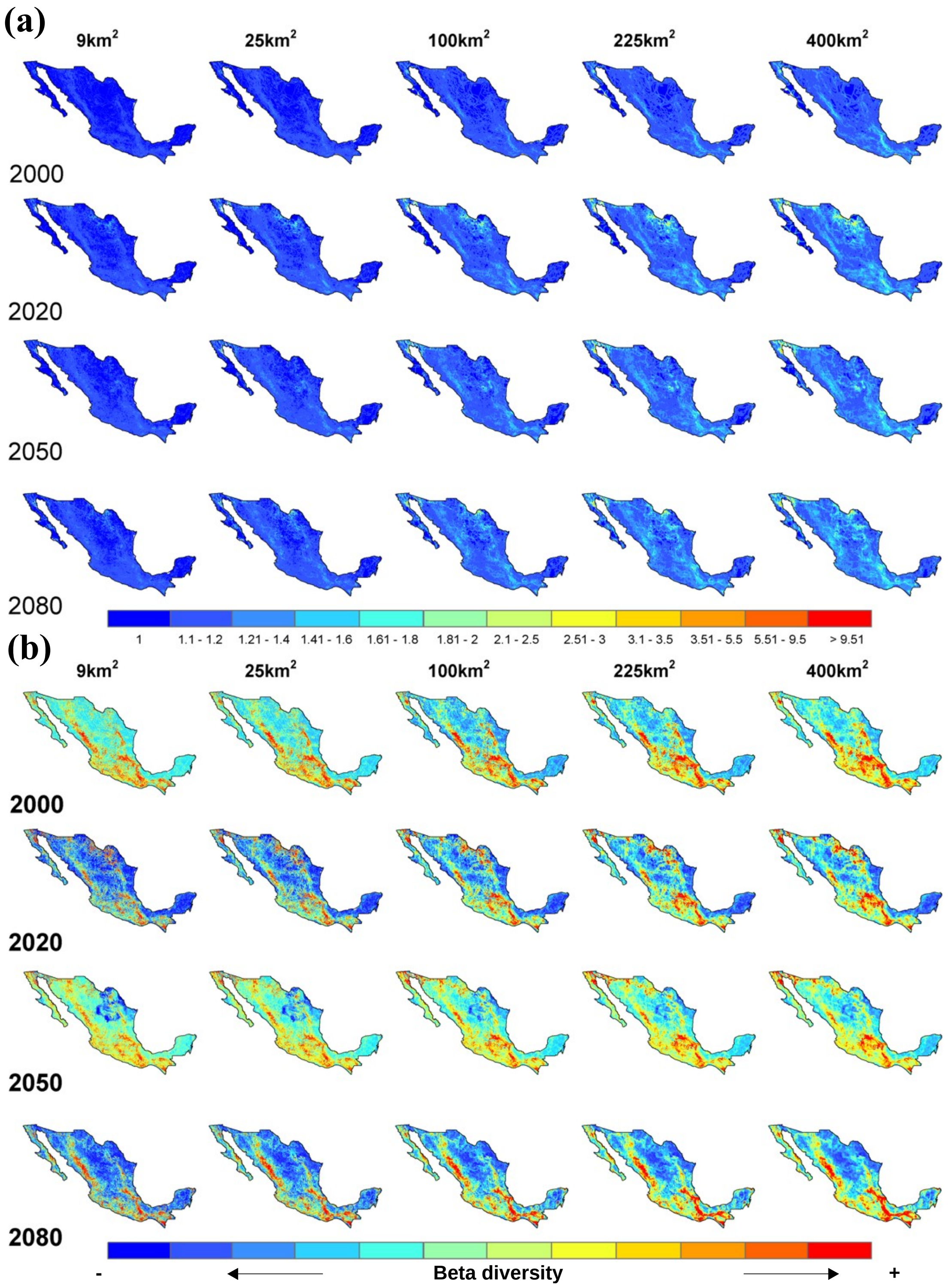


Figure SI V-12. Beta diversity patterns of Mexican amphibians using the lowest presence threshold with different window sizes and moderate dispersion with trimming parameter. Two versions of the maps are presented, (a) using the same scaling of values in each map and (b) stretched colours using two standard deviations.

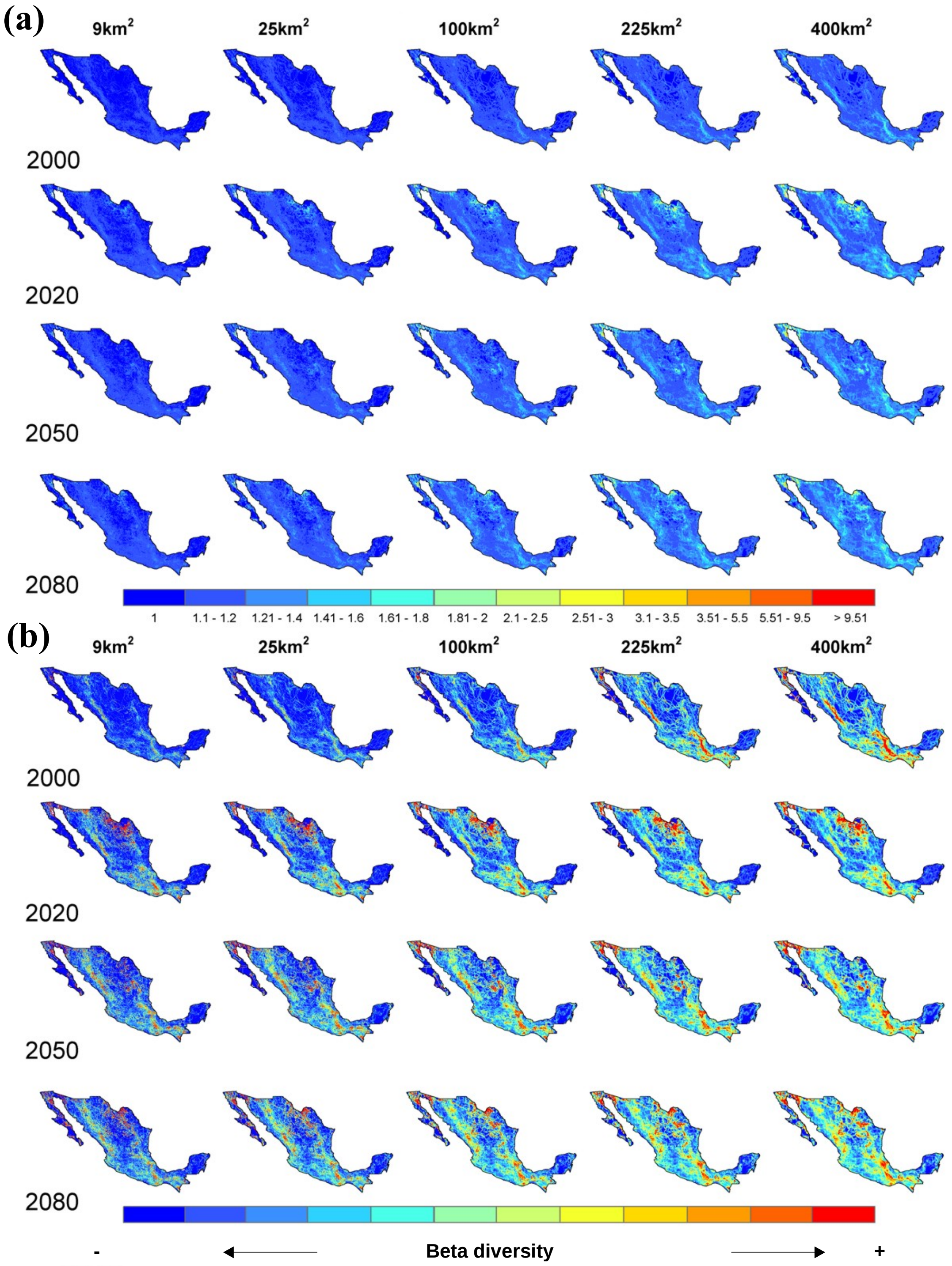


Figure SI V-13. Beta diversity patterns of Mexican amphibians using the 50% of presence probability threshold with different window sizes and <u>total dispersion</u> parameter. Two versions of the maps are presented, (a) using the same scaling of values in each map and (b) stretched colours using two standard deviations.

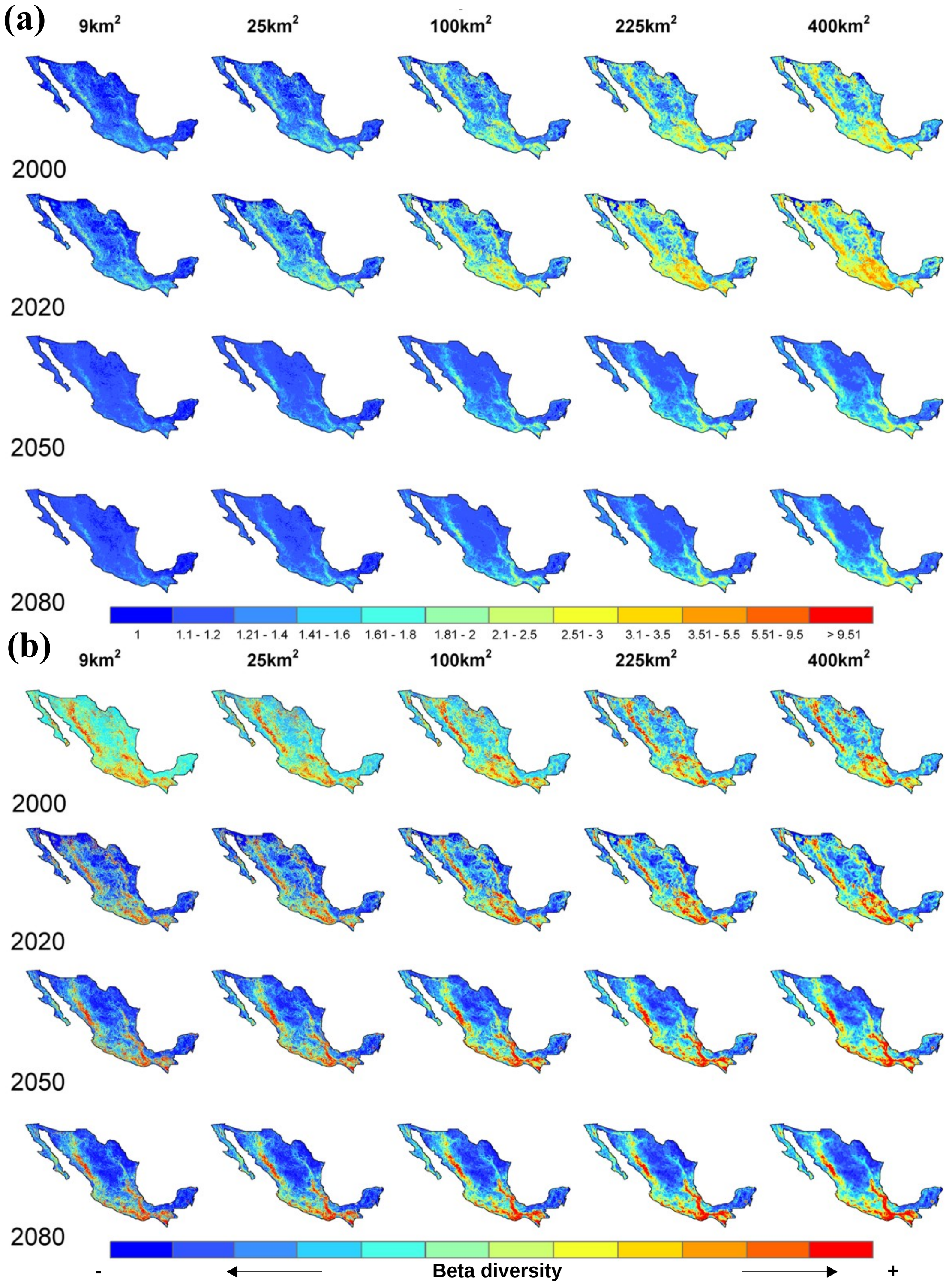


Figure SI V-14. Beta diversity patterns of Mexican amphibians using the 50% of presence probability threshold with different window sizes and zero dispersion parameter. Two versions of the maps are presented, (a) using the same scaling of values in each map and (b) stretched colours using two standard deviations.

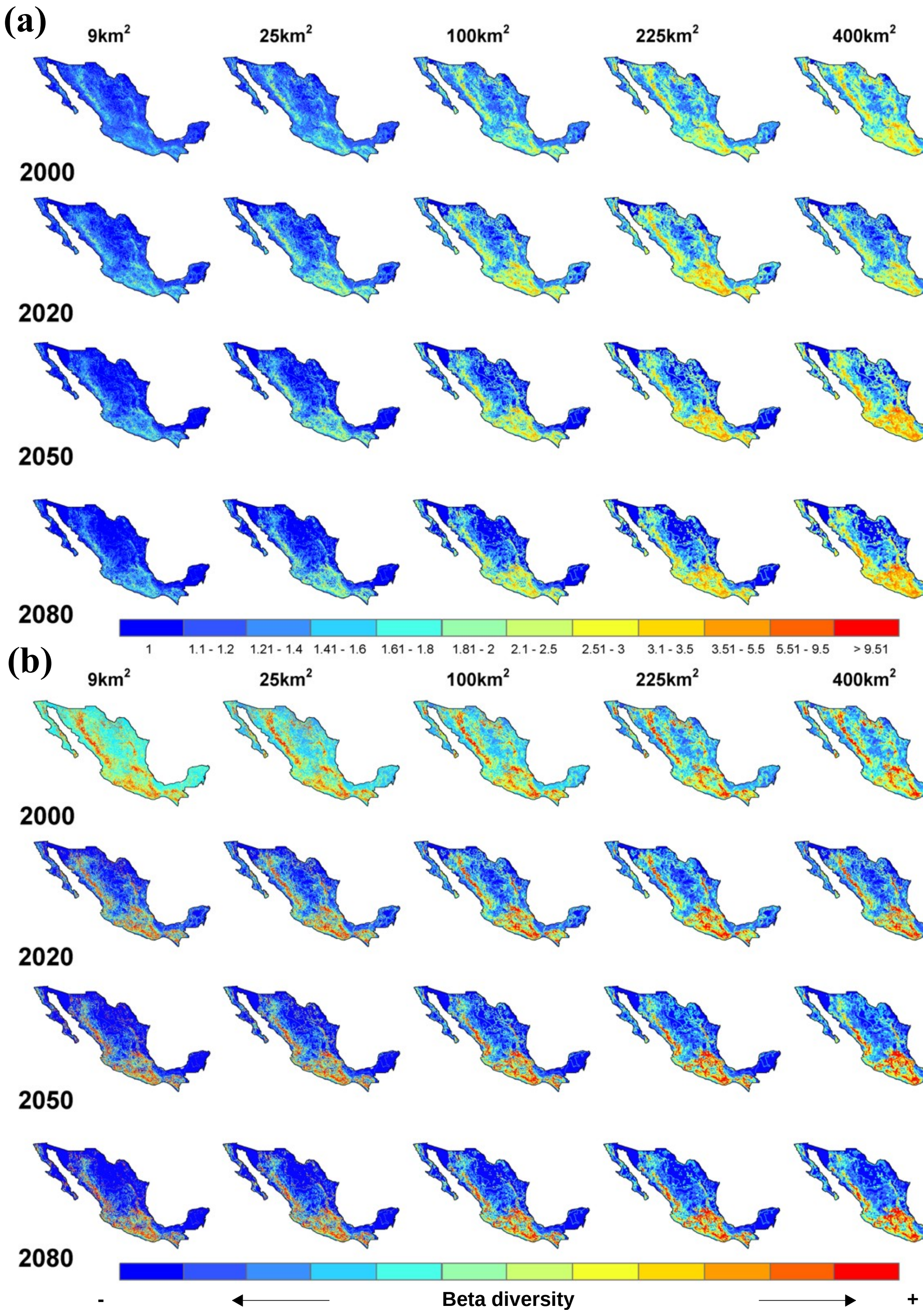


Figure SI V-15. Beta diversity patterns of Mexican amphibians using the 50% of presence probability threshold with different window sizes and moderate dispersion parameter. Two versions of the maps are presented, (a) using the same scaling of values in each map and (b) stretched colours using two standard deviations.

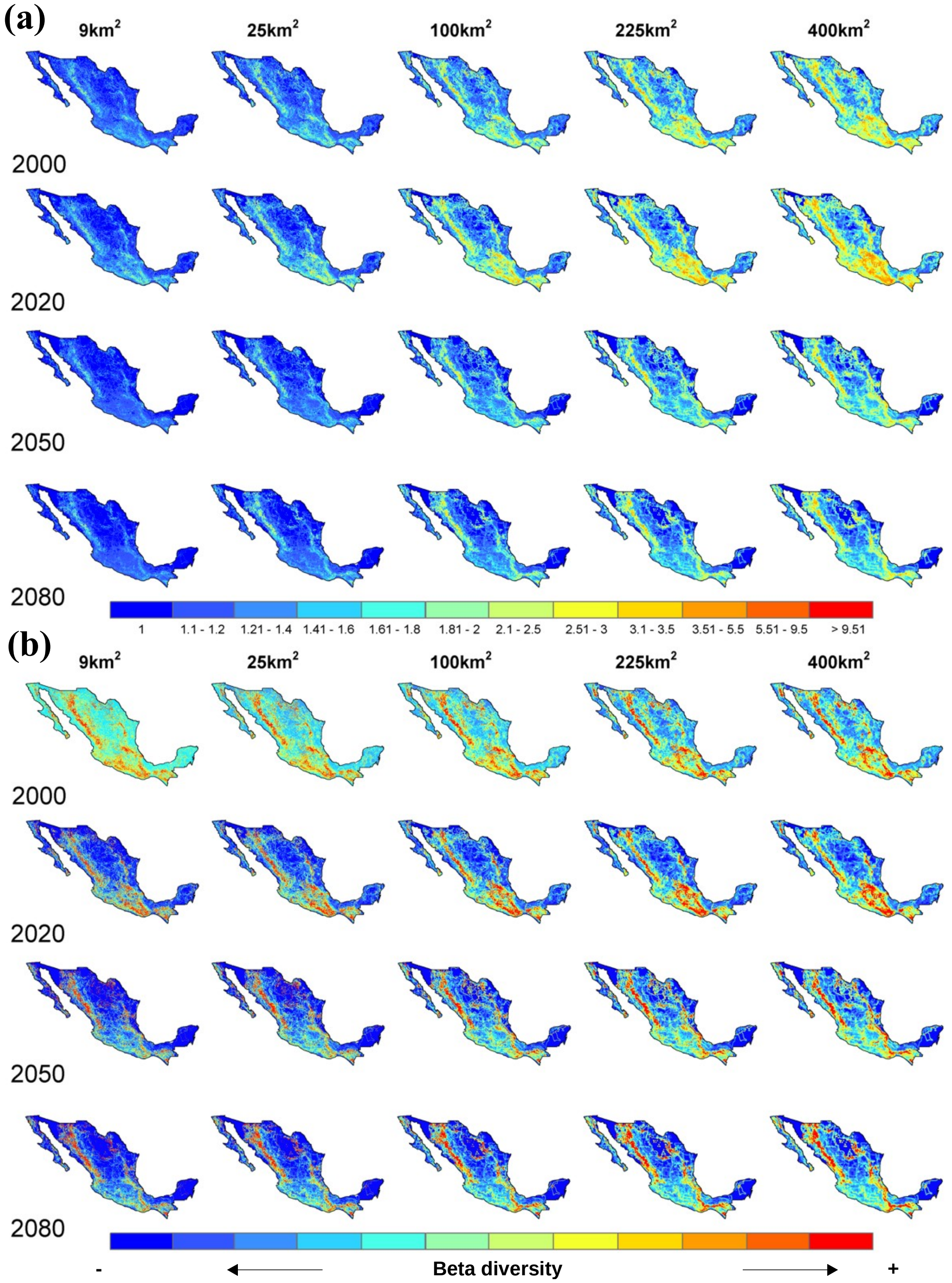


Figure SI V-16. Beta diversity patterns of Mexican amphibians using the 50% of presence probability threshold with different window sizes and <u>moderate dispersion with trimming</u> parameter. Two versions of the maps are presented, (a) using the same scaling of values in each map and (b) stretched colours using two standard deviations.

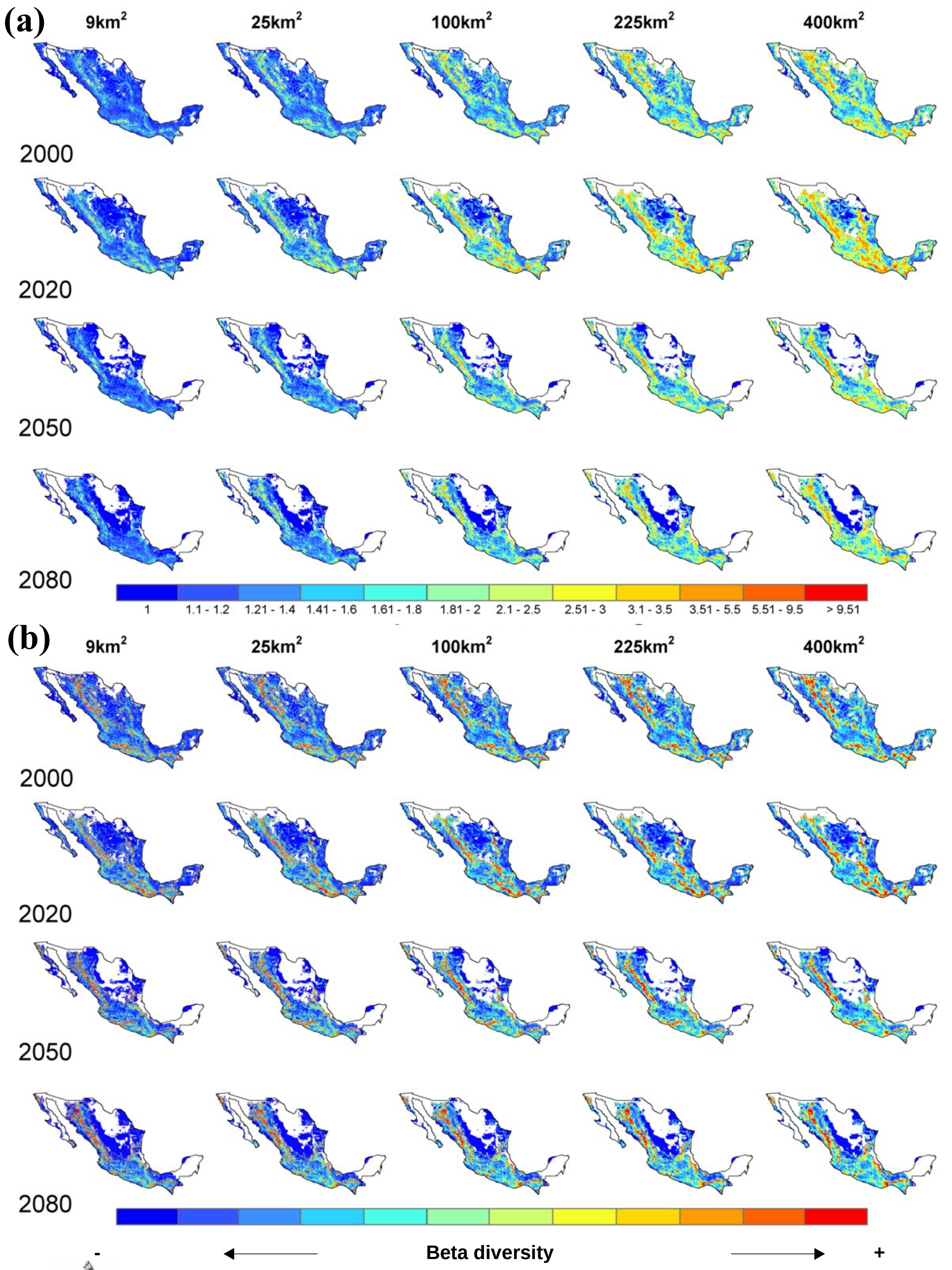


Figure SI V-17. Beta diversity patterns of Mexican amphibians using the 70% of presence probability threshold with different window sizes and total dispersion parameter. Two versions of the maps are presented, (a) using the same scaling of values in each map and (b) stretched colours using two standard deviations.

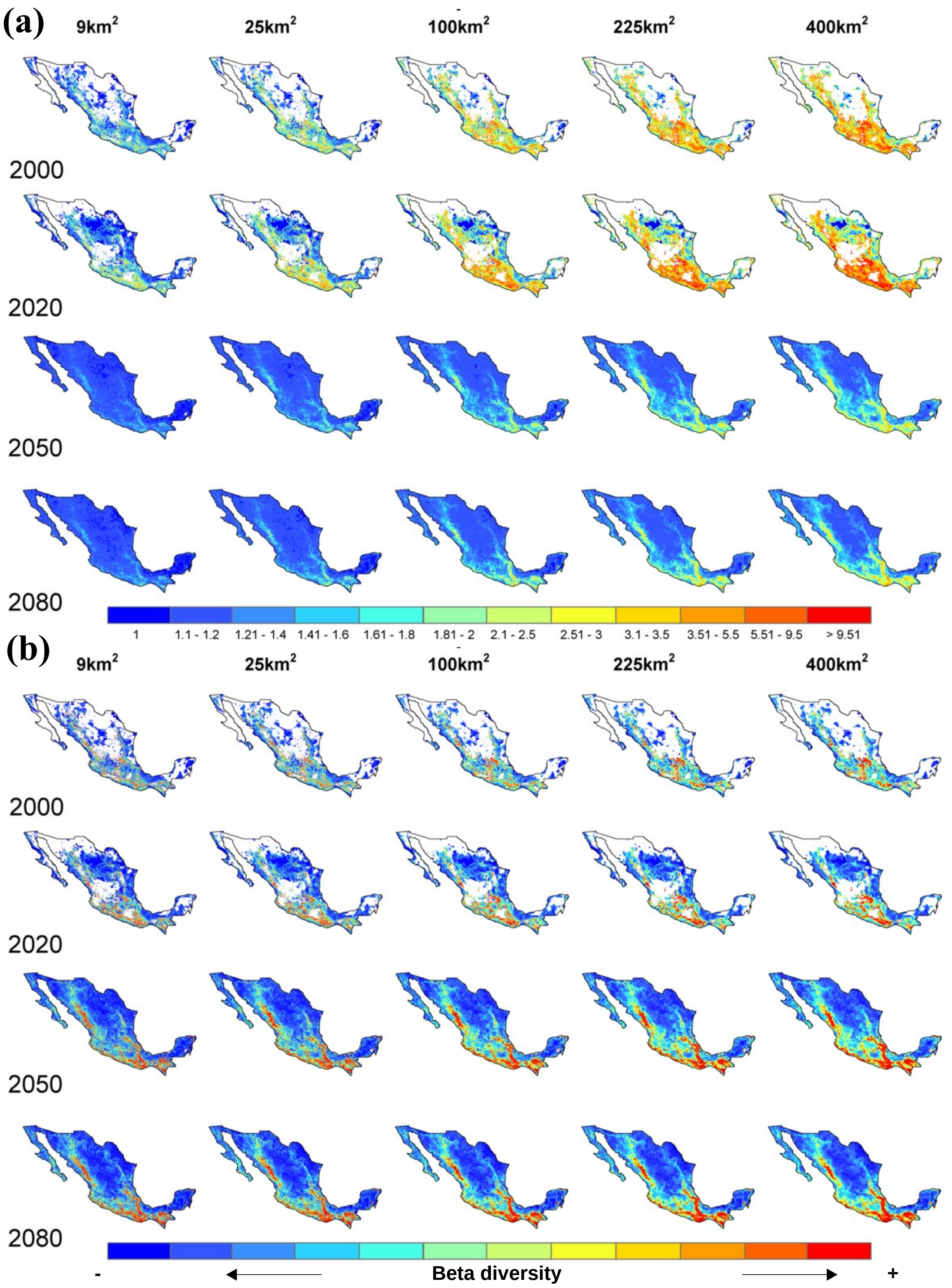


Figure SI V-18. Beta diversity patterns of Mexican amphibians using the 70% of presence probability threshold with different window sizes and <u>zero dispersion</u> parameter. Two versions of the maps are presented, (a) using the same scaling of values in each map and (b) stretched colours using two standard deviations.

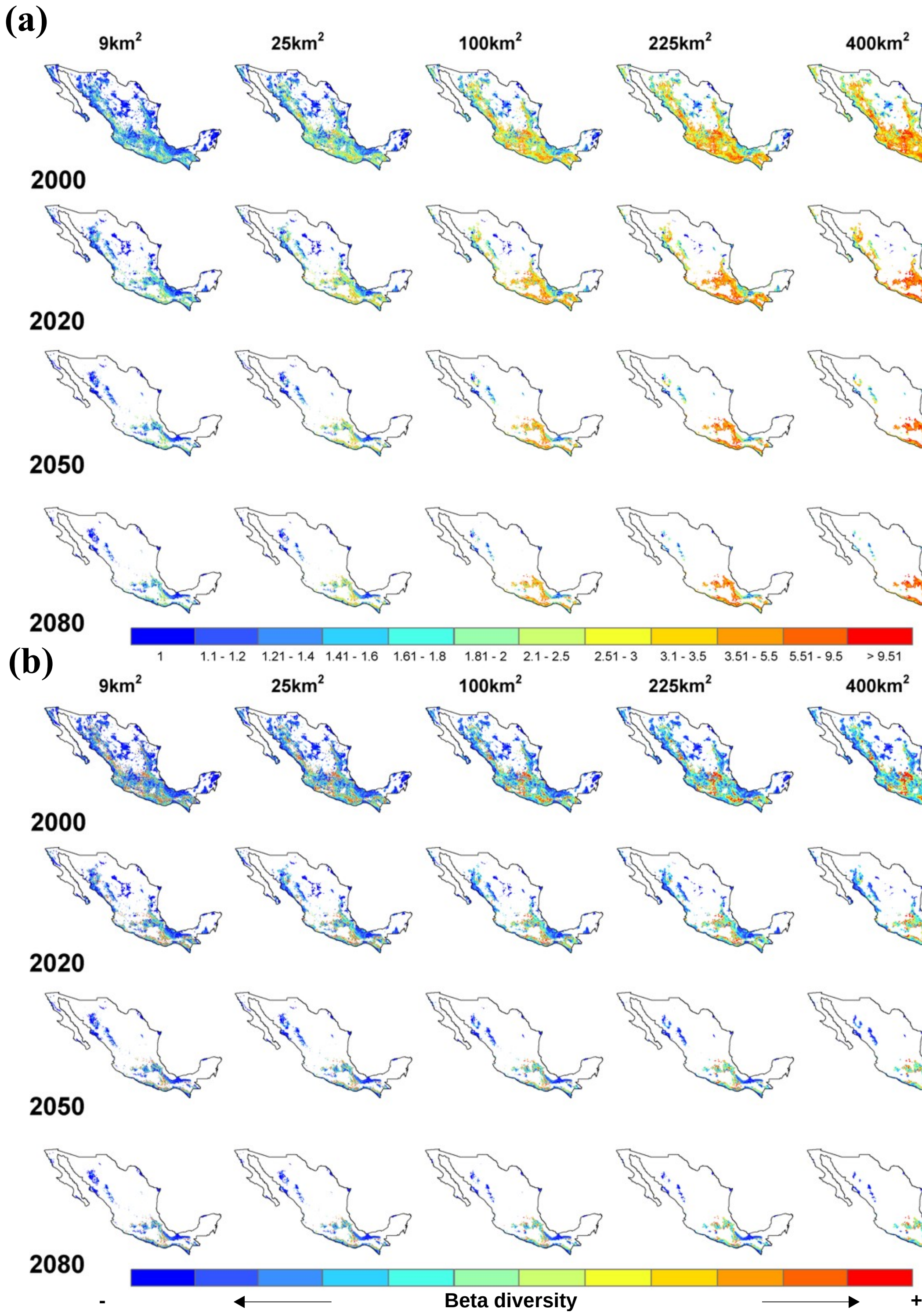


Figure SI V-19. Beta diversity patterns of Mexican amphibians using the 70% of presence probability threshold with different window sizes and <u>moderate dispersion</u> parameter. Two versions of the maps are presented, (a) using the same scaling of values in each map and (b) stretched colours using two standard deviations.

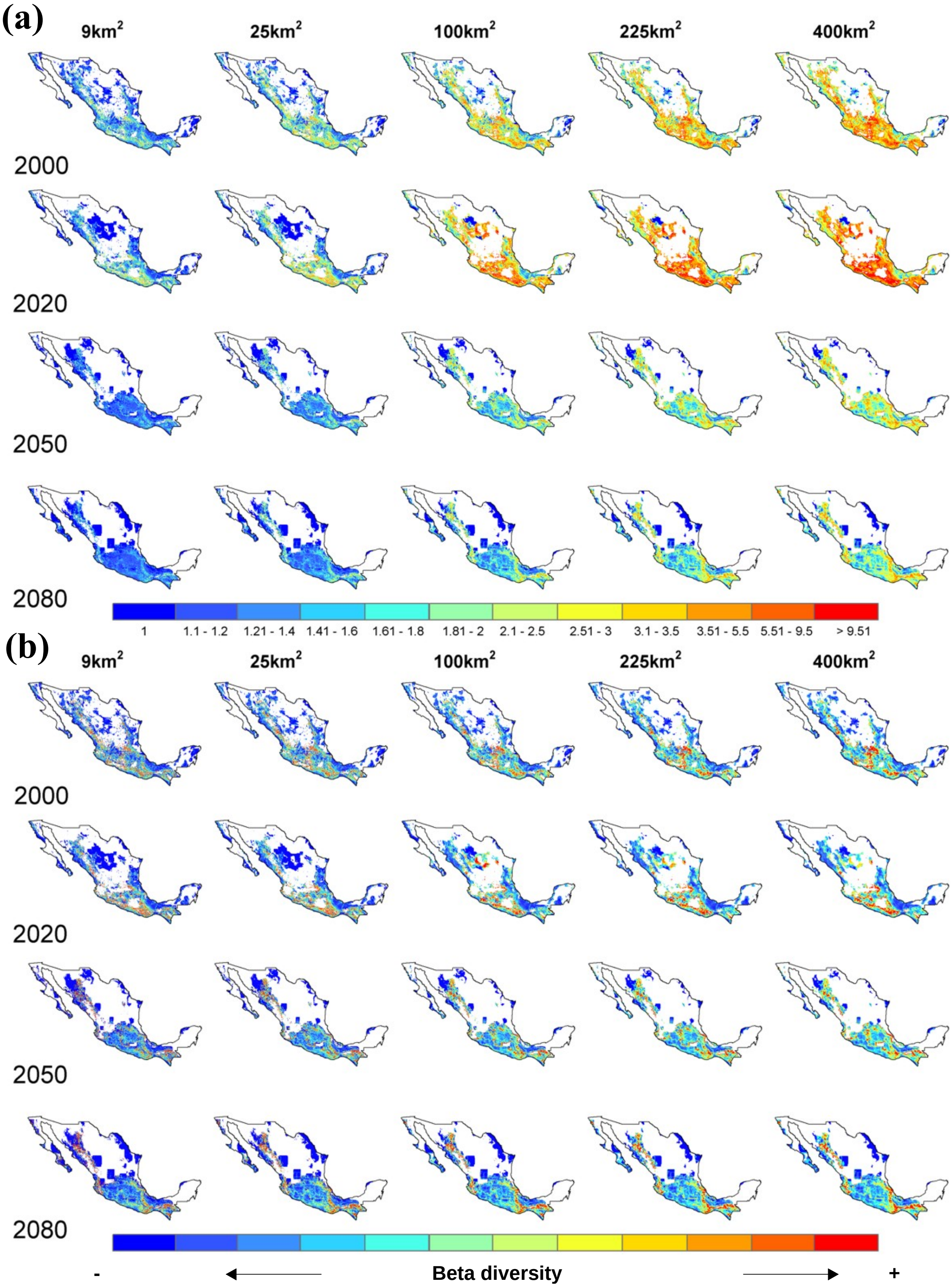
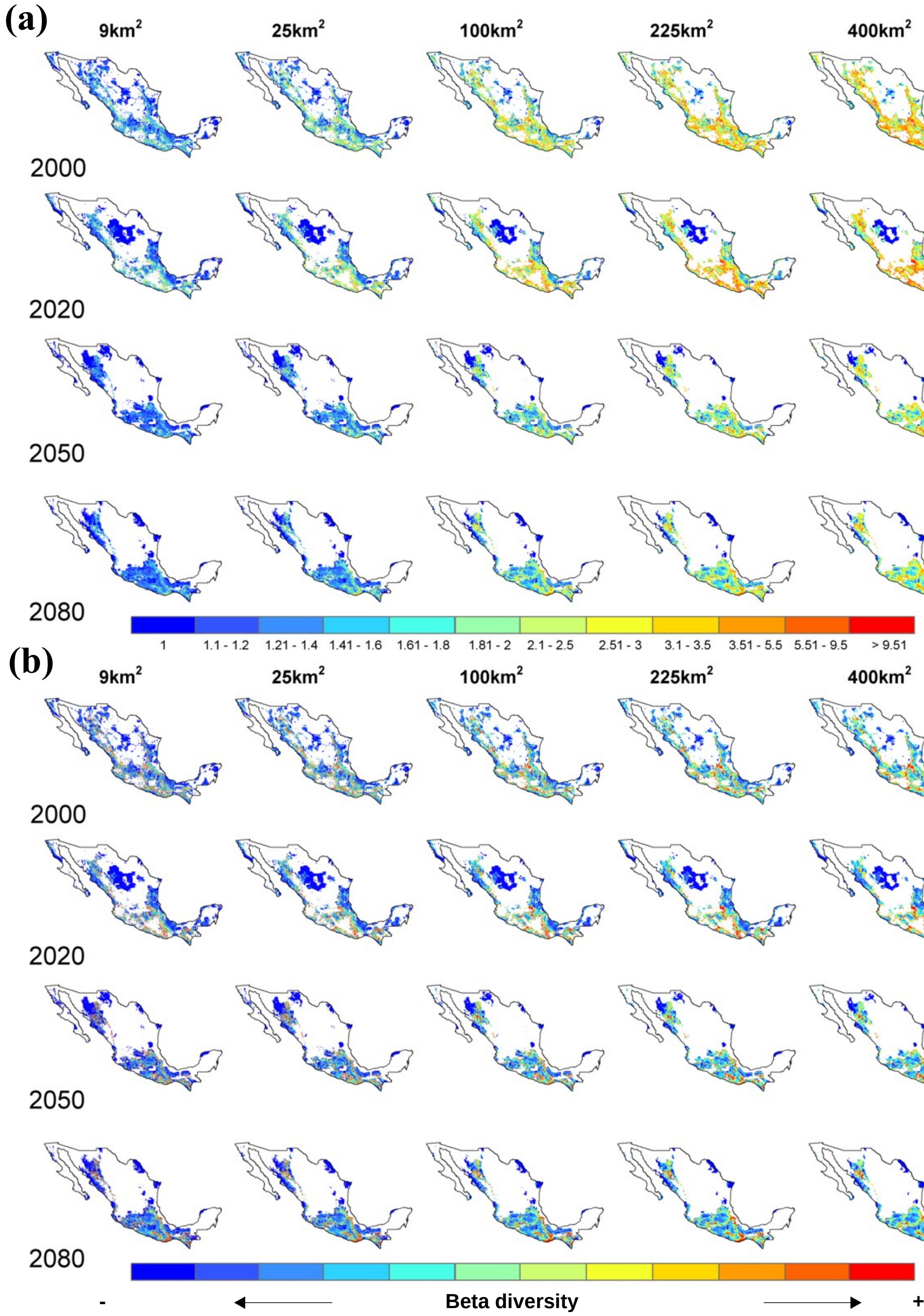


Figure SI V-20. Beta diversity patterns of Mexican amphibians using the 70% of presence probability threshold with different window sizes and moderate dispersion with trimming parameter. Two versions of the maps are presented, (a) using the same scaling of values in each map and (b) stretched colours using two standard deviations.



Coincidence among patterns of beta diversity

To evaluate quantitatively if the beta diverse zones remained coupled with the mountain ranges regardless of variation in model parameters we performed an overlay procedure, as follows. First, we used a quartile classification and selected the category in the highest quartile, to separate the 'hottest' zones in terms of beta diversity. The pixels belonging to the selected category were exported to a new raster and converted to 0-1 values, whereby pixels with zero do not belong to the highest beta diversity areas, pixels with a value of 1 do. Second, we overlaid maps and summed values to assess the coincidence among patterns generated using different parameter values. Thermometer colours were used to indicate coincidence, from blue that indicates low to red that shows high coincidence.

The purpose was to evaluate whether or not these 'hottest' beta diverse zones would vary. We evaluated different parameters separately. Thus, in Fig SI V-21 we assessed how the hottest beta diverse zones would diverge based on varying the window size used in modelling. In order to do this we fixed the dispersion parameter and the threshold of presence to the 10th percentile training presence of the logistic threshold of the distribution model. So, in each plate of Fig SI V-21 five patterns were overlapped that correspond to each window size (3, 5, 10, 15, and 20 pixels side). In Fig SI V-22 the procedure was the same but using the lowest presence threshold. Fifty and 70% of probabilities were used in Figs SI V-23 and SI V-24, respectively. In Fig SI V-25 the effects of variation in dispersion were assessed. In that case we fixed the window size (10 pixels side) and each plate shows the threshold used. Four patterns were overlapped in this case, one for each possibility of dispersion: 1) total, 2) zero, 3) moderate and 4) moderate with trimming at the baseline. In the last case, shown in Fig SI V-26, variation in threshold was assessed;

again only four patterns were overlapped: 1) 10th percentile training presence of the logistic threshold of the distribution model, 2) lowest presence threshold, 3) fifty and 4) seventy percent of probability of presence. From the figures it is possible to appreciate that the coincidence of high beta diversity zones with the major Mexican mountain ranges remains a robust pattern across simulations, although the relative importance of particular mountain ranges varies depending on parameter settings.

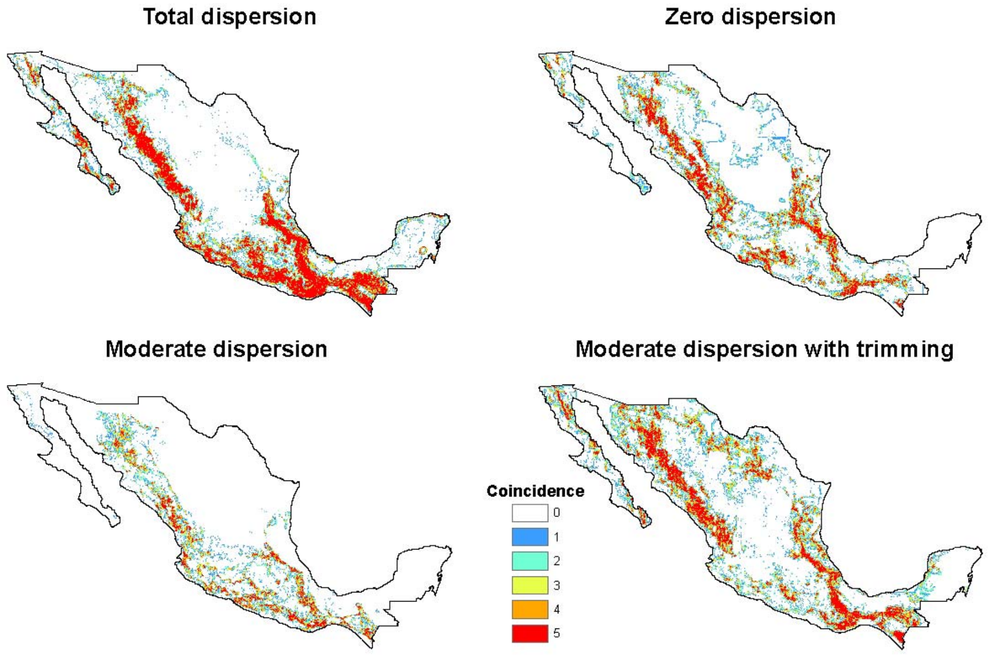


Figure SI V-21. Maps showing the coincidence among beta diversity patterns with different window sizes (3, 5, 10, 15, and 20 pixels to a side), using the 10th percentile training presence of the logistic threshold of the distribution model as a threshold of presence. The different panels are for different dispersion levels. Colours indicate degree of overlapping or coincidence: blue, no coincidence); green, coincidence among 2 patterns; yellow, among 3; orange implies coincidence among 4; and finally red implies zones where each model produced values of beta diversity in the highest quartile.

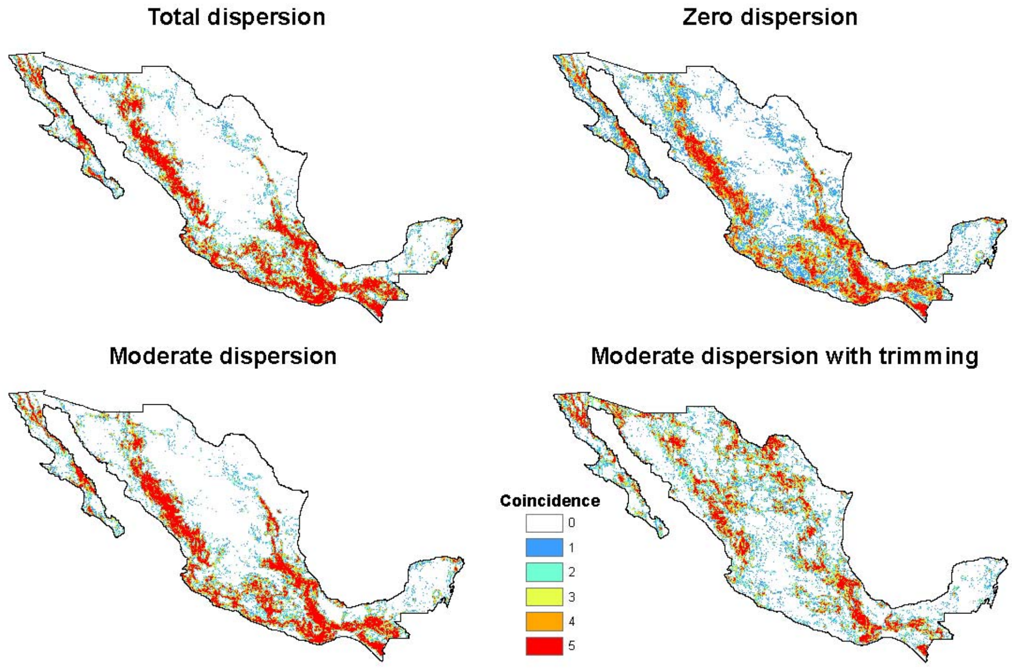


Figure SI V-22. Maps showing the coincidence among beta diversity patterns with different window sizes (3, 5, 10, 15, and 20 pixels to a side), using the lowest presence as a threshold of presence. The different panels are for different dispersion levels. Colours indicate degree of overlapping or coincidence: blue, no coincidence); green, coincidence among 2 patterns; yellow, among 3; orange implies coincidence among 4; and finally red implies zones where each model produced values of beta diversity in the highest quartile.

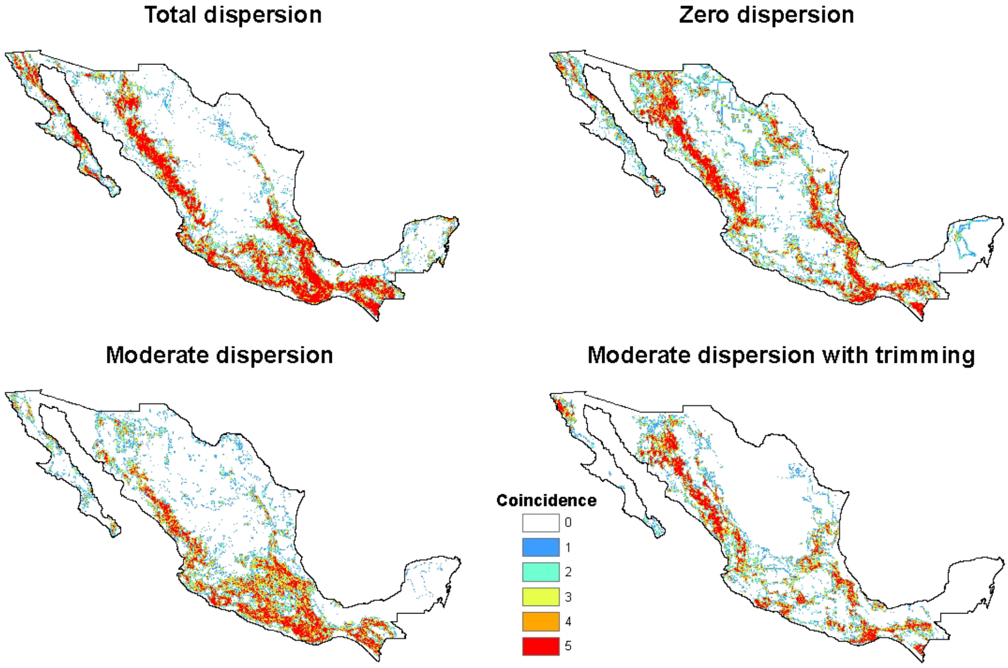


Figure SI V-23. Maps showing the coincidence among beta diversity patterns with different window sizes (3, 5, 10, 15, and 20 pixels to a side), using the 50% of probability as a threshold of presence. The different panels are for different dispersion levels. Colours indicate degree of overlapping or coincidence: blue, no coincidence); green, coincidence among 2 patterns; yellow, among 3; orange implies coincidence among 4; and finally red implies zones where each model produced values of beta diversity in the highest quartile.

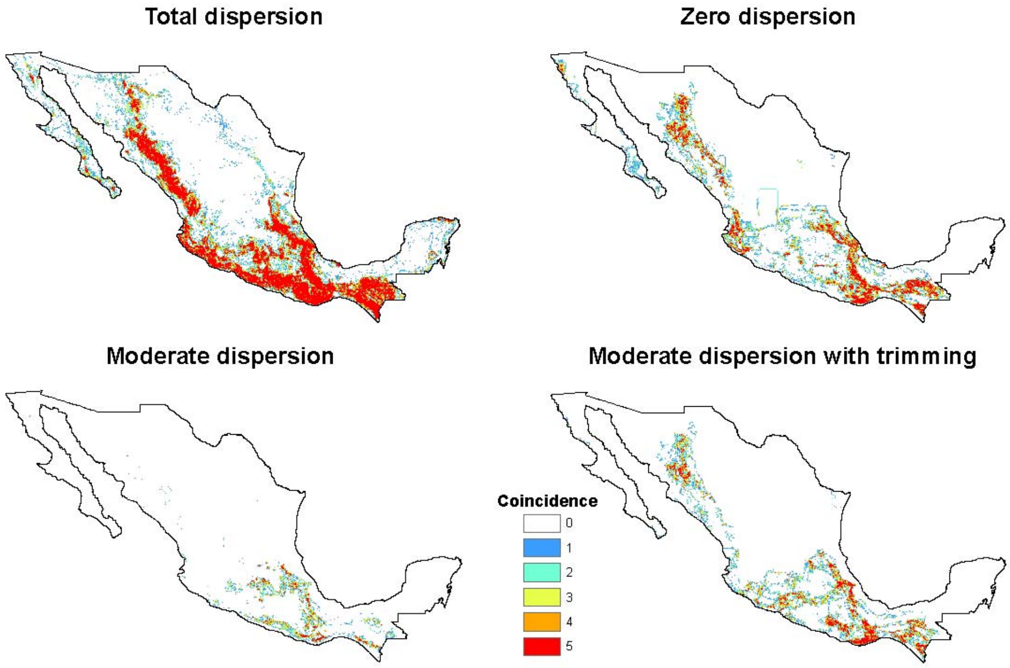


Figure SI V-24. Maps showing the coincidence among beta diversity patterns with different window sizes (3, 5, 10, 15, and 20 pixels to a side), using the 70% of probability as a threshold of presence. The different panels are for different dispersion levels. Colours indicate degree of overlapping or coincidence: blue, no coincidence); green, coincidence among 2 patterns; yellow, among 3; orange implies coincidence among 4; and finally red implies zones where each model produced values of beta diversity in the highest quartile.

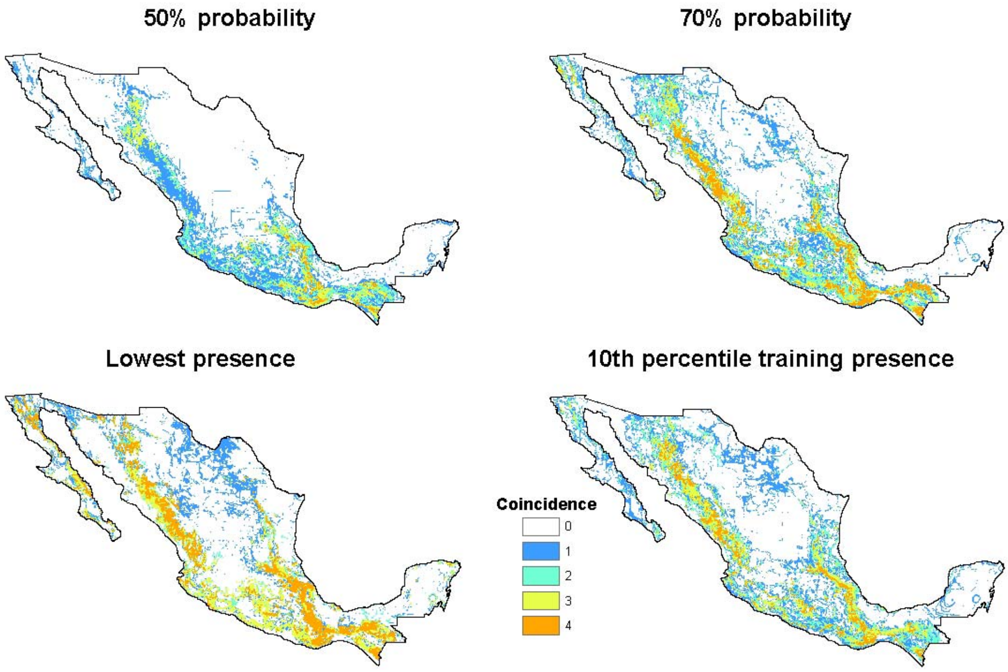


Figure SI V-25. Maps showing the coincidence among beta diversity patterns with different dispersion rates allowed; window size fixed (10 pixels side). The different panels are for different threshold of presence. Colours indicate degree of overlapping or coincidence: blue, no coincidence; green, coincidence among 2 patterns; yellow, among 3; orange implies zones where each model produced values of beta diversity in the highest quartile.

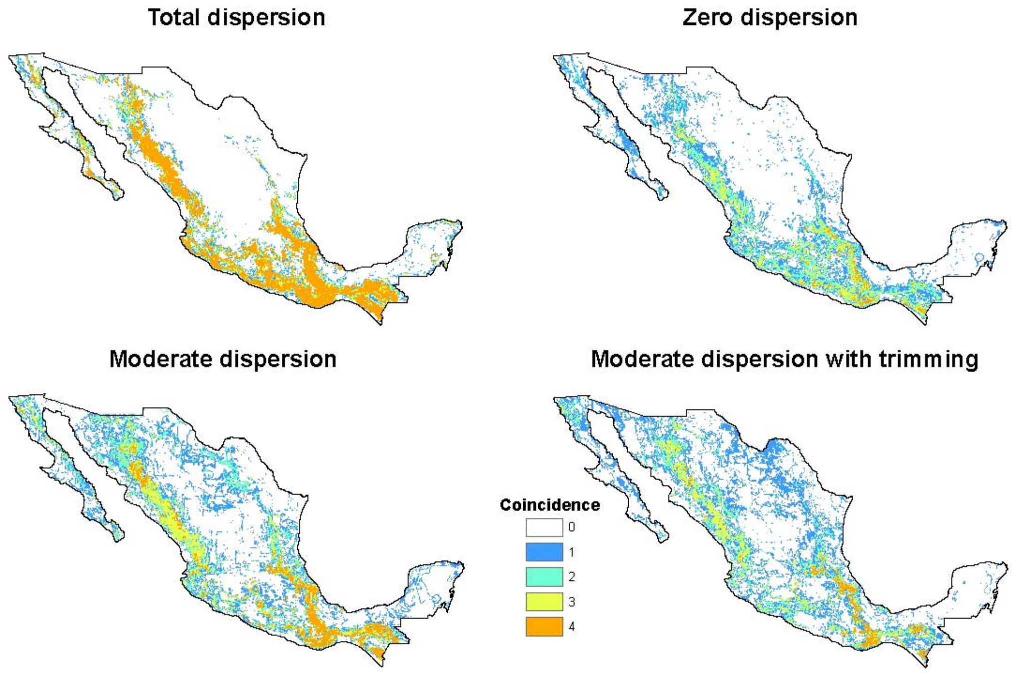


Figure SI V-26. Maps showing the coincidence among beta diversity patterns with different thresholds of presence; window size fixed (10 pixels side). The different panels are for different possibilities of dispersion. Colours indicate degree of overlapping or coincidence: blue, no coincidence; green, coincidence among 2 patterns; yellow, among 3; orange implies zones where each model produced values of beta diversity in the highest quartile.

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Craugastor alfredi, La Pera 2009

VI. THE DEMISE OF THE GOLDEN TOAD AND THE CREATION OF A CLIMATE CHANGE ICON SPECIES

“Time is fun when you are having flies”.

FrogMatters, 2008

This chapter was finished in June 2011, and submitted for review and publication in February 2012 to *Conservation and Society* (see Appendix B). The co-authors that contributed to this work were (in authorship order): Leticia M. Ochoa Ochoa, Robert J. Whittaker and Richard J. Ladle who kindly gave consent to include this article in the thesis.

Chapter word count including references, tables and appendices: 13,460

Main text: 4,327

ABSTRACT

There is an unavoidable degree of uncertainty associated with future climate projections, and even more unpredictability about the potential impact of different climate scenarios on the ecology and distribution of organisms. Conservationists face a major public communications challenge to both raise awareness and mobilize support for conservation and climate change mitigation/adaptation policies while at the same time realistically representing complex and uncertain scientific understandings. Here, we illustrate the interplay of these competing communication goals through a review of the representations of the golden toad in the print media and peer-reviewed literature. Since its disappearance the toad has become an important conservation flagship species that has been frequently portrayed as the first verified extinction attributable to global warming. Moreover, there was an increase in the certainty of published news items regarding the toad and its demise, especially in the late 1990s. The uncertainty surrounding the toad's disappearance (apparent in the primary research literature) was poorly represented in the popular press. The transformation of the toad into an iconic species for climate-change advocacy reflects the perceived need to project the negative outcomes of climate change beyond immediate horizons. Conservationists need new strategies to communicate scientific uncertainty to better inform the general public.

Keywords: climate change, conservation, distanciation, *Incilius periglenes*, media representation, politics of despair, uncertainty.

INTRODUCTION

> "Perhaps the most common outcome of the scientific process is no facts, but uncertainty."
> Friedman et al. (1999: vii)

> "For many, false prophecy is still less frightening than uncertainty."
> Reading (2004: 15)

Global concern regarding the conservation status of amphibians began to gather momentum at the first World Conference of Herpetology in 1989 (Sarkar 1996). Numerous scientists at this meeting argued there was a general declining trend among amphibian populations in different parts of the world, but with no obvious single cause (Blaustein and Wake 1990; Blaustein 1994; Houlahan et al. 2000). Several hypotheses were suggested, such as ultraviolet radiation, pesticides, introduction of alien species, toxicants, deforestation, and pathogens (e.g. reviews of Blaustein et al. 1998; Collins and Storfer 2003; Cushman 2006; and see Appendix VI-1 for individual references). These threats are not mutually exclusive and some have proved difficult to identify definitively or separate in the field (Collins and Storfer 2003), possibly because sub-population decline is inevitable in metapopulations with high demographic variability, as is characteristic of many amphibian populations (Alford and Richards 1999; Gillespie 2010).

The golden toad, *Incilius (Bufo) periglenes* (Savage 1966), is a classic example of a species for which the cause of decline and eventual extinction is poorly understood, but which nevertheless has become an iconic species within climate change discourse. The golden toad was first discovered in the cloud forest of the Monteverde region of Costa Rica in 1964 (Savage 1966). The toad's known geographic range always was extremely limited and a reserve of less than 4km^2 was established by 1972 that encompassed the entire known global population (Crump et al. 1992). Although these amphibians were difficult to survey accurately within the dense undergrowth of the cloud forest, they could be counted reliably for a few weeks in April when they emerged to mate in temporary pools (Crump et al. 1992). Unlike the vast majority of extinctions, the final disappearance of the golden toad was monitored closely and appears to have been rapid. More than 1500 toads were observed in 1987, but only a single toad was observed at the main known breeding site in 1988 and 1989 while seven adult males and two adult females were recorded 4–5 km away in 1988. No verified sightings have been reported since (Crump et al. 1992, Pounds and Crump 1994, Sarkar 1996). Published accounts of the procedures used to survey and monitor amphibians in the Monteverde cloud forest reserve are limited and rather imprecise. Pounds et al. (1997, p.1316), wrote that “Monteverde reserve has been *almost constantly* patrolled for 25 years” a comment that Wake and Vrendenburg (2008) cited as “daily monitoring”. We could not find any information in the published literature (printed or online) on the frequency of monitoring, the extent of the monitored area post-1990, what proportion of the research area has been systematically sampled, sampling method (day or night samplings), or whether any other forests in the vicinity have been searched. We should also note that the lack of systematic sampling of the reserve and/or of the wider region introduced a degree of uncertainty into the precipitousness of the observed decline (Crump et al. 1992; Sarkar 1996).

The toad’s disappearance was linked initially with the severe Neotropical droughts of 1987–1988 caused by the El Niño-Southern Oscillation (ENSO) conditions (Crump et al. 1992; Pounds and Crump 1994). However, shortly after the toad’s disappearance, Crump et al. (1992) discussed and acknowledged that other factors (e.g. non-specific pathogen attacks) might have played a role in the extinction and also commented that impacts of prior environmental degradation (initiated before monitoring work began) could not be ruled out entirely. These uncertainties were reported to the media.

The articles based on monitoring the populations in the years leading up to the crash made no mention of direct evidence for disease playing a role. Specifically, Crump et al. (1992) commented that data to address this possibility were lacking. Pounds et al. (1999) subsequently published a high-profile article in *Nature* arguing that climate change was probably responsible for the decline or disappearance of a number of species of birds, reptiles and amphibians in the area, citing the golden toad as a specific example. Pounds et al. (2006) provided additional climate-trend analyses and developed a more refined argument for the toad’s extinction based on the temperature-sensitivity of the behaviour of the pathogenic chytrid fungus *Batrachochytrium dendrobatidis* (but see Lips et al. 2008; Garner et al. 2011; Cheng et al. 2011 with counterarguments for this hypothesis). Pounds et al. stated that their data supported, with “very high confidence”, the case for large-scale climate warming being the key to the loss of a number of amphibians and implicated this temperature-sensitive chytrid as part of the causal nexus leading to amphibian declines. They focused on species in the genus *Atelopus* (harlequin frogs) for the most part, but also cited the golden toad as subject to the same drivers (Pounds et al. 2006). These later arguments did not call on any specific new evidence regarding the golden toad that added to the previous work of Crump et al. (1992) or Pounds and Crump (1994).

To attribute climate change as the single cause of any extinction event is problematic (Whitfield et al. 2007) because separating a specific climate-change influence from historical variability in climate and other environmental conditions is difficult (Anchukaitis and Evans 2010). The arguments of Pounds et al. (1999, 2006) that climate change was the main causal factor in the extinction of the golden toad coincided with a marked increase in emphasis on climate change in conservation discourse generally. This followed a shift from 1987 to 1992 in the United Nation's focus from "poverty reduction in developed countries" to the "biodiversity crisis", including climate change, biodiversity and forests (McManus 2000). Climate change was one of the main issues during the United Nations Conference on Environment and Development (UNCED) in Rio 1992, the Conference of the Parties in Geneva 1996 (COP2) and Kyoto 1997 (COP3), and the global media was paying close attention.

The focus of the international community on climate change has had inevitable consequences for conservation (Jepson and Ladle 2010), not least because many sources of conservation research funding became linked to understandable concerns about how changing climate might impact wildlife and ecosystems. The potential impacts of climate change became a topic of much discussion among conservationists, many of whom aligned relatively quickly behind this dominant theme (Ladle et al. 2005; Ladle and Jepson 2010). The overall representation of the golden toad in popular and scientific narratives, and its transformation from an obscure species of mainly herpetological interest into both a prominently cited example of a contemporary extinction event (e.g. Pearson 2011), and a global flagship species relative to climate change (Stork and Samways 1995), provides a unique window into the use of scientific information in various ways.

To better understand these uses, we present a comparative assessment of the reporting on the extinction and relevance of the golden toad in the academic literature (peer-reviewed journal articles) and in the media (internet and newspapers). We offer an interpretation of this transformation in terms of how society obtains and uses scientific information and perceives and responds to environmental messages, drawing on ideas of *distanciation* (McManus 2000). We also reflect on the potential implications for public perceptions of science and conservation.

MATERIALS AND METHODS

We searched the peer-reviewed journal literature via two databases: Scopus and the ISI Web of Knowledge. We obtained six results from Scopus that included "*Bufo periglenes*" (title, keywords, and body), and six that included "golden toad". From the ISI Web of Knowledge, we obtained 18 articles that included the term "*Bufo periglenes*" and 29 that included "golden toad" (Appendix VI-2). We did not find any peer-reviewed article that included "*Incilius periglenes*". In total, we retrieved 40 peer-reviewed articles published between 1972 and 2010.

We used the Lexis® database to search all news articles from all available sources of published information (newspapers, newswires, magazines, broadcast transcripts, and some blogs) that contained the words "golden toad" and "*sapo dorado*" (common name in Spanish). This search included articles published and captured electronically from January 1983 to March 2010. In all, we obtained 530 articles published in Spanish and English. After screening and deleting duplicated news or reports not related to amphibians (such as cultural or sports news), we compiled a database of 400 articles.

We recorded the following information for peer-reviewed and news articles: title/headline, month, year, type of article/news, name of the source, country of release, and whether the author(s) mentioned other amphibian species or other species in general. We categorized presumed causes of disappearance for *I. periglenes* or population changes for other specifically mentioned amphibian species as: climate change, habitat loss (including deforestation), pollution (including pesticides, chemical wastes), ultraviolet radiation, alien species, acid rain, ENSO (i.e. climate variability as opposed to long-term change), and diseases (including viruses and fungi). If the identified cause of population change did not fit into the above classification, we recorded it as “other causes” and recorded any additional information on population status (declining, disappearance, extinction, etc.) mentioned in the article.

We used keywords or statements in the headline or in the main body of the text such as: wiped out, extinct(ion), probably or believed to be extinct, not seen, endangered, threatened, disappeared, vanish(ed), declining, killed (fatal), mass extinction and "canaries in a coal mine" to further characterize reports in media sources and academic journals. We also recorded other information contained in media reports such as direct quotes attributed to non-governmental organizations (NGOs), university researchers and government officials, as well as events such as conferences or scientific articles related to the published news. Additionally, we surveyed 92 peer-reviewed articles, selected haphazardly from 385 papers identified via Scopus in January 2011 that cited Pounds et al. (2006), to specifically assess how authors represented this important article in the scientific literature. Literature research, data extraction and compilation to standardize interpretation and classification of the information were performed by a single person to avoid bias.

RESULTS

News items containing the term “golden toad” increased irregularly over time with four peaks in frequency (Fig. VI-1) and an annual mean of 14.8585 ± a standard deviation of 15.39. In contrast, the number of peer-reviewed articles in scientific journals containing either "golden toad" or "*Bufo periglenes*" or "*B. periglenes*" was consistently low over the study period, with a mean of 1.33 ± 1.33 articles per annum. The frequencies of news items and peer-reviewed articles were not correlated (adjusted $R^2 = 0.002$, $p = 0.31$, Fig. VI-1).

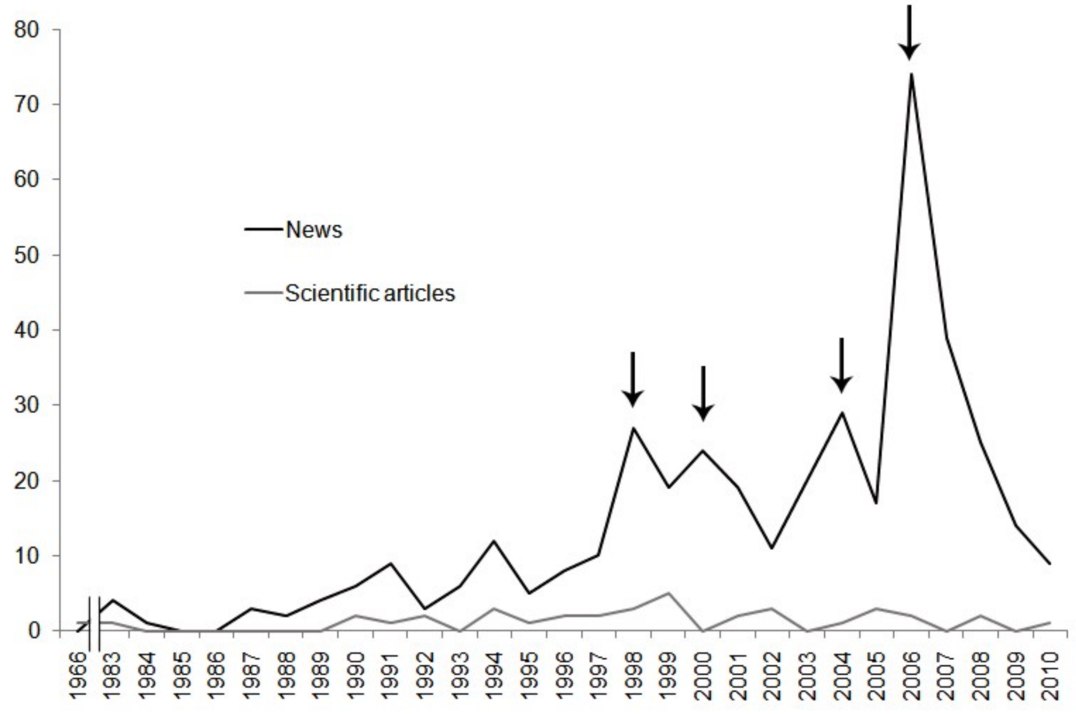

Figure VI-1. Number of peer-reviewed articles (sources ISI Web of Knowledge and Scopus) and news (via LexisNexis®) published containing the term "golden toad" and/or "*Bufo periglenes*". The description of the golden toad was in 1966; following which we could not find peer-reviewed articles until 1983. The first news in the LexisNexis® database occurred in the same year.

Authors of popular articles invoked different causes for the disappearance of *I. periglenes* from Monteverde through time. Several causes were identified shortly after the extinction event was reported: those causes typically were described as having high uncertainty. This changed over time and climate change and the amphibian fungal disease, chytridiomycosis, became the dominant reported causes. As the number of articles varied through time, we used the proportion of the number of times that different causes were mentioned within the news to illustrate these trends (Fig. VI-2). It should be noted that some of the articles discuss other amphibians in addition to *I. periglenes.*

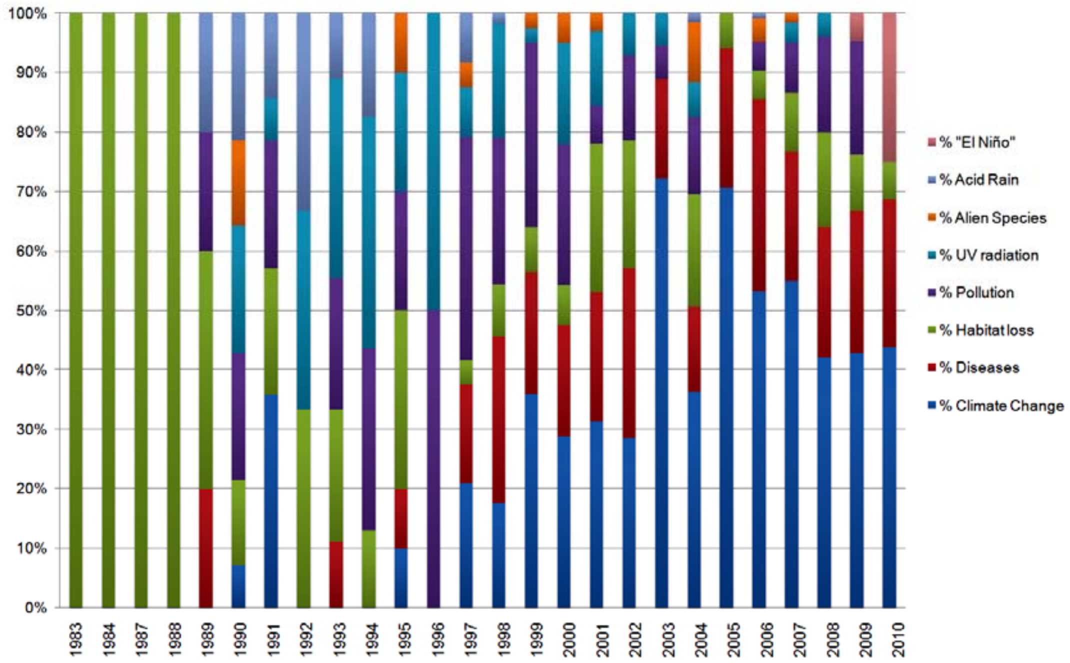

Figure VI-2. Proportional number of times *per annum* that each of the possible causes of amphibian decline that were mentioned in the news that included the golden toad. Not all the causes are necessarily related to the disappearance of the golden toad.

We found it more difficult to quantify any trends in statements regarding causes of declines in the peer-reviewed articles due to the low number of published articles containing the search terms (Appendix VI-2). From the 40 peer-reviewed articles retrieved from the search, we were only able to use 32 in the analysis. One article provided only a description of the toad, three others were specifically related to life history, and we were unable to obtain copies of another four. Most remaining articles evaluated more than one cause. A large proportion (17) of the peer-reviewed articles highlighted the golden toad as an example of unexplained decline, another seven mentioned weather variability including ENSO another five chytridiomicosis, and one the pet trade. Six articles mentioned climate change as the main factor driving the extinction (Appendix VI-2). The change in the strength of the rhetoric used by the news media to tell the story of the golden toad is also reflected in the increase in value-laden adjectives such as "wiped out" or "vanished", which peaked in 2006 (Fig. VI-3). The use of the phrase "mass extinction" in the news media also peaked that year.

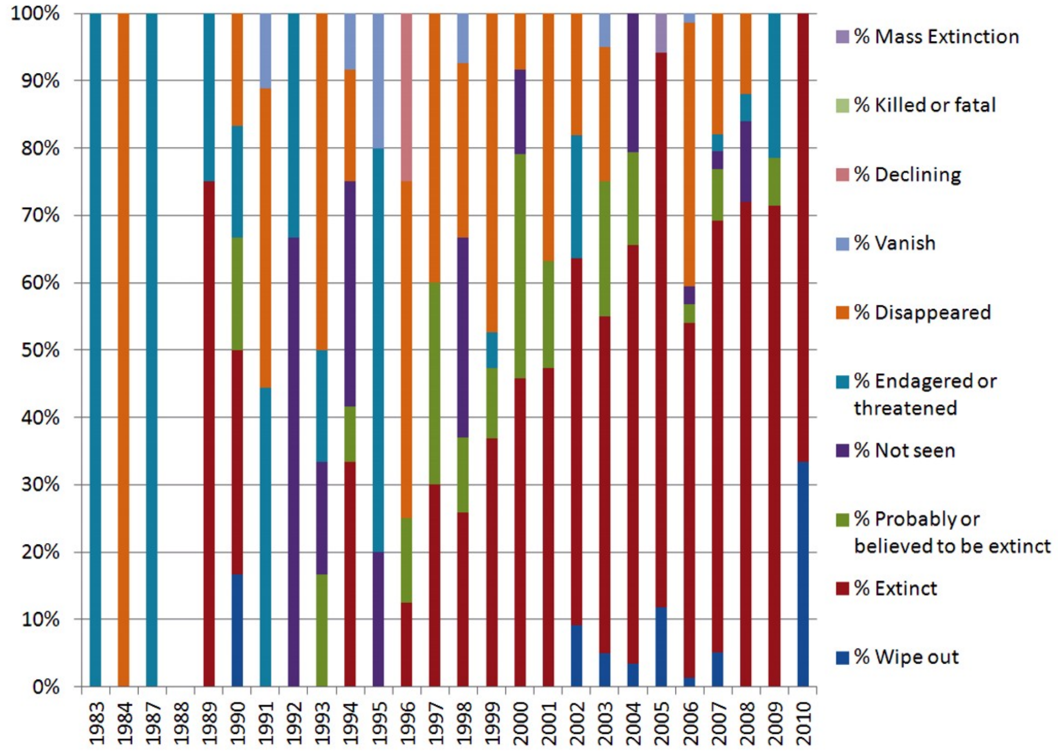

Figure VI-3. Frequency of use of different labels referring to the disappearance of the golden toad in the news items.

Whilst a relatively small number of peer-reviewed articles have been published about the golden toad, some have had considerable impact throughout the popular and scientific media, most notably, the article of Pounds et al. (2006). This article has been cited for various reasons. Forty eight articles used Pounds et al. (2006) as an example of disease impacts promoted by climate change or by climatic or environmental variability. Twenty one articles cited it as an example of species vulnerability to climate change *per se*, while six other articles referred to it as an example of chytridiomycosis, while nine challenged the hypothesis presented by Pounds et al. Finally, eight articles cited the paper as illustrating other causes of amphibian declines (Appendix VI-3).

DISCUSSION

The four peaks in the frequency of popular news items about the golden toad (Fig. VI-1) may be associated with different media events or publications. The first peak appears linked to the Kyoto conference in December 1997; the second peak (2000) could be associated with two separate events: the press releases of the WWF report "Living planet" (new versions available at http://www.panda.org) and the publication in *Nature* of the article "Quantitative evidence for global amphibian population declines" by Houlahan et al. (2000). The third peak might be linked to two high-profile publications: one in *Nature,* by Thomas et al. (2004) "Extinction risk from climate change", and the other in *Science,* by Stuart et al. (2004), entitled "Status and trends of amphibian declines and worldwide extinctions"; and to the release of the IUCN Global Amphibian Assessment (GAA). The final peak, and by far the biggest in terms of the frequency of news items, is most likely related to the publication "Widespread amphibian extinctions from epidemic disease driven by global warming" (Pounds et al. 2006).

Although-high profile academic articles may promote news stories, we found no quantitative association between the frequencies of the news-media items we surveyed and that of peer-reviewed published articles about the golden toad. This is not surprising given media outlets do not consider most peer-reviewed articles news worthy by themselves, especially those in less prominent journals, and the publication of individual peer-reviewed articles is dictated by factors not necessarily in step with the public media's focus at any given time. The observed change in the public media's descriptions of potential causes of the golden toad's extinction and of the uncertainty associated with them could have been influenced by the way climate change has come to dominate discussions of global change (Liu et al. 2011). Moreover, authors of articles in the public media arguably reflected some of the tone of high- profile scientific articles and their associated press releases, such as Thomas et al. (2004) and Pounds et al. (2006). As commented on elsewhere, the former article was widely misrepresented in the news media, partly due to misunderstanding of the uncertainties involved in complex modelling studies and partly as a result of extrapolations contained in the associated press release (Ladle et al. 2004, 2005).

Like the Thomas et al. (2004) study, the Pounds et al. (2006) article is a complex modelling study published in a high profile journal that suggested more certainty to some readers than often is stated in scientific articles. For example, the authors stated in the opening paragraph (which served as an executive summary): "we conclude with 'very high confidence' (>99%, following the Intergovernmental Panel on Climate Change, IPCC) that large-scale warming is a key factor in the disappearances [of 67% of 110 species of harlequin frogs and the golden toad]". They concluded the abstract with the non sequitur that "the urgency of reducing greenhouse-gas concentrations is now undeniable”. Language such as ‘very high confidence’ and ‘undeniable’ conveys technical meaning while also providing strong words for global news stories in the popular media. Technically speaking ‘very high confidence’ is a type of ‘hedge’ – defined by Hyland (1996) as any linguistic means used to indicate either a lack of complete commitment to the truth of a proposition, or a desire not to express that commitment categorically. Thus, ‘very high confidence’ still denotes uncertainty, albeit small, but such uncertainty can be lost on the public. Use of such a phrase can have similar consequences to those from using another technical expression common in bioclimatic envelope modelling, ‘committed to extinction’ (e.g. Thomas et al. 2004), which frequently has been simplified to “will be extinct by date *x*” by the global news media (Ladle et al. 2005).

Another interesting aspect of the media coverage of the Pounds et al. (2006) paper was the way in which the golden toad became a major element of the story, despite the main focus of the article being on a completely different genus, *Atelopus.* Although the golden toad is mentioned in the abstract alongside *Atelopus,* the article provides little further mention (and no new data) of the demise of the golden toad.

The clear narratives (“golden toad driven to extinction by climate change”, “one million species extinct by 2050”) provided by the media and conservation NGOs over the years, apparently supported by such peer-reviewed literature in the most highly cited journals, arguably made it difficult or less likely for alternative reporting to emerge in the public domain. Perhaps this helps explain why a recent article arguing that the extinction of the golden toad was caused by increased climate variability rather than directional climate change (Anchukaitis and Evans 2010) was not reported widely in public media.

The elevation of the golden toad to iconic status illustrates another consequence of how select writings in scientific journals and the popular media are related and interpreted, despite scientific uncertainties or improved information over time. The biggest NGOs were quick to use the rhetorical potential of the golden toad and have been instrumental in turning the toad into a flagship species for climate change (see Ladle and Jepson 2010). Stork and Samways (1995) defined flagship species as: ‘‘popular charismatic species that serve as symbols and rallying points to stimulate conservation awareness and action’’. The important status of the golden toad is illustrated clearly by the following quotes from Conservation International’s website (accessed August 2011), “For Ticos, as Costa Rican natives are known, reducing greenhouse gas emissions and stabilizing the climate is personally important, as the extinction of their emblematic golden toad (*Bufo [Incilius] periglenes*) due to climate change and altered weather patterns is still fresh” and from the World Wildlife Fund, “Global warming has already claimed its first species, with Costa Rica's golden toad believed to have become extinct” (Mr. Andrew Kerr, WWF, The Herald, Glasgow UK; August 31, 2000).

Conservation NGOs play an important role in determining conservation agendas, funding initiatives and interventions, liaising with politicians and policy makers, and, significantly, communicating with the public (Jepson and Ladle 2010). However, information reported in scientific journals and further reported and possibly transformed in the public media can become asymmetrical, not necessarily tethered to scientifically recognized realities of uncertainty or improved analyses, and can take on a life of its own, even among relatively informed groups. More generally, our results provide insights into how reports in the peer-reviewed literature and the popular press can be closely related when peer-reviewed articles contain sensationalist or strident headlines and poorly related when not. They also showed how information from both sources changed over time and suggested ways excerpts of scientific information, once established in the public media, can be used further in important environmental, social, and political contexts around the world.

Distanciation and Despair

Distanciation occurs when the media (of any kind) are involved in a process of separating cause and effect through the construction of space and time (McManus 2000; Rantanen 2005). In news reports there is an apparent decoupling *a priori* between cause and effect, especially when discussing global phenomena of significance, such as the care of nature. The space in *distanciation* may be created by a failure to establish the proper cause–effects links because they are too complex to explain in a brief news item. The time in *distanciation* is normally created with the context of the news, for example statements such as, “we predict, on the basis of mid-range climate-warming scenarios for 2050, that 15–37% of species in our sample of regions and taxa will be ‘committed to extinction’” (Thomas et al. 2004), help illustrate this process. Beyond other potential issues associated with such statements (see Ladle et al. 2005), uninformed readers could interpret this as “the disaster is going to occur or commence around 2050”. As information reported in the news media, this time frame is near enough to cause interest and concern in the reader (within the lifetime of the readers or their children or grandchildren), but ‘distance’ from the foundations and premises of the original information is already there (Gould 1983). Another example, advertising and advocacy for consumerism as well as for the causes and effects of climate change are everywhere. However, these phenomena rarely are linked in the media, which enables *distanciation* between our daily actions as consumers that contribute to habitat destruction and climate change and the potential consequences of both.

Experiencing historically significant events, such as a hurricane, earthquake, or an extinction event, can influence people's preoccupations, enabling the introduction of policies that may reduce the risks associated with such events in the future (Ashlin and Ladle 2007). Thus, given the *distanciation* established by the media towards climate change and biodiversity, there was an urgent need amongst concerned conservationists to identify tangible impacts that were already occurring. We suggest that it may have been this need to shorten the distance between changes in climate dynamics and potential biodiversity outcomes that lead to the promotion of the golden toad as an iconic example of the impacts of climate change on biodiversity. The urgent need to raise public awareness regarding the consequences of irrational use of natural resources seemingly has lead scientists and conservationists to make dramatic claims about extinction and its potential causes. For example E. O. Wilson claimed, "*if the situation's not abated [climate change], [we] could lose half the species of plants and animals in the world by the end of the 21st century*" (ABC News Transcripts, July 14, 2005). Such statements ultimately could be counterproductive because reporting in the public media does not necessarily reflect the uncertainty involved in climate change projections (e.g. Ladle et al. 2005) and, even if it did, the public often does not understand scientific uncertainty. Another related problem with such statements is the loss of credibility on the part of science and scientists. Credibility is based on the idea that scientists make impartial judgments based on data only; but when they align themselves with a particular side, that impartiality can come under question (Schmidt 2009).

Pessimism reigns with the realization of the dimensions of global environmental problems (Norgaard 2008). Despair is the emotion raised when individuals feel powerless to bring about desired changes and believe that nothing they do matters (Reading 2004). Consequently, despair frequently compromises the capacity to act, to improve things on behalf of others (Lapid 1989). A number of previous papers have discussed the importance of retaining or generating hope in conservation actions and projects (e.g. Orr 2004, 2007; Webb 2005). We echo these opinions, because it is surely crucial to avoid despair towards conservation: “Despair itself is the enemy of progress because in the final analysis it lacks a faith in the future” (Halpin 2001, p. 6).

More than fifteen years ago Pechman and Wilbur (1994) argued that there was insufficient information about amphibian populations to confirm the perceived worldwide decline of amphibian populations. More recently Salvidio (2009) re-analyzed 16 amphibian populations monitored for more than 15 years, and reported that all of them have shown stable long-term population dynamics. This finding is intriguing but of course 16 species and 15 years are insufficient sample sizes on a global scale for us to draw any clear conclusions from this analysis. We see no reason to doubt that amphibians are a threatened taxonomic group as a whole, with many species in danger of extinction due to a range of environmental factors, including climate change (Collins and Storfer 2003; Wake and Vredenburg 2008).

When Pechman and Wilbur (1994) raised the question of “Playing it safe or crying frog?” they were alluding to the potential negative repercussions of any incorrect reports of amphibian declines. Almost 20 years have passed since widespread amphibian declines were first reported and population declines have been reported among many species, as they have for other taxonomic groups (e.g. Malcom et al. 2005; Saino et al. 2011). Today, amphibians are no longer a forgotten group. Initiatives such as the Declining Amphibians Population Task Force (DAPTF) and others have increased general awareness and knowledge about amphibians substantially, even though there is a lack of standardized monitoring data for most amphibian species/populations (e.g. Frías et al. 2010).

Communicating science via the popular media is difficult, yet critically important. As some authors have already emphasized, scientists, as sources in the media, have to think carefully about how the information they are giving is going to be interpreted (Friedman et al. 1999). The dynamics and goals of reporting information in the popular media often differ substantially from those of reporting research results in scientific journals. This suggests we need to strive yet harder to maintain the integrity of science in the public eye by stating clearly what we know and do not know when writing for a journal or communicating more directly with the public.

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APPENDIX VI-1

Some examples of causes linked to amphibian population declining around the World (ISI Web of Knowledge Nov. 2010). Between parentheses are the numbers of articles founded related to the topic at the moment of the search. The threats were divided in major groups underlined, and divided in finer processes.

Threat type	Proposed mechanism	Consequences or change in status (examples)
Habitat loss		
Habitat transformation (18)	Amphibian species respond differentially to environmental changes.	Richness was greatest in wetlands with forest permanency (Kolozsvary and Swihart 1999).
	If intact continuous forest continues to be harvested, species that require ponds with longer hydro-periods for successful metamorphosis would be prone to population declines.	Populations decline (Neckel-Oliveira 2007).
Deforestation (68)	Whereas forest specialists suffer direct negative effect from deforestation, generalist species can take advantage of forest alteration and the presence of farm animals.	Population declines of specialist species (Cushman 2006; Furlani et al. 2009; Swift and Hannon 2010).
	Low density, population variability, and high mobility coupled with restricted habitat needs predispose woodland amphibians to local extinction caused by habitat fragmentation.	Decrease in species richness (Gibbs 1998).
Fragmentation (346)	Found an expected negative correlation between the abundance of frogs in the matrix and their vulnerability to fragmentation, however, results varied with fragment size and species traits.	Decrease in species abundance (Dixo and Metzger 2010).

Threat type	Proposed mechanism	Consequences or change in status (examples)
<u>Pollution</u>		
Pesticides and Chemical wastes (499)	Pesticides can cause variation in enzymatic levels among several tadpole species.	Appears that a conversion of native ecosystems to soybean crops may lead to increased ecological risks for anuran amphibians (Sparling et al. 2007; Davidson 2004; Rohr et al. 2008; Lajmanovich et al. 2010).
Acid rain (24)		Low pH has a negative effect in body size (Frisbie and Wyman 1995).
Heavy metals (81) Including: iron, manganese, aluminium, mercury, cadmium and bellyrium.	Cadmium inhibits acid secretion in stimulated frog gastric mucosa; Cu affects the liver metallothionein.	No apparent effect on population dynamics (Lefcort et al. 1997; Loumbourdis 2006; Gerbino et al. 2010; Cooper and Fortin 2010).
<u>Ultraviolet radiation</u> (242)		
	UV-B (280 – 315nm) can be easily absorbed by living cells and causes DNA mutation and/or cell death; induce lethal and sub-lethal effects on different ontogenetic phases of development.	Lab experiments, UB-V has an overall negative effect in *Ambystoma mexicanum*. Proportion of deformed embryos varied through the year (Frías et al. 2010). Field experiments "no differences in survival to hatching among UV-B-exposed and UV-B-shielded treatment" for *Rana muscosa, Bufo canorus*, or *Pseudacris regilla* (Vrenderburg et al. 2010). 1.1% of the distribution of *Ambystoma macrodactylum* is exposed to lethal levels of radiation (Palen and Schindler 2010). Hatching success to be unaffected by UV-B radiation. We suggest that UV-B radiation is an unlikely cause for declining populations of *Rana aurora* (Blaustein et al. 1996).

Threat type	Proposed mechanism	Consequences or change in status (examples)
		Although UV-B radiation may not contribute to the population declines of all species, it may play a role in the population decline of some species, 3 of 17 (Review of field experiments, Blaustein et al. 1998).
		By itself, UV-B caused no significant effects in *Hyla chrysoselis* and *Rana blairi* (Bruner et al. 2002).
Diseases		
Fungus (332) principally chytrids	Focused principally in chytrids.	Mass mortality of several species in Central America (Lips 1998, 1999; Lips et al. 2005; but see Kilpatrik et al. 2010).
	Batrachochytrium dendrobatidis (Bd) destroys keratinized mouthparts in anuran tadpoles, which are essential for feeding.	Bd infection reduces foraging efficiency of anuran tadpoles by altering feeding kinematics and reduces host fitness (Venesky et al. 2010).
	Potentially disrupts osmoregulation or respiration across the skin of amphibians it infects, releases toxins into the host, or both.	Results showed inhibited rehydration in individuals exhibiting clinical signs of chytridiomycosis. However, a clinical chytridiomycosis does not severely affect amphibian skin function. From 6 (*Litoria raniformis*) individuals infected, only one died (Venesky et al. 2010).
Bacteria (105)	Opportunistic pathogen associated with cutaneous infections and nodular granulomatous skin lesions.	Lab experiments. The infection does not cause death (Sánchez-Morgado et al. 2009).
	Red legged disease (bacterial dermatosepticemia).	Can cause deaths (Densmore and Green 2007).
		No lethal consequences (Davis and Cecala 2010).
Viruses (110)		Can cause mass mortality (Daszak et al. 2003; Collins and Storfer 2003)

Threat type	Proposed mechanism	Consequences or change in status (examples)
Alien species	Introduction of new predators.	Extinction but species can recover if the alien species is removed (Kats and Ferrer 2003).
Climate variability	Warmer temperatures than normal, especially during the dry season.	No clear signal, between the temperature and population decline (Alexaner and Eisched 2010).
Droughts; La Niña, El Niño events	“Climate anomalies are not a feature of all extinctions, it is not unreasonable to expect that natural climate variability can interact with species life history and ecological community and population dynamics to contribute to extinctions.”	Disappearance of *B. periglenes (*Anchukaitis and Evans 2010).
	Combination of factors, unusual warm weather and the presence of *Bd.*	Extinction (Barionuevo and Ponssa 2008)
Climate change	Thermal-optimum for *Bd* growth	Extinction (Pounds et al. 2006 but see Appendix VI-3 for cf. references).
	Climate envelope models	Extinction and displacement of distribution ranges (several authors, including Lawler et al. 2009 and Ochoa-Ochoa et al. 2012).

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Cooper, S. and C. Fortin. 2010. Metal and metallothionein content in bullfrogs: study of a whole watershed impacted by agricultural activities. *Ecotoxicology and Environmental Safety* 73: 391–399.

Cushman, S.A. 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biological Conservation* 128: 231–240.

Daszak, P., L. Berger, A.A. Cunningham, A.D. Hyatt, D.E. Green and R. Speare. 1999. Emerging infectious diseases and amphibian population declines. *Emerging Infectious Diseases* 5: 735–748.

Davis, A. and K. Cecala. 2010. Intraerythrocytic rickettsial inclusions in Ocoee salamanders (*Desmognathus ocoee*): prevalence, morphology and comparisons with inclusions of *Plethodon cinereus*. *Parasitology Research* 107: 363–367.

Davidson, C. 2004. Declining downwind: amphibian population declines in California and historical pesticide use. *Ecological Applications* 14: 1892–1902.

Densmore C.L. and D.E. Green. 2007. Diseases of amphibians. *Ilar Journal* 48: 235–54.

Dixo, M. and J. Metzger. 2010. The matrix–tolerance hypothesis: an empirical test with frogs in the Atlantic forest. *Biodiversity and Conservation* 19: 3059–3071.

Frías–Alvarez, P., V. T. Vredenburg, M. Familiar–López, J.E. Longcore, E. González–Bernal, G. Santos–Barrera, L. Zambrano and G. Parra–Olea. 2008. Chytridiomycosis survey in wild and captive Mexican amphibians. *EcoHealth* 5: 18–26.

Frisbie, M.P. and R.L. Wyman. 1995. A field simulation of the effect of acidic rain on ion balance in a woodland salamander. *Archives of Environmental Contamination and Toxicology* 28: 327–333.

Furlani, D., G.F. Ficetola, G. Colombo, M. Ugurlucan, and F. De Bernardi. 2009. Deforestation and the structure of frog communities in the humedale Terraba–Sierpe, Costa Rica. *Zoological Science* 26: 197–202.

Gerbino, A., L. Debellis, R. Caroppo, S. Curci and M. Colella. 2010. Cadmium inhibits acid secretion in stimulated frog gastric mucosa. *Toxicology and Applied Pharmacology* 245: 264–271.

Gibbs, J.P. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. *Landscape Ecology* 13: 263–268.

Kats, L.B., and R.P. Ferrer. 2003. Alien predators and amphibian declines: review of two decades of science and the transition to conservation. *Diversity and Distributions* 9: 99–110.

Kilpatrick, A.M., C.J. Briggs and P. Daszak. 2010. The ecology and impact of chytridiomycosis: an emerging disease of amphibians. *Trends in Ecology and Evolution* 25: 109–118.

Kolozsvary, M.B. and R.K. Swihart. 1999. Habitat fragmentation and the distribution of amphibians: patch and landscape correlates in farmland. *Canadian Journal of Zoology* 77: 1288–1299.

Lawler, J.J., S.L. Shafer and A.R. Blaustein. 2009. Projected climate impacts for the amphibians of the western hemisphere. *Conservation Biology* 24: 38–50.

Lajmanovich, R.C., P.M. Peltzer, C.M. Junges, A.M. Attademo, L.C. Sanchez and A. Basso. 2010. Activity levels of B–esterases in the tadpoles of 11 species of frogs in the middle Parana river floodplain: implication for ecological risk assessment of soybean crops. *Ecotoxicology and Environmental Safety* 73: 1517–1524.

Lefcort, H., R.A. Meguire, L.H.Wilson and W.F. Ettinger. 1998. Heavy metals alter the survival, growth, metamorphosis and antipredatory behavior of Columbia spotted frog (*Rana luteiventris*) tadpoles. *Archives of Environmental Contamination and Toxicology* 35: 447–456.

Lips, K.R. 1998 Decline of a tropical montane amphibian fauna. *Conservation Biology* 12: 106–117.

Lips, K.R. 1999 Mass mortality and population declines of anurans at an upland site in western Panama. *Conservation Biology* 13: 117–125.

Lips, K.R., P.A. Burrowes, J.R.Mendelson and G. Parra–Olea. 2005. Amphibian population declines in Latin America: a synthesis. *Biotropica* 37: 222–226.

Loumbourdis, N.S. 2006. Copper kinetics and hepatic glutathione levels in the copper exposed frog (*Rana ridibunda*) after Tetrathiomolybdate treatment. *Bulletin of Environmental Contamination and Toxicology* 76: 522–528.

Neckel–Oliveira, S. and M.J. Lannoo, 2007. Effects of forest disturbance on breeding habitat availability for two species of anurans in the Amazon. *Copeia* 2007: 186–192.

Palen, W.J. and D.E. Schindler. 2010. Water clarity, maternal behavior and physiology combine to eliminate UV radiation risk to amphibians in a montane landscape. *Proceedings of the National Academy of Sciences of the United States of America* 107: 9701–9706.

Pounds, J.A., M.R. Bustamante, L.A. Coloma, J.A. Consuegra, M.P.L. Fogden, P.N. Foster, E. La Marca, et al. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439: 161–167.

Rohr, J.R., et al. 2008. Agrochemicals increase trematode infections in a declining amphibian species. *Nature*, 455: 1235–1239.

Sanchez–Morgado, J.M., A. Gallagher and L.K. Johnson. 2009. *Mycobacterium gordonae* infection in a colony of African clawed frogs (*Xenopus tropicalis*). *Lab Animal* 43: 300–303.

Sparling, D.W. and G. Fellers. 2007. Comparative toxicity of chlorpyrifos, diazinon, malathion and their oxon derivatives to larval *Rana boylii*. *Environmental Pollution* 147: 535–539.

Swift, T.L. and S.J. Hannon. 2010. Critical thresholds associated with habitat loss: a review of the concepts, evidence and applications. *Biological Reviews* 85: 35–53.

Venesky, M.D., R.J. Wassersug and M.J. Parris. 2010. How does a change in labial tooth row number affect feeding kinematics and foraging performance of a ranid tadpole (*Lithobates sphenocephalus*)? *Biological Bulletin* 218: 160–168.

Vredenburg, V.T., J.M. Romansic, L.M. Chan and T.Tunstall. 2010. Does UV–B radiation affect embryos of three high elevation amphibian species in California? *Copeia* 2010: 502–512.

APPENDIX VI-2

List of the scientific articles including the terms “*Bufo periglenes*” and/or “Golden toad” resulting from the searches in both SCOPUS and the ISI Web of Knowledge available as of April 2010.

Authors	**Year**	**Title**	**Journal**	**Example of population declining by climate change**	**Weather variability**	**Other**	**Example of unexplained population declining**	**Comments**
Anchukaitis and Evans	2010	Tropical cloud forest climate variability and the demise of the Monteverde golden toad.	Proceedings of the National Academy of Sciences of the United States of America			ENSO		
Barrionuevo and Ponssa	2008	Decline of three species of the genus *Telmatobius* (Anura : Leptodactylidae) from Tucuman Province, Argentina.	Herpetologica				Yes	
Blaustein and Wake	1990	Declining amphibian populations - a global phenomenon	Trends in Ecology and Evolution				Yes	
Blaustein et al.	1999	DNA repair and resistance to UV-B radiation in western spotted frogs.	Ecological Applications				Yes	
Blaustein et al.	1998	Effects of ultraviolet radiation on amphibians: Field experiments	American Zoologist				Yes	

Authors	**Year**	**Title**	**Journal**	**Example of population declining by climate change**	**Weather variability**	**Other**	**Example of unexplained population declining**	**Comments**
Blaustein et al.	1996	DNA repair activity and resistance to solar UV-B radiation in eggs of the red-legged frog.	Conservation Biology				Yes	
Bruner et al.	2002	Developmental effects of ambient UV-B light and landfill leachate in *Rana blairi* and *Hyla chrysoscelis*.	Ecotoxicology and Environmental Safety				Yes	
Buchannan	1994	Sexual dimorphism in *Hyla squirella*: chromatic and pattern variation between the sexes	Copeia			Sexual dimorphism		
Burrowes et al.	2004	Potential causes for amphibian declines in Puerto Rico.	Herpetologica	Yes				Extension of the dry season is another aspect of climate change that has been suggested to affect tropical amphibians (Donnelly and Crump, 1998) and has been associated with the extinction of *B. periglenes* in Costa Rica.
Bustarnante et al.	2005	Changes in diversity of seven anuran communities in the Ecuadorian Andes.	Biotropica	Yes				Increase in the number of dry days.
Corser	2001	Decline of disjunct green salamander (*Aneides aeneus*) populations in the southern Appalachians.	Biological Conservation		Yes			

Authors	Year	Title	Journal	Example of population declining by climate change	Weather variability	Other	Example of unexplained population declining	Comments
Crump	1989	Life history consequences of feeding versus non-feeding in a facultatively non-feeding toad larva	Oecologia			Life history		
Crump et al.	1992	Apparent decline of the golden toad - underground or extinct.	Copeia			Too early to know		Because of its unpredictable and fluctuating breeding habitat (small pools prone to overflowing or desiccation), *B. periglenes* is a species vulnerable to vagaries of the weather. For this reason, the population might fluctuate widely in size due to variable recruitment success.
Daszak et al.	1999	Emerging infectious diseases and amphibian population declines	Emerging Infectious Diseases			Chytridiomycosis		Hypothesized link with global extinction of golden toad, *Bufo periglenes.*
Fogden	1996	Conservation of the golden toad: a brief history	Herpetological Biology					No pdf
Foster	1992	The international component of managing biological diversity	57th North American wildlife and natural resources conf - crossroads of conservation: 500 years after Columbus					No pdf

Authors	Year	Title	Journal	Example of population declining by climate change	Weather variability	Other	Example of unexplained population declining	Comments
Funk and Dunlap	1999	Colonization of high-elevation lakes by long-toed salamanders (*Ambystoma macrodactylum*) after the extinction of introduced trout populations.	Canadian Journal of Zoology				Yes	
Goerck	1997	Patterns of rarity in the birds of the Atlantic forest of Brazil.	Conservation Biology			Small catastrophe or disease		
Griffiths	2001	Conservation biology and declining Amphibian populations.	Rivi Idrobiology					No pdf
Hays et al.	1996	Developmental responses of amphibians to solar and artificial UVB sources: A comparative study.	Photochemistry and Photobiology				Yes	
Hero et al.	2005	Ecological traits of declining amphibians in upland areas of eastern Australia.	Journal of Zoology				Yes	
Jacobson	1983	Short season of the golden toad.	International Wildlife					No pdf
Jacobson and Vandenberg	1991	Reproductive ecology of the endangered golden toad (*Bufo periglenes*).	Journal of Herpetology			Pet trade	Yes	

Authors	Year	Title	Journal	Example of population declining by climate change	Weather variability	Other	Example of unexplained population declining	Comments
Lips	1999	Mass mortality and population declines of anurans at an upland site in western Panama.	Conservation Biology			Chytridiomycosis*	Yes	
Lips	1998	Decline of a tropical montane amphibian fauna.	Conservation Biology				Yes	
Lips et al.	2005	Amphibian population declines in Latin America: a synthesis.	Biotropica			Chytridiomycosis*	Yes	
Lizana and Pedraza	1998	The effects of UV-B radiation on toad mortality in mountainous areas of central Spain.	Conservation Biology				Yes	Many hypotheses have been proposed to explain this decline: natural fluctuations of the populations (see references in Blaustein et al. 1994b), global changes in climate, long drought periods, or the depletion of the ozone layer.
Nadkarni and Solano	2002	Potential effects of climate change on canopy communities in a tropical cloud forest: an experimental approach.	Oecologia	Yes		ENSO		
Nott et al.	1995	Extinctions rates - modern extinctions in the kilo-death range.	Current biology				Yes	

Authors	Year	Title	Journal	Example of population declining by climate change	Weather variability	Other	Example of unexplained population declining	Comments
Pasmans et al.	2006	Amphibian decline: the urgent need for amphibian research in Europe.	Veterinary Journal			Chytridiomycosis		The classic example of a pandemic amphibian disease is chytridiomycosis, a fungal disease caused by *Batrachochytrium dendrobatidis* that is held responsible for massive amphibian die offs and even for the extinction of several species worldwide, the most famous of which being the Costa Rica golden toad (*Bufo periglenes*).
Pechman and Wilbur	1994	Putting declining amphibian populations in perspective - natural fluctuations and human impacts.	Herpetologica			Natural causes (droughts)		The possibility remains that they are still present in underground or other retreats, and that their apparent disappearances represent extreme natural fluctuations.
Phillips	1990	Where have all the frogs and toads gone.	Bioscience				Yes	
Pounds	1990	Disappearing gold.	BBC Wildlife					No pdf
Pounds and Crump	1994	Amphibian declines and climate disturbance - the case of the golden toad and the harlequin frog.	Conservation Biology		Yes?	ENSO		
Pounds et al.	1997	Tests of null models for amphibian declines on a tropical mountain.	Conservation Biology		Unusual weather			
Pounds et al.	2006	Widespread amphibian extinctions from epidemic disease driven by global warming.	Nature	Yes				

Authors	**Year**	**Title**	**Journal**	**Example of population declining by climate change**	**Weather variability**	**Other**	**Example of unexplained population declining**	**Comments**
Pounds *et al*.	1999	Biological response to climate change on a tropical mountain.	Nature	Yes				
Savage	1972	The systematic status of *Bufo simus* with description of a new toad from western Panama.	Journal of Herpetology			Description of *B. peripattes*		
Vaira	2002	Anurans of a subtropical montane forest in northwestern Argentina: ecological survey and a proposed list of species of conservation concern.	Biodiversity and Conservation			Yes		
Wake and Vredenburg	2008	Are we in the midst of the sixth mass extinction? A view from the world of amphibians.	Proceedings of the National Academy of Sciences of the United States of America			Yes		

APPENDIX VI-3

A selection of papers citing Pounds et al. 2006. The papers were selected haphazardly, with no particular criteria in mind, but do not strictly speaking constitute a random sample. Ninety two represents in excess of 23% of the articles, selected from 385 papers January 2011, from Scopus. Acronyms: amphibian population decline (APD), and chytrid-thermal-optimum hypothesis (CTOH). *Indicate mis-citations of Pounds et al. 2006.

Article	**Example of vulnerability towards chytridiomycosis**	**Example of vulnerability towards climate change**	**Example of climate change promoting the chytridiomycosis**	**No cause mentioned**	**Example of APD but no cause related**	**Example of challenging the hypothesis CTOH**	**Quotes**
Abarca, J., G. Chaves, A. García–Rodríguez and R. Vargas. 2010. Reconsidering extinction: rediscovery of *Incilius holdridgei* (Anura: Bufonidae) in Costa Rica after 25 years. *Herpetological Review* 41: 150–152.						Yes	These disappearances have been attributed to different causes, including climate change (Pounds 1997, 2001) and emergent diseases such as chytridiomycosis (Lips et al. 2006), or the synergistic effect between these two agents (Pounds et al. 2006). However, our discovery of a population of *Incilius holdridgei* in a region with well documented chytridiomycosis (Puschendorf et al. 2006), allows a test of its vulnerability to this disease.
Agosta, S.J., N. Janz and D.R. Brooks. 2010. How specialists can be generalists: resolving the "parasite paradox" and implications for emerging infectious disease. *Zoologia* 27: 151–162.			Yes				The current EID crisis is "new" only in the sense that this is the first such event that scientists have witnessed directly.
Açakaya, R.H., S.H.M. Butchart, G.M. Mace, S.N. Stuart and C. Hilton–Taylor. 2006. Use and misuse of the IUCN red list criteria in projecting climate change impacts on biodiversity. *Global Change Biology* 12: 2037–2043.			Yes				Recent studies demonstrate that climate change can affect species viability much faster than implied by range shifts, when it interacts with other factor.

Article	Example of vulnerability towards chytridiomycosis	Example of vulnerability towards climate change	Example of climate change promoting the chytridiomycosis	No cause mentioned	Example of APD but no cause related	Example of challenging the hypothesis CTOH	Quotes
Al–Attar, A.M. 2010. Hematological, biochemical and histopathological studies on marsh frog, *Rana ridibunda*, naturally infected with *Waltonella duboisi*. *International Journal of Zoological Research* 6: 199–213.					Yes		
Alemu I, J.B., M.N.E. Cazabon, L. Dempewolf, A. Hailey, R.M. Lehtinen, R.P. Mannette, K.T. Naranjit and A.C. J. Roach. 2008. Presence of the chytrid fungus Batrachochytrium dendrobatidis in populations of the critically endangered frog Mannophryne olmonae in Tobago, West Indies. *EcoHealth* 5: 34–39.			Yes				Chytridiomycosis is presently endemic in this species, with a prevalence of about 20% and no associated clinical disease. Thus although global warming might increase the susceptibility of montane amphibians by bringing their environments within the optimum temperature range of *B. dendrobatidis* this is unlikely in the lowland and lower-montane frog *M. olmonae.*
Alford, R.A., K.S. Bradfield and S.J. Richards. 2007. Ecology: Global warming and amphibian losses. *Nature* 447.						Yes	We question the analysis of Pounds et al. which so far provides the only geographically broad test of this idea. Contrary to their working model, indicate that multiyear warm periods may be more important in amphibian declines than single warm years. By focusing on the latter, the authors' test could be inconclusive.
Alford, R.A. and S.J. Richards. 1997. Lack of evidence for epidemic disease as an agent in the catastrophic decline of Australian rain forest frogs. *Conservation Biology* 11: 1026–1029.							
Altermatt, F. and D. Ebert. 2008. Genetic diversity of *Daphnia magna* populations enhances resistance to parasites. *Ecology Letters* 11: 918–928.	Yes						Parasites are of general importance in all natural systems, and epidemics can lead to population extinctions (...Pounds et al. 2006).*

Article	Example of vulnerability towards chytridiomycosis	Example of vulnerability towards climate change	Example of climate change promoting the chytridiomycosis	No cause mentioned	Example of APD but no cause related	Example of challenging the hypothesis CTOH	Quotes
Alton, L.A., R.S. Wilson and C.E. Franklin. 2010. Risk of predation enhances the lethal effects of UV–B in amphibians. *Global Change Biology* 16: 538–545.			Yes				It has been suggested that subtle environmental changes occurring at a global scale (e.g. global climate change and increasing UV-B radiation) may be interacting with stressors acting at local and regional scales (e.g. acidification, contaminants and disease) to negatively impact amphibian populations (Pounds et al. 2006).
Anchukaitis, K.J. and M.N. Evans. 2010. Tropical cloud forest climate variability and the demise of the Monteverde golden toad. *Proceedings of the National Academy of Sciences of the United States of America* 107: 5036–5040.						Yes	Rather, the extinction of the Monteverde golden toad (*Bufo periglenes*) appears to have coincided with an exceptionally dry interval caused by the 1986–1987 El Niño event.
Berg, M.P., E. Toby Kiers, G. Driessen, M. van der Heijden, B.W. Kooi, F. Kuenen, M. Liefting, H.A. Verhoef and J. Ellers. Adapt or disperse: understanding species persistence in a changing world. *Global Change Biology* 16: 587–598.	Yes	Yes					Recent studies indicate that robustness of species interactions under climate change is determined by variation in the temperature sensitivity of their community components (Pounds et al. 2006).
Bickford, D., S.D. Howard, D. J.J. Ng and J.A. Sheridan. 2010. Impacts of climate change on the amphibians and reptiles of Southeast Asia. *Biodiversity and Conservation* 19: 1043–1062.			Yes				Additionally, increased metabolic rates often draw on energy normally allocated for maintenance (Fitzpatrick 1976; Scott and Fore 1995), resulting in increased susceptibility to disease (Pounds et al. 2006).
Blaustein, A.R. and A. Dobson. 2006. Extinctions: a message from the frogs. *Nature* 439: 143–144.			Yes				Pounds and colleagues provide compelling evidence that anthropogenic climate change has already altered transmission of a pathogen that affects amphibians, leading to widespread population declines and extinctions.
Blaustein, A.R. and P.T.J. Johnson. 2010. Conservation biology: When an infection turns lethal. *Nature* 465: 881–882.			Yes				Intensity threshold of *B. dendrobatidis* varies across species or with environmental conditions, and what part is played by environmental cofactors such as climate change.

Article	Example of vulnerability towards chytridiomycosis	Example of vulnerability towards climate change	Example of climate change promoting the chytridiomycosis	No cause mentioned	Example of APD but no cause related	Example of challenging the hypothesis CTOH	Quotes
Botkin, D.B., H. Saxe, M.B. Araújo, R. Betts, R.H. W. Bradshaw, T. Cedhagen, P. Chesson, et al. 2007. Forecasting the effects of global warming on biodiversity. *BioScience* 57: 227–236.			Yes (climatic variability)				… amphibian declines due to outbreaks of a pathogenic chytrid fungus (*Batrachochytrium dendrobatidis*) are related to the annual range of temperatures, not to the mean temperature.
Briggs, C.J., R.A. Knapp and V.T. Vredenburg. 2010. Enzootic and epizootic dynamics of the chytrid fungal pathogen of amphibians. *Proceedings of the National Academy of Sciences of the United States of America* 107: 9695–9700.				Yes			This model can easily incorporate the effects of temperature or other environmental conditions (such as water flow rate) on Bd growth.*
Brook, B.W., N.S. Sodhi and C.J.A. Bradshaw. 2008. Synergies among extinction drivers under global change. *Trends in Ecology and Evolution* 23: 453–460.			Yes				An excellent real-world example comes from the highland forests of Costa Rica, where 40% of 50 endemic frog and toad species disappeared following synchronous population crashes during the late 1980s. Recent work has linked these extinctions to an interaction between global warming and disease.
Brooks, D.R. and E.P. Hoberg. 2007. How will global climate change affect parasite–host assemblages? *Trends in Parasitology* 23: 571–574.			Yes				Accelerated perturbation in global ecosystems can initiate events that link climate change, loss of biodiversity and emerging infectious diseases.
Brooks, T.M., S.J. Wright and D. Sheil. 2009. Evaluating the success of conservation actions in safeguarding tropical forest biodiversity. *Conservation Biology* 23: 1448–1457.	Yes						Little is known about other drivers of biodiversity loss within PAs. Examples include disease, which caused the extinction of the golden toad (*Incilius periglenes*) in Costa Rica's Reserva Biológica Monteverde.
Bruijnzeel, L.A., M. Mulligan and F.N. Scatena. 2011. Hydrometeorology of tropical montane cloud forests: emerging patterns. *Hydrological Processes* 25: 465–498.		Yes					In recent years, climatic warming and drying related to global or regional climate change have become an increasingly important factor that can potentially threaten TMCF hydrological functioning, in addition to having a devastating effect on particularly vulnerable plant and animal groups like mosses and amphibians.

Article	Example of vulnerability towards chytridiomycosis	Example of vulnerability towards climate change	Example of climate change promoting the chytridiomycosis	No cause mentioned	Example of APD but no cause related	Example of challenging the hypothesis CTOH	Quotes
Bruno, J.F., E.R. Selig, K.S. Casey, C.A. Page, B.L. Willis, C.D. Harvell, H. Sweatman and A.M. Melendy. 2007. Thermal stress and coral cover as drivers of coral disease outbreaks. *Public Library of Science Biology* 5: 1220–1227.			Yes				Temperature and climate change have also been implicated in plant and animal disease outbreaks in both terrestrial and aquatic habitats.
Buckley, L.B. and W. Jetz. 2007. Environmental and historical constraints on global patterns of amphibian richness. *Proceedings of the Royal Society B: Biological Sciences* 274: 1167–1173.				Yes			Amphibians have repeatedly been used as an indicator group for environmental change*
Bush, M.B. and T.E. Lovejoy. 2007. Amazonian conservation: Pushing the limits of biogeographical knowledge. *Journal of Biogeography* 34: 1291–1293.			Yes				The synergism induced in Amazonia through simplifying ecological structure from the complexity of forest to the simplicity of soybean fields or ranchland, the increased probability of human-set fires, and complex ecological interactions mediated by climate, e.g. bacterial diseases (Pounds et al. 2006).
Bustamante, H.M., L.J. Livo and C. Carey. 2010. Effects of temperature and hydric environment on survival of the Panamanian golden frog infected with a pathogenic chytrid fungus. *Integrative Zoology* 5: 143–153.			Yes				Pounds et al. (2006) propose a “climate-linked epidemic hypothesis,” or, more specifically, a “chytrid-thermal-optimum hypothesis.”
Butler, G. 2010. Fungal sex and pathogenesis. *Clinical Microbiology Reviews* 23: 140–159.	Yes						Others cause disease in animals, such as the chytrid species *Batrachochytrium dendrobatidis*, which is devastating the global amphibian population.
Calosi, P., D.T. Bilton and J.I. Spicer. 2008. Thermal tolerance, acclimatory capacity and vulnerability to global climate change. *Biology Letters* 4: 99–102.		Yes					During periods of rapid climate change, taxa that are unable to shift their geographical ranges are particularly at risk from extinction (Pounds et al. 2006).
Cannatella, D.C. 2008. Comment on "Habitat split and the global decline of amphibians". *Science* 320.				Yes			Amphibians are important indicators of environmental degradation and climate change.

Article	Example of vulnerability towards chytridiomycosis	Example of vulnerability towards climate change	Example of climate change promoting the chytridiomycosis	No cause mentioned	Example of APD but no cause related	Example of challenging the hypothesis CTOH	Quotes
Carnaval, A.C. and J.M. Bates. 2007. Amphibian DNA shows marked genetic structure and tracks pleistocene climate change in northeastern Brazil. *Evolution* 61: 2942–2957.			Yes (climatic anomalies)				Our data show *B. dendrobatidis* to be present in Brazil in the early 1980s. When tied to Heyer et al.'s (1988) and Weygoldt's (1989) observations on local climate anomalies, our results are consistent with a hypothesis of a climate-linked epidemic event leading to amphibian declines (Pounds et al. 2006).
Carvalho, S.B., J.C. Brito, E.J. Crespo and H.P. Possingham. 2010. From climate change predictions to actions – conserving vulnerable animal groups in hotspots at a regional scale. *Global Change Biology* 16: 3257–3270.			Yes				Climate warming is projected to induce the spread chytridiomycete fungus.
Casadevall, A. and L.A. Pirofski. 2007. Accidental virulence, cryptic pathogenesis, martians, lost hosts and the pathogenicity of environmental microbes. *Eukaryotic Cell* 6: 2169–2174.			Yes?				The ongoing decimation of amphibian populations by a chytrid fungus may reflect a similar phenomenon, whereby ecological changes might select for variants with enhanced virulence.
Chown, S.L., K.J. Gaston, M. van Kleunen and S. Clusella–Trullas. 2010. Population responses within a landscape matrix: a macrophysiological approach to understanding climate change impacts. *Evolutionary Ecology* 24: 601–616.		Yes					Although the ultimate causes of amphibian declines in tropical Central America remain the subject of debate (e.g. Pounds et al. 1999, 2006; Rohr et al. 2008), changes in water availability owing to global temperature change and local habitat destruction are important (Rovito et al. 2009).
Chown, S.L. and J.S. Terblanche. 2006. Physiological diversity in insects: ecological and evolutionary contexts. *Advances in Insect Physiology* 33: 50–152.		Yes					In many cases, climate change effects are negative and have either resulted in or are predicted to give rise to species extinctions.

Article	Example of vulnerability towards chytridiomycosis	Example of vulnerability towards climate change	Example of climate change promoting the chytridiomycosis	No cause mentioned	Example of APD but no cause related	Example of challenging the hypothesis CTOH	Quotes
Cisneros–Heredia, D.F., J. Delia, M.H. Yáñez–Muñóz and H. M. Ortega–Andrade. 2010. Endemic Ecuadorian glassfrog *Cochranella mache* is critically endangered because of habitat loss. *ORYX* 44: 114–117.						Yes	Diseases and global warming have been linked to some of these declines but the causes of most remain poorly understood.
Clark, D.A. 2007. Detecting tropical forests' responses to global climatic and atmospheric change: current challenges and a way forward. *Biotropica* 39: 4–19.		Yes					As recently illustrated by an analysis of frog extinctions in Costa Rica (Pounds et al. 2006), elevational transects of continuous tropical forest offer an important opportunity for detecting the effects of climate change on tropical forest plants.
Coloma, L.A., S. Lötters, W.E. Duellman and A. Miranda–Leiva. 2007. A taxonomic revision of *Atelopus pachydermus* and description of two new (extinct?) species of *Atelopus* from Ecuador (Anura: Bufonidae). *Zootaxa* 1557: 1–32.	Yes	Yes					Ecuadorian amphibian species are under categories of extinction risk, we emphasize on the challenge of a rapid response and fundamental changes in policies and actions that are required in order to address the amphibian crisis. ... given the novel threats mostly imposed by global warming and pathogens.
Contreras, V., E. Martínez–Meyer, E. Valiente and L. Zambrano. 2009. Recent decline and potential distribution in the last remnant area of the microendemic Mexican axolotl (Ambystoma mexicanum). *Biological Conservation* 142: 2881–2885.		Yes					Climate change has also been identified as an important indirect threat for amphibian populations in recent decades.
Cooper, N., J. Bielby, G.H. Thomas and A. Purvis. 2008. Macroecology and extinction risk correlates of frogs. *Global Ecology and Biogeography* 17: 211–221.			Yes (changes in the environment)				These environmental variables may also be linked directly to extinction risk in frogs since these taxa are very sensitive to changes in the environment (Pounds et al. 2006) that can also increase their susceptibility to other threats, for example the chytrid fungus
Corey, S.J. and T.A. Waite. 2008. Phylogenetic autocorrelation of extinction threat in globally imperilled amphibians. *Diversity and Distributions* 14: 614–629.			Yes				

Article	Example of vulnerability towards chytridiomycosis	Example of vulnerability towards climate change	Example of climate change promoting the chytridiomycosis	No cause mentioned	Example of APD but no cause related	Example of challenging the hypothesis CTOH	Quotes
Crausbay, S.D. and S.C. Hotchkiss. 2010. Strong relationships between vegetation and two perpendicular climate gradients high on a tropical mountain in Hawaii. *Journal of Biogeography* 37: 1160–1174.			Yes				Some of the few studies that do show evidence of tropical biological response also demonstrate that response to climate change can be complicated by powerful secondary effects, including fire, disease and invasive species (Hemp, 2005; Pounds et al. 2006).
Crutzen, P.J. 2006. Albedo enhancement by stratospheric sulfur injections: a contribution to resolve a policy dilemma? *Climatic Change* 77: 211–219.		Yes					Already major species extinctions by current climate warming have been reported by Pounds et al.
Dalgleish, H.J., D.N. Koons and P.B. Adler. Can life–history traits predict the response of forb populations to changes in climate variability? *Journal of Ecology* 98: 209–217.		Yes					
Daly, G.L., Y.D. Lei, C. Teixeira, D.C.G. Muir, L.E. Castillo and F. Wania. 2007. Accumulation of current–use pesticides in neotropical montane forests. *Environmental Science and Technology* 41: 1118–1123.			Yes				Even though pathogens in combination with global warming have recently been implicated in the decline of amphibian populations in the Neotropics, this does not exclude a potential role of contaminants in this disturbing phenomenon.
Deichmann, J.L., G.B. Williamson, A.P. Lima and W. D. Allmon. A note on amphibian decline in a central Amazonian lowland forest. *Biodiversity and Conservation* 19: 3619–3627.		Yes					Enigmatic decline has been attributed to a number of proximal causes including climate change.
Eugster, W., R. Burkard, F. Holwerda, F.N. Scatena and L A. Bruijnzeel. 2006. Characteristics of fog and fogwater fluxes in a Puerto Rican elfin cloud forest. *Agricultural and Forest Meteorology* 139: 288–306.				Environmental conditions			Cloud forests have been reported to be very susceptible to changes in environmental conditions.

Article	Example of vulnerability towards chytridiomycosis	Example of vulnerability towards climate change	Example of climate change promoting the chytridiomycosis	No cause mentioned	Example of APD but no cause related	Example of challenging the hypothesis CTOH	Quotes
Fouquet, A., G.F. Ficetola, A. Haigh and N. Gemmell. Using ecological niche modelling to infer past, present and future environmental suitability for *Leiopelma hochstetteri*, an endangered New Zealand native frog. *Biological Conservation* 143: 1375–1384.			Yes				This has been the case for New Zealand native frogs (*Leiopelma*) with serious declines due to a climate driven epidemic of chytriomycosis (Bell et al. 2004a; Pounds et al. 2006).
Franco, A.M.A., J.K. Hill, C. Kitschke, Y.C. Collingham, D.B. Roy, R. Fox, B. Huntley and C.D. Thomas. 2006. Impacts of climate warming and habitat loss on extinctions at species' low–latitude range boundaries. *Global Change Biology* 12: 1545–1553.			Yes				Extinctions will often be driven by climate change and other threats acting in concert species.
Gachon, C.M.M., T. Sime–Ngando, M. Strittmatter, A. Chambouvet and G.H. Kim. Algal diseases: Spotlight on a black box. *Trends in Plant Science* 15: 633–640.			Yes				Climate change already affects disease patterns worldwide, and is incriminated in massive sudden extinctions (e.g. ‘frog killer fungus’).
Garner, T.W.J., J.M. Rowcliffe and M.C. Fisher. Climate change, chytridiomycosis or condition: an experimental test of amphibian survival. *Global Change Biology* 17: 667–675.						Yes	The amphibian host/*Batrachochytrium dendrobatidis* (Bd) parasite system is considered by many to be strongly influenced by changes in environmental temperature (Pounds et al. 2006; Bosch et al. 2007; Muths et al. 2008, but see Lips et al. 2008): evidence for this is equivocal.
Gilman, S.E., M.C. Urban, J. Tewksbury, G.W. Gilchrist and R.D. Holt. 2010. A framework for community interactions under climate change. *Trends in Ecology and Evolution* 25: 325–331.			Yes				Empirical evidence suggests that climate-driven changes in interacting species, including pathogen prevalence.
Grasso, R.L., R.M. Coleman and C. Davidson. Palatability and antipredator response of Yosemite Toads (*Anaxyrus canorus*) to nonnative Brook Trout (*Salvelinus fontinalis*) in the Sierra Nevada Mountains of California. *Copeia* 3: 457–462.		Yes					

Article	Example of vulnerability towards chytridiomycosis	Example of vulnerability towards climate change	Example of climate change promoting the chytridiomycosis	No cause mentioned	Example of APD but no cause related	Example of challenging the hypothesis CTOH	Quotes
Jiguet, F., R. Julliard, C.D. Thomas, O. Dehorter, S. E. Newson and D. Couvet. 2006. Thermal range predicts bird population resilience to extreme high temperatures. *Ecology Letters* 9: 1321–1330.		Yes					Projected responses of species to climate change provide strong evidence that anthropogenic climate change represents a serious threat to biodiversity.
Johnson, P.T.J. 2006. Amphibian diversity: decimation by disease. *Proceedings of the National Academy of Sciences of the United States of America* 103: 3011–3012.			Yes				Recent work by Pounds et al. (12), for example, suggests that temperature shifts promote Batrachochytrium infection at certain elevations and may therefore have indirectly driven the loss of numerous harlequin frog species in Central and South America.
Karvonen, A., P. Rintamáki, J. Jokela and E.T. Valtonen. Increasing water temperature and disease risks in aquatic systems: climate change increases the risk of some, but not all, diseases. *International Journal for Parasitology* 40: 1483–1488.			Yes				The risk of parasite and pathogen infections may also increase
Kilpatrick, A.M., C.J. Briggs and P. Daszak. The ecology and impact of chytridiomycosis: an emerging disease of amphibians. *Trends in Ecology and Evolution* 25: 109–118.						Yes	
Koch, P.L. and A.D. Barnosky. 2006. Late quaternary extinctions: state of the debate. *Annual Review of Ecology, Evolution and Systematics* 37: 215–250.		Yes					Global extinctions of some smaller animals are attributed to current warming.
Laurance, W. F. 2008. Global warming and amphibian extinctions in eastern Australia. *Austral Ecology* 33: 1–9.			Yes				Rising temperatures could also alter other features of montane areas, such as ... the diversity and virulence of pathogens.

Article	Example of vulnerability towards chytridiomycosis	Example of vulnerability towards climate change	Example of climate change promoting the chytridiomycosis	No cause mentioned	Example of APD but no cause related	Example of challenging the hypothesis CTOH	Quotes
Lawler, J.J., S.L. Shafer and A.R. Blaustein. 2010. Projected climate impacts for the amphibians of the western hemisphere. *Conservation Biology* 24: 38–50.			Yes				
Lovejoy, T.E. 2006. Protected areas: a prism for a changing world. *Trends in Ecology and Evolution* 21: 329–333.			Yes				It is a complex multi-factorial situation involving pollutants, habitat destruction, climate change and an epidemic pathogen (a chytrid fungus), with increasing evidence of synergism among these.
Loyola, R.D., C.G. Becker, U. Kubota, C.F.B. Haddad, C.R. Fonseca and T.M. Lewinsohn. 2008. Hung out to dry: choice of priority ecoregions for conserving threatened neotropical anurans depends on life–history traits. *Public Library of Science* ONE 3.	Yes						
Mainka, S. A. and G. W. Howard. 2010. Climate change and invasive species: double jeopardy. *Integrative Zoology* 5: 102–111.		Yes					Climate is changing nature before our eyes. Species extirpations (local extinctions) and extinctions of amphibians have been linked with climate change.
McGinnity, P., E. Jennings, E. DeEyto, N. Allott, P. Samuelsson, G. Rogan, K. Whelan and T. Cross. 2009. Impact of naturally spawning captive–bred Atlantic salmon on wild populations: depressed recruitment and increased risk of climate–mediated extinction. *Proceedings of the Royal Society B: Biological Sciences* 276: 3601–3610.			Yes				
Meegaskumbura, M., K. Manamendra–Arachchi, C. J. Schneider and R. Pethiyagoda. 2007. New species amongst Sri Lanka's extinct shrub frogs (Amphibia: Rhacophoridae: Philautus). *Zootaxa* 1397: 1–15.			Yes				Climate-driven epidemic disease.

Article	Example of vulnerability towards chytridiomycosis	Example of vulnerability towards climate change	Example of climate change promoting the chytridiomycosis	No cause mentioned	Example of APD but no cause related	Example of challenging the hypothesis CTOH	Quotes
Mendelson, J.R., K.R. Lips, J.E. Diffendorfer, R.W. Gagliardo, G.B. Rabb, J.P. Collins, Peter Daszak, R. Ibáñez D., et al. 2006. Biodiversity – Confronting amphibian declines and extinctions. *Science* 313: 48–48.			Yes				Global climate change may be encouraging local conditions ideal for Bd's persistence and/or spread.
Millero, F.J. 2007. The marine inorganic carbon cycle. *Chemical Reviews* 107: 308–341.		Yes					The increase in the temperature may cause the extinction of animals examine the carbonate system.
Murray, K.A., L.F. Skerratt, R. Speare and H. McCallum. 2009. Impact and dynamics of disease in species threatened by the amphibian chytrid fungus, *Batrachochytrium dendrobatidis*. *Conservation Biology* 23: 1242–1252.						Yes	There is no evidence that climatic anomalies caused these declines, either directly or as suggested by current models of climate-linked disease outbreaks.
Olivier, A., C. Barbraud, E. Rosecchi, C. Germain and M. Cheylan. Assessing spatial and temporal population dynamics of cryptic species: an example with the European pond turtle. *Ecological Applications* 20: 993–1004.			Yes (but climatic anomalies)				Climate anomalies have been proposed as triggers of die-offs by providing opportunities for fatal chytrid outbreaks.
Page, R.A. and M.J. Ryan. 2006. Social Transmission of novel foraging behaviour in bats: frog calls and their referents. *Current Biology* 16: 1201–1205.				Yes			With the catastrophic and worldwide decline of amphibians.
Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* 37: 637–669.			Yes				Pounds et al. (2006) hypothesised that recent trends toward warmer nights and increased daytime cloud cover have shifted mid-elevation sites (1000–2400 m), where the preponderance of extinctions have occurred, into thermally optimum conditions for the chytrid fungus, *Batrachochytrium dendrobatidis*.

Article	Example of vulnerability towards chytridiomycosis	Example of vulnerability towards climate change	Example of climate change promoting the chytridiomycosis	No cause mentioned	Example of APD but no cause related	Example of challenging the hypothesis CTOH	Quotes
Pauli, H., M. Gottfried, K. Reiter, C. Klettner and G. Grabherr. 2007. Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994–2004) at the GLORIA *master site Schrankogel, Tyrol, Austria. *Global Change Biology* 13: 147–156.		Yes					Climate warming-associated shifts or extirpations at the rear edges of species have been detected.
Pedersen, A.B., K.E. Jones, C.L. Nunn and S. Altizer. 2007. Infectious diseases and extinction risk in wild mammals. *Conservation Biology* 21: 1269–1279.	Yes						
Piha, H., M. Luoto, M. Piha and J. Merilä 2007. Anuran abundance and persistence in agricultural landscapes during a climatic extreme. *Global Change Biology* 13: 300–311.		Yes					Global climate change has been shown to be negatively related with the survival, distribution and abundance of amphibians, as well as influence their breeding phenology.
Pounds, J.A., A.C. Carnaval, R. Puschendorf, C. F. B. Haddad and K. L. Masters. 2006. Responding to amphibian loss. *Science* 314: 1541.			Yes				Evidence suggests that climate change and other factors may contribute to declines by triggering disease outbreaks, which might travel varying distances in wavelike patterns.
Pounds, J.A., M.R. Bustamante, L.A. Coloma, J.A. Consuegra, M. P.L. Fogden, Pru N. Foster, E. La Marca, et al. 2007. Ecology – Pounds et al. reply. *Nature* 447: E5–E6.			Yes				
Puschendorf, R. and F. Bolaños. 2006. Detection of *Batrachochytrium dendrobatidis* in *Eleutherodactylus fitzingeri*: effects of skin sample location and histologic stain. *Journal of Wildlife Diseases* 42: 301–306.	Yes						The chytrid fungus *Batrachochytrium dendrobatidis* has been implicated in amphibian declines around the world.
Puschendorf, R., F. Castañeda and J.R. McCranie. 2006. Chytridiomycosis in wild frogs from Pico Bonito National Park, Honduras. *EcoHealth* 3: 178–181.			Yes				Pounds et al. (2006) found that most of the missing harlequin frog species vanished in warmer than average years.

Article	Example of vulnerability towards chytridiomycosis	Example of vulnerability towards climate change	Example of climate change promoting the chytridiomycosis	No cause mentioned	Example of APD but no cause related	Example of challenging the hypothesis CTOH	Quotes
Raffel, T.R., J.R. Rohr, J.M. Kiesecker and P.J. Hudson. 2006. Negative effects of changing temperature on amphibian immunity under field conditions. *Functional Ecology* 20: 819–828.			Yes				Increased infection risk due to warming trends has recently been implicated in the extinction of many tropical frog species.
Ramsey, J.P., L.K. Reinert, L.K. Harper, D.C. Woodhams and L. A. Rollins–Smith. Immune defences against *Batrachochytrium dendrobatidis*, a fungus linked to global amphibian declines, in the South African clawed frog, *Xenopus laevis*. *Infection and Immunity* 78: 3981–3992.				Yes			
Reading, C.J. 2007. Linking global warming to amphibian declines through its effects on female body condition and survivorship. *Oecologia* 151: 125–131.			Yes				What has not been demonstrated, however, is how the link between 'global warming' and amphibian declines operates (Collins and Storfer 2003) though Pounds et al. (2006) have suggested that temperatures in many highland areas are shifting towards the growth optimum for the pathogenic chytrid fungus (*Batrachochytrium dendrobatidis*), thereby encouraging outbreaks.
Rodder, D., M. Veith and S. Lotters. 2008. Environmental gradients explaining the prevalence and intensity of infection with the amphibian chytrid fungus: the host's perspective. *Animal Conservation* 11: 513–517.			Yes				
Rohr, J.R., T.R. Raffel, J.M. Romansic, H. McCallum and P.J. Hudson. 2008. Evaluating the links between climate, disease spread and amphibian declines. *Proceedings of the National Academy of Sciences of the United States of America* 105: 17436–17441.		Yes					

Article	Example of vulnerability towards chytridiomycosis	Example of vulnerability towards climate change	Example of climate change promoting the chytridiomycosis	No cause mentioned	Example of APD but no cause related	Example of challenging the hypothesis CTOH	Quotes
Rosa, I.D., F. Simoncelli, A. Fagotti and R. Pascolini. 2007. Ecology: the proximate cause of frog declines? *Nature* 447.						Yes	We therefore think that the focus by Pounds et al. (2006) on a single pathogen is hard to justify because the host–parasite ecology is at present so poorly understood.
Shearer, C.A., E. Descals, B. Kohlmeyer, J. Kohlmeyer, L. Marvanová, D. Padgett, D. Porter, et al. 2007. Fungal biodiversity in aquatic habitats. *Biodiversity and Conservation* 16: 49–67.			Yes				This chytrid, *Batrachochytrium dendrobatidis*, parasitizes and kills amphibians (Berger et al. 1999) and may be responsible, along with changes in environmental factors such as temperature (Pounds et al. 2006), for the global amphibian decline.
Smith, K.G., K.R. Lips and J.M. Chase. 2009. Selecting for extinction: Nonrandom disease–associated extinction homogenizes amphibian biotas. *Ecology Letters* 12: 1069–1078.						Yes	Recent analyses indicate that there is presently little direct evidence for a role of climate as the widespread, proximate cause of amphibian declines in Lower Central America (cf. Pounds et al. 2006; Lips et al. 2008; Rohr et al. 2008).
Tylianakis, J.M., R.K. Didham, J. Bascompte and D.A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11: 1351–1363.			Yes (but ENSO)				
Underwood, E.C. and B.L. Fisher. 2006. The role of ants in conservation monitoring: If, when and how. *Biological Conservation* 132: 166–182.		Yes					Increases in CO2 and other greenhouse gases in the atmosphere are anticipated to cause detrimental changes to the environment.
Voyles, J., E.B. Rosenblum and L. Berger. 2011. Interactions between *Batrachochytrium dendrobatidis* and its amphibian hosts: a review of pathogenesis and immunity. *Microbes and Infection* 13: 25–32.			Yes				The importance of temperature also prompted the hypothesis that global climate change might create optimal thermal conditions for disease spread (i.e. the chytrid thermal optimum hypothesis).
Wasonga, D.V., A. Bekele, S. Lotters and M. Balakrishnan. 2007. Amphibian abundance and diversity in Meru National Park, Kenya. African *Journal of Ecology* 45: 55–61.		Yes					The survival of the amphibian fauna all over the world is under threat as a result of a variety of causes, apparently related to global change.

Article	Example of vulnerability towards chytridiomycosis	Example of vulnerability towards climate change	Example of climate change promoting the chytridiomycosis	No cause mentioned	Example of APD but no cause related	Example of challenging the hypothesis CTOH	Quotes
Williams, S.E., L.P. Shoo, J.L. Isaac, A.A. Hoffmann and G. Langham. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *Public Library of Science Biology* 6: 2621–2626.		Yes					
Witte, C.L., M.. Sredl, A.S. Kane and L.L. Hungerford. 2008. Epidemiologic analysis of factors associated with local disappearances of native ranid frogs in Arizona. *Conservation Biology* 22: 375–383.			Yes				
Woodhams, D.C., R.A. Alford, C.J. Briggs, M. Johnson and L.A. Rollins–Smith. 2008. Life–history trade–offs influence disease in changing climates: strategies of an amphibian pathogen. *Ecology* 89: 1627–1639.			Yes				
Woodhams, D.C., N. Kenyon, S.C. Bell, R.A. Alford, S. Chen, D. Billheimer, Y. Shyr and L.A. Rollins–Smith. 2011. Adaptations of skin peptide defences and possible response to the amphibian chytrid fungus in populations of Australian green–eyed treefrogs, *Litoria genimaculata*. *Diversity and Distributions* 16: 703–712.			Yes (butenvironental co-factors)				Environmental cofactors vary among populations. These may be particularly important in the dynamics of chytridiomycosis.
Woodhams, D.C., K. Ardipradja, R.A. Alford, G. Marantelli, L.K. Reinert and L.A. Rollins–Smith. 2007. Resistance to chytridiomycosis varies among amphibian species and is correlated with skin peptide defenses. *Animal Conservation* 10: 409–417.		Yes					
Zambrano, L., E. Vega, M.L.G. Herrera, E. Prado and V.H. Reynoso. 2007. A population matrix model and population viability analysis to predict the fate of endangered species in highly managed water systems. *Animal Conservation* 10: 297–303.					Yes		

Juvenile of *Agalychnis moreleti,* Nahá 2010

VII. THE EFFECTS OF GOVERNMENTAL PROTECTED AREAS AND SOCIAL INITIATIVES FOR LAND PROTECTION ON THE CONSERVATION OF MEXICAN AMPHIBIANS

“The community which has neither poverty nor riches will always have the noblest principles”.

Plato

This chapter was finished in April 2009, accepted in August, and published in September of the same year in *PloSOne* (see Appendix B). The co-authors that contributed to this work were (in authorship order): Leticia M. Ochoa Ochoa, J. Nicolás Urbina-Cardona, Luis-Bernardo Vázquez, Oscar Flores-Villela and Juan Bezaury-Creel, who kindly gave consent to include this article in the thesis.

Chapter word count including references, tables and appendices: 12,308

Main text: 5,144

ABSTRACT

Traditionally, biodiversity conservation gap analyses have been focused on governmental protected areas (PAs). However, an increasing number of social initiatives in conservation (SICs) are promoting a new perspective for analysis. SICs include all of the efforts that society implements to conserve biodiversity, such as land protection, from private reserves to community zoning plans some of which have generated community-protected areas. This is the first attempt to analyze the status of conservation in Latin America when some of these social initiatives are included. The analyses were focused on amphibians because they are one of the most threatened groups worldwide. Mexico is not an exception, where more than 60% of its amphibians are endemic. We used a niche model approach to map the potential and *real* geographical distribution (extracting the transformed areas) of the endemic amphibians. Based on remnant distribution, all the species have suffered some degree of loss, but 36 species have lost more than 50% of their potential distribution. For 50 micro-endemic species we could not model their potential distribution range due to the small number of records per species, therefore the analyses were performed using these records directly. We then evaluated the efficiency of the existing set of governmental protected areas and established the contribution of social initiatives (private and community) for land protection for amphibian conservation. We found that most of the species have some proportion of their potential ecological niche distribution protected, but 20% are not protected at all within governmental PAs. 73% of endemic and 26% of micro-endemic amphibians are represented within SICs. However, 30 micro-endemic species are not represented within either governmental PAs or SICs. This study shows how the role of land conservation through social initiatives is therefore becoming a crucial element for an important number of species not protected by governmental PAs.

Keywords: Amphibians, Ecological Niche Loss, Gap Analysis, Niche-Based Distributions, Protected Areas, Conservation Social Efforts, Mexico.

INTRODUCTION

The rapid growth of anthropogenic activities has expanded cattle and agriculture frontiers into natural habitats, transforming ecosystems into fragmented, semi-natural landscapes [1]. A large amount of native habitat has been transformed into numerous smaller forest patches isolated and surrounded by a matrix of pasture, cultivated land, and secondary re-growth vegetation [2, 3]. A key strategy for protecting biodiversity from external pressures has been the establishment and maintenance of Protected Areas (PAs). However, current PAs remain isolated from one another, and in many cases, natural biological pathways for plant and animal dispersal became disrupted by anthropogenic barriers [4, 5]. This anthropogenic matrix occupies, in several places, the majority of the landscape and acts as a filter for dispersal of animals between forest patches [6, 7]. In this sense, isolated PAs managed by either federal or local governments alone are not effective in maintaining biodiversity; thus, the necessity of developing representative and interconnected conservation area networks to preserve biodiversity is becoming more important [8]. Recently, several calls have been made to recognise local participation as a core element of conservation strategies [9, 10]. Social initiatives for land conservation therefore play a crucial role in increasing the range of protection of threatened and endemic species, thus ensuring their persistence. These social initiatives are based on a cooperation scheme where strong social participation is used to implement conservation actions.

In Mexico, 528 PAs have been established (Fig. VII-1) by the three government jurisdictions: 163 federal, 278 state, and 87 municipal, with a total of 18,513,089 ha constituting 9.4% of continental Mexico [11, updated to 31/12/2008]. Mexico's National Protected Area Commission (CONANP – the *Comisión Nacional* *de Áreas Naturales Protegidas*) is currently managing three provisionally demarcated natural resources protection areas, within national irrigation districts' watersheds, representing 3,123,127 additional ha. However, many of these PAs have been established for reasons unconnected to biodiversity protection, and the representation of some important ecosystems such as temperate and tropical dry forests is still not adequate.

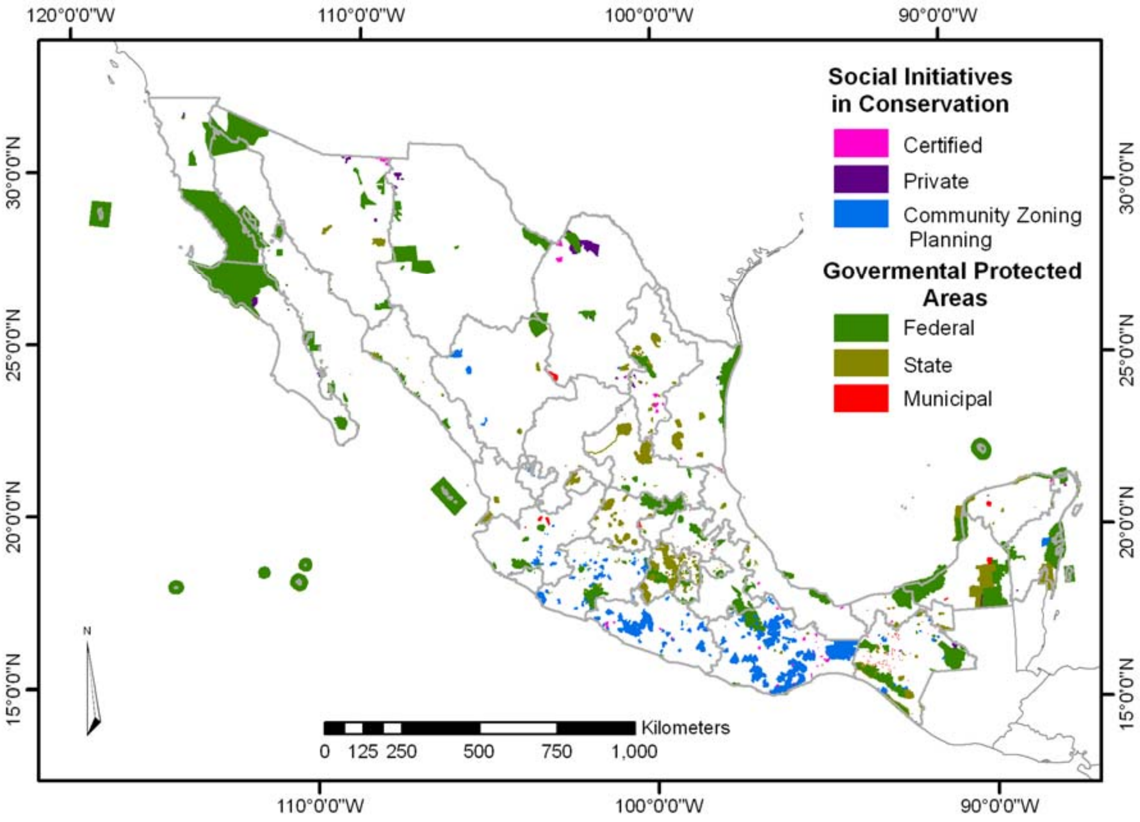

Figure VII-1. Protected Areas of Mexico. Dark green polygons represent federal governmental PAs, pale green polygons state PAs, and red polygons municipal PAs. Light blue polygons represent community land zoning efforts, pink polygons include land protection social action initiatives through private protected areas and purple polygons include certified areas by CONANP.

Social initiatives in conservation (SICs) include all the efforts from society to protect land with the ultimate purpose of conserving biodiversity. SICs are divided into two groups, private and community, depending on the nature of the land ownership (Fig-VII-1). Private and community land protection initiatives are not new in Mexico; the

Mayan “*pet kot*” was a certain patch of forest where useful trees were protected and planted to provide food, fiber, medicine, and other basic needs [12]. Probably the first known private protected area in Mexico was established around 1824 by the German botanist Karl Sartorius at El Mirador (his coffee plantation near the town of Huatusco), in the state of Veracruz [13]. Botanists and zoologists like Wilheim Karwinski, Auguste Sallé, Ferdinand Deppé, Theodore Harwegg, Karl Heller, and others who described new taxa, used El Mirador as a research station.

More recently, special governmental forestry and conservation projects such as Biodiversity Conservation by Indigenous (or Native) Communities (COINBIO – *Conservación de la Biodiversidad por Comunidades e Indígenas*), Conservation and Sustainable Management of Forest Resources in Mexico (PROCYMAF – *Proyecto de Conservación y Manejo Sustentable de Recursos Forestales en México*), and Integrated Ecosystem Management in Three Priority Ecoregions (MIE – *Proyecto de Manejo Integrado de Ecosistemas*) are utilising community zoning planning processes, some of which have generated community protected areas (Fig. VII-1).

Their owners, who manage and protect these land plots, in direct or indirect association with non-governmental organisations, have usually established private protected areas. The National Commission of Natural Protected Areas (CONANP) has promoted a certification process for private and community initiatives. This process implies a formal commitment from the owners to assign certain portions of the property (or even all of it) to conservation for a predetermined period greater than 15 years. By the end of August 2008, at least 637,123 hectares of private and community protected areas were registered in Mexico (0.3% of the country’s area), while CONANP had certified other 202,670 ha (0.1% of the country’s area).

Community zoning plans had been defined within 3,021,863 ha (1.5% of the Mexico's area) [14, 15].

Deforestation of natural areas is the greatest driver of the biodiversity crisis, causing species population extinction and risking the functionality of the world ecosystems [16]. Amphibians, one of the most abundant vertebrate groups in tropical environments [17], play an integral role in connecting aquatic and terrestrial systems by influencing primary production and the transfer of energy and organic matter along food webs, acting as herbivores, predators, and prey [18]. Mexico is the fifth richest country in terms of amphibian species, and it has one of the highest levels of endemism worldwide [19]. From the 373 species of amphibians that have been recorded for Mexico, 228 are endemics, representing more than 60% of the total amphibian fauna in the country. Most of the endemic amphibian species have restricted ranges or are rare in their natural environment [20]. Fragmentation and natural habitat loss threatens 89% of neotropical amphibians [21], affecting them through population isolation, inbreeding, edge effects, and disconnection between aquatic and terrestrial environments [also known as habitat split], both key systems for amphibian reproduction [5, 22]. Evidence suggests that habitat fragmentation poses an even greater extinction risk for endemics and highly rare species because of their habitat specialisation [23-25].

In Mexico, the states most affected by deforestation include those with the greatest number of amphibian species: Oaxaca, Chiapas, Veracruz, Guerrero, Tabasco, Tamaulipas, Campeche, Aguascalientes, Distrito Federal, and Estado de Mexico, a situation that highlights the critical urgency of establishing conservation area networks that connect forest fragments [26].

Factors affecting amphibians that are related to habitat loss (*e.g.* edge and matrix effects) are probably minimised within protected areas. This strategy still seems to be the best option for safeguarding species across multiple spatial scales, and thus *in situ* conservation of viable populations in natural ecosystems is widely recognised as a fundamental requirement for the maintenance of biodiversity [27, 28]. Thus, there is a need to evaluate currently protected amphibian diversity to determine where new protected areas should be established in order to move towards complete coverage [29-31] and define further interconnectivity requirements between protected area units. This approach is called 'gap analysis', a planning approach based on the assessment of the comprehensiveness of existing protected-area networks and the identification of gaps in their coverage [27]. In Mexico, some regional and national gap analyses have revealed that coverage of amphibians by existing national networks of protected areas is, at present, inadequate; García [32] mentioned that only 31% of the amphibians (29% endemics) are actually protected. A more recent analysis, using distribution range models, revealed that *potentially* 75% of the amphibians *are* protected by at least one of the governmental PAs [33].

The Amphibian Conservation Action Plan developed by IUCN's Species Survival Commission indicates, as one of the most important priorities for amphibian conservation, the reinforcement of the management of PAs and the establishment of additional conservation area networks to include the distribution ranges of threatened species that are not protected by the current PA systems [34]. Conservation of amphibians in highly fragmented landscapes requires special management tools, such as habitat restoration and management of forest patches to buffer edge effects, environmental changes and the invasion of species from the matrix, to ensure high habitat quality and species persistence [25, 35]. Therefore, the identification of conservation units that include and connect several ecosystems along natural (such as altitudinal) gradients is crucial to maintaining biological processes operating at broad spatial scales [26-38], alongside the conservation of micro-habitats that allow the protection of micro-endemic and rare species [21].

In this study, we mapped the *potential* and *real* geographical distribution [39] of endemic amphibian species of Mexico in order to: (a) evaluate the efficiency of the existing set of governmental protected areas with respect to the inclusion of Mexican threatened and endemic amphibian species; (b) establish the value of private and community land protection initiatives as a complementary tool to preserve the distribution ranges of threatened and endemic amphibians; and (c) determine the potential loss of distribution ranges due to habitat loss.

RESULTS

Protection within PAs and SICs

Due to the nature of transformed areas associated with established societies (at any scale) and settlements around the country, it is not surprising that the analyses showed that all species have lost habitat (Supplementary Table SI VII-1). Most of the species that we were able to model had at least a small proportion of their remnant distribution range within governmental PAs. These species are probably being protected at the periphery of their range with the core distribution area outside PAs (for further discussion, see [29, 31]). Proportions also varied widely, with no species having 100% of their range within PAs (Supplementary Table SI VII-1). Furthermore, the ranges of *Bolitoglossa riletti, Pseudoeurycea tlahcuiloh,* and *Craugastor omiltemanus* showed 0% coverage within any governmental PA. For large proportion (55.7%) of endemic amphibians—98 species—presented less than 10% of their potential range was within PAs, whilst 49 species had more than 10% but less than 20% of their potential range within the limits of a PA. For 23 species, PAs covered between 20% and 50% of their potential distribution ranges. Finally, data showed that only three species, *Ambystoma altamirani*, *Chiropterotriton magnipes*, and *Craugastor vulcani,* presented more than 50% of their potential ranges within governmental PAs, all of which have small potential range sizes. Just eight (of fifty) species whose potential range was not modelled (micro-endemic) had at least one occurrence within a PA: *Chiropterotriton cracens, C. mosaueri, Dendrotriton megarhinus, Pseudoeurycea gigantea, P. longicauda, Lithobates pueblae, Craugastor batrachylus* and *C. palenque*.

Due to the nature of land protection through social action efforts, most of the areas assigned to conservation are relatively small. Surprisingly, 167 species (95%) were represented in these areas, with most of them, however, in a small proportion of their range (no more than 40%). An important finding was that three species (*Bolitoglossa riletti*, *Pseudoeurycea riletti* and *Craugastor omiltemanus*) that were not protected in governmental PA systems *were* represented within social conservation areas. In addition, 13 micro-endemic species, those without a niche-based model, were represented within social action areas: *Bolitoglossa alberchi, B. oaxacensis, B. zapoteca, Ecnomiohyla echinata, Plectrohyla ameibothalame, P. calvicollina, P. labedactyla, Pseudoeurycea longicauda, P. mixcoatl, P. orchileucus, P. tenchalli, Thorius insperatus* and *Craugastor silvicola.*

Overall, this means that approximately 65% of endemic amphibian species potentially have less than 20% of their distribution range protected, and around 20% are not protected at all within governmental PAs. Nevertheless, 73% of endemic and

26% of micro-endemic amphibians are represented within social conservation areas. However, 30 micro-endemic species are not represented in either governmental PAs or social conservation areas.

Potential loss of distribution ranges

Based on the proportion of the remnant range sizes, we divided the species into four groups: Severely Reduced (SR), Very Reduced (VR), Moderately Reduced (MR) and Less Reduced (LR) (Supplementary Table SI VII-1). Three species conformed to the first group—SR: *Ambystoma mexicanum, A. granulosum* and *Parvimolge townsendii*, all of which have lost more than 80% of their potential range sizes. The VR group included 33 species that have lost more than 50% but less than 80% of their potential distribution ranges. The MR group contained 107 species. Finally, 33 species with less reduced status were those who have lost no more than 20% of their potential distribution range size. There was a strong correlation between potential range size and remnant range size ($Rs= 0.986$ $p> 0.001$), but there was no correlation at all between potential range size and proportion of remnant size ($Rs= 0.009$ $p> 0.9$). This means that species with a small potential range size can have a high proportion of remnant habitat, and species with large potential ranges a small proportion of remnant habitat.

According to the location of the historical records we divided the 50 micro-endemics for which we could not obtain potential distribution models, into 3 groups. The main assumption is that these records are species populations, and are still viable; however, we cannot ascertain if they were collected in secondary vegetation or if disturbance occurred after sampling. The first group considered was very reduced (VR), species that have at least one population within conserved or natural vegetation, and composed of 30 species. The second group, severely reduced (SR), is composed of 11 species that have all their populations in secondary vegetation: *Bolitoglossa zapoteca, Exerodonta abdivita, Plectrohyla calthula, P. calvicollina, P. cembra, P. psarosema, Pseudoeurycea amuzga, P. aquatica, Craugastor palenque, C. polymniae,* and *Eleutherodactylus dennisi.* For the second group the viable population assumption becomes risky, as these species are rare and usually have limited tolerance to environmental changes. That is the case for *P. aquatica*, declared potentially extinct in 2001 [40]. The third group of species, those whose entire known populations were in transformed areas and represent possible extinctions (PE), included: *Plectrohyla labedactyla, P. pachyderma, Pseudoeurycea praecellens, Thorius infernalis, T. minydemus, Craugastor taylori, C. uno, Lithobates psilonota,* and *L. pueblae.* Fortunately, until 2004 there were no species with all of their populations in urbanised zones. New specimens of *C. uno* have been collected recently (E. Smith, G. Santos-Barrera personal communication) but no information about its populations' health is known. However, these are the species of most concern, and a biological survey to determine their population existence and viability is urgently needed (Figure VII-2, SI VII-1-9, and Appendix VII-1, Table SI-1).

DISCUSSION

Our results indicate that the amount of land area conserved through social actions does not contribute *significantly* (in statistical terms) to the conservation of Mexican endemic amphibians. Nevertheless, these local efforts are of extreme importance in preserving those species that are not protected through the governmental PA system. These small patches assigned to conservation allow biodiversity connectivity with PAs, acting as stepping-stones. Taken together, social conservation initiatives are constantly growing and developing through different pathways, such as payment for environmental services, Forest Stewardship Council certification agreements, permanent forestry areas, CONANP certification, and private owners willingly leaving a piece of land for conservation. Unfortunately, not all of these actions have been fully included in spatial databases, notwithstanding current efforts to compile, maintain, and continuously actualise these spatial databases [e.g. 11, 14, 15, 41].

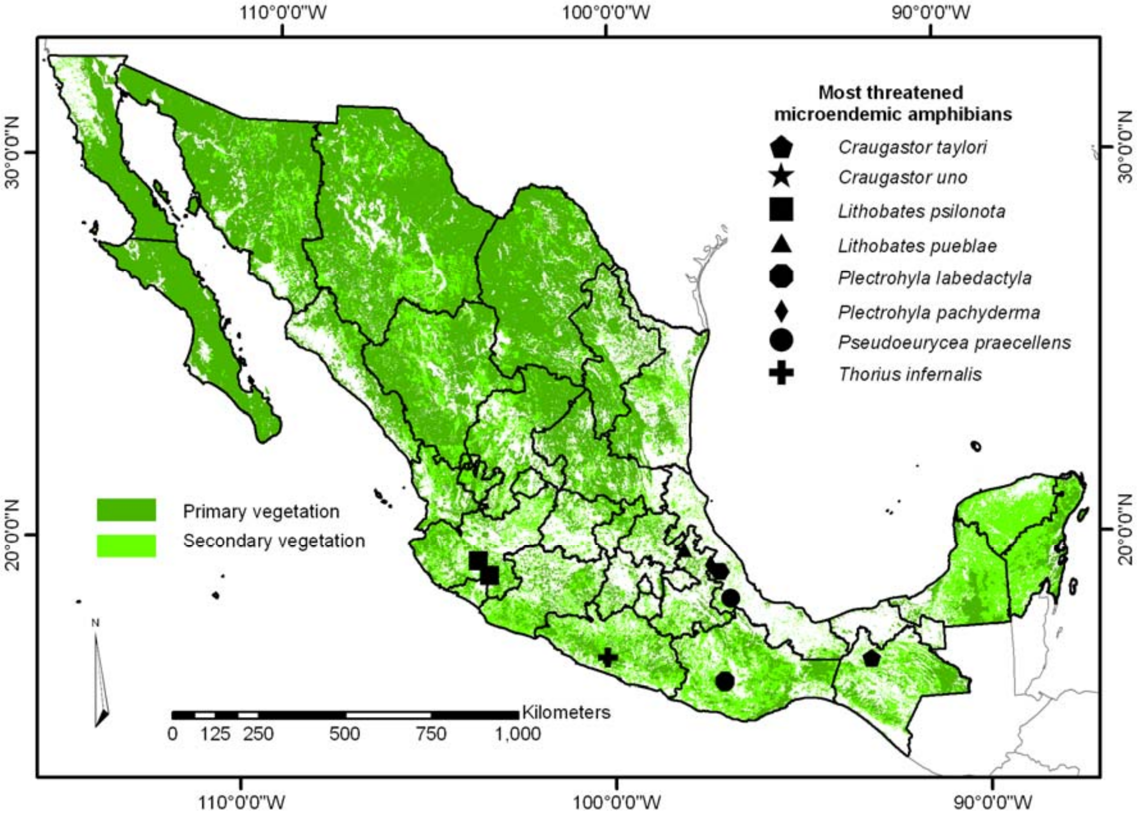

Figure VII-2. Location of the most threatened micro-endemic amphibians in Mexico. Black figures represent the database registers; transformed areas (TA) represented in white; dark-green polygons representing primary and light-green secondary vegetation. *Craugastor uno* and *Thorius infernalis* registers are very close, and the symbols in the map are overlapped, Zoom-in of each species location are available in supporting information (Figs. SI VII-1–9).

We are well aware of caveats derived from modelling species' distributions [31, 42]. Modelling based upon species occurrence data [43] over predicted areas could indicate the occurrence of some phylogenetically closely-related species that are expected to have similar ecological niches and trends [44]. However, in conservation planning, commission and omission errors could lead to preserving sites that do not actually contain the focal species. Such errors would give a false impression of the strength of PAs or SICs in the protection of overall species. For example, one of the great limitations for neotropical conservation is the lack of fine-scale Open Access GIS applications and accurate species geographical records in order to carry out robust gap analyses to implement realistic conservation management plans [35]. It then becomes compulsory to seek more precise error measures and specific validation data, not only through complex statistics but also in the field through monitoring. On the other hand, rapid assessments of species conservation status with biodiversity models could provide insightful approaches for conservation. However, we suggest that in order to make further assertions or predictions, potential distribution ranges would need to be verified in the field.

The complexity of conservation efforts

In most countries and especially in tropical regions, a complex semi-natural matrix dominates the landscape. This landscape is largely a cultural artefact determined by human activities [16]. With this in mind, conservation of biodiversity in landscapes controlled by human activities will be one of the biggest challenges in the next few decades, especially if we are taking into account the synergies caused by changes in species elevation ranges resulting from climate change [35, 45, 46]. Furthermore, it has been demonstrated that during the 20th century the tropical and subtropical regions have experienced more human pressure (population growth, increased agricultural activities, and deforestation) than ever before, threatening amphibians in the most diverse places around the world [47].

The idea of excluding people from protected areas is still supported by some conservationists [48], but in Mexico this approach has fallen out of favour due to its impracticality [49]. In ideal scenarios, conservation areas act as repositories of biota on which evolution can work into the future and may act as refuges of optimal habitat in times of stress. But in many cases, these areas provide only suboptimal habitat or the only suitable habitat remaining for species [50], and suffer from isolation, inadequate planning and management, stochastic events, and cover insufficient areas to maintain viable populations.

Typically, planning regions are exposed, at varying extents, to threats from expanding agriculture, mineral resource extraction, urbanisation, and other sources [51]. The new challenge of conservation biology is to become fully integrated into policy, planning, and management processes that regulate the use of natural resources [50]. Social costs, such as the impact of a plan on local people must be taken into account when prioritising conservation areas that are to be implemented based on budgetary factors (e.g. costs of acquiring lands) [53]. Ethical and other socio-political constraints will determine if prioritised sites will represent and ensure the persistence of biodiversity with minimum overlap with human activities [50, 51].

On the other hand, there is an increasing social concern that natural resources are decreasing around the world. This concern is mostly related to the social perception about the role played by ecosystems on the regulation of several environmental services. And the criticism of land-use policies is becoming more and more common. But conservation is rarely viewed as a local priority and is often driven by donors or other economic causes [52, 53]. However, conservation actions take place at the local level and therefore social initiatives become not only a local priority but also critical a one. In addition, in numerous areas the lack of community trust in governmental institutions has created an atmosphere in which government-led initiatives are not able to succeed. For example, in the states of Oaxaca and Guerrero in Southern Mexico—despite being the first and fourth most biologically rich states in the country, respectively, and housing a high diversity of many micro-endemic salamanders and frogs—there are very few governmental PAs (Fig. VII-1). Moreover, in the last decade at least 33 new amphibian species have been described from these two states alone [54]. Therefore, in those places, social initiatives for conservation become powerful and realistic tools.

Support and work with local communities, emphasising the need for social and economic reforms, is a crucial action for forest conservation [55, 56]. It is important to realise that no matter how many reserves or conservation plans are developed, if local communities or local stakeholders are not truly involved, no plan in conservation—other than those involving truly unpopulated and isolated areas—will be successful. Community involvement is also a basic prerequisite if connectivity between formal conservation areas is to be achieved. Our results show that although the amount of area protected through social efforts is not significant in magnitude, nevertheless for some species it represents the only protected habitat available.

In summary, if a comprehensive goal for biodiversity conservation is going to be achieved, governmental protected areas are only a starting point. There is no doubt that governmental PAs are currently playing a vital role in biodiversity conservation and that social initiatives in conservation for land protection are becoming increasingly important elements for conservation at a landscape level, especially in relation to ecological connectivity. In Mexico in the last few years the percentage of area covered by these social initiatives has increased to 1.5% [14, 15], and it is expected to grow in the near future, since local communities have become aware of the serious environmental problems in the country.

Effective conservation planning and implementation must occur as part of an overarching strategy that considers local, regional and national development strategies within the framework of a global context. The role of land conservation initiatives through social actions, as has been demonstrated for Mexican amphibians, becomes a crucial element for an important number of species not covered by governmental PAs. The importance of social participation in governmental PA creation and management cannot be overstated. Protected areas where the local population was involved since their inception - such as the Sian Ka´an Biosphere Reserve and Xcalak National Park - where due to the limited number of people involved, reaching consensuses was an easier task, contrast greatly with respect to their current governability, with other more socially complex areas such as the Montes Azules, Los Tuxtlas and Manantlán biosphere reserves, where consensus building had to take place only after the fact that the PA had already been established [J. Bezaury, pers. obs.].

Scientists, conservationists, land planners, politicians, and society in general should realise that conservation at the local level is an essential component of the solution for the biodiversity crisis, even though it will not solve the problem *per se*. For example, amphibians are threatened by other causes such as chytridiomycosis, and although in some PAs various measures are being taken (*e.g.* use of Bioclean), it is very difficult to protect amphibians against this disease through any kind of land protection [57]. In Mexico, although the presence of the fungus has been reported, there is no demographic study that confirms amphibian population decline caused by the fungus, but several populations have disappeared due to deforestation.

The effects of other threats on amphibian population dynamics, such as climate change, have not been tested in Mexico. Species migration is possible and although neither SICs nor PAs can stop the consequences of climate change, in this case SICs could play a key role in connecting between PAs, which are usually bigger and thus contain more heterogeneity. It is urgent therefore that periodic field monitoring is carried out, within and outside PAs and SICs, to determine the status of the species at risk of extinction based on periodic field data (*e.g.* Fig. SI VII-1–9).

Adopting balanced patterns of natural resource consumption that are informed by each ecosystem's carrying capacity will ultimately determine the persistence or extinction of viable populations of species. If society does not recognise this, no amount of conservation efforts will stop or even slow down the biodiversity crisis. Recognising and emphasising the priorities of local communities not only stimulates environmentally friendly land-use planning, but also produces positive effects for biodiversity conservation.

Finally, we want to highlight the work that several public and non-governmental institutions across Mexico have undertaken in developing, updating, and providing widespread, open access to spatial databases of governmental PAs and SICs for land protection for conservation of local biodiversity. These types of initiatives are essential for biodiversity analysis, such as the one at hand, and thus become the foundation for conservation planning. The development of such open-source GIS databases should be encouraged and supported by governments in other parts of the world, especially in developing countries where the pressure on natural resources is high and a baseline is needed to take prompt actions.

MATERIALS AND METHODS

We modelled the distribution range for 176 Mexican endemics amphibians using 19 world climatic environmental variables [58], spatial layers for topography, slope and topoindex from 0.01° U.S. Geological Survey's Hydro-1K [59], and a maximum entropy model approach, *MaxEnt* [60]. Maximum entropy niche-based distribution modelling is an innovative analytical approach to evaluate in a standardised way the potential geographical distribution of species along regions lacking comprehensive databases of species distribution [30, 31]. We ran *MaxEnt* under the "auto-features" mode as suggested by Phillips and Dudik [61], configuring the machine-learning algorithm to use 75% of species records for training data set and 25% for testing the model [for details see 61]. We selected the logistic output format because it is robust to unknown prevalence, being also easier to interpret as the estimated species probability of presence given the constraints imposed by environmental variables [31, 61]. In this case, grid cells with small logistic values are predicted to be unsuitable or only marginally suitable for the studied species given their assumed ecological niche. Finally, we reclassified each species map using the 10 percentile training presence of the logistic threshold of the distribution model [31].

The environmental conditions of a predicted ecological niche could be represented in multiple areas along a geographical space; [62] however, species do not use all suitable ecological niches available along the geographical space, as they are constrained by species behaviour, dispersal ability, and inter and intra-specific interactions that take place at local and landscape scales [63, 64]. Urbina-Cardona and Loyola [31] have suggested the use of *MaxEnt* instead of other presence-only methods [64-66] to assess the effectiveness of protected areas in representing endangered amphibian species because this software constrains predicted species ranges, reducing and avoiding commission errors when a model predicts the presence of a given species in particular areas, although it is known that this species is not present there. Although *MaxEnt* generates high omission errors or false negative rates, when a model predicts the absence of a species in particular areas, though it is known that this species is indeed present there [63,67], such errors are preferable when models are conceived for conservation purposes [68].

It is likely that the accuracy of niche models varies systematically across biological groups [30]. It has been demonstrated that species with restricted ecological niche distribution, such as endemics or endangered species, had thin geographical ranges generating more robust and precise niche-based models [69,70]. On the other hand, Loiselle et al. [67] determined that using distribution models that minimise false positives (such as *MaxEnt* models) for well-known taxa, priority areas highlighted for conservation matched those previously selected by experts in biogeography, ecology, and taxonomy.

Even though important efforts have been undertaken by the National Commission for the Use and Knowledge of Biodiversity (CONABIO –*Comisión Nacional para el Uso y Conocimiento de la Biodiversidad*) in creating biological databases for Mexico, currently important geographical areas still lack amphibian collection data [19]. It is also known that extent of occurrence maps obtained through niche-based models can overestimate species current distribution and geographic range sizes, biasing broad-scale ecological patterns and their correlates [71]. Due to a lack of better alternatives, range maps and estimates of species' geographic ranges based on niche-modelling techniques have become the baseline data for many broad-scale analyses in ecology and conservation biogeography [30, 72]. Niche-based distribution modelling is an efficient tool for identifying gaps in current land protection systems, especially when it highlights regions that surround PAs and, therefore, complement proposed conservation plans [51, 72, 73].

We were unable to define a distribution model for 49 species due to the availability of only a few unique records (less than 3) and consequently considered these species as micro-endemics. These species were analysed separately establishing where data points were located in transformed or pristine areas. We assumed that every occurrence data point was a population. We divided the species in three different groups, the first one with at least one population in natural vegetation classified as very reduced (VR), the second one with its entire populations in secondary vegetation as severely reduced (SR), and the third one with its entire populations in transformed areas (agricultural, forestry, farm land or urbanised), as possible local extirpations (PE). These categories were assigned in a more drastic way because these species were assumed to be micro-endemic but overall rare species.

In this study we focused on habitat loss and its repercussions in potential habitats. To evaluate the habitat loss we used the latest (2005) land-use coverage and vegetation layer developed by the Mexican National Institute of Geography and Statistics (INEGI) [74]. This layer was developed using satellite images and field verification [74] and is currently the most accurate information available for the whole country. We extracted from the data set all remnants of primary vegetation from all types to include vegetation in a “pristine” stage and also secondary vegetation that was previously deforested or degraded and is now at some stage of succession. Both vegetation stages were assumed as suitable habitats for amphibian endemic species. We are aware of the assumptions of this procedure, since it is well known that endemics commonly have small distribution ranges because of their specific ecological needs [75]. We believe that even though some species can live in disturbed areas, an important proportion of “covered” areas classified as natural vegetation suffer from the “empty forest” syndrome [76], or simply the natural patches are so small that the edge effects cannot be avoided, and some species are unable to persist [7, 25]. This compensates for the omission error, and therefore, the analyses are balanced.

In order to evaluate the proportion of species of amphibians included within governmental PAs, we utilised the published spatial distribution layers [11, 77]; these spatial databases are the first to provide information on protected areas created by state and municipal governments in Mexico. Federal Protected Areas layers used were modified from those developed by CONANP. Spatial layers for land protection through SICs in Mexico were also developed [see 14, 15, 41]. Initiatives covered by the above-mentioned layers include private and community protected areas—some of which have been certified by CONANP—and community zoning plans. This last category still has a wide uncertainty margin.

Since overlaps between governmental decrees would result in double counting of surface areas, we extracted all overlaps giving them a hierarchical priority. Federal PAs superseded state PAs (except for natural resource protection areas, where state PAs do prevail by law), and state PAs prevailed over municipal ones. Finally, only land protection initiatives through social action occurring outside governmental PAs were taken into consideration.

After extracting overlapped areas, we determined the extent of the ranges occurring inside governmental PAs and those located within lands protected through social action. We quantified the extent of ranges located within both categories and measured whether there was a significant difference in the amount of area protected through social action.

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APPENDIX VII-1

Table SI VII-1. List of endemic Mexican amphibians used in this analysis. Each species[+] has its number of unique records, values of the training model or area under the curve (AUC), size of the distribution range model, amount of remnant distribution and threatened status according with IUCN*, NOM-ECOL 2001** and remnant distribution range group***.

+ The species authors and scientific names are according to compendium from Flores-Villela (unpublished data) and the amphibian species of the world (http://research.amnh.org/herpetology/amphibia/).

*IUCN categories: CE=critically endangered, E=endangered, V=vulnerable, NT=near threatened, LT=least concern, and DD=data deficient.

**NOM-ECOL: A=threatened, P=protected, Pr=special protection.

***Group: PE=Possible extinctions, SR= severely reduced, VR= very threatened, MR= medium reduced, LR= low reduced (see text for more details).

Species Name	**IUCN**	**NOM ECOL**	**Number of unique points**	**Group**	**Training AUC**	**10 percentile training presence**		**Potential Range (ha)**	**Remnent Range (ha)**	**Remnent Range (%)**	**PA (ha)**	**PA (%)**	**Social Efforts (ha)**	**Social Efforts (%)**	**Total area protected (%)**
						p values	**Reclass value**								
Ambystoma altamirani Dugès, 1895	E	A	63	VR	1	7.45E-36	0.886	607,399	273,420	45.01	149,214	54.57	2,265	0.83	55.40
Ambystoma amblycephalum Taylor, 1940	CE	Pr	9	VR	0.999	6.76E-6	0.783	2,689,522	1,273,736	47.36	156,571	12.29	44,730	3.51	15.80
Ambystoma andersoni Krebs and Brandon, 1984	CE	Pr	6	MR	1	0.00E+00	0.925	1,013,714	786,035	77.54	17,413	2.22	17,885	2.28	4.49

Species Name	IUCN	NOM ECOL	Number of unique points	Group	Training AUC	10 percentile training presence		Potential Range (ha)	Remnent Range (ha)	Remnent Range (%)	PA (ha)	PA (%)	Social Efforts (ha)	Social Efforts (%)	Total area protected (%)
						p values	Reclass value								
Ambystoma dumerili (Dugès, 1870)	CE	Pr	17	VR	1	3.00E-08	0.852	452,168	173,759	38.43	14,533	8.36	5,646	3.25	11.61
Ambystoma flavipiperatum Dixon, 1963	DD	Pr	14	MR	0.999	4.32E-03	0.75	2,169,453	1,121,772	51.71	31,645	2.82	711	0.06	2.88
Ambystoma granulosum Taylor, 1944	CE	Pr	27	SR	1	1.92E-18	0.794	285,660	45,498	15.93	20,661	45.41	0	0.00	45.41
Ambystoma leorae (Taylor, 1943)	CE	A	7	MR	0.999	1.3E-3	0.788	943,953	638,271	67.62	146,033	22.88	49,928	7.82	30.70
Ambystoma lermaense (Taylor, 1940)	CE	Pr	16	VR	0.998	8.00E-12	0.928	192,388	68,773	35.75	22,646	32.93	2,606	3.79	36.72
Ambystoma mexicanum (Shaw and Nodder, 1798)	CE	Pr	16	SR	1	3.2E-11	0.783	277,502	38,303	13.80	11,884	31.03	1,803	4.71	35.73
Ambystoma ordinarium Taylor, 1940	E	Pr	24	MR	1	2.43E-18	0.789	1,276,051	738,480	57.87	68,359	9.26	21,142	2.86	12.12
Ambystoma rivulare (Taylor, 1940)	DD	A	11	MR	0.997	1.00E+00	0.539	6,360,043	4,197,252	65.99	559,713	13.34	590,637	14.07	27.41
Ambystoma rosaceum Taylor, 1941	LC	Pr	157	LR	0.997	0.00E+00	0.506	13,104,247	11,094,720	84.67	718,119	6.47	98,856	0.89	7.36
Ambystoma taylori	CE	Pr	1	MR	-	-	No model	-	-	-	-	-	-	-	-

Species Name	**IUCN**	**NOM ECOL**	**Number of unique points**	**Group**	**Training AUC**	**10 percentile training presence**		**Potential Range (ha)**	**Remnent Range (ha)**	**Remnent Range (%)**	**PA (ha)**	**PA (%)**	**Social Efforts (ha)**	**Social Efforts (%)**	**Total area protected (%)**
						p values	**Reclass value**								
Brandon, Maruska and Rumph, 1982															
Ambystoma velasci (Dugès, 1888)	LC	Pr	19	VR	0.996	1.96E-05	0.735	3,119,925	630,903	20.22	87,112	13.81	9,223	1.46	15.27
Anaxyrus compactilis (Wiegmann, 1833)	LC		266	MR	0.992	0.00E+00	0.45	36,028,493	20,517,538	56.95	1,246,274	6.07	164,288	0.80	6.87
Anaxyrus kelloggi (Taylor, 1938)	LC		139	MR	0.999	0.00E+00	0.588	5,253,291	2,717,114	51.72	64,557	2.38	268	0.01	2.39
Anaxyrus mexicanus (Brocchi, 1879)	NT		80	LR	0.996	2.06E-26	0.398	14,411,290	12,614,703	87.53	815,144	6.46	155,096	1.23	7.69
Bolitoglossa alberchi García-París, Parra-Olea, Brame and Wake, 2002	LC		3	MR	-	-	No model	-	-	-	-	-	-	-	-
Bolitoglossa hermosa Papenfuss, Wake and Adler, 1984	NT	Pr	3	MR	-	-	No model	-	-	-	-	-	-	-	-
Bolitoglossa macrinii (Lafrentz, 1930)	NT	Pr	17	MR	0.999	1.19E-04	0.645	3,563,056	2,833,442	79.52	76,070	2.68	517,808	18.27	20.96
Bolitoglossa oaxacensis Parra-	DD		1	MR	-	-	No model	-	-	-	-	-	-	-	-

Species Name	IUCN	NOM ECOL	Number of unique points	Group	Training AUC	10 percentile training presence		Potential Range (ha)	Remnent Range (ha)	Remnent Range (%)	PA (ha)	PA (%)	Social Efforts (ha)	Social Efforts (%)	Total area protected (%)
						p values	Reclass value								
Olea, García-París and Wake, 2002															
Bolitoglossa platydactyla (Gray in Cuvier, 1831)	NT	Pr	146	VR	0.999	0.00E+00	0.697	4,817,409	1,479,885	30.72	76,718	5.18	131,282	8.87	14.06
Bolitoglossa riletti Holman, 1964	E	Pr	13	MR	1	2.70E-04	0.824	720,989	523,901	72.66	0	0.00	30,937	5.91	5.91
Bolitoglossa veracrucis Taylor, 1951	E	Pr	1	MR	-	-	No model	-	-	-	-	-	-	-	-
Bolitoglossa yucatana (Peters, 1882)	LC	Pr	16	MR	0.999	2.18E-02	0.553	4,443,514	3,536,485	79.59	203,102	5.74	38,659	1.09	6.84
Bolitoglossa zapoteca Parra-Olea, García-París and Wake, 2002	DD		2	SR	-	-	No model	-	-	-	-	-	-	-	-
Bromeliohyla dendroscarta (Taylor, 1940)	CE		22	MR	1	3.28E-13	0.75	1,590,565	996,176	62.63	78,158	7.85	120,764	12.12	19.97
Charadrahyla altipotens (Duellman, 1968)	CE		9	MR	0.998	2.13E+01	0.296	11,343,876	8,629,706	76.07	642,558	7.45	752,640	8.72	16.17
Charadrahyla chaneque (Duellman, 1961)	CE		27	MR	0.997	1.73E-05	0.757	2,066,633	1,568,604	75.90	82,480	5.26	326,628	20.82	26.08

Species Name	IUCN	NOM ECOL	Number of unique points	Group	Training AUC	10 percentile training presence		Potential Range (ha)	Remnant Range (ha)	Remnant Range (%)	PA (ha)	PA (%)	Social Efforts (ha)	Social Efforts (%)	Total area protected (%)
						p values	Reclass value								
Charadrahyla nephila (Mendelson and Campbell, 1999)	V		28	LR	0.998	1.21E-10	0.899	540,948	478,000	88.36	7,498	1.57	122,167	25.56	27.13
Charadrahyla taeniopus (Günther, 1901)	V		50	VR	1	2.44E-37	0.843	1,078,503	504,149	46.75	79,533	15.78	554	0.11	15.89
Charadrahyla trux (Adler and Dennis, 1972)	CE		4	LR	1	2.00E-04	0.749	541,386	483,778	89.36	4,308	0.89	152,952	31.62	32.51
Chiropterotriton arboreus (Taylor, 1941)	CE	Pr	7	MR	1	1.00E+00	0.925	340,988	212,027	62.18	37,519	17.70	0	0.00	17.70
Chiropterotriton chiropterus (Cope, 1863)	CE	Pr	155	VR	0.999	0.00E+00	0.795	5,671,271	2,626,950	46.32	470,743	17.92	191,782	7.30	25.22
Chiropterotriton chondrostega (Taylor, 1941)	E	Pr	17	VR	1	5.32E-9	0.708	1,819,484	805,031	44.25	92,579	11.50	18,878	2.35	13.85
Chiropterotriton crascens Rabb, 1958	E		1	MR	-	-	No model	-	-	-	-	-	-	-	-
Chiropterotriton dimidiatus (Taylor, 1940)	E	Pr	22	MR	1	0.00E+00	0.961	59,947	33,671	56.17	2,955	8.78	0	0.00	8.78
Chiropterotriton lavae (Taylor, 1942)	CE	Pr	12	MR	1	0.00E+00	0.937	162,127	89,666	55.31	14,383	16.04	1,647	1.84	17.88

Species Name	IUCN	NOM ECOL	Number of unique points	Group	Training AUC	10 percentile training presence		Potential Range (ha)	Remnent Range (ha)	Remnent Range (%)	PA (ha)	PA (%)	Social Efforts (ha)	Social Efforts (%)	Total area protected (%)
						p values	Reclass value								
Chiropterotriton magnipes Rabb, 1965	CE	Pr	21	LR	1	5.00E-01	0.968	82,032	68,609	83.64	47,707	69.54	0	0.00	69.54
Chiropterotriton mosaueri (Woodall, 1941)	DD	Pr	2	MR	-	-	No model	-	-	-	-	-	-	-	-
Chiropterotriton multidentatus (Taylor, 1939)	E	Pr	61	MR	1	2.85E-34	0.786	3,390,979	2,452,344	72.32	635,558	25.92	3,007	0.12	26.04
Chiropterotriton orculus (Cope, 1865)	V		5	MR	0.982	1.00E+00	0.519	2,983,834	2,361,235	79.13	503,877	21.34	294,353	12.47	33.81
Chiropterotriton priscus Rabb, 1956	NT	Pr	30	LR	1	7.29E-22	0.839	358,639	321,350	89.60	14,429	4.49	7,571	2.36	6.85
Chiropterotriton terrestris (Taylor, 1941)	CE		9	MR	1	2.00E-04	0.941	258,932	150,791	58.24	35,528	23.56	0	0.00	23.56
Craugastor batrachylus Taylor, 1940	DD	Pr	3	MR	-	-	No model	-	-	-	-	-	-	-	-
Craugastor berkenbuschii (Peters, 1870)	NT	Pr	91	MR	0.999	1.28E-40	0.616	4,337,328	2,304,774	53.14	111,103	4.82	465,513	20.20	25.02
Craugastor decoratus Taylor, 1942	V	Pr	63	MR	1	1.01E-29	0.795	3,011,351	1,717,277	57.03	282,274	16.44	63,805	3.72	20.15
Craugastor glaucus	CE	Pr	3	MR	-	-	No model	-	-	-	-	-	-	-	-

Species Name	IUCN	NOM ECOL	Number of unique points	Group	Training AUC	10 percentile training presence		Potential Range (ha)	Remnent Range (ha)	Remnent Range (%)	PA (ha)	PA (%)	Social Efforts (ha)	Social Efforts (%)	Total area protected (%)
						p values	Reclass value								
Lynch, 1967															
Craugastor guerreroensis Lynch, 1967	CE	Pr	3	MR	-	-	No model	-	-	-	-	-	-	-	-
Craugastor hobartsmithi Taylor, 1937	E		61	MR	0.996	3.49E-17	0.428	18,609,199	12,151,452	65.30	773,652	6.37	781,229	6.43	12.80
Craugastor megalotympanum Shannon and Werler, 1955	CE	Pr	6	MR	0.999	1.40E-03	0.673	672,105	414,655	61.69	37,581	9.06	91,783	22.13	31.20
Craugastor mexicanus (Brocchi, 1877)	LC		193	MR	0.998	0.00E+00	0.704	6,057,599	4,162,556	68.72	447,943	10.76	632,590	15.20	25.96
Craugastor occidentalis Taylor, 1941	DD		60	MR	0.998	1.45E-17	0.451	10,449,628	7,217,352	69.07	258,003	3.57	71,188	0.99	4.56
Craugastor omiltemanus (Günther, 1900)	E	Pr	16	LR	1	0.00E+00	0.958	197,249	189,171	95.90	0	0.00	56,382	29.80	29.80
Craugastor palenque Campbell and Savage, 2000	DD		2	SR	-	-	No model	-	-	-	-	-	-	-	-
Craugastor pelorus Campbell and Savage, 2000	DD		8	MR	0.987	3.14E-03	0.283	13,756,009	9,095,125	66.12	830,408	9.13	490,361	5.39	14.52
Craugastor polymniae Campbell, Lamar and Hillis,	CE	Pr	1	SR	-	-	No model	-	-	-	-	-	-	-	-

Species Name	**IUCN**	**NOM ECOL**	**Number of unique points**	**Group**	**Training AUC**	**10 percentile training presence**		**Potential Range (ha)**	**Remnent Range (ha)**	**Remnent Range (%)**	**PA (ha)**	**PA (%)**	**Social Efforts (ha)**	**Social Efforts (%)**	**Total area protected (%)**
						p values	**Reclass value**								
1989															
Craugastor pozo Johnson and Savage, 1995	CE		6	MR	0.934	1.30E-01	0.515	7,918,374	5,913,136	74.68	4,844,302	8.19	222,998	3.76	11.95
Craugastor rhodopis (Cope, 1867)	V		166	MR	0.998	0.00E+00	0.772	6,178,527	3,595,340	58.19	329,891	9.18	471,716	13.12	22.30
Craugastor rugulosus (Cope, 1870)	LC		132	MR	0.998	0.00E+00	0.606	9,281,314	6,459,997	69.60	272,212	4.21	942,607	14.59	18.81
Craugastor montanusi Lynch, 1965	E	Pr	8	VR	1	0.00E+00	0.922	171,639	45,872	26.73	12,715	27.72	0	0.00	27.72
Craugastor silvicola Lynch, 1967	E		1	MR	-	-	No model	-	-	-	-	-	-	-	-
Craugastor spatulatus Smith, 1939	E	Pr	38	MR	1	2.24E-22	0.738	1,361,656	1,002,204	73.60	75,617	7.55	161,054	16.07	23.61
Craugastor tarahumaraensis Taylor, 1940	V	Pr	9	LR	0.986	2.00E-03	0.337	49,220,225	43,219,770	87.81	1,642,177	3.80	249,918	0.58	4.38
Craugastor taylori Lynch, 1966	DD	Pr	1	PE	-	-	No model	-	-	-	-	-	-	-	-
Craugastor uno Savage, 1984	E	Pr	1	PE	-	-	No model	-	-	-	-	-	-	-	-

Species Name	IUCN	NOM ECOL	Number of unique points	Group	Training AUC	10 percentile training presence		Potential Range (ha)	Remnent Range (ha)	Remnent Range (%)	PA (ha)	PA (%)	Social Efforts (ha)	Social Efforts (%)	Total area protected (%)
						p values	Reclass value								
Craugastor vocalis Taylor, 1940	LC	Pr	59	MR	0.998	1.60E-25	0.494	10,829,534	7,637,100	70.52	276,300	3.62	103,144	1.35	4.97
Craugastor vulcani Shannon and Werler, 1955	E		61	VR	1	2.05E-41	0.827	248,428	50,439	20.30	39,142	77.60	109	0.22	77.82
Craugastor yucatanensis Lynch, 1965	NT	Pr	9	MR	0.999	5.59E-03	0.667	4,911,430	3,897,306	79.35	857,173	21.99	50,506	1.30	23.29
Cryptotriton adelos (Papenfuss and Wake, 1987)	E		6	LR	0.999	5.5E-3	0.511	3,333,897	2,777,723	83.32	326,588	11.76	361,254	13.01	24.76
Cryptotriton alvarezdeltoroi (Papenfuss and Wake, 1987)	E		2	MR	-	-	No model	-	-	-	-	-	-	-	-
Dendropsophus sartori Fitzinger, 1843	LC		22	MR	1	2.40E-10	0.695	1,617,512	876,053	54.16	21,298	2.43	80,036	9.14	11.57
Dendrotriton megarhinus (Rabb, 1960)	V		3	MR	-	-	No model	-	-	-	-	-	-	-	-
Dendrotriton xolocalcae (Taylor, 1941)	V	Pr	5	VR	1	1.00E+00	0.861	174,937	48,775	27.88	14,670	30.08	0	0.00	30.08
Dermophis oaxacae (Mertens, 1930)	DD	Pr	24	MR	0.993	2.19E-03	0.457	6,085,644	4,522,458	74.31	555,744	12.29	501,661	11.09	23.38
Duellmanohyla chamulae	E	Pr	12	LR	0.994	2.19E-4	0.532	356,552	302,944	84.96	477	0.16	74,380	24.55	24.71

Species Name	IUCN	NOM ECOL	Number of unique points	Group	Training AUC	10 percentile training presence		Potential Range (ha)	Remnent Range (ha)	Remnent Range (%)	PA (ha)	PA (%)	Social Efforts (ha)	Social Efforts (%)	Total area protected (%)
						p values	Reclass value								
(Duellman, 1961)															
Duellmanohyla ignicolor (Duellman, 1961)	E	Pr	16	MR	1	2.70E-11	0.798	10,256,591	7,294,510	71.12	542,669	7.44	736,226	10.09	17.53
Duellmanohyla schmidtorum (Stuart, 1954)	V	Pr	11	MR	0.998	2.79E-04	0.183	15,354,346	10,644,234	69.32	831,439	7.81	815,570	7.66	15.47
Ecnomiohyla echinata (Duellman, 1961)	CE	Pr	3	MR	-	-	No model	-	-	-	-	-	-	-	-
Ecnomiohyla miotympanum (Cope, 1863)	NT		312	MR	0.995	0.00E+00	0.703	25,844,622	16,289,140	63.03	3,001,368	18.43	823,437	5.06	23.48
Ecnomiohyla valancifer (Firschein and Smith, 1956)	CE	Pr	6	MR	1	1.00E+00	0.797	195,577	123,163	62.97	33,696	27.36	25,673	20.84	48.20
Eleutherodactylus angustidigitorum (Taylor, 1940)	V	Pr	48	VR	1	1.13E-36	0.81	1,149,907	574,428	49.95	18,347	3.19	20,673	3.60	6.79
Exerodonta abdivita (Campbell and Duellman, 2000)	DD		2	SR	-	-	No model	-	-	-	-	-	-	-	-
Exerodonta bivocata (Duellman and Hoyt, 1961)	DD		6	MR	0.997	1.00E+00	0.568	2,437,964	1,907,733	78.25	234,004	12.27	255,882	13.41	25.68

Species Name	IUCN	NOM ECOL	Number of unique points	Group	Training AUC	10 percentile training presence		Potential Range (ha)	Remnent Range (ha)	Remnent Range (%)	PA (ha)	PA (%)	Social Efforts (ha)	Social Efforts (%)	Total area protected (%)
						p values	Reclass value								
Exerodonta chimalapa (Mendelson and Campbell, 1994)	E		8	MR	0.99	2.61E-03	0.219	21,955,579	13,919,444	63.40	1,107,265	7.95	1,295,807	9.31	17.26
Exerodonta juanitae (Snyder, 1972)	V	A	15	MR	0.998	8.52E-08	0.415	6,161,741	4,643,981	75.37	249,429	5.37	639,483	13.77	19.14
Exerodonta melanomma (Taylor, 1940)	V	Pr	35	MR	0.999	1.38E-12	0.612	3,735,244	2,583,017	69.15	77,191	2.99	448,367	17.36	20.35
Exerodonta pinorum (Taylor, 1937)	V	Pr	10	MR	0.998	5.04E-05	0.282	10,627,261	7,535,428	70.91	682,674	9.06	768,521	10.20	19.26
Exerodonta smaragdina (Taylor, 1940)	LC	Pr	43	MR	0.997	3.07E-09	0.546	13,121,548	8,395,180	63.98	394,302	4.70	173,654	2.07	6.77
Exerodonta sumichrasti Brocchi, 1879	LC		73	MR	0.995	8.38E-21	0.477	19,640,901	13,136,074	66.88	1,056,029	8.04	1,747,354	13.30	21.34
Exerodonta xera (Mendelson and Campbell, 1994)	V		12	MR	0.985	9.72E-03	0.157	59,600,320	41,975,516	70.43	6,202,655	14.78	1,165,790	2.78	17.55
Hyla eximia Baird, 1854	LC		711	MR	0.994	0.00E+00	0.559	28,661,689	15,964,530	55.70	1,405,576	8.80	201,306	1.26	10.07
Hyla plicata	LC	A	130	VR	0.999	0.00E+00	0.774	4,204,719	1,696,987	40.36	371,961	21.92	44,979	2.65	24.57

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						p values	Reclass value								
Brocchi, 1877															
Lithobates dunni Zweifel, 1957	E	Pr	24	MR	1	0.00E+00	0.888	28,588,818	21,411,518	74.89	1,103,416	5.15	366,628	1.71	6.87
Lithobates johni (Blair, 1965)	E	P	7	MR	0.996	2.08E-02	0.362	13,221,465	9,871,406	74.66	250,473	2.54	5,749	0.06	2.60
Lithobates magnaocularis (Frost and Bagnara, 1974)	LC		113	VR	0.997	0.00E+00	0.533	4,889,816	2,008,760	41.08	75,010	3.73	14,347	0.71	4.45
Lithobates megapoda (Taylor, 1942)	V	Pr	61	VR	0.999	4.11E-24	0.606	6,031,623	2,131,356	35.34	301,980	14.17	6,260	0.29	14.46
Lithobates montezumae (Baird, 1854)	LC	Pr	177	VR	0.999	0.00E+00	0.603	3,989,132	1,874,576	46.99	94,190	5.02	44,355	2.37	7.39
Lithobates neovolcanicus (Hillis and Frost, 1985)	NT	A	48	MR	0.999	3.92E-27	0.609	20,602,034	14,308,846	69.45	1,328,041	9.28	1,343,667	9.39	18.67
Lithobates omiltemanus (Günther, 1900)	CE	P	12	MR	0.988	1.24E-03	0.371	6,654,238	5,155,499	77.48	157,150	3.05	16,687	0.32	3.37
Lithobates psilonota (Webb, 2001)	DD		2	PE	-	-	No model	-	-	-	-	-	-	-	-
Lithobates pueblae Zweifel, 1955)	CE	P	1	PE	-	-	No model	-	-	-	-	-	-	-	-

Species Name	IUCN	NOM ECOL	Number of unique points	Group	Training AUC	10 percentile training presence		Potential Range (ha)	Remnent Range (ha)	Remnent Range (%)	PA (ha)	PA (%)	Social Efforts (ha)	Social Efforts (%)	Total area protected (%)
						p values	Reclass value								
Lithobates pustulosus (Boulenger, 1883)	LC	Pr	90	MR	0.999	4.54E-04	0.61	6,088,509	4,069,864	66.85	121,507	2.99	565,135	13.89	16.87
Lithobates sierramadrensis (Taylor, 1939)	V	Pr	38	VR	0.999	1.81E-13	0.515	11,269,737	5,535,912	49.12	1,076,380	19.44	210,774	3.81	23.25
Lithobates spectabilis (Hillis and Frost, 1985)	LC		169	VR	0.999	0.00E+00	0.644	1,592,478	583,307	36.63	49,018	8.40	13,177	2.26	10.66
Lithobates tlaloci (Hillis and Frost, 1985)	CE	P	9	MR	0.999	1.02E-05	0.603	13,569,308	8,780,599	64.71	867,629	9.88	604,390	6.88	16.76
Lithobates zweifeli (Hillis, Frost, and Webb, 1984)	LC		98	VR	0.997	7.66E-37	0.526	6,512,422	2,921,706	44.86	85,489	2.93	9,541	0.33	3.25
Megastomatohyla mixe (Duellman, 1965)	CE	Pr	6	MR	0.995	1.64E-02	0.323	13,044,805	8,720,574	66.85	707,714	8.12	737,526	8.46	16.57
Megastomatohyla mixomaculata (Taylor, 1950)	E	A	15	VR	1	0.00E+00	0.935	121,739	27,724	22.77	589	2.13	422	1.52	3.65
Megastomatohyla nubicola (Duellman, 1964)	E	A	6	VR	1	0.00E+00	0.96	213,691	59,943	28.05	10,423	17.39	4,571	7.63	25.01
Megastomatohyla pellita (Duellman, 1968)	CE		7	MR	0.997	1.00E+00	0.584	3,490,566	2,572,708	73.70	127,714	4.96	371,446	14.44	19.40

Species Name	IUCN	NOM ECOL	Number of unique points	Group	Training AUC	10 percentile training presence		Potential Range (ha)	Remnent Range (ha)	Remnent Range (%)	PA (ha)	PA (%)	Social Efforts (ha)	Social Efforts (%)	Total area protected (%)
						p values	Reclass value								
Incilius cristatus (Wiegmann, 1833)	CE	Pr	44	VR	0.997	6.87E-15	0.468	15,101,286	7,389,690	48.93	1,112,693	15.06	742,274	10.04	25.10
Incilius gemmifer (Taylor, 1940)	E	Pr	12	MR	0.999	3.48E-02	0.178	5,964,334	3,445,594	57.77	120,030	3.48	318,733	9.25	12.73
Incilius marmoreus (Wiegmann, 1833)	LC		526	MR	0.995	0.00E+00	0.527	26,436,171	16,260,446	61.51	714,829	4.40	1,190,774	7.32	11.72
Incilius mazatlanensis (Taylor, 1940)	LC		691	MR	0.996	0.00E+00	0.599	14,275,158	9,668,143	67.73	267,794	2.77	5,804	0.06	2.83
Incilius occidentalis (Camerano, 1879)	LC		641	MR	0.99	0.00E+00	0.509	45,041,798	27,965,712	62.09	1,949,074	6.97	884,892	3.16	10.13
Incilius perplexus (Taylor, 1943)	E		154	MR	0.999	0.00E+00	0.66	6,282,379	3,591,758	57.17	165,791	4.62	165,019	4.59	9.21
Incilius spiculatus (Mendelson, 1997)	E		18	MR	0.967	7.70E-01	0.054	70,610,876	45,795,809	64.86	3,724,010	8.13	2,152,745	4.70	12.83
Pachymedusa dacnicolor (Cope, 1864)	LC		598	MR	0.996	0.00E+00	0.561	16,784,217	10,047,759	59.86	358,003	3.56	278,854	2.78	6.34
Parvimolge townsendi (Dunn, 1922)	CE	A	20	SR	1	0.00E+00	0.955	140,363	27,163	19.35	2,128	7.83	276	1.01	8.85
Plectrohyla acanthodes	CE	Pr	17	MR	0.985	4.52E-09	0.703	4,743,090	3,421,225	72.13	470,127	13.74	513,498	15.01	28.75

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						p values	Reclass value								
Duellman and Campbell, 1992															
Plectrohyla ameibothalame (Canseco-Márquez, Mendelson, and Gutiérrez-Mayén, 2002)	DD		3	MR	-	-	No model	-	-	-	-	-	-	-	-
Plectrohyla arborescandens (Taylor, 1939)	E	Pr	35	VR	0.999	1.08E-14	0.659	7,033,668	3,296,155	46.86	480,252	14.57	201,681	6.12	20.69
Plectrohyla bistincta (Cope, 1877)	LC	Pr	65	MR	0.997	3.84E-02	0.492	13,474,644	9,129,476	67.75	901,781	9.88	940,211	10.30	20.18
Plectrohyla calthula (Ustach, Mendelson, McDiarmid, and Campbell, 2000)	CE		3	SR	-	-	No model	-	-	-	-	-	-	-	-
Plectrohyla calvicollina (Toal, 1994)	CE		2	SR	-	-	No model	-	-	-	-	-	-	-	-
Plectrohyla celata (Toal and Mendelson, 1995)	CE		13	LR	1	1.69E-06	0.671	1,065,394	930,963	87.38	107,787	11.58	176,932	19.01	30.58
Plectrohyla cembra (Caldwell, 1974)	CE		2	SR	-	-	No model	-	-	-	-	-	-	-	-
Plectrohyla charadricola (Duellman, 1964)	E	Pr	43	MR	0.999	2.62E-31	0.888	1,030,330	527,265	51.17	93,654	17.76	34	0.01	17.77

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						p values	Reclass value								
Plectrohyla chryses (Adler, 1965)	CE	Pr	8	LR	1	1.00E+00	0.861	323,771	306,746	94.74	6,458	2.11	99,479	32.43	34.54
Plectrohyla crassa (Brocchi, 1877)	CE	Pr	9	MR	0.977	2.79E-03	0.395	28,611,331	21,300,606	74.45	2,043,004	9.59	1,462,876	6.87	16.46
Plectrohyla cyanomma (Caldwell, 1974)	CE	Pr	11	LR	1	1.00E+00	0.843	365,086	323,176	88.52	24,501	7.58	82,194	25.43	33.01
Plectrohyla cyclada (Campbell and Duellman, 2000)	E		38	MR	0.999	4.26E-18	0.675	5,254,221	3,526,572	67.12	517,467	14.67	420,341	11.92	26.59
Plectrohyla hazelae (Taylor, 1940)	CE	Pr	15	MR	0.995	4.65E-04	0.543	12,072,789	8,130,909	67.35	870,993	10.71	669,338	8.23	18.94
Plectrohyla labedactyla (Mendelson and Toal, 1996)	DD		1	PE	-	-	No model	-	-	-	-	-	-	-	-
Plectrohyla lacertosa Bumzahem and Smith, 1954	E	Pr	12	MR	0.999	7.39E-03	0.496	4,850,518	3,738,829	77.08	384,673	10.29	432,048	11.56	21.84
Plectrohyla mykter (Adler and Dennis, 1972)	E	Pr	9	LR	1	1.80E-03	0.686	1,236,909	1,059,116	85.63	81,657	7.71	240,825	22.74	30.45
Plectrohyla pachyderma (Taylor, 1942)	CE		2	PE	-	-	No model	-	-	-	-	-	-	-	-
Plectrohyla pentheter	E		25	LR	0.999	1.68E-01	0.684	2,616,800	2,183,944	83.46	139,729	6.40	407,881	18.68	25.07

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						p values	Reclass value								
(Adler, 1965)															
Plectrohyla psarosema (Campbell and Duellman, 2000)	CE		1	SR	-	-	No model	-	-	-	-	-	-	-	-
Plectrohyla robertsorum (Taylor, 1940)	E	Pr	14	VR	1	6.00E-04	0.798	716,127	303,662	42.40	28,611	9.42	1,484	0.49	9.91
Plectrohyla sabrina (Caldwell, 1974)	CE	Pr	9	LR	1	1.00E+00	0.909	294,541	256,651	87.14	6,339	2.47	64,114	24.98	27.45
Plectrohyla siopela (Duellman, 1968)	CE		5	MR	0.992	1.79E-02	0.477	1,243,420	986,586	79.34	163,463	16.57	160,936	16.31	32.88
Plectrohyla thorectes (Adler, 1965)	CE	Pr	10	MR	0.996	1.16E-02	0.527	7,046,246	5,524,164	78.40	441,398	7.99	637,314	11.54	19.53
Plectrohyla pycnochila Rabb, 1959	CE		2	MR	-	-	No model	-	-	-	-	-	-	-	-
Pseudoeurycea ahuitzotl Adler, 1996	CE		1	MR	-	-	No model	-	-	-	-	-	-	-	-
Pseudoeurycea altamontana (Taylor, 1939)	E	Pr	16	MR	1	0.00E+00	0.92	230,265	157,465	68.38	70,860	45.00	6,223	3.95	48.95
Pseudoeurycea amuzga	DD		1	SR	-	-	No model	-	-	-	-	-	-	-	-

Species Name	IUCN	NOM ECOL	Number of unique points	Group	Training AUC	10 percentile training presence		Potential Range (ha)	Remnent Range (ha)	Remnent Range (%)	PA (ha)	PA (%)	Social Efforts (ha)	Social Efforts (%)	Total area protected (%)
						p values	Reclass value								
Pérez-Ramos and Saldaña de la Riva, 2003															
Pseudoeurycea anitae Bogert, 1967	CE	A	4	MR	0.995	1.00E+00	0.621	5,554,314	3,687,809	66.40	22,024	0.60	218,324	5.92	6.52
Pseudoeurycea aquatica Wake and Campbell, 2001	CE		1	SR	-	-	No model	-	-	-	-	-	-	-	-
Pseudoeurycea belli (Gray, 1850)	V	A	224	MR	0.995	0.00E+00	0.557	20,722,191	12,251,242	59.12	1,471,003	12.01	753,465	6.15	18.16
Pseudoeurycea cephalica (Cope, 1865)	NT	A	225	VR	0.999	0.00E+00	0.736	5,377,605	2,497,994	46.45	627,254	25.11	76,772	3.07	28.18
Pseudoeurycea cochranae (Taylor, 1943)	E	A	71	MR	0.998	8.68E-30	0.592	4,872,145	3,245,976	66.62	397,817	12.26	445,189	13.72	25.97
Pseudoeurycea conanti Bogert, 1967	E		2	MR	-	-	No model	-	-	-	-	-	-	-	-
Pseudoeurycea firscheini Shannon and Werler, 1955	E	Pr	7	MR	0.992	1.00E+00	0.511	10,489,350	6,741,673	64.27	880,163	13.06	383,815	5.69	18.75
Pseudoeurycea gadovi (Dunn, 1926)	E	Pr	30	MR	1	8.23E-19	0.847	2,198,478	1,182,410	53.78	288,488	24.40	93,142	7.88	32.28
Pseudoeurycea galeanae	NT	A	20	LR	1	1.30E-13	0.752	642,893	574,277	89.33	48,069	8.37	13,364	2.33	10.70

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						p values	Reclass value								
(Taylor, 1941)															
Pseudoeurycea gigantea (Taylor, 1939)	CE		2	MR	-	-	No model	-	-	-	-	-	-	-	-
Pseudoeurycea juarezi Regal, 1966	CE	A	44	LR	1	1.15E-28	0.898	745,194	626,463	84.07	18,271	2.92	143,436	22.90	25.81
Pseudoeurycea leprosa (Cope, 1869)	V	A	208	VR	0.999	0.00E+00	0.834	3,532,930	1,361,211	38.53	347,974	25.56	39,241	2.88	28.45
Pseudoeurycea lineola (Cope, 1865)	E	Pr	28	VR	1	1.50E-07	0.935	300,464	92,219	30.69	8,745	9.48	0	0.00	9.48
Pseudoeurycea longicauda Lynch, Wake and Yang, 1983	E	Pr	3	MR	-	-	No model	-	-	-	-	-	-	-	-
Pseudoeurycea lynchi Parra-Olea, Papenfuss and Wake, 2001	CE		7	VR	1	1.00E+00	0.966	131,050	57,818	44.12	7,673	13.27	44	0.08	13.35
Pseudoeurycea melanomolga (Taylor, 1941)	E	Pr	11	MR	0.998	3.72E-05	0.647	1,667,272	1,109,806	66.56	142,987	12.88	151,055	13.61	26.49
Pseudoeurycea mixcoatl Adler, 1996	DD		3	MR	-	-	No model	-	-	-	-	-	-	-	-
Pseudoeurycea mystax	E	A	6	MR	0.998	8.90E-03	0.533	5,596,410	4,045,761	72.29	506,855	12.53	682,693	16.87	29.40

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						p values	Reclass value								
Bogert, 1967															
Pseudoeurycea nahuacampatepetl Parra-Olea, Papenfuss and Wake, 2001	CE		1	MR	-	-	No model	-	-	-	-	-	-	-	-
Pseudoeurycea nigra (Wake and Johnson, 1989)	CE	P		MR	-	-	No model	-	-	-	-	-	-	-	-
Pseudoeurycea nigromaculata (Taylor, 1941)	CE	Pr	7	MR	0.988	1.00E+00	0.334	65,505,834	43,917,165	67.04	2,426,437	5.53	1,661,750	3.78	9.31
Pseudoeurycea orchileucus (Brodie, Mendelson, and Campbell, 2002)	E		2	MR	-	-	No model	-	-	-	-	-	-	-	-
Pseudoeurycea orchimelas (Brodie, Mendelson, and Campbell, 2002)	E		22	VR	1	1.60E-15	0.854	213,458	100,702	47.18	39,287	39.01	23,349	23.19	62.20
Pseudoeurycea parva Lynch and Wake, 1989	CE	A	4	LR	0.999	2.50E-03	0.586	1,237,082	1,090,592	88.16	106,048	9.72	278,554	25.54	35.27
Pseudoeurycea praecellens (Rabb, 1955)	CE	A	1	PE	-	-	No model	-	-	-	-	-	-	-	-
Pseudoeurycea robertsi	CE	A	19	MR	0.999	0.00E+00	0.923	81,763	54,383	66.51	26,685	49.07	0	0.00	49.07

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						p values	Reclass value								
(Taylor, 1939)															
Pseudoeurycea saltator Lynch and Wake, 1989	CE	A	7	LR	1	8.00E-04	0.77	1,064,497	929,580	87.33	102,833	11.06	162,053	17.43	28.50
Pseudoeurycea scandens Walker, 1955	V	Pr	21	MR	1	1.00E-20	0.942	599,474	409,737	68.35	94,705	23.11	794	0.19	23.31
Pseudoeurycea smithi (Taylor, 1939)	CE	A	50	MR	1	1.86E-30	0.799	1,576,905	1,014,637	64.34	115,265	11.36	191,060	18.83	30.19
Pseudoeurycea tenchalli Adler, 1996	E		1	MR	-	-	No model	-	-	-	-	-	-	-	-
Pseudoeurycea teotepec Adler, 1996	E		1	MR	-	-	No model	-	-	-	-	-	-	-	-
Pseudoeurycea tlahcuiloh Adler, 1996	CE		4	LR	1	1.00E+00	0.947	116,702	105,748	90.61	0	0.00	30,157	28.52	28.52
Pseudoeurycea unguidentis (Taylor, 1941)	CE	A	10	MR	0.96	3.80E-03	0.484	19,580,278	12,366,857	63.16	1,312,794	10.62	1,093,844	8.84	19.46
Pseudoeurycea werleri Darling and Smith, 1954	E	Pr	31	MR	1	0.00E+00	0.947	152,337	86,942	57.07	33,821	38.90	21,328	24.53	63.43
Ptychohyla acrochorda Campbell and Duellman, 2000	DD		11	MR	1	6.25E-06	0.347	2,794,606	2,022,511	72.37	223,116	11.03	289,829	14.33	25.36

Species Name	IUCN	NOM ECOL	Number of unique points	Group	Training AUC	10 percentile training presence		Potential Range (ha)	Remnent Range (ha)	Remnent Range (%)	PA (ha)	PA (%)	Social Efforts (ha)	Social Efforts (%)	Total area protected (%)
						p values	Reclass value								
Ptychohyla erythromma (Taylor, 1937)	E	Pr	6	MR	0.998	1.00E+00	0.576	3,708,083	2,908,034	78.42	170,019	5.85	438,046	15.06	20.91
Ptychohyla leonhardschultzei (Ahl, 1934)	E	Pr	51	LR	0.998	5.38E-02	0.621	5,064,791	4,183,423	82.60	220,570	5.27	741,920	17.73	23.01
Ptychohyla zophodes Campbell and Duellman, 2000	DD		27	MR	1	6.40E-23	0.897	25,844,622	16,289,140	63.03	3,001,368	18.43	823,437	5.06	23.48
Smilisca dentata (Smith, 1957)	E		8	LR	0.998	1.00E+00	0.648	371,278	328,899	88.59	26,766	8.14	81,341	24.73	32.87
Syrrhophus dennisi (Lynch, 1970)	E	Pr	2	SR	-	-	No model	-	-	-	-	-	-	-	-
Syrrhophus dilatus (Davis and Dixon, 1955)	E		11	LR	0.999	2.00E-03	0.826	2,081,371	1,685,173	80.96	94,632	5.62	320,969	19.05	24.66
Eleutherodactylus grandis (Dixon, 1957)	CE	Pr	4	MR	0.999	9.00E-04	0.804	1,020,740	609,933	59.75	45,525	7.46	40,097	6.57	14.04
Eleutherodactylus interorbitalis (Langebartel and Shannon, 1956)	DD	Pr	4	VR	1	1.00E+00	0.711	1,462,038	706,547	48.33	38,435	5.44	691	0.10	5.54
Eleutherodactylus longipes (Baird, 1859)	V		55	MR	0.999	8.56E-22	0.672	5,621,486	4,166,994	74.13	679,480	16.31	2,011	0.05	16.35

Species Name	IUCN	NOM ECOL	Number of unique points	Group	Training AUC	10 percentile training presence		Potential Range (ha)	Remnent Range (ha)	Remnent Range (%)	PA (ha)	PA (%)	Social Efforts (ha)	Social Efforts (%)	Total area protected (%)
						p values	Reclass value								
Eleutherodactylus modestus (Taylor, 1942)	V	Pr	8	MR	0.995	1.46E-02	0.607	9,547,715	6,102,119	63.91	245,410	4.02	286,361	4.69	8.71
Eleutherodactylus nitidus Peters, 1870	LC		333	MR	0.996	0.00E+00	0.56	24,201,586	14,159,980	58.51	1,041,466	7.35	713,944	5.04	12.40
Eleutherodactylus nivicolimae (Dixon and Webb, 1966)	V	Pr	10	MR	0.998	1.30E-05	0.679	5,468,321	3,794,038	69.38	264,100	6.96	42,433	1.12	8.08
Eleutherodactylus pallidus (Duellman, 1958)	DD	Pr	11	MR	1	9.00E-04	0.769	1,587,660	1,114,988	70.23	72,207	6.48	719	0.06	6.54
Eleutherodactylus rufescens (Duellman and Dixon, 1959)	CE	Pr	4	LR	1	1.00E+00	0.91	447,967	405,131	90.44	32,323	7.98	19,136	4.72	12.70
Eleutherodactylus saxatilis (Webb, 1962)	E		7	LR	1	1.00E+00	0.743	862,904	829,349	96.11	29,775	3.59	7,368	0.89	4.48
Eleutherodactylus syristes (Hoyt, 1965)	E	Pr	5	MR	0.991	2.42E-02	0.456	12,619,675	9,096,048	72.08	783,240	8.61	1,086,147	11.94	20.55
Eleutherodactylus teretistes (Duellman, 1958)	DD	Pr	14	MR	0.999	2.52E-05	0.54	4,776,759	3,525,010	73.80	81,864	2.32	6,507	0.18	2.51
Eleutherodactylus verrucipes (Cope, 1885)	V	Pr	70	MR	0.999	4.22E-32	0.821	2,435,947	1,694,518	69.56	386,520	22.81	6,334	0.37	23.18
Thorius arboreus	E		10	LR	1	4.00E-08	0.836	270,852	243,204	89.79	17,649	7.26	63,263	26.01	33.27

Species Name	IUCN	NOM ECOL	Number of unique points	Group	Training AUC	10 percentile training presence		Potential Range (ha)	Remnent Range (ha)	Remnent Range (%)	PA (ha)	PA (%)	Social Efforts (ha)	Social Efforts (%)	Total area protected (%)
						p values	Reclass value								
Hanken and Wake, 1994															
Thorius aureus Hanken and Wake, 1994	CE		6	LR	1	1.00E+00	0.845	1,497,792	1,316,202	87.88	193,811	14.73	230,979	17.55	32.27
Thorius boreas Hanken and Wake, 1994	E		11	MR	0.999	1.00E+00	0.671	180,404	93,977	52.09	12,028	12.80	340	0.36	13.16
Thorius dubitus Taylor, 1941	E	Pr	17	LR	1	3.00E-08	0.93	69,629	66,819	95.96	230	0.34	28,821	43.13	43.48
Thorius grandis Hanken, Wake and Freeman, 1999	E		6	LR	1	0.00E+00	0.937	1,570,503	1,259,591	80.20	229,571	18.23	193,646	15.37	33.60
Thorius infernalis Hanken, Wake and Freeman, 1999	CE		1	PE	-	-	No model	-	-	-	-	-	-	-	-
Thorius insperatus Hanken and Wake, 1994	DD		1	MR	-	-	No model	-	-	-	-	-	-	-	-
Thorius lunaris Hanken and Wake, 1994	E		6	LR	0.998	1.00E+00	0.766	262,368	223,219	85.08	1,584	0.71	70,494	31.58	32.29
Thorius macdougalli Taylor, 1949	V	Pr	42	MR	1	0.00E+00	0.96	29,891,220	21,279,507	71.19	2,286,325	10.74	1,113,353	5.23	15.98

Species Name	IUCN	NOM ECOL	Number of unique points	Group	Training AUC	10 percentile training presence		Potential Range (ha)	Remnent Range (ha)	Remnent Range (%)	PA (ha)	PA (%)	Social Efforts (ha)	Social Efforts (%)	Total area protected (%)
						p values	Reclass value								
Thorius magnipes Hanken and Wake, 1998	CE		8	MR	0.987	1.00E+00	0.274	118,237	69,308	58.62	7,967	11.50	2,704	3.90	15.40
Thorius minutissimus Taylor, 1949	CE	Pr	2	MR	-	-	No model	-	-	-	-	-	-	-	-
Thorius minydemus Hanken and Wake, 1998	CE		2	PE	-	-	No model	-	-	-	-	-	-	-	-
Thorius munificus Hanken and Wake, 1998	CE		9	MR	1	0.00E+00	0.957	196,965	138,660	70.40	31,624	22.81	28,388	20.47	43.28
Thorius narismagnus Shannon and Werler, 1955	CE		7	MR	1	1.00E-04	0.884	2,539,191	1,647,064	64.87	182,363	11.07	226,369	13.74	24.82
Thorius narisovalis Taylor, 1940	CE	Pr	59	LR	0.999	5.88E-35	0.661	529,756	485,238	91.60	7,307	1.51	141,068	29.07	30.58
Thorius omiltemi Hanken, Wake and Freeman, 1999	E		9	VR	1	4.00E-04	0.856	1,769,167	761,947	43.07	78,369	10.29	35,700	4.69	14.97
Thorius papaloe Hanken and Wake, 2001	E		3	MR	-	-	No model	-	-	-	-	-	-	-	-
Thorius pennatulus Cope, 1869	CE	Pr	11	MR	1	1.44E-06	0.631	956,640	609,988	63.76	75,421	12.36	99,392	16.29	28.66

Species Name	IUCN	NOM ECOL	Number of unique points	Group	Training AUC	10 percentile training presence		Potential Range (ha)	Remnent Range (ha)	Remnent Range (%)	PA (ha)	PA (%)	Social Efforts (ha)	Social Efforts (%)	Total area protected (%)
						p values	Reclass value								
Thorius pulmonaris Taylor, 1940	E	Pr	27	LR	1	1.28E-09	0.827	8,440,912	6,798,094	80.54	840,036	12.36	906,004	13.33	25.68
Thorius schmidti Gehlbach, 1959	E	Pr	5	MR	0.991	1.87E-02	0.502	385,064	258,081	67.02	93,530	36.24	9,900	3.84	40.08
Thorius spilogaster Hanken and Wake, 1998	CE		6	VR	1	4.00E-04	0.9	6,434,517	2,825,802	43.92	217,356	7.69	214,174	7.58	15.27
Thorius troglodytes Taylor, 1941	E	Pr	28	MR	1	0.00E+00	0.972	12,473,264	7,884,229	63.21	294,063	3.73	458,101	5.81	9.54
Tlalocohyla godmani (Günther, 1901)	V		25	MR	0.999	3.14E-12	0.609	22,956	16,707	72.78	1,975	11.82	1	0.01	11.83
Tlalocohyla smithii (Boulenger, 1902)	LC		391	MR	0.997	0.00E+00	0.596	4,948,893	2,654,766	53.64	109,741	4.13	76,449	2.88	7.01
Triprion petasatus (Cope, 1865)	LC	Pr		MR	-	-	No model	-	-	-	-	-	-	-	-

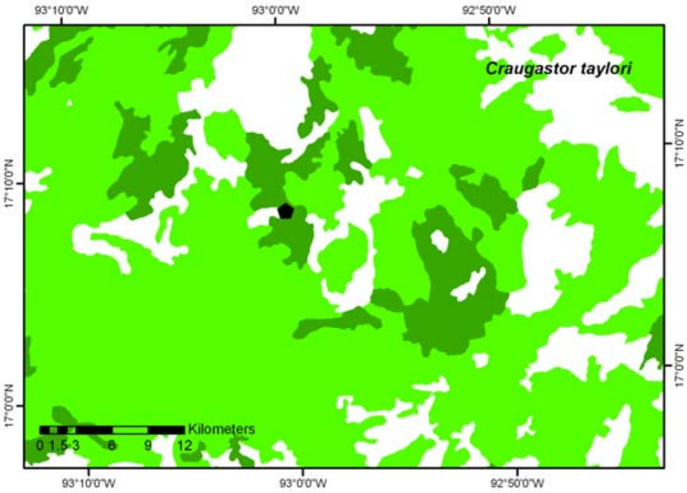

Figure SI VII-1. Zoom-in to the location of *Craugastor taylori* historical (database) records. In dark green, conserved forest; secondary forest in light green, and disturbed areas in white.

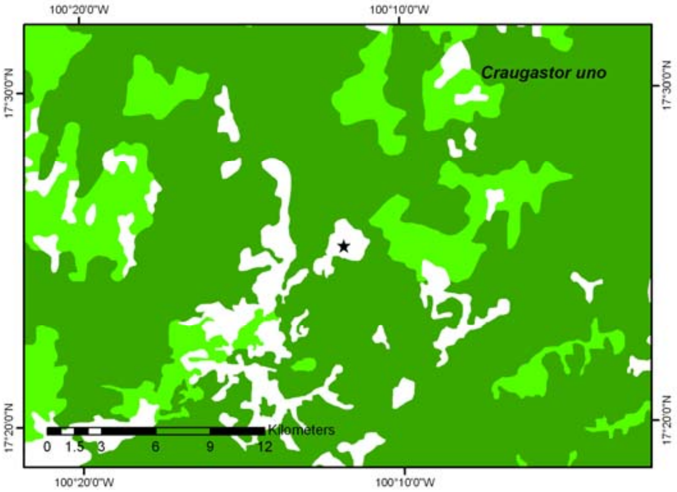

Figure SI VII-2. Zoom-in to the location of *Craugastor uno* historical (database) records. In dark green, conserved forest; secondary forest in light green, and disturbed areas in white.

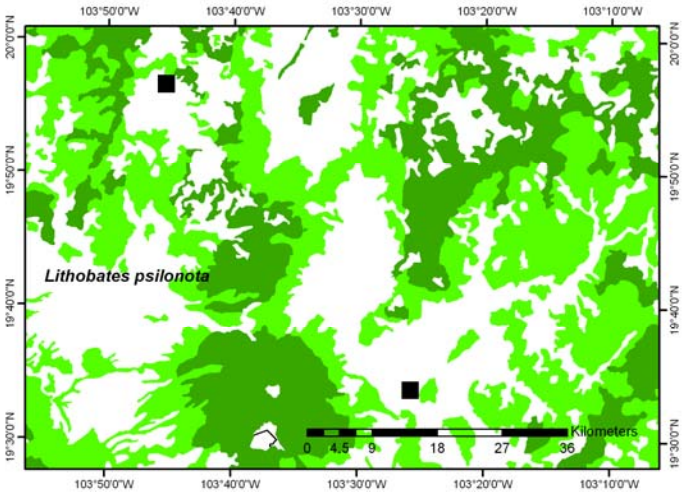

Figure SI VII-3. Zoom-in to the location of *Lithobates psilonota* historical (database) records. In dark green, conserved forest; secondary forest in light green, and disturbed areas in white.

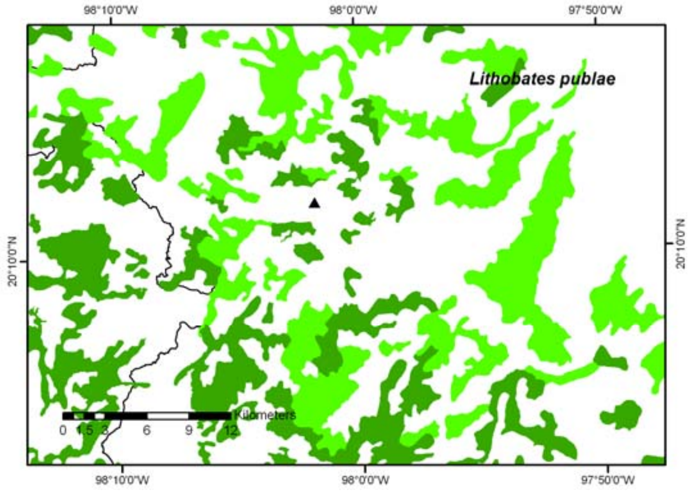

Figure SI VII-4. Zoom-in to the location of *Lithobates publae* historical (database) records. In dark green, conserved forest; secondary forest in light green, and disturbed areas in white.

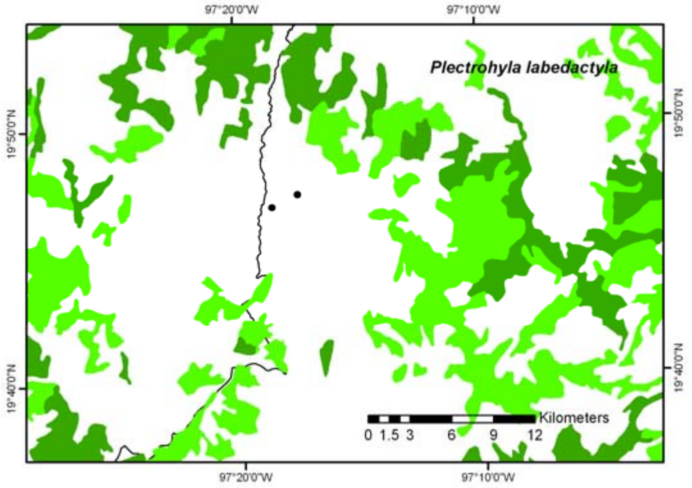

Figure SI VII-5. Zoom-in to the location of *Plectrohyla labedactyla* historical (database) records. In dark green, conserved forest; secondary forest in light green, and disturbed areas in white.

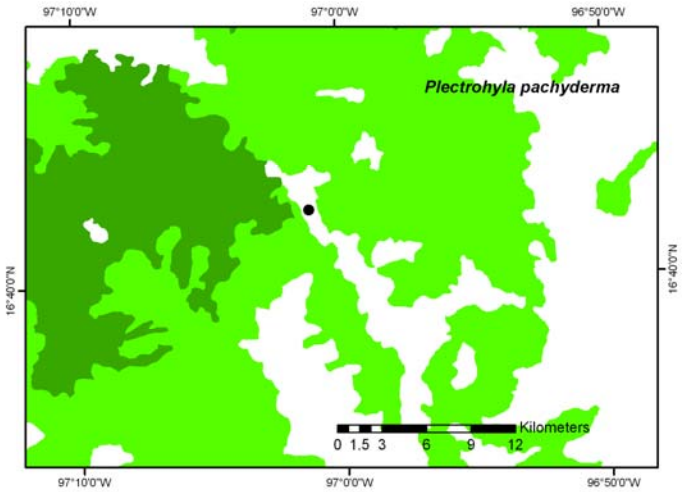

Figure SI VII-6. Zoom-in to the location of *Plectrohyla pachyderma* historical (database) records. In dark green, conserved forest; secondary forest in light green, and disturbed areas in white.

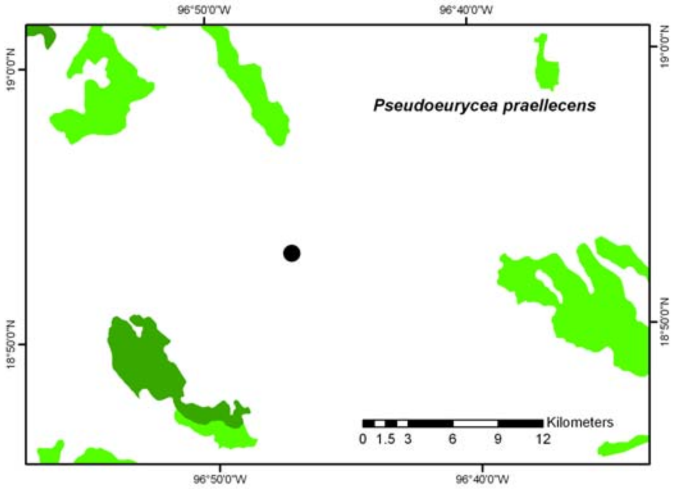

Figure SI VII-7. Zoom-in to the location of *Pseudorycea praellecens* historical (database) records. In dark green, conserved forest; secondary forest in light green, and disturbed areas in white.

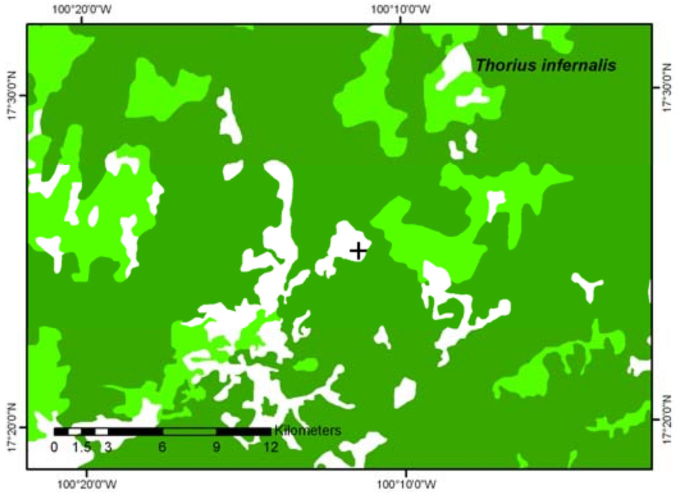

Figure SI VII-8. Zoom-in to the location of *Thorius infernalis* historical (database) records. In dark green, conserved forest; secondary forest in light green, and disturbed areas in white.

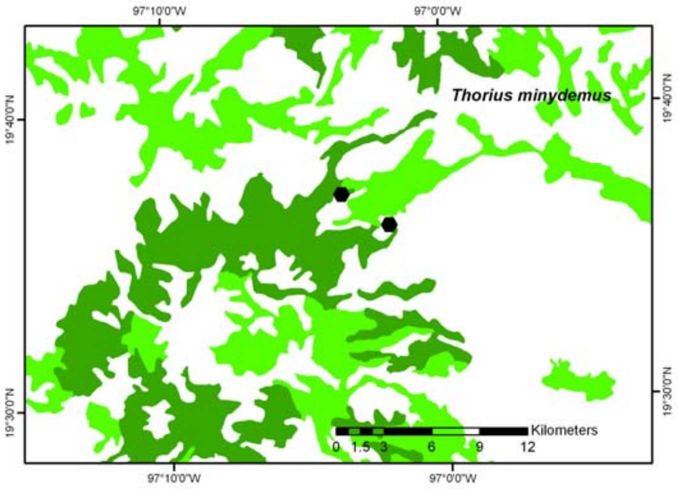

Figure SI VII-9. Zoom-in to the location of *Thorius minydemus* historical (database) records. In dark green, conserved forest; secondary forest in light green, and disturbed areas in white.

Dendrosophus microcephalus, Nahá 2010

VIII. CHOOSING THE SURVIVORS? A GIS-BASED TRIAGE SUPPORT TOOL FOR MICRO-ENDEMICS: APPLICATION TO DATA FOR MEXICAN AMPHIBIANS

“Where there are no swamps, there are no frogs”.

German proverb

This chapter was finished in December 2010, accepted in July, and published in September of the same year in *Biological Conservation* (see Appendix B). The co-authors that contributed to this work were: Leticia M. Ochoa Ochoa, Juan Bezaury-Creel, Luis-Bernardo Vázquez, and Oscar Flores-Villela who kindly gave consent to include this article in the thesis.

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Main text: 5,279

ABSTRACT

Given the current speed of land use change, we cannot expect to save all species from extinction, and so must decide how to focus limited resources to prevent the greatest number of extinctions. This paper proposes a simple conservation triage method that: evaluates the threat status for 145 micro-endemic Mexican amphibian species; assesses current potential threat abatement responses derived from existing policy instruments and social initiatives; and combines both indicators to provide broad-scale conservation strategies that would best suit amphibian micro-endemic buffered areas (AMBAs) in Mexico. To prioritize the AMBAs we used existing and newly compiled spatial databases of territorial conservation instruments, threats, and amphibian range distributions for Mexico. We identify 50% of Mexican micro-endemic amphibians as requiring urgent actions. Based on the location of the AMBAs and using existing conservation instruments, we develop a conservation strategy for the majority of these species. However, almost 25% urgently need field-base verification to confirm their persistence due to the small percentage of remnant natural vegetation within the AMBAs, before we may sensibly recommend such a strategy.

Keywords: amphibians, conservation-triage, environmental policy, GIS, social conservation initiatives, Mexico, micro-endemics.

INTRODUCTION

Since the mid 19th century an increasing preoccupation with biodiversity loss has developed among biologists, culminating with the establishment of specific areas dedicated to conservation. These ideas have been shaped within what we call conservation biology (Soulé, 1985) and conservation biogeography (Whittaker et al., 2005), and have lately permeated into different disciplines, e. g. rural development, land use planning, green technologies, etc. Conservation science has evolved at an unprecedented pace in the last couple of decades stimulated by the immediate need of more efficient and repeatable means of analysis. Systematic conservation planning (SCP) is a continuous process that provides tools for methodical identification of priority areas for conservation of biodiversity (Margules and Pressey, 2000; Margules and Sarkar, 2007). Typically formulated as a minimization approach, SCP sets out to optimize the deployment of resources that need to be allocated to conservation, normally in the form of protected areas (PAs) or other targeted conservation investment. Therefore, the SCP community has focused primarily on developing algorithms (e.g. Marxan, CosNet, ResNet) that allow the user to evaluate and propose protected area networks that optimize biodiversity conservation efforts (Sarkar et al., 2006).

The relevance of PAs for natural resources conservation has been broadly recognized (Hockings, 2003; Rodrigues et al., 2004), since they play an important role in conserving and preserving biodiversity by mitigating human disturbance (Margules and Sarkar, 2007). Herein we refer to PAs as areas that have been officially declared (but see Dudley, 2008). While of crucial importance, PAs are not the only currently available tool that can be used to preserve biodiversity (Rodrigues et al., 2004), since a wide variety of conservation instruments exists in different countries, some of which – depending on local socio-economic and political characteristics – can be better suited for this purpose than others (i.e. social conservation initiatives). Moreover, due to the complex processes and costs involved in establishing and maintaining governmental PAs, this instrument should be visualized as just one tool within the available toolkit. This situation becomes especially significant within the context of mega-diverse countries, such as Mexico, with high regional diversity (gamma) and elevated variation in species composition across communities within a landscape (beta diversity). It has been shown that 43% of the country's land is required to cover all conservation targets included within Mexico's Gap Analysis derived from the Convention of Biological Diversity (CBD) Protected Areas Program (CONABIO et al., 2007).

Most of the people involved in SCP are aware that it is impossible to conserve everything. This is because there are inevitable trade-offs when choosing areas and species to protect, given the *realpolitik* of current land use change tendencies (Prins, 1990; Reitan, 1998). Nevertheless, through the use of conservation triaging tools it is possible to develop strategies designed to minimize the levels of extinction given a specific level of resources. In essence, this approach follows the old political maxim "choose the battles that you can win". Initially, it must be recognised that the strategy adopted depends on what aspects of biodiversity are most highly valued, expressed in conservation goals or targets (e.g. what we want to protect).

Establishing conservation goals is a key but essentially subjective first step of SCP, with important consequences for PA system design. For instance, phylogenetic diversity may be targeted when considering the protection of evolutionary history, functional diversity if ecosystem function is a prime concern, and knowledge of charismatic species' natural history is critical if they are to be given priority. Previous analyses have shown, for example, that analyses focused on the phylogenetic diversity pattern (evolutionary signal) differ from those identifying species richness hotspots (Forest et al., 2007), and the latter will diverge from analyses based on range restricted (endemic) species hotspots (Lamoreux et al., 2006). Consequently, the different solutions for those targets will be spatially dissimilar (e.g. Brooks et al., 2006).

Implementation strategies will also vary. For example, in order to maintain functioning ecosystems, conservation actions should be implemented fast and effectively and must take explicit account of landscape context and ecological linkages in space and time (Daily et al., 1997; Kremen, 2005). Otherwise, conserving charismatic or beautiful species, may lead to targeting resources very precisely to manage programmes of translocation/relocation (e.g. Donlan, 2005). In all cases "choosing the survivors" should not be only related to their evolutionary history, ecosystem functionality or charisma, but also to an appraisal of the threats, resources and the survival prospects of each species within often rapidly changing local circumstances (Caughley, 1994; Devictor et al., 2010).

Species with small range sizes, i.e. micro-endemics, have high irreplaceablability scores (sensu Margules and Pressey, 2000) within SCP analyses. Thus, these species are by definition vulnerable and considered endangered (Sarkar, 1996; IUCN, 2008), particularly from stochastic events, e.g. *Incillius periglenes* (Crump et al., 1992) or *Rheobatrachus silus* (Tyler and Davies, 1985). The alliance for zero extinction (AZE) highlights the need to avoid potential extinction of micro-endemic species (Ricketts et al., 2005).

Our overarching goal is to support prioritization of conservation strategies within the context of often rapidly land use change situations, such as those currently found in Mexico, including the adoption of a wide range of conservation instruments to build-up more efficient strategies. To that end we developed a pragmatic GIS-based method, which can be used as a preliminary evaluation tool for micro-endemic persistence feasibility. We also present a newly compiled spatially referenced data base of land use planning and other policy instruments developed between 2003 and 2009 in Mexico under the auspices of multiple agencies and institutions operating within the country. The analyses are based on Mexican amphibians because they present one of the highest levels of endemism in the World (Flores-Villela, 1993).

Mexico has 372 species of amphibians, 250 of which are endemics (Frías-Alvarez et al., 2010) and 145 micro-endemics, i.e. having ranges < 5 000km^2. Most of the micro-endemics occur in mountain ranges (cf. Urbina-Cardona and Flores-Villela, 2010 for reptiles), which can be considered as areas of enhanced diversification rates (Smith et al., 2007). Thus it is important to assess the overall value of each micro-endemic species range, in terms of the richness of the area in other micro-endemics, wider ranging endemics and other native species of amphibians, i.e. to assess the *umbrella* value of those areas for conservation for Mexican amphibians.

Specific objectives of this paper include: 1) assessing the threat status of Mexican micro-endemic amphibian species; 2) evaluating the potential threat abatement conservation response derived from existing policy instruments and social initiatives; and, 3) through combining the previous indicators, propose broad scale indicators of feasible conservation strategies for amphibian micro-endemic areas (AMBAs) across Mexico. Within this assessment we include a prioritization of actions that could be performed to enable the persistence of micro-endemic amphibian species in Mexico.

MATERIALS AND METHODS

Through this method we seek to prioritize Mexican amphibian micro-endemics occurring within the AMBAs, taking into account their current threat level and to suggest policy and social conservation instruments that will facilitate their continued existence. The list of Mexican endemic amphibians was derived from UNAM's Museum of Zoology of the Sciences Faculty (MZFC) database. The database consists of geo-referenced species' presence records, gathered from various museums worldwide, and was geographically and taxonomically verified by experts (for further details, see Ochoa-Ochoa, 2006). As in any other database, sampling effort is spatially biased (see maps published in Pineda and Lobo 2009 for Mexican amphibians). According to the latest literature revision, 372 amphibian species are native to Mexico, of which 250 (> 67%) are endemics (Frías-Alvarez et al., 2010) and 145 (58%) of the latter are micro-endemics.

Micro-endemic amphibians were defined as those whose extreme collection sites were located within a 100 km linear distance (< 5,000 km^2). Buffer areas of 10km^2 radius were created around species collection localities: these areas are here termed amphibian micro-endemic buffered areas (AMBAs). Since we do not have abundance data, we have de facto assumed that each georeferenced locality in the database represents a population that can be affected by changes occurring within the resulting AMBAs. All analyses were performed using an equal-area planar projection (Conformal Lambert Conic WGS84) in ArcView 3.2 and ArcGIS 9.3.

Instead of a modelling approach, museum database records were used in order to avoid true commission errors in the representation of the species distribution range. Our approach inevitably will involve omission errors but this more conservative approach of relying only on known collection localities is to be preferred for present purposes (see Discussion). We included all the unique records without date filtering for two reasons: 1) we cannot assume that species are no longer present in their localities (e.g. assuming extinction) without performing an adequate sampling of the areas, and 2) all sensible conservation strategies should involve field-based verification before implementation of conservation actions. We are confident in this approach to conservation prioritization because micro-endemics may, in general, be assumed to be especially sensitive to environmental changes.

Within each AMBA the following indicators were evaluated:

2.1 ***Threat status level.*** The threat status for each AMBA was evaluated using the following stress factors: ***human population density and growth rate***, each derived from census data for 1990, 1995, 2000 and 2005 (INEGI, 1996a, 1996b, 2001, 2009); ***land use***, utilizing primary and secondary vegetation from INEGI series III (2005); and, ***road density*** (IMT, 2003), calculated using a 50 m buffer on both sides of each road. Depending on the amount of disturbance, a ranking value was assigned from 0 representing no significant threat, to 5 being the highest level of threat (see Appendix VIII-1). An arithmetic mean of all threat values was obtained for each species, and was assigned to each species as its threat status. Although this procedure has several caveats, it can be relatively easy to achieve in many parts of the globe and represents a useful starting point to develop more accurate species-specific or sites-specific analyses.

2.2 *Potential response index.* This qualifier includes all currently existing policy instruments and social initiatives for conservation in Mexico, captured within recently created spatially referenced databases. We assessed whether these instruments were present in the AMBAs in order to evaluate their potential response capability. These policy instruments included: different levels of "environmental zoning plans" (Ordenamiento Ecológico del Territorio, SEMARNAT-DGPAIR, 2008a,b), community zoning plans (Ordenamiento Territorial Comunitario, González et al., 2008), environmental services payment programs (CONAFOR, 2009), land with sustainable wildlife management plans (UMAS) (SEMARNAT-DGVS, 2008) or forestry practices (FSC certification) (Bezaury-Creel and Ochoa-Ochoa, 2008; Bezaury-Creel et al., 2008a), public protected areas (Bezaury-Creel et al., 2009, 2010a,b), community conserved areas (Bezaury-Creel et al., 2008b,c), field research facilities (Bezaury-Creel and Ochoa-Ochoa, 2010), World Heritage sites (Bezaury-Creel and Torres, 2010) and Ramsar sites (CONANP, 2009). Each of these policy instruments and social initiatives were assigned a quantitative value, with regards to their individual "relative strength", reflecting the expected capability of each instrument to abate potential threats. The evaluation was performed using indicators of their potential threat abatement response capacity such as: type (public, private or mixed), enforceability (compulsory or voluntary), required level of public investment (high, medium, or low) and permanence over time (see Table VIII-1).

AMBAs can contain different instruments with different relative strength-level. Therefore, a current potential threat abatement response level for each AMBA was obtained through the hierarchical sum of the relative strength index, i.e. the assignment of the highest available "relative strength index" value for public policy instruments.

Table VIII-1. Potential threat abatement response capacity of policy instruments and social initiatives. Compliance denotes if a tool is legally binding or if it is voluntary; “Int. convention” indicates an international agreement such as UNESCO’s World Heritage Convention (http://whc.unesco.org/en/danger) and the Ramsar Convention (http://www.ramsar.org). The plus signs in the Public/ Private synergy indicate the value of private instruments added to the public value to obtain the final index.

Policy Instrument or Social Initiative	**Type**	**Compliance**	**Public Investment**	**Permanence**	**Relative Strength Index**	**Public/ Private Synergy**
World Heritage Site	Public/International	Int. convention	High	Permanent Until Revoked	5	
Federal Protected Area (Core Zone)	Public/National	Compulsory	High	Permanent	5	
Ramsar Site	Public/International	Int. convention	Medium	Permanent Until Revoked	4	
Federal Protected Area (Buffer Zone)	Public/National	Compulsory	High	Permanent	4	
State Protected Area (Core Zone)	Public/State	Compulsory	Medium	Permanent	4	
Municipal Protected Area (Core Zone)	Public/Municipal	Compulsory	Medium	Permanent	4	
Field Research Stations	Public/Private	Operational	High	Permanent	4	+
State Protected Area (Buffer Zone)	Public/State	Compulsory	Medium	Permanent	3	
Municipal Protected Area (Buffer Zone)	Public/Municipal	Compulsory	Medium	Permanent	3	
Community-Conserved Areas (Certified)	Private/Public	Voluntary	Low	Owner’s Decided	3	+
Forest Stewardship Council Certified (Currently active)	Private/Private	Voluntary	None	Owner’s Decided	3	+
Community-Conserved Areas (Not certified)	Private	Voluntary	None	Owner’s Decided	3	+
Permanent Forestry Area	Private	Voluntary	None	Owner’s Decided	3	+
Regional Environmental Zoning Plan (Sub-State Coverage)	Public/National	Compulsory	Low	Periodically Reviewed	2	
Local Environmental Zoning Plan	Public/National	Compulsory	Low	Periodically Reviewed	2	
Wildlife Management Unit	Private/Public	Voluntary	Low	Owner’s Decided	2	+
Environmental Services Program (Currently active)	Private/Public	Voluntary	High	5 Year Period	2	+
Community Zoning Plan	Private	Voluntary	Medium	Owner’s Decided	2	+
Regional Environmental Zoning Plan (State Coverage)	Public/National	Compulsory	Low	Periodically Reviewed	1	
Forest Stewardship Council Certified (Currently inactive)	Private/Private	Voluntary	None	Certificate not renewed	1	
Environmental Services Program (Currently inactive)	Private/Public	Voluntary	None	Past 5 years period	1	
No Policy Instrument or Social Initiative					0	

Public/private synergy was reflected in this overall grading through the addition of the "relative strength index" value of all currently active social initiatives, or the value of a previous but currently inactive initiative when no currently active ones exist. Potential threat abatement response capacity values varied from 0 to 17. The "relative strength index" range of values varied from 1 to 5, the latter for the instrument with the strongest potential threat abatement response capacity and the former with the lowest capacity.

These additive values were normalized for each micro-endemic buffered site to determine a "potential response instrument diversity index" ranging from 0 to 5 (see Appendix VIII-2), where 0 means that no conservation instrument/initiative is currently present in the buffered site, and 5 presents a wide variety of conservation instruments/initiatives (e.g. governmental PAs, environmental services programmes, community zoning plans, etc).

2.3 ***Priority intervention value.*** This indicator was obtained through comparing the "threat status level" with the "potential response instrument diversity index" values for micro-endemic buffered sites within a threat/response matrix (Table VIII-2.1). Its values ranged from 1 – lowest threat/highest potential response to 7 - highest threat/lowest potential response. This value becomes the final product for triaging conservation efforts resulting from the support tool here proposed. The matrix can be split into two coarse categories divided by a "precautionary approach threshold" located towards the low threat/high potential response sector (value 3), of the average distribution range of priority intervention values. Above this precautionary approach threshold, efforts should be oriented towards consolidating existing conservation practices, without excluding the establishment of new instruments/initiatives. In this area, species should ideally be doing fine. Below the precautionary approach threshold, the high threat/low potential response sector is where priority interventions – expressed as “conservation strategies” – should be concentrated (Table VIII-2.2). This could mean that investments in areas with the highest threats and lowest response level would be least cost effective; with perhaps a lower priority since these species have such poor survival prospects. Nevertheless this is only a threat-response indicator and each species demands a particular strategy that should be based on specific site-based information of its potential to survive through conservation action.

Table VIII-2. 1.Threat/response matrix utilized for determining priority intervention values. Depending on the threat status values and the potential response index each AMBA was placed in the matrix.

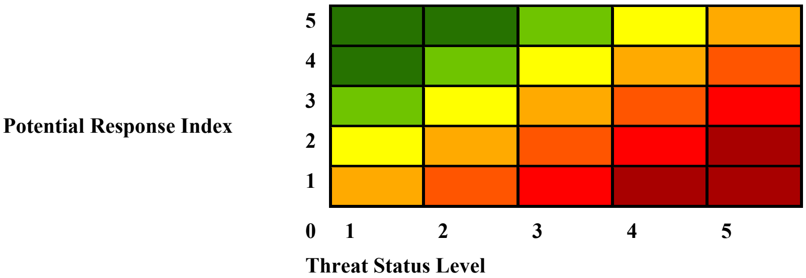
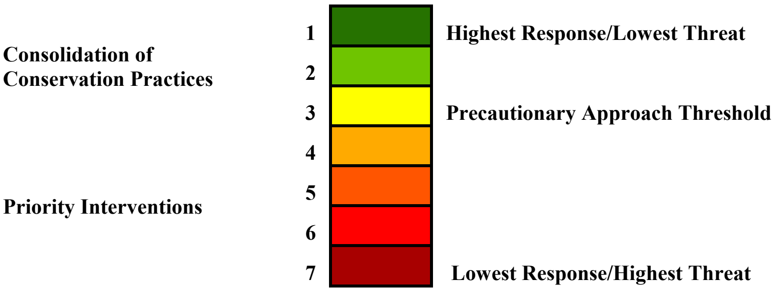


Table VIII-2. 2. Priority intervention values. The position in the matrix of each AMBA can be used to guide the course of action to follow.



2.4 *Conservation strategies*. In order to propose implementation of feasible conservation strategies, AMBAs were overlaid with Mexico’s terrestrial gap analysis results (CONABIO et al., 2007), land-use (INEGI, 2005), land tenure (OBSINTER, 2007), indigenous groups (Boege, 2008), and environmental services program eligibility zones (CONAFOR, 2007); to calculate their overlap area (see Appendix VIII-3). In doing so, the goal was to evaluate potential implementation of policy instruments and social initiatives that could assist land use threat abatement within the context of a wider integrated strategy aimed at preventing micro-endemic amphibian species extinction in Mexico. Table VIII-3 could help to establish potential implementation of different policy instruments and social initiatives. We suggest choosing the principal (P) and secondary (S) strategies, according to the feasibility of each instrument and the characteristics of each AMBA. Potential implementation of conservation strategies, utilizing either policy instruments or social initiatives, was derived from the use of a diverse set of conditions that include: national conservation or programmatic priorities, specific target ecosystems, and cultural indicators.

2.4 ***Umbrella value***. Finally, we calculated the conservation umbrella value for each AMBA as the number of additional amphibian species that would be protected by the AMBA. This value was assessed utilizing database locality records, and potential distribution, based upon range distribution database created using niche models and distribution data obtained from the literature (Ochoa-Ochoa et al., 2009a). In order to make correct comparisons among AMBAs umbrella values with different size, an adjustment by area was performed (dividing all the areas by the smallest buffer, and then dividing the number of species of each AMBA by the factor obtained).

RESULTS

The threat rank and the threat status for each species are given in Appendix VIII-1 and summarized in Fig VIII-1. A low overall threat status was obtained for 10 species, 72 species were scored as medium, 55 as high, and 8 as very-high threat status, the latter principally as a result from land use change and high human population density in their AMBAs. Our potential threat abatement response capacity ranking produced only one species with no conservation instruments/initiatives within its AMBA, *Plectrohyla miahuatlanensis,* a recently described species (value 0). The AMBAs of 15 species had a very low value of diversity of conservation initiatives (value 1), 27 AMBAs had a low value, 37 an intermediate value (level 3), 43 a high value, and eight a very high value (value 5) (Appendix VIII-2).

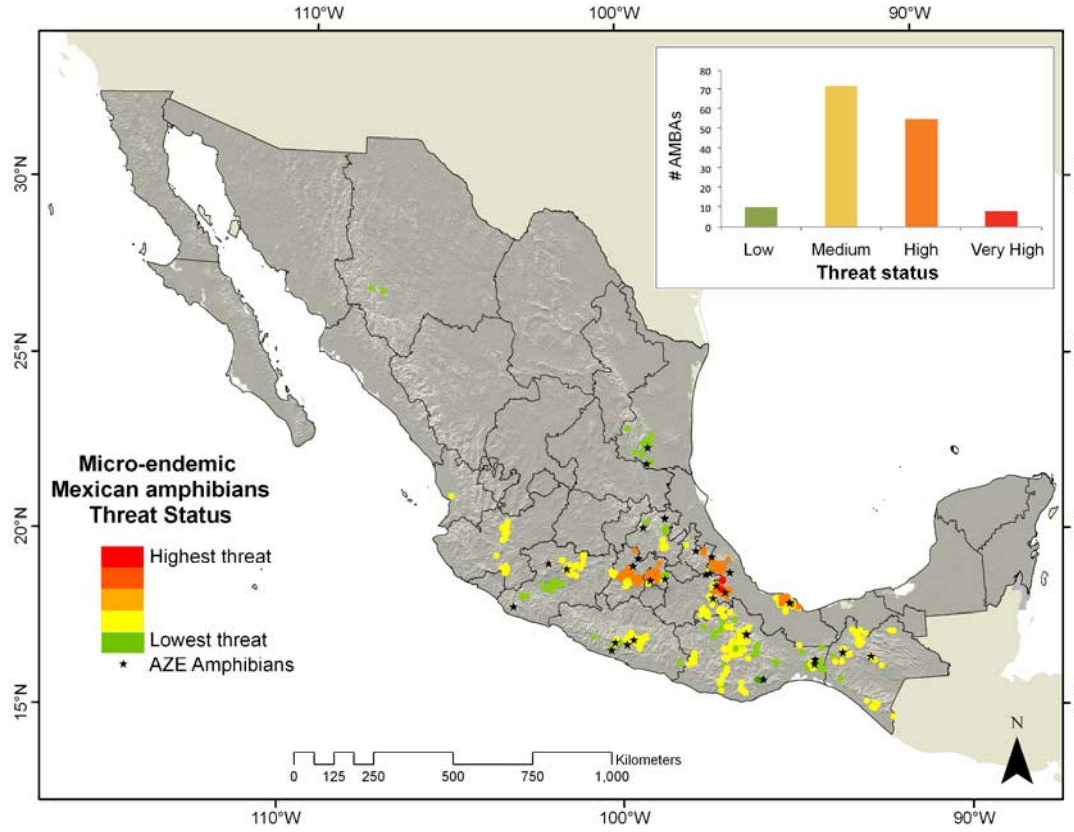


Figure VIII-1. Threat status of Mexican micro-endemic amphibian buffered areas (AMBAs). The graph shows the number of AMBAs in each threat status category. AZE is a global initiative to select sites where species are in imminent danger of disappearing, in this case amphibians (http://www.zeroextinction.org/).

Priority intervention values resulting from the threat/response matrix categorization are summarized in Figure VIII-2. The results indicate that 32 AMBAs require consolidation of existing conservation practices. That means that their values in the matrix were below 3. Five of these species need field verification to confirm their persistence due to the low percentage of remnant vegetation:

Table VIII-3. Conservation strategies implementation. This table suggests generic potential implementation feasibility for different policy instruments and social initiatives. Based upon the results of the Gap Analyses or specific characteristics of these areas (columns), different policy instruments or social initiatives were recommended as principal (P) or secondary (S) strategies.

Policy Instrument or Social Initiative	GAP Analysis Extreme Importance	GAP Analysis High Importance	GAP Analysis Medium Importance	Temperate and Tropical Timber Producing Forests	Aquatic and sub-aquatic vegetation	Land tenure	Indigenous Groups	Program Eligibility Area
Federal Protected Area	P	S						
State Protected Area	P	P	S					
Municipal Protected Areas	S	S	P					
Ramsar Site	S	S	S		P			
Environmental Services Program	S	S	S					P
Environmental Zoning Plan	P	P	P					
Community Zoning Plan						P	P	
Community-Conserved Areas (Communal)						P	P	
Community-Conserved Areas (Private)						P		
Permanent Forestry Area				P				
Forest Stewardship Council Certified				P				

The implementation of conservation strategies was based upon national conservation or programmatic priorities, such as the GAP analysis results of priority areas for biodiversity conservation (CONABIO et al., 2007); specific target ecosystems (e.g. CONAFOR, 2007); and cultural indicators (Boege, 2008). Thus, 24 AMBAs could be suggested as possible candidates for federal protected area status, 44 for state protected area status and 34 for municipal protected area status, because they correspond respectively with GAP analysis sites of extreme, high, and medium importance. Only the AMBA for *Ambystoma taylori* could be considered as a potential Ramsar site. AMBAs within the 2007 eligible environmental services project areas include 39 sites designated for hydrological services, 24 sites for agro-forestry, and 58 sites for biodiversity services. Community zoning plans are considered feasible for 73 AMBAs. Eventually, community conserved areas could be established within at least 72 AMBAs and private community conserved areas could reasonably be promoted in 59 of these. Permanent forestry areas, some of which could in time be considered for Forest Stewardship Council certification, could provide a productive landscape alternative for at least 49 AMBAs (Appendix VIII-3).

Most AMBAs had a high umbrella value for other amphibians (Appendix VIII-1). The analysis of the locality records database indicated that 19 AMBAs could also protect over 20 additional species each (although not necessarily different species among sites). The umbrella value obviously increased when using the potential distribution range database rather than just the locality records. For example the AMBA for *Thorius smithi* obtained the highest umbrella value: it could potentially help to protect 51 species (in addition to *T. smithi*), while the number of AMBAs protecting 20 more species is increased to 67 using the modelled distributions data set. Based only on micro-endemic records occurring in the same region, the AMBAs from the species of the genera *Thorius*, *Pseudoeurycea* and *Plectrohyla* have the highest umbrella values (up to 16 species each).

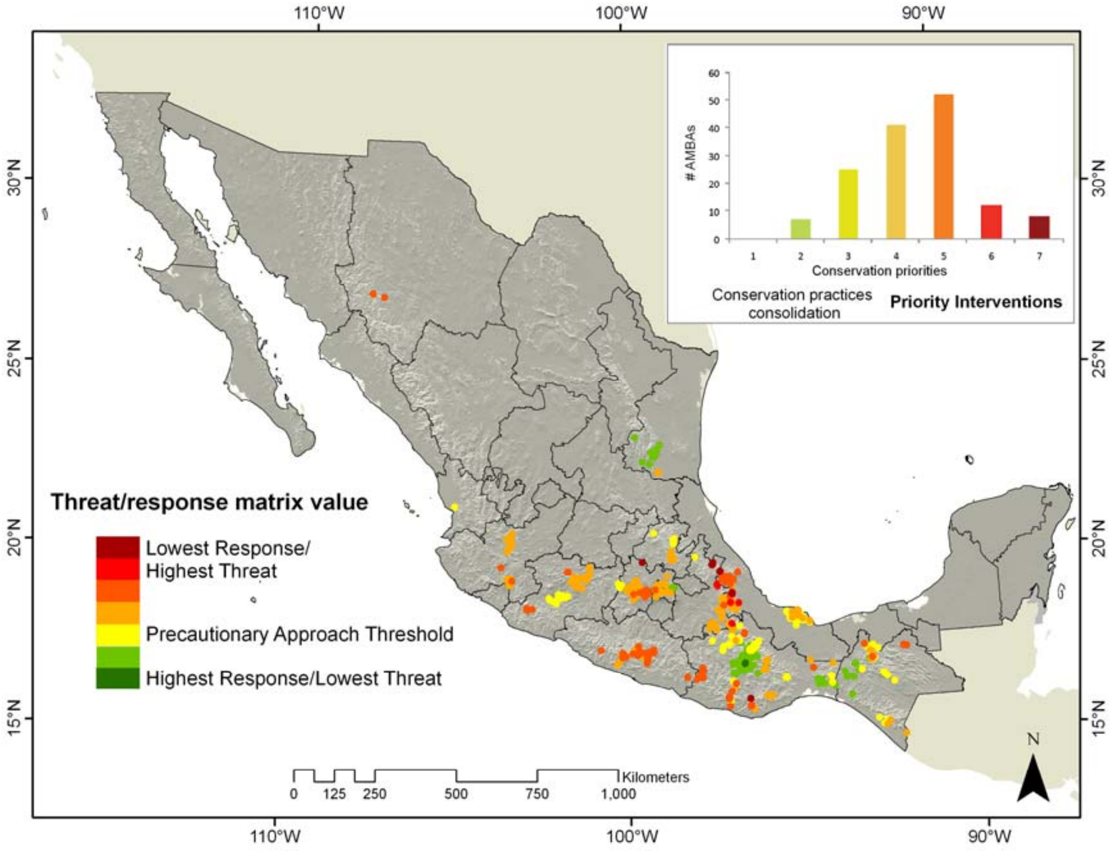


Figure VIII-2. Threat /response level matrix for the Mexican micro-endemic amphibian buffered areas (AMBAs). The graph shows the number of AMBAs in each category of priority interventions according to the data in Table VIII-2.2.

DISCUSSION

Successful conservation strategies do not only depend on increasing PAs number or coverage, but also on quality and connectivity with adjacent natural areas (Jackson and Gaston, 2008; Ladle and Whittaker, 2011). Therefore to ensure the success of protected areas, other conservation efforts need to be implemented at a landscape level to provide connectivity. Moreover, effective economic support programs that promote and support social conservation initiatives are required to increase protected areas effectiveness and values. Thus, in the triage tool proposed here rank values of private initiatives were individually added to the baseline public rank in this exercise. Private initiatives are definitively required for around 80% of PAs land in order to achieve effective conservation results (a bottom-up strategy), and cannot be considered as a conservation investment overkill. Previous analyses have indicated that private initiatives in protecting amphibian diversity in Mexico are vital for 26% of micro-endemic species (Ochoa-Ochoa et al., 2009b).

Resources for conservation are very limited thus a prioritized risk list is urgently needed to guide conservation resource allocation. That is the aim of the triage conservation tool presented here. At the same time it is known that assessing the threat status of any population in the absence of a standardized monitoring programme is challenging (Parrish et al., 2003; Gallant et al., 2007; Bakker and Doak, 2009). This triage tool should be used as coarse indicator for regional level decision taking: a case-by-case analysis should never be abandoned as a requirement for designing effective conservation strategies. To illustrate this we refer to two cases dealing with the AMBAs for *Craugastor pozo* and *Ambystoma mexicanum*. The former case represents a situation where these analyses may tend to average conflicting indexes and thus be inclined to suggest a better picture than the on-the-ground reality; the second case represents a situation where although the assessment seems correct the conservation actions that need to be taken are very habitat specific.

In the first case, *C. pozo* AMBA presents a high value conservation instruments index and a medium level of threat, which placed it in our “consolidation of conservation practices” category. However, field verified interactions (L. Ochoa pers. obs.) between *C. pozo* and human activities (litter extraction to sell as organic fertilizer) suggest that this species is actually being subjected to greater pressures that those expected from the presence of existing instruments and initiatives. Implementation of a monitored litter extraction management program, in coordination with local communities, is urgently needed to preserve, restore and maintain this habitat and associated traditional land use practices. Thus, *C. pozo* AMBA should be in the high conservation priority category; a judgement that was not, however, reflected in the coarse scale analysis conducted herein.

In the second example, *A. mexicanum* AMBA includes areas with unsuitable habitat outside the Xochimilco and Chalco wetlands. These unsuitable areas have federal PAs, a World Heritage site and environmental services program. Nevertheless, the most significant conservation action that needs to be implemented for the long-term survival of *A. mexicanum* is to increase the quality and quantity of water available within its wetland habitats. Hence, the prospects for this species are not strongly related to/dependent on the territorial policy instruments and social initiatives utilized in the present analyses.

Overall, the results seem to agree with the conclusion of the Global Amphibian Assessment, by Stuart et al. (2008) that Mexico ranks as the second country in the world for numbers of threatened amphibians species. This is because most of the AMBAs have medium to low potential threat abatement response capability (below 3, Appendix VIII-2), therefore very few AMBAs fall in the category of merely requiring conservation consolidation strategies. Nevertheless, in a recent review of the status of Mexican amphibians, Frías-Alvarez et al. (2010) reported that notwithstanding the numerous negative reports of amphibians' species and populations in Mexico, there is a consistent lack of demographic studies that quantitatively address the population trends of Mexican amphibians. As an example, 26 species included in the analyses may already be extinct (Baena and Halffter, 2008; Ochoa-Ochoa et al., 2009b). However, none of them has been officially declared extinct owing in part to a lack of field confirmation surveys.

We have also identified 37 amphibians (Appendix VIII-3) for whom field-based verification is urgently needed because remnant vegetation cover in their AMBAs is very low. It is of general knowledge that habitat loss remains the major threat for biodiversity globally (Alford and Richards, 1999; Millennium Ecosystem Assessment 2005; Gallant et al., 2007). For example, it has been shown that the loss of canopy cover affects the distribution of amphibians negatively, causing an impoverishment in number of juveniles, number of adults, and in turn amphibian species richness (Urbina-Cardona et al., 2006). Thus, it is imperative to conduct field-based verification on those areas where possibly extinct micro-endemic species were recorded to assess presence/absence and threat status of those species. Subsequently, declare them officially extinct, or implement appropriate conservation strategies, as the case may be.

Another aspect of the triage tool presented is the use of buffered sites from collection records remains a limitation of our analysis. Two possible sources of error should be highlighted: that the amphibian in question may be much more restricted (commission errors), or that amphibian has other populations that has not yet been documented (omission errors). For the former case a finer analysis must be achieved, for the latter source of error there are other tools that can be more useful, such as environmental niche modelling (Pearson et al., 2007). However, sampling in unexplored regions remains inevitable.

A typical triage result output, based upon limited resources for conservation efforts, would involve lower investment on the highest response/lowest threat sites and avoided investment on the lowest response/highest threat sites (Table VIII-2.1).

However, this scenario might be not necessarily realistic. For example, in the optimum side of the potential response matrix, i.e. highest response; federal protected areas are currently Mexico's most effective conservation strategy and the highest-ranking public policy tool in this exercise. Nonetheless, only 20% of the land within these PAs is actually public land (Bezaury-Creel and Gutiérrez-Carbonell, 2009). This implies that in order to implement any conservation strategy land owners must be involved. On the opposite side, the lowest response/highest threat situations do not necessarily imply a waste of conservation resources because amphibians may not necessarily provide an adequate surrogate for other groups (Rodrigues and Brooks, 2007). Therefore triage analyses should be carried out also for other groups. Moreover, it would be easier and more straight-forward to establish conservation strategies for a subset of species from different groups than dealing with all biodiversity, especially in megadiverse countries.

Although conservation policy instruments in Mexico are not specifically targeted at amphibians, they can certainly benefit from already-established instruments. For example, environmental agencies could (i) promote the incorporation of conservation provisions specifically for amphibians within AMBAs with existing environmental zoning plans and wildlife management units (UMAS), and (ii) encourage stakeholders to include amphibian programs (e.g. conservation, monitoring, etc.) in their next iteration or permit renovation process. Thus, eventually, plans and permits would have a more holistic view; including consideration not only of amphibians, but other taxa as well.

To conclude, there is no doubt that micro-endemics can easily disappear if their habitat is not preserved (Ricketts et al., 2005). Thus, they are good candidates for targeting in conservation investment, particularly in a country with many micro-endemic species. Especially since most of the species within our analyses had a high umbrella value meaning that protecting these areas could result in the protection of several more amphibian species (Appendix VIII-3). In general, micro-endemic species inhabit mountain ranges. These zones have high herpetofaunistic diversity possibly related to elevated diversification rates (e.g. Smith et al., 2007) and elevated heterogeneity. It is foreseen that these characteristics will be maintained even under a climate change scenario (Flores-Villela and Goyenechea, 2003; Ochoa-Ochoa et al., *submitted*). Therefore, these areas should be a priority for conservation action to allow successful migration and resorting of animal and plant communities during future episodes of climate change (Dawson et al., 2011).

CONCLUSIONS

The exercise presented here represents a coarse tool of analysis involving different strategies and conservation instruments (Table VIII-1). Although this triage tool is wrapped up in a SCP framework it should certainly not be used as the single tool for selecting areas, but only for prioritizing them and selecting preliminary strategies that could be implemented in the field. It can also be used to reduce the gap between assessment and implementation (Cowling et al., 2004), because it is specifically focused on existing conservation instruments and their implementation feasibility when proposing an overarching strategy. Based on these considerations, it would be possible to allocate (or re-allocate) resources to different places within the country to reinforce and enlarge a pre-existing conservation areas network. Choosing successful survivors should be based on the threat/response matrix (Tables VIII-2.1 and VIII-2.2). This triage tool could also ultimately help to identify places too devastated to be worth further conservation investment. Implementation of monitoring programs in devastated areas is always important, even if it is only to document extinctions. Our analyses highlight the need for local field-based verification for a substantial proportion of amphibian species. The triage tool proposed here could be of significant use in resource allocation exercises at a national level, but we should not forget that local biological and social situational analyses are always an essential prerequisite for designing successful conservation strategies for each AMBA or landscape.

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APPENDIX VIII-1

Threat status of Mexican micro-endemic amphibians based on buffered sites of 10km ratio and "umbrella value" or how many additional amphibian species would be protected within these areas corrected by sizes. Columns are described as follows: **Species** = Name of the species. **Author** = Author (s) of the description of the species, empty brackets indicate a change from the original description name (e.g. the genus has changed). **Year** = Year of the description of the species. **Umbrella values** = number of additional amphibian species that would be protected by the AMBA, based on database records and on potential distribution. For all umbrella values an adjustment by area was performed (dividing all the areas by the smallest buffer, and then dividing the number of species of each AMBA by the factor obtained). **% Veg remnant** = % of non-transformed vegetation in the AMBA. **% Roads** = the area in % occupied by roads. Due the spatial information of roads is given in lines we create a buffer zone of 50m to each side along the road-line. **Rate of population growth (annual) =** percentage of population growth per annum**. Population density =** Number of inhabitants per hectare. Ranks were assigned as follow: **Land cover rank** if the buffered site had 100 % of vegetation coverage then the rank was = 0, >90% = 1, 70- 89.9% = 2, 50- 69.9% = 3, 30-49.9% = 4, and less than 30% = 5. **Population density rank** if the population density was 0 hab/ha then rank was =0, < 0.1 hab/ha = 1, 0.11 to 1 hab/ha = 2, 1.1 to 5 hab/ha = 3, 5.1 to 10 hab/ha = 4, and > 10 hab/ha **=** 5. **Population growth rank** if the population growth was 0% per year then the rank was = 0, up to 1 % annual =1, up to 2 % annual = 2, up to 4 % annual = 3, up to 6% annual = 4, and more than 6 % annual = 5. **Roads density rank** if there were no roads then the rank was = 0, less than 5% = 1, up to 10% = 2, up to 20% = 3, up to 30% = 4, and more than 30%. After the ranks of each threat were obtained we calculated the arithmetic mean of the threat ranks to obtain an overall **threat status** value for each AMBA.

Species	Author	Year	Umbrella value Database records	Umbrella value Potential	Umbrella value micro-endemic	% Veg remnant	% Roads	Rate of population growth (annual)	Population density (hab/ha)	Land cover rank	Population density rank	Population growth rank	Roads density rank	Overall threat status
Incilius pisinnus	Mendelson, Williams, Sheil & Mulcahy	2005	**3**	**5**	**0**	41.20%	3.30%	1.10%	0.92	4	2	2	2	**2.5**
Craugastor batrachylus	Taylor	1940	**9**	**10**	**1**	62.40%	4.70%	0.80%	0.18	3	2	1	2	**2**
Craugastor galacticorhinus	Canseco-Márquez & Smith	2004	**7**	**28**	**1**	53.50%	5.90%	6.40%	0.85	3	2	5	3	**3.25**

Species	Author	Year	Umbrella value Database records	Umbrella value Potential	Umbrella value micro-endemic	% Veg remnant	% Roads	Rate of population growth (annual)	Population density (hab/ha)	Land cover rank	Popu-lation density rank	Popul-ation growth rank	Roads density rank	Overall threat status
Craugastor glaucus	Lynch	1967	**9**	**11**	**1**	56.80%	7.90%	5.20%	2.64	3	3	4	3	**3.25**
Craugastor guerreroensis	Lynch	1967	**23**	**28**	**3**	79.20%	13.90%	3.20%	0.43	2	2	3	4	**2.75**
Craugastor megalotympanum	Shannon & Werler	1955	**12**	**11**	**2**	25.80%	9.00%	1.60%	1.19	5	3	2	3	**3.25**
Craugastor montanus	Lynch	1965	**10**	**11**	**1**	51.80%	6.50%	3.90%	1.7	3	3	3	3	**3**
Craugastor omiltemanus	Günther	1901	**11**	**11**	**2**	84.50%	13.10%	3.40%	1.61	2	3	3	4	**3**
Craugastor palenque	Campbell & Savage	2000	**11**	**14**	**0**	48.10%	2.60%	4.40%	0.99	4	2	4	2	**3**
Craugastor pelorus	Campbell & Savage	2000	**9**	**9**	**1**	38.10%	7.00%	4.10%	0.92	4	2	4	3	**3.25**
Craugastor polymniae	Campbell, Lamar & Hillis	1989	**8**	**32**	**3**	90.20%	8.50%	1.50%	0.14	1	2	2	3	**2**
Craugastor pozo	Johnson & Savage	1995	**7**	**11**	**0**	49.50%	3.10%	2.40%	0.59	4	2	3	2	**2.75**
Craugastor silvicola	Lynch	1967	**5**	**33**	**1**	83.30%	0.20%	2.20%	0.01	2	1	3	1	**1.75**
Craugastor taylori	Lynch	1966	**21**	**33**	**3**	56.50%	8.00%	4.00%	0.39	3	2	4	3	**3**
Craugastor vulcani	Shanon & Werler	1955	**5**	**4**	**1**	14.50%	6.30%	2.10%	0.97	5	2	3	3	**3.25**
Eleutherodactylus dennisi	Lynch	1970	**10**	**20**	**1**	33.00%	4.90%	0.50%	0.32	4	2	1	2	**2.25**
Eleutherodactylus dixoni	Lynch	1991	**19**	**20**	**3**	76.80%	14.30%	3.20%	0.52	2	2	3	4	**2.75**
Eleutherodactylus grandis	Dixon	1957	**16**	**25**	**3**	27.70%	19.10%	0.60%	58.55	5	5	1	4	**3.75**
Eleutherodactylus nivicolimae	Dixon & Webb	1966	**9**	**11**	**0**	46.80%	4.80%	1.20%	1.42	4	3	2	2	**2.75**
Eleutherodactylus rufescens	Duellman & Dixon	1959	**5**	**11**	**0**	85.90%	1.60%	0.60%	0.14	2	2	1	2	**1.75**
Eleutherodactylus verruculatus	Peters	1870	**28**	**52**	**3**	17.00%	23.50%	3.00%	2.34	5	3	3	5	**4**

Species	Author	Year	Umbrella value Database records	Umbrella value Potential	Umbrella value micro-endemic	% Veg remnant	% Roads	Rate of population growth (annual)	Population density (hab/ha)	Land cover rank	Population density rank	Population growth rank	Roads density rank	Overall threat status
Charadrahyla altipotens	Duellman	1968	**6**	**9**	**1**	71.10%	4.20%	4.70%	0.28	2	2	4	2	**2.5**
Charadrahyla chaneque	Duellman	1961	**13**	**15**	**3**	66.90%	9.10%	3.50%	0.46	3	2	3	3	**2.75**
Charadrahyla tecuani	Campbell, Blancas-Hernández & Smith	2009	**9**	**24**	**0**	90.00%	3.80%	7.20%	0.05	2	1	5	2	**2.5**
Charadrahyla trux	Adler & Dennis	1972	**10**	**21**	**5**	85.20%	11.40%	3.40%	0.14	2	2	3	4	**2.75**
Duellmanohyla chamulae	Duellman	1961	**10**	**18**	**1**	44.40%	8.30%	4.50%	1.14	4	3	4	3	**3.5**
Duellmanohyla ignicolor	Duellman	1961	**13**	**15**	**3**	75.30%	9.50%	4.90%	0.42	2	2	4	3	**2.75**
Ecnomiohyla echinata	Duellman	1962	**14**	**21**	**5**	80.70%	10.20%	2.30%	0.18	2	2	3	4	**2.75**
Ecnomiohyla valancifer	Firschein & Smith	1956	**16**	**15**	**3**	16.40%	11.00%	2.30%	1.99	5	3	3	4	**3.75**
Exerodonta abdivita	Campbell & Duellman	2000	**7**	**27**	**1**	80.90%	3.30%	3.70%	0.36	2	2	3	2	**2.25**
Exerodonta bivocata	Duellman & Hoyt	1961	**16**	**23**	**3**	65.60%	12.10%	4.50%	0.96	3	2	4	4	**3.25**
Exerodonta chimalapa	Mendelson & Campbell	1994	**6**	**11**	**0**	77.30%	1.60%	1.10%	0.08	2	1	2	2	**1.75**
Exerodonta xera	Mendelson & Campbell	1994	**3**	**5**	**0**	68.50%	3.20%	3.50%	1.71	3	3	3	2	**2.75**
Hyla arboricola	Taylor	1941	**6**	**6**	**1**	74.70%	9.50%	3.90%	1.3	2	3	3	3	**2.75**
Megastomatohyla mixomaculata	Taylor	1950	**10**	**14**	**1**	28.20%	17.60%	2.70%	4.73	5	3	3	4	**3.75**
Megastomatohyla nubicola	Duellman	1964	**19**	**25**	**2**	19.20%	25.00%	2.90%	5.35	5	5	3	5	**4.5**
Megastomatohyla pellita	Duellman	1968	**11**	**15**	**1**	77.40%	6.40%	5.30%	0.39	2	2	4	3	**2.75**
Plectrohyla ameibothalame	Canseco-Márquez, Mendelson & Gutiérrez-Mayén	2002	**3**	**8**	**0**	63.40%	2.60%	1.10%	0.11	3	2	2	2	**2.25**

Species	Author	Year	Umbrella value Database records	Umbrella value Potential	Umbrella value micro-endemic	% Veg remnant	% Roads	Rate of population growth (annual)	Population density (hab/ha)	Land cover rank	Population density rank	Population growth rank	Roads density rank	Overall threat status
Plectrohyla calthula	Ustach, Mendelson, McDiarmid & Campbell	2000	**9**	**24**	**2**	92.90%	7.20%	1.00%	0.18	1	2	2	3	**2**
Plectrohyla calvicollina	Toal	1994	**17**	**22**	**4**	87.40%	9.50%	2.90%	0.21	2	2	3	3	**2.5**
Plectrohyla celata	Toal & Menselson	1995	**19**	**19**	**6**	87.90%	22.00%	2.10%	0.18	2	2	3	5	**3**
Plectrohyla chryses	Adler	1965	**11**	**13**	**3**	77.70%	14.70%	2.30%	0.64	2	2	3	4	**2.75**
Plectrohyla cyanomma	Caldwell	1974	**21**	**32**	**9**	91.90%	26.70%	1.20%	0.12	1	2	2	5	**2.5**
Plectrohyla ephemera	Meik, Canseco-Márquez, Smith & Campbell	2005	**1**	**23**	**0**	99.30%	1.90%	5.20%	0.13	1	2	4	2	**2.25**
Plectrohyla labedactyla	Mendelson & Toal	1996	**7**	**29**	**3**	82.90%	4.10%	1.80%	0.15	2	2	2	2	**2**
Plectrohyla miahuatlanensis	Meik, Smith, Canseco-Márquez & Campbell	2006	**6**	**30**	**1**	69.70%	3.00%	5.90%	0.42	3	2	4	2	**2.75**
Plectrohyla mykter	Adler & Dennis	1972	**9**	**12**	**3**	90.10%	12.50%	2.90%	0.17	1	2	3	4	**2.5**
Plectrohyla pachyderma	Taylor	1942	**12**	**25**	**1**	21.00%	4.40%	5.30%	5.69	5	4	4	2	**3.75**
Plectrohyla psarosema	Campbell & Duellman	2000	**10**	**32**	**2**	92.50%	7.10%	1.70%	0.21	1	2	2	3	**2**
Plectrohyla pycnochila	Rabb	1959	**18**	**25**	**4**	66.30%	12.40%	4.90%	3.77	3	3	4	4	**3.5**
Plectrohyla sabrina	Caldwell	1974	**24**	**24**	**8**	87.00%	24.50%	2.60%	0.1	2	1	3	5	**2.75**
Plectrohyla siopela	Duellman	1968	**9**	**14**	**2**	31.20%	11.90%	2.60%	1.22	4	3	3	4	**3.5**
Ptychohyla acrochorda	Campbell & Duellman	2000	**17**	**19**	**6**	82.50%	20.50%	2.00%	0.31	2	2	2	5	**2.75**
Ptychohyla erythromma	Taylor	1937	**12**	**14**	**2**	81.00%	13.00%	0.70%	0.47	2	2	1	4	**2.25**

Species	Author	Year	Umbrella value Database records	Umbrella value Potential	Umbrella value micro-endemic	% Veg remnant	% Roads	Rate of population growth (annual)	Population density (hab/ha)	Land cover rank	Population density rank	Population growth rank	Roads density rank	Overall threat status
Lithobates chichicuahutla	Cuellar, Méndez de la Cruz & Villagrán Santa Cruz	1996	**3**	**10**	**1**	23.20%	6.00%	1.60%	0.42	5	2	2	3	**3**
Lithobates dunni	Zweifel	1957	**2**	**4**	**0**	35.60%	7.10%	2.10%	3.91	4	3	3	3	**3.25**
Lithobates lemosespinali	Smith & Chiszar	2003	**5**	**9**	**0**	94.00%	3.30%	3.30%	0.07	1	1	3	2	**1.75**
Lithobates omiltemanus	Günther	1900	**11**	**11**	**2**	81.60%	11.00%	2.30%	0.54	2	2	3	4	**2.75**
Lithobates psilonota	Webb	2001	**13**	**16**	**1**	37.20%	5.90%	0.60%	1.01	4	3	1	3	**2.75**
Lithobates pueblae	Zweifel	1955	**15**	**31**	**0**	35.30%	4.80%	2.50%	3.66	4	3	3	2	**3**
Lithobates tlaloci	Hillis & Frost	1985	**4**	**5**	**1**	13.50%	11.70%	0.40%	68.64	5	5	1	4	**3.75**
Ambystoma amblycephalum	Taylor	1940	**3**	**7**	**0**	51.30%	7.00%	1.40%	0.94	3	2	2	3	**2.5**
Ambystoma andersoni	Krebs & Brandon	1984	**8**	**20**	**2**	35.70%	10.50%	0.80%	1.94	4	3	1	4	**3**
Ambystoma bombypellum	Taylor	1940	**1**	**13**	**0**	10.30%	3.60%	6.20%	0.82	5	2	5	2	**3.5**
Ambystoma dumerili	Dugès	1870	**4**	**9**	**0**	46.90%	7.70%	1.20%	1.31	4	3	2	3	**3**
Ambystoma flavipiperatum	Dixon	1963	**3**	**4**	**0**	40.80%	3.70%	3.60%	7.19	4	4	3	2	**3.25**
Ambystoma granulosum	Taylor	1944	**3**	**4**	**0**	12.40%	8.30%	3.70%	6.5	5	4	3	3	**3.75**
Ambystoma lermaense	Taylor	1940	**4**	**5**	**1**	25.30%	9.30%	3.00%	8.89	5	4	3	3	**3.75**
Ambystoma leorae	Taylor	1943	**6**	**8**	**1**	71.80%	3.10%	3.00%	0.45	2	2	3	2	**2.25**
Ambystoma mexicanum	Shaw	1789	**4**	**5**	**1**	7.90%	11.50%	0.70%	68.44	5	5	1	4	**3.75**
Ambystoma taylori	Brandon Maruska & Rumph	1981	**3**	**10**	**1**	28.30%	5.00%	1.60%	0.4	5	2	2	3	**3**
Bolitoglossa alberchi	García-Paris, Parra-Olea, Brame & Wake	2003	**3**	**17**	**1**	86.00%	0.10%	5.70%	0.04	2	1	4	1	**2**

Species	Author	Year	Umbrella value Database records	Umbrella value Potential	Umbrella value micro-endemic	% Veg remnant	% Roads	Rate of population growth (annual)	Population density (hab/ha)	Land cover rank	Popu-lation density rank	Popul-ation growth rank	Roads density rank	Overall threat status
Bolitoglossa hermosa	Papenfuss Wake & Adler	1984	**11**	**18**	**3**	80.60%	8.30%	-0.40%	0.17	2	2	1	3	**2**
Bolitoglossa oaxacensis	Parra-Olea, García-Paris & Wake	2002	**20**	**35**	**3**	83.90%	6.60%	4.30%	0.19	2	2	4	3	**2.75**
Bolitoglossa riletti	Holman	1964	**6**	**9**	**0**	63.70%	3.90%	5.40%	0.43	3	2	4	2	**2.75**
Bolitoglossa veracrucis	Taylor	1951	**2**	**17**	**0**	43.30%	1.90%	3.90%	0.13	4	2	3	2	**2.75**
Bolitoglossa zapoteca	Parra-Olea, García-Paris & Wake	2002	**4**	**14**	**1**	96.80%	2.30%	-1.40%	0.06	1	1	1	2	**1.25**
Chiropterotriton crascens	Rabb	1958	**19**	**26**	**2**	78.00%	7.00%	2.00%	0.12	2	2	2	3	**2.25**
Chiropterotriton dimidiatus	Taylor	1939	**4**	**5**	**0**	39.80%	3.90%	3.90%	3.85	4	3	3	2	**3**
Chiropterotriton lavae	Taylor	1942	**17**	**23**	**4**	38.50%	19.60%	6.20%	1.69	4	3	5	4	**4**
Chiropterotriton mosaueri	Woodall	1941	**8**	**24**	**0**	72.50%	3.10%	1.40%	0.24	2	2	2	2	**2**
Chiropterotriton terrestris	Taylor	1941	**9**	**15**	**0**	54.90%	5.00%	1.70%	0.64	3	2	2	2	**2.25**
Cryptotriton adelos	Papenfuss & Wake	1987	**14**	**16**	**6**	77.40%	18.90%	4.10%	0.35	2	2	4	4	**3**
Cryptotriton alvarezdeltoroi	Papenfuss & Wake	1987	**20**	**22**	**3**	36.20%	11.30%	2.80%	0.95	4	2	3	4	**3.25**
Dendrotriton megarhinus	Rabb	1960	**16**	**34**	**0**	90.40%	1.40%	5.20%	0.07	1	1	4	2	**2**
Dendrotriton xolocalcae	Taylor	1941	**20**	**23**	**1**	45.70%	6.00%	2.30%	0.79	4	2	3	3	**3**
Ensatina eschscholtzii	Gray	1850	**10**	**12**	**2**	20.20%	20.20%	2.80%	6.81	5	4	3	5	**4.25**
Pseudoeurycea ahuitzotl	Adler	1996	**6**	**34**	**4**	86.40%	10.30%	2.90%	0.16	2	2	3	4	**2.75**
Pseudoeurycea amuzga	Pérez-Ramos & Saldaña de la Riva	2003	**0**	**26**	**0**	92.20%	3.00%	1.40%	0.24	1	2	2	2	**1.75**
Pseudoeurycea anitae	Bogert	1967	**13**	**21**	**3**	78.10%	5.00%	3.90%	0.35	2	2	3	2	**2.25**

Species	Author	Year	Umbrella value Database records	Umbrella value Potential	Umbrella value micro-endemic	% Veg remnant	% Roads	Rate of population growth (annual)	Population density (hab/ha)	Land cover rank	Popu-lation density rank	Popul-ation growth rank	Roads density rank	Overall threat status
Pseudoeurycea aquatica	Wake & Campbell	2001	**11**	**33**	**3**	90.90%	8.20%	1.00%	0.19	1	2	1	3	**1.75**
Pseudoeurycea aurantia	Canseco-Márquez & Parra-Olea	2003	**10**	**32**	**4**	85.20%	11.70%	2.30%	0.26	2	2	3	4	**2.75**
Pseudoeurycea conanti	Bogert	1967	**14**	**23**	**1**	56.60%	3.90%	5.80%	0.34	3	2	4	2	**2.75**
Pseudoeurycea firscheini	Shannon & Werler	1955	**15**	**21**	**2**	44.30%	13.40%	3.30%	0.79	4	2	3	4	**3.25**
Pseudoeurycea gigantea	Taylor	1939	**8**	**15**	**3**	56.10%	9.10%	2.80%	0.46	3	2	3	3	**2.75**
Pseudoeurycea lineola	Cope	1865	**7**	**8**	**1**	30.50%	13.60%	2.80%	5.5	4	4	3	4	**3.75**
Pseudoeurycea longicauda	Lynch Wake & Yang	1983	**6**	**13**	**0**	53.20%	4.60%	3.30%	2.3	3	3	3	2	**2.75**
Pseudoeurycea lynchi	Parra-Olea, Papenfuss & Wake	2001	**12**	**20**	**3**	39.80%	14.80%	4.80%	1.48	4	3	4	4	**3.75**
Pseudoeurycea maxima	Parra-Olea, García-Paris, Papenfuss & Wake	2005	**8**	**11**	**1**	66.90%	4.40%	5.90%	0.45	3	2	4	2	**2.75**
Pseudoeurycea melanomolga	Taylor	1941	**13**	**14**	**3**	29.60%	15.80%	3.00%	5.36	5	4	3	4	**4**
Pseudoeurycea mixcoatl	Adler	1996	**10**	**25**	**4**	86.30%	14.50%	3.60%	0.21	2	2	3	4	**2.75**
Pseudoeurycea mixteca	Canseco-Márquez & Gutiérrez-Mayen	2005	**4**	**8**	**0**	50.20%	2.70%	0.20%	0.13	3	2	1	2	**2**
Pseudoeurycea mystax	Bogert	1967	**6**	**21**	**1**	74.00%	3.10%	3.90%	0.45	2	2	3	2	**2.25**
Pseudoeurycea naucampatepetl	Parra-Olea, Papenfuss & Wake	2001	**24**	**34**	**6**	51.50%	25.10%	4.60%	1.01	3	3	4	5	**3.75**
Pseudoeurycea nigra	Wake & Johnson	1989	**21**	**38**	**1**	58.80%	6.10%	4.50%	1.47	3	3	4	3	**3.25**
Pseudoeurycea obesa	Parra-Olea, García-Paris, Hanken & Wake	2005	**6**	**26**	**2**	44.10%	10.60%	3.50%	0.96	4	2	3	4	**3.25**

Species	Author	Year	Umbrella value Database records	Umbrella value Potential	Umbrella value micro-endemic	% Veg remnant	% Roads	Rate of population growth (annual)	Population density (hab/ha)	Land cover rank	Popu-lation density rank	Popul-ation growth rank	Roads density rank	Overall threat status
Pseudoeurycea orchileucos	Brodie, Mendelson & Campbell	2002	**39**	**33**	**6**	79.00%	18.70%	2.40%	0.43	2	2	3	4	**2.75**
Pseudoeurycea orchimelas	Brodie, Mendelson & Campbell	2002	**8**	**7**	**1**	18.80%	8.00%	2.20%	1.13	5	3	3	3	**3.5**
Pseudoeurycea papenfussi	Parra-Olea, García-Paris, Hanken & Wake	2005	**30**	**49**	**15**	89.80%	39.10%	1.00%	0.18	2	2	1	5	**2.5**
Pseudoeurycea parva	Lynch & Wake	1989	**11**	**20**	**0**	96.20%	1.40%	1.10%	0.02	1	1	2	2	**1.5**
Pseudoeurycea praecellens	Rabb	1955	**34**	**53**	**2**	1.40%	18.90%	1.80%	1.9	5	3	2	4	**3.5**
Pseudoeurycea quetzalanensis	Parra-Olea, Canseco-Márquez & García-Paris	2004	**11**	**21**	**0**	32.30%	3.40%	6.70%	1.83	4	3	5	2	**3.5**
Pseudoeurycea robertsi	Taylor	1938	**6**	**10**	**1**	55.00%	5.60%	5.10%	1.32	3	3	4	3	**3.25**
Pseudoeurycea ruficauda	Parra-Olea, García-Paris, Hanken & Wake	2004	**7**	**23**	**2**	51.40%	13.00%	4.50%	0.91	3	2	4	4	**3.25**
Pseudoeurycea saltator	Lynch & Wake	1989	**18**	**24**	**8**	87.40%	22.40%	1.30%	0.09	2	1	2	5	**2.5**
Pseudoeurycea scandens	Walker	1955	**3**	**5**	**1**	70.80%	8.60%	3.10%	1.5	2	3	3	3	**2.75**
Pseudoeurycea smithi	Taylor	1938	**4**	**4**	**0**	72.90%	3.00%	0.70%	0.11	2	2	1	2	**1.75**
Pseudoeurycea tenchalli	Adler	1996	**13**	**33**	**6**	87.10%	15.60%	0.70%	0.27	2	2	1	4	**2.25**
Pseudoeurycea teotepec	Adler	1996	**15**	**37**	**7**	87.40%	15.90%	4.30%	0.14	2	2	4	4	**3**
Pseudoeurycea tlahcuiloh	Adler	1996	**10**	**25**	**4**	91.70%	12.10%	3.30%	0.09	1	1	3	4	**2.25**
Pseudoeurycea tlilicxitl	Lara-Góngora	2003	**7**	**12**	**1**	57.20%	4.00%	2.10%	1.98	3	3	3	2	**2.75**
Pseudoeurycea unguidentis	Taylor	1941	**11**	**13**	**4**	74.40%	16.80%	2.50%	2.87	2	3	3	4	**3**

Species	Author	Year	Umbrella value Database records	Umbrella value Potential	Umbrella value micro-endemic	% Veg remnant	% Roads	Rate of population growth (annual)	Population density (hab/ha)	Land cover rank	Popu-lation density rank	Popul-ation growth rank	Roads density rank	Overall threat status
Pseudoeurycea werleri	Darling & Smith	1954	**9**	**8**	**1**	25.20%	9.40%	2.10%	1.28	5	3	3	3	**3.5**
Thorius arboreus	Hanken & Wake	1994	**22**	**31**	**10**	87.10%	27.40%	1.40%	0.11	2	2	2	5	**2.75**
Thorius aureus	Hanken & Wake	1994	**23**	**32**	**10**	87.40%	27.50%	1.40%	0.12	2	2	2	5	**2.75**
Thorius boreas	Hanken & Wake	1994	**16**	**23**	**7**	86.20%	23.30%	0.40%	0.14	2	2	1	5	**2.5**
Thorius dubitus	Taylor	1941	**14**	**19**	**2**	46.80%	13.00%	3.00%	0.83	4	2	3	4	**3.25**
Thorius grandis	Hanken, Wake & Freeman	1999	**10**	**22**	**4**	89.30%	11.70%	4.20%	0.1	2	1	4	4	**2.75**
Thorius infernalis	Hanken, Wake & Freeman	1999	**14**	**40**	**5**	85.50%	14.70%	1.30%	0.23	2	2	2	4	**2.5**
Thorius insperatus	Hanken & Wake	1994	**32**	**52**	**16**	90.40%	40.00%	1.00%	0.19	1	2	1	5	**2.25**
Thorius lunaris	Hanken & Wake	1998	**8**	**21**	**2**	51.10%	6.90%	6.50%	0.95	3	2	5	3	**3.25**
Thorius macdougalli	Taylor	1949	**9**	**9**	**3**	80.80%	14.50%	1.10%	0.25	2	2	2	4	**2.5**
Thorius magnipes	Hanken & Wake	1998	**13**	**16**	**2**	51.80%	12.00%	3.00%	0.72	3	2	3	4	**3**
Thorius minutissimus	Taylor	1949	**5**	**22**	**2**	95.30%	3.70%	-0.60%	0.11	1	2	1	2	**1.5**
Thorius minydemus	Hanken & Wake	1998	**23**	**32**	**6**	39.90%	24.70%	5.80%	1.97	4	3	4	5	**4**
Thorius munificus	Hanken & Wake	1998	**16**	**21**	**3**	37.40%	20.50%	5.20%	1.35	4	3	4	5	**4**
Thorius narismagnus	Shannon & Werler	1955	**22**	**19**	**3**	21.90%	11.20%	2.20%	2.17	5	3	3	4	**3.75**
Thorius omiltemi	Hanken, Wake & Freeman	1999	**10**	**14**	**3**	87.00%	13.40%	2.50%	0.28	2	2	3	4	**2.75**
Thorius papaloae	Hanken & Wake	2001	**5**	**15**	**1**	77.40%	8.40%	1.40%	0.32	2	2	2	3	**2.25**
Thorius pennatulus	Cope	1869	**15**	**19**	**2**	26.10%	19.90%	2.60%	5.8	5	4	3	4	**4**
Thorius pulmonaris	Taylor	1939	**5**	**6**	**2**	61.70%	9.90%	3.00%	2.07	3	3	3	3	**3**
Thorius schmidti	Gehlbach	1959	**6**	**16**	**1**	50.00%	5.70%	4.90%	0.93	4	2	4	3	**3.25**
Thorius smithi	Hanken & Wake	1994	**39**	**51**	**11**	81.10%	16.50%	4.80%	0.03	2	1	4	4	**2.75**
Thorius spilogaster	Hanken & Wake	1998	**8**	**23**	**2**	53.30%	7.00%	6.50%	0.97	3	2	5	3	**3.25**
Thorius troglodytes	Taylor	1941	**10**	**14**	**2**	52.90%	10.20%	1.80%	0.71	3	2	2	4	**2.75**

APPENDIX VIII-2

Calculating aggregate potential threat abatement response capacity of policy instruments and social initiatives for each AMBA and corresponding category within the threat/response level matrix.

Individual potential threat abatement response capacity values for different policy instruments and social initiatives were taken from the relative strength Index in Table VIII-1 (from main text), where each of those policy instruments and social initiatives was assigned a quantitative value, base on their individual “relative strength” for responding to risks to ecological integrity.

Current aggregate potential threat abatement response level for each AMBA was obtained through the sum of the individual values of the relative strength index according to the following considerations:

- From protected areas and international conservation instruments (pale green) only the highest value was added.
- Field research stations value was added in all cases (pale orange).
- All values for current social initiatives were added (pale blue).
- Values from Environmental Zoning Plans (pale pink) and non-current social initiatives (pale brown) were only added when none of the other instruments was present.

This sum represents an indicator the “instrument diversity index”, which was then transformed into an aggregate potential threat abatement response capacity denominated as a “potential response index” by ranking the instrument diversity index values (0 = 0, from 1 to 3 = 1, from 4 to 5 = 2, from 6 to 8 = 3, from 9 to 13 = 4, and higher or equal to 14 = 5). Priority intervention values were assigned following the threat/response level matrix in tables VIII-2.1 and VIII-2.2 from main text.

SPECIES	World heritage sites	Federal Protected Area (Core Zone)	Ramsar Site	Federal Protected Area (Buffer Zone)	State Protected Area (Core Zone)	Municipal Protected Area (Core Zone)	State Protected Area (Buffer Zone)	Municipal Protected Area (Buffer Zone)	Field research stations (public or private)	Community-Conserved Areas (Certified)	Forest Stewardship Council Certified (Current)	Community-Conserved Areas (Not certified)	Permanent Forestry Area	Environmental Services Program (Current)	Wildlife Management Unit (UMA)	Community Zoning Plan	Regional Environmental Zoning Plan (State Coverage)	Zoning Plan (Sub-State Coverage)	Local Environmental Zoning Plan	Forest Stewardship Council Certified (Not current)	Environmental Services Program (Not current)	Instrument Diversity Index	Potential Response Index	Priority Intervention Value (Table VIII-2)	Overall Threat status (from Appendix VIII-1)
Ambystoma amblycephalum			4				3							2		2	1				1	8	3	**4**	2.5
Ambystoma andersoni			4				3															4	2	**6**	3
Ambystoma bombypellum							3										1					3	1	**7**	3.5
Ambystoma dumerili			4				3							2		2	1				1	8	3	**5**	3
Ambystoma flavipiperatum			4	4				3						2		2	1				1	8	3	**5**	3.25
Ambystoma granulosum				4			3	3	4					2			1		2		1	10	4	**4**	3.75
Ambystoma leorae				4			3		4					2	2		1				1	12	4	**3**	2.25
Ambystoma lermaense			4	4			3	3						2	2		1				1	8	3	**5**	3.75
Ambystoma mexicanum	5		4	4			3		4					2			1				1	11	4	**4**	3.75
Ambystoma taylori																					1	1	1	**7**	3
Bolitoglossa alberchi														2		2						4	2	**5**	2
Bolitoglossa hermosa														2		2						4	2	**5**	2
Bolitoglossa oaxacensis														2		2						4	2	**5**	2.75
Bolitoglossa riletti														2		2						4	2	**5**	2.75
Bolitoglossa veracrucis										3				2		2						7	3	**4**	2.75
Bolitoglossa zapoteca																2						2	1	**5**	1.25
Charadrahyla altipotens														2		2					1	4	2	**5**	2.5
Charadrahyla chaneque							3	3		3	3	3		2		2				1	1	16	5	**2**	2.75

SPECIES	World heritage sites	Federal Protected Area (Core Zone)	Ramsar Site	Federal Protected Area (Buffer Zone)	State Protected Area (Core Zone)	Municipal Protected Area (Core Zone)	State Protected Area (Buffer Zone)	Municipal Protected Area (Buffer Zone)	Field research stations (public or private)	Community-Conserved Areas (Certified)	Forest Stewardship Council Certified (Current)	Community-Conserved Areas (Not certified)	Permanent Forestry Area	Environmental Services Program (Current)	Wildlife Management Unit (UMA)	Community Zoning Plan	Regional Environmental Zoning Plan (State Coverage)	Zoning Plan (Sub-State Coverage)	Local Environmental Zoning Plan	Forest Stewardship Council Certified (Not current)	Environmental Services Program (Not current)	Instrument Diversity Index	Potential Response Index	Priority Intervention Value (Table VIII-2)	Overall Threat status (from Appendix VIII-1)
Charadrahyla tecuani																2						2	1	**6**	2.5
Charadrahyla trux														2		2					1	4	2	**5**	2.75
Chiropterotriton crascens					4		3					3		2							1	9	4	**3**	2.25
Chiropterotriton dimidiatus				4			3							2	2		1		2			8	3	**5**	3
Chiropterotriton lavae				4			3							2			1				1	6	3	**6**	4
Chiropterotriton mosaueri				4										2			1					6	3	**4**	2
Chiropterotriton terrestris		5		4										2			1					7	3	**4**	2.25
Craugastor batrachylus					4		3					3		2	2						1	11	4	**3**	2
Craugastor galacticorhinus														2								2	1	**7**	3.25
Craugastor glaucus			4				3					3		2								9	4	**4**	3.25
Craugastor guerreroensis										3						2						5	2	**5**	2.75
Craugastor megalotympanum		5	4	4			3		4					2	2						1	13	4	**4**	3.25
Craugastor montanus		5	4	4			3					3		2								10	4	**4**	3
Craugastor omiltemanus										3				2		2					1	7	3	**5**	3
Craugastor palenque	5			4				3														5	2	**6**	3
Craugastor pelorus							3	3		3				2		2	1					10	4	**4**	3.25
Craugastor polymniae				4			3			3				2		2					1	11	4	**3**	2
Craugastor pozo		5		4			3	3	4			3		2							1	14	5	**2**	2.75
Craugastor silvicola																2						2	1	**5**	1.75

SPECIES	World heritage sites	Federal Protected Area (Core Zone)	Ramsar Site	Federal Protected Area (Buffer Zone)	State Protected Area (Core Zone)	Municipal Protected Area (Core Zone)	State Protected Area (Buffer Zone)	Municipal Protected Area (Buffer Zone)	Field research stations (public or private)	Community-Conserved Areas (Certified)	Forest Stewardship Council Certified (Current)	Community-Conserved Areas (Not certified)	Permanent Forestry Area	Environmental Services Program (Current)	Wildlife Management Unit (UMA)	Community Zoning Plan	Regional Environmental Zoning Plan (State Coverage)	Zoning Plan (Sub-State Coverage)	Local Environmental Zoning Plan	Forest Stewardship Council Certified (Not current)	Environmental Services Program (Not current)	Instrument Diversity Index	Potential Response Index	Priority Intervention Value (Table VIII-2)	Overall Threat status (from Appendix VIII-1)
Craugastor taylori			4								3			2		2				1		11	4	**4**	3
Craugastor vulcani		5	4	4			3		4					2	2		1				1	13	4	**4**	3.25
Cryptotriton adelos				4			3			3	3	3		2		2				1	1	17	5	**3**	3
Cryptotriton alvarezdeltoroi								3						2								5	2	**6**	3.25
Dendrotriton megarhinus		5		4			3							2		2			2		1	9	4	**3**	2
Dendrotriton xolocalcae				4			3							2								6	3	**5**	3
Duellmanohyla chamulae								3						2		2						7	3	**5**	3.5
Duellmanohyla ignicolor										3	3	3		2		2				1	1	13	4	**3**	2.75
Ecnomiohyla echinata				4			3			3	3	3		2		2				1	1	17	5	**2**	2.75
Ecnomiohyla valancifer		5	4	4			3		4					2	2						1	13	4	**4**	3.75
Eleutherodactylus dennisi										3					2							5	2	**5**	2.25
Eleutherodactylus dixoni										3						2						5	2	**5**	2.75
Eleutherodactylus grandis				4			3		4					2			1				1	10	3	**5**	3.75
Eleutherodactylus nivicolimae				4			3							2		2	1				1	8	3	**4**	2.75
Eleutherodactylus rufescens																	1					1	1	**5**	1.75
Eleutherodactylus verruculatus														2							1	2	1	**7**	4
Ensatina eschscholtzii				4			3			3				2							1	9	4	**5**	4.25
Exerodonta abdivita														2								2	1	**6**	2.25

SPECIES	World heritage sites	Federal Protected Area (Core Zone)	Ramsar Site	Federal Protected Area (Buffer Zone)	State Protected Area (Core Zone)	Municipal Protected Area (Core Zone)	State Protected Area (Buffer Zone)	Municipal Protected Area (Buffer Zone)	Field research stations (public or private)	Community-Conserved Areas (Certified)	Forest Stewardship Council Certified (Current)	Community-Conserved Areas (Not certified)	Permanent Forestry Area	Environmental Services Program (Current)	Wildlife Management Unit (UMA)	Community Zoning Plan	Regional Environmental Zoning Plan (State Coverage)	Zoning Plan (Sub-State Coverage)	Local Environmental Zoning Plan	Forest Stewardship Council Certified (Not current)	Environmental Services Program (Not current)	Instrument Diversity Index	Potential Response Index	Priority Intervention Value (Table VIII-2)	Overall Threat status (from Appendix VIII-1)
Exerodonta bivocata								3						2		2						7	3	**5**	3.25
Exerodonta chimalapa		5		4			3							2		2						9	4	**2**	1.75
Exerodonta xera				4			3							2		2						8	3	**4**	2.75
Hyla arboricola										3						2					1	5	2	**5**	2.75
Incilius pisinnus				4			3									2	1					6	3	**4**	2.5
Lithobates chichicuahutla																					1	1	1	**7**	3
Lithobates dunni			4				3							2		2	1				1	8	3	**5**	3.25
Lithobates lemosespinali														2								2	1	**5**	1.75
Lithobates omiltemanus										3						2					1	5	2	**5**	2.75
Lithobates psilonota														2		2	1					5	2	**5**	2.75
Lithobates pueblae			4	4						3				2			1					9	4	**4**	3
Lithobates tlaloci	5		4	4			3		4					2			1				1	11	4	**4**	3.75
Megastomatohyla mixomaculata			4	4			3							2							1	6	3	**5**	3.75
Megastomatohyla nubicola				4										2							1	6	3	**6**	4.5
Megastomatohyla pellita														2		2					1	4	2	**5**	2.75
Plectrohyla ameibothalame				4			3							2		2						8	3	**4**	2.25
Plectrohyla calthula														2		2						4	2	**5**	2
Plectrohyla calvicollina				4						3	3	3		2		2				1	1	17	5	**2**	2.5

SPECIES	World heritage sites	Federal Protected Area (Core Zone)	Ramsar Site	Federal Protected Area (Buffer Zone)	State Protected Area (Core Zone)	Municipal Protected Area (Core Zone)	State Protected Area (Buffer Zone)	Municipal Protected Area (Buffer Zone)	Field research stations (public or private)	Community-Conserved Areas (Certified)	Forest Stewardship Council Certified (Current)	Community-Conserved Areas (Not certified)	Permanent Forestry Area	Environmental Services Program (Current)	Wildlife Management Unit (UMA)	Community Zoning Plan	Regional Environmental Zoning Plan (State Coverage)	Zoning Plan (Sub-State Coverage)	Local Environmental Zoning Plan	Forest Stewardship Council Certified (Not current)	Environmental Services Program (Not current)	Instrument Diversity Index	Potential Response Index	Priority Intervention Value (Table VIII-2)	Overall Threat status (from Appendix VIII-1)
Plectrohyla celata										3	3	3		2		2				1	1	13	4	**4**	3
Plectrohyla chryses										3				2		2					1	7	3	**4**	2.75
Plectrohyla cyanomma										3	3	3		2		2				1	1	13	4	**3**	2.5
Plectrohyla ephemera										3				2		2					1	7	3	**4**	2.25
Plectrohyla labedactyla											3			2		2				1		7	3	**4**	2
Plectrohyla miahuatlanensis																						0	0	**7**	2.75
Plectrohyla mykter										3				2		2					1	7	3	**4**	2.5
Plectrohyla pachyderma							3										1				1	3	1	**7**	3.75
Plectrohyla psarosema														2		2						4	2	**5**	2
Plectrohyla pycnochila			4				3	3				3		2								9	4	**4**	3.5
Plectrohyla sabrina										3	3	3		2		2				1	1	13	4	**3**	2.75
Plectrohyla siopela				4			3							2			1				1	6	3	**5**	3.5
Pseudoeurycea ahuitzotl														2		2						4	2	**5**	2.75
Pseudoeurycea amuzga																2						2	1	**5**	1.75
Pseudoeurycea anitae											3			2		2				1		7	3	**4**	2.25
Pseudoeurycea aquatica														2		2						4	2	**4**	1.75
Pseudoeurycea aurantia				4			3			3				2		2					1	11	4	**3**	2.75
Pseudoeurycea conanti										3				2		2					1	7	3	**4**	2.75

SPECIES	World heritage sites	Federal Protected Area (Core Zone)	Ramsar Site	Federal Protected Area (Buffer Zone)	State Protected Area (Core Zone)	Municipal Protected Area (Core Zone)	State Protected Area (Buffer Zone)	Municipal Protected Area (Buffer Zone)	Field research stations (public or private)	Community-Conserved Areas (Certified)	Forest Stewardship Council Certified (Current)	Community-Conserved Areas (Not certified)	Permanent Forestry Area	Environmental Services Program (Current)	Wildlife Management Unit (UMA)	Community Zoning Plan	Regional Environmental Zoning Plan (State Coverage)	Zoning Plan (Sub-State Coverage)	Local Environmental Zoning Plan	Forest Stewardship Council Certified (Not current)	Environmental Services Program (Not current)	Instrument Diversity Index	Potential Response Index	Priority Intervention Value (Table VIII-2)	Overall Threat status (from Appendix VIII-1)
Pseudoeurycea firscheini				4			3							2								6	3	**5**	3.25
Pseudoeurycea gigantea				4										2			1				1	6	3	**4**	2.75
Pseudoeurycea lineola			4	4			3			3				2							1	9	4	**4**	3.75
Pseudoeurycea longicauda		5		4			3					3		2		2	1		2		1	12	4	**3**	2.75
Pseudoeurycea lynchi				4			3							2			1				1	6	3	**5**	3.75
Pseudoeurycea maxima														2		2						4	2	**5**	2.75
Pseudoeurycea melanomolga				4			3							2			1				1	6	3	**6**	4
Pseudoeurycea mixcoatl										3				2		2					1	7	3	**4**	2.75
Pseudoeurycea mixteca				4			3							2		2						8	3	**4**	2
Pseudoeurycea mystax														2		2						4	2	**5**	2.25
Pseudoeurycea naucampatepetl				4			3							2			1				1	6	3	**5**	3.75
Pseudoeurycea nigra				4			3	3				3		2								9	4	**4**	3.25
Pseudoeurycea obesa				4			3							2								6	3	**5**	3.25
Pseudoeurycea orchileucos										3	3			2		2				1		10	4	**3**	2.75
Pseudoeurycea orchimelas		5	4	4			3		4					2	2		1				1	13	4	**4**	3.5
Pseudoeurycea papenfussi										3		3		2		2					1	10	4	**3**	2.5
Pseudoeurycea parva								3						2		2						7	3	**3**	1.5
Pseudoeurycea praecellens										3				2								5	2	**6**	3.5

SPECIES	World heritage sites	Federal Protected Area (Core Zone)	Ramsar Site	Federal Protected Area (Buffer Zone)	State Protected Area (Core Zone)	Municipal Protected Area (Core Zone)	State Protected Area (Buffer Zone)	Municipal Protected Area (Buffer Zone)	Field research stations (public or private)	Community-Conserved Areas (Certified)	Forest Stewardship Council Certified (Current)	Community-Conserved Areas (Not certified)	Permanent Forestry Area	Environmental Services Program (Current)	Wildlife Management Unit (UMA)	Community Zoning Plan	Regional Environmental Zoning Plan (State Coverage)	Zoning Plan (Sub-State Coverage)	Local Environmental Zoning Plan	Forest Stewardship Council Certified (Not current)	Environmental Services Program (Not current)	Instrument Diversity Index	Potential Response Index	Priority Intervention Value (Table VIII-2)	Overall Threat status (from Appendix VIII-1)
Pseudoeurycea quetzalanensis														2							1	2	1	**7**	3.5
Pseudoeurycea robertsi				4			3							2			1				1	6	3	**5**	3.25
Pseudoeurycea ruficauda				4			3							2								6	3	**5**	3.25
Pseudoeurycea saltator										3	3	3		2		2				1	1	13	4	**3**	2.5
Pseudoeurycea scandens				4			3			3	3	3		2		2				1	1	17	5	**2**	2.75
Pseudoeurycea smithi					4		3					3		2	2						1	11	4	**2**	1.75
Pseudoeurycea tenchalli										3				2		2					1	7	3	**4**	2.25
Pseudoeurycea teotepec														2		2						4	2	**6**	3
Pseudoeurycea tlahcuiloh														2		2						4	2	**5**	2.25
Pseudoeurycea tlilicxitl				4			3		4					2			1				1	10	4	**3**	2.75
Pseudoeurycea unguidentis				4			3			3	3	3		2		2				1	1	17	5	**3**	3
Pseudoeurycea werleri		5	4	4			3		4					2	2						1	13	4	**4**	3.5
Ptychohyla acrochorda										3	3	3		2		2				1	1	13	4	**3**	2.75
Ptychohyla erythromma										3				2		2					1	7	3	**4**	2.25
Thorius arboreus										3	3	3		2		2				1	1	13	4	**3**	2.75
Thorius aureus										3	3	3		2		2				1	1	13	4	**3**	2.75
Thorius boreas										3	3	3		2		2				1	1	13	4	**3**	2.5
Thorius dubitus				4			3							2								6	3	**5**	3.25

SPECIES	World heritage sites	Federal Protected Area (Core Zone)	Ramsar Site	Federal Protected Area (Buffer Zone)	State Protected Area (Core Zone)	Municipal Protected Area (Core Zone)	State Protected Area (Buffer Zone)	Municipal Protected Area (Buffer Zone)	Field research stations (public or private)	Community-Conserved Areas (Certified)	Forest Stewardship Council Certified (Current)	Community-Conserved Areas (Not certified)	Permanent Forestry Area	Environmental Services Program (Current)	Wildlife Management Unit (UMA)	Community Zoning Plan	Regional Environmental Zoning Plan (State Coverage)	Zoning Plan (Sub-State Coverage)	Local Environmental Zoning Plan	Forest Stewardship Council Certified (Not current)	Environmental Services Program (Not current)	Instrument Diversity Index	Potential Response Index	Priority Intervention Value (Table VIII-2)	Overall Threat status (from Appendix VIII-1)
Thorius grandis														2		2						4	2	**5**	2.75
Thorius infernalis														2		2						4	2	**5**	2.5
Thorius insperatus										3		3		2		2					1	10	4	**3**	2.25
Thorius lunaris				4										2							1	6	3	**5**	3.25
Thorius macdougalli										3	3	3		2		2				1	1	13	4	**3**	2.5
Thorius magnipes				4			3							2								6	3	**5**	3
Thorius minutissimus																2						2	1	**5**	1.5
Thorius minydemus				4			3							2			1				1	6	3	**6**	4
Thorius munificus				4			3							2			1				1	6	3	**6**	4
Thorius narismagnus		5		4			3		4					2	2						1	13	4	**4**	3.75
Thorius omiltemi										3				2		2					1	7	3	**4**	2.75
Thorius papaloae				4			3							2		2						8	3	**4**	2.25
Thorius pennatulus				4						3				2								9	4	**5**	4
Thorius pulmonaris				4			3			3	3	3		2		2				1	1	17	5	**3**	3
Thorius schmidti				4			3							2								6	3	**5**	3.25
Thorius smithi										3	3	3		2		2				1	1	13	4	**3**	2.75
Thorius spilogaster				4										2							1	6	3	**5**	3.25
Thorius troglodytes				4			3							2								6	3	**4**	2.75

APPENDIX VIII-3

Potential strategies per micro-endemic amphibians' buffered areas (AMBAs) derived from specific characteristics of each region. CZP = Conservation Zoning Plans; CCAcp = Community Conserved Areas (c=communal, p=private); PA=Protected Areas (m = Municipal, s = State, f = Federal ; ESP = Environmental Services Program (b = biological, h = hydrological, a = agro-forestry); PAF = Permanent Forestry Area; FSC = Forest Stewardship Council certification. Conservation priorities come from Appendix VIII-2. "Ejido" and "Community" are two types of distinct communal land tenure in Mexico.

Species	**% Indigenous territory**	**% Gap extreme priority**	**% Gap high priority**	**% Gap medium priority**	**% "Ejido" land tenure**	**% Community land tenure**	**% ESP Eligible zones agro-forestry**	**% ESP Eligible zones biodiversity**	**%ESP Eligible zones hydrological**	**% Temperate & tropical timber forests**	**% Wetlands**	**Conservation priorities**	**% Remnant vegetation**	**Feasible strategies**
Ambystoma amblycephalum	3%	16%	0%	42%	34%	8%	1%	33%	39%	36%	0%	4	51%	Field Verification, CZP, CCAp, PAm.
Ambystoma andersoni	0%	68%	0%	0%	49%	11%	0%	0%	53%	31%	0%	6	36%	Field Verification, CZP, ESPb, CCAcp.
Ambystoma bombypellum	0%	0%	0%	0%	45%	0%	1%	0%	0%	0%	0%	7	10%	Field Verification, CZP, ESP b, h, CCAp, PAs, or PAm.
Ambystoma dumerili	29%	0%	0%	38%	29%	20%	1%	87%	78%	31%	2%	5	47%	Field Verification, CZP, CCAp, ESP a, b, PAf.
Ambystoma flavipiperatum	0%	0%	0%	14%	33%	3%	0%	21%	18%	25%	2%	5	41%	Field Verification, CCAcp.
Ambystoma granulosum	6%	0%	17%	2%	53%	4%	1%	12%	7%	9%	0%	4	12%	Field Verification, CZP, ESP b, h, CCAcp, PAs.

Species	% Indigenous territory	% Gap extreme priority	% Gap high priority	% Gap medium priority	% "Ejido" land tenure	% Community land tenure	% ESP Eligible zones agro-forestry	% ESP Eligible zones biodiversity	%ESP Eligible zones hydrological	% Temperate & tropical timber forests	% Wetlands	Conservation priorities	% Remnant vegetation	Feasible strategies
Ambystoma leorae	0%	51%	33%	11%	66%	8%	3%	57%	86%	58%	0%	3	72%	
Ambystoma lermaense	1%	0%	48%	12%	33%	16%	4%	29%	32%	13%	0%	5	25%	Field Verification, CZP, ESP a, b, CCAcp, PAs.
Ambystoma mexicanum	0%	10%	7%	23%	13%	0%	6%	12%	14%	2%	4%	4	8%	Field Verification, CCAp.
Ambystoma taylori	0%	0%	0%	18%	73%	0%	5%	61%	0%	1%	12%	7	28%	Field Verification, CZP, PFA - FSC, CCAcp, PAs, or PAm.
Bolitoglossa alberchi	93%	23%	75%	2%	1%	72%	64%	60%	13%	0%	0%	5	86%	CZP, ESP b, CCAcp,
Bolitoglossa hermosa	0%	7%	79%	0%	67%	8%	49%	57%	0%	38%	0%	5	81%	CZP, ESP b, CCAcp, PAm.
Bolitoglossa oaxacensis	45%	78%	0%	22%	0%	77%	61%	0%	0%	56%	0%	5	84%	Field Verification, CZP, ESP b, CCAcp, PAm.
Bolitoglossa riletti	49%	19%	16%	17%	35%	62%	68%	3%	0%	50%	0%	5	64%	CZP, ESP a, PFA - FSC, CCAc,
Bolitoglossa veracrucis	22%	55%	25%	20%	53%	5%	100%	58%	69%	0%	0%	4	43%	Field Verification.CZP, ESP b, h, CCAcp, PAs,
Bolitoglossa zapoteca	47%	37%	0%	0%	0%	95%	0%	0%	0%	92%	0%	5	97%	CZP, PFA - FSC, CCAc, PAs.
Charadrahyla altipotens	31%	15%	0%	45%	3%	77%	24%	18%	16%	41%	0%	5	71%	Field Verification, CZP, ESP b, Ramsar, CCAc.
Charadrahyla chaneque	62%	37%	26%	8%	28%	37%	34%	36%	37%	22%	0%	2	67%	

Species	% Indigenous territory	% Gap extreme priority	% Gap high priority	% Gap medium priority	% "Ejido" land tenure	% Community land tenure	% ESP Eligible zones agro-forestry	% ESP Eligible zones biodiversity	%ESP Eligible zones hydrological	% Temperate & tropical timber forests	% Wetlands	Conservation priorities	% Remnant vegetation	Feasible strategies
Charadrahyla tecuani	0%	0%	0%	46%	100%	0%	70%	0%	0%	86%	0%	6	90%	CZP, ESP a, PFA - FSC, CCAc, PAm.
Charadrahyla trux	0%	28%	72%	0%	57%	36%	41%	15%	0%	42%	0%	5	85%	CZP, CCAc, new ESP PAs.
Chiropterotriton crascens	0%	9%	75%	0%	48%	0%	41%	99%	59%	23%	0%	3	78%	
Chiropterotriton dimidiatus	0%	9%	61%	18%	41%	0%	10%	9%	25%	5%	0%	5	40%	Field Verification, CZP, ESP b, PFA - FSC, CCAp, Pas.
Chiropterotriton lavae	0%	43%	25%	0%	24%	0%	21%	100%	83%	26%	0%	6	39%	Field Verification, ESP b, h, CCAp, PAs, or PAm.
Chiropterotriton mosaueri	16%	70%	15%	15%	18%	51%	0%	0%	0%	35%	0%	4	73%	
Chiropterotriton terrestris	2%	38%	11%	48%	11%	9%	6%	27%	0%	11%	0%	4	55%	
Craugastor batrachylus	0%	3%	52%	0%	47%	0%	29%	32%	19%	26%	0%	3	62%	
Craugastor galacticorhinus	100%	84%	16%	0%	6%	19%	0%	1%	0%	27%	0%	7	54%	CZP, new ESP, CCAp, PAf.
Craugastor glaucus	69%	25%	0%	0%	41%	16%	6%	0%	0%	50%	0%	4	57%	
Craugastor guerreroensis	0%	45%	1%	0%	57%	21%	74%	76%	1%	70%	0%	5	79%	CZP, CCAc, new ESP PAs, or PAm.

Species	% Indigenous territory	% Gap extreme priority	% Gap high priority	% Gap medium priority	% "Ejido" land tenure	% Community land tenure	% ESP Eligible zones agro-forestry	% ESP Eligible zones biodiversity	%ESP Eligible zones hydrological	% Temperate & tropical timber forests	% Wetlands	Conservation priorities	% Remnant vegetation	Feasible strategies
Craugastor megalotympanum	7%	6%	34%	28%	55%	0%	39%	83%	34%	0%	1%	4	26%	Field Verification.
Craugastor montanus	17%	13%	31%	10%	55%	9%	35%	79%	10%	11%	0%	4	52%	
Craugastor omiltemanus	0%	44%	45%	0%	63%	7%	19%	34%	26%	42%	0%	5	85%	Field Verification, CZP, ESP b, CCAcp,
Craugastor palenque	55%	5%	17%	0%	55%	0%	65%	3%	0%	0%	0%	6	48%	CZP, ESP b, h, PAs, CCAcp, or PAm.
Craugastor pelorus	31%	14%	16%	23%	44%	2%	14%	2%	45%	4%	0%	4	38%	Field Verification.
Craugastor polymniae	95%	0%	80%	0%	1%	92%	6%	100%	87%	42%	0%	3	90%	
Craugastor pozo	18%	6%	10%	13%	37%	8%	34%	15%	11%	27%	0%	2	50%	
Craugastor silvicola	94%	46%	54%	0%	0%	63%	100%	41%	0%	0%	0%	5	83%	Field Verification, CZP, CCAcp, PAm.
Craugastor taylori	31%	36%	2%	5%	73%	2%	50%	17%	0%	15%	3%	4	57%	
Craugastor vulcani	20%	7%	15%	19%	51%	3%	58%	59%	16%	0%	0%	4	15%	Field Verification.
Cryptotriton adelos	94%	56%	34%	2%	9%	81%	7%	86%	62%	26%	0%	3	77%	
Cryptotriton alvarezdeltoroi	35%	26%	18%	6%	32%	3%	25%	4%	7%	3%	0%	6	36%	Field Verification, CZP, CCAcp, PAs.

Species	% Indigenous territory	% Gap extreme priority	% Gap high priority	% Gap medium priority	% "Ejido" land tenure	% Community land tenure	% ESP Eligible zones agro-forestry	% ESP Eligible zones biodiversity	%ESP Eligible zones hydrological	% Temperate & tropical timber forests	% Wetlands	Conservation priorities	% Remnant vegetation	Feasible strategies
Dendrotriton megarhinus	0%	14%	79%	7%	47%	0%	35%	100%	80%	61%	0%	3	90%	
Dendrotriton xolocalcae	0%	0%	47%	0%	63%	1%	24%	100%	6%	2%	0%	5	46%	CZP, CCAcp, new ESP PAs.
Duellmanohyla chamulae	44%	20%	29%	9%	61%	3%	25%	20%	24%	8%	0%	5	44%	Field Verification, CZP, ESP b, CCAcp, PAm.
Duellmanohyla ignicolor	100%	25%	70%	0%	32%	38%	17%	75%	31%	0%	0%	3	75%	
Ecnomiohyla echinata	99%	29%	56%	8%	4%	76%	19%	100%	88%	17%	0%	2	81%	
Ecnomiohyla valancifer	0%	19%	31%	13%	51%	0%	42%	67%	25%	0%	1%	4	16%	Field Verification, CZP, ESP b, h, CCAcp, PAs, or PAm.
Eleutherodactylus dennisi	0%	0%	0%	0%	47%	1%	41%	0%	0%	33%	0%	5	33%	CZP, ESP b, h, CCAp, PAf.
Eleutherodactylus dixoni	0%	28%	14%	0%	57%	11%	66%	67%	11%	61%	0%	5	77%	Field Verification, CZP, CCAcp,
Eleutherodactylus grandis	0%	59%	23%	0%	0%	0%	8%	0%	57%	8%	0%	5	28%	Field Verification, ESP a, CCAp, PAf.
Eleutherodactylus nivicolimae	0%	26%	22%	0%	53%	0%	22%	17%	32%	32%	0%	4	47%	CZP, ESP b, h CCAcp, PAm.

Species	% Indigenous territory	% Gap extreme priority	% Gap high priority	% Gap medium priority	% "Ejido" land tenure	% Community land tenure	% ESP Eligible zones agro-forestry	% ESP Eligible zones biodiversity	%ESP Eligible zones hydrological	% Temperate & tropical timber forests	% Wetlands	Conservation priorities	% Remnant vegetation	Feasible strategies
Eleutherodactylus rufescens	0%	49%	0%	6%	10%	0%	44%	65%	0%	84%	0%	5	86%	ESP b, PFA - FSC, CCAp, PAs.
Eleutherodactylus verruculatus	0%	76%	16%	0%	11%	0%	62%	100%	9%	0%	0%	7	17%	Field Verification, ESP a,b, CCAp, PAf.
Ensatina eschscholtzii	5%	57%	11%	7%	30%	0%	71%	84%	28%	4%	0%	5	20%	Field Verification, CCAp, ESP a, b, PAf.
Exerodonta abdivita	72%	0%	100%	0%	45%	24%	23%	57%	0%	0%	0%	6	81%	CZP, ESP a, b, h, CCAcp, PAf, PAm.
Exerodonta bivocata	68%	37%	40%	15%	72%	5%	19%	4%	12%	13%	0%	5	66%	CZP, ESP a, b, PFA - FSC, CCAcp, PAs.
Exerodonta chimalapa	26%	21%	6%	43%	18%	21%	66%	41%	14%	64%	0%	2	77%	
Exerodonta xera	21%	15%	52%	4%	40%	40%	1%	83%	2%	24%	0%	4	69%	CZP, ESP b, CCAc, PAs.
Hyla arboricola	4%	21%	21%	7%	47%	15%	22%	29%	15%	36%	0%	5	75%	CZP, ESP b, CCAcp, PAs.
Incilius pisinnus	0%	3%	0%	0%	74%	0%	5%	2%	1%	37%	0%	4	41%	Field Verification, CZP, CCAcp, PAs.
Lithobates chichicuahutla	0%	0%	0%	4%	59%	0%	5%	69%	0%	4%	2%	7	23%	Field Verification, CZP, CCAcp.
Lithobates dunni	12%	10%	0%	16%	36%	10%	2%	56%	42%	25%	1%	5	36%	Field Verification, CZP, ESP a, b, CCAp, PAf.

Species	% Indigenous territory	% Gap extreme priority	% Gap high priority	% Gap medium priority	% "Ejido" land tenure	% Community land tenure	% ESP Eligible zones agro-forestry	% ESP Eligible zones biodiversity	%ESP Eligible zones hydrological	% Temperate & tropical timber forests	% Wetlands	Conservation priorities	% Remnant vegetation	Feasible strategies
Lithobates lemosespinali	100%	0%	0%	10%	87%	0%	0%	48%	0%	54%	0%	5	94%	CZP, CCAc, new ESP PAs.
Lithobates omiltemanus	1%	32%	21%	3%	50%	11%	34%	25%	12%	45%	0%	5	82%	Field Verification, CZP, ESP b, CCAcp.
Lithobates psilonota	0%	19%	0%	0%	27%	0%	7%	0%	3%	32%	0%	5	37%	Field Verification, CCAp.
Lithobates pueblae	68%	47%	0%	32%	2%	0%	22%	64%	0%	11%	0%	4	35%	Field Verification.
Lithobates tlaloci	0%	14%	14%	13%	15%	1%	11%	8%	18%	3%	4%	4	14%	Field Verification, CCAp.
Megastomatohyla mixomaculata	5%	52%	9%	8%	26%	0%	51%	99%	59%	6%	0%	5	28%	Field Verification, ESP a, b, h, CCAp, PAf.
Megastomatohyla nubicola	2%	76%	15%	2%	26%	0%	70%	99%	28%	0%	0%	6	19%	Field Verification, ESP a, b, CCAp, PAf.
Megastomatohyla pellita	66%	37%	0%	56%	0%	63%	44%	38%	35%	51%	0%	5	77%	CZP, ESP- a, b, h CCAcp.
Plectrohyla ameibothalame	16%	12%	0%	27%	1%	95%	0%	34%	0%	30%	0%	4	63%	
Plectrohyla calthula	100%	43%	57%	0%	0%	92%	18%	100%	27%	9%	0%	5	93%	CZP, CCAc, new ESP PAf, or PAm.
Plectrohyla calvicollina	30%	0%	0%	14%	3%	96%	0%	100%	57%	67%	0%	2	87%	

Species	% Indigenous territory	% Gap extreme priority	% Gap high priority	% Gap medium priority	% "Ejido" land tenure	% Community land tenure	% ESP Eligible zones agro-forestry	% ESP Eligible zones biodiversity	%ESP Eligible zones hydrological	% Temperate & tropical timber forests	% Wetlands	Conservation priorities	% Remnant vegetation	Feasible strategies
Plectrohyla celata	100%	50%	44%	6%	14%	82%	8%	100%	77%	20%	0%	4	88%	
Plectrohyla chryses	0%	48%	21%	1%	60%	11%	24%	37%	15%	39%	0%	4	78%	CZP, CCAcp, new ESP PAs.
Plectrohyla cyanomma	100%	53%	36%	11%	0%	98%	2%	100%	99%	36%	0%	3	92%	
Plectrohyla ephemera	100%	27%	71%	0%	0%	96%	43%	32%	41%	83%	0%	4	99%	
Plectrohyla labedactyla	65%	0%	0%	0%	16%	65%	0%	0%	0%	83%	0%	4	83%	
Plectrohyla miahuatlanensis	29%	0%	0%	54%	2%	5%	10%	48%	12%	68%	0%	7	70%	CZP, PFA - FSC, CCAp, PAm.
Plectrohyla mykter	0%	49%	51%	0%	67%	13%	28%	30%	17%	41%	0%	4	90%	CZP, ESP a, b, PFA - FSC, CCAc, PAs.
Plectrohyla pachyderma	2%	0%	38%	44%	10%	2%	14%	24%	10%	4%	0%	7	21%	Field Verification, CCAp, PAm.
Plectrohyla psarosema	100%	51%	49%	0%	0%	88%	23%	100%	16%	12%	0%	5	93%	CZP, CCAc, new ESP PAf, or PAm.
Plectrohyla pycnochila	88%	38%	7%	21%	37%	33%	9%	4%	0%	32%	0%	4	66%	
Plectrohyla sabrina	100%	60%	39%	1%	12%	83%	9%	100%	78%	13%	0%	3	87%	
Plectrohyla siopela	0%	41%	27%	25%	57%	0%	4%	100%	57%	25%	0%	5	31%	Field Verification, CZP, ESP b, h, CCAcp, PAs.

Species	% Indigenous territory	% Gap extreme priority	% Gap high priority	% Gap medium priority	% "Ejido" land tenure	% Community land tenure	% ESP Eligible zones agro-forestry	% ESP Eligible zones biodiversity	%ESP Eligible zones hydrological	% Temperate & tropical timber forests	% Wetlands	Conservation priorities	% Remnant vegetation	Feasible strategies
Pseudoeurycea ahuitzotl	0%	31%	45%	0%	1%	60%	21%	0%	0%	68%	0%	5	86%	CZP, ESP a, CCAcp, PAs.
Pseudoeurycea amuzga	55%	47%	0%	3%	47%	32%	100%	0%	0%	58%	0%	5	92%	CZP, CCAc, new ESP PAs.
Pseudoeurycea anitae	48%	38%	0%	14%	7%	73%	30%	0%	0%	52%	0%	4	78%	
Pseudoeurycea aquatica	100%	53%	47%	0%	0%	95%	8%	100%	46%	6%	0%	4	91%	CZP, ESP b, CCAc, PAf, or PAm.
Pseudoeurycea aurantia	86%	0%	65%	0%	0%	95%	4%	100%	59%	40%	0%	3	85%	
Pseudoeurycea conanti	17%	0%	2%	10%	3%	47%	26%	49%	33%	44%	0%	4	57%	CZP, CCAc, CCAcp.
Pseudoeurycea firscheini	11%	37%	0%	2%	48%	0%	0%	52%	49%	15%	0%	5	44%	Field Verification, CZP, CCAp.
Pseudoeurycea gigantea	0%	39%	33%	26%	36%	0%	2%	100%	90%	42%	0%	4	56%	Field Verification, CZP, ESP a, CCAp, PAf.
Pseudoeurycea lineola	17%	42%	4%	17%	35%	0%	65%	63%	35%	6%	0%	4	31%	Field Verification, ESP a, b, CCAcp, PAs.
Pseudoeurycea longicauda	6%	0%	7%	55%	39%	28%	8%	0%	76%	46%	0%	3	53%	

Species	**% Indigenous territory**	**% Gap extreme priority**	**% Gap high priority**	**% Gap medium priority**	**% "Ejido" land tenure**	**% Community land tenure**	**% ESP Eligible zones agro-forestry**	**% ESP Eligible zones biodiversity**	**%ESP Eligible zones hydrological**	**% Temperate & tropical timber forests**	**% Wetlands**	**Conservation priorities**	**% Remnant vegetation**	**Feasible strategies**
Pseudoeurycea lynchi	0%	21%	36%	15%	24%	0%	27%	87%	48%	16%	0%	5	40%	Field Verification, ESP b, CCAp, PAm.
Pseudoeurycea maxima	48%	25%	2%	12%	37%	59%	60%	3%	0%	53%	0%	5	67%	CZP, ESP a, PFA - FSC, CCAc, PAs.
Pseudoeurycea melanomolga	0%	33%	20%	14%	43%	0%	27%	100%	54%	22%	0%	6	30%	Field Verification, CZP, ESP b, h, CCAp, PAs, or PAm.
Pseudoeurycea mixcoatl	0%	61%	34%	2%	72%	24%	17%	62%	0%	56%	0%	4	86%	CZP, ESP b, PFA - FSC, CCAc, PAf, or PAm.
Pseudoeurycea mixteca	62%	0%	16%	11%	3%	95%	0%	78%	0%	19%	0%	4	50%	
Pseudoeurycea mystax	93%	47%	13%	9%	0%	41%	6%	80%	0%	46%	0%	5	74%	Field Verification, CZP, ESP a, b, CCAp, PAf.
Pseudoeurycea naucampatepetl	0%	44%	46%	0%	42%	0%	15%	100%	100%	43%	0%	5	52%	CZP, CCAp.
Pseudoeurycea nigra	9%	83%	0%	0%	38%	0%	43%	53%	74%	47%	0%	4	59%	
Pseudoeurycea obesa	99%	65%	35%	0%	12%	39%	13%	26%	0%	13%	0%	5	44%	Field Verification, CZP, CCAcp, PAs.
Pseudoeurycea orchileucos	100%	32%	68%	0%	46%	41%	14%	100%	24%	0%	0%	3	79%	

Species	% Indigenous territory	% Gap extreme priority	% Gap high priority	% Gap medium priority	% "Ejido" land tenure	% Community land tenure	% ESP Eligible zones agro-forestry	% ESP Eligible zones biodiversity	%ESP Eligible zones hydrological	% Temperate & tropical timber forests	% Wetlands	Conservation priorities	% Remnant vegetation	Feasible strategies
Pseudoeurycea orchimelas	18%	11%	23%	24%	43%	4%	33%	72%	24%	0%	1%	4	19%	Field Verification, CZP, ESP a, b, h, CCAp, PAf.
Pseudoeurycea papenfussi	100%	59%	31%	9%	0%	98%	1%	100%	100%	37%	0%	3	90%	
Pseudoeurycea parva	36%	9%	39%	41%	14%	44%	53%	94%	18%	79%	0%	3	96%	
Pseudoeurycea praecellens	0%	56%	0%	3%	62%	0%	100%	0%	0%	0%	0%	6	1%	Field Verification, CZP, CCAcp.
Pseudoeurycea quetzalanensis	72%	38%	0%	22%	2%	0%	57%	20%	0%	14%	0%	7	32%	Field Verification, CZP, ESP a, CCAp, PAs.
Pseudoeurycea robertsi	2%	7%	86%	0%	61%	12%	0%	90%	51%	35%	0%	5	55%	CZP, ESP a, CCAcp, PAf.
Pseudoeurycea ruficauda	90%	83%	17%	0%	28%	42%	3%	42%	0%	26%	0%	5	51%	Field Verification, CZP, ESP a, CCAcp, PAf.
Pseudoeurycea saltator	100%	58%	31%	11%	3%	94%	9%	100%	90%	25%	0%	3	87%	
Pseudoeurycea scandens	54%	9%	20%	16%	5%	77%	1%	60%	42%	59%	0%	2	71%	
Pseudoeurycea smithi	0%	8%	28%	24%	43%	0%	35%	48%	19%	0%	0%	2	73%	

Species	% Indigenous territory	% Gap extreme priority	% Gap high priority	% Gap medium priority	% "Ejido" land tenure	% Community land tenure	% ESP Eligible zones agro-forestry	% ESP Eligible zones biodiversity	%ESP Eligible zones hydrological	% Temperate & tropical timber forests	% Wetlands	Conservation priorities	% Remnant vegetation	Feasible strategies
Pseudoeurycea tenchalli	0%	73%	26%	0%	83%	12%	18%	70%	0%	51%	0%	4	87%	
Pseudoeurycea teotepec	0%	55%	41%	0%	29%	51%	20%	0%	0%	46%	0%	6	87%	CZP, ESP b, h, CCAc, PAs.
Pseudoeurycea tlahcuiloh	0%	61%	39%	0%	33%	59%	24%	1%	0%	37%	0%	5	92%	CZP, CCAc, new ESP PAf, or PAm.
Pseudoeurycea tlilicxitl	0%	20%	50%	22%	33%	25%	0%	24%	85%	40%	0%	3	57%	
Pseudoeurycea unguidentis	62%	16%	17%	24%	3%	89%	0%	91%	52%	49%	0%	3	74%	
Pseudoeurycea werleri	12%	5%	32%	32%	54%	0%	41%	79%	33%	1%	1%	4	25%	Field Verification.
Ptychohyla acrochorda	90%	31%	67%	3%	36%	53%	15%	90%	42%	10%	0%	3	83%	
Ptychohyla erythromma	0%	31%	36%	0%	70%	3%	44%	53%	22%	43%	0%	4	81%	
Thorius arboreus	100%	61%	32%	7%	1%	96%	8%	100%	99%	26%	0%	3	87%	
Thorius aureus	100%	59%	31%	10%	1%	96%	7%	100%	99%	31%	0%	3	87%	
Thorius boreas	100%	31%	49%	20%	0%	97%	1%	100%	82%	43%	0%	3	86%	

Species	% Indigenous territory	% Gap extreme priority	% Gap high priority	% Gap medium priority	% "Ejido" land tenure	% Community land tenure	% ESP Eligible zones agro-forestry	% ESP Eligible zones biodiversity	%ESP Eligible zones hydrological	% Temperate & tropical timber forests	% Wetlands	Conservation priorities	% Remnant vegetation	Feasible strategies
Thorius dubitus	11%	39%	0%	1%	49%	0%	0%	49%	54%	19%	0%	5	47%	Field Verification, CZP, CCAp, ESP b, h, PAf.
Thorius grandis	0%	53%	43%	0%	32%	54%	23%	2%	0%	38%	0%	5	89%	CZP, ESP b, CCAc, PAs.
Thorius infernalis	0%	27%	73%	0%	82%	12%	53%	13%	0%	20%	0%	5	86%	CZP, ESP a, CCAc, PAs, or PAs.
Thorius insperatus	100%	63%	30%	7%	0%	98%	1%	100%	100%	35%	0%	3	90%	
Thorius lunaris	2%	56%	11%	11%	26%	0%	10%	100%	98%	33%	0%	5	51%	ESP b, h, CCAp, PAf.
Thorius macdougalli	90%	24%	52%	15%	6%	78%	8%	100%	56%	26%	0%	3	81%	
Thorius magnipes	5%	36%	0%	0%	43%	0%	0%	37%	48%	21%	0%	5	52%	Field Verification, CZP, ESP b, CCAp, PAm.
Thorius minutissimus	62%	55%	0%	0%	0%	100%	0%	0%	0%	94%	0%	5	95%	CZP, PFA - FSC, CCAc, PAf.
Thorius minydemus	0%	39%	27%	0%	22%	0%	21%	100%	85%	29%	0%	6	40%	Field Verification, ESP b, h, CCAp, PAs, or PAm.
Thorius munificus	0%	59%	19%	4%	30%	0%	18%	100%	83%	27%	0%	6	37%	Field Verification, CCAp, ESP b, h, PAf.
Thorius narismagnus	0%	3%	43%	23%	64%	0%	45%	86%	37%	0%	0%	4	22%	Field Verification, CZP, ESP b, h, CCAcp, PAs, or PAm.
Thorius omiltemi	0%	55%	36%	1%	67%	18%	16%	36%	16%	46%	0%	4	87%	CZP, CCAc, new ESP PAf, or PAm.

Species	% Indigenous territory	% Gap extreme priority	% Gap high priority	% Gap medium priority	% "Ejido" land tenure	% Community land tenure	% ESP Eligible zones agro-forestry	% ESP Eligible zones biodiversity	%ESP Eligible zones hydrological	% Temperate & tropical timber forests	% Wetlands	Conservation priorities	% Remnant vegetation	Feasible strategies
Thorius papaloae	69%	0%	20%	0%	19%	71%	3%	100%	18%	60%	0%	4	77%	
Thorius pennatulus	27%	69%	0%	3%	42%	1%	73%	47%	19%	2%	0%	5	26%	Field Verification, CZP, CCAp.
Thorius pulmonaris	44%	11%	11%	15%	8%	73%	0%	53%	41%	38%	0%	3	62%	
Thorius schmidti	83%	49%	42%	0%	28%	5%	0%	41%	0%	27%	0%	5	50%	CZP, new ESP PAs, CCAcp or PAm.
Thorius smithi	100%	85%	15%	0%	9%	87%	19%	100%	81%	0%	0%	3	81%	
Thorius spilogaster	2%	59%	11%	11%	24%	0%	10%	100%	100%	35%	0%	5	53%	ESP b, h, CCAp, PAf,
Thorius troglodytes	13%	32%	0%	0%	44%	0%	0%	40%	49%	23%	0%	4	53%	CZP, ESP b, h, CCAp, PAf,

Duellmanohyla zoque sp. nov., Nahá 2010

IX. GENERAL DISCUSSION

“We think too small, like the frog at the bottom of the well. He thinks the sky is only as big as the top of the well. If he surfaced, he would have an entirely different view”.

Mao Tse-Tung

AMPHIBIAN CONSERVATION IN A CHANGING WORLD

Sólo se muere una vez.
(You only die once)

Currently, global changes and the prospect of numerous species extinctions are an everyday feature of the environmental news. The perspectives offered at the beginning of the millennium ecosystem assessment are possibly the worst one could expect (Norgaard, 2007). Everything seems to be wrong. There is too much pollution, too much deforestation, too many people, and there seems to be little economic and political will to solve the problems. With the realization of the extensive scale of the current global environmental problems, pessimism reigns in the air. And yet the veiled truth is that we know very little about the status of the majority of the species in the world.

Amphibians constitute one of the most threatened groups of species (Alford & Richards, 1999; Collins & Storfer, 2003; Alford *et al.*, 2007). In the last decades amphibians have captured the attention of many ecologists and environmentalists, with influential studies reporting population declines (e.g. Lips, 1998, 1999; Lips *et al.*, 2005). The paradigm of population decline in amphibians has now been supported by more than 10 years of amphibian science. Statements such as “populations of amphibians are declining in all regions where they are found” (e.g. Blaustein *et al.*, 2004, p. 35) are common. Nevertheless, there are few long term monitoring studies that support this theory; in fact analyses based on long term monitoring (i.e. more than 15 years) have shown no declining trend (e.g. Salvidio, 2009).

Moreover, we are in an early stage of knowledge about the dynamic processes involved in amphibian community ecology across many regions of the planet. As we could see in figure I-2 of the general introduction (Chapter I) Neotropical amphibians are the most threatened (e.g. La Marca *et al.*, 2005; Rovito *et al.*, 2009). But this figure may also show a clear bias in where amphibian studies have been performed. Recognition of such a bias does not mean that Neotropical amphibians are not threatened, rather it is simply we lack of knowledge of threats to tropical amphibians in other regions, as a result of ongoing pressure on the natural resources, especially harvesting driven by temperate countries. One crude example of natural resource exploitation is of precious woods, i.e. mahogany, ebony, cedar, etc., which were very popular in the 1970s and early 1980s in Europe. But there are other examples of tropical resources exploitation, which includes industrial agriculture, such as bananas, cotton, palm oil, etc.

According to the Global Amphibian Assessment and the IUCN (update of 2011), respectively, nearly 30%/29.7% (~2059) of the amphibians, from the 6,771/6,936 amphibian species described (Frost, 2011; AmphibiaWeb, 2012), “are known to be threatened or extinct”. This category includes 38 species known to be extinct, 120 probably extinct, and 1,901 threatened (IUCN 2011). A combination of the two categories “threatened” and “extinct” is certainly problematic for conservation: while *something* can be done for a threatened species, *nothing* can be done for an extinct one - it is gone forever. Why then, are the IUCN red list analyses presented in this way? This approach is definitively puzzling. It is very likely that the aim behind it is to create awareness about species conservation. There is no doubt amphibians are a group threatened by extinction, but they are not the only threatened taxonomic group (i.e. corals, mammals, reptiles, plants, fish, etc.), and if everything is classified as a priority, nothing can actually be treated as a priority. Unfortunately, instead of encouraging conservation actions these claims could end up causing despair.

Dramatic statements that overstate the evidence have been a huge problem in conservation, particularly in the last half century, connected first with deforestation, including reliance on species–area relationships (SAR) to predict the number of extinctions (e.g. Tanentzap *et al.*, 2012); and now also connected with climate change science (e.g. Wake & Vrendenburg, 2008). It is known that deforestation can wipe out entire species populations, although there has been a lot of debate about the form of SAR that extinction rates by deforestation will follow. Conversely, there is an undeniable uncertainty in climate change projections (e.g. Keller *et al*., 2004). For example, chapter V shows that setting low dispersal capability in climate change projections (i.e. zero dispersion) generates high levels of species extinctions, but also that higher thresholds for presence in the models generate high rates of extinctions in the projections. Thus, the prevalence of species in projections for future diversity, at least for species richness or α-diversity, depends entirely on the settings, including the scenario of warming and the algorithm used (e.g. Pearson *et al.*, 2006). Although, α-diversity pattern is very likely to change in the near future we don't know exactly how. Thus, instead of focusing on α-diversity it probably would be better to focus conservation resources on β-diversity, because its overall geographic pattern will remain *stable* under climate change scenarios, making it a safe bet for conservation investment. Zones of high β-diversity are associated with topographic formations, although the values projected varied between the projected periods and p will also vary with different warming scenarios. The results indicate that heterogeneous zones associated with mountain ranges will remain particularly important for amphibian diversity and thus areas for continued conservation prioritization in the face of climate change. Historically these findings make sense, in biogeographical and biological terms, especially when a strong association can be observed among the mountain ranges and the number of endemic species – a relationship previously discerned in relation to Pleistocene refuges (i.e. Smith *et al.*, 2007). This is very likely to be valid for other groups of Mexican species, although patterns of β-diversity will vary depending on the group.

β-diversity zones for reptiles and mammals were also found to occur along mountain ranges, although not exactly in the same regions, while birds follow a different pattern, showing high values in the Mexican Plateau (see Chapter IV). Although each vertebrate group seems to be responding in a different way to environmental heterogeneity at coarser scales (from 0.125 to 2 degrees, from ~160km^2 to ~40,000km^2), climatic heterogeneity seems to be the prevailing factor associated with β-diversity in each group. It has been suggested that mountain ranges could function as ‘biogeographic crossroads” (Hortal & Lobo, 2006). These areas could act as natural corridors that would permit populations to persist by allowing migration to new habitats under conditions of changing climate. Although climate change most likely will have different effects on each group, to concentrate conservation resources on heterogeneous zones could be a good option to preserve the greatest possible diversity under a broad array of future climate-change scenarios.

Considering finer scales of analysis it was possible to observe that the drivers of amphibian metacommunities vary between landscapes (see Chapter II). The variation observed may reflect the contrasting governance regimes of the two areas studied, which directly affects the spatial structure of the patches (i.e. conserved forest, open areas, etc.). Thus, if governance of protected areas is an important driver in amphibian communities this should be one of the principal aspects to focus on in conservation. Although this aspect seems to be an obvious one, it is often ignored in scientific assessments. But recognising and emphasising the priorities of local [human] communities not only may stimulate environmentally-friendly land-use planning, but may also produce positive effects for biodiversity conservation (see Chapter VII). This leads to conscious and committed people taking care of their land not only because they recognise it as an important issue but also because their primary needs are satisfied.

It is also necessary to recognise that wilderness is a perception recently created. Human societies have been intensively modifying landscapes since the discovery of agriculture around 12,000 years ago (beginning of the Neolithic era), but they have been impacting on the environment far longer. They live in and manage landscapes; it is a fact. It would probably be better to have every piece of land well managed than just a small isolated amount of nature “untouched”. Because environmental changes happen, they are also a fact. Communities and metacommunities will go through re-arrangements as the environmental conditions in the landscape change (see Chapter III). These variations in the metacommunity structure will be mainly caused by the individual response of each species, which in the breading (i.e. rainy) season, are in search of the most adequate place to reproduce. Therefore, in well managed landscapes species will be able to move as their physiological needs require, and this will ensure species persistence in the long term. By contrast, in isolated populations/communities it seems unlikely that many of the species will be likely to migrate successfully in reference to be environmental change.

Recently, conservation paradigms, practices and policies have become a focus of research by anthropologists, geographers, biologists, and others.

Nevertheless, the relationship between conservation practitioners and academics has at times been difficult due to a lack of communication. Conservation NGOs play an important role in determining conservation agendas, funding initiatives and interventions, liaising with politicians and policy makers. And, most importantly, communicating with the public (Ladle *et al.*, 2005). However, information published in scientific journals and further reported (and possibly transformed) in the public media can become asymmetrical, not necessarily tethered to scientifically recognized realities of uncertainty or up-to-date analyses. This ‘modified information’ can take on a life of its own, even among relatively informed groups. This extract of scientific information, once established in the public media, can be further used in important environmental, social, and political contexts around the world (see Chapter VI).

Communicating science via the popular media is difficult, yet critically important, especially since it is relatively easy to create *distanciation* around an issue (McManus, 2000), which can indirectly foster feelings of despair amongst the public (Fig. IX-1). As some authors have already emphasized, scientists, as sources of information in the media, have to think carefully about how the information they are providing is going to be interpreted (Friedman *et al.*, 1999). The dynamics and goals of reporting information in the popular media often differ substantially from those of reporting research results in scientific journals. This suggests that we [as scientists] need to strive yet harder to maintain the integrity of science in the public eye by stating clearly what we know and do not know when writing for a journal or communicating more directly with the public.

When the media publish strident phrases regarding conservation issues and nothing ‘evident’ (in the public’s daily life) happens, people feel used or cheated, realizing the media has appealed to their most deep sentiments ‘apparently’ for nothing. Therefore, scepticism, regarding not just climate change, but other environmental issues, gains followers. This generates not only more distanciation towards the environmental problems but also despair in environmentally conscious people because they feel that they are “losing the battle”.

Currently the media advertises the “green” version of products but the patterns of consumption have to maintain (or even increase) the actual rate. So, no real change there. The aim is still business and profits. Nevertheless, the media can help to re-establish the links between our daily actions and the consequences of these actions for the environment. It can facilitate the acknowledgement that there is a hidden cost to our world of abundance: that there are pervasive impacts on *all* aspects of our environment (Goleman, 2009). It has also a psychological cost: the increasingly common feeling of emptiness.

The key part of the previous paragraph is the *media* (singular of medium, *Lat. medius* = middle). As can be observed increasingly frequently, people (the public) act as responsibly as they can towards the environment based on the limited information provided by the mass media. However, the media has forgotten that its place is, as its name says, in the “middle”. Media writers should not be generators of information but transmitters. Perhaps it is not their fault, because they must cover a lot of transmission time, and when they do not have enough information, they generate it, and when they generate it, they do what is best for *business*. The exhortation regarding this aspect is that scientists, as a community, must responsibly take their place in the communication process and educate the public to learn to live with uncertainty. It will be the only way to reduce/shorten the already large distance between the public and environmental problems. And if impartial scientists are not there to fill the blanks, someone else will. Maybe it will be a person well-intentioned, maybe it will not. But as long as they are not scientists, they will always privilege some ideology over information. Moreover, when this ideology doesn't fit the personal ideas of the audience, *distanciation* takes place again. It is impossible to have a single ideology that fits the personal ideas of every member of the audience. But what scientists can provide is complete information, including uncertainties. This information does not need to fit any ideas. Information can win its own right to be in everyone's consciousness.

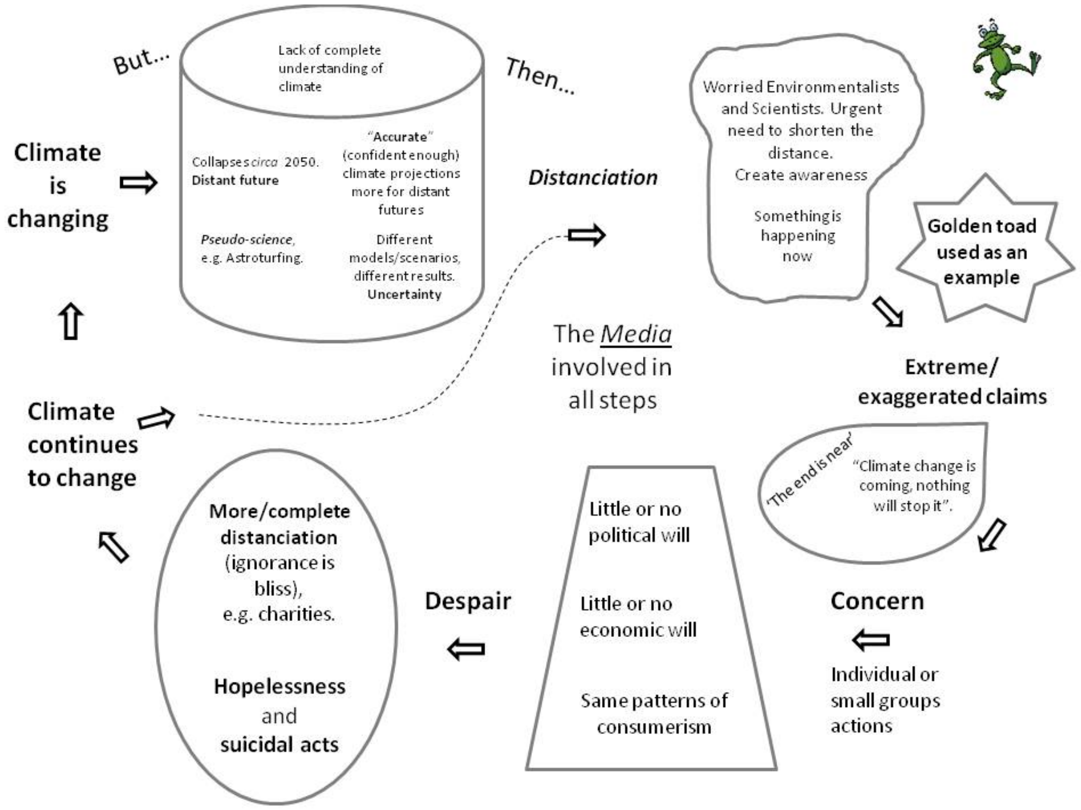

Figure IX-1. Schematization of the *distanciation* process and some of its consequences, including despair. "Astroturfing is a form of advocacy in support of a political, organizational, or corporate agenda, designed to give the appearance of a 'grassroots' movement" (Wikipedia accessed March 2012).

It is absolutely important to stress that the frame of mind within a society plays an important role in its future. "The ability to imagine and anticipate the future is a defining aspect of the human condition" (Reading, 2004, p. 3). When societies cannot imagine a better future, pessimism and despair may lead to suicidal acts.

Despair almost always compromises people's capacity to act radically, and to improve things on behalf of others (e.g. Nesse, 1999). It can also undermine confidence because individuals feel powerless to bring about desired changes and believe that nothing they can do matters (Reading, 2004). Despair leads us either to give up 'the elusive quest' entirely or to proceed self-indulgently to 'do one's own thing' in the current extremely permissive context (Lapid, 1989). The mentality of 'keep to your own business' is spread and even promoted. Therefore the sense of community is undermined. The notion of striving for the greater good stops. If it is not associated with a sense of promoting the well-being of the community, then encouraging acts that effect behavioural change is very difficult.

Adopting balanced patterns of natural resource consumption that are informed by each ecosystem's carrying capacity will ultimately determine the persistence or extinction of viable populations of species. If society does not recognise this, no amount of conservation efforts will stop or even slow down the biodiversity crisis.

Human societies have to realize that the promoted life style (i.e. the *American dream*), technological improvements, even generating and spreading knowledge, each have a cost for nature. But we are also part of nature. Moreover, we have the skills to manage nature to select areas for conservation and the resources for managing each of them. In other words, we can choose the survivors. Thus we can prioritize and implement tools that help us to reduce the gap between assessment and implementation (see Chapter VIII) and allocate (or re-allocate) resources to different places to reinforce and enlarge a pre-existing conservation area network. It is also time to accept that it will not be possible to save all species.

Even if the worst climate change projections, combined with deforestation, diseases, etc. (e.g. Hof *et al*., 2011) are ultimately correct, we are at the start of a road of uncertainty and unfortunately we will have to wait to see how the uneven effects play out around the world (warming, cooling, droughts, massive rains, etc.). If the worst climate projections are right, most likely there will be several extinctions. But it is almost certain that poor human societies will be the ones to suffer more and this can create other kinds of problems, such as riots, revolutions, wars, etc., which have detrimental consequences for the environment. In the case of other non-human species, it is possible to provide pathways: corridors through social initiatives, i.e. private or communitarian reserves, environmental zoning plans and even through the establishment of infrastructure for environmental service provision (see Chapters VII and VIII). In the last case, more intrusive programs could be promoted, such as the one that is currently being carried out in Central America by the AmphibianArk organization (http://www.amphibianark.org/, 2012). There, amphibians are collected and maintained in captivity in order to assist species' survival. Nevertheless, conserving the remaining forest patches, to create corridors, links or pathways among them will most likely increase the chance of persistence for most species, including amphibians.

The development and implementation of monitoring programmes is essential to evaluate how [amphibian] metacommunities and species distributions respond to environmental changes, especially in zones that are forecast to suffer the most drastic decreases (see Chapter V). Monitoring is always important, even if it is only to document extinctions. It also is absolutely crucial to perform adequate analyses to establish the status of populations, especially in fluctuating environments such as the seasonal tropics.

I have started monitoring two areas in south Mexico, La Pera and Nahá. In addition to continuing to monitor them, I hope to expand monitoring programs to other areas through collaborations within Mexico and other parts of Latin America. This thesis contributes to the knowledge of Mexican amphibian ecology and to the understanding of the processes underlying amphibian responses to environmental changes. I am confident that some of the analyses presented in this thesis (i.e. Chapter II, III, IV and V) will serve as an inspiration for young (and not so young) amphibiologists in Mexico. Some others will serve as tool for implementing conservation measures (i.e. Chapter VII and VIII). Finally, I expect that the reflection made in Chapter VI and in this chapter will awake some positive responses regarding sociological and political issues in conservation.

Understanding the variations of diversity drivers among landscapes could result in a more efficient management of protected areas to conserve biodiversity in the long term. In addition there is an urgent need to develop a more complete understanding of temporal patterns of diversity, and consequently the underlying processes that shape and maintain biodiversity, which is essential knowledge for protecting species adequately in human landscapes (the most pervasive form of landscape there is) in the long term. Finally I would like to stress the vital importance of finding or maintaining ways for people to fulfil their needs while halting the spread of the culture of consumerism. This will be the only way to achieve success in conservation.

Probably it is time for an environmental revolution; because the environmental crisis has gone on long enough. I would like to end with a quote from José Martí (1982, p.62):

"... Pero los pueblos no están hechos de los hombres como debieran ser, sino de los hombres como son. Y las revoluciones no triunfan, y los pueblos no se mejoran si aguardan a que la naturaleza humana cambie; sino que han de obrar conforme a la naturaleza humana y de batallar con los hombres como son, - o contra ellos."

"... But societies are not made of people as they should be, but of people as they are. And revolutions do not succeed, and people do not get better if you wait to change human nature, but must work according to human nature and do battle with people as they are - or against them. "

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Tlalocohyla picta, Nahá 2010

X. APPENDIX A. A NEW SPECIES OF TREEFROG OF THE GENUS *DUELLMANOHYLA* (ANURA: HYLIDAE) FROM SOUTHERN MEXICO

“Variety is the spice of life”.

American proverb

This Appendix was finished in August 2010, and submitted for review and publication to *Copeia*. The co-authors that contributed to this work were (in authorship order): Luis Canseco-Márquez, J. Luis Aguilar-López, Ricardo Luría-Manzano, Eduardo Pineda, and Leticia M. Ochoa Ochoa. Resubmission was encouraged and new genetic analyses were required. The required analyses are in process.

Chapter word count including references, tables and appendices: 3,700

Main text: 2,715

ABSTRACT

We describe a new species of treefrog of the genus *Duellmanohyla* from southern Mexico. The new species is characterized by a pinkish-red eye and the presence of a mental gland. It can be easily distinguished from the other Mexican species of the *Duellmanohyla* genus by coloration pattern, presence of mental gland and nuptial excrescences. Advertisement calls from a population in Chiapas also is described. The number of species of *Duellmanohyla* in Mexico has increased to five with the description of this new species.

Resumen. Se describe una nueva especie del género *Duellmanohyla* para el sur de México. La nueva especie se caracteriza por tener el iris color rosa, así como por la presencia de una glándula mental. Se diferencia fácilmente de las otras especies mexicanas del género por el patrón de coloración, la presencia de glándula mental y de excresencias nupciales. Se proporciona además información sobre el canto para la población de Chiapas. Con la descripción de esta nueva especie, el número de especies del género *Duellmanohyla* para México aumenta a cinco.

INTRODUCTION

The region known as "Selva Zoque" in southern Mexico includes part of the regions of Chimalapas in eastern Oaxaca, Uxpanapa in southern Veracruz, and "El Ocote," a protected area in Chiapas. Tropical rainforest is the principal vegetation in the region (Salas-Morales et al. 2001). Although "Selva Zoque" represents the largest non-fragmented extension of tropical rainforest in Mexico and presumably harbors a great biodiversity, unfortunately its fauna has been poorly studied. Studies of amphibians and reptiles in the Uxpanapa-Chimalapas region are scarce. However, the region has always fascinated herpetologists. Duellman (1960) described the distribution of 36 species of amphibians from the Isthmus of Tehuantepec, where few localities are from Uxpanapa, Veracruz. More recently, Navarro et al. (2008) documented 35 species of amphibians and 105 species of reptiles from several localities of Chimalapas, Oaxaca. Muñoz-Alonso, et al. (1996) described the herpetofauna of "El Ocote" in Chiapas.

In 1993, during a fieldtrip carried out in the tropical rainforest of the Chimalapas' region (Southeast Oaxaca), one of us (LCM) collected a single enigmatic female of a non-identified hylid frog that since then has been in the collection of Museo de Zoología, UNAM (MZFC). More recently, in 2008 and 2009, as part of their master and PhD theses, JLAL and LMOO respectively, while conducting explorations in the Uxpanapa, Veracruz, and Chiapas, respectively, obtained more specimens of the same hylid frog. Comparison of this new material with the female collected in 1993 revealed that the specimens represent the same species, a new hylid frog belonging to the genus *Duellmanohyla,* that is described herein.

MATERIALS AND METHODS

All measurements and terminology follow Duellman (2001). Measurements were made with calipers under a stereo microscope and rounded to 0.1 mm. Those from bilateral structures were taken on the right side of each specimen. Sex was determined by the presence of secondary sexual characters in males (nuptial excrescences and mental gland). Webbing formulae for hands and feet follow those of Myers and Duellman (1982). Descriptions of coloration in life were recorded. Spontaneous vocalizations of males of *D. zoque* were recorded from June 1st to September 25th 2009 in two different natural protected areas (PA) in Chiapas, southern Mexico: La Pera (16º 56.98’ N; 93º 20.83’ W) and Nahá (16º 57.55’ N; 91º 36.23’ W), as part of the doctoral project of L.M. Ochoa-Ochoa. Air temperature and humidity were measured in different parts of the PA every minute with a data-logger (LogTag Humidity and Temperature Data Logger), 24.1-25.6ºC and 85-100%, 20.7-23.2ºC and 80-100%, respectively. Sound recordings of 10 min were made between 20.00 and 01.00 hours using a portable digital recorder (Sony ICD-P630F) and a unidirectional microphone (AudioThecnica ATR 55). Four 10-min recordings of 11 males were made. The frogs called from leaves or branches (from 0.30 to 2 m) near the edges of the streams (< 1 m). Recording distance varied depending on accessibility of the calling location (but less than 10 m always). The recording aim was to have an extra record of populations’ sizes. Some vocalizations and predations were filmed with a digital camera (Sony DSC-H20 10.1MP).

Vocalizations were saved as *.wav files and subsequently were analyzed and edited using Syrinx and Wavelab 6 software. Calls were edited at sampling frequencies of 22 and 44 kHz, and analyzed with fast Fourier transformation (FFT) of 128 points. Further search among populations is planned in order to determine the geographic distribution of the new species.

Duellmanohyla zoque, new species (Figs. X-1–3)

Figure X-1. Specimens in life of *Duellmanohyla zoque*. A: Male holotype (MZFC 24004, 36.4 mm SVL); B: Female paratype (UTA A 59271, 55.65 SVL); C, D: Specimens from La Pera Chiapas.

Holotype.— UNAM-MZFC 24004 (original number RLM 062) an adult male (Fig. X-1A) 6.5 km SSE from Paso del Moral, Uxpanapa, Veracruz, Mexico, taken on 6 July 2008 in tropical rainforest at 76 m elevation (17° 10.84' N, 94° 35.13' W).

Paratypes.— UNAM-MZFC 18667, adult female from Chalchijapa (Chimalapas region), Oaxaca, collected on 9 May 1993 in tropical rainforest at 600 m (17º 3.25'N, 94º 39.23' W). Three females from Paso del Moral, Veracruz at 230m, 17º 10.8' N, 94º 35.39' W (MZFC 24005-06; UTA A 59271): same data as the holotype.

Other specimens (not collected) are from Chiapas, La Pera and Nahá. In "La Pera" were seen: on 2 June 2009 one juvenile at 828 m elevation (16º 53.93' N, 93º 19.85' W), on 17 August 2009 one juvenile and one male at 854 m elevation (16º 53.62' N, 93º 20.71' W), on 21 August 2009 six males and two juveniles at 800 m elevation (16º 53.63"N-93º 20.71’ W), and two males at 828 m elevation (16º 54.53’N, 93º 20.83’ W). In Nahá only two males were seen on 22 July 2009 (16º 54’ N, 93º 20.72’ W) and 24 September 2009 (16º 54.02’ N, 93º 20.72’ W) respectively.

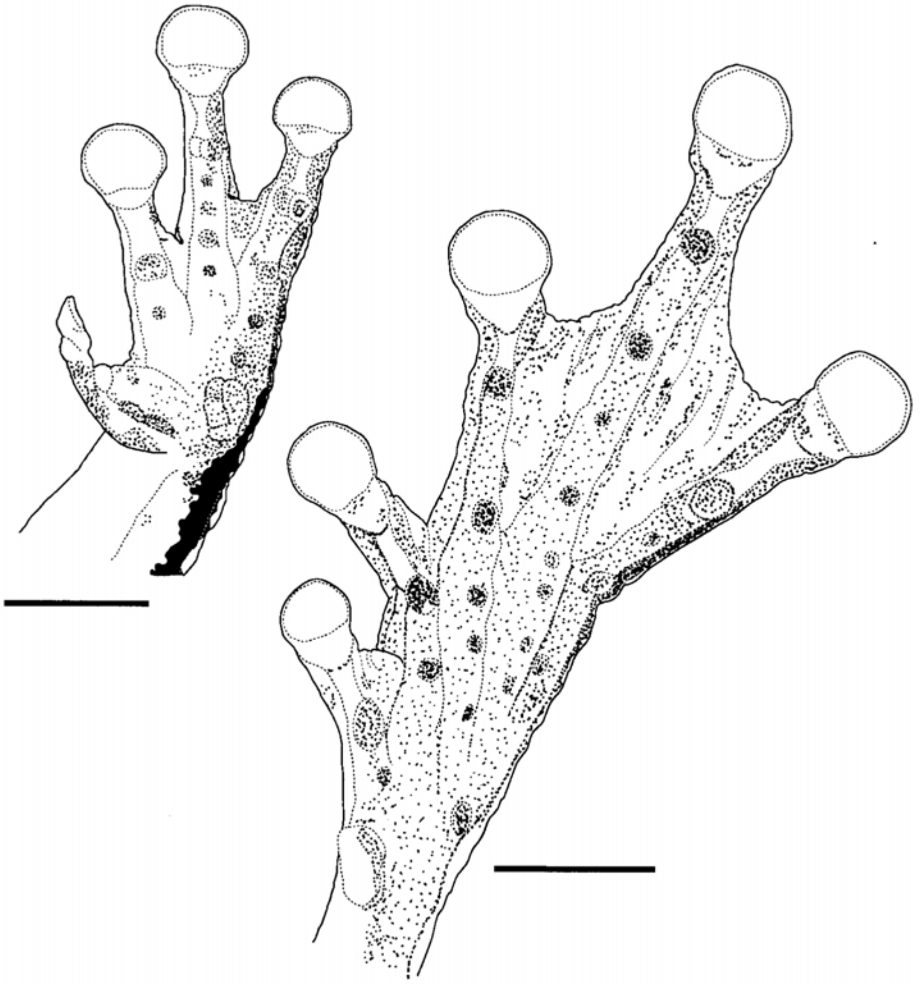

Figure X-2. Ventral aspect of hand and foot of *Duellmanohyla zoque*, holotype (MZFC 24004). Scale bar = 3 mm.

Diagnosis.— *Duellmanohyla zoque* is characterized by a green dorsum with white spots or brown dorsum with dark-brown spots (bright green in *D. ignicolor* and *D. chamulae*, brown in *D. schmidtorum*) lacking ventrolateral glands (present in all other Mexican species of the genus), iris pale pink with brown reticulations (red in *D. chamulae* and *D. schmidtorum* and golden in *D. ignicolor*). *Duellmanohyla zoque* is the largest species in the genus (Table X-1), SVL in male, 36.4 mm and 57.2 mm in females. Males have a mental gland, which is known in only two other species in the genus, *D. chamulae* and *D. ignicolor* (Table X-1). The coloration is similar to that of *Ptychohyla acrochorda*, a species in northern Oaxaca, which differs from the former by the presence of a tarsal fold, and absence of a mental gland.

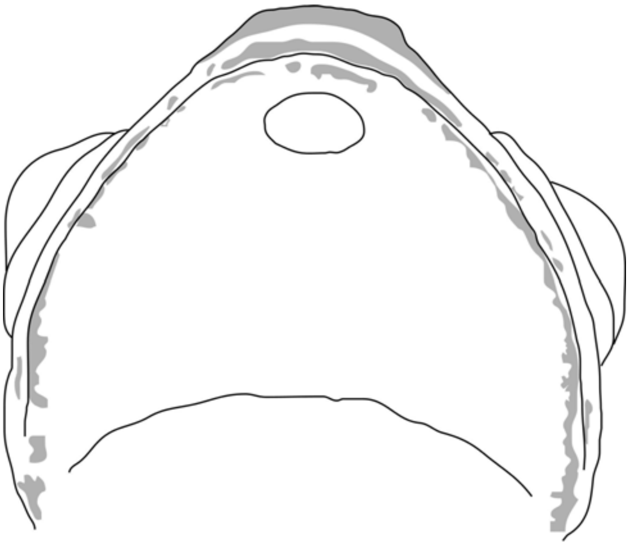

Figure X-3. Mental gland of the holotype of *Duellmanohyla zoque* (MZFC 24004).

Description of the holotype.— An adult male, SVL 36.4 mm, tibia length 20.9 mm; tibia length/SVL 0.57; foot length 15.4 mm; foot length/SVL 0.42; head length 12.7 mm; head length/SVL 0.34; head width 12.8 mm; head width/SVL 0.35; eye diameter 4.8 mm; tympanum diameter 1.9 mm; tympanum/eye 0.39. Snout in lateral view truncate, slightly rounded in dorsal view; canthus distinct and slightly angular; loreal region concave; lips moderately thick, not flared; nostrils protuberant; internarial distance 2.2 mm; top of head flat; interorbital distance 4.3 mm. Supratympanic fold well developed, extending from posterior corner of eye above tympanum to point above insertion of forearm, covering upper edge of tympanum; tympanum distinct, rounded. Forearm moderately robust; ulnar tubercles unequally elevated. Prepollex ossified, large, blunt. Nuptial excrescences small, composed of fine brown spines located on prepollical protrusion, inner and outer surface of Finger I, and dorsal surface of webbing between Fingers I and II; subarticular tubercles rounded, distal one on Fingers III and IV bifid; discs on fingers large, disc of the third finger slightly smaller than diameter of the tympanum; webbing formula II 1½—3 III 2½—2 IV (Fig. X-2). Heels overlapping when hind limbs adpressed; tibiotarsal articulation extending slightly beyond nostril; tarsal fold absent; row of tubercles forming a dermal ridge, extending from heel to disc of fifth toe; heel tubercle present; subarticular tubercles rounded; length of toes from shortest to largest 1-2-3-5-4; webbing formula I 1—2 II 1½—2 III 1—2 IV 2 —1 V (Fig. X-2).

Toes are moderately long; discs of toes same size as those on fingers (Fig. X-2). Cloacal opening directed posteroventrally at midlevel of thighs with several curved folds below the cloacal opening; cloacal sheath short; a few white tubercles below and lateral to vent. Skin on dorsum smooth; that of throat, chest, belly and ventral surface of thighs granular. Ventrolateral glands absent; small, ovoid mental gland present (Fig. X-3). Tongue cordiform with posterior notch; vomerine teeth five on right side, six on left, situated on small, elliptical elevations between ovoid internal nares. Vocal slits absent.

In life, dorsum of head, body, forelimbs, and hind limbs green with brown blotches and numerous irregular white spots concentrated on posterior part of dorsum; well-defined white stripe along upper jaw; flanks mottled with irregular white spots on pale brown background; narrow white stripe on ventrolateral edge of forearm and hand, and on the ventrolateral edge of tarsus and foot; brown stripe parallele to the white stripe on forearm, extending onto Finger IV; similar brown stripe on tarsus. White stripe above cloacal opening; brown patch with a few small white spots below cloacal opening. Belly, chin, chest, and ventral surface of limbs white. Ventral surface of the Finger IV and webbing between Fingers

III and IV sdark brown; and all ventral surface of foot, including webbing, dark brown. Iris pale pink with brown reticulations (Fig. X-1).

Vocalizations.—One or two notes comprise the advertisement calls of *Duellmanohyla zoque*. The most common call (±61% of ll calls) consists of a short single note "crrrc" (Fig. X-4A), the second (27% of calls) consists of a single note "guiac" (Fig. X-4B), and less frequently, (12% of calls) the advertisement call is composed of the two former notes, here designated mixed calls (Fig. X-4C-E). The duration of the calls is 192 ms–1.720 s (634 ± 351.7 ms, *n* = 90 calls from 4 males). Intervals between calls are 300 ms–46.5s (8.520 ± 9.872 s, n = 90 calls from 4 males); intervals longer than one minute were excluded. The mixed calls are the longest (958.5 ± 301.4 ms, *n* = 24 calls from 2 males), and the simple calls composed only by "guiac" are commonly the shortest calls (312.7 ± 131 ms, *n* = 24 from calls from 2 males).

The "crrrc" advertisement calls consists of 5–14 pulses, with mean dominant frequencies of 1231 Hz (± 373.6) to 2915 Hz (± 533.6); among these calls we registered the highest frequency (3570 Hz). The "guiac" call consists of one duplicated note with a mean frequency range of 1066.8 Hz (± 274.3) to 2841 Hz (± 583.3); among these calls we registered the lowest frequency (468 Hz). Harmonics were not evident in the spectrogram because the recording media avoid them. Running water and crickets produced primarily background noise, at the calling sites, at high frequencies (4 to 7 Khz).

Etymology.— The species name refers to the "Selva Zoque", a region that includes part of the historical range of Zoque culture, an ethnic group that has inhabited this area since immemorial times, comprising the tropical rainforest in Uxpanapa (Veracruz), Chimalapas (Oaxaca) and El Ocote (Chiapas).

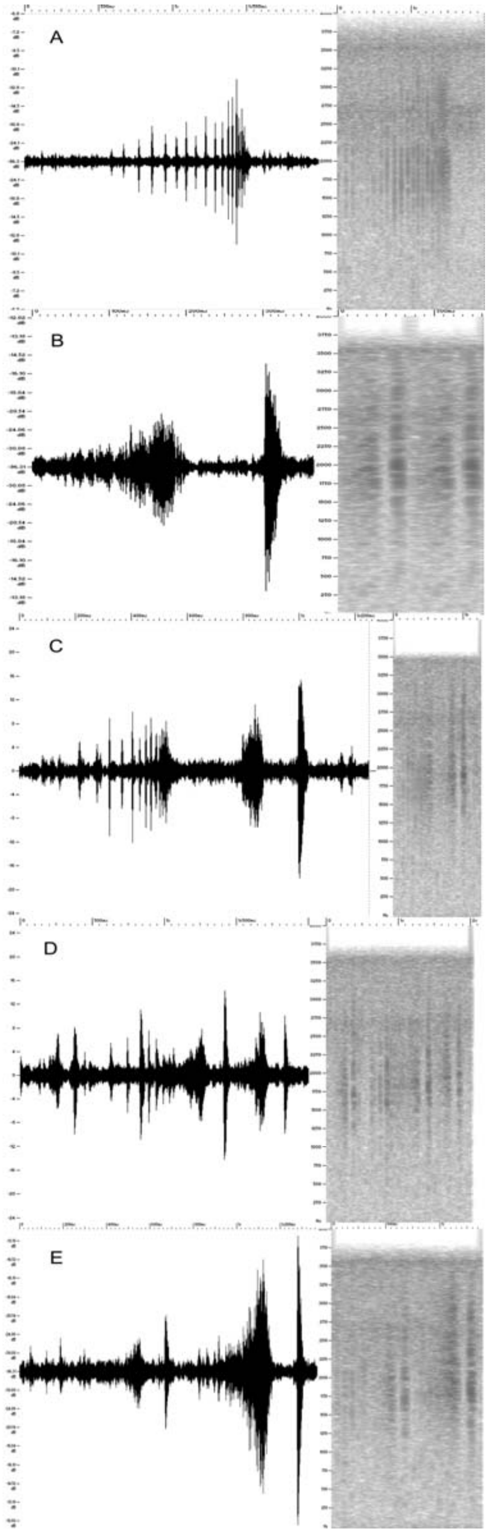

Figure X-4. Advertisement call of *Duellmanohyla zoque*.

Variation.— Variation in body measurements among four females and the single male is summarized in Table 2. Two females (MZFC, 18667, 24005) lack the scattered white spots on dorsum, additionally, one female from Uxpanapa (MZFC 24006) has a concentration of black spots along the edge of the lower lip (UTA A 59271) and has a concentration of brown spot on the chin and chest, absent in the other specimens. Variation in vomerine teeth in females is as follows: 5/7 (MZFC 18667); 6/6 (UTA A 59271); 5/4 (MZFC 24005) and 6/5 (MZFC 24006).

Habitat and Distribution.— This arboreal species occurs in undisturbed tropical rainforest in Veracruz, Oaxaca and Chiapas at elevations between 76-828 m in southern Mexico (Fig. X-5). The specimens were collected at night, with the exception of that from Chimalapas, Oaxaca, which was sleeping on a leaf at 8:30 h near a stream. The male holotype was on a bush in the river; females from Uxpanapa, Veracruz, were on *Heliconia* leaves. All were captured at 20:00-01:00h at 1.50 m above the ground.

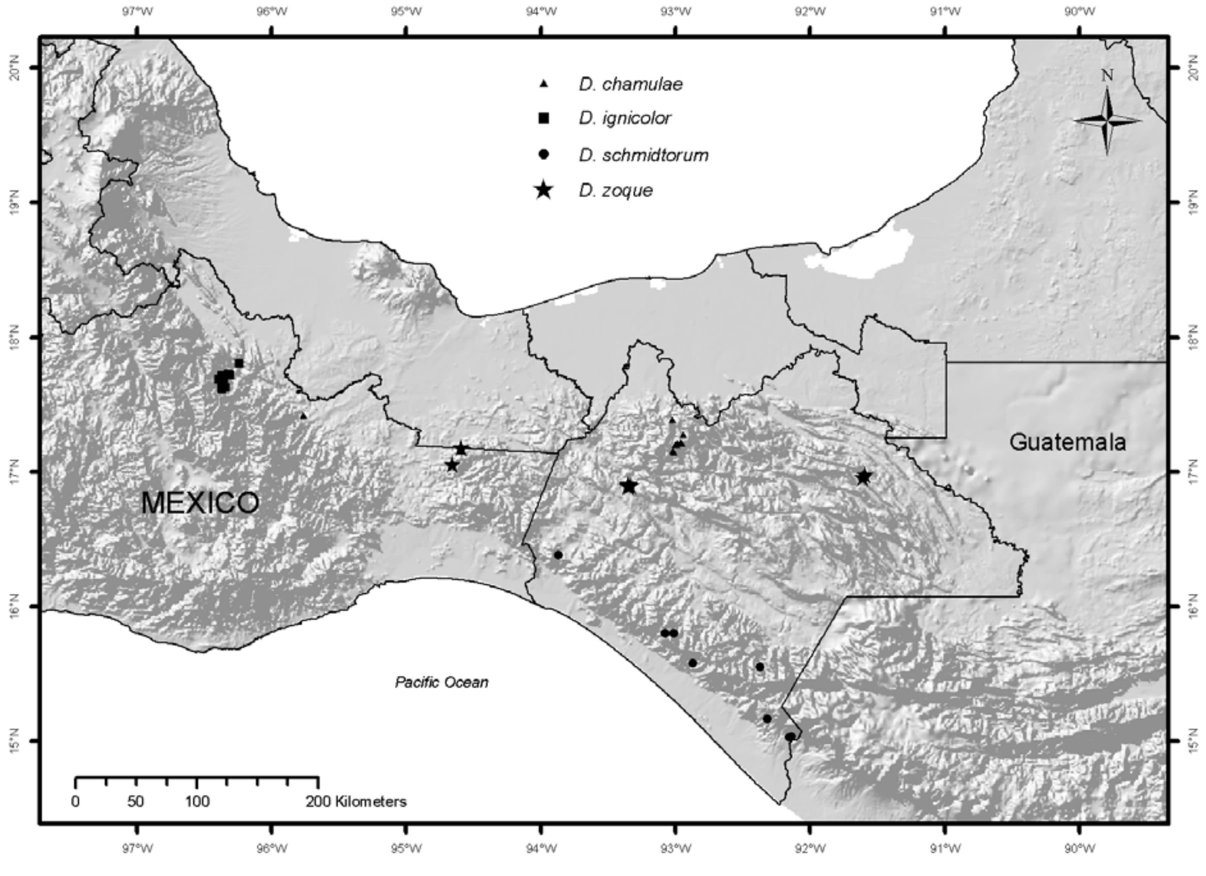

Figure X-5. Geographic distribution of the species of *Duellmanohyla* in Southern México.

The new species was collected in June 1993 in Chalchijapa (Chimalapas region), July 2008 and March 2009 in Uxpanapa (Veracruz). It was also observed in natural protected areas La Pera in June 2009 (El Ocote region) and in Nahá in July 2009 (northeastern of Lacandona region) both in Chiapas. A spider of the Family Ctenidae was observed feeding on one froglet (Fig. X-6).

Figure X-6. Spider (Araneae: Ctenidae) eating a froglet of *Duellmanohyla zoque,* in La Pera protected area, Chiapas. Maps generated with ArcGIS 9.3.1 (ESRI, 2009).

Other species of amphibians and reptiles that we found in the type locality include:

Incilius macrocristatus, I. valliceps, Hyalinobatrachium fleischmanni, Craugastor berkenbuschii, C. loki, Eleutherodactylus leprus, Duellmanohyla chamulae, Smilisca baudinii, S. cyanosticta, Lithobates maculatus, Bolitoglossa alberchi, Sceloporus internasalis, Anolis barkeri, Anolis compressicaudus, Scincella cherriei, Lepidophyma tuxtlae, Clelia scytalina, Imantodes cenchoa, Geophis carinosus, Stenorrhina degenhardtii, Ninia sebae and *Bothrops asper.*

Conservation status.—The few individuals found lead us to think that *Duellmanohyla zoque* is rare within the amphibian communities sampled. It was only found in pristine forest. Deforestations rates in the south of Mexico are among the highest in the World (Klepeis and Vance 2003); therefore, if deforestation continues, the existence of the species may be compromised.

DISCUSSION

Duellmamohyla zoque is similar to *Ptychohyla acrochorda* in coloration. However, the latter is endemic to the Sierra de Juárez in northern Oaxaca and it is characterized by having a chest gland absent in *D. zoque*, and by the absence of a mental gland, which is present in *D. zoque*. Although the distribution range of *Duellmanohyla zoque* is near to those of *Ptychohyla euthysanota* and *P. macrotympanum, D. zoque* differs morphologically by iris coloration, because the two species of *Ptychohyla* have golden iris. Additionally, *D. zoque* is distinguished from *P. macrotympanum* by the absence of ventrolateral glands, and from *P. euthysanota* by dorsal coloration—green with white spots in *D. zoque* and reddish bronze in *P. euthysanota*.

The Central American genus *Duellmanohyla* (Campbell and Smith, 1992) is composed of nine species (Duellman, 2001), including the species described here (Table X-1) and ranges from southern Mexico to western Panama. Four species occur in Mexico (Fig. X-7): *D. chamulae,* from northern slopes of the central highlands of Veracruz, Oaxaca and Chiapas (350-1700 m); *D. ignicolor*, from northern slopes of the Sierra Juárez, Oaxaca (680-1850 m); *D. schmidtorum*, from Pacific slopes of the Sierra Madre from extreme eastern Oaxaca, México, to southwestern Guatemala (1300-2200 m) (Duellman, 2001); and *D. zoque* from Veracruz, Oaxaca and Chiapas (76-800 m).

Figure X-7. Species of *Duellmanohyla* from México. A. *D.ignicolor* (Santiago Tlatepusco, Santa María Usila, Oax); B. *D. chamulae*, (Paso del Moral, Veracruz); C. *D. schmidtorum*, (Finca Prusia, Municipality of Albino Corzo, Chiapas); D. *D. zoque* (Paso del Moral, Veracruz, paratype, MZFC 24005).

In Mexico, the genus was known only from Chiapas and Oaxaca, but occurrence of *Duellmanohyla chamulae* in Veracruz (Aguilar-López et al., *in press*), as well as the new species described here, adds another genus for the amphibian fauna of this state. Campbell and Smith (1992), and Duellman (2001) have proposed hypotheses of the relationships of members in the genus *Duellmanohyla*, based mostly on morphological characters. In both analyses, the species occurring in Mexico form a single clade, supported by five and four synapomorphies, respectively. Also, they concur that, within this clade, *D. ignicolor* and *D. chamulae* are more closely related by the presence of a mental gland. Additionally both species have a green dorsal coloration and inhabit the Atlantic versant of southern Mexico, whereas *D. schmidtorum* has a brown dorsum and occurs in the Pacific versant of southern Mexico and adjacent Guatemala (Campbell and Smith 1992). The presence of this gland in *D. zoque*, besides its distribution (Atlantic slopes of southern Mexico) and dorsal coloration (green or brown with brown blotches and white spots), suggest that this species is closely related to *D. ignicolor* and *D. chamulae*. However, if this is accepted, it would imply a loss of ventrolateral glands and appearance of nuptial excrescences in *D. zoque*, so its relationships with the other species of the genus remain unclear until a more robust analysis can be performed. In their molecular analysis, Faivovich et al. (2005) and Wiens et al (2010), include only two and three species, respectively and Wiens et al. (2010) mentioned the possibility that the *Duellmanohyla* may not be monophyletic.

ACKNOWLEDGMENTS

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Table X-1. Morphometric variation in *Duellmanohyla zoque*: range (in millimeters) followed by mean in parentheses.

Measurement	Male (n=1)	Females (n=4)
SVL	36.4	46.2-56.8 (53.4)
Tibia length	20.9	28.9-34.7 (32.2)
Foot length	15.4	20.9-25.2 (23.6)
Head length	12.7	17.2-20.7 (19.3)
Head width	12.8	17.4-21.4 (19.9)
Diameter of eye	4.8	5.2-5.6 (5.4)
Diameter of tympanum	1.9	2.4-3.0 (2.7)

Table X-2. Selected characteristics of all species of *Duellmanohyla* genus. Data of other species obtained from Duellman (2001).

	D. zoque	*D. schmidtorum*	*D. chamulae*	*D. ignicolor*	*D. Salvavida*	*D. soralia*	*D. urachnocroa*	*D. rufioculis*	*D. lythrodes*
Maximum SVL in males (mm)	36.4	32.4	30.5	30.9	28	32.3	36.8	30	32.6
Maximum SVL in females (mm)	57.2	38.3	31.8	33.1	34.3	37.7	39.9	39.9	Unknown
Iris coloration	pink	Red	Red	Golden	Bright red	Bright red	Bright red	Red	Bright red
Ventrolateral glands	Absent	Present	Present	Present	Absent	Absent	Absent	Absent	Absent
Mental gland	Present	Absent	Present	Present	Absent	Absent	Absent	Absent	Absent
Nuptial excrescenses	Present	Absent	Absent	Absent	Present	Present	Present	Present	Present
Dorsal coloration	Bright green with irregular white spots	Brown	Bright green	Bright green	Dull green	Brown to black with green lichenous spots	Bright green	Reddish brown	Green or brown
Labial stripe	A fine present along the lip	Present	Present	Absent	White labial stripe	Absent	Present	Present	Present
Flanks	Mottled with dark brown and white cream	With white lateral stripe	With white lateral stripe	Without pattern	White lateral stripe	Absent	White lateral stripe	Present	Present
Tarsal fold	Absent	Absent	Absent	Absent	Present	Present	Present	Present	Absent
Forearm	With a row of tubercles	With fold	?	With a row of tubercles	With a row of tubercles	With a row of tubercles	With fold	Some whit a row of tubercles	Weak dermal fold
Distribution and elevation	Atlantic versant in Veracruz, Oaxaca and Chiapas (Mexico) at 76-828 m elev.	Pacific versant in Oaxaca, Chiapas (Mexico) and Guatemala at 1300-2200 m elev.	Atlantic versant in Southern Veracruz, Oaxaca and northern Chiapas at 350-1700 m elev.	Atlantic versant in northern Oaxaca at 680-1800 m elev.	Northern Honduras at 90-1400 m elev.	Eastern Guatemala and Western Honduras at 40-1570 m elev.	Costa Rica and Western Panamá at 300-1720 m elev.	Caribbean and Pacific slopes of Costa Rica at 775-1580 m elev.	Extreme Northeastern Costa Rica adjacent Panamá at 170-800 m elev.

Craugastor laticeps, Nahá 2010

XI. APPENDIX B. CONSENT LETTERS FROM CO-AUTHORS AND ADDITIONAL MATERIAL REGARDING THE STATUS OF THE SUBMITTED ARTICLES

"Individually, we are one drop. Together, we are an ocean."

Ryunosuke Satoro

CHAPTER IV. PROOF OF SUBMISSION AND STATUS

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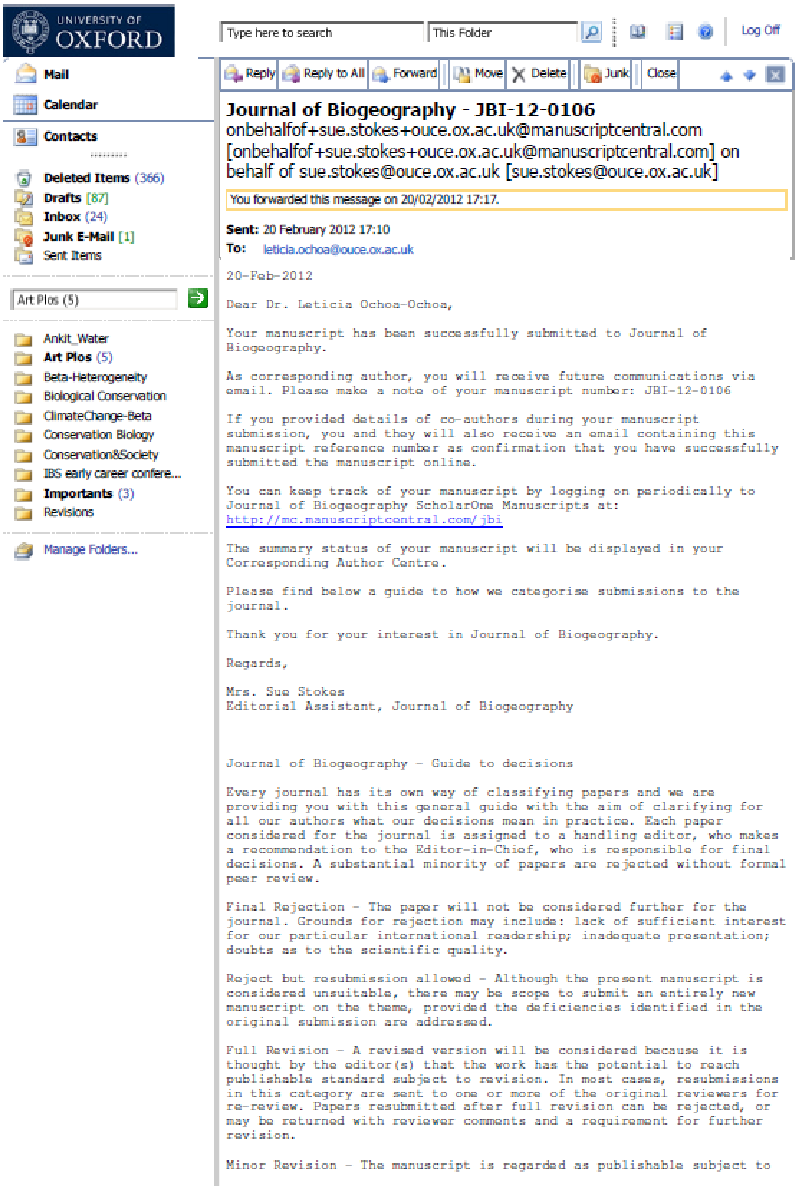

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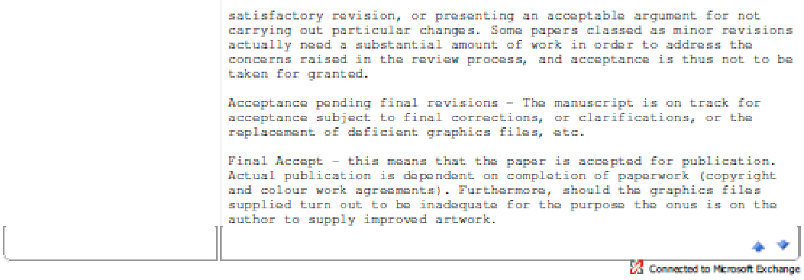

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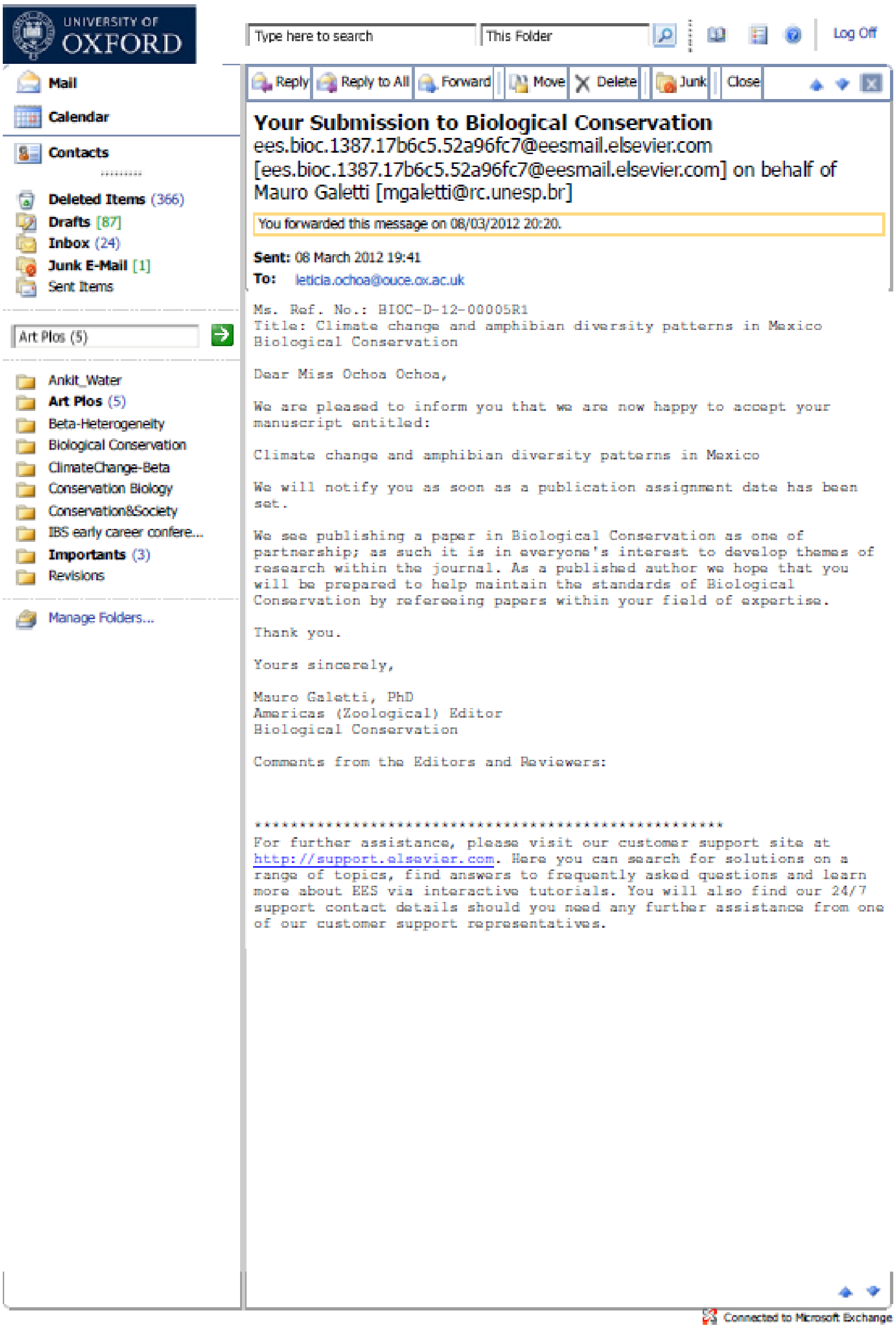

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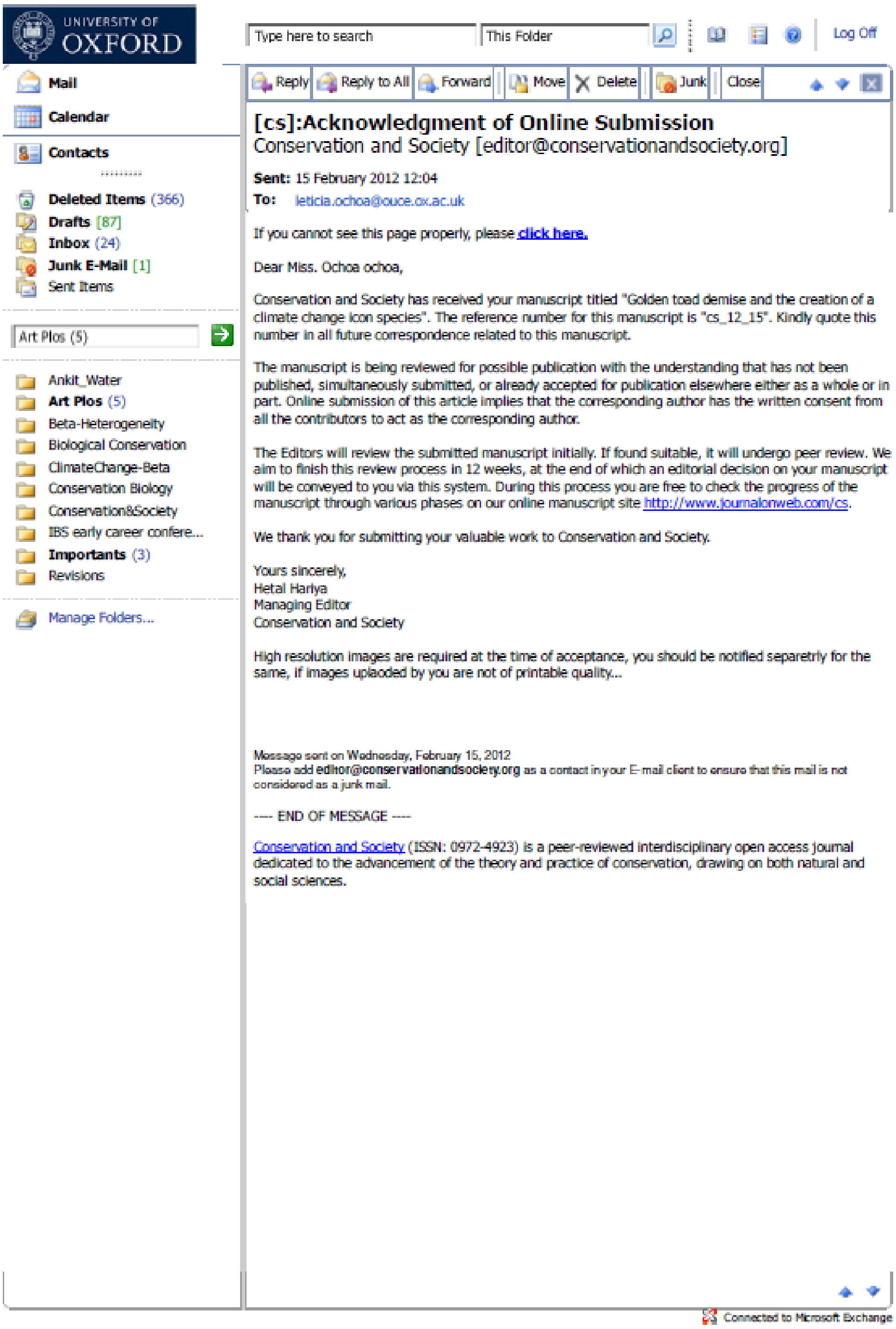

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CHAPTER VII. PROOF OF SUBMISSION AND STATUS

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The Effects of Governmental Protected Areas and Social Initiatives for Land Protection on the Conservation of Mexican Amphibians

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Abstract

Traditionally, biodiversity conservation gap analyses have been focused on governmental protected areas (PAs). However, an increasing number of social initiatives in conservation (SICs) are promoting a new perspective for analysis. SICs include all of the efforts that society implements to conserve biodiversity, such as land protection, from private reserves to community zoning plans some of which have generated community-protected areas. This is the first attempt to analyze the status of conservation in Latin America when some of these social initiatives are included. The analyses were focused on amphibians because they are one of the most threatened groups worldwide. Mexico is not an exception, where more than 60% of its amphibians are endemic. We used a niche model approach to map the potential and *real* geographical distribution (extracting the transformed areas) of the endemic amphibians. Based on remnant distribution, all the species have suffered some degree of loss, but 36 species have lost more than 50% of their potential distribution. For 50 micro-endemic species we could not model their potential distribution range due to the small number of records per species, therefore the analyses were performed using these records directly. We then evaluated the efficiency of the existing set of governmental protected areas and established the contribution of social initiatives (private and community) for land protection for amphibian conservation. We found that most of the species have some proportion of their potential ecological niche distribution protected, but 20% are not protected at all within governmental PAs. 73% of endemic and 26% of micro-endemic amphibians are represented within SICs. However, 30 micro-endemic species are not represented within either governmental PAs or SICs. This study shows how the role of land conservation through social initiatives is therefore becoming a crucial element for an important number of species not protected by governmental PAs.

Citation: Ochoa-Ochoa L, Urbina-Cardona JN, Vázquez L-B, Flores-Villela O, Bezaury-Creel J (2009) The Effects of Governmental Protected Areas and Social Initiatives for Land Protection on the Conservation of Mexican Amphibians. PLoS ONE 4(9): e6878. doi:10.1371/journal.pone.0006878

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Competing Interests: The authors have declared that no competing interests exist.

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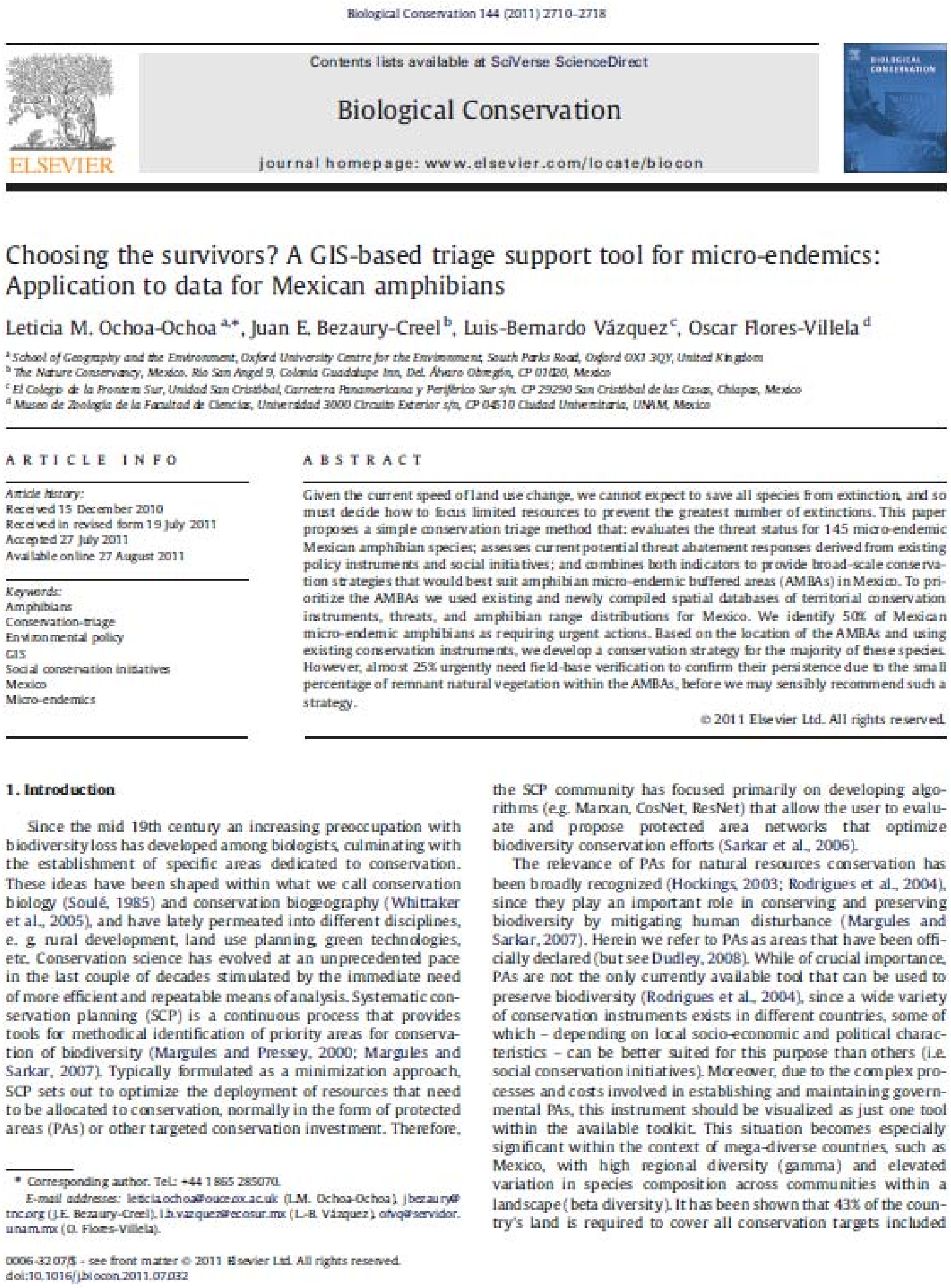
Introduction

The rapid growth of anthropogenic activities has expanded cattle and agriculture frontiers into natural habitats, transforming ecosystems into fragmented, semi-natural landscapes [1]. A large amount of native habitat has been transformed into numerous smaller forest patches isolated and surrounded by a matrix of pasture, cultivated land, and secondary re-growth vegetation [2,3]. A key strategy for protecting biodiversity from external pressures has been the establishment and maintenance of Protected Areas (PAs). However, current PAs remain isolated from one another, and in many cases, natural biological pathways for plant and animal dispersal become disrupted by anthropogenic barriers [4,5]. This anthropogenic matrix occupies, in several places, the majority of the landscape and acts as a filter for dispersal of animals between forest patches [6,7]. In this sense, isolated PAs managed by either federal or local governments alone are not effective in maintaining biodiversity; thus, the necessity of developing representative and interconnected conservation area networks to preserve biodiversity is becoming more important [8]. Recently, several calls have been made to recognise local participation as a core element of conservation strategies [9,10]. Social initiatives for land conservation therefore play a crucial role in increasing the range of protection of threatened and endemic species, thus ensuring their persistence. These social initiatives are based on a cooperation scheme where strong social participation is used to implement conservation actions.

In Mexico, 528 PAs have been established (Fig. 1) by the three government jurisdictions: 163 federal, 278 state, and 87 municipal, with a total of 18,513,089 ha constituting 9.4% of continental Mexico [[11], updated to 31/12/2008]. Mexico's National Protected Area Commission (CONANP – the *Comisión Nacional de Áreas Naturales Protegidas*) is currently managing three provisionally demarcated natural resources protection areas, within national

CHAPTER VIII. PROOF OF SUBMISSION AND STATUS



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Choosing the survivors? A GIS-based triage support tool for micro-endemics: Application to data for Mexican amphibians

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ABSTRACT

Given the current speed of land use change, we cannot expect to save all species from extinction, and so must decide how to focus limited resources to prevent the greatest number of extinctions. This paper proposes a simple conservation triage method that: evaluates the threat status for 145 micro-endemic Mexican amphibian species; assesses current potential threat abatement responses derived from existing policy instruments and social initiatives; and combines both indicators to provide broad-scale conservation strategies that would best suit amphibian micro-endemic buffered areas (AMBAs) in Mexico. To prioritize the AMBAs we used existing and newly compiled spatial databases of territorial conservation instruments, threats, and amphibian range distributions for Mexico. We identify 50% of Mexican micro-endemic amphibians as requiring urgent actions. Based on the location of the AMBAs and using existing conservation instruments, we develop a conservation strategy for the majority of these species. However, almost 25% urgently need field-base verification to confirm their persistence due to the small percentage of remnant natural vegetation within the AMBAs, before we may sensibly recommend such a strategy.

1. Introduction

Since the mid 19th century an increasing preoccupation with biodiversity loss has developed among biologists, culminating with the establishment of specific areas dedicated to conservation. These ideas have been shaped within what we call conservation biology (Soulé, 1985) and conservation biogeography (Whittaker et al., 2005), and have lately permeated into different disciplines, e. g. rural development, land use planning, green technologies, etc. Conservation science has evolved at an unprecedented pace in the last couple of decades stimulated by the immediate need of more efficient and repeatable means of analysis. Systematic conservation planning (SCP) is a continuous process that provides tools for methodical identification of priority areas for conservation of biodiversity (Margules and Pressey, 2000; Margules and Sarkar, 2007). Typically formulated as a minimization approach, SCP sets out to optimize the deployment of resources that need to be allocated to conservation, normally in the form of protected areas (PAs) or other targeted conservation investment. Therefore, the SCP community has focused primarily on developing algorithms (e.g. Marxan, CosNet, ResNet) that allow the user to evaluate and propose protected area networks that optimize biodiversity conservation efforts (Sarkar et al., 2006).

The relevance of PAs for natural resources conservation has been broadly recognized (Hockings, 2003; Rodrigues et al., 2004), since they play an important role in conserving and preserving biodiversity by mitigating human disturbance (Margules and Sarkar, 2007). Herein we refer to PAs as areas that have been officially declared (but see Dudley, 2008). While of crucial importance, PAs are not the only currently available tool that can be used to preserve biodiversity (Rodrigues et al., 2004), since a wide variety of conservation instruments exists in different countries, some of which – depending on local socio-economic and political characteristics – can be better suited for this purpose than others (i.e. social conservation initiatives). Moreover, due to the complex processes and costs involved in establishing and maintaining governmental PAs, this instrument should be visualized as just one tool within the available toolkit. This situation becomes especially significant within the context of mega-diverse countries, such as Mexico, with high regional diversity (gamma) and elevated variation in species composition across communities within a landscape (beta diversity). It has been shown that 43% of the country's land is required to cover all conservation targets included

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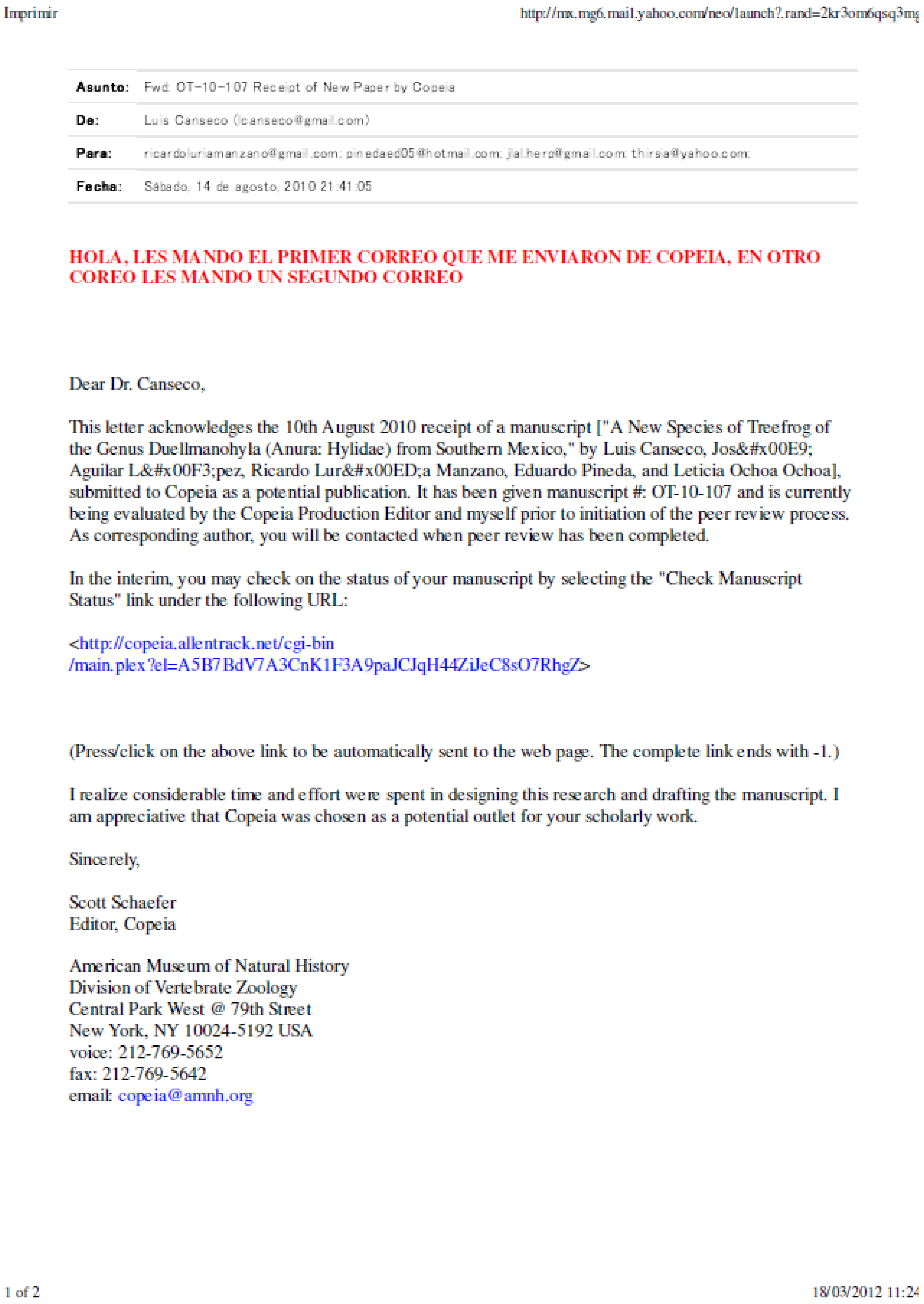
APPENDIX A. PROOF OF SUBMISSION AND STATUS



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Asunto: Fwd: OT-10-107 Receipt of New Paper by Copeia
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Para: ricardoluriamanzano@gmail.com; pinedaed05@hotmail.com; jlal.herp@gmail.com; thirsia@yahoo.com;
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HOLA, LES MANDO EL PRIMER CORREO QUE ME ENVIARON DE COPEIA, EN OTRO COREO LES MANDO UN SEGUNDO CORREO

Dear Dr. Canseco,

This letter acknowledges the 10th August 2010 receipt of a manuscript ["A New Species of Treefrog of the Genus Duellmanohyla (Anura: Hylidae) from Southern Mexico," by Luis Canseco, José Aguilar López, Ricardo Luría Manzano, Eduardo Pineda, and Leticia Ochoa Ochoa], submitted to Copeia as a potential publication. It has been given manuscript #: OT-10-107 and is currently being evaluated by the Copeia Production Editor and myself prior to initiation of the peer review process. As corresponding author, you will be contacted when peer review has been completed.

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I realize considerable time and effort were spent in designing this research and drafting the manuscript. I am appreciative that Copeia was chosen as a potential outlet for your scholarly work.

Sincerely,

Scott Schaefer
Editor, Copeia

American Museum of Natural History
Division of Vertebrate Zoology
Central Park West @ 79th Street
New York, NY 10024-5192 USA
voice: 212-769-5652
fax: 212-769-5642
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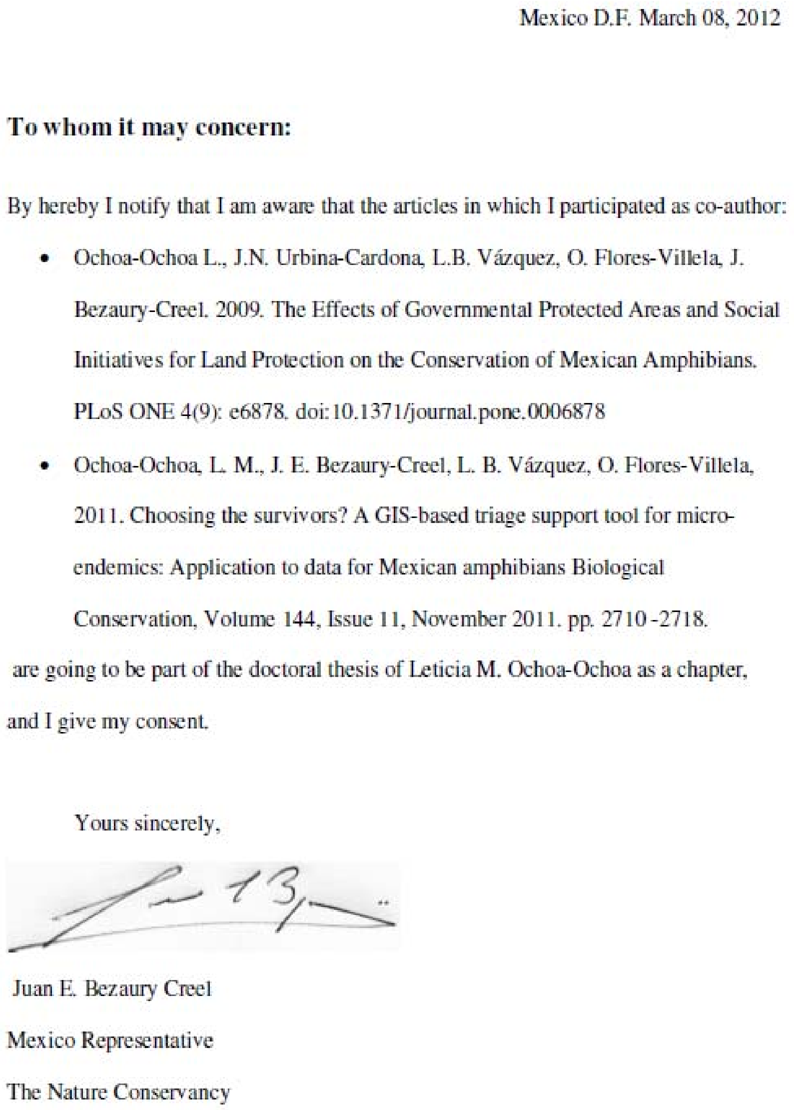
1 of 2 18/03/2012 11:24

CONSENT LETTERS

Consent Letters from the co-authors of some of the chapters; and are in alphabetical order.



Mexico D.F. March 08, 2012

To whom it may concern:

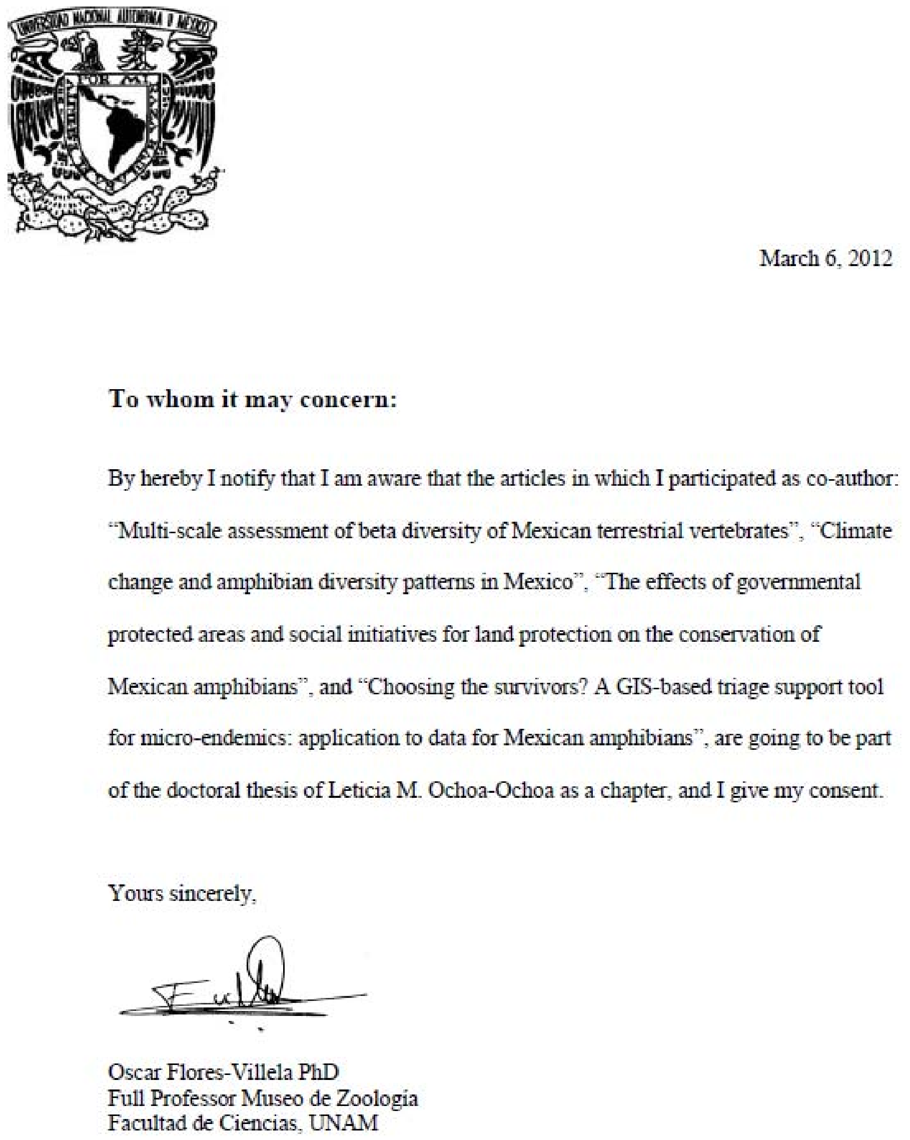
By hereby I notify that I am aware that the articles in which I participated as co-author:

- Ochoa-Ochoa L., J.N. Urbina-Cardona, L.B. Vázquez, O. Flores-Villela, J. Bezaury-Creel. 2009. The Effects of Governmental Protected Areas and Social Initiatives for Land Protection on the Conservation of Mexican Amphibians. PLoS ONE 4(9): e6878. doi:10.1371/journal.pone.0006878
- Ochoa-Ochoa, L. M., J. E. Bezaury-Creel, L. B. Vázquez, O. Flores-Villela, 2011. Choosing the survivors? A GIS-based triage support tool for micro-endemics: Application to data for Mexican amphibians Biological Conservation, Volume 144, Issue 11, November 2011. pp. 2710 -2718.

are going to be part of the doctoral thesis of Leticia M. Ochoa-Ochoa as a chapter, and I give my consent.

Yours sincerely,

Juan E. Bezaury Creel
Mexico Representative
The Nature Conservancy



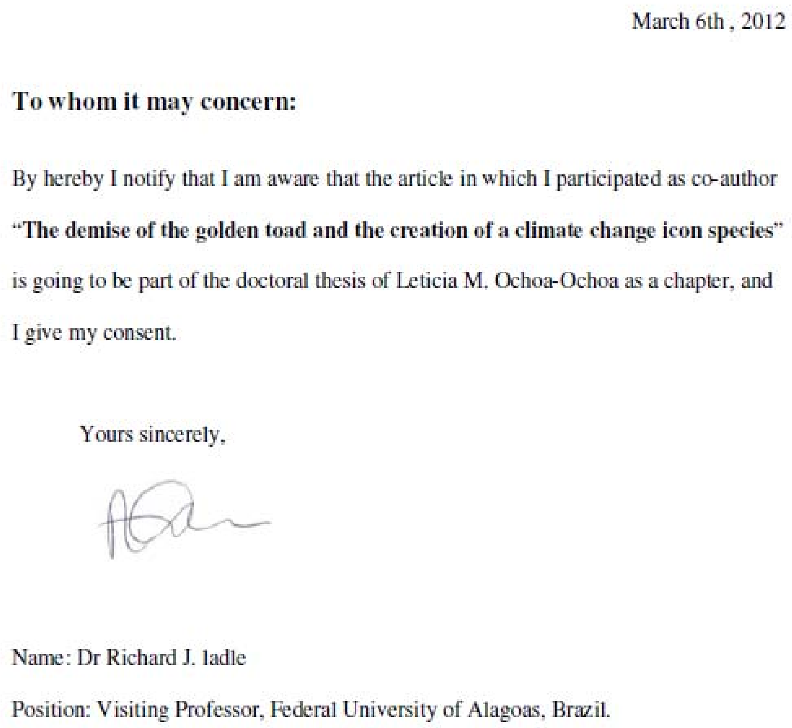
March 6, 2012

To whom it may concern:

By hereby I notify that I am aware that the articles in which I participated as co-author: “Multi-scale assessment of beta diversity of Mexican terrestrial vertebrates”, “Climate change and amphibian diversity patterns in Mexico”, “The effects of governmental protected areas and social initiatives for land protection on the conservation of Mexican amphibians”, and “Choosing the survivors? A GIS-based triage support tool for micro-endemics: application to data for Mexican amphibians”, are going to be part of the doctoral thesis of Leticia M. Ochoa-Ochoa as a chapter, and I give my consent.

Yours sincerely,

Oscar Flores-Villela PhD
Full Professor Museo de Zoología
Facultad de Ciencias, UNAM



March 6th , 2012

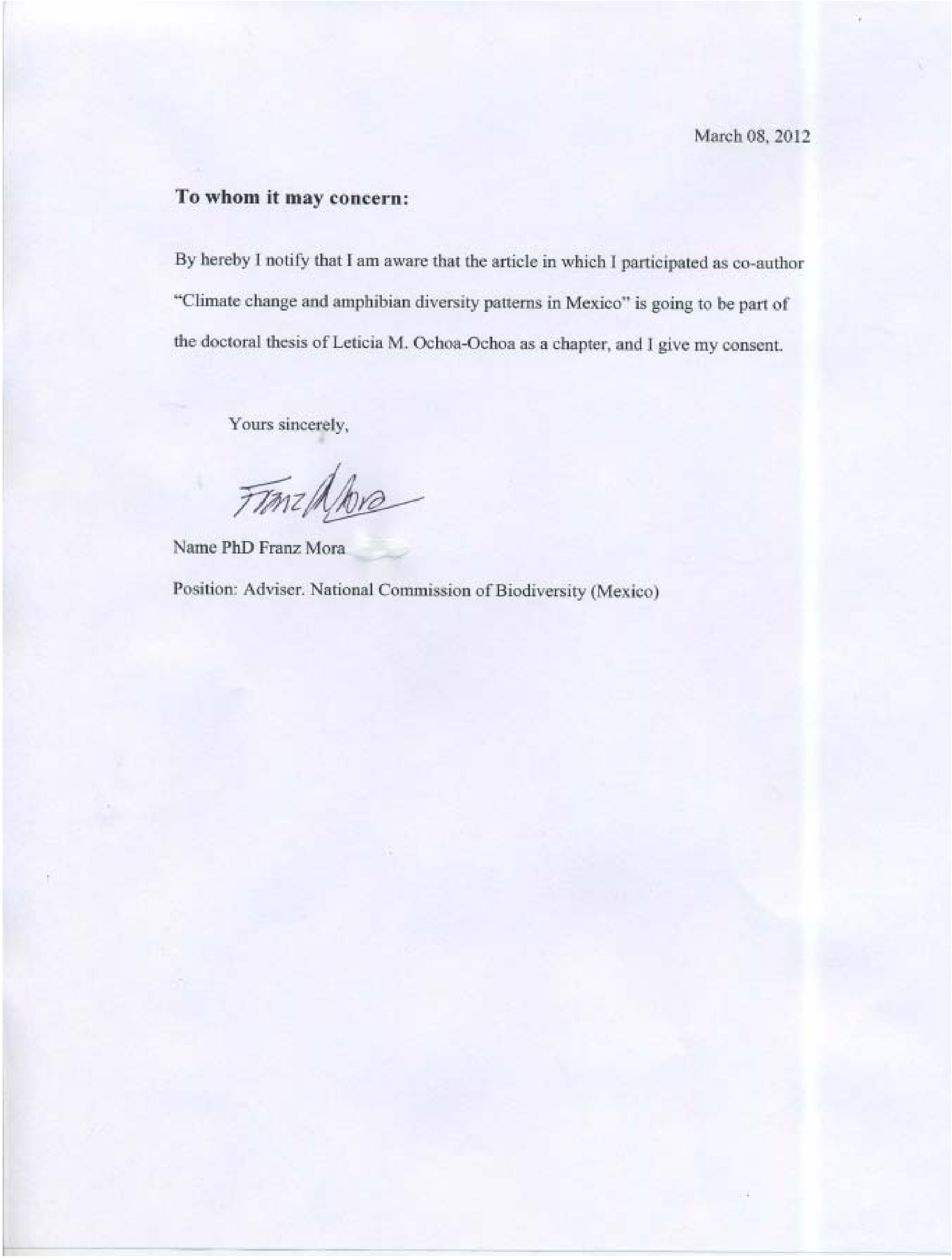
To whom it may concern:

By hereby I notify that I am aware that the article in which I participated as co-author **"The demise of the golden toad and the creation of a climate change icon species"** is going to be part of the doctoral thesis of Leticia M. Ochoa-Ochoa as a chapter, and I give my consent.

Yours sincerely,

Name: Dr Richard J. ladle

Position: Visiting Professor, Federal University of Alagoas, Brazil.



March 08, 2012

To whom it may concern:

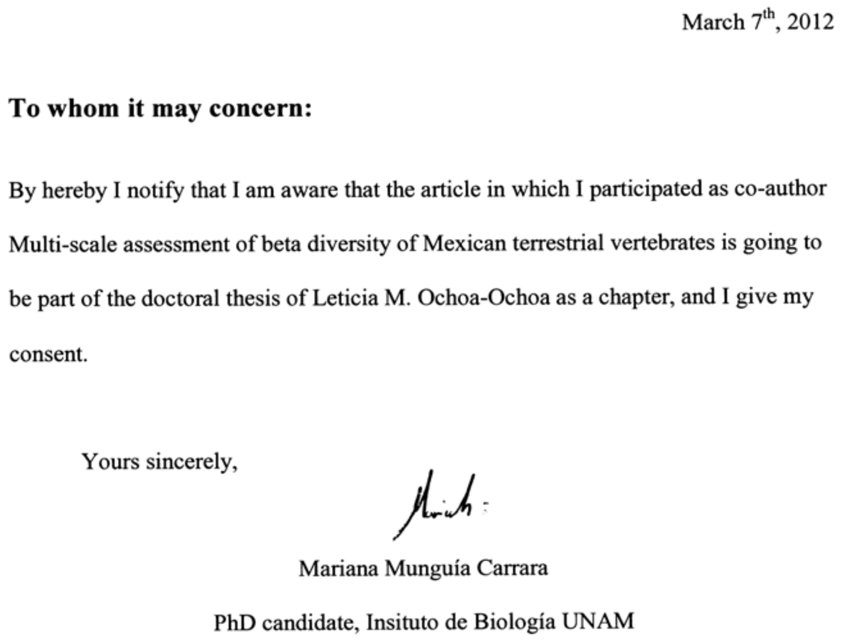
By hereby I notify that I am aware that the article in which I participated as co-author "Climate change and amphibian diversity patterns in Mexico" is going to be part of the doctoral thesis of Leticia M. Ochoa-Ochoa as a chapter, and I give my consent.

Yours sincerely,

Franz Mora

Name PhD Franz Mora

Position: Adviser. National Commission of Biodiversity (Mexico)



March 7th, 2012

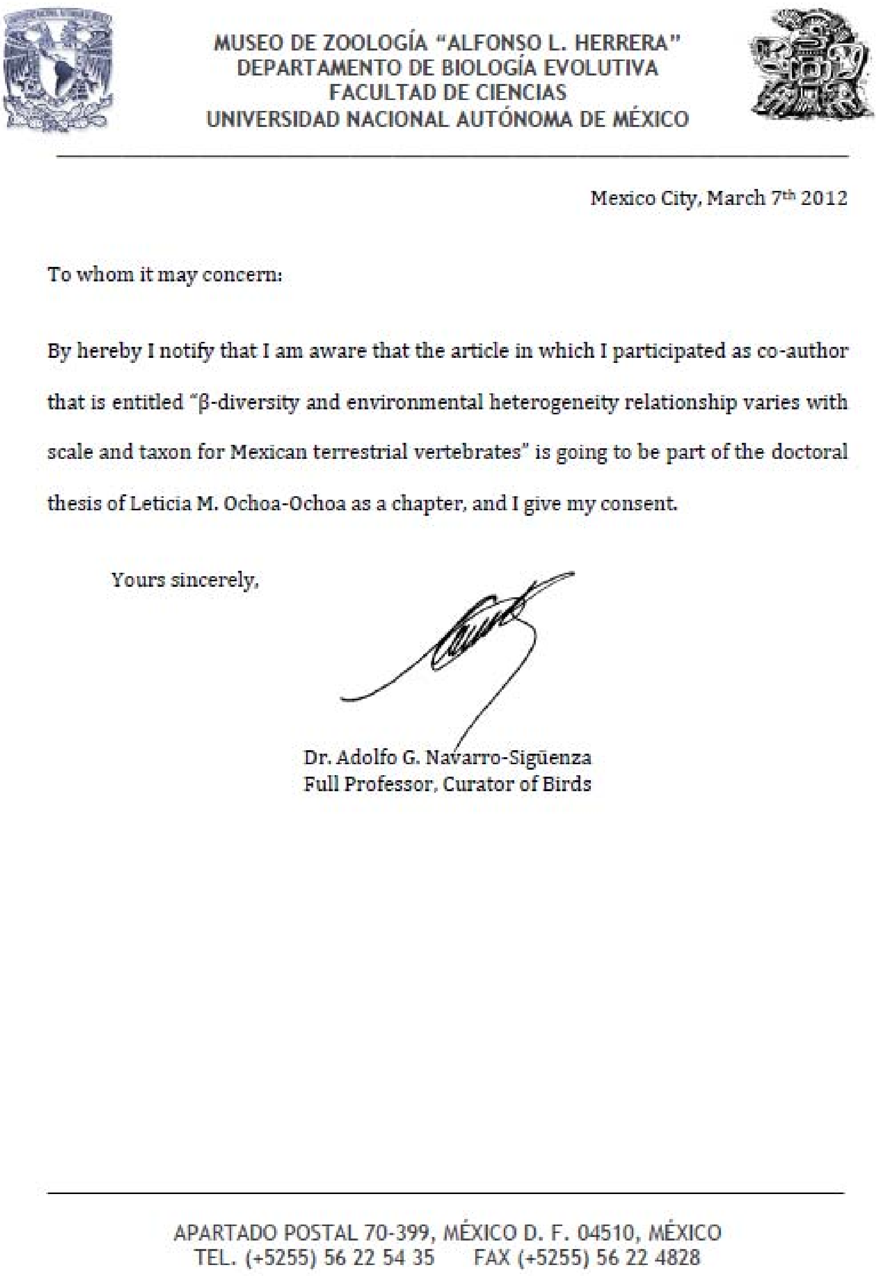
To whom it may concern:

By hereby I notify that I am aware that the article in which I participated as co-author Multi-scale assessment of beta diversity of Mexican terrestrial vertebrates is going to be part of the doctoral thesis of Leticia M. Ochoa-Ochoa as a chapter, and I give my consent.

Yours sincerely,

Mariana Munguía Carrara

PhD candidate, Insituto de Biología UNAM



MUSEO DE ZOOLOGÍA "ALFONSO L. HERRERA"
DEPARTAMENTO DE BIOLOGÍA EVOLUTIVA
FACULTAD DE CIENCIAS
UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

Mexico City, March 7th 2012

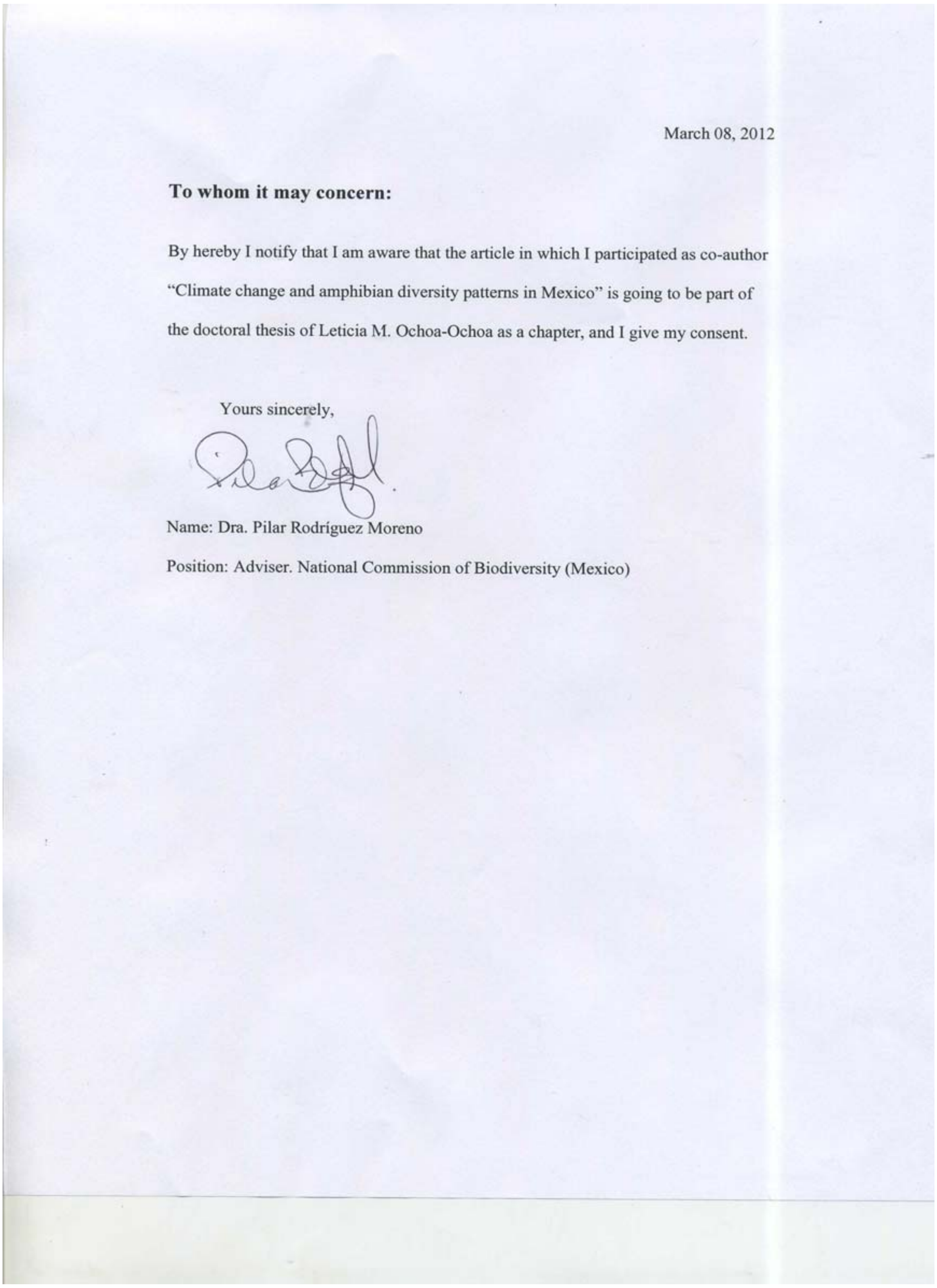
To whom it may concern:

By hereby I notify that I am aware that the article in which I participated as co-author that is entitled "β-diversity and environmental heterogeneity relationship varies with scale and taxon for Mexican terrestrial vertebrates" is going to be part of the doctoral thesis of Leticia M. Ochoa-Ochoa as a chapter, and I give my consent.

Yours sincerely,

Dr. Adolfo G. Navarro-Sigüenza
Full Professor, Curator of Birds

APARTADO POSTAL 70-399, MÉXICO D. F. 04510, MÉXICO
TEL. (+5255) 56 22 54 35 FAX (+5255) 56 22 4828



March 08, 2012

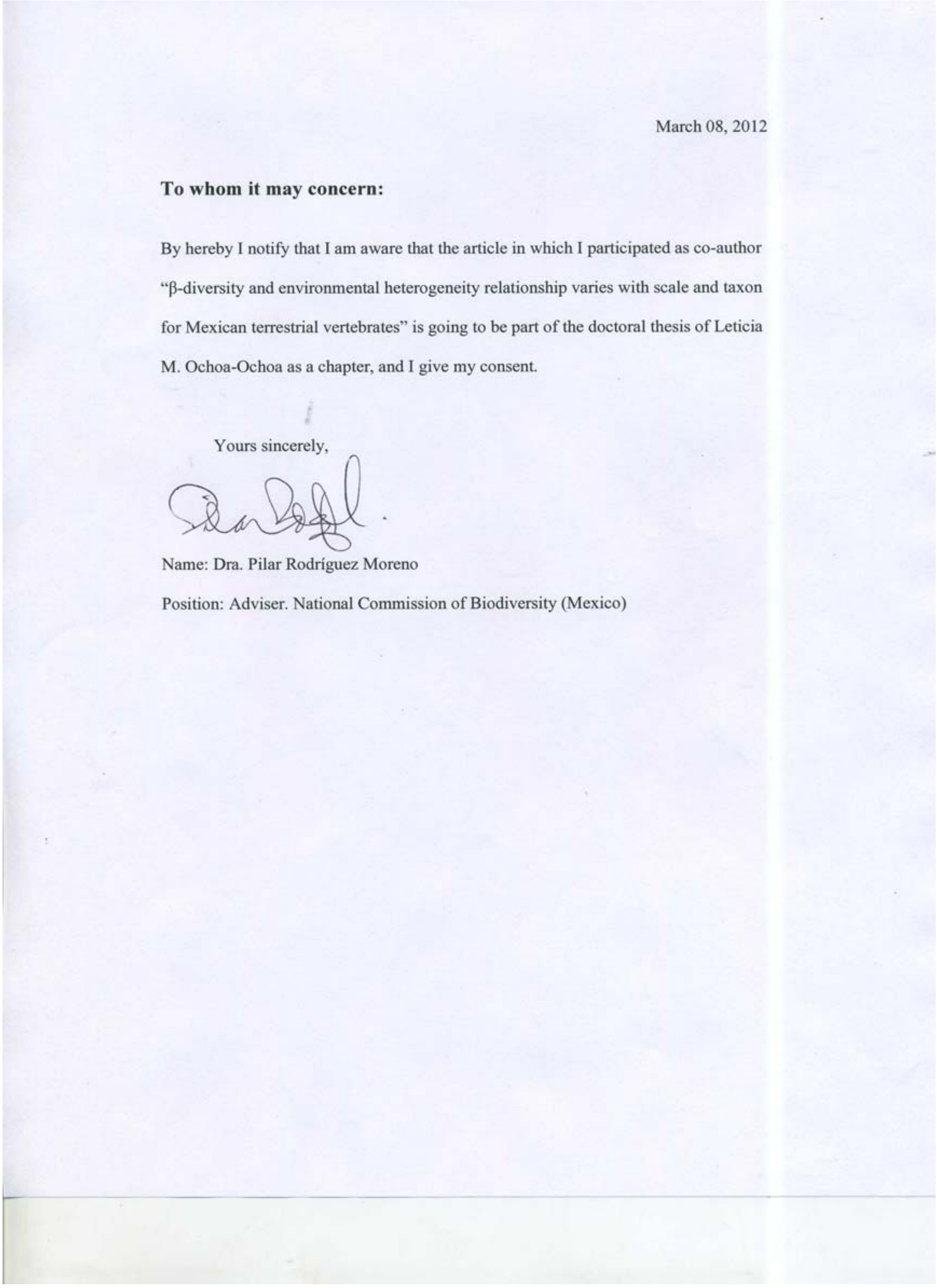
To whom it may concern:

By hereby I notify that I am aware that the article in which I participated as co-author "Climate change and amphibian diversity patterns in Mexico" is going to be part of the doctoral thesis of Leticia M. Ochoa-Ochoa as a chapter, and I give my consent.

Yours sincerely,

Name: Dra. Pilar Rodríguez Moreno

Position: Adviser. National Commission of Biodiversity (Mexico)



March 08, 2012

To whom it may concern:

By hereby I notify that I am aware that the article in which I participated as co-author "β-diversity and environmental heterogeneity relationship varies with scale and taxon for Mexican terrestrial vertebrates" is going to be part of the doctoral thesis of Leticia M. Ochoa-Ochoa as a chapter, and I give my consent.

Yours sincerely,

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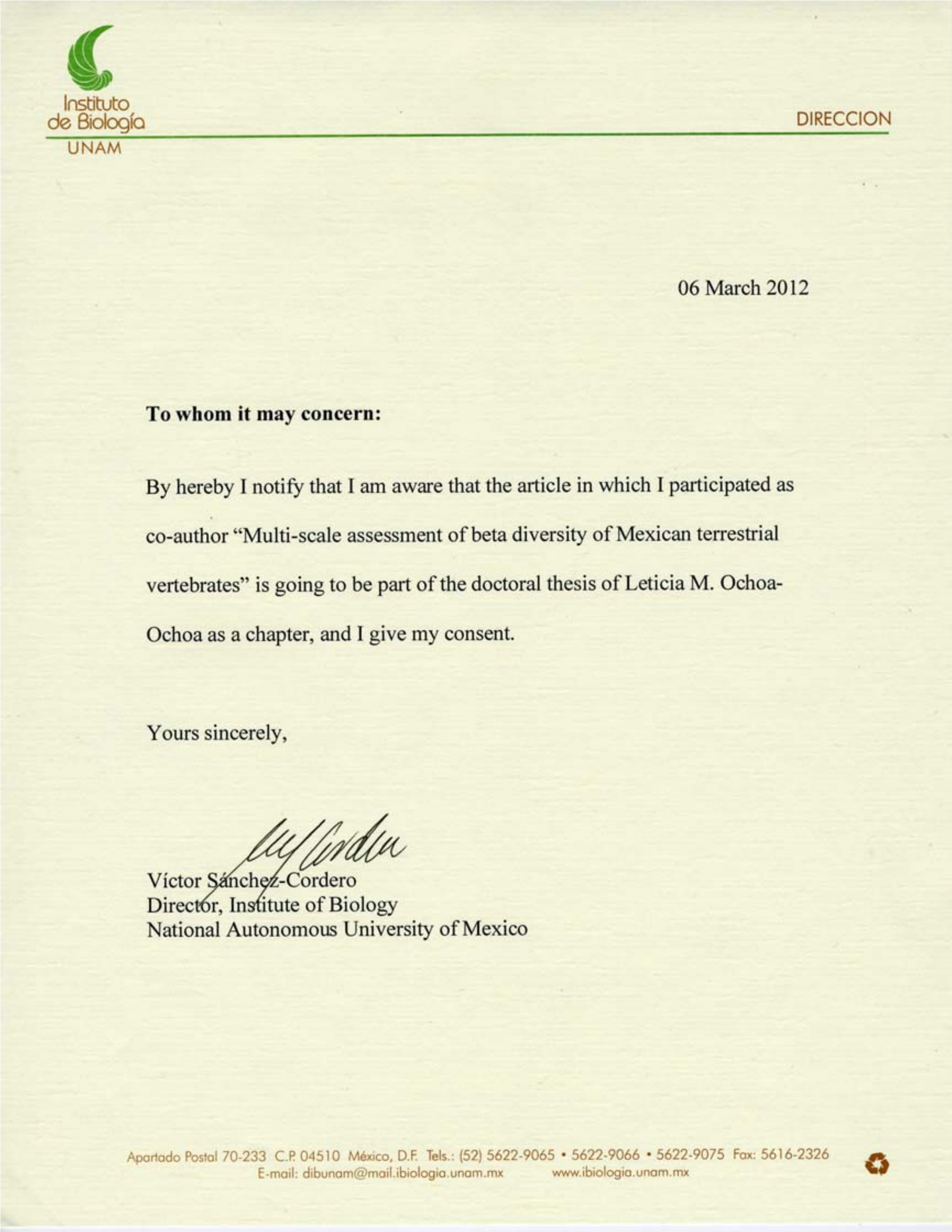
Position: Adviser. National Commission of Biodiversity (Mexico)



Instituto
de Biología
UNAM

DIRECCION

06 March 2012

To whom it may concern:

By hereby I notify that I am aware that the article in which I participated as co-author "Multi-scale assessment of beta diversity of Mexican terrestrial vertebrates" is going to be part of the doctoral thesis of Leticia M. Ochoa-Ochoa as a chapter, and I give my consent.

Yours sincerely,

Víctor Sánchez-Cordero
Director, Institute of Biology
National Autonomous University of Mexico

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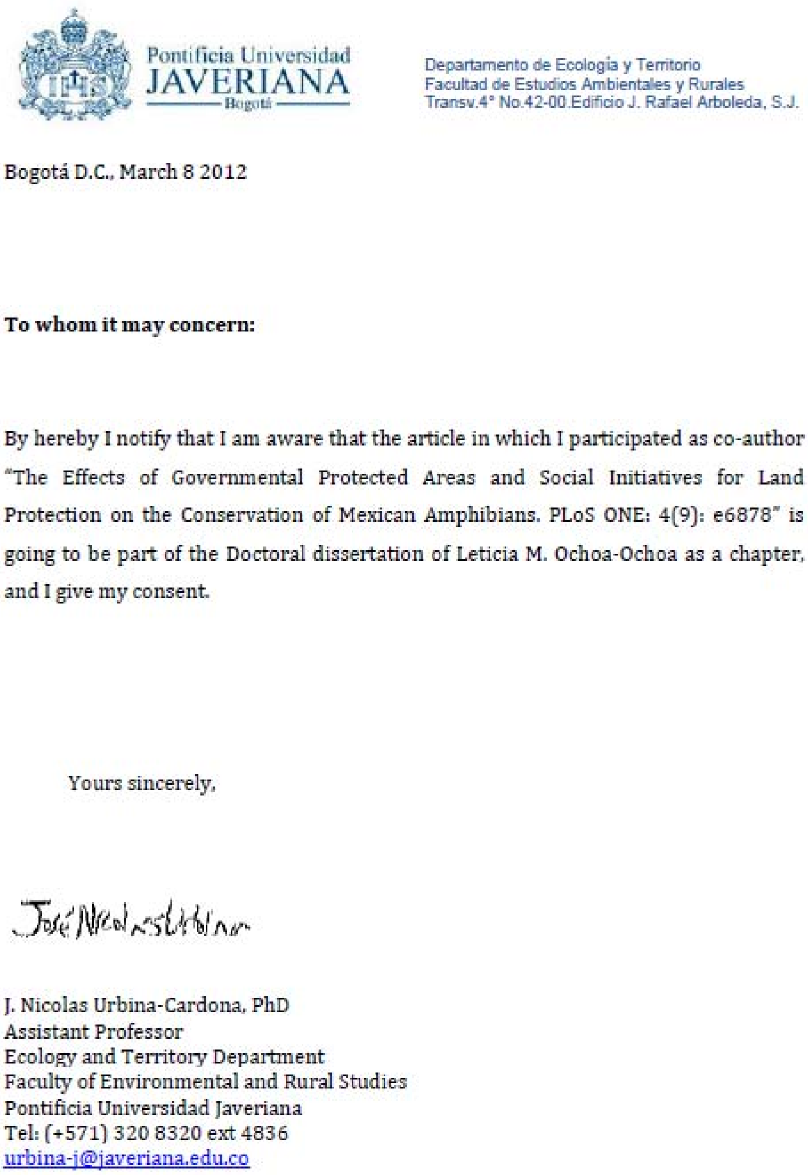

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Facultad de Estudios Ambientales y Rurales
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To whom it may concern:

By hereby I notify that I am aware that the article in which I participated as co-author "The Effects of Governmental Protected Areas and Social Initiatives for Land Protection on the Conservation of Mexican Amphibians. PLoS ONE: 4(9): e6878" is going to be part of the Doctoral dissertation of Leticia M. Ochoa-Ochoa as a chapter, and I give my consent.

Yours sincerely,

José Nicolas Urbina

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Assistant Professor
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Unidad San Cristóbal

CP/022/12
March 06 2012

To whom it may concern:

By hereby I notify that I am aware that the article in which I participated as co-author "Choosing the survivors? A GIS-based triage support tool for micro-endemics: application to data for Mexican amphibians" which was published in *Biological Conservation*, and "The role of land protection through governmental protected areas and social action in biodiversity conservation: the case of Mexican amphibians" which was published in PLOS One, are going to be part of the doctoral thesis of Leticia M. Ochoa-Ochoa as a chapter, and I give my consent.

Yours sincerely,

Dr. Luis Bernardo Vázquez
Senior professor and researcher
Head Posgraduate Department
Unidad San Cristóbal

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SCHOOL OF GEOGRAPHY AND THE ENVIRONMENT

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UNIVERSITY OF
OXFORD

29h March 2012

Amphibian diversity in a changing World: a view from Mexico ~

Thesis submitted for the degree of Doctor of Philosophy by Leticia M. Ochoa-Ochoa

I consent to the inclusion of manuscripts to which I have contributed as a co-author within the above thesis. I also confirm that for all chapters within the thesis, apart from Appendix A, Leticia Ochoa-Ochoa is first author and has carried out the leading role, as is consistent with her position as first author. My own role has been confined to discussion, commenting on drafts, and so forth, consistent with my role as supervisor of the thesis.

Yours sincerely

Robert J Whittaker