Climate and biodiversity in the Andean Dry Puna

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Abstract

Arid mountain systems and their biological diversity are particularly vulnerable to changes in climate. The aim of this thesis was to evaluate climate variability and its impacts on ecological systems at different spatial and temporal scales, focusing on the Dry Puna ecoregion in the Central Andes, around the triple frontier of Argentina, Bolivia and Chile, and using a combination of climate data, data from remote sensors, and ecological surveys. I expanded on earlier generalized climatic trends by empirically assessing climate variability since 1980 with a larger set of weather stations at high elevation. I found no consistent temporal trends in temperature and rainfall, but high inter-annual variation in rainfall associated with El Niño Southern Oscillation (ENSO) effects. Climate and topography affected vegetation productivity (measured as the Normalized Difference Vegetation Index NDVI) in the Dry Puna in various ways. Primary productivity was overall low but higher in the High Plateau, under the humid influence of the Amazon. There was no significant temporal trend in productivity in the study area since 1980 and NDVI variability was chiefly driven by ENSO conditions (lower during El Niño years, with dry and hot summers). At a finer scale, vegetation types responded to low rainfall in different ways; tussock grasslands were the most affected by low rainfall; wetlands and scrublands the most resilient. The aridity of the Dry Puna also poses particular ecological limitations to animals. Using species distribution models and resource selection functions I showed that mesocarnivores coexist in this low productive ecosystem by selecting key resources at different degrees and scales, including free water, clusters of prey and refuge. The endangered Andean cat *Leopardus jacobita*, the most specialized, was also the most selective at finer scales and showed the larger spatial overlap with its preferred prey the southern mountain viscacha *Lagidium viscacia*. Using bioclimatic models at the continental level, I predicted that suitable habitats for Andean cats will decline under future scenarios of climate change by up to a third by 2080. Although 15% would still be represented within the current network of protected areas, there will be a dramatic decline in the northern reach of the species range. Given the dearth of earlier climatic and ecological studies in the Dry Puna, this thesis makes a substantial contribution to better understand the impact of climate on the productivity of this dry environment, and how threatened species may interact and respond to current and projected climate conditions.

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Dedicated to Caliboro, the place where I learnt to love nature.

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Chapter 1:

Introduction

1.1. Background

1.1.1. Dry mountains

Mountains are key elements of the biosphere, being widely recognized as important water sources, and with an essential role in the water cycle (Beniston et al. 1997, Viviroli et al. 2003, Viviroli et al. 2007). They provide freshwater to half of the human population for consumption, industry, irrigation and hydropower (Viviroli et al. 2009). Mountains are characterized as water towers because they deliver disproportional runoff compared to the respective lowlands, being a significant source of water for the nearby lowlands (Viviroli et al. 2007). This is particularly important in arid and semiarid zones, where mountains contain water reservoirs, such as glaciers and snow (Viviroli et al. 2003), storing water for the dry season in important areas of the Mediterranean Basin, the Sahara, Sub-Saharan Africa and the Central Andes (FAO et al. 2011).

Many mountains are biodiversity hotspots with endemic and mountain-adapted specialists (Körner 2003). This is the result of the presence of several climatic zones across small distances and strong evolutionary pressures; for example some species evolved from lowland species following mountain lifts; others evolved influenced by topographic barriers and habitat patchiness, which make dispersal and colonization difficult (Price and Geist 2013). Examples of high altitude biodiversity hotspots are the Central Asian mountains, with the highest alpine flora diversity and distinctiveness in the Northern Hemisphere (Agakhanjanz and Breckle 1995), the Tropical Andes, the mountains of Southwest China and the Eastern Himalayas (Myers et al. 2000).

Among high altitude systems, dry mountains cover 8.5% of the Earth's surface, combining all high altitude areas with a ratio of mean annual precipitation to mean annual potential evapotranspiration lower than 0.65 (FAO et al. 2011). The largest expanse of dry mountains are in Asia (almost 6 million km^2), and the smallest in South America (977,454 km^2) and Europe (91,881km^2) (FAO et al. 2011). They are typically fragile ecosystems, because in addition to water scarcity, life is constrained by steep slopes, poor soils and extreme weather (FAO et al. 2011). As a result of these strong environmental constrains dry highlands host mountain and arid-adapted specialists which contribute to the overall diversity of mountain systems. In spite of their importance as biodiversity hotspots and as sources of water in dry regions, dry mountains are among the least studied and most

unknown environments in the world, and we therefore have a limited understanding of the ecological processes sustaining their biodiversity (FAO et al. 2011).

1.1.2. Climate change and climatic projections in mountains

Climate change is having strong environmental impacts on mountain ecosystems, wich are considered among the most vulnerable areas to warming and changes in precipitation (Beniston 2003, Diaz et al. 2003). Temperature is changing at high elevations more markedly than in lowlands (Diaz and Bradley 1997, Diaz et al. 2003, Vuille et al. 2003, Pepin and Lundquist 2008, Liu et al. 2009). For example, warming on the Tibetan Plateau between 1955 and 1996 was higher than in other regions at the same latitude, suggesting that mountains are particularly affected (Xu et al. 2009). Current estimates indicate high rates of warming in arid mountains, ranging from an increase of 4-5 ºC by 2055 in arid mountains of Central and West Asia (worst case scenario) and 3-4 ºC in the Central Andes and the Sahara mountains (Nogués-Bravo et al. 2007, FAO et al. 2011).

In the Tropical Andes changes in climate are evident (Vuille and Bradley 2000, Vuille et al. 2003, Urrutia and Vuille 2009), including the retreat of glaciers (Vuille et al. 2008a), with far reaching consequences. Rainfall and snow are initially stored as ice in glaciers, and/or as water in wetlands, which then is slowly released into the lowlands (Juen et al. 2007, Vuille et al. 2008a, Urrutia and Vuille 2009). Climate change can generate modifications in these hydrologic systems that affect the availability of water for human consumption, grazing and industrial activities in the lowlands below (Vergara et al. 2007, Urrutia and Vuille 2009).

Trends and projections of climate variables in mountains are particularly difficult to estimate. One of the major limitations to our understanding of patterns and consequences of climate change in mountains is the general scarcity of weather stations at high altitudes worldwide. For this reason climate models necessarily extrapolate from limited empirical information, which compromises the precision of the predictions in mountain systems. Moreover, global and regional climate models largely underestimate the complex climate features produced by mountain topography (Nogués-Bravo et al. 2007, Scherrer and Körner 2011). There is a general agreement of the urgency to gather and analyse more climatic information at local scales, in order to improve our understanding and capacity to predict the direction and consistency of climate change in mountains.

1.1.3. Climate and primary productivity in arid mountains

Research to improve our understanding and predictions of climate change is particularly relevant for dry mountains, where changes in climate can cause serious alterations to arid ecosystems (Whitford 2002, Placzek et al. 2009). Indeed, these are considered among the most responsive ecosystems to climate change (Melillo et al. 1993, Whitford 2002), because water is a critical resource, controlling diversity, abundance and coexistence of organisms (Noy-Meir 1973, Ali et al. 2000, Enright et al. 2005). Any change in the water cycle (precipitation, run-off, evaporation or evapotranspiration) will affect the availability of water to plants, which in dry highland are also stressed by high solar radiation; solar radiation will potentiate the effects of increasing temperatures, via increasing evaporation, diminishing soil moisture and reducing the volume of water in wetlands, snow cover and ground sources (McCluney et al. 2011). These changes, spatially and temporally, might produce unexpected shifts in the abundance and diversity of species (Holmgren et al. 2001, De La Maza et al. 2009, McCluney et al. 2011).

Several studies in arid and semiarid ecosystems have documented considerable changes in primary productivity in response to variations in precipitation (Nicholson et al. 1990; Tucker et al., 1991; Tucker and Nicholson, 1999; Rasmusson, 1998). In dry mountains empirical data suggest that grasslands might actually degrade due to the combination of warmer and drier conditions, in contrast with the expected increase of primary productivity with increasing temperature in these areas (Dirnböck et al. 2003).

Clearly precipitation is a key climatic variable affecting the distribution and productivity of vegetation communities in arid mountains, and understanding these relationships will help understand how arid ecosystems respond to climate change, including cascading effects on animal populations and human activities. As climate change is also causing more extreme climatic events such as heat waves and droughts (IPCC 2014), understanding how these will affect arid mountain ecosystems is a pending task.

1.1.4. Climate and vegetation in arid mountains

Vegetation characteristics vary along regional gradients of temperature and precipitation in many regions of the world (Woodward and Williams 1987, Walter and Breckle 2002). In mountains, minimum temperatures have long been viewed as an important climatic factor controlling plant distribution and imposing constrains to species' ranges more generally

(Woodward and Williams 1987). Plants in high mountains have adapted by developing physiological and morphological adaptations to extreme low temperatures and water stress, enabling them to grow and reproduce in such harsh environmental conditions (Körner 2003). Indeed, the complex terrain of the mountains creates diverse and favourable habitats for plant species, thus determining heterogeneous and patchy responses of vegetation following microclimatic variations created by topography (Körner 2003). Because of the complexity of microclimates and of the species' adaptations to life in mountains, shifts in water availability under climate change might produce diverse effects. Vegetation types might respond to changes differently, depending on their tolerance to specific ranges of environmental conditions and their patterns of growth, survival and reproduction (Porter et al. 2000).

1.1.5. Impacts on biodiversity in arid mountains

Growing evidence of the impacts of climate change upon mountain biodiversity indicates that species are shifting their distributions upwards as a result of global warming (Parmesan 2006, Seimon et al. 2007, Raxworthy et al. 2008). Under various scenarios of climate projections, mountains animals from different regions show an upslope shift in their distribution, including bird species (La Sorte and Jetz 2010), neotropical hummingbirds (Buermann et al. 2011) and Tibetan ungulates (Luo et al. 2014).

In addition to range shifts at the level of species, understanding animal responses to climate in arid highlands requires a finer scale of analyses in order to account for the clustered nature of critical resources and the sptatil scales at which animals might perceive them. Variations in topography and slope determine the location of free water for wildlife, and create thermal refuges for species at various elevations, to which species' will respond according to their particular adaptations and degree of tolerance or specialization.

Carnivores, because of their position at the top of the food chain, can be useful indicators to study the relationships between climate and the fauna of dry highlands, adapted to extreme weather and water scarcity (Sergio et al. 2008). Research on highland carnivores is notably scarce due to their cryptic nature, remote distributions and large-scale habitat requirements. Understanding how carnivores utilize critical resources in arid mountains, such as water and refuge which are scarce and presumably at high demand, can bring light into the fundamental question of the mechanisms promoting carnivore coexistence in low

productive ecosystems. Ecological studies at finer spatial scales are needed in order to incorporate microclimate variations, food, refuge and free water, and multi-species approaches to understand the coping strategies developed by predators with various degrees of specialization. Highland specialists typically have restricted distributions as they depend on rare habitats or resources to survive, being outcompeted by the more generalist sympatric predators, and for that reason they are vulnerable to extinction.

1.2. The Central Andean Dry Puna: study area and ecological indicators

One of the most intriguing and less studied dry mountains in the world is the Central Andean Dry Puna. This is the driest region of the Andes and a global conservation priority due to its biological distinctiveness and vulnerability (Dinerstein et al. 1995). The mean annual precipitation is less than 400mm and highly variable in space. The area is located in a transition zone between tropical and extratropical atmospheric circulation, and influenced by El Niño Southern Oscillation (ENSO), with the Andes Cordillera imposing a strong barrier effect (Garreaud et al. 2009).

The vegetation of the Dry Puna is patchy and fragmented, dominated by grasslands, scrublands and localized wetlands including lagoons and salt flats. At a first glance the Dry Puna looks uninhabited, but this ecoregion supports relative high diverse and endemic biodiversity, including among the most charismatic, three flamingo species (*Phoenicopterus chilensis*, *Phoenicoparrus andinus,* and *Phoenicoparrus jamesi*), the chinchilla (*Chinchilla lanigera*), vicuña (*Vicugna vicugna*) a camelid with the finest fibre, the rare and endangered Andean cat (*Leopardus jacobita*), and the queñoa (*Polylepis tarapacana*), the tree that grows at highest elevation in the world. This biodiversity shows important adaptations to extreme conditions including adaptations to low partial pressures of oxygen such as high blood oxygen affinity in chinchillas (*Chinchilla brevicaudata*) and vicuñas (Chiodi 1970, Ostojic et al. 2002, Storz 2007), to prevent water loss in chinchillas (Cortes et al. 2003), and to consume fibrous and ligneous vegetation such as incisive teeth with continuous growth and highly digestive efficiency in vicuñas (Sponheimer et al. 2003, Borgnia et al. 2010). Others such as the southern mountain viscachas (*Lagidium viscacia*) and Andean toads (*Bufo spinulosus*) show markedly diurnal activity and basking behaviour to cope with the extreme thermal environment at high elevation (Mann 1978, Lambrinos

and Kleier 2003). Among carnivores, Andean cats share with snow leopards (*Panthera uncia*) morphological adaptations to cope with the low temperatures such as long hair with dense woolly under fur (McCarthy et al. 2003).

Climate change has been well documented in the Tropical Andes (Vuille et al. 2000, Vuille et al. 2003) with glaciers retreating at a significant speed (Vuille et al. 2008b, Rabatel et al. 2013) and tree lines climbing up the Andean slopes (Feeley et al. 2011). Less is known however, about the Dry Puna in the Central Andes. Climate models project higher temperatures than today (Bradley et al. 2004, Bradley et al. 2006, Urrutia and Vuille 2009a), and there is little agreement among models on future trends in precipitation. Seth et al. (2010) and Thibeault et al. (2010) predicted a slight increase in precipitations during the rainy season by the end of this century, whereas Urrutia and Vuille (2009) and Minvielle and Garreaud (2011) predicted precipitation to decrease.

Similarly, research on current and future effects of climate on the flora and fauna of the Dry Puna is lacking. The Dry Puna ecosystem offers a particularly interesting model system because it is highly susceptible to changes in moisture (Grosjean and Veit 2005). Any change in water availability will affect vegetation growth, with a domino effect across the ecosystem and unknown consequences for a number of endemic species such as the Andean cat, and for the supply of water to human populations further down the Andes. Understanding how the Dry Puna ecosystem responds to climatic variability will make an important contribution to predict the eventual consequences of long-term climate change, and to develop mitigation mechanisms to prevent ecological disasters affecting biodiversity and human welfare.

This thesis focuses on the area around the triple frontier between Argentina, Chile and Bolivia, which corresponds to the Central Andean Dry Puna ecoregion (Olson et al. 2001). The study area encompasses part of the High Andes Plateau or ‘Altiplano’, part of the chain of high peaks that form the international boundary between the countries, and the Andean slopes dropping westwards towards the Atacama Desert in Chile. The Altiplano is the second largest high-elevation plateau in the world, runs above 3,000m across parts of Peru, Bolivia, Chile and Argentina and has been an important centre of adaptive radiation for Andean species, adapted to the harsh climatic conditions of extreme altitude (Marquet 1994, Ruggiero et al. 2001).

The study area is dominated by volcanoes and endorreic basins, with salt pans and shallow lagoons. The climate is characterized by low atmospheric pressure, low air density, extreme diurnal variations in temperature and minimal atmospheric humidity (Aceituno 1996, Garreaud et al. 2003), with low annual precipitation, concentrated in the summer months (Vuille et al. 2000, Garreaud et al. 2003). Vegetation growth is limited and the green biomass is largely concentrated around wetlands, forming cushion bogs and other riparian vegetation that largely depend on water from underground sources (Squeo et al. 2006). These bogs and wetlands, locally known as 'bofedales' and 'vegas' are essential for herbivores, mainly rodents and camelids with adaptations to consume high fibre vegetation, and for humans alike, as they provide water and pasture for their domestic animals.

Understanding how arid ecosystems such as the Dry Puna respond to changes in climate is an important but difficult question, because it involves several interacting factors operating at various time scales, including long-term processes for which data is often not available. This thesis proposes an effective approach to study spatial and temporal responses of ecosystems to climate change, in the use of ecological indicators, including those derived from remote sensing.

Ecological indicators can be defined as surrogates for the response of ecosystem components in space and time (Niemi and McDonald 2004, Armon and Hänninen 2015). For example, the Normalized Difference Vegetation Index (NDVI) is a useful ecosystem function indicator, a proxy for net primary productivity/green biomass and soil moisture (Pettorelli et al. 2005, Wang et al. 2007). NDVI has been used for temporal ecological studies with good results in dry areas (Malo and Nicholson 1990, Zhao et al. 2011). To study the Dry Puna biodiversity and ecosystem processes, I examined the relationship between NDVI and precipitation, which in turn is a good proxy for direct water availability for plants (Austin 2007). Precipitation in the form of snow, and snow cover, are almost negligible in the study system, because precipitation occurs almost exclusively in the summer and winter snowfalls are very rare, originated by cold upper-air low pressure systems coming from the Pacific that penetrates to the area (Vuille and Ammann 1997). Little is know about underground water and the mechanisms for water recharge, due to a dearth of information and the complexity of the hydrological systems (Molina 2006, Uribe et al. 2015).

In order to study changes in primary productivity in the Dry Puna I analysed the magnitude and distribution of NDVI values in relation to climatic variables over the last three decades. Using rainfall and NDVI as indicators of water availability, this thesis investigates how vegetation reacts to dry years to achieve a more comprehensive understanding of the dynamics of this biological system in relation to climate variations in time and space.

In terms of animal responses to climate change, carnivore species are good indicators of the health of the ecosystem as a whole, and of prey-predator interactions in an area where food resources, refuge and water are limited and patchy (Sergio et al. 2008). In particular, the Dry Puna is a good system to study competition among carnivores for limited resources, including the more profitable prey. For example, within the guild of medium size carnivores, the Andean cat is the only species limited to dry and cold climates, and seemingly adapted to predate on mountain viscachas, many times larger than other rodents species. Because of its restricted climatic niche, the Andean is also a useful species to explore the potential effects of climate change on mountain specialists, by projecting its future distribution under various scenarios of climate change.

1.3. Objectives and thesis outline

The overall aim of this thesis is to characterise the Dry Puna climate variability, and to understand the effects of climate upon the ecosystem. To achieve this objective I combine climatic records with remote sensing and field data, and analyse them at diverse temporal and spatial scales.

I tackle three specific objectives:

1. To assess recent patterns of climatic variation within the complex landscape of an arid mountain, using empirical data on rainfall and temperature, and incorporating variations in El Niño Southern Oscillation (ENSO), altitude, longitude and latitude (Chapter 3).

2. To test the resilience and dependence of primary productivity and vegetation on rainfall in the Dry Puna, including the role of localized factors such as topography, and considering short and long term responses (Chapters 4 and 5).

3. To assess how patterns of use of key resource in dry highlands, including water, prey and refuge, affect the structure of the community of medium sized carnivores (i.e., Andean cats, Pampas cats (*Leopardus colocolo*) and culpeo foxes (*Lycalopex culpaeus*)), and how long-term climate change might affect the distribution of the more specialized Andean cat (Chapter 6 and 7).

The thesis is organized in the following chapters:

Chapter 1: Introduction

General introduction to relevant topics of the thesis, overall aim and objectives and a brief overview of thesis chapters.

Chapter 2: Literature review: mountain climates, biodiversity and environmental indicators, with a focus in the Dry Puna

A general review of the state of knowledge of the relationships between climate and mountain biodiversity worldwide and for the Andes and Dry Puna in particular. This review provides background information for all thesis chapters and it includes a detailed description of the study area.

Chapter 3: Climate complexity in the Central Andes: a study case on empirically - based regional variations in the Dry Puna

This chapter responds to the need to measure and understand current climatic variability in the Dry Puna, a climatic system comparatively under-studied in the Andean region. I analyse spatial and temporal patterns of variation in temperature and rainfall between 1980 and 2010 using 28 weather stations located above 2,300m in the Dry Puna of Bolivia and Chile. This region is under the influence of tropical and extratropical atmospheric

circulations, ENSO and with the Andes imposing a barrier effect and drastic topographic changes, and therefore predicted to show important variation, that it is also not accounted for in global models. Global and regional models project an increase in temperature for the Dry Puna, but no clear trends in rainfall. By using empirical data from all available weather stations, this chapter provides a first assessment of changes in climate in this region and a first validation of the climatic extrapolations of global climate surfaces for the Dry Puna. I expect high rainfall and temperature variability within the study area, in response to local topography and elevation, but also with regards to the exposure to global circulation systems, for example at each side of the Andes and along a south-north axis (due to the influence of the humid Amazonia climate).

Chapter 4: Climate linked variations in primary productivity in the Dry Puna

There is a crucial need to understand how future climate might affect biodiversity in dry highlands, with complex climates and specialized organisms. Previous studies of climate and NDVI in the Andes were carried out at global or continental scales using global climatic surfaces (Paruelo et al. 2004, Zeng et al. 2013, Barbosa et al. 2015). Here I describe, for the first time, patterns of variation in NDVI in the Dry Puna using actual climate records rather than climatic surfaces. I test for variations in primary productivity between 1982 and 2006 around 28 weather stations, by comparing time series of NDVI data at 8km resolution against time series of temperature, rainfall and ENSO. I expect primary productivity to be mainly influenced by rainfall, with strong signs from ENSO fluctuations (as in other regions of the Andes) and to exhibit strong spatial patterns of variation and both short- and long-term responses to rainfall.

Chapter 5: Vegetation response to low rainfall in the Dry Puna

Since precipitation has been suggested as one of the main climatic variables affecting vegetation in the Dry Puna (Morales et al. 2004, Soliz et al. 2009), dry periods can have considerable effects on vegetation. Complementing the previous chapter, I study vegetation productivity using higher resolution satellite imagery in order to capture the spatial heterogeneity of mountain vegetation. To understand the resilience of ecosystems to climate change I explore the magnitude and direction of vegetation responses to low rainfall in the Dry Puna. I compare their productivity, measured as NDVI at 30m of

resolution, in a 'normal' and a 'dry' year, using Landsat TM images, digital elevation models, and field surveys. Spatially, productivity is expected to be higher in northern and eastern aspects where solar radiation is higher and which receive a humid influence from the Amazon. Temporally, productivity should be higher during 'normal' than 'dry' years, possibly with the exception of the vegetation types associated to wetlands and supported by underground water sources.

Chapter 6: Use of localized resources shape the community of carnivores in the Dry Puna

The guild of medium-size carnivores in the Dry Puna is composed by a highly specialized carnivore, the Andean cat, and two generalist meso-carnivores, the Pampas cat and the culpeo fox, the latter two also present in other ecosystems further down the Andes Cordillera. The prevailing thesis is that the Andean cat can maintain local populations in sympatry with these generalist carnivores, because it is more efficient at exploiting the more profitable mountain viscachas, a rocky specialist and the largest rodent in the Dry Puna (Walker et al. 2007; Napolitano et al. 2008; Marino et al. 2010). I use occurrence data from carnivores and prey to explore habitat associations and patterns of use of three critical resources: wetlands that concentrate water and green biomass; rocky outcrops and broken terrain which provide refuge to both prey and predators; and prey presence. I provide crucial information to understand how Dry Puna carnivores share the use of these localized resources, according to their physiological adaptations and degree of specialisation/generalism. I expect patterns of resource use to differ between specialist and generalist species, including the spatial scales at which carnivores perceive and select rare resources (Pita et al. 2011).

Chapter 7: Predicting the future of mountain carnivores taking into account climate, prey availability and protected area networks

Global warming tends to insulate highland species into mountaintops, threatening the survival of many important endemic species worldwide (Parmesan 2006, La Sorte and Jetz 2010, Luo et al. 2014). The distribution of Andean cats is largely associated to arid and cold conditions and as a result the species might be highly sensitive to global warming (Marino et al. 2011). Understanding the processes driving shifts in the Andean cat range

under climate change will help predict the future of many other Andean vertebrates. To achieve this objective I modelled Andean cat and viscacha distributions, using corrected scenarios of climate change and incorporating the existent biological knowledge as explicitly as possible. I assess the future conservation status of Andean cats by analysing the future representativeness of suitable habitats within the current network of protected areas, and considering the spatial and genetic structure of the existing populations. As warming affect the Andes, I expect the Andean cat range to shif up the Andean slopes and a decline in suitable habitats.

Chapter 8: General discussion

Concluding remarks of this thesis, including a holistic interpretation of the results in relation to the conservation of the biodiversity of the Central Andean Dry Puna under current and projected climate variability.

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Chapter 2:

Literature review: mountain climates, biodiversity and environmental indicators, with a focus in the Dry Puna

2.1. Mountains

2.1.1. The importance of mountains

Interest in mountains has been increasing in recent decades due to their significant role in a sustainable human future. They contain one of the most important indicators of climate change, glaciers, being among the most sensitive regions to climate change (Diaz et al. 2003b).

The definition of what are mountains is diverse in the geographical literature, with several existing characterizations of mountains systems. Some are delimited mainly by subjective features, as described by Roderick Peattie (Peattie 1936), who pointed out that mountains should be impressive and enter in the imagination of people who live close to them (Price et al. 2013). Likewise, there are several objective criteria to define mountains, such as altitude, local relief or steepness, and geologic, climatic and floral characteristics (Price et al. 2013). Generally, it is suggested that mountains range in altitude from 600m to 8,848m, exhibit high relief and steepness of slope, and have strong relative environmental gradients within a short distance (Gosling and Bunting 2008). Following these criteria, mountains display strong climatic and ecological variability (Gosling and Bunting 2008).

Mountain systems cover around 25% of the global land surface, and although they are generally considered to be marginal for human habitation due to their harsh environmental conditions and inaccessibility, 26% of the world's population lives in or near mountain areas (Meybeck et al. 2001, Diaz et al. 2003b).

Mountains are important elements of the global biosphere, containing diverse ecosystems. The effects of elevation in determining vegetation belts in mountain areas can be compared to the different latitudinal climatic zones, and these elevation gradients produce hotspots of unique biodiversity (Diaz et al. 2003b). Moreover, mountains are fragile and extremely vulnerable to perturbations and ecosystem changes (Messerli et al. 1997), particularly to variations in temperature and precipitation (e.g. Diaz 2003 and Arroyo et al. 1998). Indeed, it has been suggested that mountain environments comprised of snow, glaciers and high altitude biodiversity, are among the environments most vulnerable to global climate change (Diaz et al. 2003b).

Mountains also play an important role in the Earth's climate systems. For example, mountains affect atmospheric circulation and climate through perturbations of large-scale atmospheric flow patterns, and influence the formation of clouds and precipitation in their surroundings (Beniston et al. 1997). However, the lack of observational climate data from remote mountain areas and the complexity of their relief makes it difficult to incorporate these areas in general circulation models, hindering the understanding of climate characteristics in mountains and their effects on general systems (Beniston et al. 1997).

Mountains provide important natural resources such as water, biodiversity, mineral resources, and hydropower. Mountains are a key element of the hydrological cycle (Beniston et al. 1997), evidenced in their large discharge of water, compared to lowlands. As a fundamental source of freshwater for lowland regions and further beyond, mountain systems affect both seasonal and long-term water storage (Diaz et al. 2003b, Viviroli et al. 2007). Globally, some 32% of the water discharged annually comes from mountains (Viviroli et al. 2003), with the proportion varying according to the region. The role of mountains in hydrological systems is greater when they are adjacent to dry lowlands; for example, in semi-arid or arid regions, mountains can contribute 50-90% of total annual discharge (Messerli 2009) and supply as much as 90% of freshwater for human consumption, irrigation, and industrial use in adjacent dry lowlands (Meybeck et al. 2001, Diaz et al. 2003b).

In dry areas, mountains serve as "wet islands", harbouring water reservoirs for the dry season, depending on factors such as their glacier's size, volume, and durability of snow cover (Viviroli et al. 2003). Mountains are thefore particulary important in dry areas, serving as water towers to the lowlands, such as the mountains of the Mediterranean Basin, the Sahara, Sub-Saharan Africa and the Central Andes (FAO et al. 2011).

FAO et al. (2011) defines dryland mountains as all hyper-arid, arid, semi-arid and dry-subhumid mountain areas with an aridity index (i.e. ratio of annual precipitation to potential evapotranspiration) of less than 0.65. According to this, dry mountains cover 12 million km^2 with almost half of the total area located in Asia. Dryland mountains are characterized by several environmental constraints, such as a water scarcity, highly heterogeneous topography, steep and poor soils, and extreme weather and climate with droughts and heat waves (FAO et al. 2011). Water, the main constraint for life in this environment, occurs as glaciers, snow packs, salty lakes, lagoons, rivers, streams and underground water (FAO et al. 2011).

Human reliance on mountain water is growing each year due to an increase in the world population and economic activities such as mining and industrialization. Because of this dependence, changes in climate can have great impacts on the broader hydrologic system, leading to serious and undetermined effects in the socio-economy of human populations living in mountains and surrounding lowlands (Beniston et al. 1997).

Already, it has been documented that temperature changes in highlands have been greater than in lowlands (Diaz and Bradley 1997, Diaz et al. 2003a, Vuille et al. 2003, Pepin and Lundquist 2008, Liu et al. 2009). A good example of this is in the Tropical Andes, where changes in climate have been already observed (Vuille et al. 2000, Vuille et al. 2003, Urrutia and Vuille 2009) and glaciers are retreating (Vuille et al. 2008). Rainfall and snow are initially stored as ice in glaciers or as water in wetlands, saving this resource for the following seasons, when water is released into the lowlands (Juen et al. 2007, Vuille et al. 2008, Urrutia and Vuille 2009). Climate change could generate serious modifications in the hydrologic system, affecting the availability of water for human consumption, grazing and other industrial activities in the lowlands (Vergara et al. 2007, Urrutia and Vuille 2009).

2.1.2. Mountains and biodiversity

Mountains are characterized by a high level of endemism, with some species having evolved from lowland species, and others under the influences of topographic barriers and habitat patchiness, with difficult dispersal and colonization (Price and Geist 2013). As a general rule, the number and diversity of animal and plant species decreases with altitude, with the exception of some altitude cloud forest or desert mountains, which catch moisture and are more diverse and productive at higher elevations (Hadley et al. 2013, Price and Geist 2013). In the Himalayas and the Andes, between 20-30° latitude, vascular plants reach their highest altitude at 5,800 to 6,400m (Webster 1961). Overall, the species number and composition vary for each mountain area, depending on environmental conditions such as size, elevation, age, history of mountain uplift, and climate (Price and Geist 2013). Under the challenging conditions of dry mountains environments, species have developed strategies to cope with serious limitations such as water scarcity and extreme weather and climate. This results in areas with exceptional biodiversity (including endemicity) and ecosystems services, which often qualify them as priority ecoregions for global conservation (Olson and Dinerstein 2002, FAO et al. 2011).

The alpine life zone is restricted to the area of natural vegetation above the treeline, which is the highest altitude at which trees can grow (Körner 2003). However, this has to be taken with caution, as some tree species occur only at high altitudes, and some other natural variables could create unusually low timberlines (Körner 2003, Price et al. 2013). In general, alpine areas have low temperatures, high solar radiation, low soil nutrient levels, low atmospheric pressure, strong winds, and short growing seasons (Körner 2003). Despite such harsh environmental conditions, some plants have the ability to survive because they have adapted to water stress and extremely low temperatures, or have developed modifications to grow and reproduce, such as changes in growth form, including low stature (Körner 2003). Some plants have developed mechanisms of freezing tolerance or avoidance (Squeo et al. 1996), and others support water scarcity by having a small leaf area to avoid transpiration, or longer root systems to extract water from deeper or surrounding soils. A diversity of conditions in altitude, slope, aspect or shade provide diverse and favourable habitats or refuges for particular species (Körner 2003).

2.2. Climate change and mountains

2.2.1 Climate change

During the last decade changes in climate have emerged as a major environmental problem. The United Nations' Intergovernmental Panel for Climate Change (IPCC) defines climate change as “statistically significant variation in either the mean state of the climate or in its variability, persisting for an extended period (typically decades or longer). Climate change may be due to natural internal processes or external forcing, or persistent anthropogenic changes in the composition of the atmosphere or in land use” (IPCC, 2001). The United Nations Framework Convention on Climate Change (UNFCCC) defines climate change as "a change of climate which is attributed directly or indirectly to human activity that alters the composition of the global atmosphere and which is in addition to natural climate variability observed over comparable time periods".

Carbon dioxide (CO_2), methane (CH_4), nitrous oxide (NO) and water vapour are normal components of the atmosphere that trap the energy that comes from the Earth; when the concentration of these gases increase, the Earth's surface temperature increases (Primack and Ros 2002). In the last century, these greenhouse gas emissions have increased so

markedly that concentrations of carbon dioxide, methane and nitrous oxide are now at record levels, mainly due to economic and population growth (IPCC 2014).

The climate of a region is determined by long term weather, including seasonal variability, complicating long term predictions (Cowie 2012). However, today's climate is clearly changing on temporal scales that are much shorter compared to past glacial periods (Thuiller 2007). Observations clearly demonstrate a general warming of the climate system, with an increasing mean air and ocean global temperature (IPCC 2014). The IPCC has recently concluded with strong certainty that human activities during the last 100 years are responsible for this observed global warming (IPCC 2014).

Other evidence of climate change includes the rise of sea level at a global scale, changes in patterns of precipitation, glacial melting, changes in the frequency of climatic events, and increasing frequency and magnitude of extreme climatic events as droughts or floods (Haeberli and Beniston 1998, Vuille et al. 2008, IPCC 2014). All these changes may have serious consequences on the structure and function of natural systems, altering rainfall regimes and hydrological systems, affecting water availability, or provoking increased runoff or landslides (Messerli et al. 2004, Viviroli et al. 2007). Similarly, species' response to warming might include changes in migration, seasonal patterns, abundance and even extinction of animals and plants (Thomas et al. 2004, Bellard et al. 2012, IPCC 2014).

Our knowledge of the future state of climate is mainly based on different models that have been developed, some of which include large scale interactions between atmospheric and oceanic components and other relevant processes mediated by soil and vegetation. Models that simulate the global climate are called General Circulation Models (GCM) and have a coarse spatial resolution (generally hundreds of kilometres). Although future projections of climate change vary depending on the type of GCM, in general GCMs predict large changes in precipitation and temperature in South America (IPCC 2007), which agree with the biological and physical impacts already described for the continent (Rosenzweig et al. 2008, Vuille et al. 2008). Regional Climate Models (RCMs) are developed for specific geographic areas at finer spatial resolutions (50-25km). RCMs are driven by climate-related variables calculated by GCMs and commonly include atmosphere, earth surface components, and fundamental processes in the climate system (Jones et al. 2004). However, confidence is often higher for continental scale models than for regional models, due to the limited capacity of models to simulate some aspects of regional climate change (Cowie 2012).

2.2.2. Climate change in mountains

Changes predicted for mountains areas vary according to temporal and spatial scales. In general, mountain regions have warmed in the last century according to latitude, with higher warming occurring at high altitudes in the tropics than in temperate regions (Kohler et al. 2014). In addition, important environmental boundaries, such as tree and snow lines, have been documented to be moving upland under warming conditions, affecting ecosystems and decreasing water supplies (Kohler et al. 2014).

In the case of the Andean mountains, models predict that the region will warm by 0.5–1 °C during the period 2020–2029 (IPCC 2007). Although the Central Andes is weakly resolved in current global models, due to their relative coarse resolution, these climate predict higher temperatures than today. For example, a projected scenario using seven GCMs suggested an increase in temperature of >2.5°C for the Andes mountains between 10°S to 40°S, including Bolivia, Chile and Argentina (Bradley et al. 2004). Moreover, a mean of eight different GCMs projected a maximum temperature increase and enhanced warming with altitude for the High Andes of Peru, Bolivia and northern Chile under a high emission scenario (Bradley et al. 2006). Furthermore, a RCM also projected warming in the tropical Andes and predicted an increase in temperature at higher elevations (Urrutia and Vuille 2009).

On the other hand, there is little agreement among models about future trends in precipitation in mountains ranges. In the Andes precipitation is projected to increase at the equator and decrease towards the south (Gosling and Bunting 2008). For the Central Andean Puna, Seth et al. (2010) and Thibeault et al. (2010) studied nine GCMs and predicted a slight increase in precipitation during the rainy season by the end of the century. In contrast, Urrutia and Vuille (2009) suggested precipitation in the rainy season will decrease by the end of this century, mainly caused by weaker easterly winds and strengthened westerlies leading to drier overall conditions in these areas. Minvielle and Garreaud (2011) predicted a decrease in summer precipitation of between 10 and 30%, while the rest of the year the Andes Puna would persist as dry as at present.

2.2.3. Effects of climate change on mountain biodiversity

Climate change can affect biodiversity at different levels, including changes in species' phenology (Edwards and Richardson 2004), physiology (Hughes 2000) and geographic distribution (Parmesan 1996, Hickling et al. 2006, Lenoir et al. 2008). These effects may drive some species to extinction (Parmesan and Yohe 2003, Thomas et al. 2004), thereby altering the effectiveness of protected areas in geographically covering the species distribution in the future (Parmesan and Yohe 2003, Hannah 2010).

Evidence of climate change impacting mountain biodiversity has been already observed (Parmesan 2006). Indeed, many studies predict important impacts on mountain biodiversity, with many taxa shifting their distributions upwards as a result of global warming (Parmesan 2006, Seimon et al. 2007, Lenoir et al. 2008, Raxworthy et al. 2008, Harsch et al. 2009, Luo et al. 2014) and cold-adapted plants declining in favour of warm-adapted ones, particulary in European's alpine systems (Gottfried et al. 2012). In the South American Andes, Marcora et al. (2008) suggested that warming will restrict the mountain tree queñoa (*Polylepis australis*) to the uppermost altitudes, and Feeley et al. (2011) showed an upward shift in most tropical tree ranges due to an increase in temperature. As species move higher up the mountain slopes, there will inevitably be a reduction in the extent and quality of their suitable habitats, and the development of vertical discontinuities may hinder their capacity to disperse (Colwell et al. 2008, La Sorte and Jetz 2010).

In mountain areas, the potential for species to adapt to climate change will also be affected by the structure and extension of topographic features, the geographical range size of the species, and the projected temperature changes. Geographical range contractions and a decline in population numbers could eventually lead to "mountaintop extinctions" (Colwell et al. 2008, La Sorte and Jetz 2010).

2.3. Ecological Indicators

Environmental processes often present a level of complexity that is difficult to measure in its entirety, requiring different study approaches and involving several measures or indices (Armon and Hänninen 2015). Indicators are effective, simple, fast and cost effective measures, which indicate, with reasonable precision, change in an environmental process or phenomenon of interest (Armon and Hänninen 2015).

Threats and pressures on ecosystems are growing every day; among these we find the impacts of climate change on biodiversity. Climate change can be measured using various indicators, such as measurements of extreme temperature over time, changes in precipitation, wind speed, storms and CO_2 concentration (Møller 2015). These indicators are usually easy to measure, require minimum equipment, and generally provide longstanding data (Møller 2015).

On the other hand, the ecological data required to understand biological responses to climate change are difficult to obtain, since measuring populations, species or communities is expensive and requires longer acquisition time. In these cases, surrogates are used as a proxy for detecting change (Noss 1990). The choice of indicators is important, and depends on many factors (e.g., data available in the study area), yet at a minimum, the indicator chosen must be consistent in time and space, to show changes in environmental conditions, and must provide relevant information of the phenomenon in study (Møller 2015).

According to Dale and Beyeler (2001) ecological indicators that would meet these criteria should: “be easily measured, be sensitive to stresses on the system, respond to stress in a predictable manner, be anticipatory, predict changes that can be averted by management actions, be integrative, have a known response to disturbances, anthropogenic stresses, and changes over time, and have low variability in response”.

At present the indicators most commonly used to study the biological impact of climate change are changes in phenology and distribution of species (Møller 2015). In arid areas, the key indicators used to measure degradation and desertification over time are net primary productivity, presence/absence of indicative plant species, vegetation cover, soil organic matter, and some chemical and physical soil properties (Wiesmeier 2015). In terms

of changes in species range size, a larger distributional range under favourable climatic conditions is associated with a greater population size and genetic variation which allows a better response in the face of climate change (Wakeley 1998, Møller 2015). Moreover, it is expected that populations with larger ranges have a greater capacity of dispersal distance (Møller 2015).

One of the most important tools to detect environmental change is remote-sensing technology. Satellite data, with its global coverage and wide range of instruments, can provide information over decades for important environmental parameters such as topography, sea surface temperature and phenology, among others (Revenga et al. 2005, Sherbinin et al. 2014). The normalized vegetation index (NDVI) is a vegetation index extracted from satellite images to monitor the response of vegetation to climate (Malo and Nicholson 1990, Nemani et al. 2003, Wang et al. 2003). NDVI correlates strongly with the photosynthetically active radiation absorbed by vegetation and is thus widely recognized as a good indicator of vegetation productivity and green biomass (Tucker and Sellers 1986, Sellers et al. 1994, Myneni et al. 1997, Wang et al. 2003, Pettorelli et al. 2005). NDVI is calculated using the near infra-red (NIR) and the red spectral (RED) bands reflected by the vegetation and captured by the sensor, employing the following formula: NDVI = [(NIR − RED)/(NIR + RED)] (Pettorelli et al. 2005, Chuvieco 2008). The importance of using NDVI in plant ecology and the increasing number of studies incorporating this indicator in animal ecology have been highlighted by Pettorelli et al. (2005) and (2011), who recognize NDVI as a key tool for understanding the biological responses to climate change, by providing important information about vegetation dynamics that relate animal populations and environmental variability.

2.4. The Central Andean Dry Puna: study area

The Central Andean Dry Puna is located in southern Andean Cordillera Occidental, on the border between Argentina, Bolivia and Chile, and it is crossed by the tropic of Capricorn. It includes the departments of Potosi in Bolivia; the provinces of Jujuy and Salta in Argentina; and the regions of Tarapaca, Antofagasta, and Atacama in Chile (Figure 2.1). The area is located within the Tropical Andes hotspot, the most biologically rich region of the planet (Myers et al. 2000). The terrain varies among mountain ranges. The High

Plateau or Altiplano, a sedimentary–volcanic plateau, runs at over 3,000m for 1,800km in southern Peru, Bolivia, northern Chile and northern Argentina, and its width varies between 350 and 400km (Allmendinger et al. 1997, Ordoñez et al. 2009).

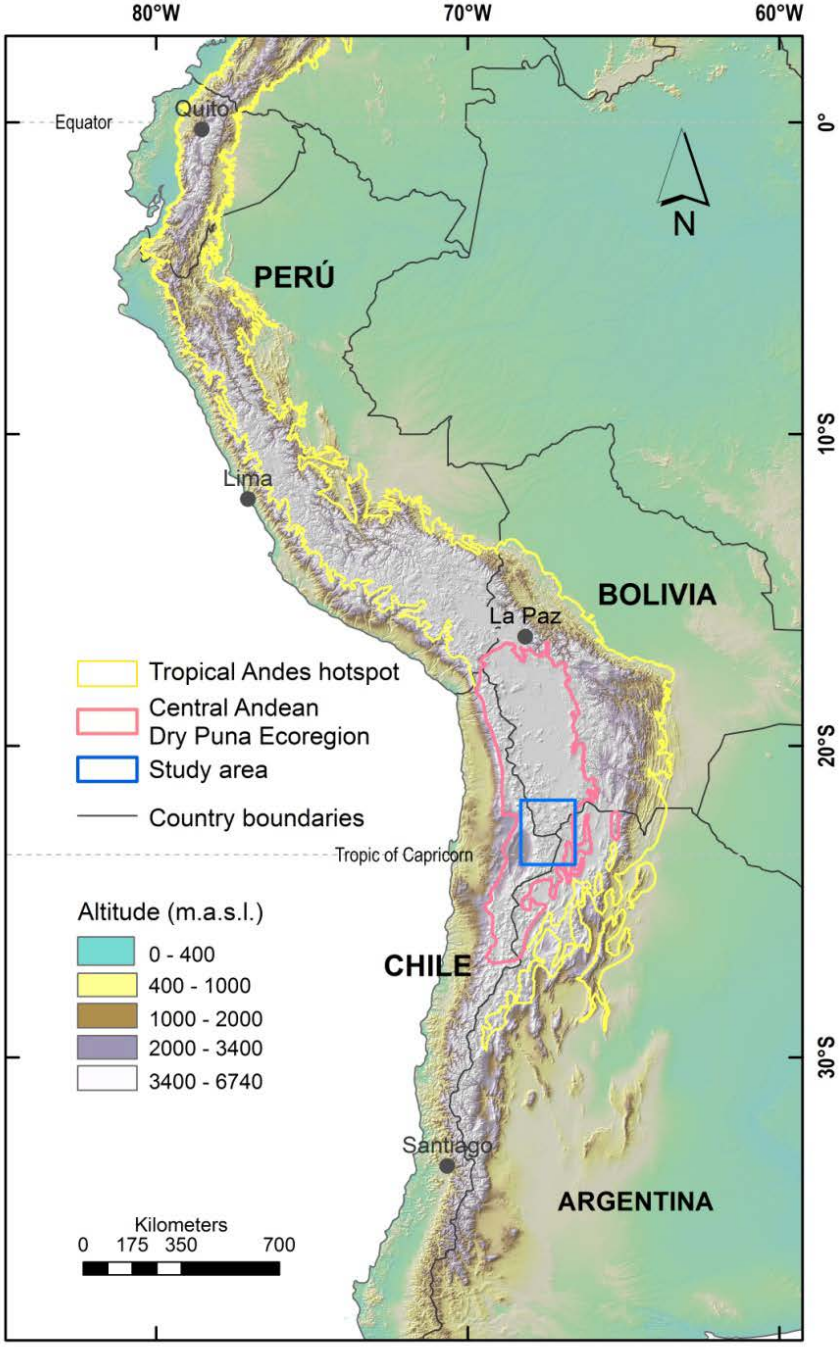

Figure 2.1. Location of the study area, the Central Andean Dry Puna ecoregion, and the Tropical Andes Hotspot in South America.

The Central Andean Dry Puna has been included under several ecological or biogeographical classifications as Puna, Altiplano and Central Andes (Cabrera 1968,

Cabrera and Willink 1973, Udvardy 1975, Rivas-Martínez and Navarro 1994). In this study I follow the World Wildlife Fund (WWF) ecoregion classification, which considers the study area to be part of the Central Andean Dry Puna ecoregion, within the Neotropical region (Olson et al. 2001, Olson and Dinerstein 2002, WWF 2015), including the south-western part of the Altiplano and the high mountains surrounding it, as well as the western slopes of the Andes above 3,000m (Figure 2.1).

The climate of the study area presents low temperatures, reduced atmospheric humidity, low air density, intense solar radiation and extreme diurnal variations in temperature (Aceituno 1996, Garreaud et al. 2009). The climate is semi-arid, with a mean annual precipitation of less than 400mm, which presents a high spatial variability. There is a strong seasonality in rainfall, which is restricted to the austral summer (December to March), when more than 70% of the total precipitation occurs in the form of an intense convective precipitation (Garreaud et al. 2003, Garreaud et al. 2009). During the other austral seasons, the dry influence of the mid-level westerly flow from the Pacific produces almost no rainfall (Vuille and Ammann 1997, Garreaud et al. 2003).

Rainfall in the Central Andean Dry Puna is associated with convective cloud cover over the Central Andes and the southwestern part of the Amazon. This summer rainfall is mainly driven by intensity and displacement southward of the Bolivian High, an upper-level high pressure cell formed by the heating liberated by the convection in the Amazonas basin, which increases the emergence of upper level easterly winds over the Central Andes. These winds bring moisture from the East tropical Amazon basin and Gran Chaco area (Garreaud et al. 2003, Vuille and Keimig 2004) and the intense solar heating of the surface produces a destabilization of the local troposphere (Garreaud et al. 2009).

During the summer season there is a great variability in the temporal distribution of precipitation, caused by the position and intensity of the Bolivian High. Rainy days are grouped in periods of approximately seven days occurring when the Bolivian High is more intense and displaced to the south. These are followed by a similar number of dry days with opposing conditions of the Bolivian High (Garreaud 1999, Garreaud et al. 2003, Garreaud et al. 2009).

Rainfall shows a strong longitudinal gradient in the Central Andean Dry Puna: the western region presents stability and dryness due to the subsidence produced by the subtropical South East Pacific Anticyclone and the cold Sea Surface Temperatures. In contrast, the

eastern area is more humid and warmer, due to the wet and unstable conditions coming from the Amazon (Garreaud and Aceituno 2001, Garreaud et al. 2003). In addition, there is also a latitudinal climatic gradient in the Puna characterized by a significant reduction in precipitation and humidity conditions from north to south (Vuille and Keimig 2004, Garreaud et al. 2009).

Rainfall in the area also presents large inter-annual variability, which is related to the El Niño Southern Oscillation (ENSO) (Aceituno 1988, Vuille 1999, Vuille et al. 2000, Garreaud and Aceituno 2001). In La Niña years, when there is a cooling of the tropical Pacific and the troposphere reduces the westerly flows, the weather tends to be wet. El Niño years tend to be dry, due to warming of the Pacific that increases the westerly flows, bringing dry air to the Andes and diminishing the rainfall. However, in some years this pattern does not occur (e.g., a wet El Niño year in 1972/73 and a dry La Niña year in 1988/89; Garreaud et al. 2003, Vuille and Keimig 2004).

The landscape of the study area consists of high elevation dryland with endorheic basins, systems of gorges, ravines and rivers, with characteristic wetlands that are the most remarkable trait of the hydrological system. These wetlands, which include salty lagoons, freshwater lagoons and salt pans, are systems of shallow lagoons formed over evaporitic endorheic basins during the Tertiary period, 1.8–65 million years ago (Farías et al. 2009). In these aquatic ecosystems environmental conditions for life are extreme, being subject to intense ultraviolet radiation, large daily air temperature fluctuations, high salinity levels, low nutrient concentrations and the presence of heavy metals, especially arsenic (Mantelli et al. 2003, Farías et al. 2009, Ordoñez et al. 2009). As moisture comes from the east in the study area, the salt flats on the west side are in the process of fossilization, because they receive only occasional or irregular recharge in the form of underground water and sporadic flooding. To the central and east of the study area, salt pans are at intermediate stages between saline lakes and salt flats, and some of them have thermal springs (Demergasso et al. 2004). Important wetlands in the area are peatlands and meadows associated with permanent water courses or temporarily flooding (Squeo et al. 2006).

In general, there is little and localized information on surface and groundwater and on mechanisms for water recharge in the region (Molina 2006). Previously water body recharge in the High Andes was thought to be very limited (Grosjean et al. 1995, Messerli et al. 1997), but evidence of groundwater recharge in the Dry Puna is increasing (Magaritz et al. 1990, Houston 2007, 2009, Uribe et al. 2015). According to Houston (2009), the

groundwater in the study area presents unique characteristics, with aquifers located along a borad range of elevations and commonly compartmentalized by tectonic activity and uplift of volcanic-sedimentary basins. However, the mechanism and magnitude of the recharge are still poorly understood due to lack of information and the complexity of the hydrological systems (Uribe et al. 2015). One example is the Linzor basin, in Chile, which shows a highly variable diffuse recharge concentrated in wet years and no recharge in years with precipitation lower than 120mm (Houston 2009).

Among the main salt flats and lagoons in the study area are the Lagunas de Vilama in Argentina at 4,500m, and Tara and Aguas Calientes at 4,400m in Chile. The Salar de Tara basin integrates territories of Argentina, Bolivia and Chile, receiving the Zapaleri River as a major contributor, which originates in Bolivia, flows to Argentina and then continues through Chile (Figure 2.2). Other rivers are mostly temporary and exhibit low flow, with the exception of the Quetena River, in Bolivia, which is permanent and feeds important wetlands (Alurralde 2006).

Figure 2.2. Salar de Tara in Chile. The basin integrates areas from Argentina, Bolivia and Chile.

The vegetation in the study area is patchy and fragmented, dominated by tussock grasslands and azonal wetlands, with areas of barren soil and rocky outcroppings. The complex mountain topography affect the flow of air masses, creating sheltered habitat areas and generating different climatic conditions for vegetation growth.

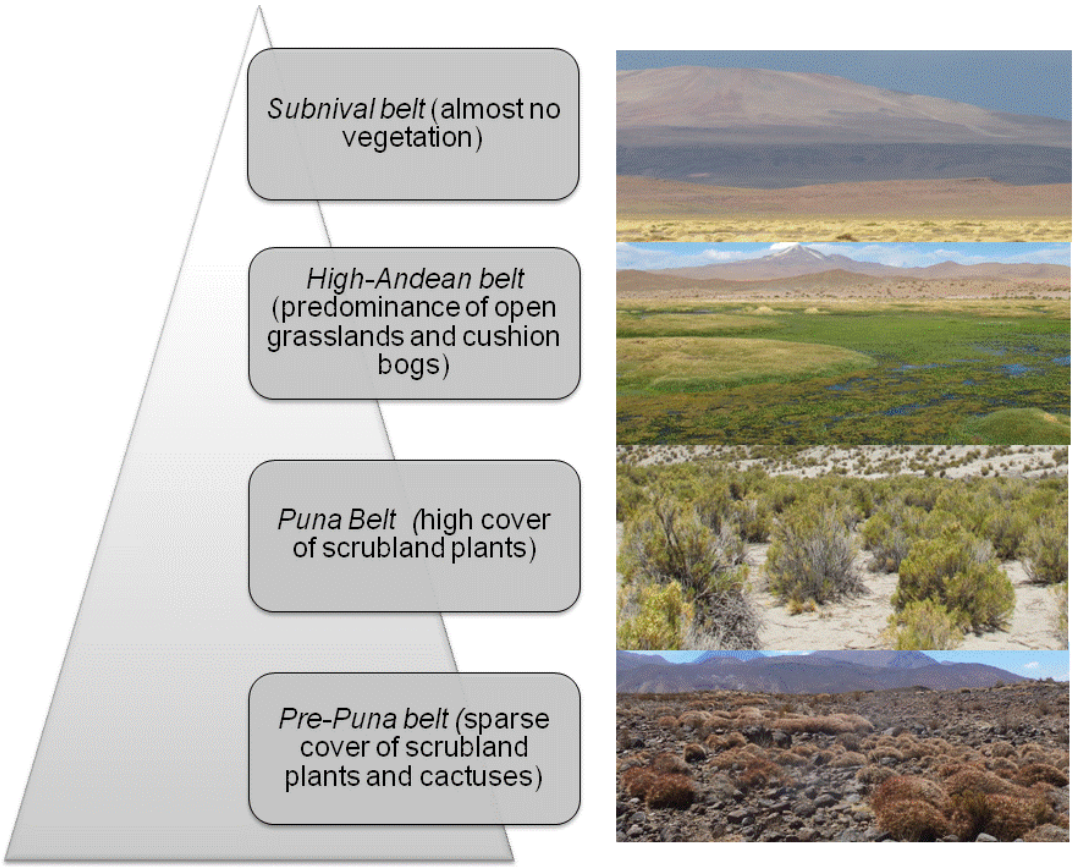

Figure 2.3. Vegetation belts present in the Dry Puna (from Villagrán et al. 1981, Arroyo et al. 1988, Marquet et al. 1998).

For vegetation belts are present in the study area (Figure 2.3): the Prepuneño or Pre-Puna (with low scrubland plants and cacti), the Puneño or Puna (a large extension of scrubland plants known as tolares), the Altoandino or High Andean (predominantly comprised of large open grasslands and localized cushion bogs) and the Subnival (almost devoid of vegetation) (Villagran et al. 1981, Arroyo et al. 1988, Marquet et al. 1998). The scrubland includes xerophilous shrubs such as *Parastrephia quadrangualris*, *Fabiana denudate* and *Chuquiraga atacamensis*, the grassy steppes consist predominantly of *Festuca chryssophyla* and *Stipa frigida* (Villagrán et al. 1981, Villagrán et al. 1982, Villagran et al. 1983, Gutierrez et al. 1998). The cushion bogs and riparian vegetation include *Distichia muscoides*, *Plantago rigida*, *Azorella compacta* and *Werneria aretioides* (Marquet et al.

1998, Luebert and Pliscoff 2006). Within this wetland vegetation, a typical Puna vegetation type are 'bofedales', cushion plant peatlands associated with high water tables, with *Oxychloe andina* and *Patosia clandestina* as the most common species (Squeo et al. 2006). Arroyo and Cavieres (2013) postulate that the physical delimitation of the Puna is the most difficult of all high Andes ecosystems, and there are no published figure for the complete vascular flora of the area.

The systems of wetlands concentrate water, a scarce resource in this ecosystem, and sustaine the highest primary productivity in the area. Arroyo et al. (1998) and others have shown high dependence of cushion bogs and riparian vegetation on fresh-water distribution. Most animals, including the camelids vicuña (*Vicugna vicugna*) (Figure 2.4) and guanaco (*Lama guanicoe*) strongly depend on wetland vegetation (Messerli et al. 1997, Villagrán and Castro 1997, Squeo et al. 2006). These wetlands are also key habitats for waterbirds and rodents, and they provide pasture for domestic herbivores, enabling limited human settlement (Villagrán and Castro 1997). Limited vegetation growth and the plants' adaptations to the harsh climate, reduce the number of plants available as food in the Dry Puna, and their palatability for micro-mammals (Cortes et al. 2002, Tirado et al. 2012). There is important bird diversity associated to wetlands, both of terrestrial and aquatic species, including three flamingo species (*Phoenicopterus chilensis, Phoenicoparrus andinus, and Phoenicoparrus jamesi)* (Caziani and Derlindati 2000, Valqui et al. 2000, Caziani et al. 2007), horned coot (*Fulica cornuta*), Puna teal (*Anas puna*), Andean gull (*Larus serranus*) and suri (*Pterocnemia pennata*) (Caziani et al. 2001). Comparatively, less is known about the populations of carnivores, including the Andean cat (*Leopardus jacobita*), a mountain endemic and specialized predator of southern mountain viscacha (*Lagidium viscacia*) (Figure 2.4), Pampas cat (*Leopardus colocolo*), culpeo fox (*Lycalopex culpaeus*) and puma (*Puma concolor*) (Walker et al. 2007, Lucherini et al. 2009, Reppucci et al. 2011).

Figure 2.4. Vicuñas (top) and southern mountain viscacha (bottom) in the Dry Puna.

The Dry Puna is of particular conservation concern due to its high level of floral and faunal endemisms. Species have developed remarkable adaptations for survival to the extreme temperatures, dryness and altitude (Messerli et al. 1997, Olson et al. 2001). Animal adaptations in the Puna, include adaptations to altitude, such as high blood oxygen affinities in chinchillas (*Chinchilla brevicaudata*) (Ostojic et al. 2002), highly efficiency of digestion of vicuñas to consume the fibrous and ligneous Puna vegetation (Sponheimer et al. 2003, Borgnia et al. 2010) and the remarkably diurnal activity and basking behaviour in Andean toads (*Bufo spinulosus*) to cope with low temperatures (Lambrinos and Kleier 2003).

In the triple frontier between Argetina, Chile and Bolivia, the network of protected areas includes 9,141km^2 of High Andean habitats. There are one National Reserve and two RAMSAR sites in Chile, a National Reserve and a RAMSAR site in Bolivia, and a RAMSAR site in Argentina - part of the Regional Reserve Las Chinchillas but which has not yet implemented (Figure 2.5). In Chile, the Flamencos National Reserve consists of seven sectors, three of which are located in the triple frontier region: Tara and Aguas Calientes (367km^2), and Pujsa (57km^2). The Flamencos National Reserve was created in 1990, and Tara was incorporated as a RAMSAR site in 1995 (CONAF 2008). In Bolivia, the Eduardo Avaroa National Reserve was created in 1973 and expanded in 1981; since 2009 it is also part of Los Lipez RAMSAR site, which extends over an area of 7,147km^2 (SaviaGlobal 2006). Lastly, Lagunas de Vilama in Argentina was appointed a RAMSAR site in 2000 covering 1,570km^2.

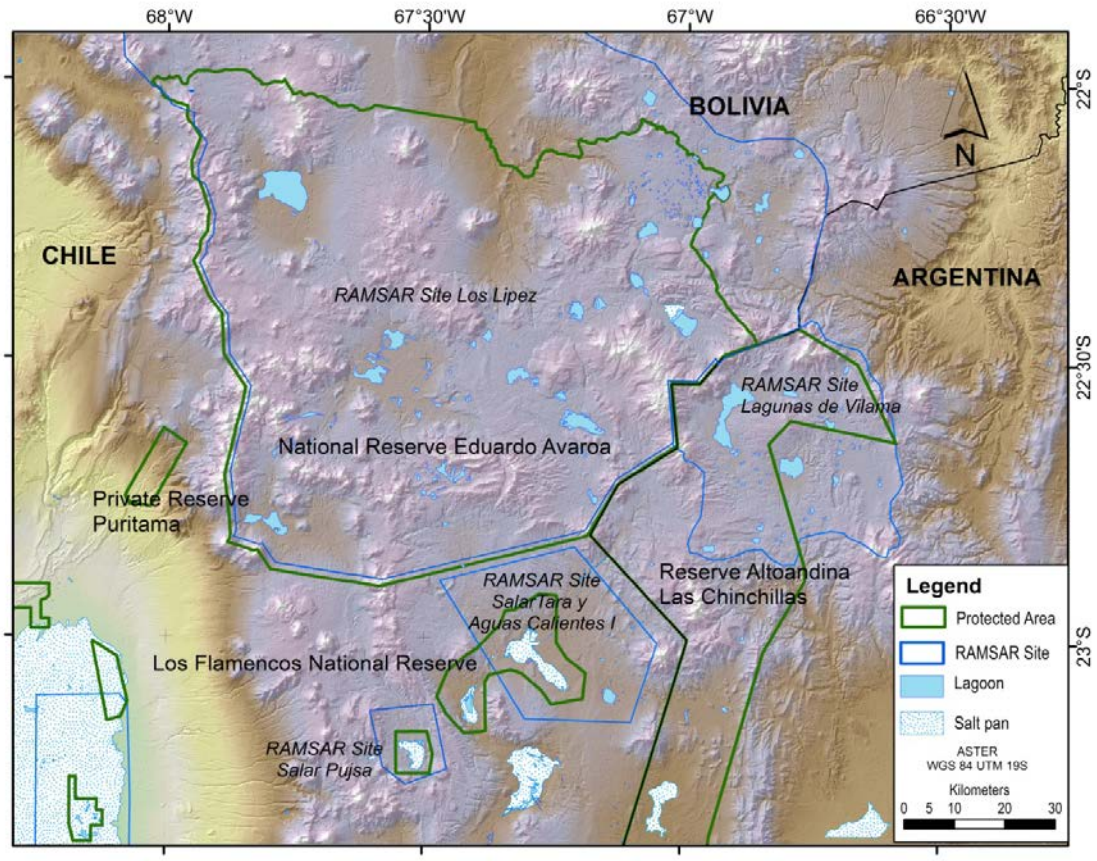

Figure 2.5. Location of protected areas in the triple frontier of Argentina, Bolivia and Chile.

It is inherently difficult to study the effects of anthropogenic disturbances on High Andean biodiversity. Although the study area has a low population density, it has been inhabited

for over 1,000 years by cultures restricted primarily to raise llamas (*Lamas glama*) in wetlands and steppes (Schiappacasse et al. 1989). The Dry Puna natural vegetation has been affected by camelid grazing and firewood collection for centuries (Figure 2.6), but currently llamas are kept mostly for own consumption, and for fiber and wool production (SaviaGlobal 2006, Clark 2012). In some localized areas, intense grazing by llamas and sheep have degraded the vegetation (SaviaGlobal 2006), and the extraction of *Polylepis tarapacana* and *Azorella compacta* for burning has decimated these species (Olson et al. 2001, WWF 2015). Another potential human impact on this ecosystem is water extraction for mining and for human settlements in the lowlands, although the scale and severity of this impact is poorly known.

Figure 2.6. Herd of llamas in Quetena, Eduardo Avaroa National Reserve, Bolivia.

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Chapter 3:

Climate complexity in the Central Andes: a study case on empirically-based local variations in the Dry Puna

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Abstract

Mountain ecosystems are thought to be especially sensitive to climate change, but empirical evidence is scarce as there are only few and scattered meteorological records that exist from high elevations. As a result, predicting climatic patterns and trends in mountains is a challenge. We analysed temperature and precipitation data to assess and understand local variation in the highland climate of the driest region of the Andes, which is located at the confluence of circulation systems and influenced by drastic topographic changes, including the barrier effect of the Andes. Records from 28 weather stations, located above 2,300m in the Central Andean Dry Puna in Bolivia and Chile, revealed no general statistical trends between 1980 and 2010, and high variability across localities. Warming was evident at 2,300m towards the Atacama Desert, and again in the plateau above 4,000m. The precipitation, concentrated during the summer months, revealed increasing trends only in the north-eastern portion of the study area, which is under humid tropical influence from the Amazon basin. The effect of ENSO was most evident along the western slopes of the Andes, reflecting influence of the Pacific and the barrier effect of the Andes. While meteorological data from high elevations are limited to a few stations and incomplete time series, they provide valuable empirical evidence of climatic variability in the Central Andean Dry Puna, which can be contrasted against current climatic surfaces. Such comparisons reveal that local-scale variations in mountain climates are not reflected in interpolated global data sets at coarser spatial scales.

3. 1. Introduction

Globally, climate change is causing an overall increase in temperature, changes in the quantity and variability of precipitation, and a general increase in the occurrence of extreme events such as heat waves, droughts and floods (IPCC 2014). However, climate change expresses itself differently in different regions of the world and in mountain areas in particular, more climatic information at the local scale is needed to improve our understanding and capacity to predict the direction and consistency of climate change.

Critically, mountain ecosystems are considered to be highly sensitive to warming and changes in precipitation (Diaz et al. 2003, La Sorte and Jetz 2010), including the Tropical Andes where glaciers have been retreating during the last 50 years (Rabatel et al. 2013, Vuille et al. 2008). Here, using meteorological station data, Vuille and Bradley (2000) showed an increasing trend of 0.33ºC/decade between 1975 and 2000, while Vuille et al. (2003) showed an increasing rate of 0.15ºC/decade for 1950-1994 and obtained a similar warming trend with the ECHAM4 model and the CRU05 dataset. More restricted studies in the Central Andes, such as Seiler et al. (2013), analysed data for 1965-2004 showing an increasing trend in temperature greater than 0.1ºC/decade in the Bolivian Andes, and Falvey and Garreaud (2009) suggested a warming trend of 0.25ºC/decade for the Andes in the north of Chile. Trends in precipitation are unclear; while Vuille et al. (2003) found no overall trend between 1950 and 1994, Seiler et al. (2013) found areas with decreasing and increasing rainfall trends in summer between 1985-2004 in the south of the Bolivian High Plateau.

Models of future climate change in the Tropical Andes predict higher temperatures than today (Bradley et al. 2004, Bradley et al. 2006). At finer scales, a Regional Climatic Model for 2071 to 2100, also predicts warming, especially at higher elevations (Urrutia and Vuille 2009). Increasing temperatures could seriously affect mountain ecosystems through snow melting and evaporation rates, which will in turn alter water availability in the area. Projections in precipitation are associated with larger uncertainties than those for temperature changes. Some precipitation projection models suggest slight increments in summer rainfall for the Central Andes Dry Puna (Seth et al. 2010, Thibeault et al. 2010) while others predict a decrease in precipitation by the end of this century (Minvielle and Garreaud 2011, Urrutia and Vuille 2009).

While some efforts have been devoted to study climate trends and predict climate change in the Tropical Andes under future scenarios, rather less attention has been paid to measure and understand current climatic variability in the Central Andean Dry Puna, although the impacts upon ecosystems can be more critical in this area, as the general tendency for dry areas is to get drier as the Earth warms up (IPCC 2014). Also, there is almost no validation of climatic extrapolations of global climate surfaces in this area. The only exception is the work of Vuille et al. (2003), who used the CRU05 to make their validation analysis for the whole Tropical Andes. One of the reasons for this is the scarcity of weather stations at high altitudes, not only here but worldwide.

The south of the Central Andean Dry Puna of Bolivia and Chile (Olson et al. 2001) is one of the driest areas of the Andes and includes part of the second highest plateau in the world. This is a key location to study climatic variability because the area sits in a transition zone between tropical and extra-tropical atmospheric circulation and precipitation patterns (Messerli et al. 1997) and it experiences a strong elevation gradient over a short distance, from the Atacama Desert at 2,000m to the top of the Western Plateau in Bolivia at over 5,000m and with the Andes acting as a major climatic barrier. Due to convergence of large-scale climatic systems and more localized effects of the topography, we expected complex patterns of climate variation in the study area. Rainfall in the area is mainly restricted to the austral summer, between December to March, in the form of intense convective precipitation (Garreaud et al. 2003). This summer convection is mainly driven by: 1) the intensity and location of the Bolivian High (an upper-level high pressure cell formed by the heating liberated by the convection in the Amazonas basin) 2) the emergence of upper level easterly winds over the Central Andes, bringing moisture from the Amazon and Chaco, and 3) surface heating which destabilizes the local troposphere (Garreaud et al. 2003, Vuille and Keimig 2004, Garreaud et al. 2009). The near-complete absence of rain during the rest of the year is due to the dry influence of the mid-level westerly flow from the Pacific Ocean (Garreaud et al. 2003, Vuille and Ammann 1997), produced by synergistic interactions between subsiding dry air masses associated to the South Pacific anticyclone and the cold Humboldt current (Vuille and Baumgartner 1993, Vuille and Ammann 1997). Large-scale phenomena caused by ocean-atmosphere interactions such as El Niño Southern Oscillation (ENSO) and the Pacifical Decadal Oscillation (PDO), also affect temperature and precipitation in the Andes (Vuille et al. 2000, Garreaud and Aceituno 2007). Finally, although it has been suggested that mountain

regions are warming faster than the lowlands surrounding them, there is no general agreement on how rates of warming change with elevation in the Tropical Andes (Rangwala and Miller 2012). Some studies indicate that higher areas are getting warmer (Diaz and Bradley 1997), while others have found the opposite effect (Vuille and Bradley 2000) or no altitude dependency as Vuille et al. (2003) suggested.

In this study we explored the complexity of climatic behaviours in an arid region of the Central Andes, considering spatial and temporal patterns of variation in temperature and precipitation across 28 weather stations between 1980 and 2010. Our study combines records from weather stations located between 2,300 and 4,400m, including two stations located in the limits of the Atacama Desert, which have already been used to extrapolate information to the Andes. We analysed time series records in relationship to local topography and atmospheric circulation systems such as the Southern Oscillation and compared our results against global current climatic surfaces.

3.2. Methods

3.2.1. Temperature and precipitation data

We collected records of monthly mean temperature and precipitation from 50 weather stations located above 2,200 m provided by the Dirección General de Aguas of Chile (DGA), Dirección Meteorológica of Chile (DCM) and Servicio Nacional de Meteorología e Hidrología of Bolivia (SENAMHI). These stations are part of the national weather database in each country (Figure 3.1).

Our analyses were restricted to the period 1980- 2010 to avoid the climatic shift documented between the cold (negative) and warm (positive) phases of the PDO between 1975 to 1977 in the Pacific Ocean (Giese et al. 2002), which caused abrupt warming in Chile, because this event is bound to affect trend estimation (Bown and Rivera 2007).

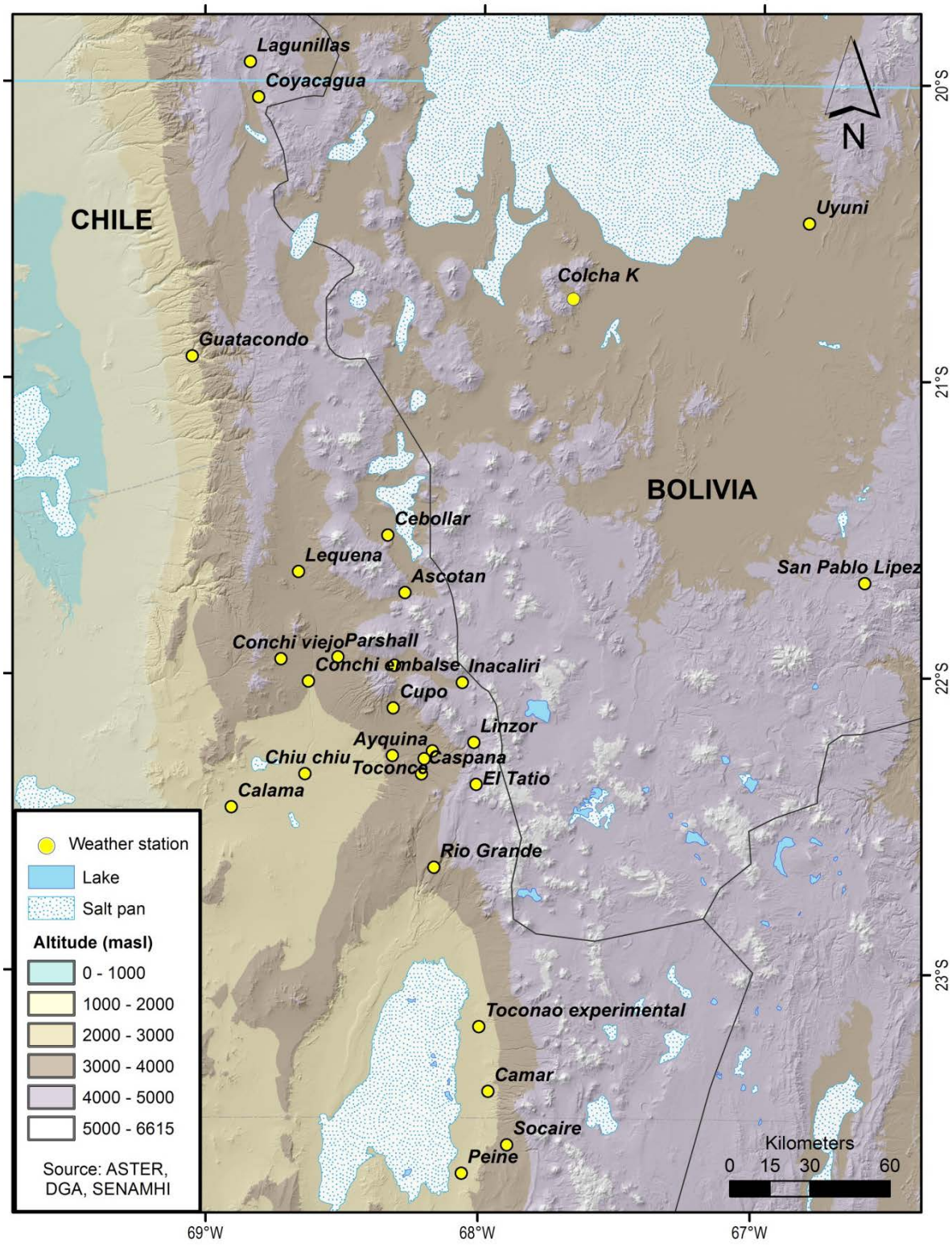

Figure 3.1. Location of selected weather stations in the Central Andean Dry Puna of Chile and Bolivia.

We compiled series of monthly means for temperature and rainfall, keeping only the months with more than twenty days of rainfall or temperature data. These thresholds were

below the standards of the Expert Team of Climate Change Detection and Indices (ETCCDI), but represent a pragmatic compromise between the need to include as many stations as possible and ability to calculate accurate estimates of monthly means.

We averaged monthly values to obtain annual and seasonal time series, as follows:

- ***Summer temperature:*** mean temperature of December, January and February
- ***Winter temperature***: mean temperature of June, July and August
- ***Annual temperature***: mean temperature from January to December
- ***Summer rainfall***: amount of rainfall in mm between December and March, period during which rainfall is concentrated (Garreaud et al. 2003); Figure 3.7.

Our selection criteria meant eleven temperature time series and 26 precipitation time series were available for analyses. The weather stations analysed had at least 19 years of seasonal temperatures, 15 years of annual temperatures and 21 years of rainfall data. When data on temperature or rainfall were missing for one season or year, these were excluded from the analysis and ignored for trend estimations. The weather stations were located between 2,289 m and 4,348m; 23 stations in the Antofagasta Region, two in the Tarapaca Region of Chile, and three stations from Potosí Department, Bolivia (Figure 3.1). Details on the location of meteorological stations, coordinates, missing data and data sources are presented in Table 3.1.

Detailed station metadata were unavailable, and the possibility of checking data errors against neighbouring weather stations was very limited. Thus we used a Homogeneity test to explore if variability in the dataset could be caused by unrelated factors such as instrument errors. We used the software RHtests V3 (http://cccma.seos.uvic.ca/cgi-bin/etccdi/main_programs/download_RHtest?a=RHtestsV3.r) to detect and adjust change points in the time series (Caesar et al. 2011). For this purpose, we log-transformed precipitation data (Wang and Feng 2010) and zeros were changed to 0.00001. Time series data were homogenized by the quantile-matching (QM) adjustment (Wang 2008, Wang et al. 2010). Non-significant change points were identified. A number of change points that were not statistically significant were identified in temperature time series (i.e., in Coyacagua, Lagunilla, Caspana, Linzor, Conchi embalse, Calama and Uyuni) and precipitation (i.e., Ascotan, Camar, Caspana and Lipez), so no adjustments were made, and we assumed all time-series to be homogenous.

Climatic variable	Station	Latitude UTM N	Longitude UTM E	Elevation (m)	Data availability (years)		
					Summer	Winter	Annual
Temperature	Linzor	7541022	600525	4,100	23	25	20
	Lagunillas	7795488	516877	4,020	19	23	15
	Coyacagua	7782237	519943	4,013	21	23	15
	ColchaK	7706413	639694	3,700	23	23	20
	Uyuni	7734766	726204	3,669	29	29	24
	Parshall	7573030	549639	3,318	28	29	23
	Caspana	7529298	580938	3,260	21	25	17
	Conchi embalse	7563959	538601	3,010	26	26	24
	Chiu chiu	7529341	537228	2,524	28	28	27
	Peine	7380025	595828	2,460	25	22	21
	Calama DCM	7513670	510287	2,293	28	30	27
Rainfall	Tatio	7525364	601396	4,370	25		
	San Pablo Lipez	7600349	746891	4,230	29		
	Linzor	7541022	600525	4,100	26		
	Inacaliri	7563405	596197	4,040	30		
	Ascotan	7597006	574737	3,970	26		
	Ojos San Pedro	7569874	570766	3,800	29		
	Cebollar	7618527	568307	3,730	21		
	ColchaK	7706413	639694	3,700	23		
	Uyuni	7734766	726204	3,669	30		
	Conchi viejo	7572283	528324	3,491	25		
	Cupo	7553917	570293	3,370	27		
	Lequena	7604891	534878	3,320	31		
	Parshall	7573030	549639	3,318	31		
	Toconce	7537855	584990	3,310	30		
	Caspana	7529298	580938	3,260	26		
	Socaire	7390668	612822	3,251	28		
	Rio Grande	7494340	585521	3,250	30		
	Salado embalse	7534950	581941	3,200	27		
	Ayquina	7536146	570041	3,031	29		
	Conchi embalse	7563959	538601	3,010	28		
	Camar	7410651	605765	2,700	31		
	Chiu chiu	7529341	537228	2,524	29		
	Toconao experim	7434788	602384	2,500	26		
	Guatacondo	7685507	495076	2,460	30		
	Peine	7380025	595828	2,460	30		
	Calama DGA	7517023	509645	2,300	26		

Table 3.1.Weather stations used for this study with their geographical location, data and sources.

3.2.2. Data analyses

ANOVA and Kruskal-Wallis analyses were performed to examine relationships between temperature, rainfall, and El Niño Southern Oscillation (ENSO) in the whole area. We obtained ENSO time series from Multivariate ENSO Index (MEI) Earth System Research Laboratory, http://www.esrl.noaa.gov/psd/enso/mei/#data, NOAA (Wolter and Timlin 2011). We considered a categorical classification of El Niño and La Niña years for ANOVA analyses (MEI rank http://www.esrl.noaa.gov/psd/enso/mei/rank.html), where MEI ranks from 1 to 19 for La Niña and 46 to 65 denote El Niño conditions. We averaged ENSO for the appropriate season or year. Because of the high climatic variability across stations, we also analysed the relationship between these teleconnection patterns at a local scale. For this we performed Pearson's correlations between ENSO and the seasonal temperature, annual temperature and summer precipitation time series at each weather station.

We used Mann-Kendall tests to assess trends and account for non-linearity and non-normality in precipitation data series. This nonparametric method is regularly used to detect trends in meteorological data (Yang et al. 2012, Jiang et al. 2013), because it is less influenced by outliers (Zhang et al. 2010, Caesar et al. 2011). The slope of the trend was calculated using Sen's slope estimates (Sen 1968) and also we used linear regressions to analyse temperature time series which allowed us to compare the results with other studies in the Andes. A significance level of $\alpha = 0.05$ was applied for all trends.

To explore geographic variations of trends, we compared Sen's slopes across latitude, longitude and elevation gradients (derived from a Digital Elevation Model, SRTM (Rabus et al. 2003) using linear models. Models were compared using Akaike criteria to select the model and explanatory variables that best explained the obtained trends (Burnham and Anderson 2002). We used R software for all analyses (R Development Core Team), including Kendall and RKT packages for Mann Kendall analyses (McLeod 2011, Marchetto 2012) and Pgirmess package for Kruskal-Wallis tests. For spatial analysis we used ArcGIS 10, Spatial Analyst extension (ESRI 2011).

To compare these empirical data with current climatic surfaces, we extracted monthly precipitation and mean temperature for each station from highest spatial resolution (30 arc second), freely distributed climate surfaces available at www.globalclimatedata.org (Mosier et al. 2013). These global surfaces were generated using a Delta downscaling

method based on long-term temporal coverage of the Climate Research Unit (CRU), Willmott & Matsuura (W&M), Global Precipitation Climatology Centre (GPCC) and WorldClim datasets (Hijmans et al. 2005). The Delta downscaled data used in this research was produced using the W&M time-series inputs, as these data performed better than the CRU grid (Mosier et al. 2013). We used the unmodified Delta downscaled data (Org) and a Delta downscaled data that has undergone a post-processing bias correction step (Bias) (as described at http://globalclimatedata.org/methods). The monthly precipitation and mean temperature values extracted were averaged across each season and each year to assess trends by Mann Kendall test. Pearson's correlations were developed to analyse the relationship between these time series.

3.3. Results

3.3.1. Temperature

Mean monthly temperature was variable across stations. The warmest summer was in 1986 in Peine, Chile (average 21.6°C), including hottest month (22.3°C in January 1986). The coldest winter was registered in Lagunillas, Chile in 2008 (-3.5°C) and the coldest month was in Uyuni, Bolivia, in July 1981 (-4.1°C).

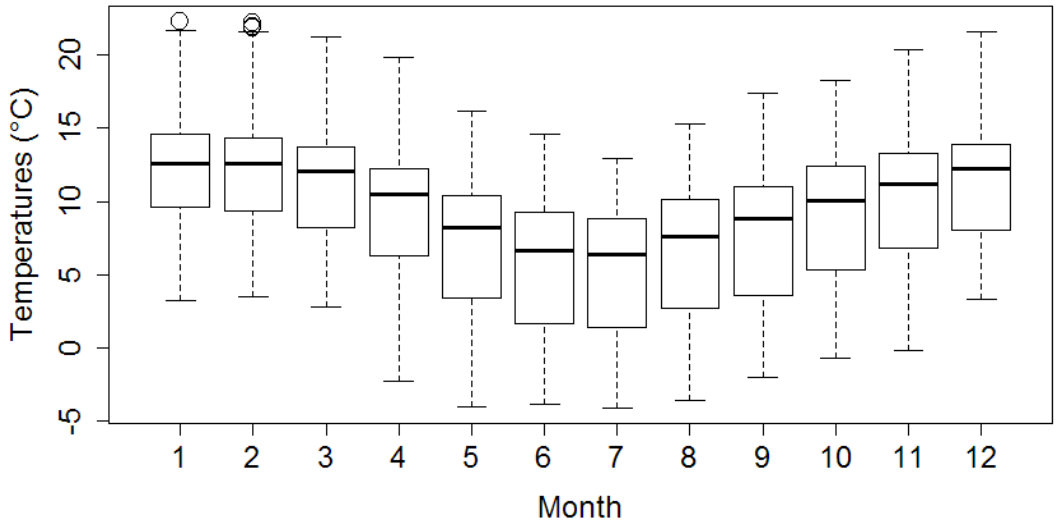

Figure 3.2. Monthly temperature between 1980 and 2010 in the Central Andean Dry Puna. The boxes represent the upper and lower quartiles, and the whiskers are 1.5 times the size of the boxes; the dots are outliers outside this threshold.

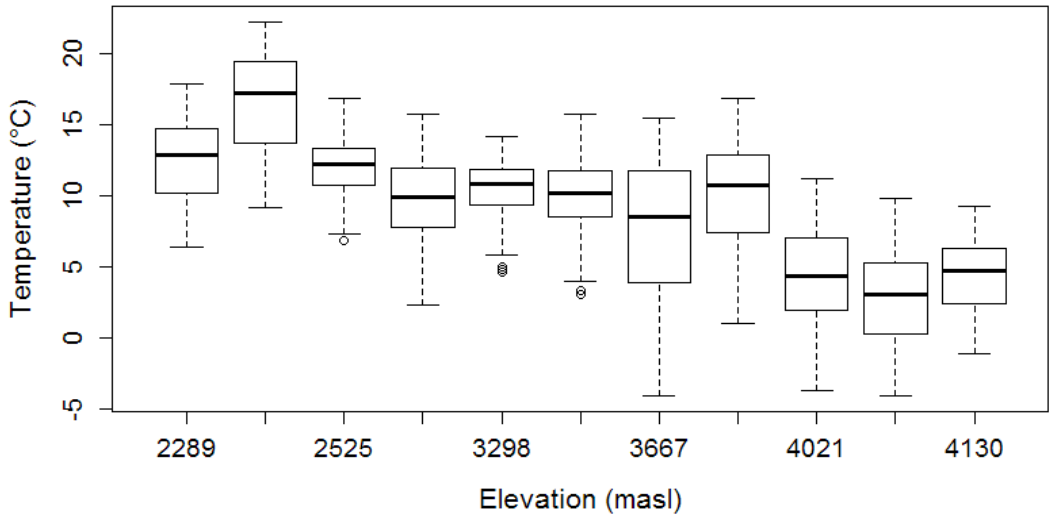

Figure 3.3. Mean temperature in each station at different elevations in the Central Andean Dry Puna of Chile and Bolivia between 1980 and 2010. The boxes represent the upper and lower quartiles, and the whiskers are 1.5 times the size of the boxes; the dots are outliers outside this threshold.

Monthly mean temperature decreased with increasing altitude of the weather station, at a rate of -0.5°C per 100m (SD 0.00009°C) (linear model, F(1,3574): 3295, p<0.0, R-sq: 0.48) (Figure 3.3). Furthermore, the best linear model showed a cooling trend to western areas and to the north as well as at increasing altitudes (monthly average was 4°C in the northernmost station and 16°C in the southern extreme (linear model, F(3,3572): 1442, p<0.0, R-sq: 0.54).

Monthly temperatures were also significantly affected by ENSO (linear model, F(2,3573): 5.937, p<0.003, R-sq: 0.003). Temperatures were significantly higher during El Niño than during La Niña years (Tukey's test p<0.044, CI 0.01 and 1.08) or normal years (Tukey's test p<0.003, CI -0.987 and -0.158) (Figure 3.4a). ENSO was positively correlated with temperature (seasonal or annual) in four weather stations located on the western slopes (Table 3.2), especially during summer.

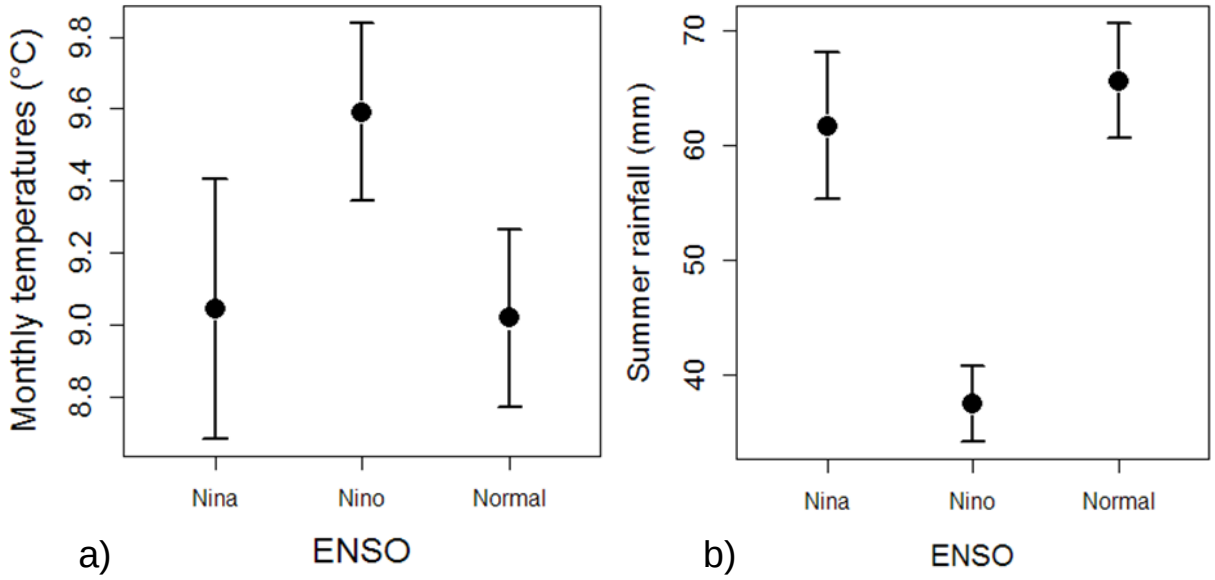

Figure 3.4. a) Mean temperature and b) summer rainfall during ENSO phases in the Central Andean Dry Puna of Chile and Bolivia between 1980 and 2010.

Weather station	Summer	Winter	Annual
Coyacagua	0.078	0.096	-0.087
Lagunillas	0.089	0.267	0.318
Parshall	**0.689**	**0.474**	**0.546**
Conchi embalse	**0.613**	**0.482**	**0.556**
Chiuchiu	**0.61**	**0.533**	**0.622**
Linzor	0.01	0.183	-0.009
Caspana	0.305	0.268	0.328
Peine	0.311	-0.001	0.118
Calama	**0.678**	**0.538**	**0.415**
ColchaK	0.223	-0.037	0.007
Uyuni	0.221	0.164	0.297

Table 3.2. Estimated Pearson's correlations between temperatures series and ENSO (MEI= Multivariate El Niño–Southern Oscillation Index). Bold values indicate significant correlation at the 5% level.

Long-term trends in temperature were not consistent (Figure 3.5a and Table 3). Warming was significant across four weather stations, both in terms of annual, summer and winter

indices (3, 2 and 3 stations respectively). Meanwhile a cooling trend was observed in three stations (2 in annual and summer and 3 in winter).

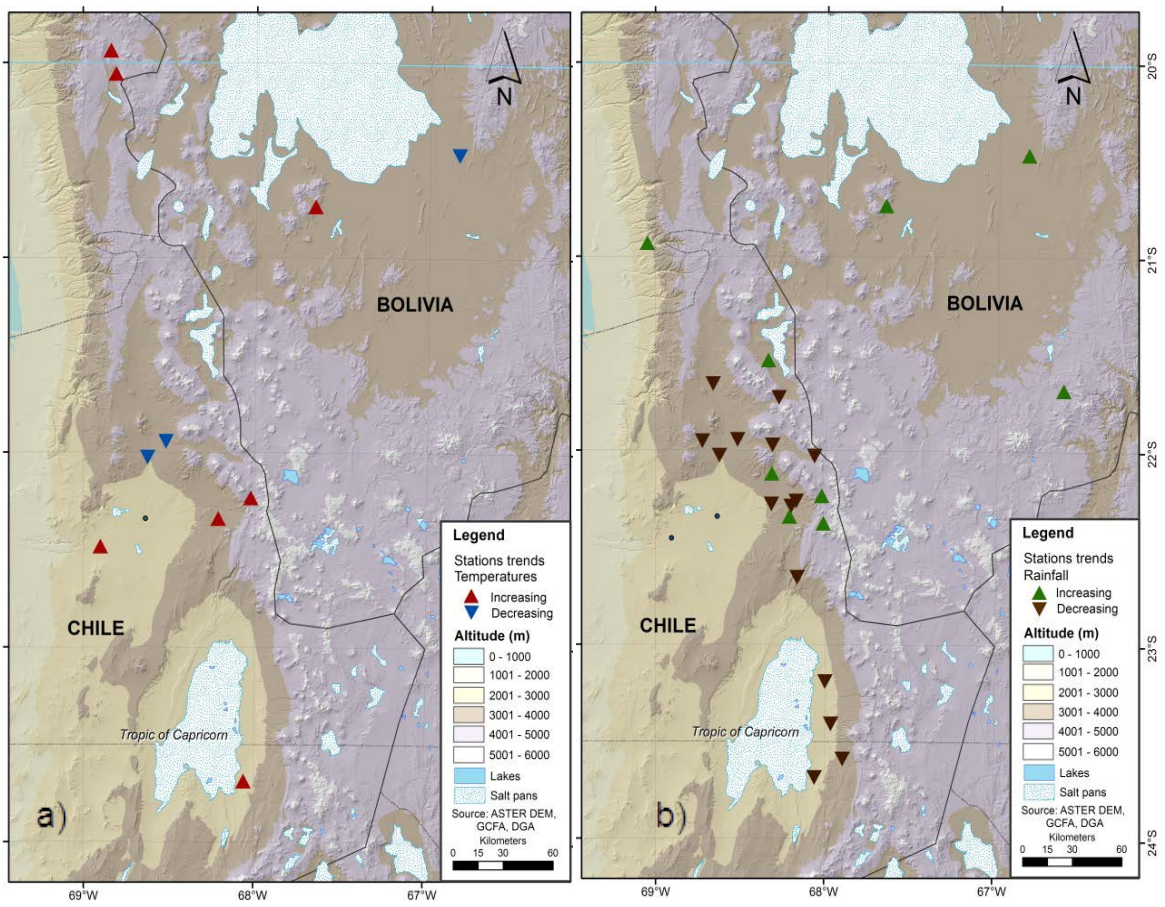

Figure 3.5. Summer trends in a) temperatures and b) rainfall in the Central Andean Dry Puna of Chile and Bolivia between 1980 and 2010.

When we examined just those weather stations with the most complete data and significant trends: Calama (2,300m) and Linzor (4,100m); both showed warming at an annual, summer and winter basis, whereas Conchi Embalse (3,010m) showed cooling in both annual and seasonal measures.

The results of Mann Kendall tests and linear regressions were highly consistent in their levels of significance, magnitude of trends (with the exception of the summer temperature series from Conchi Embalse) and their direction (with the exception of annual temperature at Uyuni station).

Estimated trends in temperature for individual stations during the period 1980 to 2010 (Mann Kendall test)

	Annual temperature		Summer temperature		Winter temperature	
Weather stations	Sen's slope	p-value	Sen's slope	p-value	Sen's slope	p-value
Coyacagua	0.026	0.092	0.028	0.116	**0.067**	0.012
Lagunillas	-0.038	0.067	0.045	0.05	**-0.086**	0.005
Parshall	**-0.059**	0.032	**-0.048**	0.021	**-0.087**	0.004
Conchi Embalse	**-0.043**	0.021	**-0.08**	0.008	**-0.048**	0.014
Chiuchiu	-0.024	0.139	0	1	-0.025	0.206
Linzor	**0.05**	0.003	0.013	0.383	**0.083**	0.002
Caspana	0.035	0.174	0.012	0.526	-0.001	1
Peine	0.002	0.928	0.026	0.262	0.014	0.535
Calama	**0.021**	0.019	**0.029**	0.004	0.023	0.143
ColchaK	**0.122**	0.002	**0.157**	0.001	**0.113**	0.015
Uyuni	-0.001	0.96	-0.005	0.836	0.02	0.536

Table 3.3. Estimated trends by Mann Kendall test analysis for annual, summer and winter temperatures for individual stations during the period 1980 to 2010. Bold values indicate significance at 0.05 level.

Geographically, weather stations fell into two groups regarding rates of change: warming in the lower-lying stations (below 3,000m) decreased with altitude, and the opposite pattern was revealed across stations above 3,000m - with the exception of Lagunillas (Figure 3.6). Linear models, however, failed to detect a significant effect. Patterns were more evident within the group of high weather stations (above 3,000m) (Figure 3.1). With the exception of the eastern-most station of Uyuni, warming in summer temperatures increased towards the north (β = 5.264e-07, $p < 0.019$) and east (β = 1.436e-06, $p < 0.009$) (best model F(3, 3): 21.98, $p<0.015$, R-sq: 0.913). Annual averages showed similar effects but this was only significant for longitude ($p < 0.012$) (best model F (2, 4): 9.555, $p < 0.03$, R-sq: 0.74) not latitude.

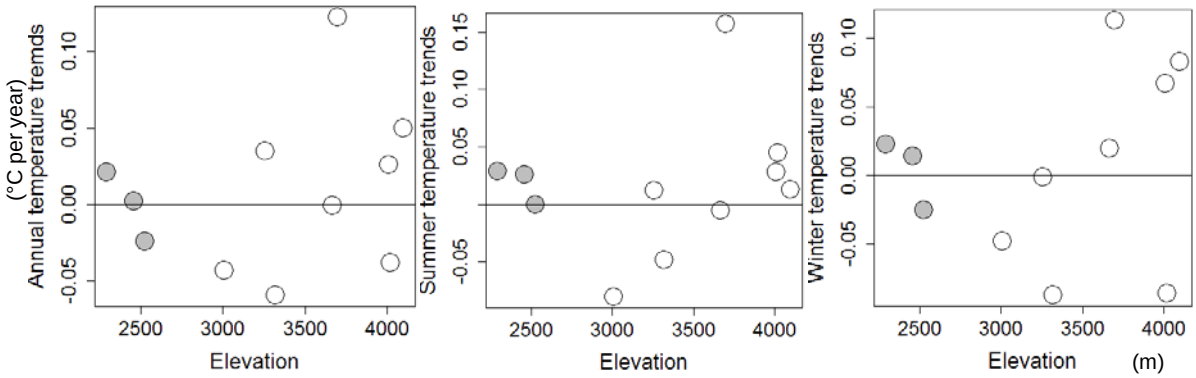

Figure 3.6. Relationship between elevation (m) and trends in summer, winter and annual temperature (°C per year), for 11 weather stations in Central Andean Dry Puna of Chile and Bolivia between 1980 and 2010 (grey circles are stations located lower than 3,000m).

According to both climatic surfaces available (i.e., Unmodified and bias Delta-downscaled data), warming is occurring across all areas where weather stations are located, but trends were not significant for stations located in the northern (Lagunillas and Coyacagua) and eastern (Uyuni) limits of the study area (Table 3.4). Generally, correlations were stronger between stations and the unmodified surface than with the bias surface. Pearson correlations between all empirical measures of temperature and each of the climatic surfaces were high for two weather stations only (Calama and Colcha K), and for summer temperatures in Peine and winter temperatures in Linzor and Uyuni (Table 3.5).

Number of stations with positive and negative trends during 1980 to 2010
*(significant at the 0.05 level)

	Temperature (n=11)			Rainfall (n=26)
Stations data	Annual	Summer	Winter	Summer
Positive trend	6(3)	8(2)	6(3)	11(0)
Negative trend	5(2)	3(2)	5(3)	15(1)
Delta downscale data Org				
Positive trend	11(9)	11(8)	11(9)	25(5)
Negative trend	0	0	0	1(0)
Delta downscale data Bias				
Positive trend	11(8)	11(8)	11(7)	14(0)
Negative trend	0	0	0	12(0)

Table 3.4. Number of weather stations with positive and negative temperature and rainfall trends and their significance at 0.05 level, in the Central Andean Dry Puna of Chile and Bolivia.

Pearson's correlations between temperatures from weather station and the Delta downscale method

	Annual		Summer		Winter	
Stations	Org	Bias	Org	Bias	Org	Bias
Calama	0.54	0.56	0.62	0.63	0.42	0.41
ColchaK	0.80	0.67	0.85	0.68	0.64	0.63
Peine			0.46	0.46		
Linzor					0.45	
Uyuni					0.45	

Table 3.5. Significant Pearson's correlation at 0.05 level between temperatures from weather station and the Delta downscale method in the Central Andean Dry Puna of Chile and Bolivia.

3.3.2. Precipitation

Precipitation was highly variable during the year (Figure 3.7) and across stations. The driest station was Calama with 1.1mm per year and the wettest San Pablo de Lipez with 99.2mm per year (which also had the wettest month with 547.6 mm recorded in January 1997). Precipitation during the rainy season varied between 1.2 and 267.2mm (CV 0.45 to 2.09) (Figure 3.8) and increased with elevation at a rate of 6.6mm per 100m (linear model, F(1, 2942): 952.4, p<0.0, R-sq: 0.2443), with very little precipitation in weather stations below 3,000m (Figure 3.8). The best model that explained variability in summer rainfall (linear model, F(3, 2940): 550.5, p<0.0, R-sq: 0.359) indicated increasing rainfall towards the north and east, and at high elevations.

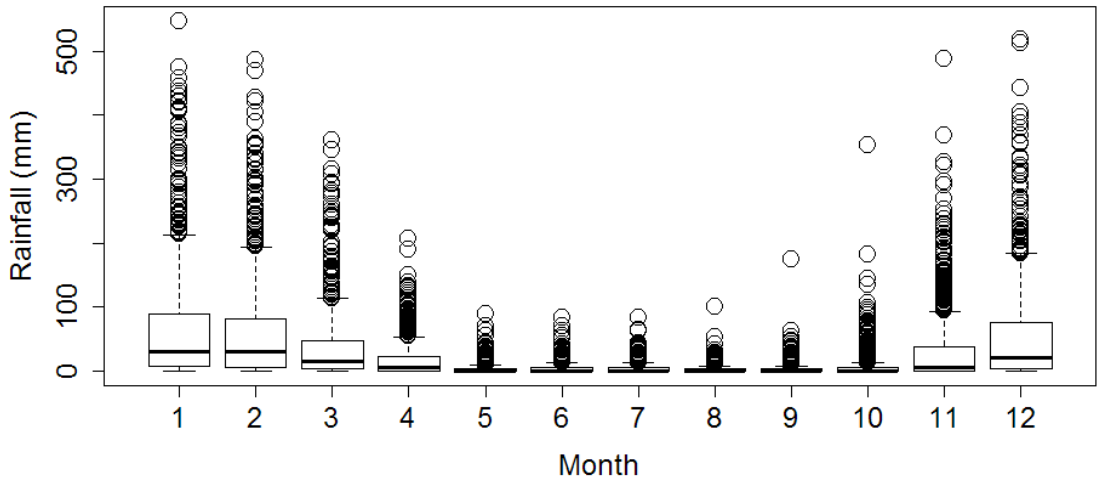

Figure 3.7. Monthly rainfall between 1980-2010 in the Dry Puna of Chile and Bolivia. The boxes represent the upper and lower quartiles, and the whiskers are 1.5 times the size of the boxes (dots are outliers located above this threshold).

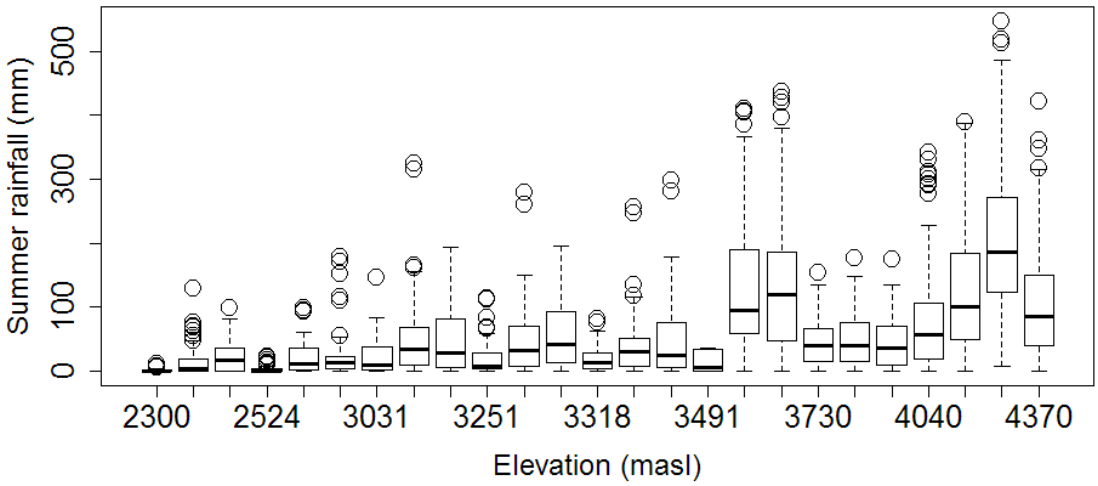

Figure 3.8. Mean summer rainfall in weather stations at different elevations in the Dry Puna of Chile and Bolivia between 1980-2010. The boxes represent the upper and lower quartiles, and the whiskers are 1.5 times the size of the boxes (dots are outliers located above this threshold).

Large-scale climatic phenomena determined significant differences in rainfall between El Niño and La Niña, and between La Niña and normal months, rainfall was significantly higher during La Niña months (Kruskal-Wallis chi-squared = 53.8533, df = 2, p-value < 2.023e-12). Also between El Niño and La Niña, and El Niño and normal, summer rainfall was significantly lower (Kruskal-Wallis chi-squared = 69.1576, df = 2, p-value < 0.0) (see Figure 3.4b). At a local scale, correlations showed negative associations between precipitation and ENSO, with the exception of Peine station. However, this relationship was statistically significant only for eight stations, all located in the western slopes of the Andes (Table 3.6).

Long-term trends in rainfall varied across the study area (Table 3.7 and Figure 3.5b). A declining trend was evident between 1980 and 2010 in 15 stations, although the trend was significantly negative at only site (Toconao experimental at 2,500m). Rainfall increased over the study period at the 11 other stations. Areas with decreasing rainfall are mainly located to the west and south of the study area, and areas with increasing precipitation to the north-east. Even when estimated trends in summer precipitation were aggregated across weather stations within these two geographic groups ("north-east", with increasing trend, and "south-west" with decreasing precipitation), trends were not significant (See Table 3.8).

The best linear model (F(2, 22): 6.301, p<0.007, R-sq: 0.3064) showed positive relationships between precipitation trends and longitude and latitude (increasing to the east and to the north) but not with elevation.

When compared to climatic surfaces, trends differed between the data from weather stations, the data from the unmodified climatic surface and the bias climatic surfaces, and also, between both climatic surfaces. In general, weather station data appeared to be more similar to the data obtained from bias surfaces. However, the number of significant trends from stations or from both climatic surfaces data was very low. The positive trends for unmodified surfaces were in the north and east (i.e., Cebollar, Ascotan, San Pablo Lipez, Uyuni y ColchaK stations). In contrast, the negative trend was located in the south (Socaire) close to the negative trend obtained from station data. No significant trends were obtained for bias surfaces, however, non-significant negative trends were also located to the west and south (Table 3.4).With reference to correlation between time series, only data from Uyuni station were positively correlated with the data obtained from bias climatic surface (cor 0.401, p-value = 0.028).

Summer precipitation and ENSO

Weather stations	MEI
Cebollar	**-0.443**
Ascotan	**-0.438**
Lequena	-0.274
Parshall	-0.307
Ojos San Pedro	-0.337
Inacaliri	**-0.388**
Conchiviejo	-0.122
Conchiembalse	-0.195
Chiuchiu	-0.174
Cupo	**-0.441**
Linzor	**-0.452**
Toconce	**-0.371**
Ayquina	-0.311
Salado embalse	**-0.402**
Tatio	-0.353
Guatacondo	-0.168
Camar	-0.33
Socaire	-0.262
Peine	0.004
RioGrande	**-0.393**
Caspana	-0.338
Toconao experimental	-0.167
Calama	-0.256
ColchaK	-0.133
Calama	-0.256
Uyuni	-0.291
San Pablo Lipez	-0.557

Table 3.6. Pearson's correlations coefficients obtained between summer precipitation and ENSO. Bold numbers indicate significant correlation at the 5% level

Estimated trends in summer precipitation between 1980 to 2010 (Mann Kendall test)

Weather stations	Sen's slope	p-value
Cebollar	0.7	0.53
Ascotan	-0.74	0.32
Lequena	-0.28	0.6
Parshall	-0.28	0.56
Ojos San Pedro	-1.37	0.22
Inacaliri	-0.47	0.75
Conchi viejo	-0.17	0.73
Conchi Embalse	-0.09	0.63
Chiuchiu	0	0.91
Cupo	0.08	0.88
Linzor	0.53	0.79
Toconce	-0.95	0.28
Ayquina	-0.34	0.41
Salado Embalse	-0.02	1
Tatio	1.38	0.62
Guatacondo	0.25	0.1
Camar	-0.44	0.2
Socaire	-0.9	0.07
Peine	-0.21	0.3
Rio Grande	-1.05	0.32
Caspana	0.19	0.86
Toconao experimental	**-1.08**	0.04
Calama	0	0.51
ColchaK	4.39	0.11
Uyuni	1.53	0.41
San Pablo de Lipez	1.01	0.75

Table 3.7. Mann Kendall test coefficients of the year effect upon summer rainfall. Bold values indicate trends significant at 0.05 level.

Weather stations	Sen's slope	p-value
North-east: *Guatacondo, Cebollar, Uyuni, San Pedro Lipez and ColchaK*	0.016	0.174
South-west: *Rio Grande, Toconao, Camar, Socaire and Peine*	-0.022	0.096

Table 3.8. Comparison of estimated trends in summer precipitation between 1980 and 2010 on aggregated weather stations (after standardizing the data). Mann Kendall test coefficients of year effect upon summer rainfall did not show any significant trends at P=0.05 level.

3.4. Discussion

Patterns of climatic variations in the Central Andean Dry Puna of Chile and Bolivia revealed a complex regional climate, which differed from the current climatic surfaces. The spatial patterns that emerged from our study contribute to understand the drivers of climatic variation in this arid region of the Central Andes, which is marked by a varied topography. The regional climate was determined by a cooling elevation effect combined with longitudinal and latitudinal effects. From the north east comes the humid influence from the tropics producing more rainfall, and from the south west, comes the influence of the subtropical subsidence of the Southern Pacific High, which mainly generates strong arid conditions of the Atacama Desert.

We found no common trends in precipitation or temperature records over three decades (1980 to 2010) across the study area. Warming was observed in the Atacama Desert and in the High plateau, but the opposite trend was evident along the western slopes of the Andes. There was a boundary effect at 3,000m, above which temperature trends increased with elevation. Below this elevation threshold, desert ecosystems at the lowest elevation showed increasing temperature trends. Previous studies have suggested warming trends across the area (Vuille and Bradley 2000, Vuille et al. 2003, Falvey and Garreaud 2009, Seiler et al. 2013). Seiler et al (2013) found an increasing trend in winter temperatures and a mix of cooling and warming areas for summer which is similar to the results obtained in our study. The warming trend described by Falvey and Garreaud (2009), of 0.25ºC/decade for the Andes in the north of Chile, considered only the Calama weather station at 2,300m (Falvey and Garreaud 2009), which our study found had different results compared to the other stations at higher altitudes. As expected from previous studies elsewhere in South America, temperatures in this region of the Andes are affected by ENSO, resulting in hot years, and especially summers, during El Niño events (Vuille and Bradley 2000, Seiler et al. 2013).

With regards to precipitation, rainfall during the rainy season has declined over the last three decades in most of the analysed stations which are located in the southwest, but trends were not significant. Our study shows a similar result to that of Vuille (2003), who presented two stations in the area with non-significant decreasing trends between 1950 and

1994, and Seiler et al. (2013), who mapped a decrease in summer rainfall trends for the Bolivian part of our study area.

Precipitation showed strong interannual variation, due to the influence of El Niño years. In most areas, trends in summer rainfall were positively related to longitude and latitude effects, although not significantly so. Precipitation trends tended to be positive to the east and north of the study area, suggesting long-term increments in rainfall due to the influence of the Amazon basin, which coincides with a study from north-west Argentina (Villalba et al. 1998) and one from Bolivia (Ronchail 1995). Moreover, our results are in concordance with studies that suggest there is strengthening of the tropical Hadley atmospheric circulation and increasing convergence in low troposphere and divergence in upper troposphere, which is making inner tropics wetter and outer tropics drier (Chen et al. 2002, Vuille et al. 2003, Vuille et al. 2008). The negative trend in rainfall towards the west and south of the study area is bound to strengthen the dry conditions associated to the 'Arid Diagonal' that crosses the Andes from the Atacama Desert towards Argentina. Furthermore, it will exaggerate the aridity of western flanks of the Andes between 24º – 25ºS, intensifying this biogeographical barrier for many plant and animal species (Arroyo et al., 1988, Chacón et al., 2012).

The empirical data analysed here reveal a somewhat different climate behaviour than the one observed in the climate surfaces of monthly precipitation and mean temperature obtained from Moiser et al. (2013). One possible explanation for this discrepancy is that the Global Historical Climatology Network (GHCN) database (Lawrimore et al. 2011), used to build W&M surfaces, includes only one weather station near the study area and all others are located at low altitudes. This means that monthly "data" over the Central Andean Dry Puna are being influenced by interpolation with stations outside of the region and at lower elevations. In addition, the elevation data obtained from the Worldclim dataset is of poor accuracy for high mountains (Hijmans et al. 2005). Our results are in concordance with previous studies that suggest the poor representation of mountain areas with spatially complex topography of climate variables on climate surfaces based on few altitude stations and with limited spatial resolution (Garreaud et al. 2009, Morales et al. 2012).

Our study illustrates several important caveats for the study of climate change in mountain regions. For instance, the extreme location and lack of metadata for the meteorological instruments may influence the accuracy of measurements. Although there are some

reservations about the quality of the data from weather stations at high altitudes, our empirical data coincide across several stations (e.g., in peaks of rainfall in 2001 in Tatio, Caspana, Salado Embalse, Ayquina, Toconce, Linzor, Cupo, Camar and Rio Grande). Secondly, low numbers, sparseness, and lack of metadata of stations may impact the effectiveness of homogeneity tests. Additionally, as other studies pointed out, in order to study synoptic climatology in mountain areas it is fundamental to understand local differences in climatic trends. Vuille (2011) argued that data obtained from stations in high altitudes are specific to the locality because of the complex topography of these areas and that their individual measurements might not directly represent the regional environment. According to Pepin and Lundquist (2008) the topography of each location in mountains areas may create several microclimates that could affect trends. However, we found that mountain peaks and hill slopes showed similar trends and magnitudes in their trends, in contrast with flat areas and engraved valley sites, which had high variation. Moreover, as the area is located between tropical and extra-tropical circulation and is affected by westerly and easterly influences, differences on windward and sheltered slopes may well also affect temperature and precipitation trends in our study site. The same applies for differences in the amount of radiation received, with northern slopes warmer than southern ones, and good data on cloud cover and snowfall would help to study changes in albedo, which may also affect temperatures (Pepin and Lundquist 2008, Rangwala and Miller 2012). Despite these caveats, this is the first study that analyzes all the stations in this dry area, and presents crucial information to understand the climate variability in the area.

Overall, we conclude on the basis of currently available data that temperature or rainfall trends are not consistent within the Dry Puna of Chile and Bolivia. On the other hand, factors associated with longitude and latitude aid our understanding of the spatial distribution of trends in precipitation and temperature. General warming may not be easily predicted or interpolated at local scales, especially in mountain areas characterized by microclimatic conditions related to a spatially complex topography.

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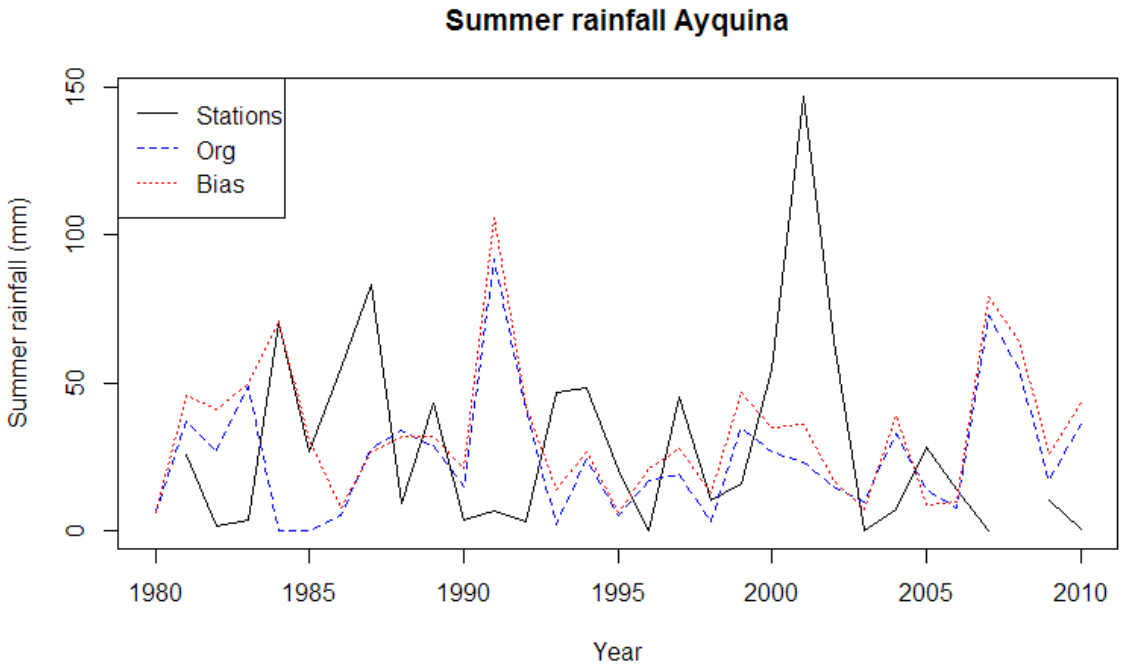
3.6. Supplementary material

S3.1. Summer rainfall time series of eight meteorological stations, with the corresponding predictions from global climate surfaces.

Time series of climatic data recorded at weather stations (black lines) and from global climate surfaces; unmodified Delta downscaled data ("Org", in blue line) and Delta downscaled data after post-processing bias corrections ("Bias", in red line) (Mosier et al. 2013).


Summer rainfall Ayquina
Stations
Org
Bias
Summer rainfall (mm)
0
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1980
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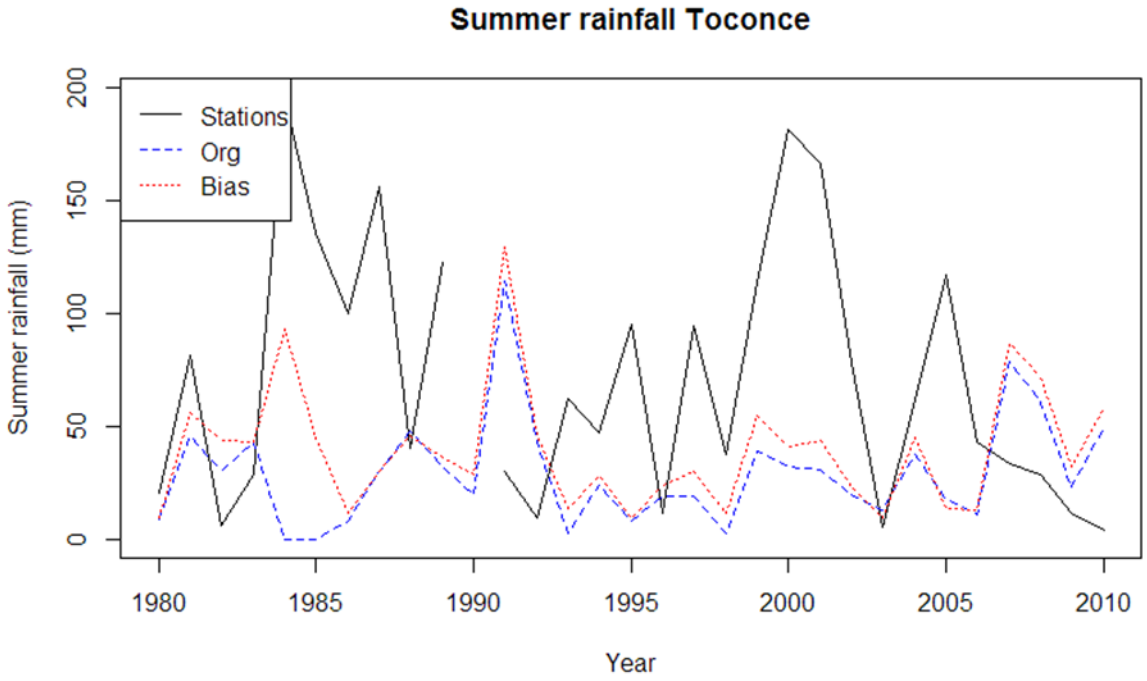
2010
Year


Summer rainfall Toconce
Stations
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Bias
Summer rainfall (mm)
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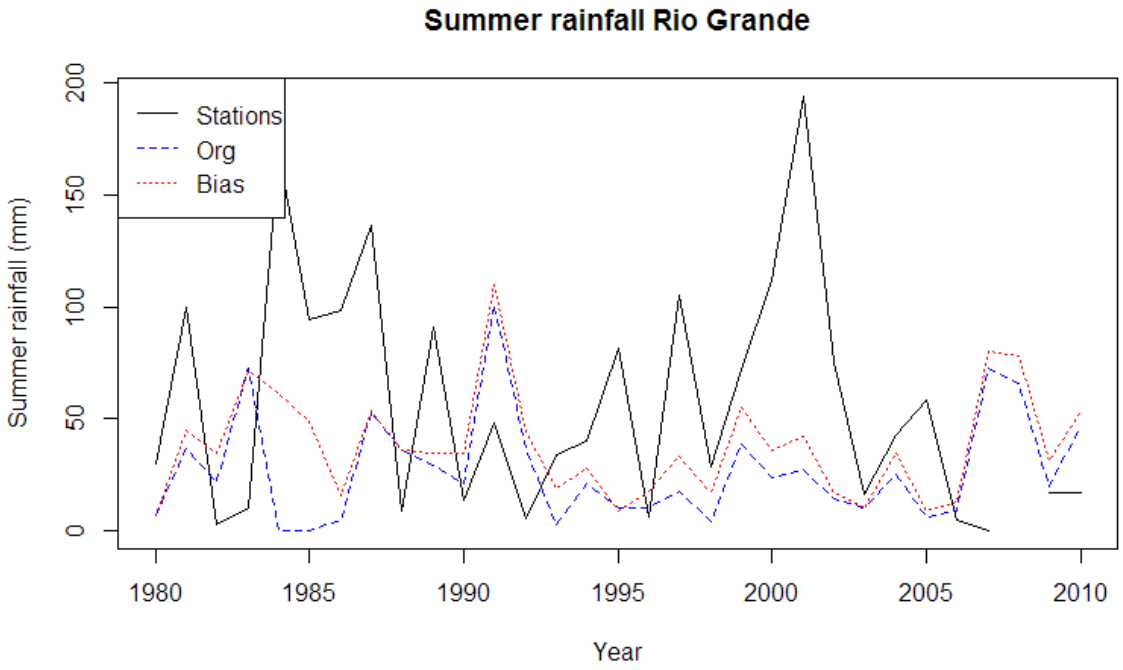
Summer rainfall Rio Grande
Stations
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Bias
Summer rainfall (mm)
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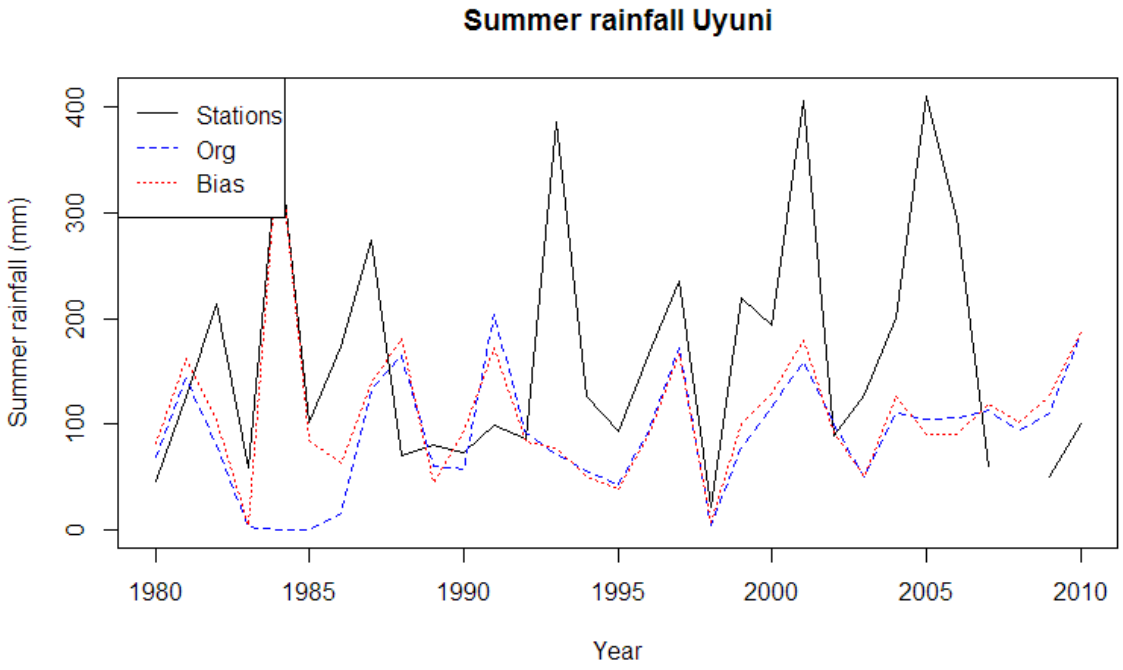
Summer rainfall Uyuni
Stations
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Bias
Summer rainfall (mm)
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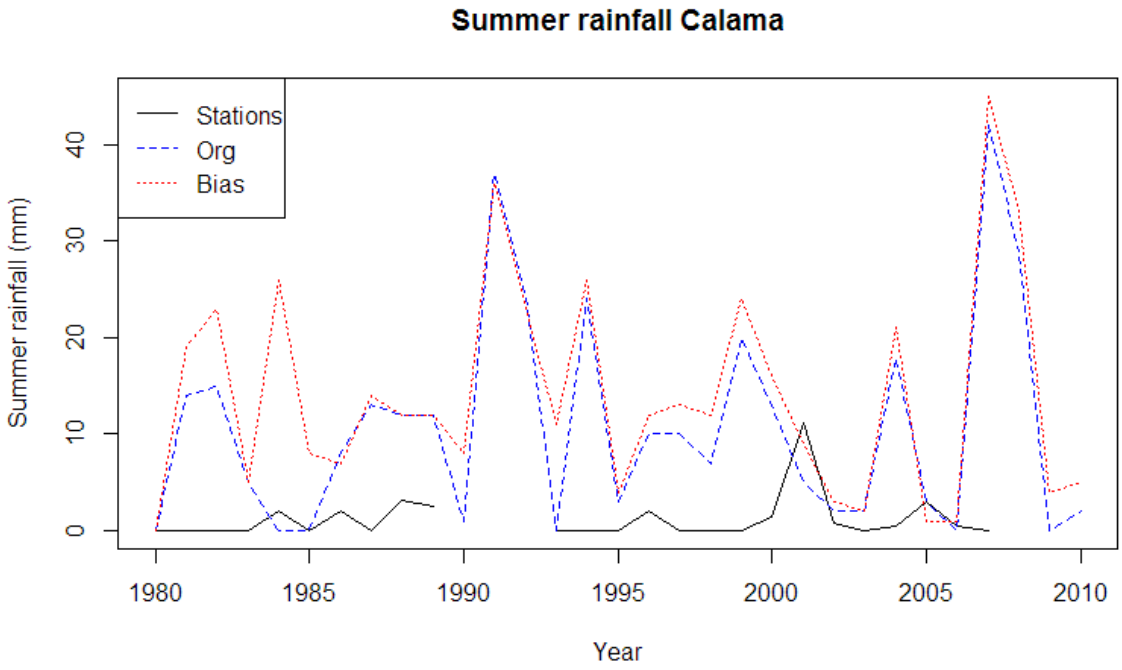
Year


Summer rainfall Calama
Stations
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Bias
Summer rainfall (mm)
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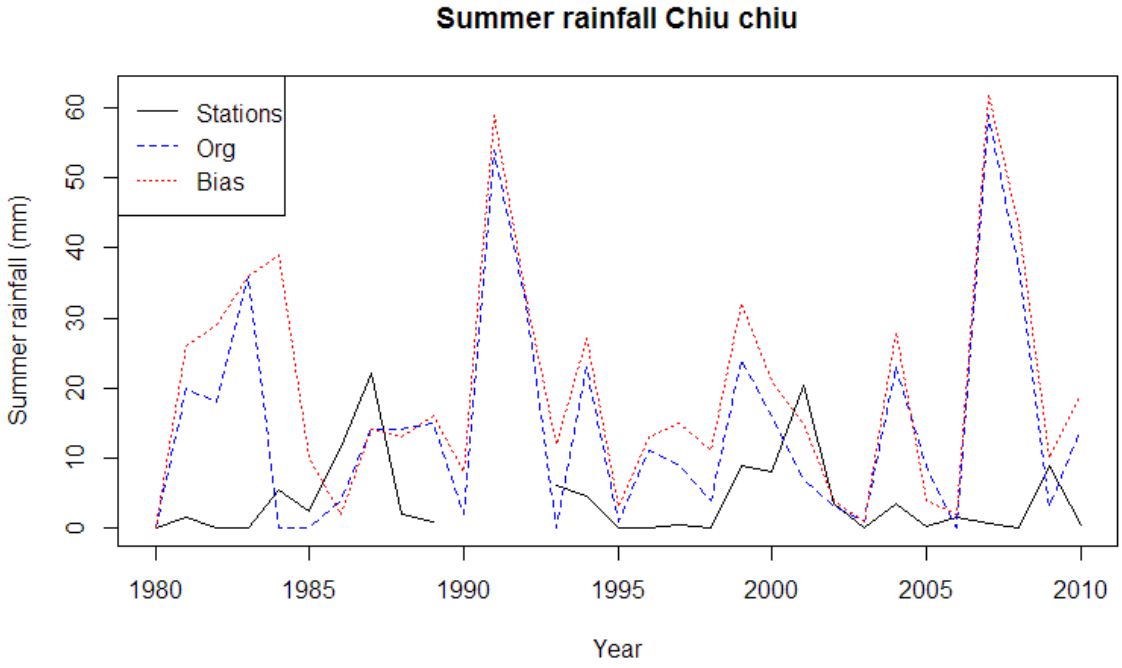
Year


Summer rainfall Chiu chiu
Stations
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Bias
Summer rainfall (mm)
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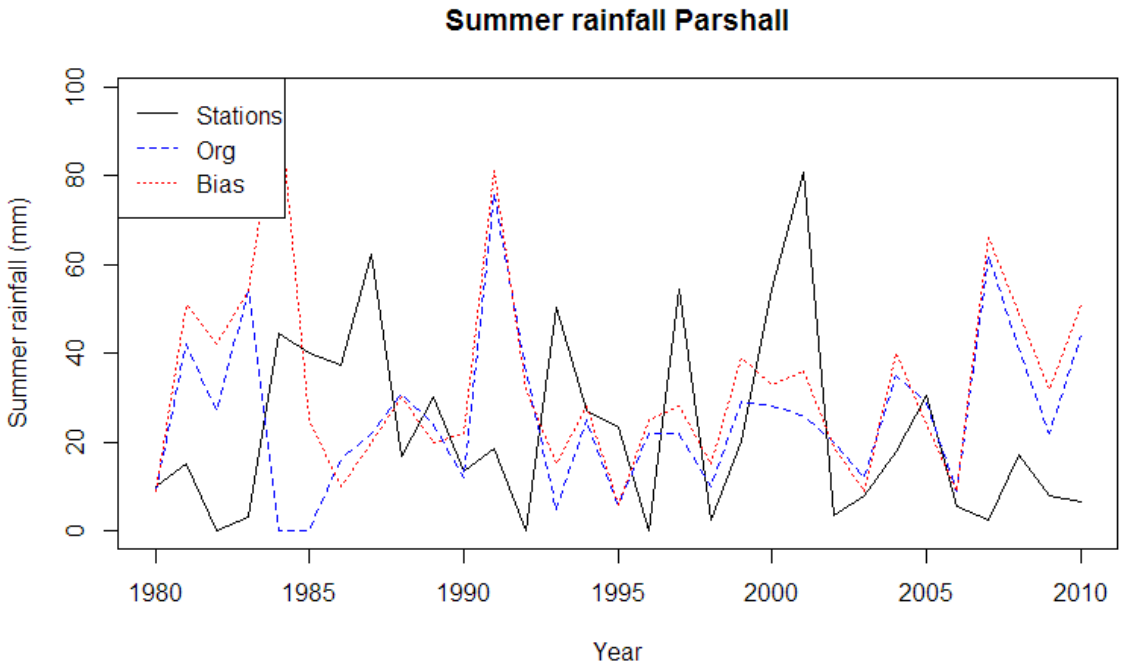
2010
Year


Summer rainfall Parshall
Stations
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Bias
Summer rainfall (mm)
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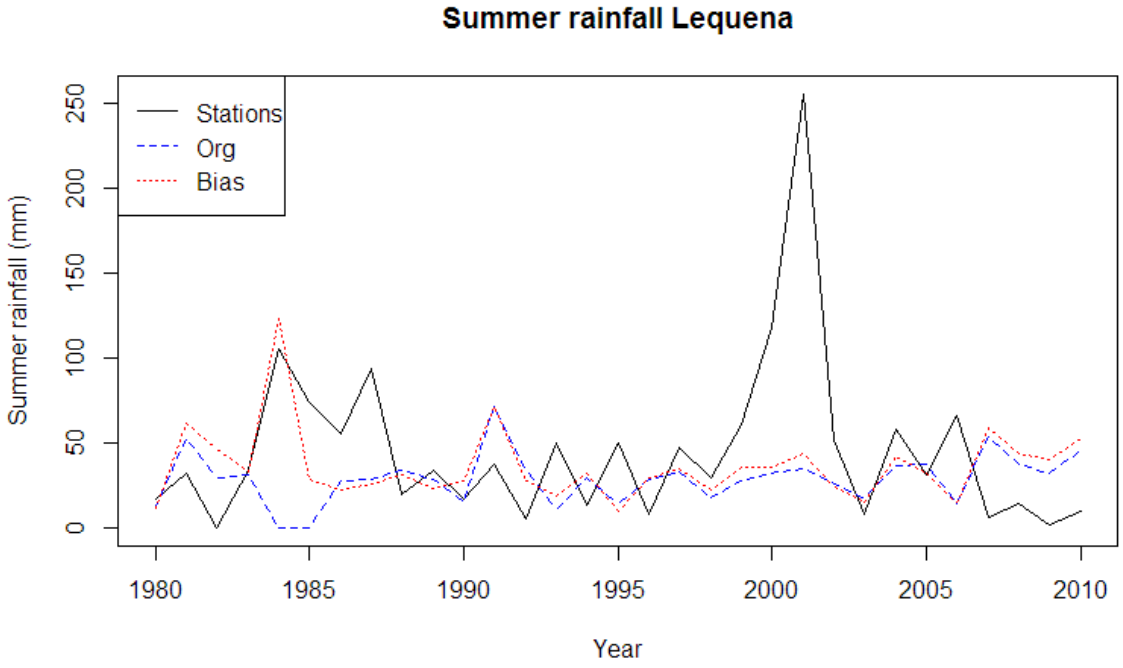
Summer rainfall Lequena
Stations
Org
Bias
Summer rainfall (mm)
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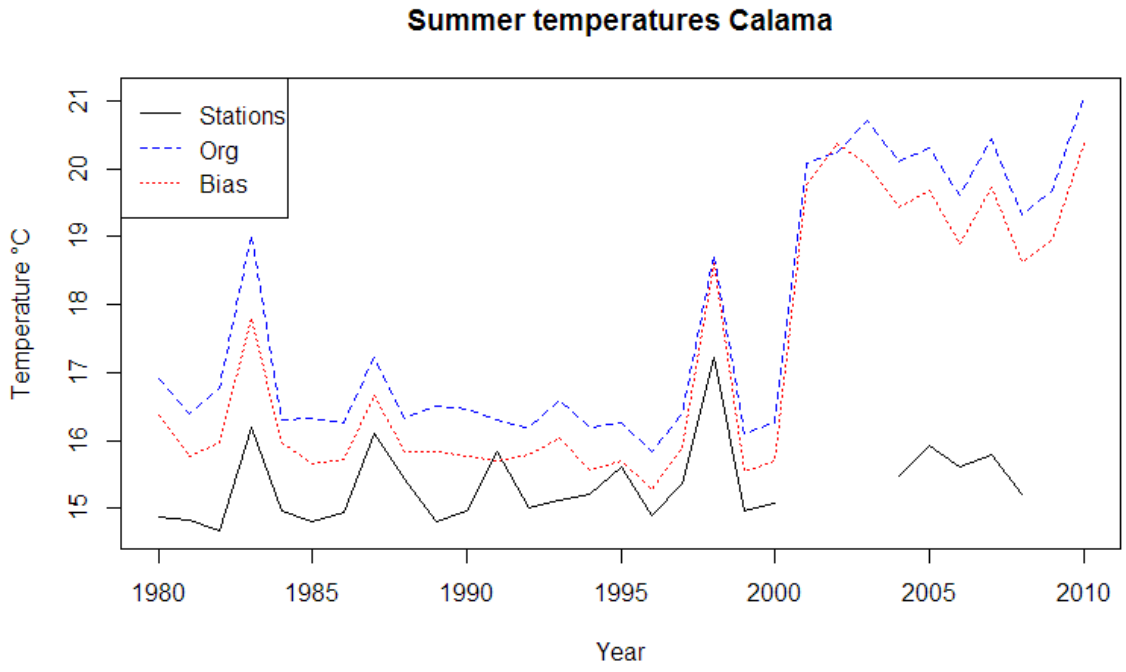
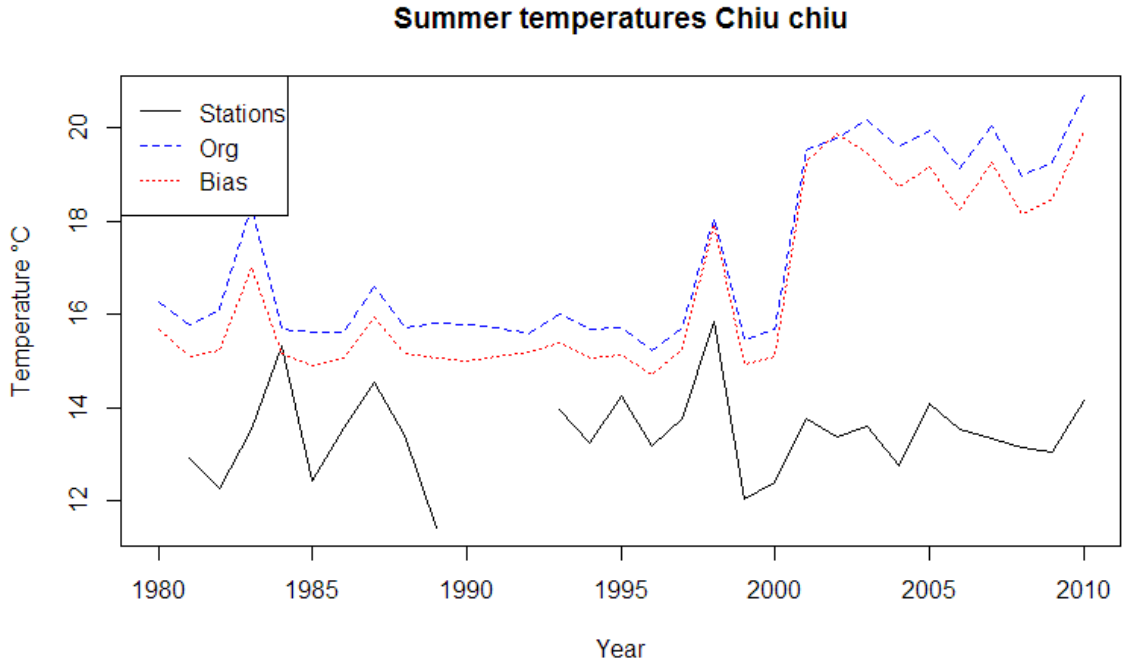
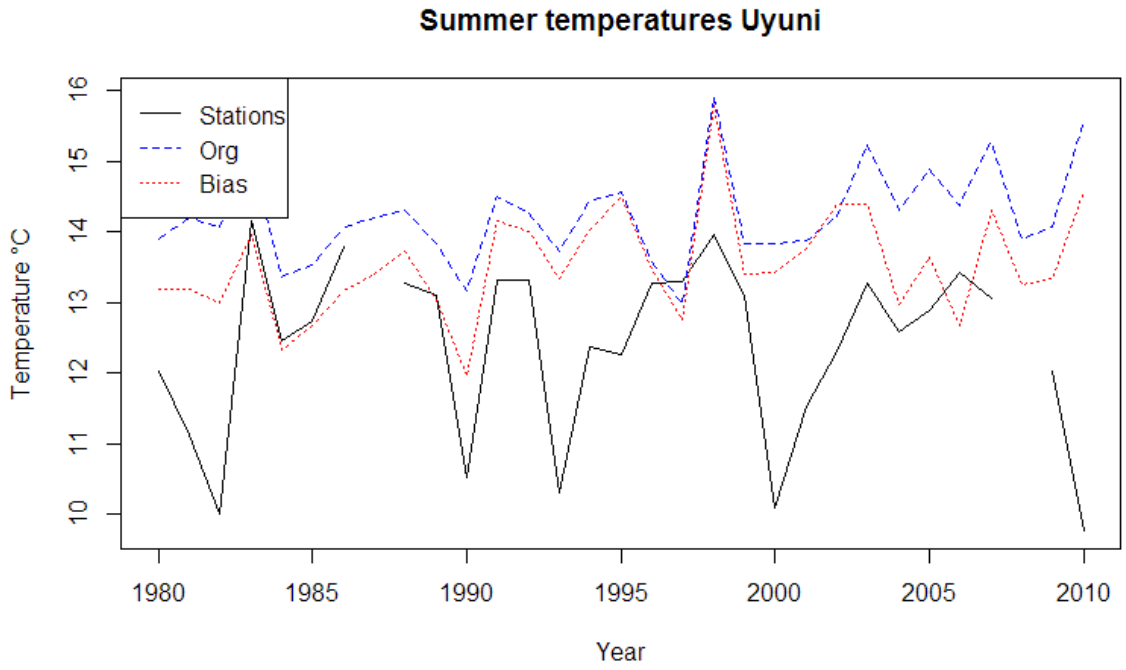
S3. 2. Summer and winter temperature time series of four meteorological stations






Summer temperatures Uyuni
Stations
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Bias
Temperature °C
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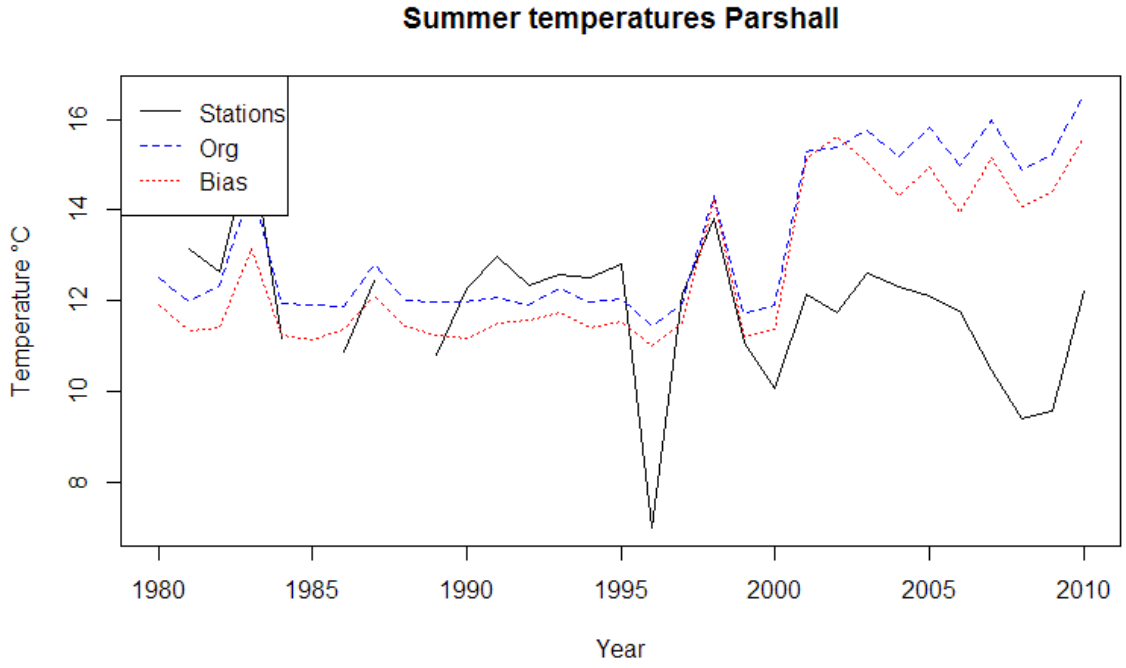
Summer temperatures Parshall
Stations
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Temperature °C
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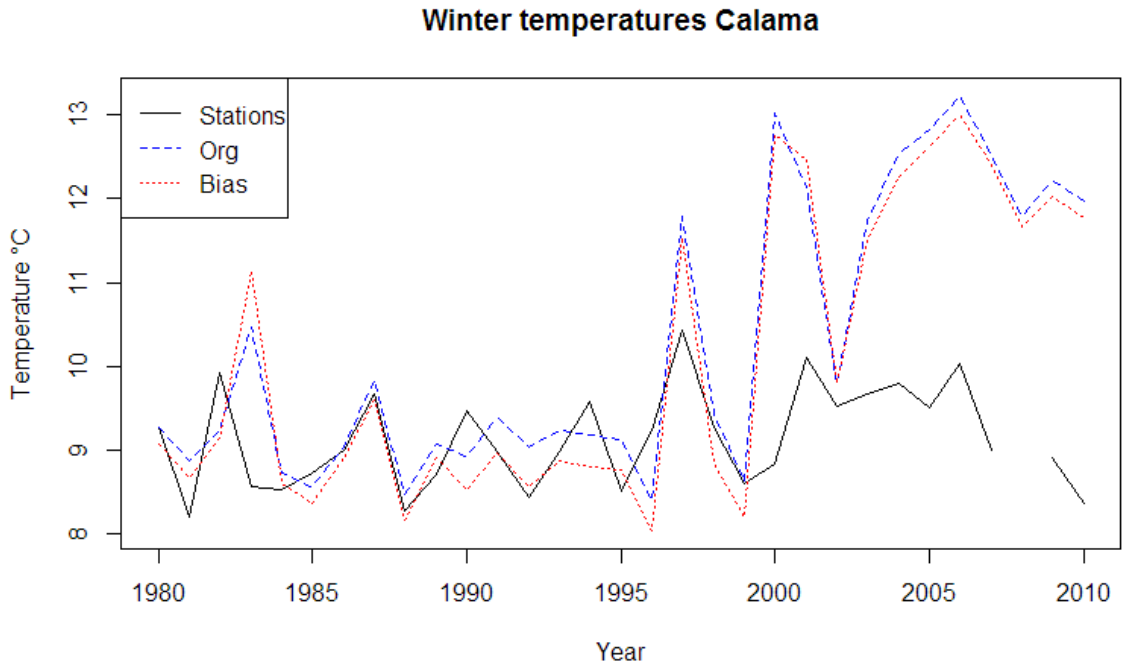
Winter temperatures Calama
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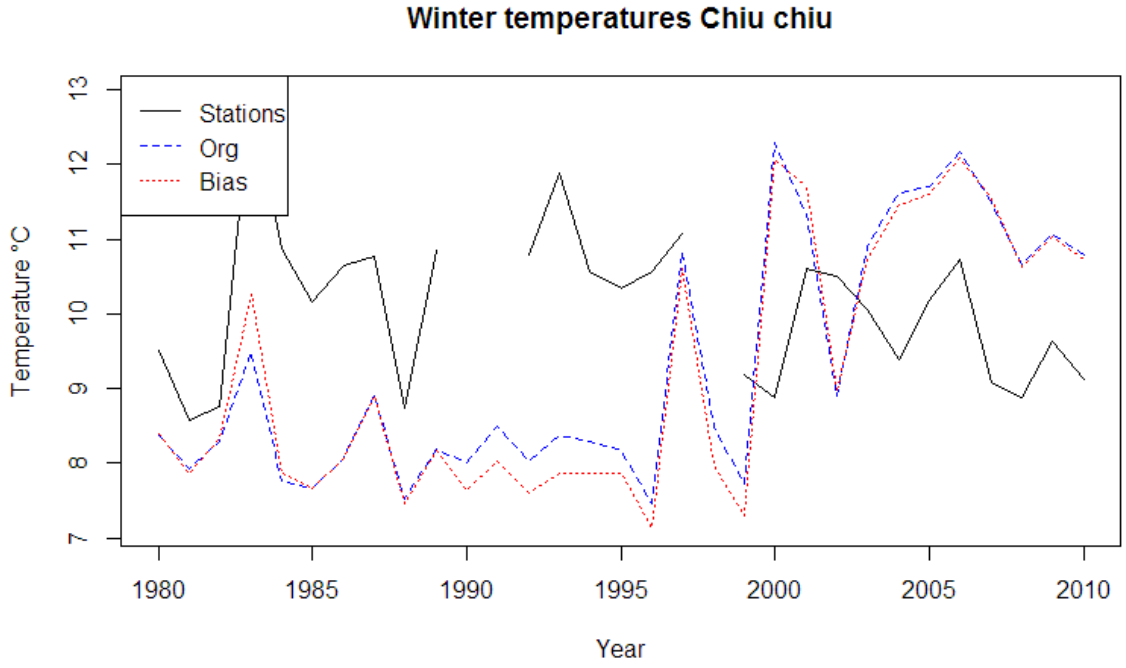
Winter temperatures Chiu chiu
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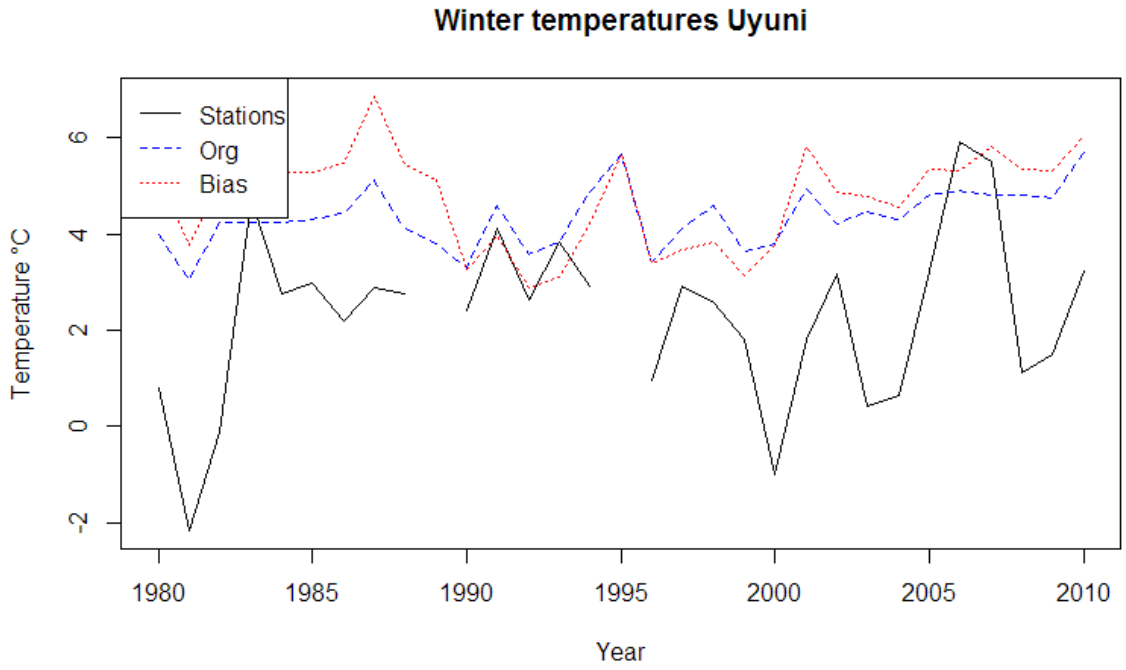
Winter temperatures Uyuni
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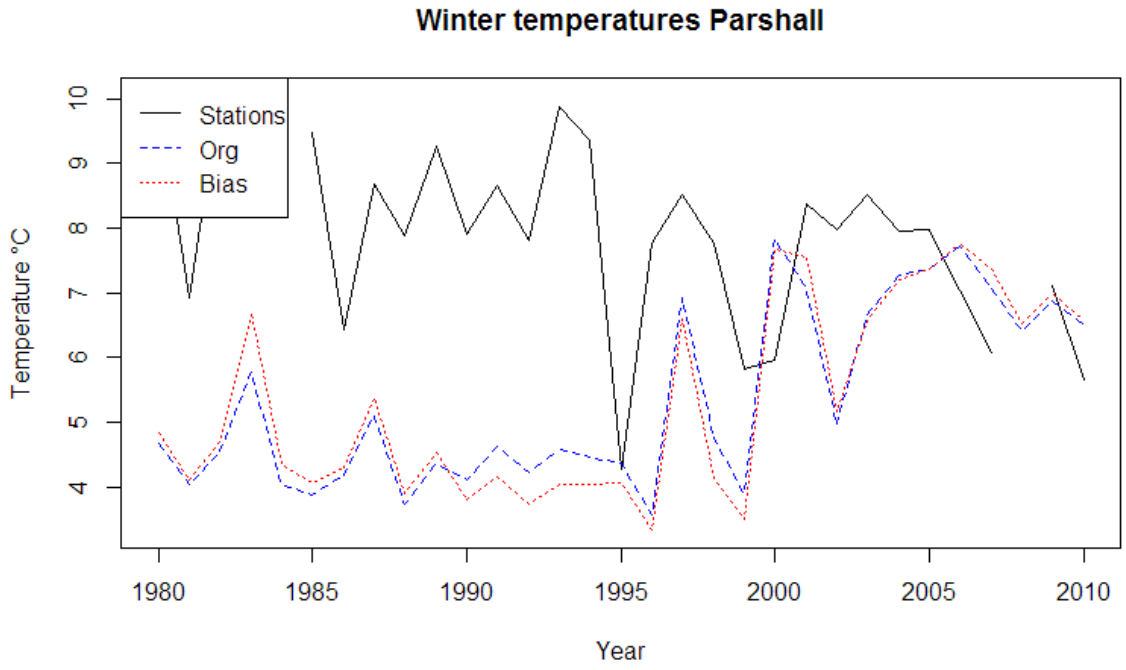
Winter temperatures Parshall
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Chapter 4:

Climate-linked variations in primary productivity in the Dry Puna

Abstract

There is an urgent need to understand how climate change affects biodiversity in arid and semi-arid mountains, with complex regional climates and specialized organisms. The Dry Puna in the Central Andes, seemingly under a process of desertification, is one of the least studied. The Dry Puna climate is characterized by summer rainfall and it is influenced by large scale and local forces, such as El Niño Southern Oscillation (ENSO) and the barrier effect of the Andes respectively. The aim of this chapter is to identify relationships between empirical climate data and various metrics of primary productivity in the Dry Puna, using the Normalized Difference Vegetation Index, a proxy for vegetation greenness and biomass, accounting for temporal trends and topographic factors. Climatic records between 1982 and 2006 were derived from 28 meteorological stations above 3,000m around the triple frontier between Argentina, Bolivia and Chile, encompassing parts of the High Plateau and the Western Slopes of the Andes. Time series of NDVI were derived from GIMMS databases for the vicinity of each weather station, to capture distinct local variations in weather and vegetation, and across the study area. There were no consistent trends in primary productivity at local or regional level and, as expected, NDVI dynamics was dominantly influenced by ENSO fluctuations (with highest productivity as the ENSO index decrease, during La Niña summers) . However, when comparing across geographic areas, NDVI correlated positively with precipitation along the Western Slopes under Pacific influence (drier and hotter than the High Plateau of Amazonian influence). The more productive areas showed more pronounced inter-annual variability in NDVI and, within a given year, NDVI responses to the amount of summer rainfall took longer to peak along the Western Slopes than in the High Plateau. This study illustrates the usefulness of NDVI to monitor and predict short and long term responses of productivity to climate in arid mountains, and indicates that in the Dry Puna primary productivity is vulnerable to future increases in the frequency El Niño events.

4.1. Introduction

Mountains have spatially complex climates and support a significant part of the global biological diversity, but they are particularly fragile and susceptible to changes in temperature and precipitation (Diaz et al. 2003, Messerli et al. 2004, Nogués-Bravo et al. 2007, La Sorte and Jetz 2010). The impacts of climate change upon mountain biodiversity and ecosystem services are particularly worrying in arid regions (Placzek et al. 2009), where water is scarce and central to the regulation of vegetation growth (Noy-Meir 1973). Considering that changes in temperature and precipitation can have far-reaching effects upon primary productivity in arid lands, it is surprising that this topic remains under-studied in many dry highlands (IPCC 2007, Sharma 2009). One of the least studied in the world is the Dry Puna, the driest region of the Andes and considered a global conservation priority due to its biological distinctiveness and vulnerability (Dinerstein et al. 1995).

Primary productivity is a useful parameter to study the impacts of climate change on vegetation dynamics in highlands, where field based studies are logistically difficult and therefore rare. Primary productivity is commonly estimated as the Normalized Difference Vegetation Index (NDVI), derived from satellite images (Wang et al. 2003, Pettorelli et al. 2005), which correlates strongly with the photosynthetically active radiation absorbed by vegetation. NDVI has been used to study vegetation responses to climate change in mountains worldwide (Ding et al. 2007, Zhong et al. 2010) and it is considered a good indicator of productivity and green biomass in arid and semi-arid regions (Tucker et al. 1985, Nicholson et al. 1990, Herrmann et al. 2005, Knapp et al. 2006, De La Maza et al. 2009). NDVI dynamics in arid and semi-arid regions is typically driven by variations in rainfall, water balance and soil moisture, which reflect in plant growth and primary production (Holmgren et al. 2006, De La Maza et al. 2009).

Low temperatures and a short rainy season, restricted to the summer months (Garreaud et al. 2003, Chapter 3), imposes substantial constraints on plant life in the Dry Puna. There the vegetation is low and sparse, dominated by shrubs and tussocks, with patches of green biomass locally associated to wetlands in valleys and depressions (Arroyo and Cavieres 2013). Paleoecological studies indicate that the vegetation of the Dry Puna has been strongly affected by precipitation; specifically, the tree growth of *Polylepis tarapacana*, the tree at highest elevation in the world, shows positive correlations between growth and

the previous season's rainfall (Morales et al. 2012, Soliz et al. 2009). However, studies relating climate and productivity/NDVI in the Andes have been conducted only at continental scale (Paruelo et al. 2004, Van Leeuwen et al. 2013, Zeng et al. 2013, Barbosa et al. 2015) and using gridded climate datasets, which interpolate the climate of the Dry Puna from a very small number of weather stations at high elevation. These datasets fail to capture the complex climatic variability of the Andes (Garreaud et al. 2009, Morales et al. 2012), as demonstrated by a localized study which incorporated additional weather stations (Chapter 3).

In order to assess climatically-linked local-scale variations in primary productivity in the Dry Puna, this study explores NDVI trends and compares them with climate records between 1982 and 2006 from 28 weather stations at 3000-4400m The study area, located on the triple frontier between Argentina, Bolivia and Chile, is a transition zone between tropical and extra tropical atmospheric circulations and with the Andes Cordillera imposing a strong barrier effect (Messerli et al. 1997). On inter-annual time scales, rainfall is affected by El Niño-Southern Oscillation (ENSO) (Vuille 1999, Chapter 3) but the local weather is also modulated by the different topography, which includes the High Plateau above 3,500m and the Western Slopes of the Andes, descending abruptly towards the Atacama Desert at 2,300m (Chapter 3). We therefore predict strong ENSO-related fluctuations in primary productivity, with superimposed topographic influences. During El Niño events conditions are dry and hot, potentially limiting plant growth during the summer months. In La Niña years, when changes in the Pacific surface temperatures intensify and displace the Bolivian High circulation system southwards, productivity should increase, particularly in the High Plateau, with the increasing influx of moisture via pronounced easterly wind anomalies from Amazon basin and Gran Chaco (Vuille 1999, Garreaud et al. 2003, Vuille and Keimig 2004).

To test these hypotheses we explored short- and long-term responses in primary productivity with respect to temperature, rainfall, ENSO records, and geographic and topographic patterns. By restricting NDVI-climate comparisons to the vicinity of the weather stations we avoided the assumption that climate at one location can be safely used to explain NDVI at a larger scale or, in other words, that gridded climate datasets are good predictors of local climates in mountains. The study have implications for our understanding of ecosystem processes in arid highlands, and of the ecological impacts of climate change upon biodiversity and humans.

4.2. Methods

4.2.1. Study area

The study area is located around the triple frontier between Argentina, Bolivia and Chile (20.5° to 24°S, 66° to 69°W), in the Central Andean Dry Puna ecoregion, above 3,000m (Figure 4.1). The monthly average temperature ranges from 0 to 16°C in summer and from -4 to 12°C in winter (Chapter 3). Annual rainfall is concentrated in the austral summer (December to March) with a mean of 85mm, ranging from 0 to 639mm (Chapter 3); rainfall outside this rainy season is negligible (Garreaud et al. 2003). Rainfall is in the form of intense convective precipitation, affected by the location and intensity of the Bolivian High (Garreaud et al. 2003, Garreaud et al. 2009) and by the easterly winds that bring humidity from the east tropical Amazon basin and Gran Chaco (Vuille and Keimig 2004). The vegetation is sparse and characterized by flora with a high degree of specialization, with physiological adaptations to water stress and extremely low temperatures , typical of in mountain areas (Körner 2003). The vegetation is dominated by shrubs, tussock grasslands, and clusters of cushion bogs that remain green throughout the year; other vegetation types are associated to salt pan margins and wetlands (Arroyo and Cavieres 2013).

In this mountain environment human presence is low, agriculture limited to the vicinity of water sources in sheltered areas and the effects of livestock grazing are mainly localized (Villagrán and Castro 1997, SaviaGlobal 2006, Clark 2012). Another anthropogenic impact is the localized extraction of water in settlements and mines, but information on this impact is scarce.

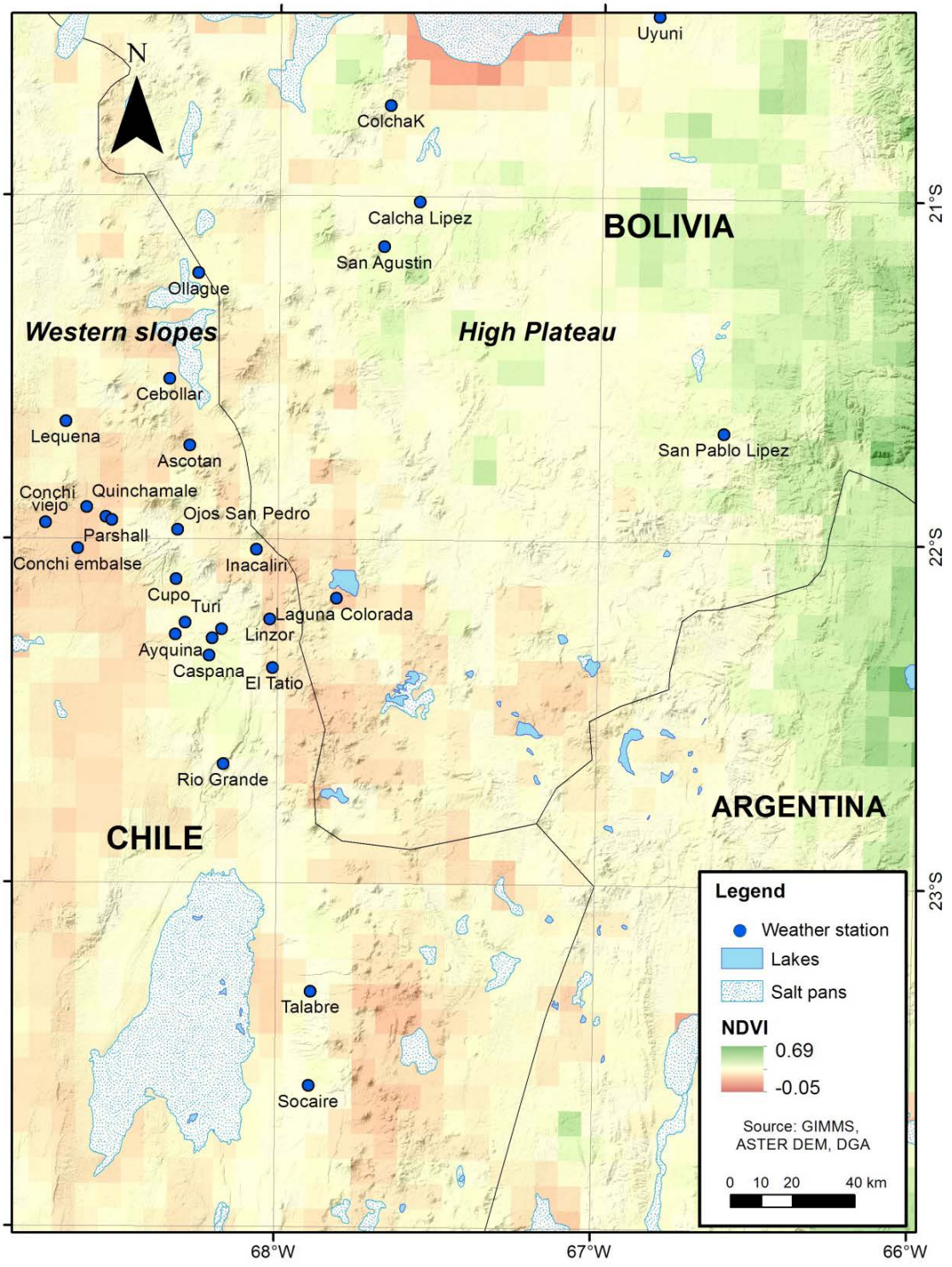

Figure 4.1. Study area with location of weather stations and GIMMS data, showing NDVI maximum values during the last two weeks of March 2005, at the end of the rainy season.

4.2.2 NDVI data

The Normalized Difference Vegetation Index or NDVI is extracted from satellite images and it is the most commonly used to monitor primary productivity, because it strongly correlates with photosynthesis and biomass (Wang et al. 2003, Pettorelli et al. 2005, Pettorelli et al. 2013). NDVI combines the spectral information reflected by vegetation and captured by sensor in the red band (RED) and the near infrared band (NIR) (Pettorelli et al. 2013). The index is calculated as a ratio between these two bands as follows: NDVI = (NIR − RED)/ (NIR + RED) (Pettorelli et al. 2005, Horning et al. 2010). NDVI values fluctuate between -1.0 to 1.0, with values lower or close to 0 indicating absence of vegetation (Horning et al. 2010).

The NDVI data used in this study were obtained from the Advanced Very High Resolution Radiometer (AVHRR), processed by the Global Inventory Modelling and Mapping Studies (GIMMS), at a spatial resolution of 8km and temporal resolution of 15 days (Tucker et al. 2005). GIMMS provide bi-weekly NDVI values and is the longest dataset of consistent NDVI values currently available, spanning from mid-1981 to 2006; alternative NDVI databases do not cover the period corresponding to the climatic records, for example MODIS, with better spatial resolution but starting in 2000.

The GIMMS dataset is corrected for atmospheric and sensors distortions. However, other noise in the data can be caused by clouds and shadows, which generally tend to decrease the values of the NDVI (Pettorelli et al. 2005, Pettorelli et al. 2013). To minimize these errors we applied the maximum value composite method (MVC), creating a monthly dataset from the two bi-weekly images, selecting the highest NDVI value of each month to characterize NDVI time series (Zhang et al. 2013, Pettorelli et al. 2013).

We calculated three response variables that are potentially important in dry highlands. For annual parameters we considered the time period between December and the following November, to include the rainy season (December-March) fully.

- ***NDVI maximum***: maximum value of the NDVI over the 12 month period. This represents the maximum photosynthetic capacity of the system, an important parameter to study productivity in Dry Puna, a system with generally low values of NDVI.

- ***NDVI range***: difference between the maximum and minimum NDVI value within each 12 month period. This parameter reflects the vegetation capacity to respond to annual climatic variation.
- ***NDVI lag***: number of months between the end of the rainy season (March) and the month with the highest NDVI within the 12 month period; when the peak fell within the rainy season, the NDVI lag was recorded as zero. This parameter measures short-term responses to the amount of summer rainfall.

These metrics were calculated for each 8km cell containing a weather station and the NDVI maximum across all pixels within the study area.

4. 2.2. Climatic data

We used climatic data from 28 weather stations, located between 3,000 and 4,400m across the study area and with at least 10 years of records between 1982 and 2006 (Table 4.1 and Figure 4.1). The data was provided by the Chilean and Bolivian governments (DGA, Direccion General de Aguas Chile and SENAMI, Servicio Nacional de Meteorología e Hidrología Bolivia). Of them, only nine weather stations had sufficient temperature records (Table 4.1). Months with less than twenty days of measurements were excluded from the analyses.

Meteorological station	Elevation (m)	Latitude UTM N (m)	Longitude UTM E (m)	Data source
Ayquina*	3,013	7536146	570041	DGA, Chile
Conchi embalse *	3,035	7563959	538601	DGA, Chile
Turi	3,069	7539945	573179	DGA, Chile
Quinchamale	3,073	7577204	541503	DGA, Chile
Socaire	3,240	7390668	612822	DGA, Chile
Salado embalse	3,243	7534950	581941	DGA, Chile
Talabre	3,252	7421051	613538	DGA, Chile
San Pedro Conchi	3,253	7574081	547692	DGA, Chile
Rio Grande	3,288	7494340	585521	DGA, Chile
Toconce	3,297	7537855	584990	DGA, Chile
Caspana*	3,298	7529298	580938	DGA, Chile
Lequena	3,314	7604891	534878	DGA, Chile
Parshall*	3,338	7573030	549639	DGA, Chile
Cupo	3,364	7553917	570293	DGA, Chile
Conchi Viejo	3,476	7572283	528324	DGA, Chile
Uyuni*	3,667	7734766	726204	SENAMI Bolivia
Ollague	3,704	7652551	577704	DGA, Chile
Cebollar	3,737	7618527	568307	DGA, Chile
Calcha Lipez	3,788	7675339	648960	SENAMI Bolivia
Ojos San Pedro	3,800	7569874	570766	DGA, Chile
ColchaK*	3,828	7706413	639694	SENAMI Bolivia
San Agustin	3,831	7660921	637516	DGA, Chile
Ascotan	3,988	7597006	574737	DGA, Chile
Inacaliri	4,016	7563405	596197	DGA, Chile
Linzor*	4,130	7541022	600525	DGA, Chile
San Pablo Lipez*	4,270	7600349	746891	SENAMI Bolivia
Laguna Colorada	4,301	7547638	621917	SENAMI Bolivia
Tatio*	4,373	7525364	601396	DGA, Chile

Table 4.1. Weather stations with more than 10 years of useful data between 1982 and 2006 in the triple frontier of Argentina, Bolivia and Chile. * stations with sufficient temperature records. UTM coordinates in WGS84 19S.

To account for interannual climatic variation we used the Multivariate ENSO Index (MEI), a continuous index representing the coupled ocean-atmosphere system over the tropical Pacific Ocean, obtained from the Earth System Research Laboratory, NOAA (www.esrl.noaa.gov/psd/enso/mei/mei.html (Wolter and Timlin 2011). This index integrates sea level pressure, zonal and meridional components of the surface winds, sea surface temperature, surface air temperature, and total cloudiness fraction of the sky

(Wolter and Timlin 2011). Large positive values of MEI are associated with El Niño events and negative values with La Niña periods.

We calculated three climatic parameters with potential to affect primary productivity in the Dry Puna:

- ***Summer temperature****:* average of monthly temperature between December and March –the warmest quarter of the year
- ***Winter temperature:*** average of monthly temperature between May and July - the coldest period of the year
- ***Summer rainfall****:* total precipitation between December and March, the rainy season.
- ***Summer ENSO:*** average of monthly MEI between December and March.

4. 2.4. Statistical analyses

Regression analyses were used to explain variations in NDVI metrics (maximum, range and lag) at the level of weather station, with relation to temperature, rainfall, ENSO, topography and geographical covariates, all of which with potential to affect primary productivity in the Dry Puna. Elevation, in meters, was derived from the Shuttle Radar Topography Mission SRTM (Rabus et al. 2003) and resampled from geographic coordinates to WGS 84 UTM 19S. Geographic location, latitude and longitude, were obtained for each weather station in coordinates in WGS 84 UTM 19S. We also compared NDVI variables between two groups of weather stations at different elevation: a) the High Plateau group, including 13 weather stations above 3,500m in the north-east of the study area, influenced by Amazonian rainfall, and b) the Western Slopes group, wit 15 stations between 3,000 and 3,500m along the Andean slopes, with Pacific influence.

To explore variations in NDVI we used mixed models, a type of regression model, based on the maximum restricted likelihood method, which combines general mixed population models with models for individual units (Zuur et al. 2009, Omuto et al. 2010), in this case the weather stations. In this way the model accounts for the differences between and within weather stations. To account for temporal dependence across the NDVI time series, we included a first-order autoregressive structure that accounts for the effect of the previous year using the corAR1() option (Zuur et al. 2009). As only a third of the weather stations provided reliable temperature records, we constructed one set of models with just rainfall

as a predictor (n=28 localities) and another including both temperature and rainfall (n=9 localities).

Pearson's correlations between pairs of predictors were all lower than 0.7 and therefore they were all considered for the regression models (Dormann et al. 2013). Models of various complexities were constructed with different combinations of predictors, weather station as random factor, and autocorrelation structure. The corrected Akaike Information Criteria (AICc) was used to compare the fit of competing models (Burnham and Anderson 2002, Grueber et al. 2011). The top models (those with a ΔAICc less than 2), were combined to calculate an average effect size coefficient for each predictor in the final model (Burnham and Anderson 2002, Grueber et al. 2011). To measure model's fit we calculated the adjusted R square.

We also explored long-term trends in NDVI maximum across the study area, using the nonparametric Mann Kendall test, suited to detect trends in non-linear data, as it is the least influenced by outliers (Zhang et al. 2010, Caesar et al. 2011). For each 8km-pixel we obtained the Theil-Sen median slope and we used the Mann Kendall p values to test for significance. We also analyzed trends spatially by country, namely Argentina, Bolivia and Chile, the latter representing the western slope of the Andes.

All spatial analyses were conducted with the software ArcGIS 10, Spatial Analyst extension and trends were calculated using the Earth Trends Modeler (ETM) in the Clark Labs TerrSet software version 18.21. Statistical analyses were performed in R (R Development Core Team), packages nlme (Pinheiro et al. 2014), RKT (Marchetto 2012) and MuMIN (Bartoń 2013).

4. 3. Results

4.3.1. Climate – productivity links

Values of NDVI maximum across all weather stations varied between 0, around the Linzor station, and 0.222 in the Socaire station (Figure 4.1), with an overall mean of the stations means of 0.104 (SD 0.037) between 1982 to 2006 (Table 4.2). As expected, the best regression models predicting variations in NDVI maximum were a function of variations in ENSO and rainfall across the study period (Table 4.3). Primary productivity decreased as

the ENSO index increased, resulting in lower productivity during the relatively dry El Niño years, and higher productivity during the wetter La Niña years. Models with geographic predictors did not have better predictive power. Accordingly, the ENSO effect was not longer evident within geographic sub-groups of weather stations (i.e. High Plateau and Western Slopes) (Table 4.3). However, productivity was positively (and significantly) affected by rainfall across localities in the Western Slopes, with a positive but non-significant ENSO effect (Table 4.3). Differences between NDVI maximum in the Western Slopes and the High Plateau stations were not significant (ANOVA of NDVI maximum $F(1,698)$: 0.419 $p<0.518$, R-sq: -0.0008) (Table 4.2).

	Study area (n=28)			Western Slopes (n=15)			High Plateau (n=13)		
	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min
NDVI max	0.105	0.222	0.046	0.108	0.222	0.046	0.101	0.209	0.047
NDVI range	0.034	0.152	0.007	0.034	0.152	0.007	0.031	0.101	0.008
Summer rainfall (mm)	85.4	639.1	0	0.046	0.324	0	0.131	0.639	0
Summer temperature (°C)	10.7	16.1	-0.8	12.3	15.4	0	8.7	16.1	-0.8
Winter temperature (°C)	4.9	12.5	-4.8	8.7	12.5	4.3	2	7.6	-4.8
Summer ENSO	0.3	2.8	-1.2	0.3	2.8	-1.2	0.3	2.8	-1.2
Longitude (m)	593740	746891	528324	567593	613538	528324	623909	746891	568307
Latitude (m)	7571314	7734766	7525364	7533574	7604891	7390668	7614860	7734766	7525364
Altitude (m)	3571	4373	3013	3237	3476	3013	3956	4373	3667

Table 4.2. Descriptive statistics (mean of each stations mean, maximum and minimum value) comparing primary productivity, climate variables, location and elevation of weather stations in the overall study area and in the two defined geographic groups (Western Slopes and High Plateau) between 1982 to 2006.

As expected, the best models predicting variations in *NDVI maximum* were a function of variations in ENSO and rainfall (in models excluding temperature) (Table 4.3). Primary productivity decreased as the ENSO index increased, resulting in lower productivity during the relatively dry El Niño years, and higher productivity during the wetter La Niña years. Only the subset of localities in the Western Slopes showed a positive (significant) contribution of rainfall and a smaller (non-significant) ENSO effect (Table 4.3). Models with geographic predictors did not have better predictive power.

		Response variable: NDVI maximum		
		All localities (n=28)	High Plateau (n=13)	Western Slopes (n=15)
	adjR^2	0.81	0.83	0.79
ENSO	Coefficient	**-1.367**	-1.481	-0.364
	lower CI	-2.454	-3.019	-1.984
	upper CI	-0.28	0.028	1.256
Summer rainfall (mm)	Coefficient	-	-	**0.073**
	lower CI			0.037
	upper CI			0.109

Table 4.3. Average fixed effects, with 95% confidence intervals (CI), from two top ranking models fitted to the time series of NDVI maximum in the Dry Puna, with rainfall, ENSO, latitude, longitude and altitude as predictors, weather station as a random factor, and autocorrelation structure of order 1 / year effect. In bold significant effects (i.e. CI excludes zero).

Models incorporating both temperature and rainfall as predictors were limited to a few weather stations (n=9). These indicated a positive effect of winter temperatures and a negative effect of summer temperatures on *NDVI maximum*, but confidence intervals of the coefficients were broad and included zero (Table 4.4).

		Response variable: *NDVI maximum*
		Localities with temperature records (n=9)
	adjR^2	0.78
ENSO	Coefficient	-2.133
	lower CI	-4.763
	upper CI	0.496
Summer temperature (°C)	Coefficient	-0.316
	lower CI	-2.732
	upper CI	2.099
Winter temperature (°C)	Coefficient	1.413
	lower CI	-0.709
	upper CI	3.534

Table 4.4. Average fixed effects, with 95% confidence intervals (CI), of four top ranking models (Δ AICc <2) fitted to the time series of *NDVI maximum* using ENSO, rainfall, temperature, latitude, longitude and elevation as predictors, weather station as random factor and autocorrelation structure of order 1 / year effect.

Another important aspect of primary productivity in drylands is inter-annual variability (*NDVI range).* Variations in *NDVI range* across the study period were better explained by *NDVI maximum*, summer rainfall and ENSO: higher intra-annual variability was linked to greener vegetation, wetter summers, and lower ENSO index values (Table 4.5). Models that also included temperature revealed an additional effect of winter temperature (i.e. the milder the winter the higher the *NDVI range*) (Table 4.5). The analysis by geographic group showed that differences in NDVI range between locations in the Western Slopes and the High Plateau were not significant (ANOVA $F_{(1,698)}$: 1.1 $p<0.295$, R-sq:-0.00014) (Table 4.2).

		Response variable: *NDVI range*	
		All localities (n=28) *	Localities with temperature records (n=9) **
	adjR^2	0.68	0.78
ENSO	Coefficient	-0.45	1.141
	lower CI	-1.299	-2.91
	upper CI	0.392	0.622
Summer rainfall (mm)	Coefficient	**0.05**	**0.03**
	lower CI	0.034	0.01
	upper CI	0.058	0.05
Winter temperature (°C)	Coefficient	-	**1.78**
	lower CI		0.399
	upper CI		3.161
Summer temperature (°C)	Coefficient	-	-0.764
	lower CI		-2.296
	upper CI		0.766
NDVI maximum	Coefficient	**0.913**	**0.992**
	lower CI	0.852	0.889
	upper CI	0.974	1.094

Table 4.5. Average fixed effects from 2 (*) and 7 (**) top ranking models fitted to the time series of *NDVI range* in the Dry Puna using climate, longitude, latitude, elevation and NDVI maximum data as predictors. CI: 95% confidence intervals. All models included weather station as random factor and autocorrelation structure of order 1 / year effect. In bold significant effects (i.e. CI excludes zero).

Shorter-term responses of primary productivity were measured as the lag in months, between the end of the rainy season and the following NDVI peak. This lag was affected by the *NDVI maximum* and the longitude of the locality: less productive areas and those located in the Western Slopes took the longest to reach the peak (*NDVI maximum* effect: -0.01355, CI: -0.020; -0.007; longitude effect: -0.000013, CI: -0.000016 to -0.000009; adjR^2= 0.05). The analysis by geographic group (High Plateau versus Western Slopes) detected significant differences in the time-lag (linear model, $F_{(1,698)}$: 21.75, p<0.000, R-sq: 0.02883; Tukey's test p<0.000, CI 0.4787899 and 1.174954) (Table 4.2). On the Western Slopes NDVI peaked between April and August, on average 3.0 (SD: 2.3) months after the end of the rains; in the High Plateau the peak was between March and July, on average 2.2 months (SD 2.3) after end of the rainy season.

4.3.2. Overall trends in primary productivity

There were no consistent trends in the *NDVI maximum* across the study area between 1982 and 2006 (Figure 4.2). Table 4.6 shows that *NDVI maximum* generally declined in Chile and Argentina, and increased in Bolivia.

	Theil-Sen slopes		
	Mean	SD	Range
Argentina	-0.018	0.754	8.621
Bolivia	0.203	0.456	3.529
Chile	-0.198	0.351	3.468

Table 4.6. Trends in productivity (*NDVI maximum*): mean of Theil-Sen slopes, SD: standard deviation and range, between 1982 and 2006 across all the study area.

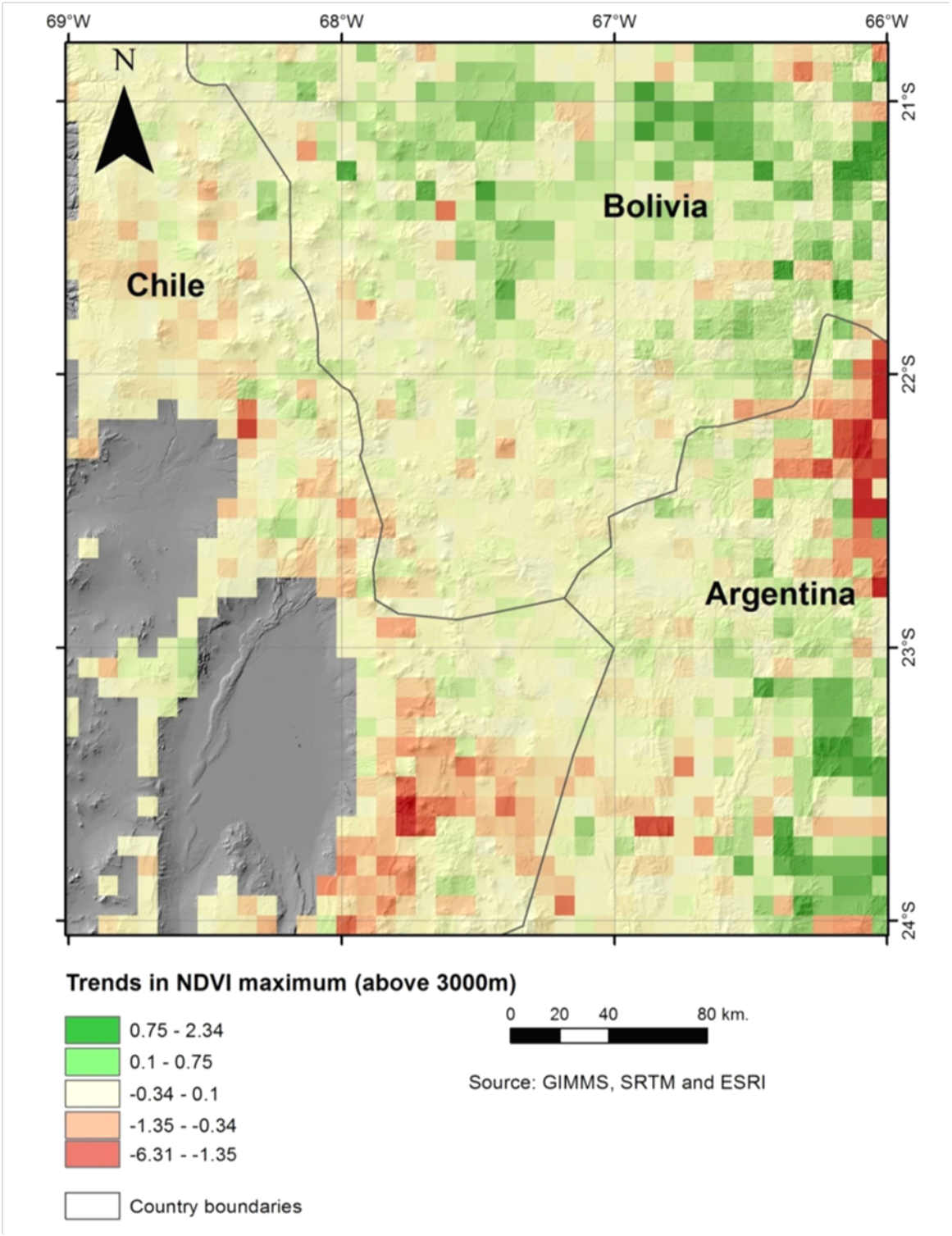

Figure 4.2. Trends in annual productivity between 1982 and 2006, depicted as Theil-Sen median slopes of the time series of the *NDVI maximum* in each 8 km pixel.

Figure 4.3 shows clusters of pixels with significant increasing trends, in shades of green; clusters with significant decreasing trends in shades of red; and many areas that remained unchanged.

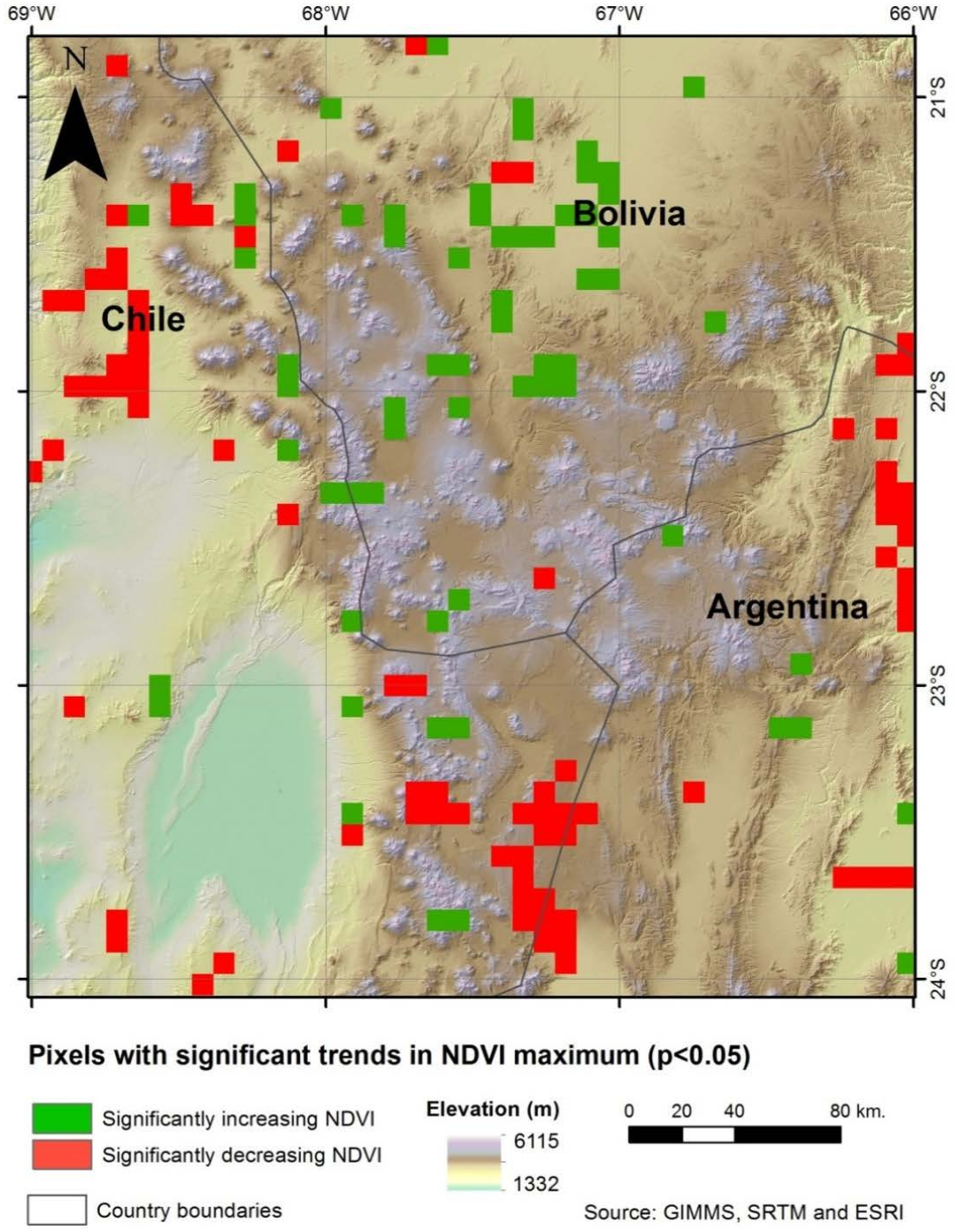

Figure 4.3. Pixels with significantly ($p<0.05$) increasing or decreasing trend in *NDVI maximum* between 1982 and 2006. The remaining pixels did not experience significant change.

The proportion of the study area that showed significant trends between 1982 and 2006 was therefore relatively low (Table 4.7): 91% remained unchanged, 3.8% showed increased productivity and 4.9% a decreasing trends. The majority of the pixels with significant declining productivity were located in Chile and to a lesser degree in Argentina, while it generally increased in Bolivia (Table 4.7 and 4.8).

Trends in *NDVI maximum*: % of area

NDVI	Study area	Argentina	Bolivia	Chile
Unchanged	91.2	24.9	39.6	26.8
Increasing	3.8	0.4	2.4	1.0
Decreasing	4.9	1.6	0.4	3.0

Table 4.7. Percentage of area with positive, null or negative significant trend in *NDVI maximum* between 1982 and 2006.

Trends in *NDVI maximum*: Mean Theil-Sen slope (SD)

NDVI	Argentina	Bolivia	Chile
Increasing	1.066 (0.324)	0.489 (0.370)	0.311 (0.200)
Decreasing	-1.149 (1.175)	-0.306 (0.319)	-0.459 (0.300)

Table 4.8. Significant trends in productivity (*NDVI maximum*): mean of Theil-Sen slopes and SD: standard deviation between 1982 and 2006 by country.

4.4. Discussion

To study climatic-linked patterns of variation in primary productivity, this study combined localized time series of NDVI values and climatic data from weather stations at high elevation in the Dry Puna, between 1982 and 2006. By relying on empirical rather than climate models or interpolated data, we addressed the inherent limitation of poor spatial definition in gridded datasets, particularly when applied to mountain areas with complex topography. We also explored overall patterns of productivity trends across the study area, to generalize the observed patterns of change.

The lack of consistency in primary productivity trends in the study area was expected from observed absence of local climatic trends over the last 30 years (Chapter 3) and with research conducted using similar data at a broader scale in the Andean region for the period 1982–2011 (Van Leeuwen et al. 2013). While there is evidence of a steady process of desertification in the Dry Puna since 1930, based on tree-ring analyses and precipitation reconstructions (Morales et al. 2012), primary productivity remained constant over two decades in most areas.

Our results are in general agreement with global studies in subtropical arid and semiarid regions that are experiencing strong climate-driven inter-annual variability in primary productivity (Zeng et al. 2013). In the Dry Puna there was a dominant role of the Pacific Ocean climate cycle ENSO in the dynamics of primary productivity, a positive relationship between productivity and ENSO events leading to higher rainfall that is supported by many studies worldwide (Holmgren et al. 2006, De La Maza et al. 2009, Van Leeuwen et al. 2013). Positive effects of precipitation on vegetation in semiarid and arid areas have been widely documented (Nicholson et al. 1990, Herrmann et al. 2005, De La Maza et al. 2009, Fabricante et al. 2009, Jin and Goulden 2014). For example, Herrmann et al. (2005) suggested that rainfall was the main factor affecting vegetation dynamics in the Sahel, and Nicholson et al. (1990) found strong associations between monthly NDVI and rainfall in previous months across Africa. Interestingly, ENSO events-rainfall relationships are not always consistent in the Dry Puna (Vuille 1999, Vuille et al. 2000) where areas in the East showed lower correlations than areas in the West (Vuille and Keiming, 2004). Correlations between rainfall and ENSO in our study area were significant but relatively low (r=-0.23), similarly to weak relationships reported by Christie et al. (2009) in the Andean High

Plateau. In consequence, rainfall-mediated effects of ENSO upon productivity were also weak in the study area, where variations in rainfall were only directly reflected in changes in productivity along the western slopes of the Andes - furthest away from the main rain sources to the north-east of the study area and where the vegetation is probably more sensitive to increasing rainfall.

ENSO can also exert effects on vegetation growth through changes in temperature. In arid areas, higher temperatures increase evapotranspiration, further diminishing water availability for plants and reducing their productivity. Coincidently, our study showed that during El Niño events, with drier and hotter summers, primary productivity decreased. Also, temperature affected primary productivity negatively in the Dry Puna due to very low temperatures during the dry winter months. However, a larger sample is necessary to further test this relationship.

In a low productive area, such as the Dry Puna, the dynamic responses of vegetation are an important component of changes in productivity. In terms of relative change within a year cycle, the most productive vegetation in the study area experienced a broader range of NDVI values, compared to the less productive areas, and particularly in wet summers. In relation to the speed of the response to increasing summer rainfall, also the most productive vegetation responded faster, particularly in the north-eastern areas, closer to main sources of moisture. Further studies, at higher spatial resolution, could tease apart whether NDVI dynamics also varies with vegetation types, such as cushion bogs, tussock grasslands and scrublands in the case of the Dry Puna. Also, studies at higher resolution can better capture the patchy and fragmented nature of the Dry Puna vegetation, determined by micro climatic conditions that create shelter for plants.

These results have important implications for predictions of the impacts of climate change on productivity; new evidence from projected climate changes confirms an increasing frequency of extreme El Niño events (Power et al. 2013, Cai et al. 2014, Cai et al. 2015), leading to higher temperatures and lower precipitation in the Dry Puna. Given the evidence of ENSO effects on primary productivity provided by this study, more frequent El Niño events can have serious effects on vegetation productivity and on the ecosystem as a whole, particularly on the south-western part of the study area, one of driest region of the Andes. Extreme and/or more frequent El Niño events would strengthen the barrier effect of the Arid Diagonal which, crossing the Andes from Chile to Argentina to the south of the

study area, limiting latitudinal migration of species of conservation concern such as Leopardus jacobita (Marino et al. 2011) and Vicugna vicugna (Marin et al. 2007).

The models presented in this study are useful tools to project productivity under future scenarios of climate change in arid mountains, and to monitor NDVI short and long-term responses to climate variability. The main limitation of this and similar studies is the scarcity of weather stations at high elevation worldwide, with a poor representation of the climate variability within mountains (in our study area, for example, there are no systematic climatic records from the Argentine side of the triple frontier). Yet, by limiting our study to the area surrounding weather stations, we bring a level of confidence to our results that cannot be ensured when using global climate datasets. Future research should use more detailed data, such as those derived from Landsat images, to enhance our understanding of the impact of climate variability on these ecosystems (Pettorelli et al. 2005, Krishnaswamy et al. 2013) and efforts should be placed on collecting and systematizing information of anthropogenic impacts in order to understand the combined influence of climate and human disturbance on Dry Puna ecosystems.

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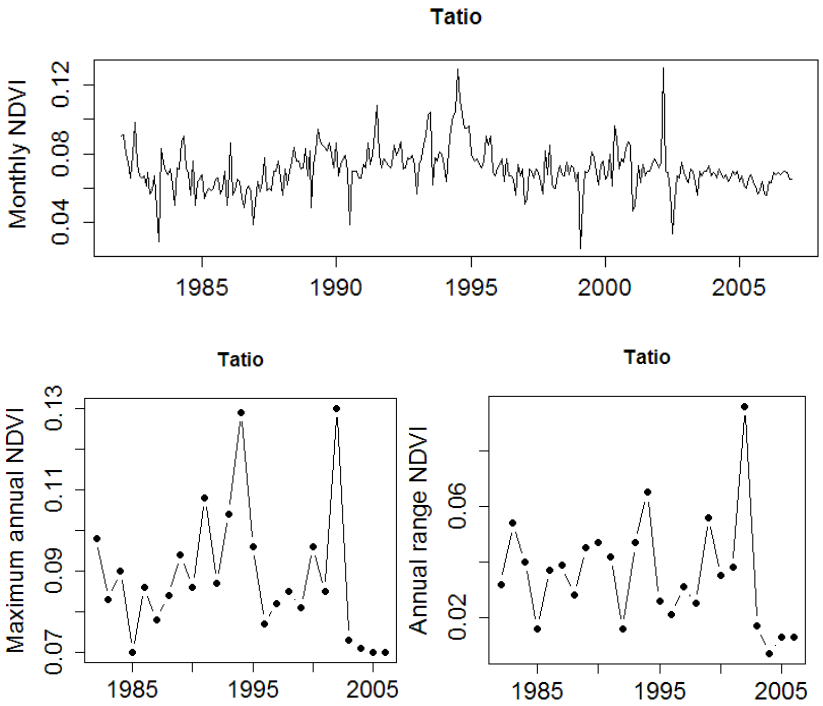
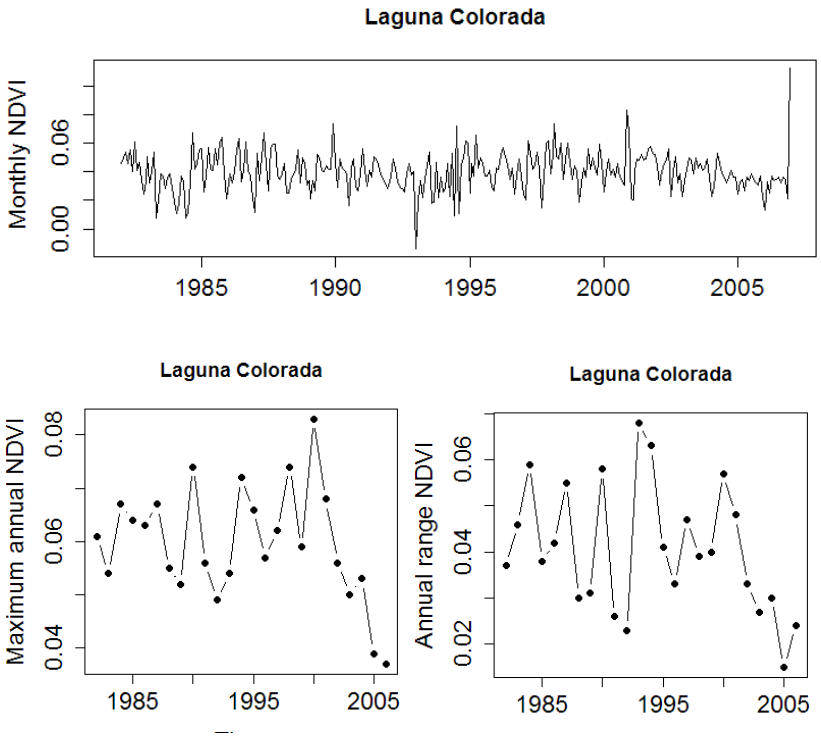
4.6. Supplementary material

S4. 1. Time series of monthly maximum NDVI, annual maximum NDVI and annual range from selected sites.

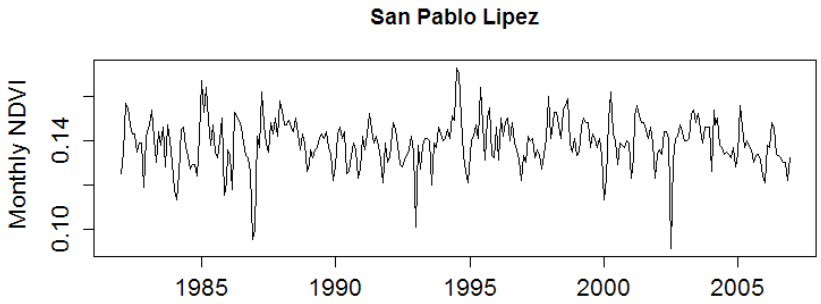
1. Tatio (4,373m)

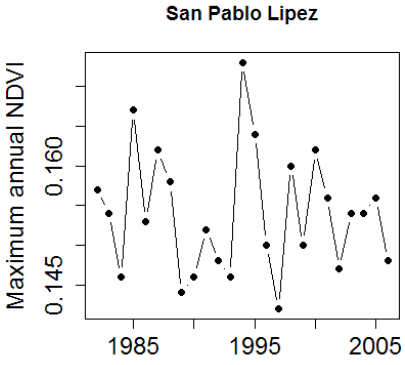


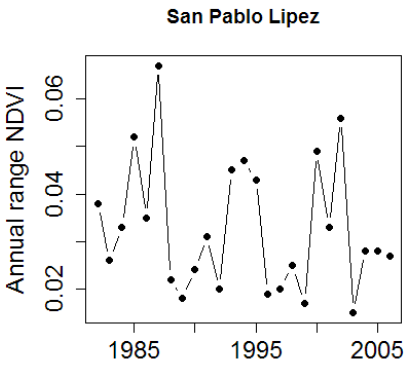
2. Laguna Colorada (4,301m)



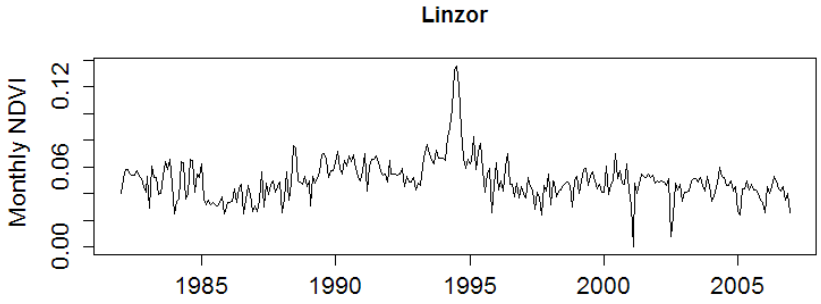
3. San Pablo Lipez (4,270m)

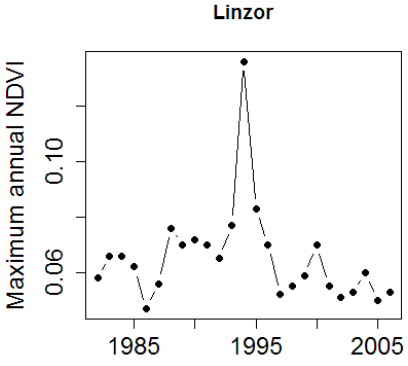


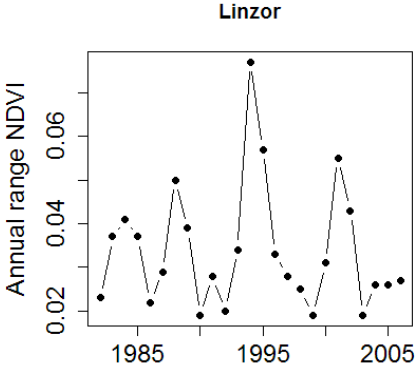




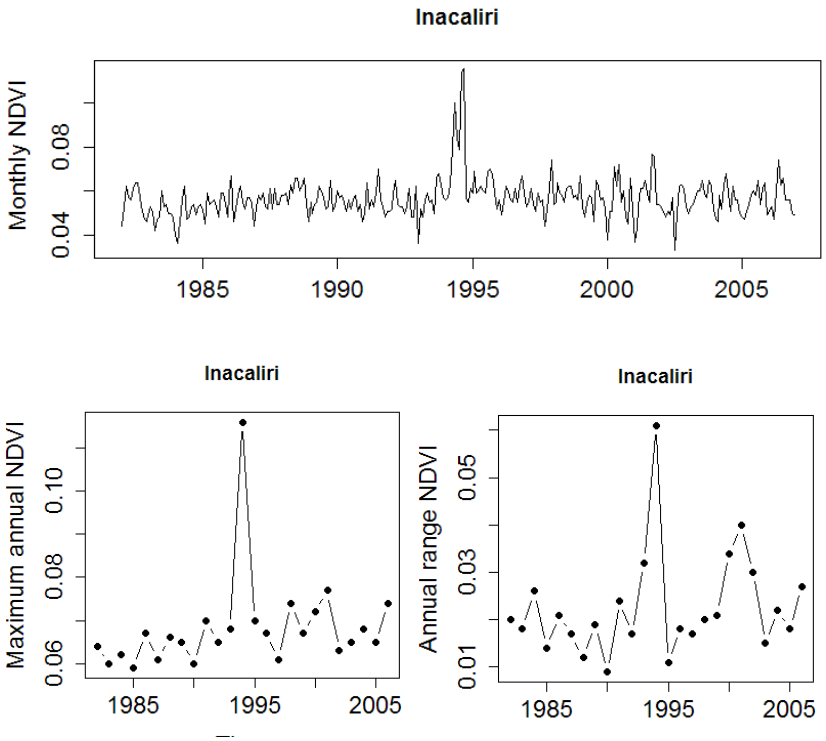
4. Linzor (4,130m)



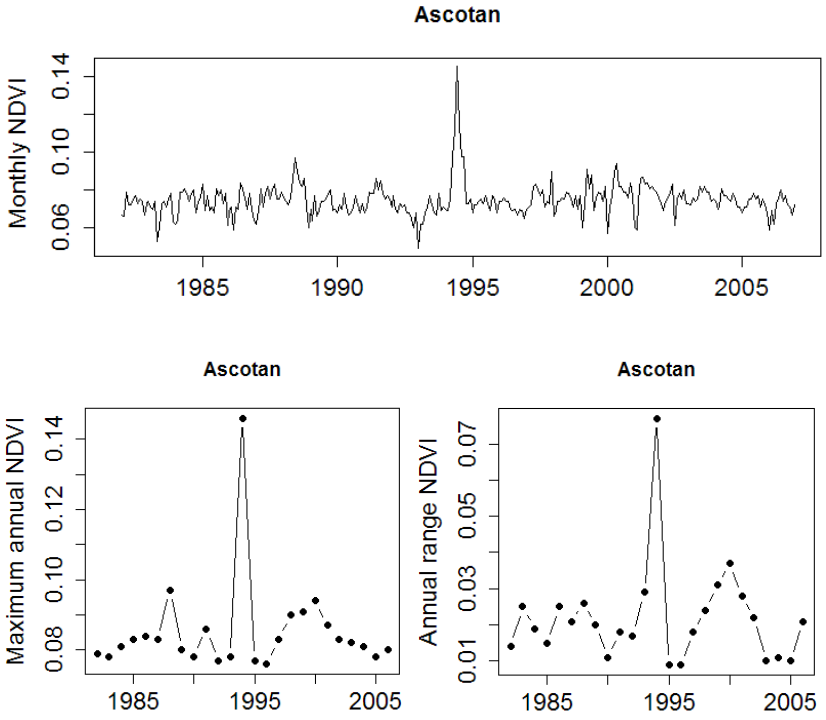




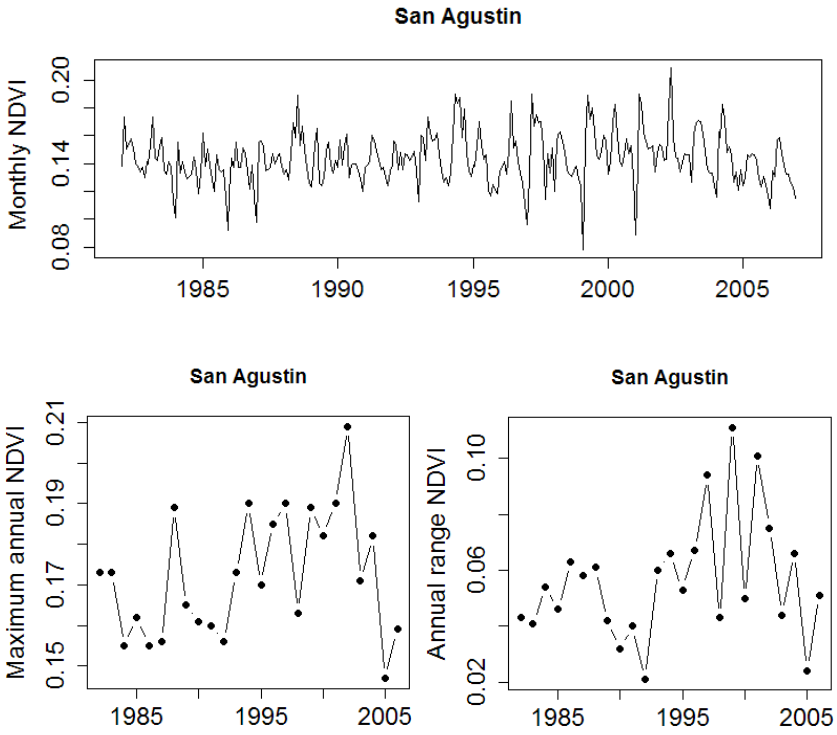
5. Inacaliri (4,016m)



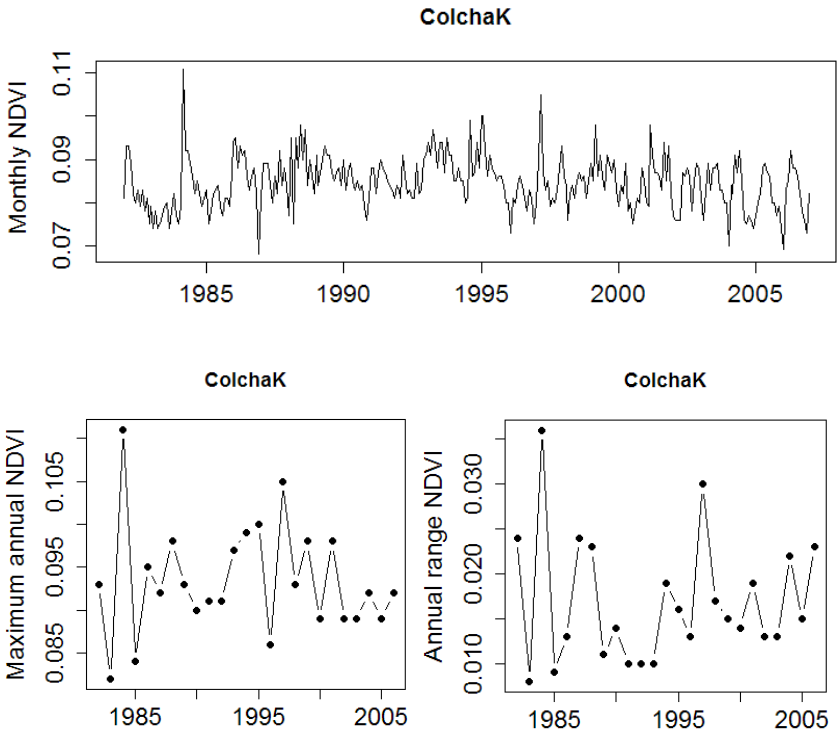
6. Ascotan (3,988m)



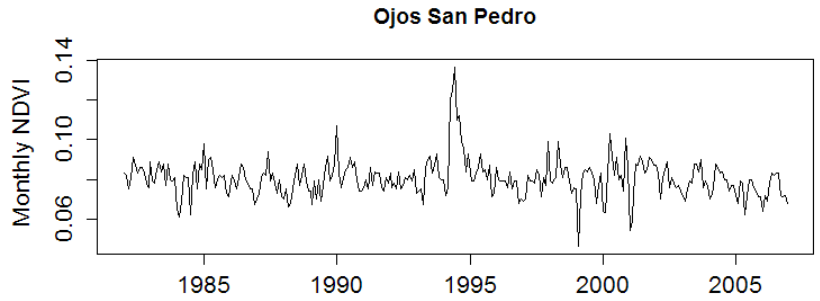
7. San Agustin (3,831m)

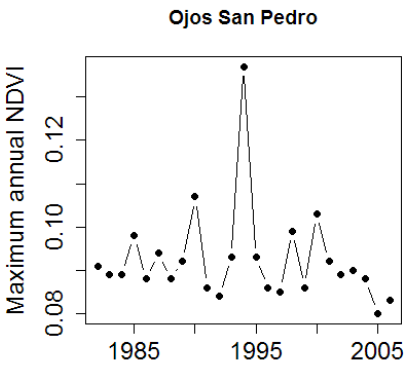


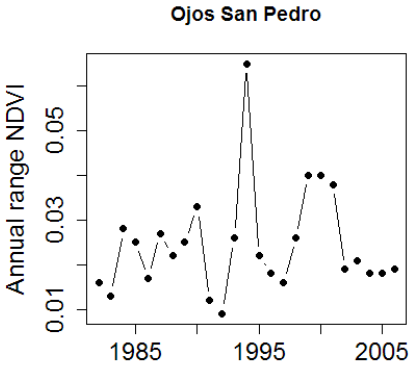
8. Colcha K (3,828m)



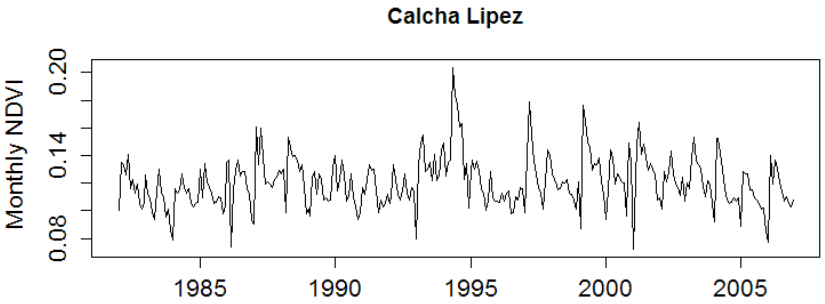
9. Ojos San Pedro (3,800m)

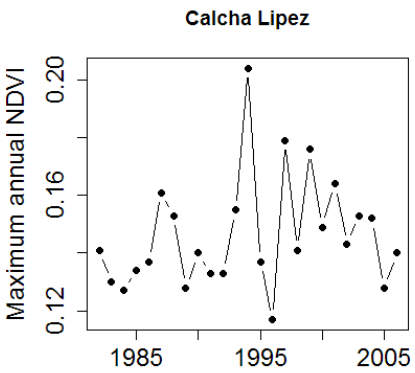


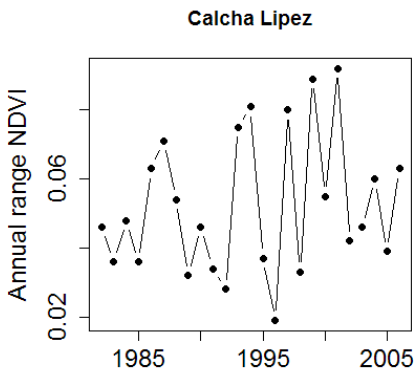




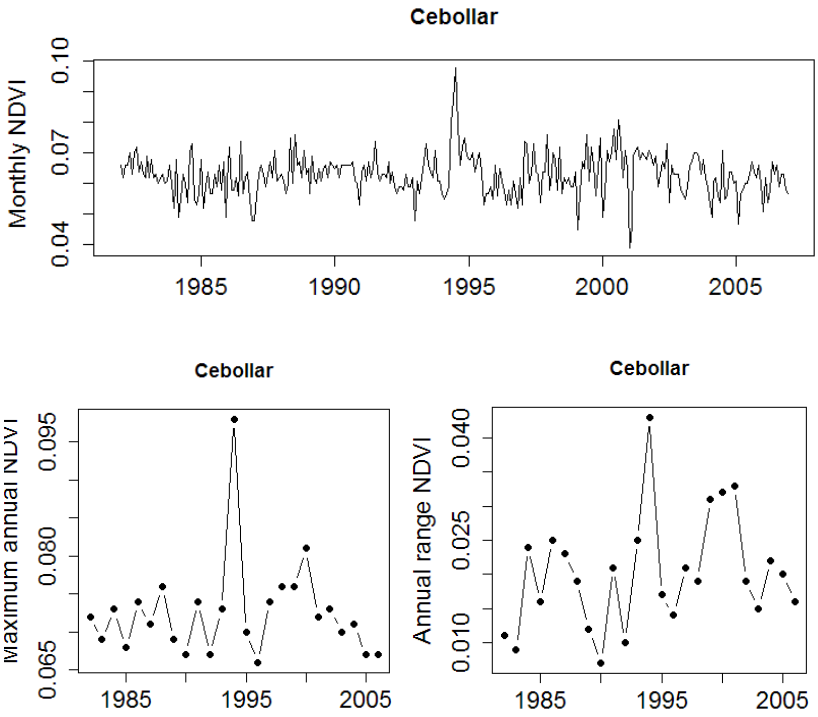
10. Calcha Lipez (3,788m)



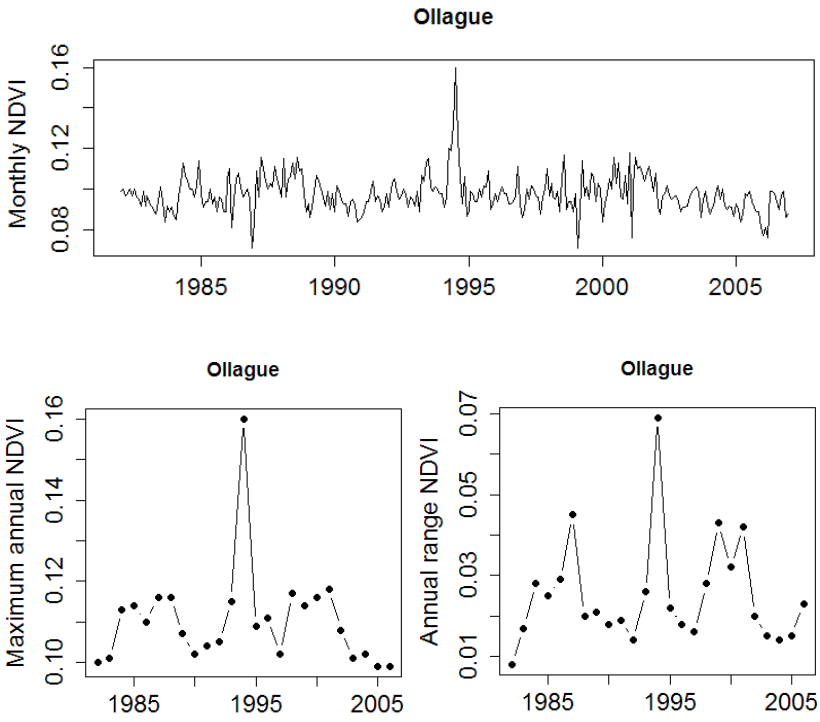




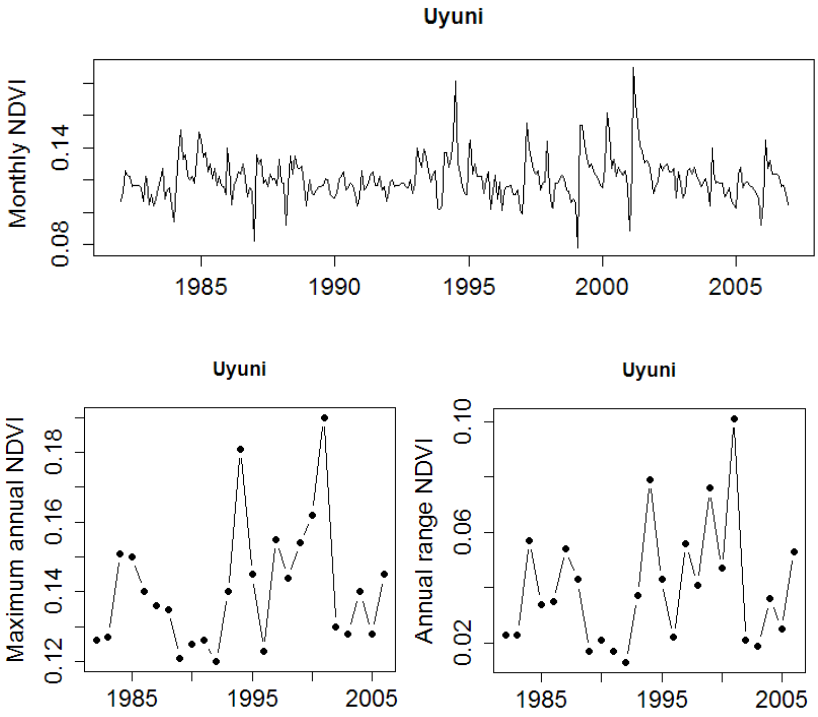
11. Cebollar (3,737m)



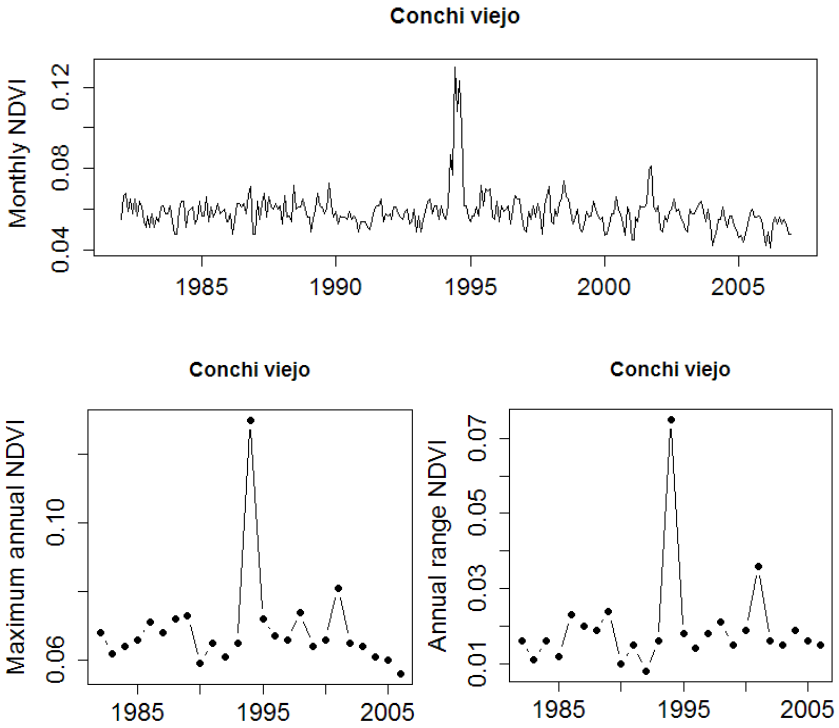
12. Ollague (3,704m)



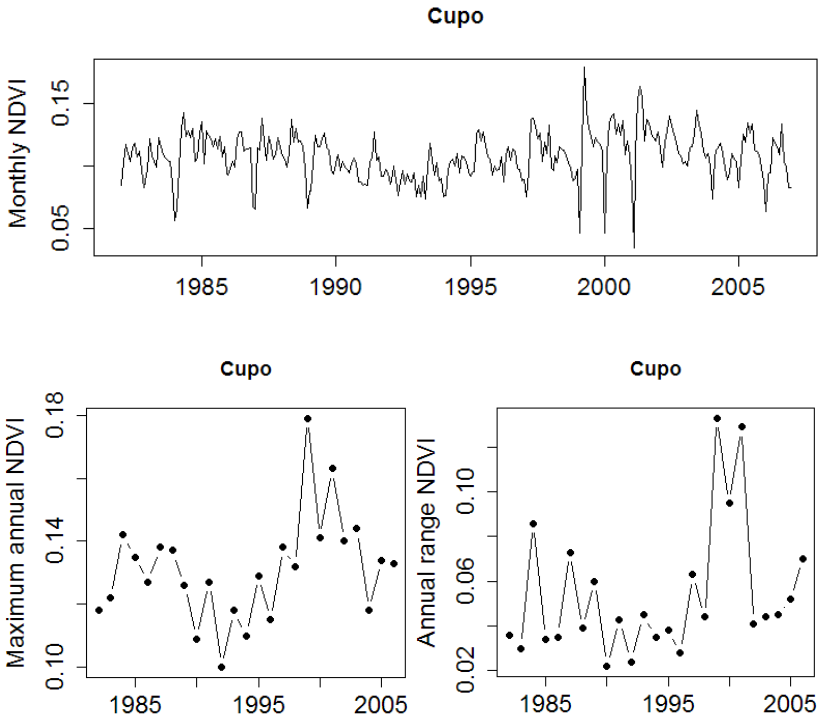
13. Uyuni (3,667m)



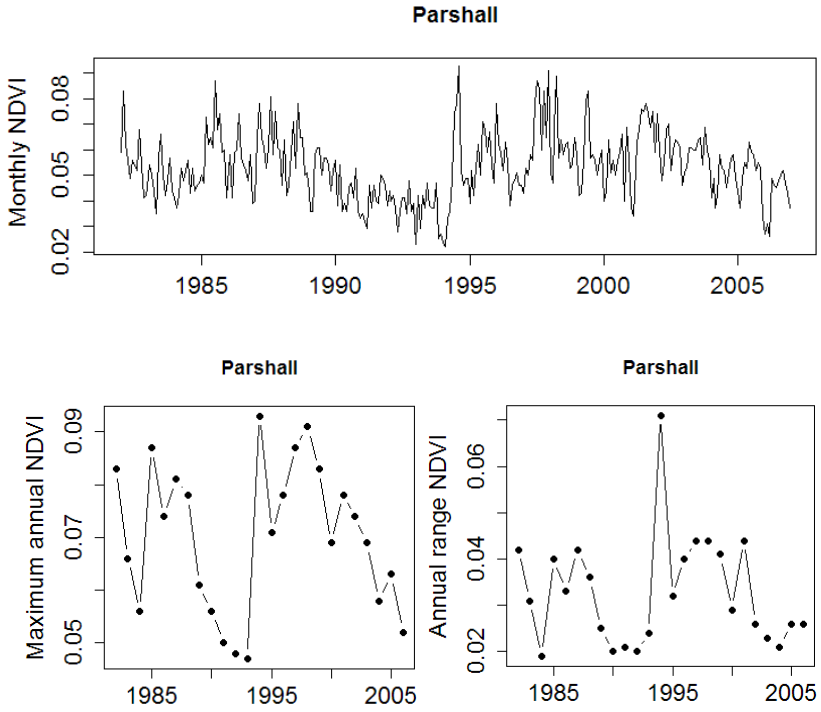
14. Conchi viejo (3,476m)



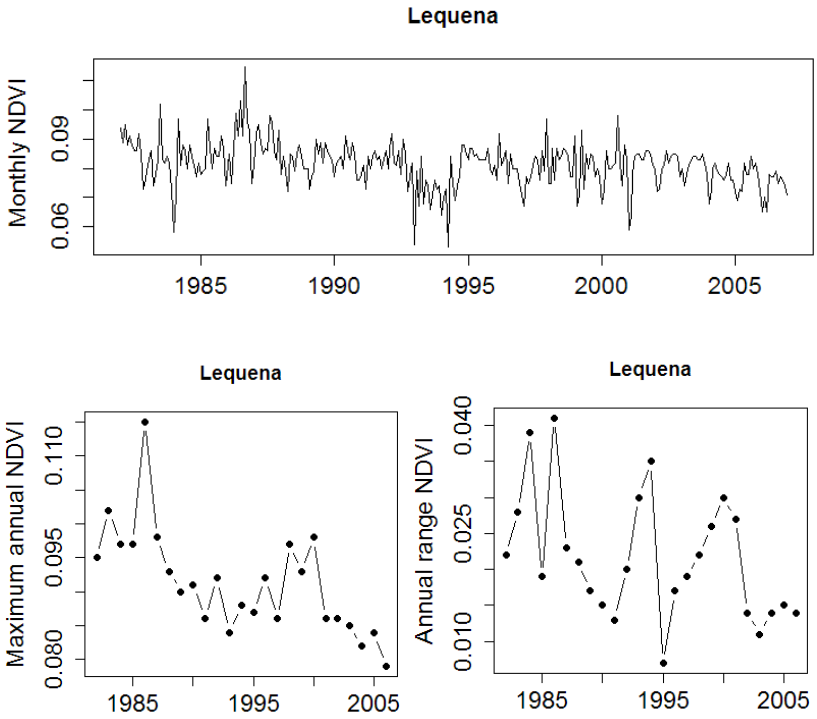
15. Cupo (3,364m)



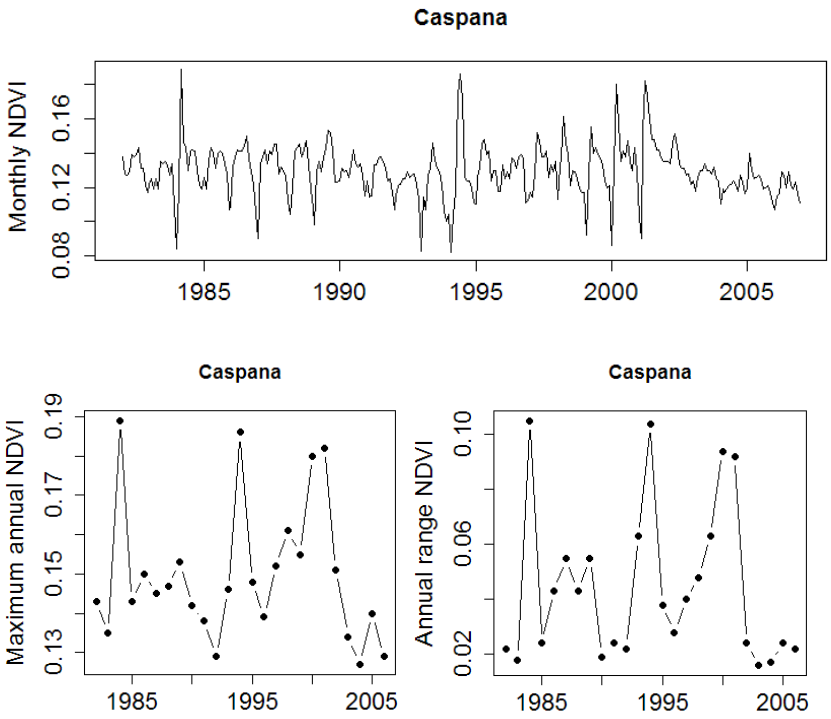
16. Parshall (3,338m)



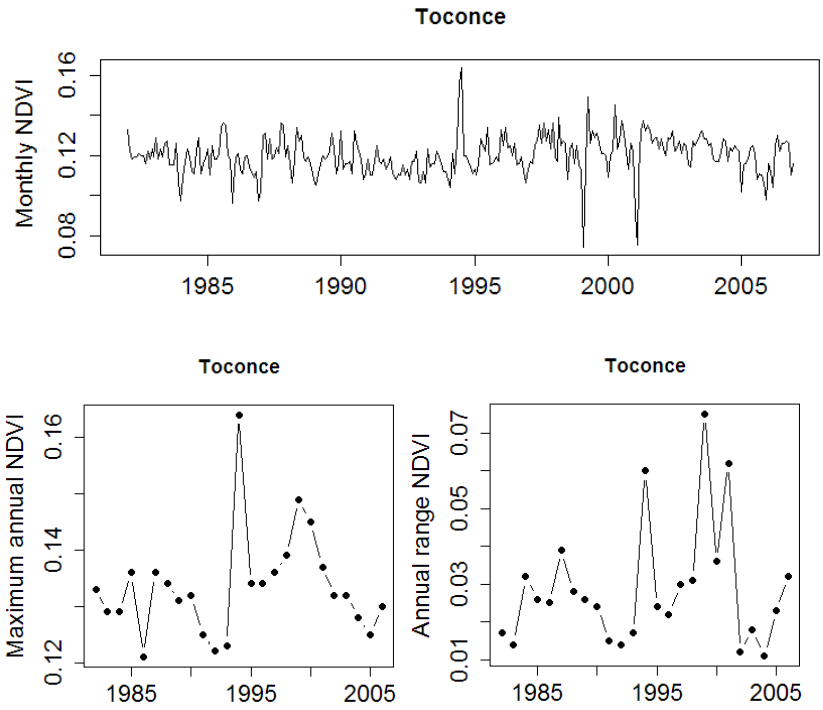
17. Lequena (3,314m)



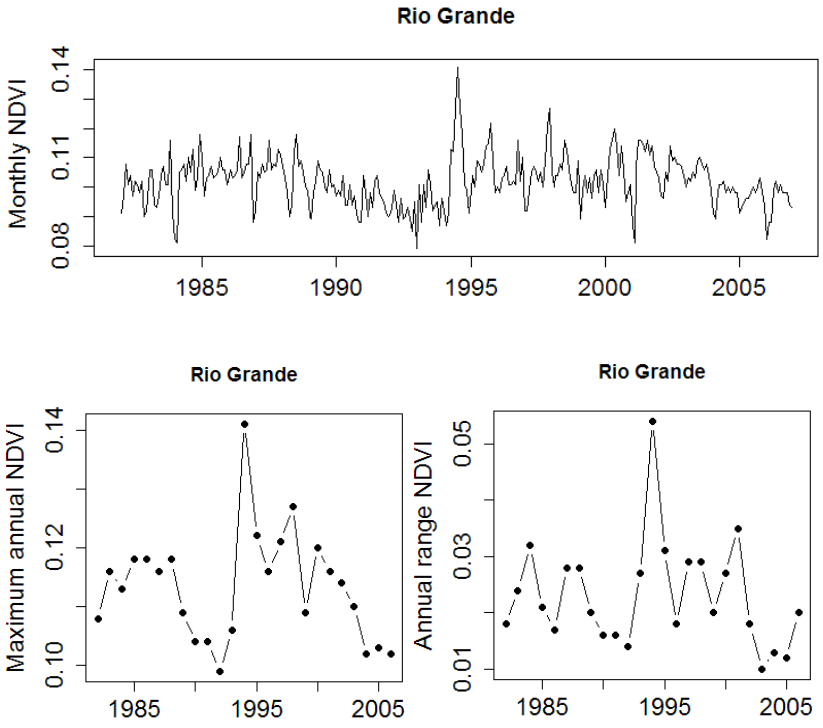
18. Caspana (3,298m)



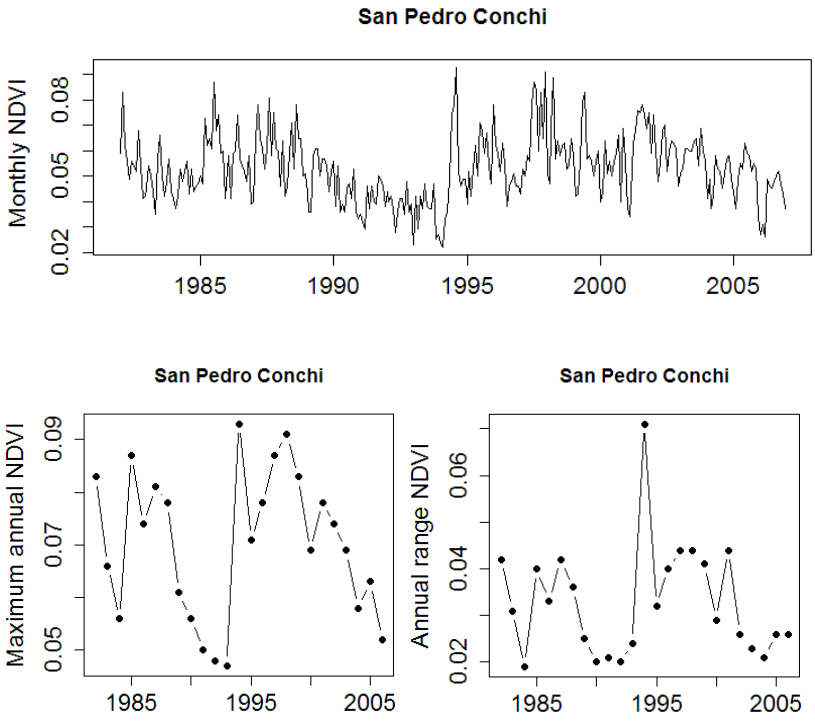
19. Toconce (3,297m)



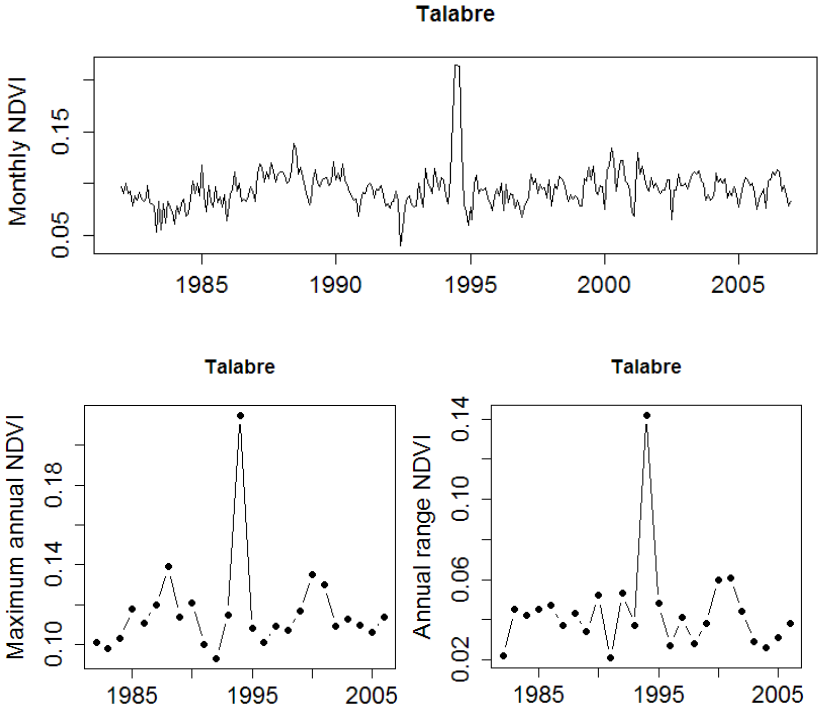
20. Rio Grande (3,288m)



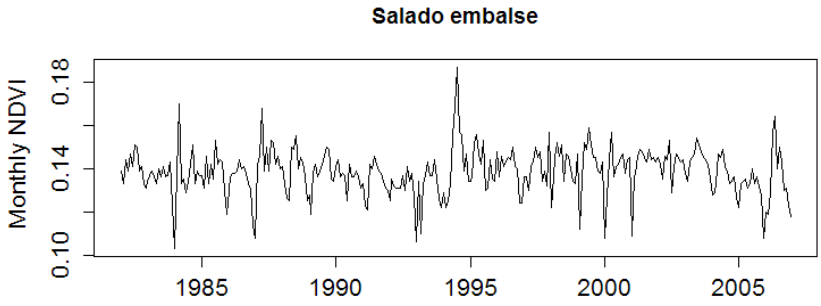
21. San Pedro Conchi (3,253m)

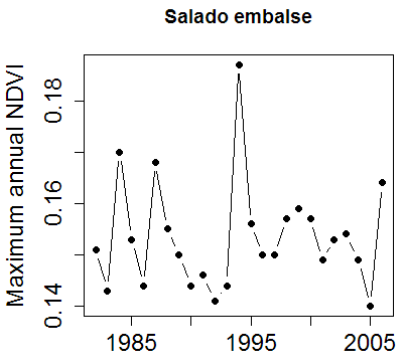


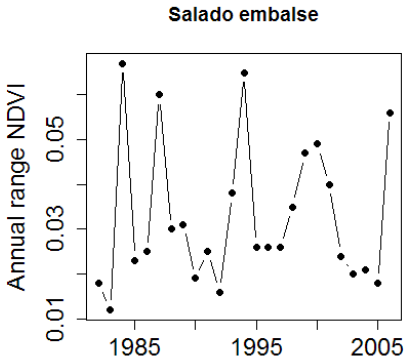
22. Talabre (3,252m)



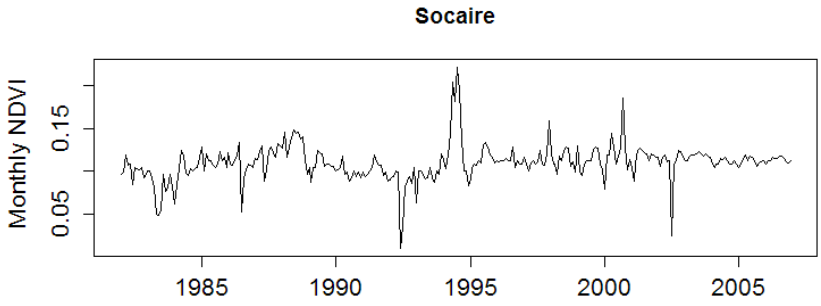
Salado embalse (3,243m)

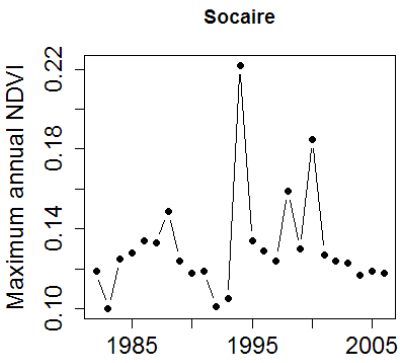


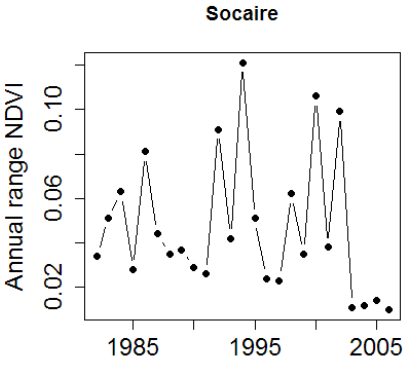




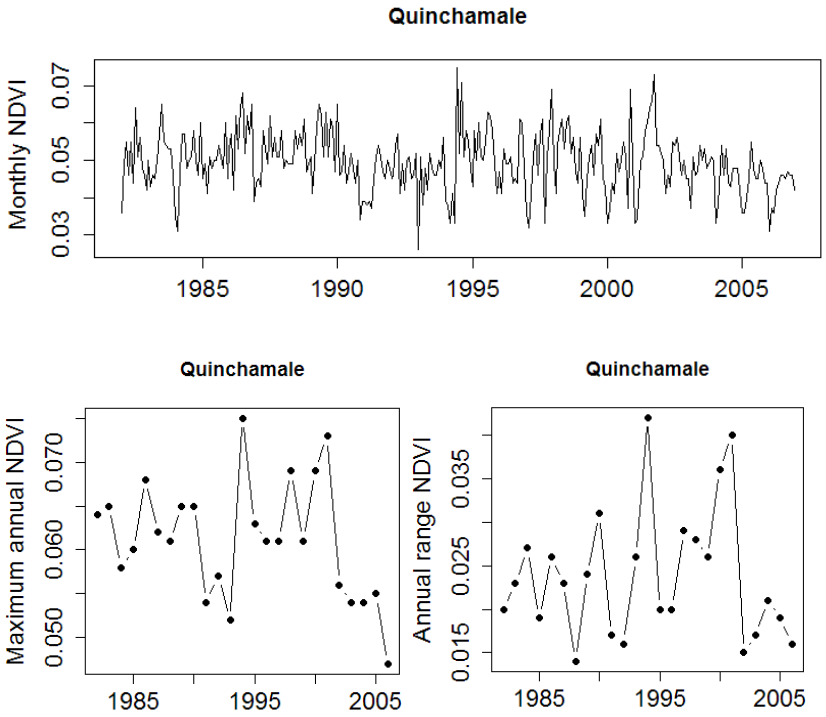
23. Socaire (3,240m)



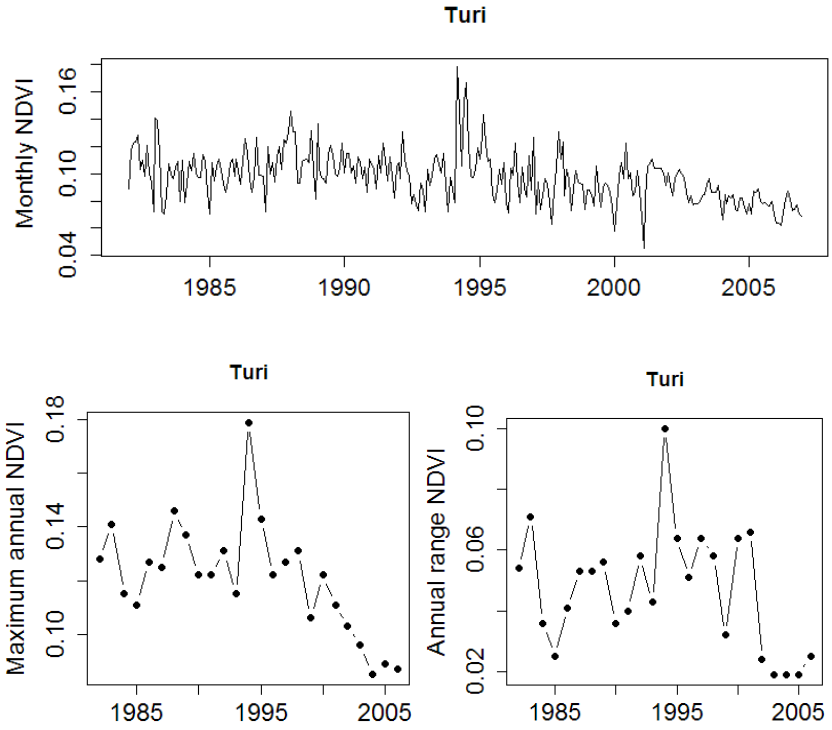




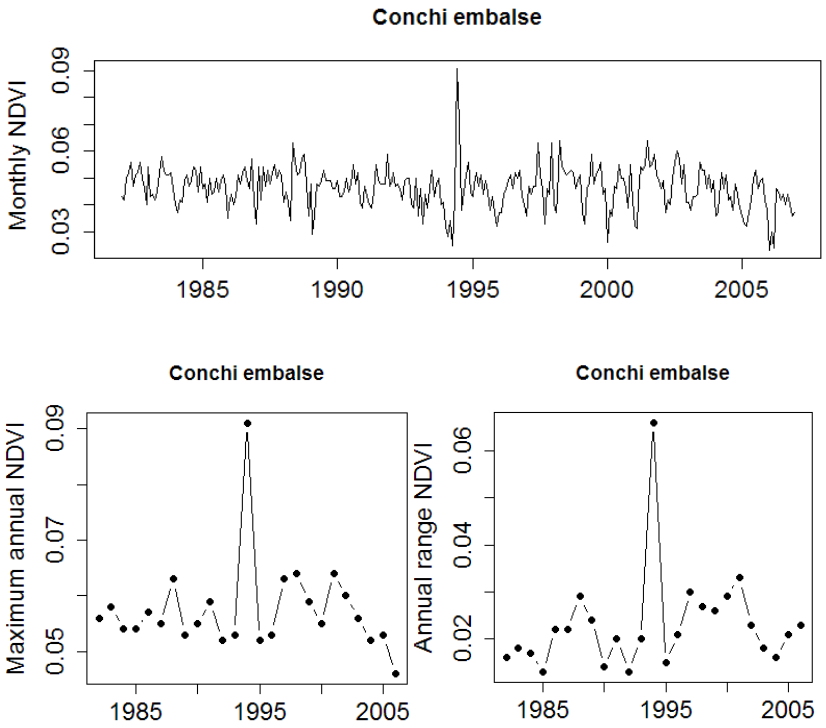
24. Quinchamale (3,073m)



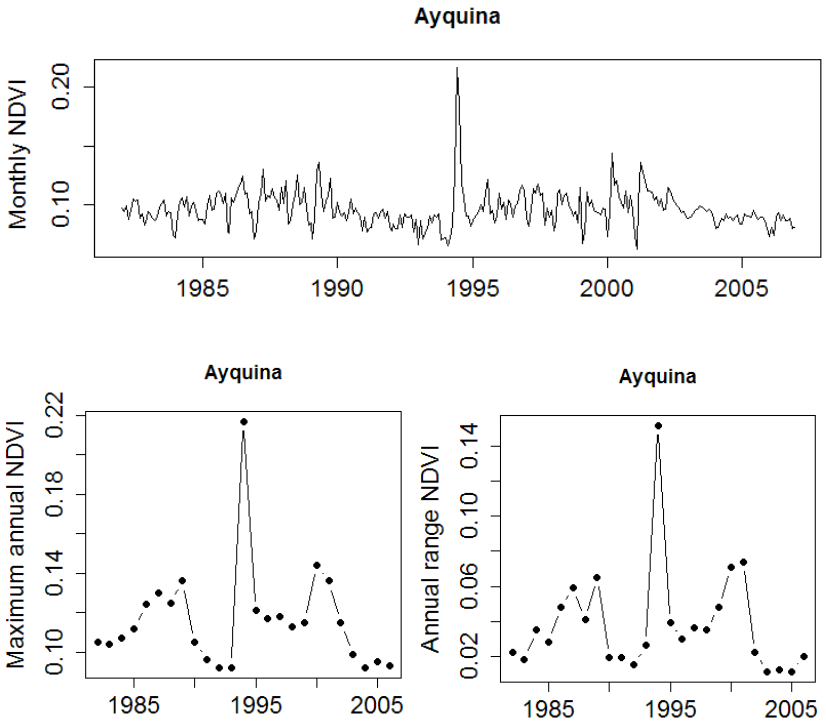
25. Turi (3,069m)



26. Conchi embalse (3,035m)



27. Ayquina (3,013m)



Chapter 5:

Vegetation responses to low rainfall in the Dry Puna

Abstract

Climate change can have serious consequences for primary productivity in dry mountains, where water is a limiting factor and plants are exposed to high radiation, strong winds and daily extremes of temperature. Plant species' adaptations and topography create a complexity of responses to climatic variation in mountains, which are not always captured by large-scale studies using coarse NDVI (Normalized Difference Vegetation Index) data. We therefore assessed responses of primary productivity to rainfall in the Dry Puna by analysing detailed NDVI metrics (at 30m resolution) across the study area and in subsets of pixels of different vegetation types, calibrated by extensive ground-truthing. Using general linear models and pairwise tests we investigated links between primary productivity, topography and low rainfall, by comparing a 'normal' and a 'dry' year (respectively, 1985 and 2009, with 131 and 12mm of rainfall over the rainy season), selected from a three-decade time series of climatic records with no significant trend. Overall, NDVI declined with elevation and increased along steeper and north-facing slopes, and towards the north-east of the study area (more humid, under Amazonian influence). With respect to a normal year, primary productivity declined in a low-rainfall year, and the decline was most pronounced in the more productive areas (north-eastern High Plateau and on the western slopes of the Andes). The more affected vegetation type was grassland dominated by Festuca tussocks and other mixed vegetation types with grasses and scrubs. Scrublands, dominated by Parastrephia spp. and Chuquiraga spp, where the most resilient to water scarcity. Also the vegetation associated to wetlands, dominated by Oxychloe spp and Distichia spp, which appeared to increase in productivity during the dry year. We conclude that rainfall is an important driver of productivity in the Dry Puna and that the potential impacts of climate change can be understood with increased specificity and accuracy when analyses are conducted at the level of vegetation type, with implications for the conservation of the Puna biodiversity.

5.1. Introduction

Interest on the impacts of climate change upon ecosystem function is increasing worldwide as temperature increases, rainfall becomes less predictable, and extreme events such as heat waves, droughts and floods are more frequent and of higher magnitude (IPCC 2014). In particular, there is a need to understand how directional changes in rainfall might affect primary productivity in mountains, among the most sensitive ecosystems to these phenomena (Beniston et al. 1997, Diaz et al. 2003).

Studies of primary productivity in arid and semi-arid regions, based on indexes derived from satellite images such as the Normalized Difference Vegetation Index (NDVI) (Malo and Nicholson 1990, Nemani et al. 2003, Pettorelli et al. 2005), show that the productivity dynamics in these regions are mainly driven by the effects of precipitation upon plant growth (Holmgren et al. 2006, De La Maza et al. 2009).

In mountain environments the complexity of the terrain creates microclimatic conditions and refuges from extreme weather, generating heterogeneous and patchy vegetation, with plants diversely adapted to the high-elevation, water stress and extreme temperatures (Körner 2003). Plants might develop deep or horizontally expanded roots to access water; some are perennial and others annual, of low stature or growing in the shape of rosettes close to the ground (Körner 2003, Hadley et al. 2013). Because of these various adaptations, their responses to climate change can be highly specific, shaped by physiological and morphological adaptations and their levels of habitat specificity (Körner 2003). There is, however, an important knowledge gap on fine-scale vegetation responses to rainfall variations in dry highland systems.

To address this question, we investigated the relationships between primary productivity (NDVI) and low rainfall in the Dry Puna, the most arid region of the High Andes, including the effects of topography and vegetation type. High elevation and water scarcity limit vegetation growth in the Dry Puna, and primary productivity is therefore very low (Chapter 4). The dominant vegetation types are grasslands and heaths, dispersed within a matrix of bare soil and rocks; green biomass is concentrated in and around wetlands in depressions and valleys, and expectedly more resilient to changes in rainfall as these are also fed from underground water (Squeo et al. 2006). Precipitation in the Dry Puna is largely limited to the austral summer months, without consistent trend over the past

decades in the study area (i.e. 1981-2010, Chapter 3), and positively correlated with large-scale changes in NDVI over that period (Chapter 4, using GIMMS NDVI datasets at a spatial resolution of 8km). Years with unusually low precipitation therefore provides opportunities to measure the responses of vegetation by comparing the distribution and magnitude of change of NDVI between a 'normal' and a 'dry' year at a higher spatial resolution using Landsat satellite images, with a resolution of 30m, and after calibrating NDVI values to vegetation types. We discuss how reduced precipitation can affect primary productivity in arid and spatially complex mountains, including differences in the responsiveness and resilience of vegetation types with diverse adaptations.

5.2. Methodology

5.2.1. Study area

The study area is located in the Central Andean Dry Puna ecoregion, around the triple frontier between Bolivia, Chile and Argentina, covering 40,915km2 of land above3,300m, corresponding to the Puna and High-Andean vegetation belts (Arroyo and Cavieres 2013). The study area encompasses parts of the High Plateau, which receives humidity from the Amazon and Gran Chaco basins (Vuille and Keimig 2004), and the drier Western Slopes of the Andes, under Pacific influence. The climate is arid to semi-arid, with precipitation concentrated during the summer months December to March (Garreaud et al. 2003) and with an average summer rainfall ranged between 16 and 260mm for the period 1982-2006, across 28 weather stations at high elevation (Chapter 4).

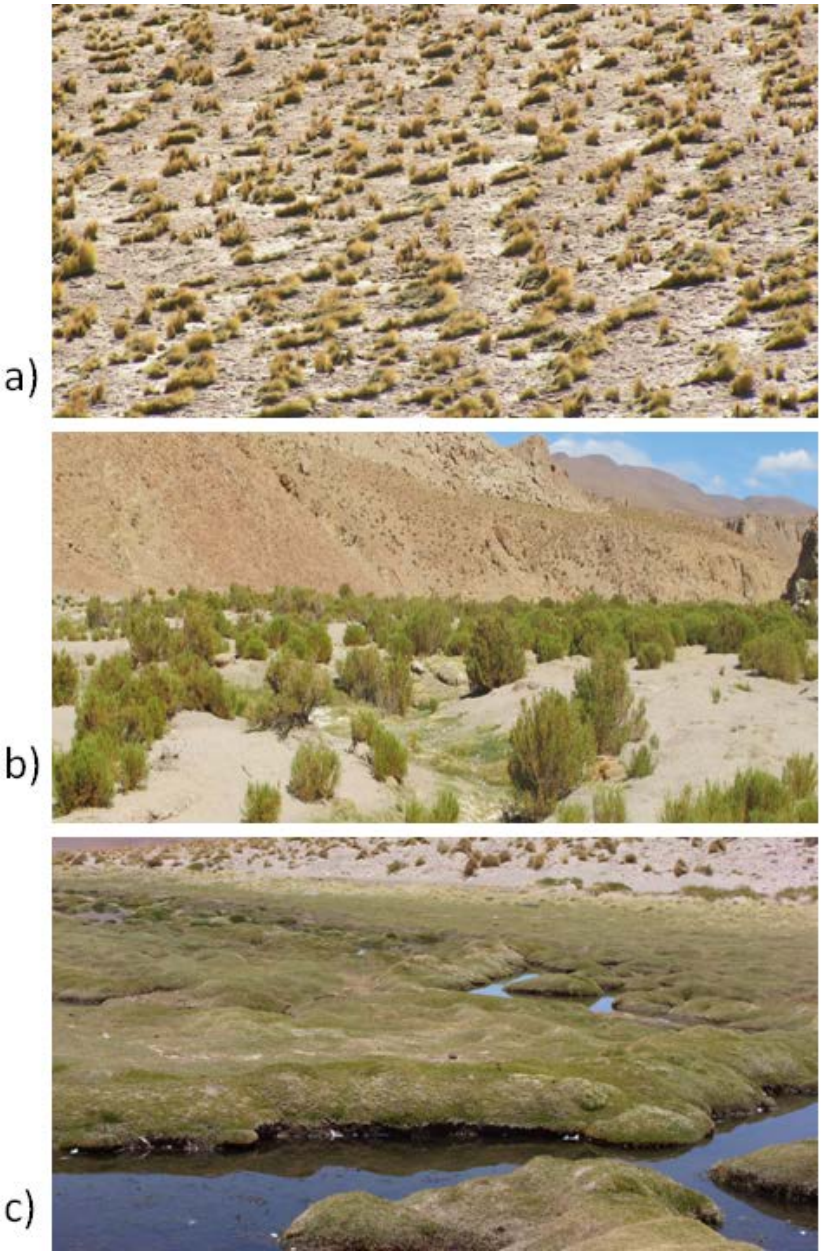


Figure 5.1. Main vegetation types in the Dry Puna; a) grasslands b) scrublands and c) wetland vegetation, locally called *vegas* and *bofedales*.

The landscape is dominated by rocky and barren ground and the vegetation is sparse. Grasslands are formed by tussocks of *Festuca orthophylla* and *Stipa frigid* and scrublands are dominated by *Parastrephia quadrangualris, Fabiana denudate* and *Chuquiraga atacamensis* (Figure 5.1a, b). The vegetation associated to wetlands is composed by cushion plants of *Distichia* spp. and *Oxychloe* spp. and grasses such as *Festuca hypsophila* and *Cortaderia atacamensis* (Villagran et al. 1981, Villagrán et al. 1982, Marquet et al. 1998, Arroyo and Cavieres 2013) (Figure 5.1c). Wetland-associated vegetation is dense

and evergreen, permanently irrigated by rainfall, snow-melting streams and/or underground water (Squeo et al. 2006, Otto et al. 2011). The contribution of snow melting is however negligible, as precipitation occurs almost exclusively in summer and winter snowfalls are rare - originated by cold upper-air low pressure systems from the Pacific penetrating the area (Vuille and Ammann 1997).

The extreme environmental conditions limit human establishment in the Dry Puna; small settlements are close to water sources and valleys, suitable to graze herds of llamas (*Lama glama*) and for small-scale agriculture (Villagrán and Castro 1997, SaviaGlobal 2006, Clark 2012). At lower elevations, settlements and mining operations extract underground water, with potential impacts on the highland ecosystems, not well understood due to the lack of reliable information.

5.2.2. Rainfall time series and selection of 'normal' and 'dry' years

A precipitation time series was created using rain gauge data from seven weather stations above 3,300m, provided by the Dirección General de Aguas Chile and the Servicio Nacional de Meteorología e Hidrología in Bolivia, between 1981 and 2010. We selected weather stations that were included within the limits of the Landsat images used for this study and with at least 25 years of data, namely: Lequena, Parshall, Cupo, Linzor, Ojos San Pedro, Inacaliri and Ascotan. Annual rainfall was characterized by the accumulated amount of rainfall over the summer months (December to March of the next year); rainfall outside this period was negligible. The average summer rainfall for the seven weather stations was 72mm and none of the time series showed a significant trend (Chapter 3). In order to compare years of different rainfall amounts we selected, from within 'normal' and 'dry' periods, a pair of years that were sufficiently apart to avoid temporal autocorrelation and that were also represented by good-quality satellite images (see section below). An image from 1985 was chosen to represent 'normal' rainfall conditions (average 131mm across the seven weather stations) and one from 2009 to represent 'dry' conditions (average 12mm; within the 15th and 30th percentiles of three and two of the weather stations, respectively) (Figure 5.2).

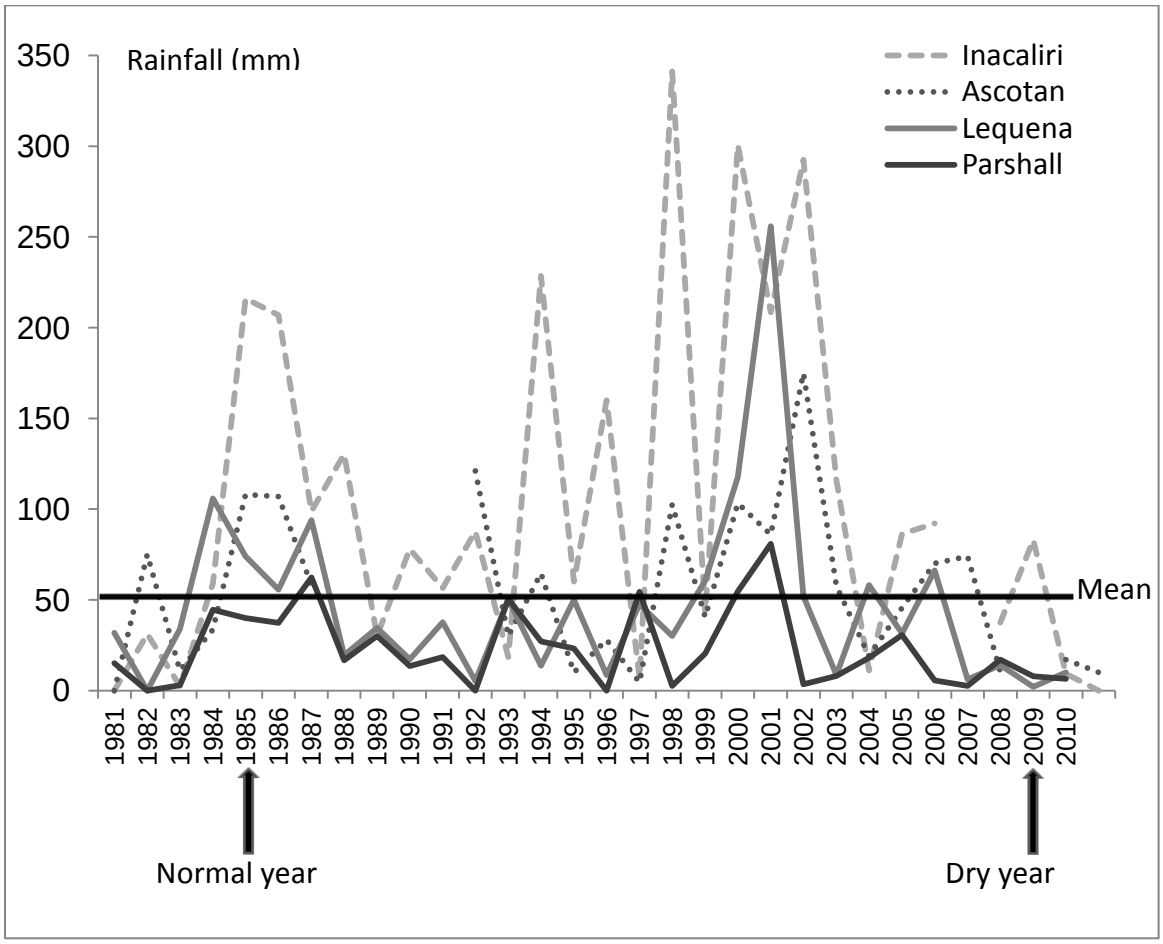


Figure 5.2. Time series of rainfall data from four weather stations in the study area (located around the triple frontier of Argentina, Bolivia and Chile).

5.2.3. Primary productivity data

NDVI values were derived from multispectral information provided by Landsat Thematic Mapper (TM) images. With a spatial resolution of 30m, Landsat images contain information at a sufficient resolution to study changes on NDVI at the vegetation type level, which cannot be obtained with MODIS at 250m. The Landsat images used corresponded to Path Rows 233 75 and 233 76 (obtained from Earth Explorer, U.S. Geological Survey's Earth Resources Observation and Science EROS, http://edcsns17.cr.usgs.gov/NewEarthExplorer/). These were the only images available without error lines or clouds to represent years within the 'normal' and 'dry' periods, that were geometrically corrected and from the same time of the year (17/05/1985 and 17/04/2009, respectively, towards the end of the rainy season) . All images were

atmospherically and radiometrically corrected using Landcor (Zelazowski et al. 2011). Topographic corrections were not implemented, as these tend to weaken the vegetation signal (Nordberg and Evertson 2003) and have often failed to remove cast shadow effects in Landsat images of mountain areas (Zhang et al. 2011). ERDAS 10 software was used to resample the Landsat images from geographic coordinates to the projected system WGS 84 19S (using a Nearest Neighbourhood Resample Method) and to calculate NDVI values.

NDVI is considered a good indicator of vegetation productivity and biomass in arid and semi-arid regions (Nicholson et al. 1990, Herrmann et al. 2005, De La Maza et al. 2009, Fabricante et al. 2009). This index combines the spectral information reflected by vegetation, captured by satellites in the visible and near infrared bands (corresponding to bands 3 and 4 in Landsat TM images respectively). NDVI is calculated as a ratio between these bands, as per the standard formula: NDVI= (Band 4 –Band 3)/ (Band 4+ Band3) (Tucker and Sellers 1986, Pettorelli et al. 2013). NDVI values vary between -1.0 to 1.0. Pixels with NDVI values lower than 0.05, a commonly accepted threshold for vegetation presence, were excluded from the analyses (Tucker et al. 1986, Tucker and Sellers 1986, Myneni et al. 1997, Liang et al. 2005).

Changes in NDVI were calculated between the 'normal' and 'dry' year, pixel by pixel, using the method of subtractive differences (Chuvieco, 2008), so that *NDVI change* = *NDVI normal* year – *NDVI dry year*. A new image was created representing changes in NDVI (*NDVI change*). All spatial analyses were conducted in ArcGIS 10 (ESRI, 2010).

5.2.4. Data analyses

5.2.4.1. Spatial patterns of NDVI and NDVI change

A random sample of 10,000 pixels were obtained from each image (*NDVI normal*, *NDVI dry* and *NDVI change*) and analysed with General Linear Models to explore NDVI patterns with respect to geographic location (i.e. latitude and longitude in metres, WGS 84 UTM 19S projection) and topography. Topographic variables included elevation (m), slope (degrees) and aspect (direction of the slope), derived from 1 arc-second resolution ASTER databases (Advanced Spaceborne Thermal Emission and Reflection Radiometer, NASA Land Processes Distributed Active Archive Center and USGS/EROS 2001. http://gdex.cr.usgs.gov/gdex/) and resampled from geographic coordinates to WGS84 19S. Two measures of aspect were calculated: eastness=sine(aspect) (where 1 is east-facing and

-1 west-facing) and northness=cosine(aspect) (1 north-facing and -1 south-facing) (Clark et al., 1999). Spatial analyses were conducted in ArcGIS 10 (ESRI, 2010). As *NDVI normal* and *NDVI dry* showed positive skewness, a log transformation was applied to run general linear models. Goodness of fit was assessed with the adjusted R^2.

5.2.4.2. Changes by vegetation type

NDVI values of the dominant vegetation types were calibrated from extensive ground-truthing data collected by the authors in collaboration with the Andean Cat Alliance. Because of the large size of the study area, with many inaccessible places and military minefields in the frontiers, we sampled 885 points that could be reached by car or walking, covering the main vegetation formations (Figure 5.3). Data was collected between Dec 2010/Jan 2011 and Dec 2011/Jan 2012, following a standardized methodology that included estimation of ground, rock and vegetation cover by dominant species, within an area of 5m radius, using the Braun-Blanquet scale (5= 100-75%; 4= 74-50%; 3= 49-25%; 2= 24-5%; 1= < 5%) (Cossios et al. 2007).

Vegetation samples were grouped into seven categories based on the dominant species and vegetation cover (only the vegetation associated to wetlands had a vegetation cover >50%):

- ***Grassland:*** vegetation dominated by tussocks of *Festuca* and *Stipa* spp.
- ***Open grassland:*** as above, with <25% cover
- ***Scrubland:*** vegetation dominated by shrubs of the genus *Parastrephia, Chuquiraga* and *Fabiana*
- *O**pen scrubland:*** as above, with <25% cover
- ***Mixed scrubland:*** mixture of shrubs and grasses; same dominant species as the vegetation types above
- ***Open mixed scrubland:*** as above, with <25% cover
- ***Wetland vegetation***: dominated by plants of the Juncaceae family such as *Oxychloe andina* and *Patosia clandestine*; locally known as ‘vegas’ and ‘bofedales’.

Values of *NDVI normal*, *NDVI dry* and *NDVI change* were extracted for each pixel corresponding to the location of a ground-truthing sample and compared between ‘dry’ and

'normal' years across vegetation types, using Paired T-test analyses (with sample locations of the same vegetation type as units of replication).

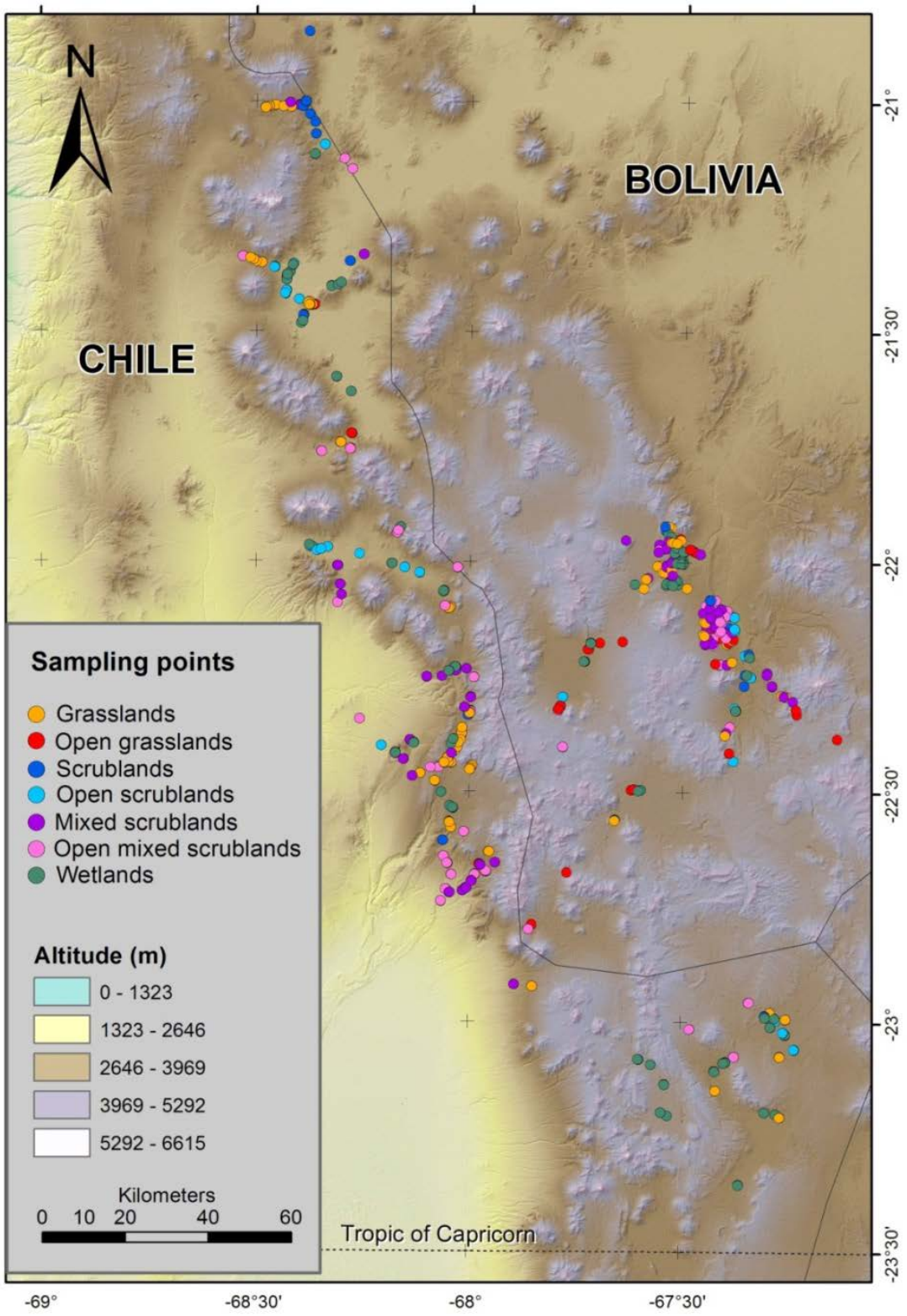


Figure 5.3. Map with the location of ground-truthing samples, coloured-coded by vegetation type, in the area covered by two Landsat images above 3,300m.

5.3. Results

5.3.1. Spatial patterns of NDVI and NDVI change

Primary productivity was heterogeneously distributed across the study area. There were vast areas without vegetation, particularly around the high peaks. The most productive areas were towards the north-east in the High Plateau in Bolivia and on the Western Andean slopes in Chile (Figure 5.4).

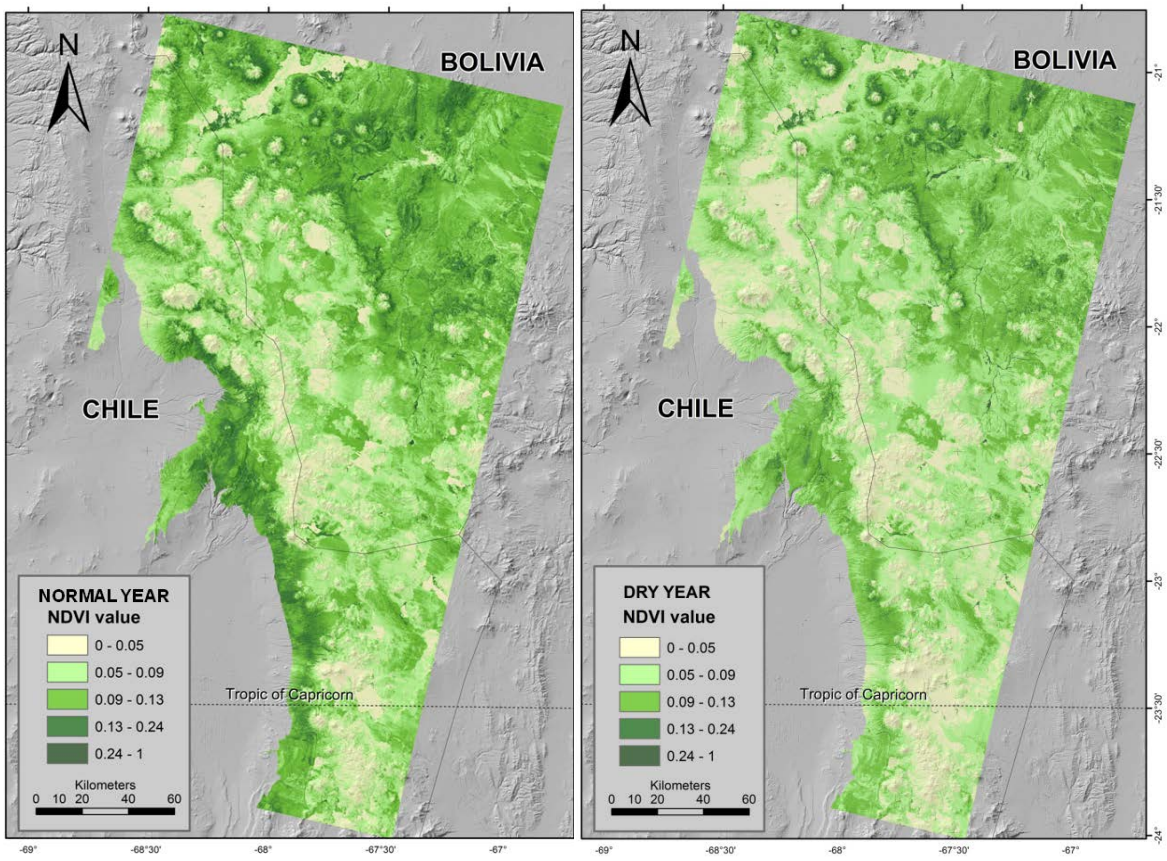


Figure 5.4. NDVI values during a *normal* (left) and a *dry* year (right) in the study area above 3,300m.

Associations between NDVI values and elevation, aspect (northness), latitude and longitude were significant and consistent across 'normal' and 'dry' years (linear model $F_{(6, 9757)}$: 310.5, p<0.000, R-sq: 0.1598 and $F_{(6, 9757)}$: 269.1, p<0.000, R-sq: 0.1414 respectively) (Table 5.1). Primary productivity increased with decreasing elevation (as expected from

increasing temperatures), increasing slope (e.g. Western Slopes of the Andes), northern orientations (receiving more sunlight and moisture), and towards the northeast of the study area (with more humidity) (Table 5.1). Productivity was on average higher in the 'normal' than in the 'dry' year (*NDVI normal:* 0.106 ±0.03, *NDVI dry:* 0.093 ±0.03, n= 10,000 pixels each year). *NDVI change*, was larger towards the south-west of the study area at lower elevation and with steeper slopes (Table 5.1, linear model, $F_{(6, 9757)}$: 177.7, p<2.2e-16, R-sq: 0.09798).

Figure 5.5 showed that areas with larger NDVI changes, and specifically with reduced productivity during the 'dry' year (Figure 5.5, in red), were mainly confined to the Western Slopes, but also in the northern part of the High Plateau. The more productive areas (with higher NDVI during a 'normal' year) showed stronger responses to dry conditions than the less productive areas (Figures 5.4 and 5.5). Small patches of increased productivity during the 'dry' year were clustered around the highest peaks, lagoons and salt pans (e.g. Salar de Tara, Salar de Pujsa, Laguna Pastos Grandes, Laguna Capina, Laguna Salada and Salar Quisquiro) (Figure 5.6). This is likely an artifact from the reflection of salt, water and snow captured by the satellite.

	NDVI dry		*NDVI normal*		*NDVI change*	
Predictors	Coefficient	p value	Coefficient	p value	Coefficient	p value
Longitude	**6.000E-07**	0.000	**2.559E-07**	0.000	**-7.467E-08**	0.000
Latitude	**3.000E-07**	0.000	**1.189E-07**	0.000	**-3.797E-08**	0.000
Elevation	**-6.180E-05**	0.000	**-1.123E-04**	0.000	**-1.413E-05**	0.000
Slope	**1.822E-03**	0.000	**2.708E-03**	0.000	**3.100E-04**	0.000
Eastness	3.767E-04	0.816	3.157E-03	0.049	4.949E-04	0.091
Northness	**5.234E-03**	0.001	**6.530E-03**	0.000	3.802E-04	0.197

Table 5.1. Summary of linear models adjusted to NDVI metrics (log transformed) from a random sample of 10,000 pixels of NDVI in a 'normal' year, a 'dry' year and their difference (*NDVI change).* Significant relationships highlighted in **bold**.

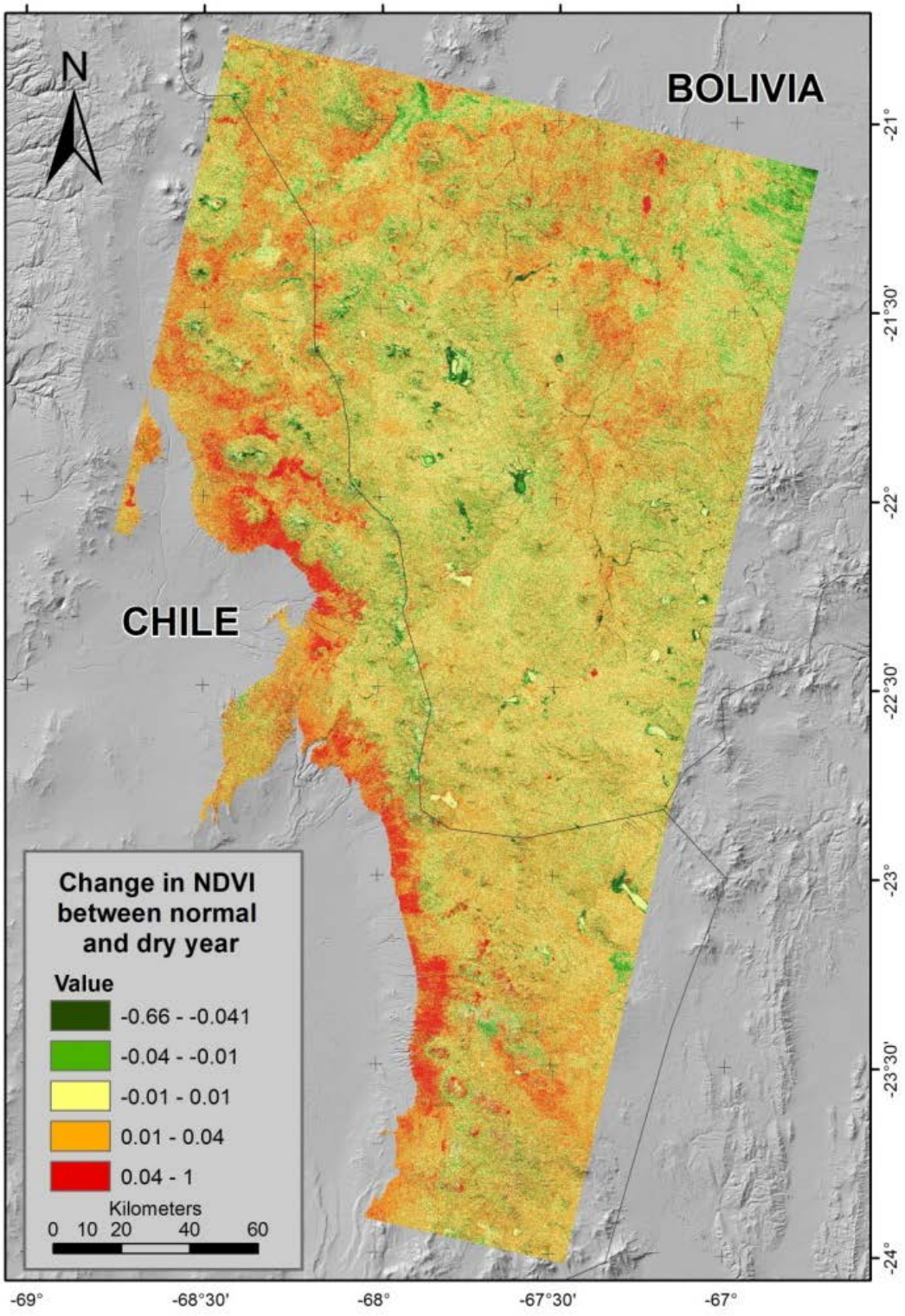


Figure 5.5. Changes in NDVI between a 'normal' and a 'dry' year (=*NDVI change*) above 3,300m. Areas in red indicate zones where primary productivity dropped most markedly.

5.3.2. Changes by vegetation type

Wetlands and scrublands were the most productive vegetation types; open grasslands and open scrublands the least productive (Table 5.2). Across all vegetation types, mean *NDVI normal* was higher (0.116 ±0.06) than the mean *NDVI dry* (0.109 ±0.08).

Vegetation types	*NDVI normal* mean (SD)	*NDVI dry* mean (SD)	*NDVI change* mean (SD)	Altitude mean (SD)	Samples (n)
Grassland	0.101 (0.03)	0.085 (0.03)	0.016 (0.02)	4,260 (194)	215
Open grassland	0.098 (0.03)	0.086 (0.03)	0.012 (0.02)	4,265 (245)	60
Scrubland	0.132 (0.08)	0.145 (0.13)	-0.013 (0.06)	4,110 (197)	37
Open scrubland	0.091 (0.05)	0.084 (0.08)	0.007 (0.05)	3,945 (242)	67
Mixed scrubland	0.122 (0.03)	0.107 (0.04)	0.015 (0.03)	4,129 (276)	142
Open mixed scrubland	0.110 (0.04)	0.095 (0.05)	0.014 (0.03)	4,146 (320)	133
Wetland vegetation	0.146 (0.11)	0.156 (0.12)	-0.011 (0.07)	4,111 (284)	231

Table 5.2. Mean NDVI values across vegetation types during a *normal* and a *dry* year, and the difference between them. SD: standard deviation; n= number of ground sample points.

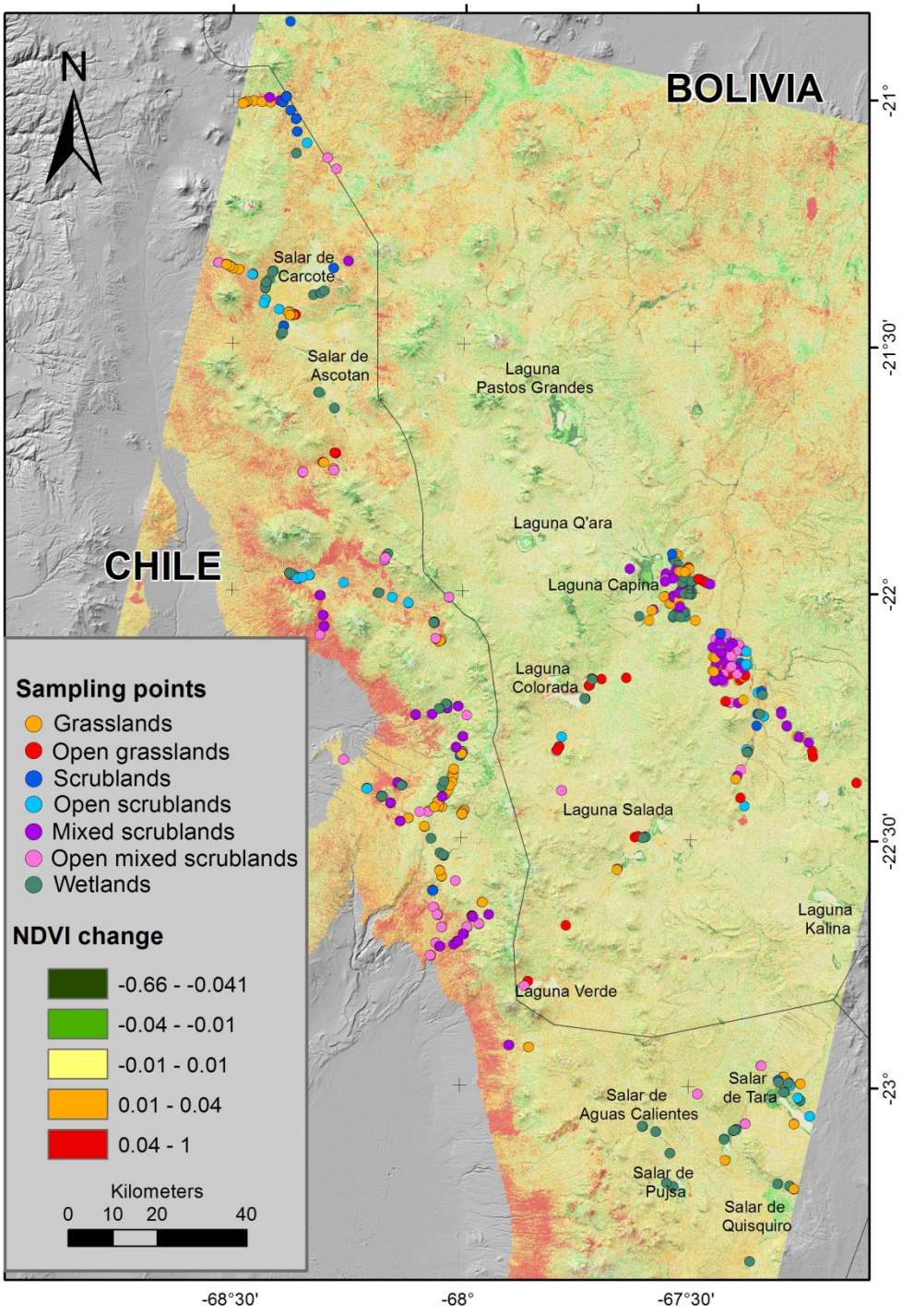
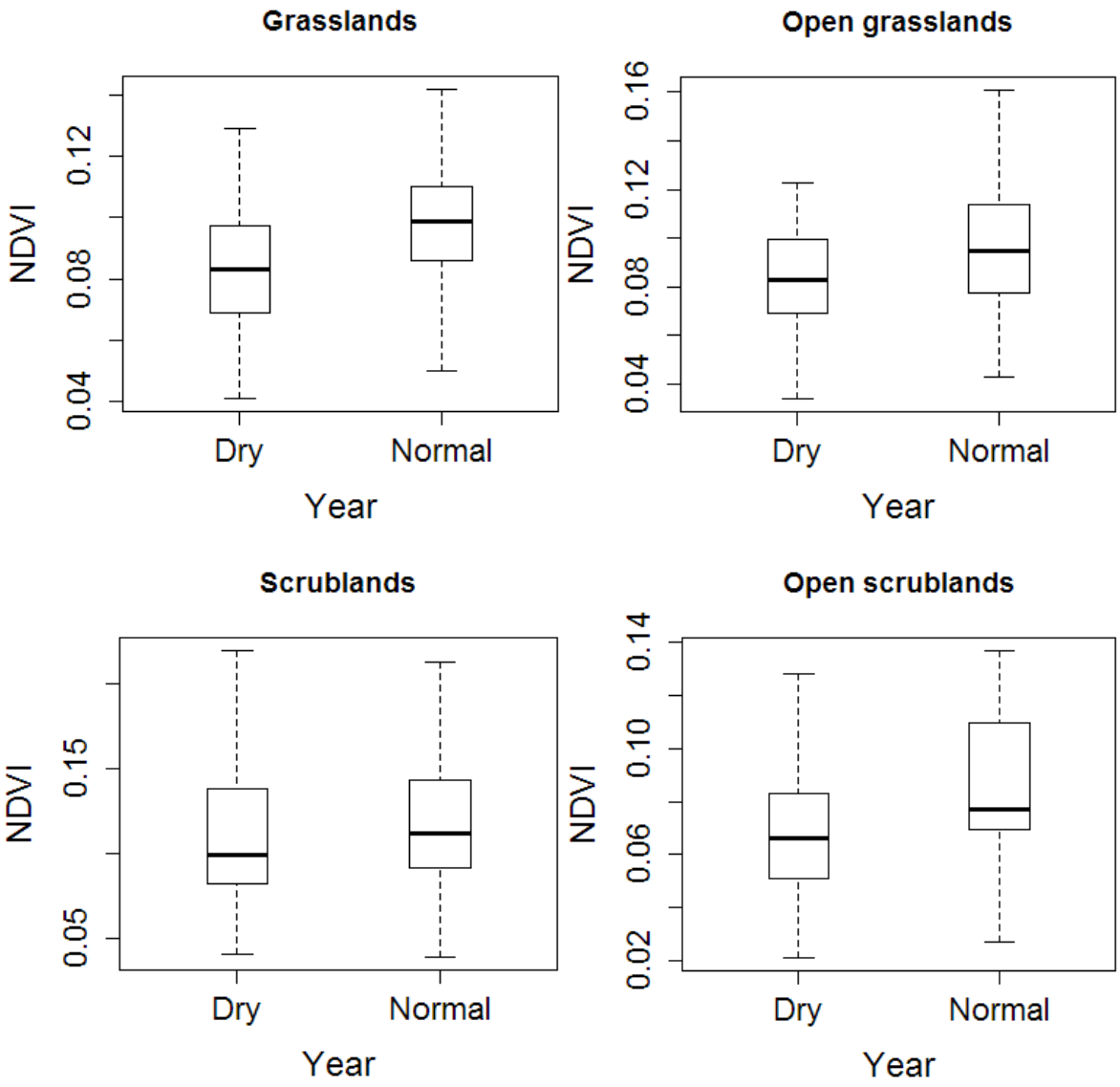


Figure 5.6. Map with the locations of ground-truthing samples, coloured-coded by vegetation type and changes in NDVI between a *normal* and a *dry* year (*=NDVI change*) above 3,300m. Areas in green indicate zones where primary productivity increased during the dry year.

Most vegetation types showed significantly lower productivity during the *dry* than *normal* year (Table 5.2 and Figure 5.7), including grasslands (Paired t test: t = -10.0488, p<0.0), open grasslands (Paired t test: t = -5.4626, p<0.0), open scrublands (Paired t test: t =-2.1268 , p<0.037), mixed scrublands (Paired t test: t = t = -6.7664, p<0.0) and open mixed scrublands (Paired t test: t =-8.3128 , p<0.0). Scrubland did not show significant change and the vegetation associated to wetlands increased their productivity during the dry year (Paired t test: t = 2.4987 p<0.013) (Figure 5.7).



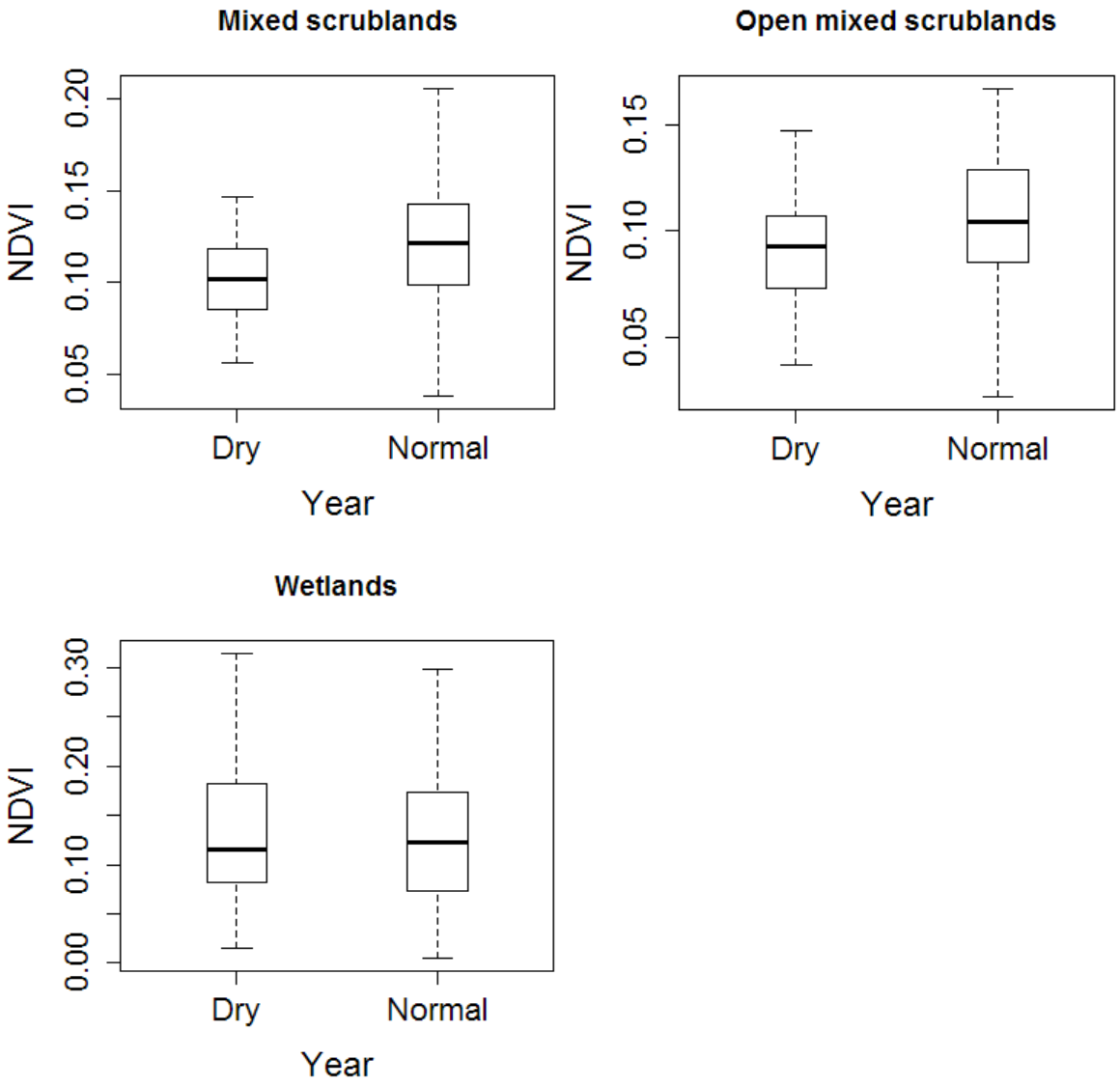


Figure 5.7. Boxplots showing differences in productivity for each vegetation type between the *dry* and the *normal* year in sample points above 3,300m within the study area.

5. 4. Discussion

This study exemplifies how plant productivity responds to changes in rainfall in dry mountains, and how these responses are modulated by geographic and topographical patterns, and by dominant vegetation types.

Like in other arid mountains, the distribution of primary productivity in the Dry Puna was affected by a spatially complex topography, including differences in altitude, slope, orientation and location. Productivity decreased consistently with increasing altitude, as temperature becomes too extreme for plants to grow. However, productivity was relatively high in the High Plateau, receiving humid influences from the Amazon, and again along the Andean slopes, probably because steep slopes create microclimatic conditions and refuges to vegetation from wind and freezing temperatures. In the western slopes of the Andes, located further away from the sources of moisture, productivity was more sensitive to increases in the summer rainfall, which activates the soil seed bank, as suggested by Luebert and Pliscoff (2006). Primary productivity was also higher in northern orientations, due to joint conditions of higher temperatures (more hours of sun light) and moisture coming from the Amazon basin. In accordance with our results, Rundel et al. (2002) described that, in the dry Andes of northern Chile, woody species in northern orientations were drought deciduous with an adaptive strategy to maximize photosynthesis activity during the wet season; in contrast, species in south facing slopes were mainly evergreen and semi evergreen, with lower rates of photosynthesis.

Whilst NDVI patterns were largely defined by topography and geographic location, rainfall still played a major role in driving vegetation change in the Dry Puna, as overall vegetation greenness was lower in a dry year compared to a normal year. However, the responses of primary productivity to reduced precipitation varied across vegetation types. Similar to other alpine areas, low productive grasslands are the predominant vegetation in the Dry Puna, and the vegetation associated to small wetlands was the most productive, maintaining vegetation greenness in high altitude areas (Körner 2003, Squeo et al. 2006, Baldassini et al. 2012, Izquierdo et al. 2015). Vegetation-specific changes in primary productivity can be explained by the particular adaptations of dominant plant species to water scarcity. For example, in a dry year greenness declined significantly across plant communities with *Festuca* tussocks which, according to Monteiro (2011), prioritize

investing on morphological traits associated to longevity and defense, over those related to high productivity. During dry years, therefore, *Festuca* tussocks reduce their above-ground phytomass compared with a normal rainfall year (Monteiro et al. 2011). They also have an efficient way to utilize moisture, with short roots that form a large sphere in between widely spaced tussocks, resulting in higher water availability per tussock (Monteiro and Körner 2013). This is a successful strategy to maximize access to rainfall water that allows tussocks to tolerate dry periods (Monteiro et al. 2011). On the other hand, the observed resilience of scrublands to low rainfall in the Dry Puna can be explained by their comparatively longer and deeper root systems, which allow them to access water at higher depths (Arroyo et al. 1988, Schenk and Jackson 2002).

Also the *vegas* and *bofedales* associated to wetlands showed resilience to dry conditions, as expected because they obtain moisture from streams, rivers and from underground water storages (Squeo et al. 2006). Indeed, this vegetation type was comparatively more productive during the dry year. It is possible that as water levels in wetlands and streams recede there is new surface with suitable conditions available for riparian vegetation to expand, and vegetation encroaches in newly-exposed humid soils. It is important to note that the dynamics between wetlands and their water sources in the Dry Puna is not well understood (Squeo et al. 2006). Although there is some evidence of underground recharge in the Dry Puna (Houston 2007, 2009, Uribe et al. 2015), the mechanism and magnitude of this complex hydrological system are poorly known due to lack of adequate data (Uribe et al. 2015). Recharge appears to be seriously affected by the amount of rainfall in the area, with no recharge in years with precipitation lower than 120mm (Houston 2009). It is a research priority to understand the Dry Puna hydrological system, and its direct effect on the primary productivity of the *vegas* and *bofedales.*

Climate models predict higher temperatures in the Dry Puna (Urrutia and Vuille 2009), uncertain trends in precipitation, and an enhanced frequency of extreme El Niño events (Power et al. 2013, Cai et al. 2014, Cai et al. 2015) which will bring hot and dry summers, and associated lower productivity (Chapter 4). Considering the high inter-annual precipitation variability in the Dry Puna, the resilience of wetland vegetation to water scarcity can contribute to maintain them as centers and refuge for biodiversity during dry periods. Wetlands are in fact centers of biodiversity in the area, as birds, rodents and native camelids are associated with wetlands or are highly reliant on wetland vegetation (Messerli et al. 1997, Villagrán and Castro 1997, Squeo et al. 2006). Wetland vegetation is also a key

feeding habitat for domestic herbivores such as llamas, on which local communities depend on (Villagrán and Castro 1997). On the other hand, grasslands dominated by tussocks of *Festuca orthophylla* are a central part of the structure of the Dry Puna ecosystem (Catorci et al. 2011) and have an important role for the communities in the area, as they are also preferred by llamas (Patty et al. 2010). Consequently, a decrease in rainfall might have a social impact besides the ecological effects associated with changes in plant community assemblage and species composition (Catorci et al. 2014).

Although there was not overall trend in rainfall or productivity in the area over the last two decades, a longer-term desertification trend is affecting the Andes Altiplano since 1930 (Morales et al. 2012), with potential negative effects on the ecosystem, including the reduction of wetlands size. This can be similar to the fossilization process that affected former saline lakes that are now salt pans in the area (Demergasso et al. 2004). Further studies are needed to deepen our understanding of the possible effects of climate change on Puna ecosystems. It is important to mention that plant growth may not only depend on current, but also on previous years' rainfall conditions and that the effects might be accumulative. While the years selected for our comparison do belong to multi-year periods of 'normality' and 'aridity' in the study area, including more years and delayed effects will provide a clearer picture of the impacts of climate change upon primary productivity. A key limitation for such studies is the availability of good quality satellite images of high spatial and temporal resolution.

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Chapter 6:

Use of localized resources shape the community of carnivores in the Dry Puna

Abstract

Carnivores inhabiting arid highlands share the use of localized resources such as free water, refuge and clusters of prey, according to their physiological adaptations and degree of specialism/generalism. We studied the guild of meso-carnivores in the Dry Puna, one of the most arid regions of the Andes, to explore species' patterns of resource use that might indicate niche segregation at fine resolution, allowing carnivores to coexist in a low productivity ecosystem. The guild included the endangered and specialized Andean cat *Leopardus jacobita*, the similar-sized Pampas cat *L. colocolo*, and the more generalist culpeo fox *Lycalopex culpaeus.* A combination of species distribution modelling and resource selection functions revealed differential selectivity for areas close to wetlands (where free water and green biomass are concentrated in the Dry Puna), broken terrain with rocky cliffs (which provide refuge to both prey and predators), elevation, and northern aspects (more exposed to solar radiation and moisture from the Amazon). The generalist culpeos showed the least resource preference and responded to the environment at larger spatial scales. In contrast, the Andean cat showed more localized responses and a proportionally larger spatial overlap with its preferred prey, the southern mountain viscacha *Lagidium viscacia*. There was also evidence that the two cat species segregated spatially, as their suitable habitats overlap by 30 and 40%, and the Pampas cat (only) showed a preference for lower elevations. Differential preferences and scales of selection, for limiting resources appear to contribute to the coexistence of carnivores in this low productive environment.

6.1. Introduction

Typically in arid highlands local topography creates thermal refuges and determines the location of free water. The way in which species utilize these critical resources will depend on their physiological and behavioural adaptations, shaping community structure (e.g., McCain 2007, Pickering and Green 2009, Pryke and Samways 2010). Carnivore species tend to be cryptic and have large-scale habitat requirements, making the study of any links between species occurrence and the spatial distribution of environmental variables challenging (García-Rangel and Pettorelli 2013). In order to examine the conditions and mechanisms that allow predators to coexist in high-altitude, low productivity ecosystems, we explored localized patterns of resource use by a guild of medium-size carnivores in the Andes' Dry Puna in the Central Andes. This is a model community to study patterns of use of limited resources by carnivores, and the potential mechanisms favouring their coexistence. The Dry Puna guild of meso-carnivores includes the endangered Andean cat *Leopardus jacobita*, a mountain specialist with a restricted distribution, and two more generalist species that also occur in a diversity of habitats at lower elevation, the Pampas cat *L. colocolo* and the larger culpeo or Andean fox *Lycalopex culpaeus*. Advances in analytical tools, including statistical methods to measure resource selection and habitat suitability from presence/presence data, have paved the way for such studies of carnivore communities (Durant et al. 2010, Pettorelli et al. 2010, Schuette et al. 2013), including communities in dry environments (e.g., Saharan desert, Brito et al. 2009) and also rare predators which depend on specific habitats, such as the Iberian lynx *Lynx pardinus* (Fernández et al. 2006) and the flat-headed cat *Prionailurus planiceps* (Wilting et al. 2010).

Ecological studies of Andean cats are few and sparse because they are extremely elusive and rare, and therefore this is one of least known species of the small cats (Nowell et al. 1996, Yensen and Seymour 2000, Villalba et al. 2004, Marino et al. 2010). It is well-established, however, that the three predators share a pool of prey species in the High Andes, mainly rodents and aquatic birds, and that the Andean cat is the most specialized predator of southern mountain viscacha *Lagidium viscacia* (Walker et al. 2007, Napolitano et al. 2008, Viscarra 2008, Marino et al. 2010) and also the least abundant (Lucherini 2003, Perovic et al. 2003, Walker et al. 2007, Reppucci et al. 2011). The prevailing thesis is that

Andean cats can maintain local populations in sympatry with the more generalist carnivores because they are more efficient at exploiting a rare resource, such as the viscacha (Walker et al. 2003). No evidence have been found of time partitioning in their daily activity patterns (although culpeos appear to be more strictly nocturnal; Marino et al. 2010).

In order to explore the mechanisms by which the rare Andean cats can coexist with generalist competitors, we first formalized a biological model of the Dry Puna carnivore community, identified potentially limiting factors, and then contrasted our predictions against occurrence data from predators and prey around the triple frontier between Argentina, Bolivia and Chile, one of the driest regions in the High Andes. Theory predicts that the potential for competition depends on the species' relative abundances and their shared use of resources (Begon et al. 2009), and that coexistence can be facilitated by niche segregation (Farrell et al. 2000), for example with respect to the use of limiting resources, which for the carnivores in the Dry Puna are highly clustered and include rodent prey, free water and refuge. Acknowledging that these interactions might occur at many spatial scales (Wiens 1989), we considered multi-scaled habitat selection as a way to understand niche segregation and species coexistence (Indermaur et al. 2009). We expected predators and prey to select some critical resources at fine scales, namely: high altitude wetlands (known as *vegas* and *bofedales*) which concentrate free water and green biomass, and conspicuous rocky outcrops (known as *roquedales*) and other broken terrain, which provide refuge to both viscachas and Andean cats. If the thesis of specialisation holds true, patterns of resource use will differ between specialist and generalist species, including the spatial scales at which animals perceive and select them (Pita et al. 2011).

In order to capture these habitat associations we combined species distribution modelling with resource selection functions. For the first we used the machine learning technique known as Maximum Entropy Modelling (Maxent), a widely recognized tool to study rare and cryptic species, as it requires presence-only data and performs particularly well in range-restricted and specialized organisms (Elith et al. 2006, Pearson et al. 2007, Elith and Leathwick 2009, Franklin and Miller 2009, Thorn et al. 2009, Wilting et al. 2010). Maxent fits response curves to the data and predicts the spatial distribution of suitable habitats, according to a set of environmental constraints and optimum conditions. The second approach, resource selection functions, characterizes the probability of a species' presence from combinations of key environmental variables in 'used' and 'unused' habitat units,

using linear-modelling techniques (Manly et al. 1993, Massolo and Meriggi 1998, Boyce and McDonald 1999, Palomares 2001). The study includes spatial scales of environmental heterogeneity that might be relevant for habitat selection in arid highlands, including: a broad elevation range (to account for variations in the elevation range of mountain species); complete hydrological systems (in this case, typically closed basins of the High Plateau); and high resolution field data (to represent localized resources such as prey and refuge in the resource selection functions). The results bring light into the role that specialization may play in structuring the community of carnivores in extreme environments such as the dry highlands.

6.2. Methods

6.2.1. Study area

The study area covers 26,800km^2 around the triple frontier between Argentina, Bolivia and Chile, located within the Central Andean Dry Puna eco-region (Olson et al. 2001) (Figure 6.1). The average elevation is 4,436m (SD 567). The highest peaks are along the international boundaries and define major basins at each side of the frontier; these are typically closed basins with one main lake (permanent or seasonal) or salt pan – e.g., Vilama complex of lagoons in Argentina, the salt pans of Chalviri in Bolivia, salt pans of Tara in Chile (Fig. 6.1). The climate is dry and cold, with intense solar radiation, strong daily amplitude in temperature, and low precipitation, concentrated over the summer months (Garreaud et al. 2003). The northeastern part of the study area in Argentina and Bolivia receives humid influences from the Amazon basin; the western slopes on the Chilean side are on the rain shadow of the Andes and more affected by Pacific atmospheric influences (Garreaud et al. 2003).

The landscape is dominated by extensive areas of exposed sandy soils and rocky terrain, devoid of any substantial plant cover above 5,000m; the vegetated areas are open grasslands (*Festuca* and *Stipa* spp.) and shrublands (dominated by *Parastrephia* and *Lepidophyllum* spp.), with wetlands known as *vegas* and *bofedales* (dominated by *Oxychloe* and *Distichia* spp.) in valleys and depressions (Cabrera 1976, Arroyo and Cavieres 2013).

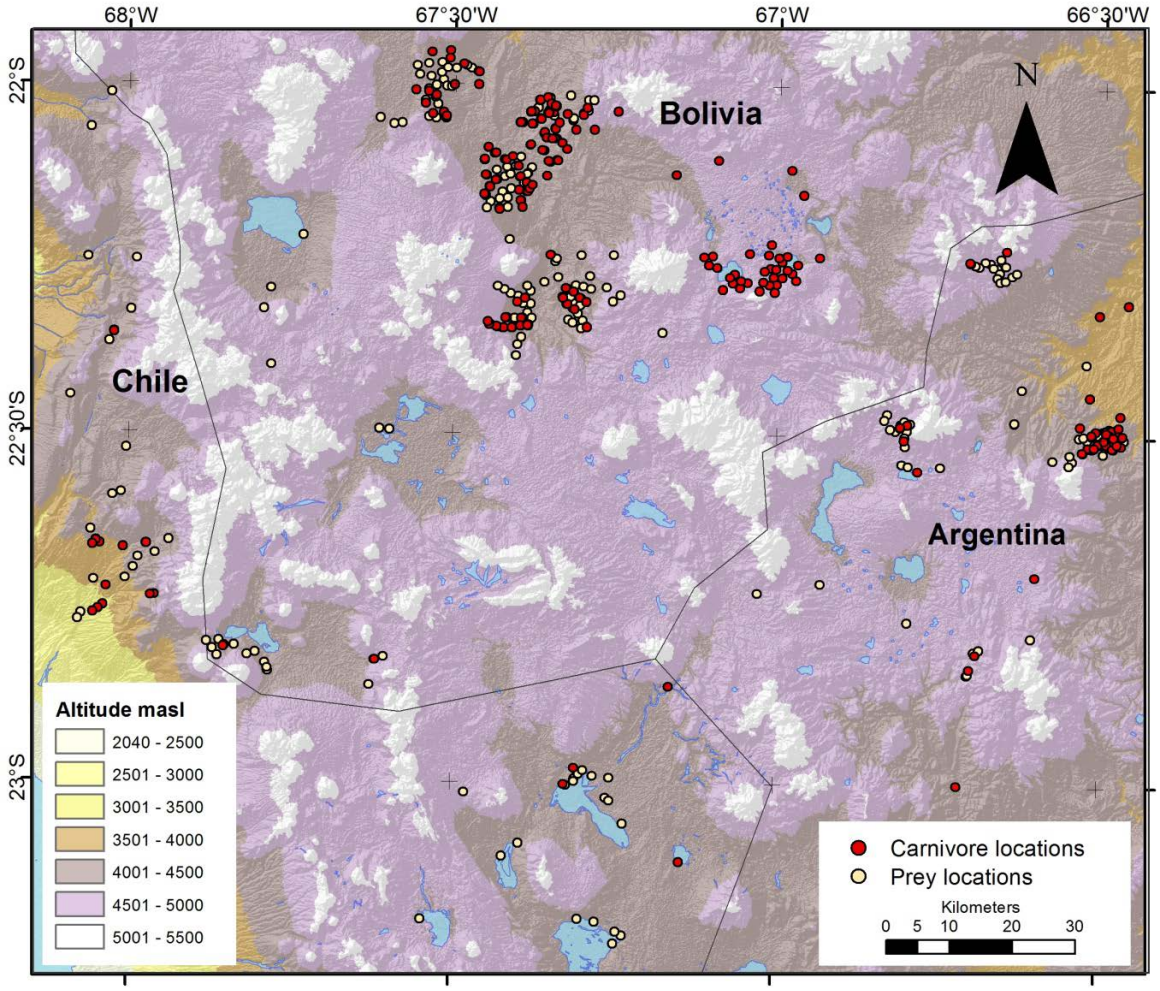

Figure 6.1. Dry Puna study area around the triple frontier between Argentina, Bolivia and Chile, with records of carnivore and prey species. All land above 5,000m is virtually devoid of vegetation.

6.2.2. Biological model (Figure 6.2.)

Within the guild of medium-size carnivores, the Andean cat (4-4.5kg) is the only species chiefly restricted to the Puna ecoregion (Redford and Eisenberg 1992; Rau et al. 1998). Pampas cats (5 kg) and culpeos (8-12 kg) are also found in several other habitat types at lower elevations. The Andean cat is present in Argentina, Bolivia, Chile, and Peru, between 3,000 to 5,500m, but predominantly above 4,000m. In the Dry Puna culpeos are the more abundant, and Andean cats the rarest (Lucherini 2003, Perovic et al. 2003, Walker et al. 2007, Reppucci et al. 2011).

Andean and Pampas cats are of similar size and with similar diets; they mostly prey on high-altitude rodents such as small cricetine mice (30-50g), *Ctenomys* spp. 'tucos' (200g,

specialized burrowers associated to sandy, loose soils) and the larger southern mountain viscacha (1.6kg, a rocky specialist). However, the diets of Pampas cats and culpeos are more diverse and flexible than that of Andean cats, and include aquatic birds, reptiles and insects, and large mammals -particularly for the culpeos, which consume carrion from vicuña (*Vicugna vicugna*), guanaco (*Lama guanicoe*) and the domestic llama (*L. glama*) (Walker et al. 2007, Napolitano et al. 2008, Viscarra 2008, Novaro et al. 2010). Comparatively, viscachas contribute more to the diet of Andean cats. The viscachas are generalist herbivores that inhabit rocky habitats with suitable crevices and tunnels, where they nest, escape predators (Walker et al. 2000), and sunbathe for considerable periods of time for thermoregulation (Galende et al. 1998, Cortes et al. 2002). In this open landscape, broken terrains offer refuge to both Andean cats and viscachas, particularly the rocky formations known as '*roquedales*', but also boulders, ridges and cliffs (Napolitano et al. 2008, Marino et al. 2010, Villalba et al. 2012). Other rodents such as the tucos escape predators and extreme weather by living underground. In the Dry Puna rodents are predominantly herbivores, and their abundance is expected to vary with vegetation type and cover along environmental gradients of elevation, slope and orientation (Chapter 5) - e.g., in the study area the northern aspects receive more solar radiation and humidity, and are therefore more productive. The availability of free water will be a limiting factor for both prey and carnivores in the Dry Puna. The high-altitude marshes known as *vegas* and *bofedales* are key components of the ecosystem. The systems of bogs and shallow pools follow the local drainage and are refreshed by subterranean water and melting ice to a lesser degree (Squeo et al. 2006). These wetlands are permanent sources of free water and act as discrete productivity pockets, maintaining green biomass all year round.

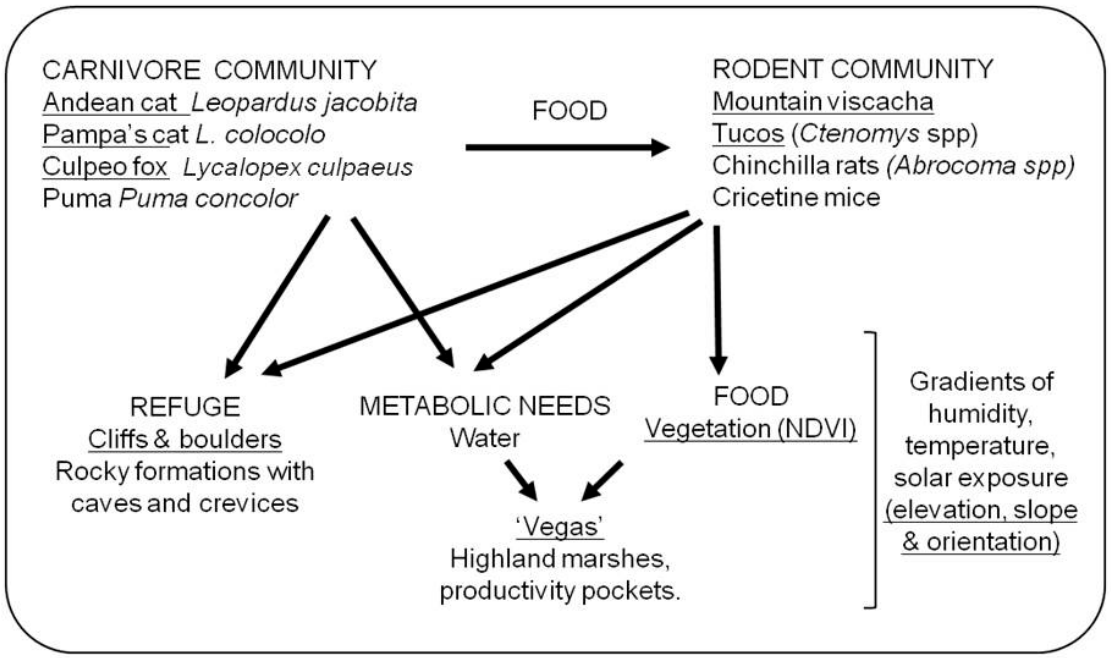

Figure 6.2. Conceptual model of the High Andes ecosystem –species and environmental factors captured in our predictive models are underlined.

6.2.3. Species distribution modelling

Datasets are confirmed records of carnivores from the triple frontier collected between 1980 and 2010, including: direct sightings, images from camera traps, genetically-identified faeces, skins and skulls (Andean Cat Alliance database www.gatoandino.org, field data compiled by the author, and including records from transects mentioned below). Presence records of viscacha and tucos were obtained between 2007 and 2011 from observations of pellets and mounds/holes respectively, collected by the author and collaborators from the Andean Cat Alliance.

The presence data represents well the diversity of environments in the Dry Puna, but are largely clustered because of the sheer size and remoteness of the study area, and the resulting uneven survey effort (Figure 6.1). To minimize the unwanted effects of this sampling bias, a spatial filter was implemented to reduce the number of occurrences to one within 1km Euclidian distance (Filter SDM toolbox Spatial Rarefy Occurrence Data (Brown 2014)). Additionally, Maxent parameters were fine-tuned to avoid over fitting around these data clusters –see below. After filtering, the final dataset consisted of 37 records of Andean cats, 65 of Pampas cats, 50 of tucos and 233 of viscachas.

The environmental data for landscape level analysis were derived from remote sensing datasets (summarized in Table 6.1.), resampled to 30m resolution. In order to represent various spatial scales of selection, a moving window was implemented to each environmental layer; centered on each raster cell, an average value was calculated from cells at specified distances, namely: 30m, 500m, 1km and 5km (Focal statistics tool, ArcGIS 10.1 ESRI, 2010). A new raster layer was created for each window size.

Variable	**Units /classes**	**Source / calculation**
Landscape level - remote sensing		
Elevation	Meters	Derived from Advance Space Thermal Emission and Radiometer (ASTER), resolution 1 arc-second. NASA Land Processes Distributed Active Archive Center (LP DAAC) and USGS/EROS 2001. http://gdex.cr.usgs.gov/gdex/. All layers were resampled from geographic coordinates to WGS84 UTM19S.
Slope	Degrees	
Eastness	= sine(aspect) -1 west to 1east	
Northness	=cosine(aspect) -1 south to 1north	
Distance to 'vegas'	Meters	Derived from four Landsat Thematic Mapper (TM) images, resolution 30m, Path Row 232 75/76 and 233 75/76 from 2001, Earth Explorer, USGS and EROS, http://edcsns17.cr.usgs.gov/NewEarthExplorer/). Images were resampled from geographic coordinates to the projected system WGS 84 19S using a Nearest Neighbourhood Resample Method (ERDAS Imagine 10). A supervised classification using the Maximum likelihood classification method (Joshi et al. 2006) was used to classify pixels into main vegetation types, based on extensive ground-truthing conducted in December-January 2010 and December 2011 (habitat samples = 500). Fifty percent of the samples were used as training data, and the other half to verify the accuracy of the classification using Kappa statistics. The land cover categories identified were: salt pan, water, *vegas* and *bofedales* (vegetation associated to wetlands), grassland, scrubland, and areas without vegetation. The distance from each cell to a vega or bofedal was calculated as predictor for subsequent modelling.
NDVI (Normalized Difference Vegetation Index)	-1 to 1.	NDVI is as a good indicator of vegetation productivity and it is used to estimate the green biomass (Tucker, 1985). NDVI was derived from four Landsat Thematic Mapper (TM) images, resolution 30m, Path Row 232 75/76 and 233 75/76 from 2001 (Earth Explorer, USGS and EROS, http://edcsns17.cr.usgs.gov/NewEarthExplorer/). Images were resampled to WGS 84 19S (Nearest Neighbourhood Resample Method). NDVI values were calculated as follows: NDVI = (NIR − VIS)/ (NIR + VIS), where NIR is the near infrared light and VIS the visible light reflected by the vegetation (Pettorelli et al., 2006). Negative NDVI values indicate absence of vegetation; while higher values are associated with greater density and greenness of the plant canopy (Justice et al., 1985).
Local scale - 'habitat samples' along transects		
Rugosity	1 to 4	Mean slope calculated across 'habitat samples' within each transect. Scale: 1=flat (0-5°), 2= gentle slope (up to 15°), 3= slope (>15 to 45°); 4= abrupt (>45°).
'Roquedal'	percentage	Percentage of 'habitat samples' within each transect with presence of boulders, ridges or cliffs.
Vegetation cover	1 to 5	Mean cover across 'habitat samples' within each transect. Braun-Blanquet scale: 5= 100-75%; 4= 74-50%; 3= 49-25%; 2= 25-5%; 1= < 5%.
Viscacha	percentage	Percentage of 'habitat samples' within each transect with pellets

Table 6.1. Environmental predictors used for the species distribution models and resource selection functions in the Dry Puna of Argentina, Bolivia and Chile.

The Maxent algorithm finds the probability distribution of maximum entropy (closest to the uniform) subject to the constraints imposed by the information available in the presence data and the environmental conditions across the study area (Phillips et al. 2006). The criteria for the choice of background area was to represent well the macro-topography of the High Andes around the triple frontier (including the western slopes of the Cordillera towards Chile and the high altitude plateau in Bolivia and Argentina). The elevation ranged from 2,040m on the Chilean side to 5,981m in the High Plateau.

The following Maxent options and parameters were selected (Maxent version 3.3.3, (Phillips et al. 2006): 'features'=Linear, Quadratic and Products (the latter to take into account interactions between variables); regularization multiplier= 1.0; Maximum iterations= 1,000; occurrence datasets randomly partitioned into a training (80%) and testing dataset (20%). As a measure of model fit Maxent calculates for each the area under the Operating Characteristics Curve (AUC, which varies from 0.5=random to 1=perfect discrimination). To assess the contributions of each environmental variables to the Maxent prediction we examined response curves, Jack-knife analyses, and estimates of 'percentage contribution' and 'permutation importance' -the first is heuristically defined from the Maxent optimal solution and sensible to highly correlated variables; the second represents the relative reduction in training-data AUC resulting from randomization of the variable in question with the AUC of the model with this only that variable as reference (a large decrease in AUC indicates that the model depends heavily on that variable) (Phillips et al. 2006, Phillips and Dudik 2008).

Initially, uni-variate Maxent models were run for each combination of predictor species across the selected spatial scales (30m, 500m, 1km and 5km). The best performing scale for each variable was identified from the models' AUC and retained for the multivariate models (Table 6. 2). When Pearson correlations between pairs of variables were larger than 0.7, the variable less directly related to the factor of interest was eliminated. Highly correlated predictors were identified using the Correlation and Summary Stats tool from SDM toolbox (Brown 2014).

6.2.4. Resource selection functions

We searched for signs of carnivore (droppings) and viscachas (pellets) along 244 transects, 20m wide and 400m long, where environmental variables were recorded every 20m within a 5m-radius 'habitat sample' (standardized methodology applied across countries, following (Cossios et al. 2007)). Transects were selected to cover the different environments in areas that could be accessed by road or walking (the study area is large and inaccessible in many places, due to topography and minefields). As Andean and Pampas cat dropping are indistinguishable to the eye, they were analysed together as 'small cats'. Viscacha pellets have been used as an abundance index in the Patagonian steppes (Walker et al. 2000, Walker et al. 2008). The environmental variables measured at each habitat sample are summarized in Table 6.1.

Logistic regressions with a logit link function were used to model the probability of presence of carnivores and prey, as depicted by the presence of their faeces. By considering transects as the sampling units we minimized the risk of low-detectability and pseudo-absences. Autocorrelation between the proposed predictors was lower than 0.5, so all were used in the models. We constructed and compared models representing all the combinations of predictor variables and used the AIC (Akaike Information Criteria, Burnham and Anderson 2002) to select the model/s with highest probability of being the 'true' model (models with accumulated 95% AIC weights were combined into an 'averaged model') (Bartoń 2013).

6.2.5. Spatial overlap

Assessment of niche differences using Maxent involves calibration of machine-learning functions that relate environmental variables to georeferenced data on species occurrence; niche overlap is then estimated through the projection of those functions across a landscape (i.e., the overlap is calculated in geographical space) (Broennimann et al. 2012). Maxent spatial predictions were first converted into binary maps (habitat - non habitat) using as cut-off criteria the maximum training sensitivity plus specificity (MSS) threshold; recommended because it maximizes sensitivity and specificity (Liu et al. 2005). The MSS for Andean cats was 0.47, Pampas cats 0.44, culpeos 0.42, viscachas 0.48 and tucos 0.41.

The analyses were implemented in Idrisi software (Eastman 2006), ArcGIS 10 (ESRI 2010) and R (R Development Core Team 2015).

6.3. Results

6.3.1. Niche modelling

The predictors that contributed most to variations in Andean cat habitat suitability were distance to 'vega' and northness, while Pampas cats were most sensitive to changes in eastness orientation and elevation. In both cases Maxent provided a good fit to the data (AUC > 0.8) (Table 6.2). Culpeos were most affected by slope and orientation (eastness) but the model provided a poorer fit (AUC 0.7) (Table 6.2).

	Andean cat		Pampas cat		Culpeo fox		Viscacha		Tuco	
	PC	PI	PC	PI	PC	PI	PC	PI	PC	PI
Distance to *vega*	43.8	50.0	13.1	10.0			17.1	20.0	49.5	51.7
Northness	40.7	34.4	14.3	19.4	17.3	15.5	38.2	15.3	11.6	11.2
Slope	8.2	13.2	10.8	9.5	41.6	44.5			22.6	34.0
Elevation			37.3	42.9			12.4	38.0		
Eastness			24.4	18.3	38.1	32.5	21.6	22.4		
AUC (sdv)	0.813 (0.065)		0.839 (0.060)		0.716 (0.083)		0.776 (0.035)		0.870 (0.060)	

Table 6.2. Summary of variables' contributions to Maxent predictions, and the fit of the models for meso-carnivores and their main prey in the triple frontier of Argentina, Bolivia and Chile. PC=percentage contribution; PI=permutation importance.

The species that responded to distance to '*vega*' did so at finer spatial scales (0.3km and 1km); other landscape variables were only important at the larger spatial scale (5km). Culpeos showed habitat associations only at the 5km scale (Table 6.3.).

The response of Andean cats to distance to '*vega*' was sharper, and with more predictive power, than that of the Pampas cat (habitat suitability for Andean cats dropped quickly over the first 3km away from a '*vega*') (Figure 6.4.). All carnivores, and the viscacha, showed preference for the northern aspects; these receive more solar radiation and for longer hours (Table 6.2 and 6.3).

	Andean cat		Pampas cat		Culpeo fox		Viscacha		Tuco	
	Scale (km)	AUC	Scale (km)	AUC	Scale (km)	AUC	Scale (km)	AUC	Scale (km)	AUC
Distance to *vega*	**1**	**0.723**	**0.3**	**0.646**	0.3	0.473	0.3	0.616	**0.3**	**0.761**
Eastness	0.3	0.601	**0.3**	**0.651**	**5**	**0.555**	1	0.598	1	0.639
Northness	**5**	**0.739**	5	0.779	5	0.645	**5**	**0.644**	5	0.585
Slope	1	0.625	0.3	0.579	**5**	**0.656**	1	0.580	**5**	**0.701**
Elevation	1	0.670	**5**	**0.797**	5	0.638	**0.3**	**0.727**	5	0.743

Table 6.3. Results of univariate Maxent models fitted to meso-carnivore and prey species in the Dry Puna. The table shows the spatial scale at which each of the predictors provided the best fit to the data (measured as the Area Under the ROC Curve = AUC). Highlighted in bold are the variables that contributed most to the predictions in the models shown in Table 6.2.

Overall, Andean cats showed the more localized environmental responses; Pampas cats' selection was mainly associated to elevation (optimum at around 3,500m, decreasing gradually towards lower and higher elevations) and culpeos selected flat or gently-sloping areas, irrespective of elevation (Figure 6.3).

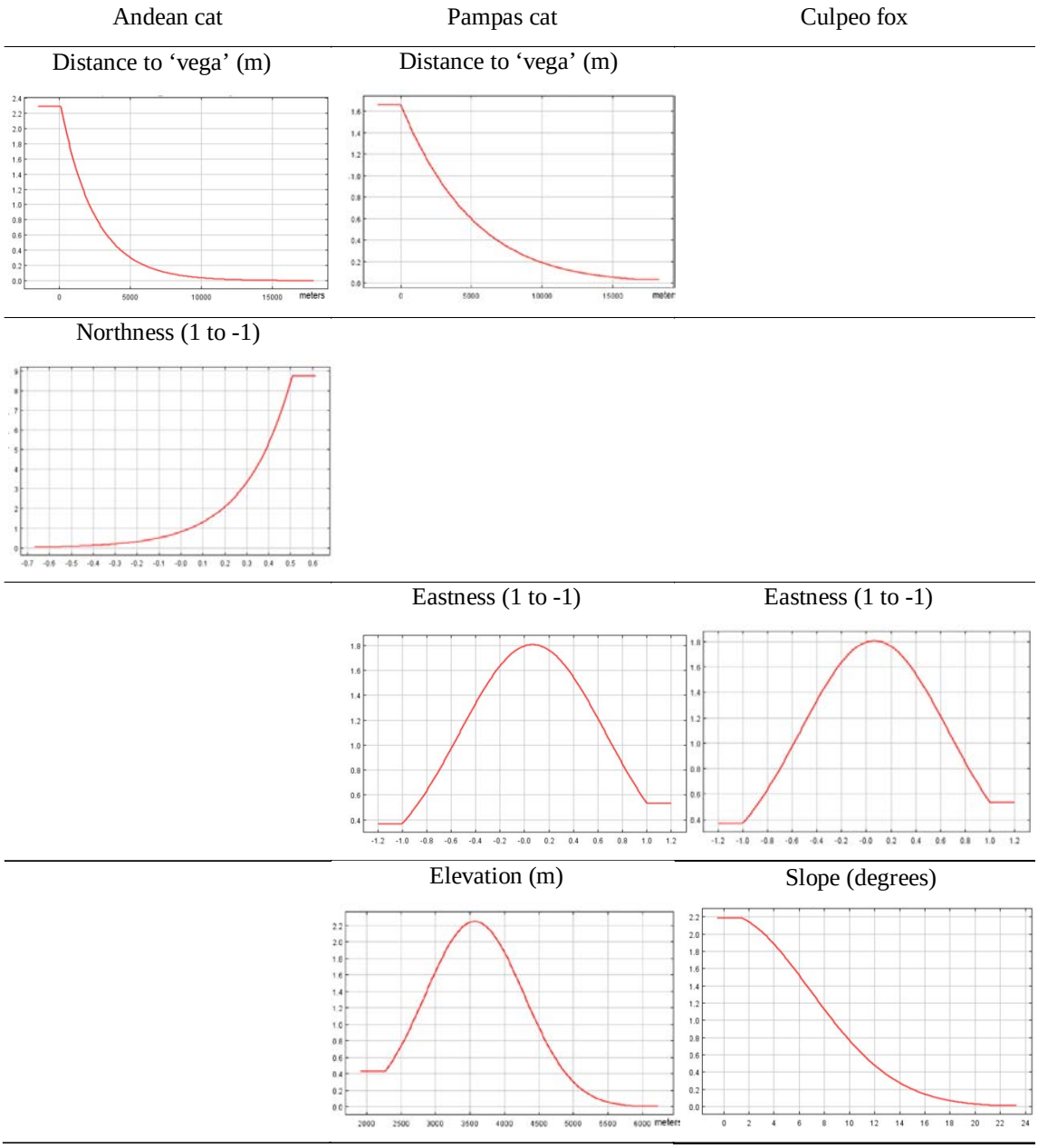

Figure 6.3. Response curves showing changes in the carnivores' habitat suitability (y axis, measured as Maxent's raw output) as each environmental variable changes (x axis), keeping all others at their average sample value.

The species distribution models also revealed different ecological requirements of the two larger rodent prey in the study area; with a better fit to the tuco data with respect to the viscacha model (Table 6.2 and Figure 6.4). The best habitats for tucos were flat or gently sloping areas in the vicinity of '*vegas*'; habitat suitability for viscachas was clearly associated to orientation (both northness and eastness) and elevation, with an optimum at around 4,000m (Figure 6.5).

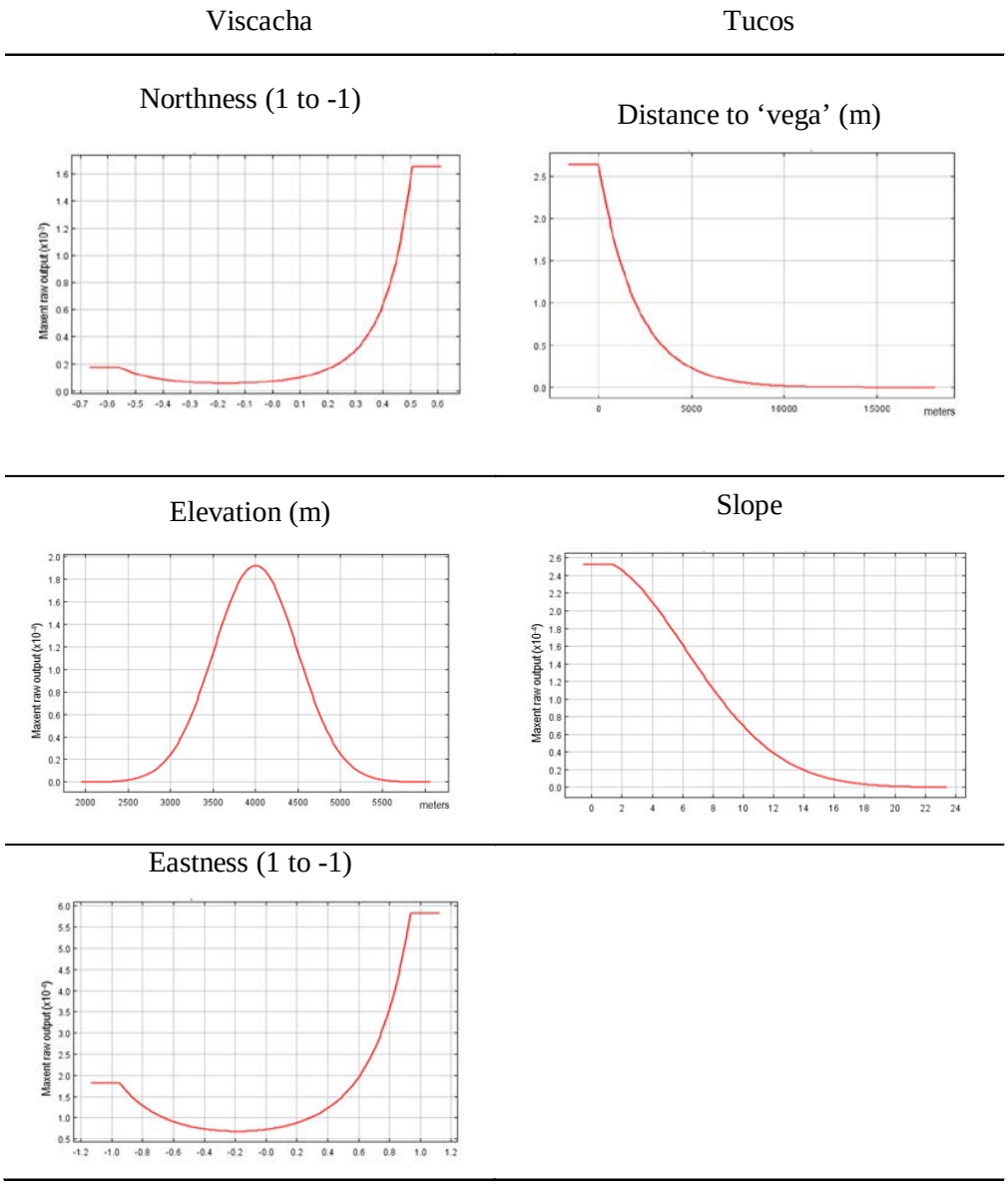

Figure 6.4. Response curves showing changes in prey habitat suitability (y axis, measured as Maxent's raw output) as each environmental variable changes (x axis), keeping all others at their average sample value.

6.3.2. Resource selection functions

The resource selection functions incorporated additional data reflecting micro-topography, vegetation, and prey availability. The two cats species ('cats model' in Table 6.4) selected broken terrains, with viscachas and close to '*vegas*'; the presence of rocky formations known as '*roquedales*' did not contribute much to the models (Table 6.4). The effect of elevation was most likely related to the Pampas cat's known preferences for relatively lower elevation, also discriminated by the species distribution models. The fit and

predictive power of the cats' model was good, and comparatively better than that of the culpeo model (Table 6.5). Culpeos appeared to avoid broken terrain and were associated with more vegetated areas, irrespective of slope and orientation (Table 6.4); slope and orientation were relevant at the larger spatial scale in the culpeo distribution model.

The resource selection function for the viscachas provided a good fit to the data (Table 6.5) and, as predicted, viscachas showed a preference for '*roquedales*' and other broken terrains, northern aspects (key for thermoregulation), and eastern slopes with more vegetation cover (more productive).

	Cats model			Culpeo fox model			Viscacha model		
	Coefficient	lower CI	upper CI	Coefficient	lower CI	upper CI	Coefficient	lower CI	upper CI
Distance to 'vega'	-0.241	-0.468	-0.047	-0.014	-0.201	0.104	-0.097	-0.287	0.060
Elevation	-1.942	-4.870	-0.071	-0.119	-2.746	1.820	1.315	-1.296	4.701
Rugosity	0.724	0.251	1.200	-0.444	-1.120	-0.003	1.585	0.606	2.654
Viscacha	0.017	0.004	0.032	0.005	-0.002	0.018	-	-	-
'Roquedal'	0.705	-0.053	2.063	0.090	-0.556	1.144	2.240	1.346	3.364
Eastness	-0.120	-0.774	0.187	-0.099	-0.723	0.208	0.606	0.004	1.174
Northness	0.079	-0.421	0.934	0.007	-0.565	0.622	0.648	0.088	1.479
Vegetation cover	-0.060	-1.107	0.685	1.308	0.568	2.047	0.835	0.000	1.788
NDVI	0.427	-3.136	6.044	-3.529	-9.972	0.558	-4.816	10.730	-0.975

Table 6.4. Results of resource selection functions predicting the probability of presence of the two cat species (Andean and Pampas cats combined), culpeo and viscacha. The table shows model-averaged coefficients for main effects (with shrinkage) and their confidence intervals (CI - lower: 2.5%, upper: 97.5%) –highlighted in grey are the size effects whose confidence intervals exclude zero.

	Cats model	Culpeo model	Viscacha model
Presences	59	53	192
Absences	185	191	52
Nagelkerke R^2	0.366	0.164	0.491
AUC	0.829	0.719	0.882
Kappa	0.429	0.113	0.602
Sensitivity *	0.946	0.968	0.634
Specificity*	0.424	0.113	0.937
Balanced accuracy	0.685	0.541	0.786

Table 6.5. Fit and predictive power of resource selection functions modelling the probably of presence of cats (Andean and Pampas cats combined), culpeo and viscacha. *(positive class=0).

6.3.3. Spatial overlap

The differential responses of all three carnivores to the environmental conditions were reflected in the distribution of suitable habitats and their overlap (Figure 6.5 and 6.7). While Andean cats selected areas close to wetlands at high elevation, Pampas cats were more evenly distributed, preferring intermediate elevations along the western and eastern slopes of the Andes. Culpeos were the least selective at the scale of this study (Figure 6.5). The total area of suitable habitat therefore decreased from that of the more generalist culpeo to that of the more specialized Andean cat (Figure 6.6). Optimal habitats for viscachas and tucos were highly localized (Figure 6.5) and their extension was similar to that of the Andean cat's (Figure 6.6).

Percentage overlap (*)			
Andean cat	Pampas cat	Culpeo fox	
	31.3	27.8	Andean cat
38.9		19.3	Pampas cat
53.4	29.9		Culpeo fox
45.6	30.2	22.0	Mountain viscacha
51.5	29.6	33.2	Tucos

Table 6.6. Percentage overlap between the areas predicted as suitable for predators and prey in the study area (derived from Maxent binary maps) * with respect to the total area of the species at the top of the column.

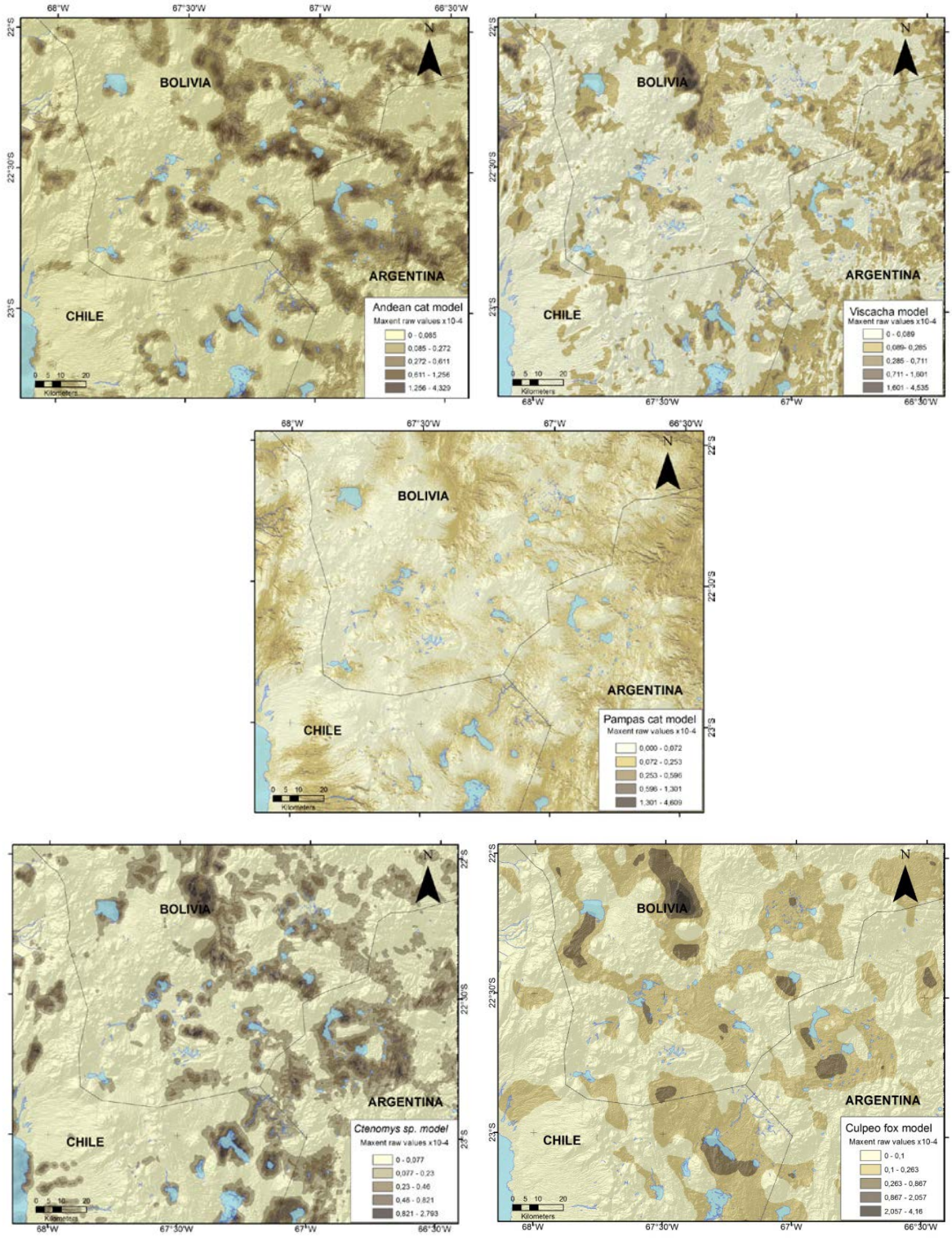

Figure 6.5. Maxent predictions of habitat suitability for three meso-carnivores and two prey species (Maxent raw output) in the triple frontier of Argentina, Bolivia and Chile.

The overlapping distribution of suitable habitats for the three carnivores covered small area (Figure 6.6). The proportional overlap ranges between 20 and 50% approximately (Table

6.6) with Pampa's and Andean cat sharing relatively smaller proportion of their suitable habitats. Andean cats shared the largest proportion of habitat with that of viscachas and tucos, in comparison with the other two carnivores (Table 6.6).

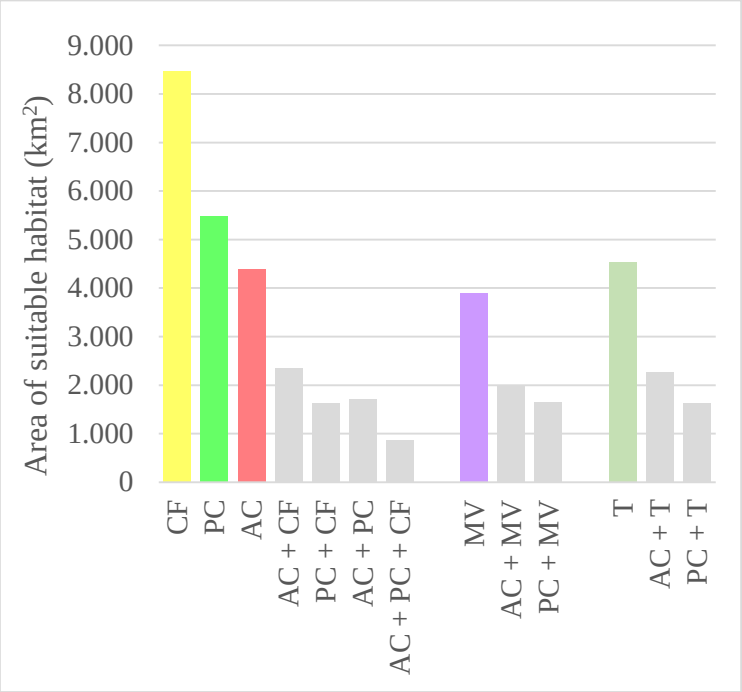

Figure 6.6 Estimated area of suitable habitat for predator and prey species in the triple frontier of Argentina, Bolivia and Chile (calculated from habitat-non habitat binary maps) and their overlapping areas (+). CF: culpeo fox; AC: Andean cat; PC: Pampas cat; MV: mountain viscacha; T: tucos.

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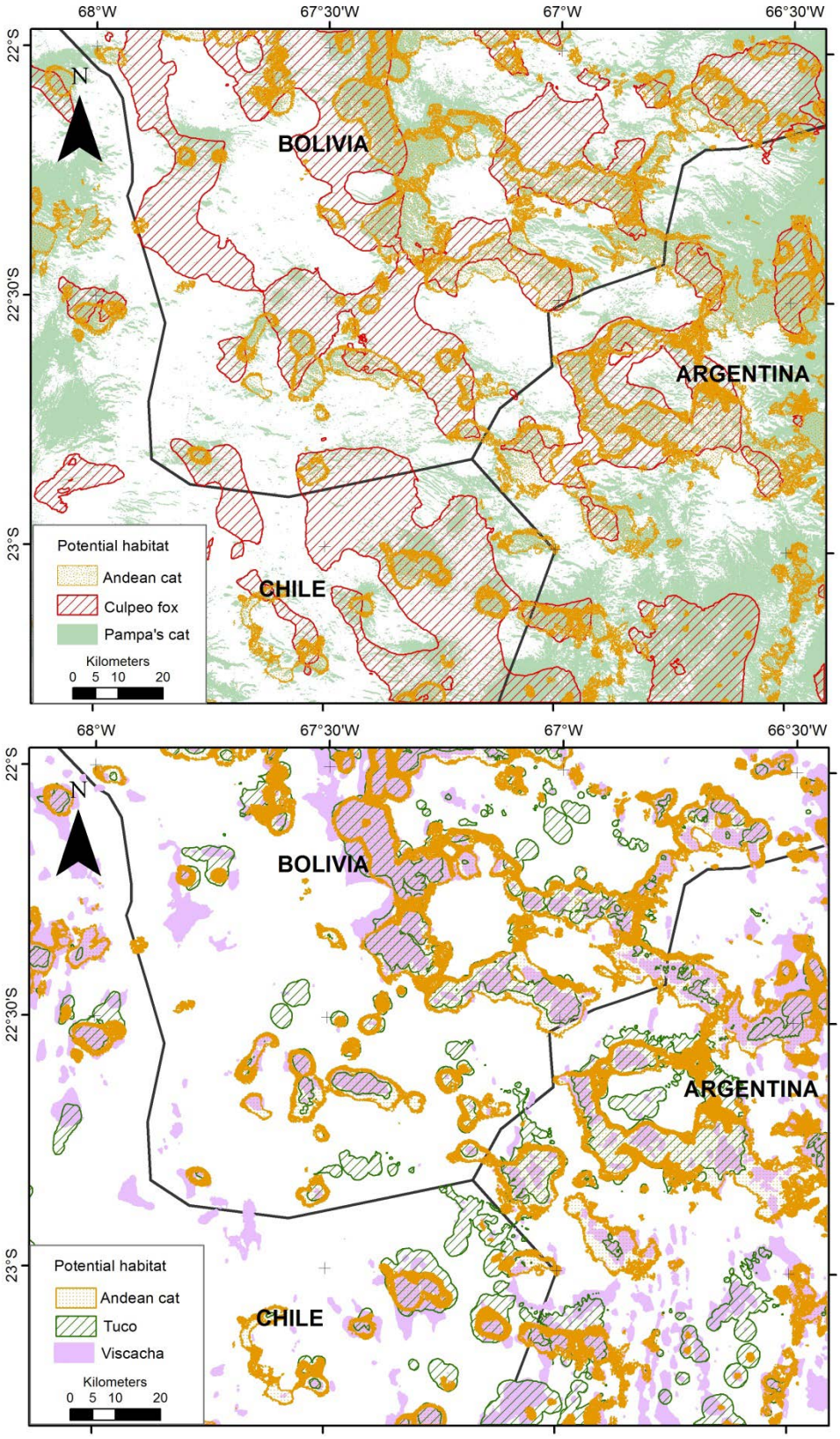

Figure 6.7. Overlapping distributions of suitable habitats (a) among the three carnivore species, and (b) among Andean cats and the two prey species modelled.

6.4. Discussion

Carnivores inhabiting dry and cold environments at high elevation have to share a limited pool of prey species, access to water and refuge, all of which are constrained and patchy in distribution in the Dry Puna. Patterns of habitat use by three coexisting meso-carnivores revealed differences in their ecological niches at local and landscape levels, supporting the notion of spatial segregation as a mechanism promoting coexistence. The observed differences agreed with our predictions, based on the species' degree of specialization and the various spatial scales at which they select habitats.

According to the competitive exclusion principle two ecologically similar species cannot coexist unless they develop some niche segregation (Hardin 1960). We expected some degree of partitioning in the realized niche of the three carnivores, where food, water and refuge are rare resources at high demand. Segregation might occur at the temporal, trophic and/or habitat selection level, but until now there are no evidence of clear segregation in any of the mentioned dimensions of this carnivores' ecological niche. While it is impossible to prove niche segregation without an experiment setting, but it is important to elaborate hypothesis to understand better how the community of carnivores work, particularly when it includes endangered species. Our conceptual model incorporated information on the trophic niche of the three carnivores and predicted that a key component structuring the carnivore guild will be the availability of viscachas, the preferred prey of Andean cats. We also proposed fine scale habitat differentiation as an important mechanism of coexistence in this arid ecosystem, in association to access to free water (concentrated in wetlands known as '*vegas*') and suitable rocky formations offering refuge from competitors and extreme weather. Accordingly, broken terrain (measured as an index of 'rugosity' and as abundance of rocky outcrops or '*roquedales*') and proximity to water (measured as distance to wetlands or '*vegas*'), were good predictors of the presence of Andean cats and viscachas, and these preferences occurred at fine spatial scales. Similarly, the burrowing *Ctenomys* spp. showed localized preferences for flat areas and gentle slopes near wetlands. Habitat preferences at the landscape level were also evident and these were positively related to higher primary productivity (e.g., northern orientations receiving humidity from the Amazon and with enhanced exposure to solar radiation). However, the more generalist culpeos showed lower preferences and suitable

habitats were the most widely distributed. A main difference between the two cat species was the Pampas cats preference for mid-elevations, indicating that the highest land might be marginal for the species or close to their physiological limit (optimal elevation 3,500m), in accordance with other studies in this region (Perovic et al. 2003, Napolitano et al. 2008).

The adaptations and life history traits of the coexisting species can help us understand the way in which they exploit resources. Andean cats for instance use broken terrains, placing themselves close to the viscachas and with easy access to the only type of cover available at such altitudes. While Pampas cats also prey on viscachas, they have also shown more flexibility, with different prey contributing to local diets within the study area including burrowing tucos and flamingos (*Phoenicopterus chilensis, Phoenicoparrus andinus, and Phoenicoparrus jamesi*) (Marino et al. 2010) -our study did not include flamingos, which seasonally concentrate in the shallow lakes. In turn, suitable habitats for Andean cats had the highest proportionally overlap with that of viscachas and tucos across the study area. The best conditions for viscachas were along the north - eastern slopes, which are the warmest and more productive, and areas with more vegetation cover, as expected for a generalist feeder that depends on rock outcrops for refuge and which exhibit frequent basking behaviour for thermoregulation. In contrast, tucos preferred flat areas close to '*vegas*', where conditions for burrowing are optimal due to the accumulation of soft, sandy soils. Like most subterranean rodents, *Ctenomys* spp live in deep, soft and well- drained soils, which reduce thermal stress and the costs of burrowing (Albanese et al. 2010).

Our study confirms that in the Dry Puna the guild of medium-size carnivores and their prey select resources at multiple scales, and that the coexistence of carnivores in low productivity environments can be facilitated by resource partitioning. Other studies demonstrating differential selectivity included the carnivore assemblage in Tanzania's Serengeti (Durant et al. 2010) and in a mixed-use landscape in Kenya, nearly all 12 carnivore species had a unique combination of environmental variables influencing occupancy patterns, supporting the hypothesis of spatial niche partitioning (Schuette et al. 2013).

Body size is expected to influence the scale of perception and animals' movements – e.g., large carnivores with large home ranges would perceive a more homogeneous landscape (e.g., Gehring and Swihart 2003). Accordingly, within the Dry Puna meso-carnivore guild, the smallest Andean cat was more selective than the larger culpeo (with ability to cover more ground, access a broader range of habitats, and acquire more varied food types) and

spatial segregation was more marked between the similarly-sized cats. Clearly the importance of interference competition will be scale dependent, and in competitive environments like the Dry Puna local exclusion and regional coexistence between competitors would appear to occur simultaneously (e.g., Amarasekare 2003). Even within overlapping ranges, spatial avoidance might be also accomplished through the use of microhabitats and by reducing the chance of encountering predators, for example by hiding in rock crevices and caves, less accessible to larger predators. The habit of Pampas and Andean cats to deposit faeces in latrines strategically located in rocky outcrops and near caves, can also facilitate mutual avoidance and coexistence (Marino et al 2010).

The Dry Puna case study supports the notion that cohabitation will be advantageous when species have different degrees of habitat and/or trophic specialization. Another example is the community of Mediterranean carnivores, which includes the highly specialized Iberian lynx and the generalist red fox *Vulpes vulpes* (Soto and Palomares 2015). The Iberian lynx feeds almost exclusively upon wild rabbits and select breeding dens at a fine spatial scale (e.g., all litters in one study were born inside hollow trunks with very large cavities, irrespective of the surrounding habitat (Fernández and Palomares 2000). Similarly, within the carnivore-guild of the Altai mountains, in East/Central Asia, the smaller weasel *Mustela altaica* has a concurrent distribution to that of its main prey the pika *Ochotona* spp. but frequents areas used by pikas mainly during the day, avoiding the more nocturnal/crepuscular habits of the stone marten *Martes foina* and red fox (Bischof et al. 2014). Also, among the 12 carnivores studied in mixed-used landscape in Kenya, the activity patterns of apex predators and meso-carnivores also differed (Schuette 2013), revealing temporal niche partitioning.

The role of temporal segregation in promoting coexistence in the Dry Puna could be important but largely speculative. Data from camera traps (summarized in Marino et al. 2010) indicates that the two cats have similar activity patterns, and both consume diurnal and nocturnal prey, and that culpeos are more strictly nocturnal/crepuscular. For Andean cats temporal partitioning is a more likely a strategy to reduces the chances of physical confrontation with the more abundant and larger carnivores. Indeed, the rarity and elusiveness of Andean cats probably emerges as an ecological process to avoid interspecific killing within the carnivore guild.

Methodological considerations

Data is a common limitation in carnivore studies, particularly if they are rare and elusive species and inhabit vast and unproductive landscapes such as the Dry Puna. By combining two methodologies this study surmounted some of these limitations, and complementary results strengthened our findings. Transect data from used-unused samples with detailed landscape information enabled a more accurate discrimination and quality assessment of suitable habitats, and the detection of crucial features not immediately obvious at broader scales (e.g., Fernández and Palomares 2000). For example, rocky outcrops provided refuge to viscachas and cats, and were important predictors, yet they were difficult to map over large areas. Fine-scale predictors also allowed to base habitat suitability directly on the availability of particular resources (i.e., food, refuge) rather than variables acting as their proxy. By considering multi-scaled levels of habitat selection, we also achieved a better characterization of the species habitat profiles and ecological requirements. Even within the guild of medium-sizes carnivores there is no single best scale for habitat differentiation, with implications for understanding how the target species perceive and respond to their environment. For generalist species such as culpeos broad ecological niches and less habitat-specificity can weaken the ability for presence-only approaches to describe and model distributions (e.g., Durant el al 2010). Poor prediction might also reflect missing variables associated to the availability of large mammal prey for culpeos, and /or the fact that the study area, which offers a good representation of the habitat used by Andean cats, covers only one of the various ecosystems where the other two carnivores exist.

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Chapter 7:

Predicting the future of mountain carnivores taking into account climate, prey availability and protected area networks

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Abstract

Mountain specialists are threatened by climate change in particular ways, tending to insulate them in mountaintops. Organism responses, however, can vary according to their position on the food chain and their ecological flexibility, so efforts should be made to implicate this natural variation into predictive distribution models. Here, we modelled the distributions of the Andean cat *Leopardus jacobita* and its preferred prey, the viscacha *Lagidium viscacia*, to assess the future conservation status of this endangered carnivore. Using corrected climatic surfaces, we estimated that the area suitable for Andean cats might decline up to 30% by 2080. Habitat loss will be more acute in the North, while the southern range will extend into lower elevations. The core range will shift upwards by up to 225m, while the southern range will move polewards by 1°. Viscachas will remain available as prey in southern and central ranges. By 2080 protected areas would encompass 10 to 15% of suitable Andean cat habitat. We conclude that the impacts of climate change would differ across the species range, and reinforce the biogeographical barriers that structured extant populations: the southern populations, genetically distinct and in seemingly less suitable habitat, are less vulnerable; the northern populations in the Peruvian Andes face the highest risk of prey and habitat loss and a decline in habitat representativeness within protected areas by 2080. To ensure the long-term survival of Andean cats, protection should target habitat in the Northern and southern range, where new opportunities for conservation will emerge in the future.

7.1. Introduction

Climate change is recognized as one of the main threats to global biodiversity (Millennium Ecosystem 2005, Brodie et al. 2012) and yet its effects are largely unknown for many species (McMahon et al. 2011). Growing evidence indicates that species are changing their distribution as a result of global warming (Root et al. 2003, Parmesan 2006, Rosenzweig et al. 2008, Chen et al. 2011) particularly in mountain ecosystems, considered highly vulnerable to climatic change (Diaz et al. 2003, Nogués-Bravo et al. 2007, Kohler et al. 2010, La Sorte & Jetz 2010). Mountain specialists are particularly at risk because they have restricted climatic niches and adaptations to specific environmental conditions, such as freezing temperatures (Grabherr et al. 1994, Bach & Price 2013). They also tend to occur over small areas with complex topography, and many are endemic. Studies from mountain regions across the world reveal that plants and animals are shifting their distributions upwards as a result of global warming (Parmesan 2006, Seimon et al. 2007, Lenoir et al. 2008, Raxworthy et al. 2008, Harsch et al. 2009, Luo et al. 2014). Such upslope shift threaten to 'trap' them in mountain top refugia, in progressively smaller and fragmented populations. Under such conditions, their likelihood of extinction due to demographic stochasticity and reduced genetic variability might increase substantially (Soulé 1987, Caughley 1994).

Species distribution modelling can provide important insights into the response of mountain specialists to climate change, including changes in their potential distributions (Guisan & Thuiller 2005, Franklin & Miller 2009) and degree of protection within existing networks of protected areas. Bioclimatic envelope models are used to describe a species' spatial climatic requirements by relating location data to climatic variables, such as temperature and precipitation, at present and under future climatic scenarios (Thomas et al. 2004, Thuiller et al. 2005). As typically species show individualistic responses to climate change, climate models are better implemented at single species level (Peterson et al. 2002, Thomas et al. 2004, Peterson et al. 2011). On the other hand, common adaptations and lack of detailed information for many highland species means that models of species such as the endangered Andean cat (*Leopardus jacobita*) can help understand the response of others living in similar climatic conditions.

A previous model of the Andean cat climatic niche showed that the species distribution is characterized by arid and cold conditions, and that it might therefore be sensitive to global warming (Marino et al. 2011). The processes driving future shifts in Andean cat distribution will be also representative of the likely impact of climate change upon many other Andean vertebrates (Marino et al. 2011). Using the Andean cat as a model, this study explores changes in the distribution of mountain carnivores, using projections of climate change from across the Andean region. The Andean cat is a South American endemic, largely restricted to arid and semi-arid areas of the High Andes and one of the least known felids of the world (Nowell et al. 1996; Yensen & Seymour 2000); it is listed as Endangered by IUCN (Villalba et al. 2016). This small felid (4 – 4.5kg) is typically associated to rocky outcrops in the Andes of Argentina, Bolivia, Chile and Peru (Yensen and Seymour 2000, Villalba et al. 2004, Marino et al. 2010), but also exists at lower elevations in the Argentine Patagonia, in the austral extreme of its range. Andean cats eat mainly rodents and some birds, and are seemingly more efficient exploiters of rock-specialists such as chinchillas (*Chinchilla* spp.) and mountain viscachas (*Lagidium viscacia*) than the sympatric carnivores (Walker et al. 2007, Napolitano et al. 2008, Marino et al. 2010). Chinchillas (*C. lanigera* and *C. brevicaudata*) were presumably a major prey for Andean cats in the past, but these are now extinct from most of its range due to overexploitation for their fur (Iriarte and Jaksic 1986). Currently the mountain viscacha (2–2.5kg) contributes the most biomass to the Andean cat's diet in Argentina, Chile and Bolivia (Walker et al. 2007b, Napolitano et al. 2008, Marino et al. 2010) and it is present across the southern Andes cordillera and the northern Patagonian steppe (Walker et al. 2003, Walker et al. 2007a). This generalist herbivore spends most of the time in rocky areas, using rock crevices to rest, sunbathe, and as a refuge from predators (Walker et al. 2000). By combining predictions for both Andean cats and mountain viscachas in the future, we are accounting for potential biological interactions between predators and prey, in the case of a specialized carnivore.

Predicting species range shifts is a pre-requisite for the conservation planning of many endangered species under changing climates. At the same time, the academic community warns of the inherent risks involved in modelling future species distribution, particularly when there is uncertainty in projected climates and when the underlying biological assumptions are not clearly addressed (Araújo and Peterson 2012). For example, predictions are often interpreted from a static viewpoint, assuming that species conserve

their climatic niches and ecological requirements, and that they have the dispersal capacity to track changes in climate (Barbet-Massin et al. 2010). We sought to minimize these limitations by using an improved climatic dataset (i.e. corrected by topography and based on weather stations from high elevation) and by incorporating the existent biological knowledge as explicitly as possible, including the Andean cat's dependency upon mountain viscachas. The Andean cat, like other mountain organisms, is bound to suffer a decline in its distribution as temperature increases along the Andean slopes. However, as the species is exposed to an important degree of climatic variation along its elongated range (which spans in latitude between 10 ºS and 40 ºS over 3,400 km), climate change my impact differentially the northern and southern populations.

Our ultimate aim is to assess the future conservation status of Andean cats and contribute guidelines to improve their protection, considering the spatial and genetic structure of the existing populations and helping detect gaps in the protected area network (Mittermeier et al. 2004). Information on the representativeness of critical habitats within protected area networks is a valid tool to derive conservation priorities. We discuss opportunities and alternatives to enhance the protection of the Andean cat niche under global warming, and address these emergent questions in the field of biology and conservation.

7.2. Methods

7.2.1. Location data

Andean cats are rare, exist at low densities and are elusive, all of which make field studies challenging. We used species occurrence data compiled by the Andean Cat Alliance (Appendix S.7.1) with important personal contributions (see Marino et al. 2011, based on the same database). The dataset included direct sightings, genetically-identified faeces, camera trap photographs, skins and skulls. To correct for sampling biases, we implemented a 3 km filter, which reduced the dataset to 135 presence points. In the process we eliminated spatial autocorrelation amongst most of the predictors. Data clusters can contain important ecological signals that enhance a model predictive power (F. Dormann et al. 2007, Kramer-Schadt et al. 2013), and can be particularly relevant for specialist predators such as the Andean cat.

Mountain viscacha records were obtained from the literature (Marquet et al. 2010), the Andean Cat Alliance database (which includes records collected by the authors), and the Global Biodiversity Information Facility (GBIF 2014) (Appendix S.7.1). The records cover the period since 1980 to date, and include direct sighting localities of individuals or their faecal pellets (which are easily identified in the field). To correct for sampling biases a 3 km filter was also implemented. The database used for modelling contained 230 location points.

7.2.2. Climatic variables

Climatic variables for current and future scenarios were obtained from surfaces produced by Pliscoff et al. (2014), who improved the Hadley Centre Coupled Model (HADCM3) version 3 climate change model by including additional information from 930 weather stations located in Chile, Peru, Bolivia and Argentina at 1 km spatial resolution. We used climatic scenarios for 2050 and 2080 from HADCM3 (Johns et al. 2003) with CO2 emissions scenarios A2 (high emissions) and B2 (low to medium emissions) (Nakićenović & III. 2000). While there are newer emission scenarios available (IPCC 2014), these have not been improved yet with local meteorological data, critical for modelling of mountain species.

To model the distribution of Andean cats we selected climatic variables associated to tolerance for cold temperatures and aridity. In order to reduce redundancy due to co-linearity, from each pair of variables with Pearson's correlations higher than 0.7 - the variable with more direct biological significance was maintained. The resulting final set contains six climatic predictors (Mean Diurnal Range, Temperature Seasonality, Minimum Temperature of Coldest Month, Annual Precipitation, Precipitation Seasonality, and Precipitation of Coldest Quarter). Following a similar process, we selected six climatic predictors for the mountain viscacha model (Mean Diurnal Range, Temperature Seasonality, Minimum Temperature of Coldest Month Mean Temperature of Wettest Quarter, Precipitation of Warmest Quarter).

7.2.3. Species distribution modelling

To predict species' distributions we applied a maximum entropy algorithm using the software Maxent 3.3.0 (Phillips et al. 2006). Maxent is widely used to model current and

future species distributions from presence only data, with particularly successful outcomes when applied to specialized species (Elith et al. 2006; Phillips et al. 2006) and those with small ranges or sample sizes (Wisz et al. 2008). The extent of the background was determined by the coverage of corrected climatic layers for the region (between latitudes 10° and 55° S and longitude 63° and 80°), which were considered suitable for our Maxent model (e.g.(Acevedo et al. 2012) because they include the known distributions of Andean cats and mountain viscachas and neighbouring areas where suitable environmental conditions might exist in future, including a good representation of the asymmetric climatic conditions at each side of the Andes and of the Patagonian steppes at the southern limit of the species' range. We selected the following Maxent options: linear, quadratic and product features; regularization factor= 1; 10 replicates; 1000 iterations, and we split occurrence locations into 80% and 20% for model training and testing. Model evaluation was performed using the area under the curve (AUC) value - values between 1 and 0.75 are considered indicative of robust models (Elith and Burgman 2002; Franklin and Miller 2009). The Maxent output, best interpreted as an indicator of habitat suitability, was then transformed into a binary map (suitable-unsuitable), from which we calculated changes in total area, and shifts in latitude and elevation (derived from SRTM Rabus et al. 2003). We considered two cutting points: a) the minimum training presence or MTP threshold, which by including all suitable habitats with known Andean cat presences produced the more conservative prediction (i.e. included the southern range), and b) the maximum training sensitivity plus specificity or MSS threshold, which maximizes sensitivity and specificity (Liu et al. 2005) and resulted in a smaller predicted range. As a result six binary maps were produced to represent present and future distributions of Andean cat's habitats, and another six for the mountain viscacha.

7.2.4. Conservation status

To measure the representation of Andean cat habitats within the network of protected areas of Argentina, Bolivia, Chile and Peru, we overlapped the International Union for Conservation of Nature (IUCN) World Database of Protected Areas 2009 (WDPA 2009) over the binary maps of the species current and future distributions. The original WGS84 datum of layers was projected to UTM coordinates for these calculations. All spatial analyses were performed in ArcGIS 10 (ESRI 2011).

7.3. Results

7.3.1. Andean cat distribution models

The Andean cat current distribution model provided a good fit (mean AUC 0.945, SD: 0.015). The species climatic niche was characterized by cold and dry winters and highly seasonal rainfall (Figure S.7.2.1). The variable with the most useful and unique information was the Minimum Temperature of the Coldest Month (as indicated by Jack-knife tests of variable importance Figure S.7.2.2) followed by Precipitation Seasonality (Table S.7.2.1).

A core of optimal habitat was identified in the Central Andes, with a mean altitude of 4,008m (CV 14.2%), corresponding to the central and northern portions of the species range (Figure 7.1). Less suitable habitats were located in the southern range, with a mean altitude of 3,308m (CV 28.2%) and containing the most recent records of Andean cats from northern Patagonia. The southern range was better represented using the MPT suitability threshold, which produced a larger potential range, on average 400m lower than that obtained with the MSS threshold.

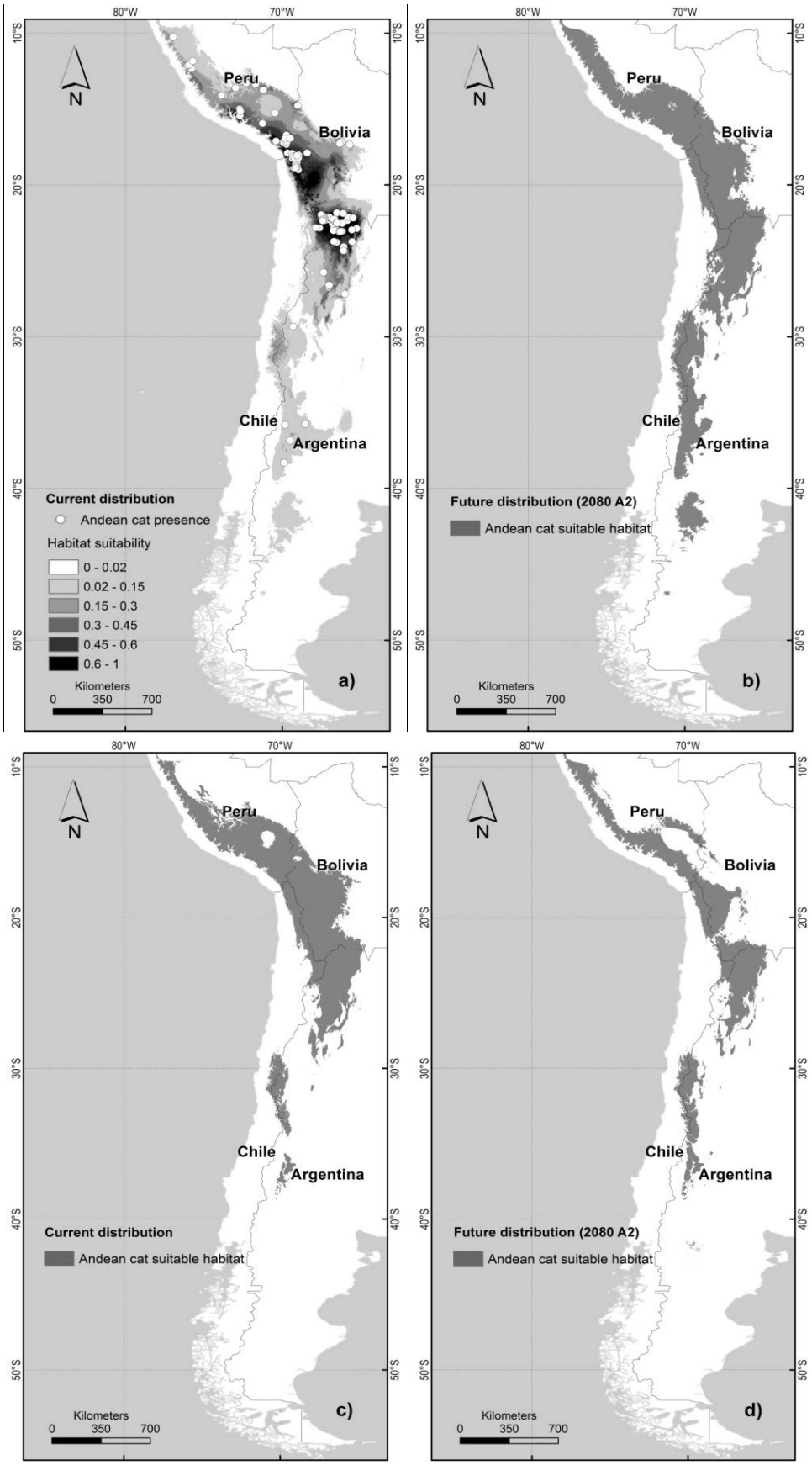

Figure 7.1. Maxent predictions of Andean cat habitat suitability under current and future climate conditions, using two alternative suitability thresholds: minimum training presence (MTP) (a and b) and maximum sensitivity-specificity threshold (MSS) (c and d). Map a)

shows the detailed Maxent's logistic output and the 135 presence records used to train the models.

The area predicted as suitable for Andean cats in 2080 was smaller than that obtained under current climatic conditions (Figure 7.1). Suitable habitats declined by 14.7% and 29.8% under the A2 scenario, using the MTP and MSS thresholds respectively. However, habitat loss did not affect the southern part of the distribution, where the area increased by 81% and 69% (under scenarios A2 and B2 respectively, with the MSS threshold) (Figure 7.2).

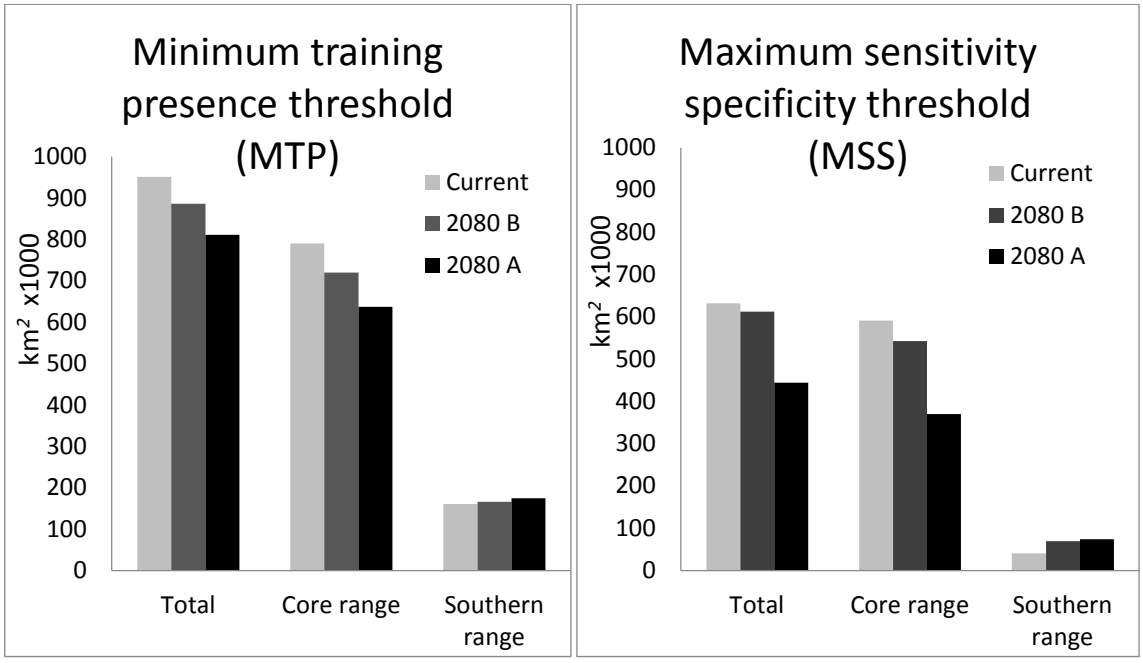

Figure 7.2. Area suitable for Andean cats across the species range (total), the core and southern ranges, showing variations under current and future climatic scenarios for 2080.

Concomitantly the average elevation shifted upwards by approximately 100m by 2080 under scenario A2 (from 3,573m and 3,962m at present, to 3,701m and 4,048 m, using MPT and MSS thresholds respectively). This elevation shift was most marked in the central core area (225m and 151m under scenarios A2 and B2 respectively) in comparison with the southern range (80m and 111m, scenarios A2 and B2 respectively; and close to zero using the MSS threshold) (Table 7.1). In addition, there was a general shift southwards of almost 1° under scenario A2 (Table 7.2).

Core range

	Minimum training presence (MTP)				Maximum sensitivity-specificity (MSS)			
Elevation	Mean	CV%	max	min	Mean	CV%	max	Min
Current	3815	20.1	6575	842	4008	14.2	6326	1139
2080 B2	3966	16.0	6740	1003	4037	16.0	6730	962
2080 A2	4040	14.6	6740	1051	4196	11.8	6740	1447

Southern range

	minimum training presence (MTP)				maximum sensitivity-specificity (MSS)			
Elevation	Mean	CV%	max	min	Mean	CV%	max	min
Current	2381	50.4	6191	599	3308	28.2	5368	959
2080 B2	2492	47.7	6730	605	3314	30.8	6730	962
2080 A2	2461	49.0	6730	631	3308	30.4	6730	926

Table 7.1. Predicted elevation shifts in Andean cat distribution by 2080.

	Latitudinal shift (km)		
	2080 scenario A2	2080 scenario B2	Habitat threshold of binary map
Total range	-98	-31	Minimum training presence threshold (MTP)
Core	-9	-1	
South	-53	9	
Total range	-180	-72	Maximum sensitivity-specificity threshold (MSS)
Core	-22	-169	
South	-49	-59	

Table 7.2. Latitudinal shifts calculated from the centroid of the current and future (2080) habitat polygons - calculated from binary maps using two habitat thresholds: minimum training presence (MTP) and maximum sensitivity-specificity (MSS). Negative values indicate southwards movement (polewards).

7.3.2. Mountain viscacha distribution models

The distribution model for mountain viscacha under current climatic conditions also provided a good fit (AUC 0.923, SD: 0.022). Overall, the mountain viscacha niche was characterized by variable daily and yearly temperatures (Table S.7.2.1). The most important predictor was the Temperature Mean Diurnal Range, which had the most useful and unique information, followed by the Mean Temperature of Wettest Quarter and Temperature Seasonality. The response curves indicated that habitat suitability increased with increasing temperature diurnal range, reaching an optimal at around 23°C (Figure S.7.2.3 and S.7.2.4).

Mountain viscacha habitat was concentrated in the Central Andes but extended towards southern latitudes at lower elevation, tracking areas with broad temperature variations. When the MTP threshold of habitat suitability was applied, the potential range encompassed the Patagonia in its entirety, including Andean temperate forests and other areas the species is not present. The MSS cutting point produced a more realistic prediction (although 9% of the records fell outside the predicted range) and so this predicted range was used for further analyses. The mean altitude of the mountain viscacha potential distribution was 2,956m and its overlap with the Andean cats range was 56%. The potential habitat for mountain viscachas decreased under future climatic scenarios by 54% under the 2080 A2 scenario (Table 7.3). The geographic range of the mountain viscacha will suffer a major contraction in its northern portion, and also towards the southern limit of the species, at latitudes higher than 40°S (Figure 7.3).

		Vizcacha habitat			Overlap Vizcacha + Andean cat
		Area (km^2)	Altitude		Area km2
			Mean	Sd	
Current	MTP	2,840,809	1,611	1,567	935,412
	MSS	734,076	2,956	1,410	351,388
2080A2	MTP	2,167,166	1,862	1,627	780,716
	MSS	428,341	3,142	1,287	188,393

Table 7.3. Total area and mean elevation of the potential distributions of mountain viscachas and mountain viscacha-Andean cat overlap, under present and future climatic conditions -calculated from binary maps using two habitat thresholds: minimum training presence (MTP) and maximum sensitivity-specificity (MSS).

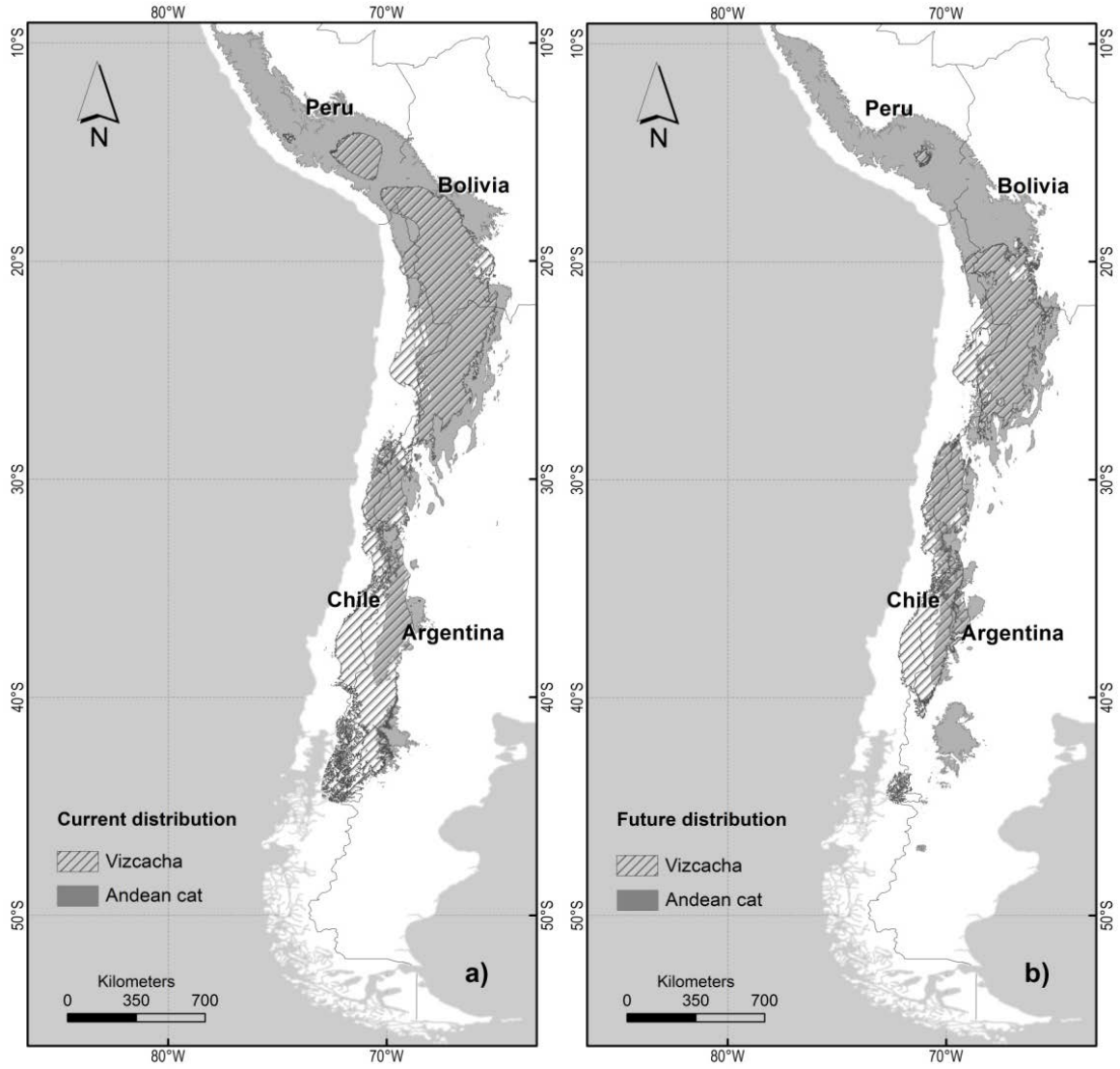

Figure 7.3. Predicted distribution of mountain viscachas and Andean cats under current (a) and future (b) climatic conditions in 2080. Binary maps were created using the maximum sensitivity-specificity (MSS) for the mountain viscacha and the minimum training point (MTP) for the Andean cat.

7.3.3 Representativeness within Protected Areas

Depending on the threshold used to separate suitable from non-suitable habitat, the potential distribution of Andean cats in South America spanned over 192,643km^2 (MTP) or 147,854km^2 (MSS). Argentina contained the largest extension of habitat, followed by Peru, Bolivia and Chile– using MTP, the more conservative threshold (Figure 7.4). The potential distribution of Andean cats overlapped with 64 protected areas (representing 8% of the total area), of which 14 have confirmed records of Andean cats. Andean cat habitats were proportionally less well represented within the network of protected areas in Chile and Peru, in comparison with Argentina and Bolivia (minimum 1% in Chile, maximum 4% in Argentina) (Table 7.4). Representativeness diminished as a whole and in each country when protected areas were overlapped over the future potential distribution – Peru will remain with virtually no Andean cat habitat protected by 2080 (Table 7.4). When considering the overlapping distributions of mountain viscacha and Andean cat habitats in the future, the decline in the area protected was similar to that calculated for Andean cats only.

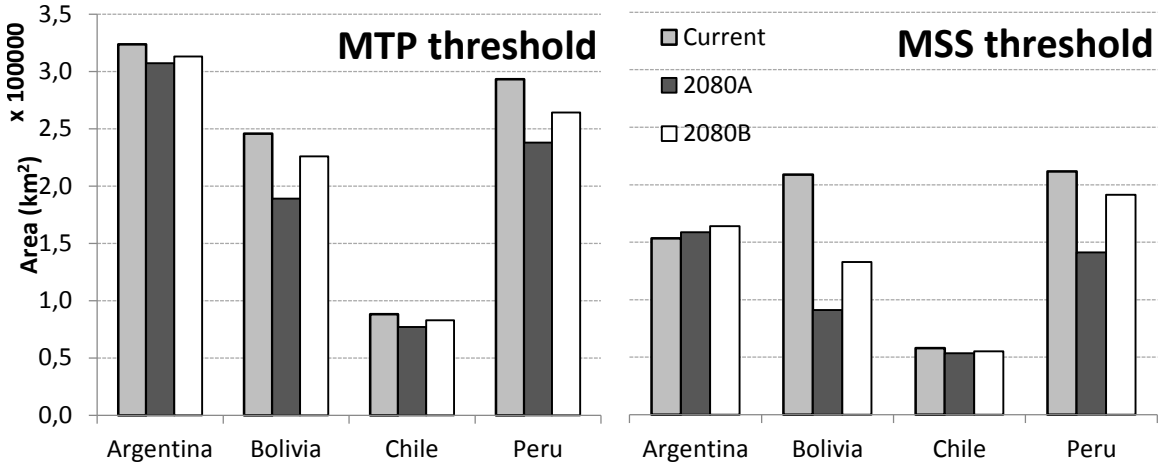

Figure 7.4. Distribution of habitats climatically suitable for Andean cat, arranged by country and climatic scenario, and using two approaches to create the binary maps, the minimum training point (MTP) and the maximum training sensitivity plus specificity (MSS) thresholds.

Andean cat habitat protected		**Habitat threshold**									
		Minimum training presence					**Maximum sensitivity-specificity**				
		Total	Arg.	Bolivia	Chile	Perú	Total	Arg.	Bolivia	Chile	Perú
Current	Pas	64	20	23	8	13	47	14	19	5	9
	km^2	73,542	37,350	22,096	6,321	7,775	55,367	24,598	19,087	5,771	5,910
2080 A2	PAs	53	17	18	10	8	42	15	11	9	7
	km^2	65,835	36,742	17,163	6,171	5,759	47,153	25,050	11,504	5,715	4,884
		-10.40%					*-14.80%*				
Overlapping (Andean cat + viscacha) habitat protected											
Current	PAs	64	20	23	8	13	22	10	9	2	1
	km^2	70,866	36,822	21,071	6,321	6,651	34,176	22,063	9,683	603	1,827
2080 A2	PAs	52	17	18	10	7	19	11	4	4	0
	km^2	61,397	36,128	13,496	6,093	5,680	30,293	21,765	7,947	580	0
		-13.40%					*-11.40%*				

Table 7.4. Representativeness of Andean cat habitats, and Andean cat- mountain viscacha overlapping habitats, within the national network of IUCN protected areas at present and in 2080 (A2 emission scenario) - calculated from binary maps using two habitat thresholds: minimum training presence (MTP) and maximum sensitivity-specificity (MSS).

7.4. Discussion

The climatic niche of Andean cats - cold and dry, with extreme diurnal variations in temperature- is distributed along the mountain grasslands and scrublands of the Andes, from the Wet Puna ecoregion in Peru, through the Dry Puna, and down into the Patagonian Steppe. Using species distribution modelling we extrapolated these suitable climates into the future to assess the risk that climate change might pose to an endangered species adapted to these cold and arid highlands.

Our results indicate that Andean cats are susceptible to the effects of global warming. Under the more pessimistic climatic projection, Andean cats might be displaced from a third of their current range. This prediction, however, varied according to the choice of habitat threshold value between 10 and 30%. While it is generally recommended to avoid thresholding (Merow et al. 2013), this is a critical step to measure range contractions /extensions and shifts using from species distribution models. We implemented both the threshold recommended in the literature (which minimizes errors of commission and omission) and the more intuitive threshold that maintains all habitats values with known records. This was more conservative and included the southern extreme of the distribution fully, an area with recent records and presumably less suitable, which will not contract under climate change according to our predictions. The same habitat threshold, however, lead to an unrealistic estimation of the distribution of mountain viscachas – based on their known distribution and biology. These results exemplify that in species distribution modelling the critical choice of habitat threshold should involve due consideration of the species biology, as well as of the distribution of survey effort, and the potential for marginal ranges to be favoured by climate change.

The habitat suitable for Andean cats will shift upwards under climate change, as predicted for other mountain specialists, including plants (Dullinger et al. 2012), birds (La Sorte & Jetz 2010), neotropical hummingbirds (Buermann et al. 2011) and Tibetan ungulates (Luo et al. 2014) . This kind of displacement, resulting from increasing temperatures, pushes organisms towards mountain tops, without openings for colonization elsewhere. For Andean cats, and other Andean species, the land above 5,000m, now virtually a cold desert, might become more suitable in the future.

The Andean cat model also predicts a poleward shift (as predicted for several species moving towards the poles by (Parmesan & Yohe 2003, Chen et al. 2011), with an increase in the suitable area at the extreme of the species range, where the species climatic niche descends to lower elevation into the arid Patagonian steppes. This result illustrates the diversity of impacts that climate change might have upon single species, not only in terms of habitat availability but also on its distribution and fragmentation. In the Andean region, the projected climatic trends appear to reinforce the effects of major climatic barriers that impose biogeographical boundaries to many plants and animals, known as the 'Andean knee' in Bolivia and the 'South American Arid Diagonal' in Chile and Argentina (e.g. Chesser 2000, Marin et al. 2007, Weigend et al. 2010) -- their effects were most accentuated under the high emission scenarios. The South American Arid Diagonal separated the Andean cat's core distribution from its southern range some 200,000 years ago, leaving a genetic signal at the time of the separation of two main lineages (Cossíos et al. 2012); in addition, two northern haplotypes also differentiated at the place of the climatic transition in the Andean knee (Cossíos et al. 2012). Our prediction is that the core and southern ranges will continue to lose connectivity, possibly becoming isolated in the future, a process that started when Andean cat dispersal was strongly constrained by post-glacial warming (Cossíos et al. 2012). The results indicate that genetically distinct Andean cat populations are affected differently by climatic conditions, which merit intensified surveys efforts in the southern range to enable populations to be modelled separately. Models derived from within-species data can produce different and better projections, and a better understanding of how intraspecific variation might buffer against adverse effects of climate change (Pearman et al. 2010, Valladares et al. 2014, Swab et al. 2015)

In understanding the responses of carnivores to climate change, it is crucial to consider prey-predator dynamics, as the predators' options will be modulated by contemporary changes in the distribution of the prey. This particularly relevant for a trophic specialist, such as the Andean cat, a seemingly more efficient exploiter of rock dwelling viscachas and chinchillas (Walker et al. 2007b, Napolitano et al. 2008, Marino et al. 2010). In our study, the predicted distribution of Andean cats overlapped closely with the distribution of chinchillas and mountain viscachas. Our predictions indicate that the concurrence of Andean cat and mountain viscacha distributions will persist in the future, and so prey availability should not prevent Andean cat shifting range due to climate change. The exception is at the northern extreme of the species' range, where we predict their habitats

will contract. Lack of data for the short-tailed chinchilla, prevented its inclusion in the model. Andean cats and mountain viscachas show a strict association to rocky formations with boulders and crevices, where they find refuge from predators and extreme weather (Walker et al. 2007a, Marino et al. 2010). This critical resource is localized and fragmented, but it cannot be accounted for at the spatial resolution of the present model. The availability and distribution of rocky formations will determine the quality of a given area within the climatically suitable range of Andean cats and mountain viscachas, a parameter that become relevant at the scale of protected areas.

Land use and land cover changes can constrain the responses of species to climate change. The High Andean climate is unfavourable for most human activities, but the environmental impacts of widespread livestock grazing, off-road tourism and mining operations are increasing concerns, particularly in Chile and Bolivia. These and other anthropogenic disturbances such as hunting of chinchillas and viscachas and killing of cats by man and domestic dogs, can have negative effects on local Andean cat populations (Villalba et al. 2004, Cossíos et al. 2007, Lucherini & Merino 2008). These threats however are highly localized, and their impacts unknown, and therefore difficult to capture in species distribution models at the level of species and with our current knowledge.

Conservation implications

Our results confirm the need for new conservation planning for Andean cats, as their habitat will be decreasing due to global warming. The analysis of habitat representativeness within protected areas is an important application of species distribution models, providing detailed and spatially explicit information on the conservation status of a species. Currently, less than 10% of the potential range of Andean cats is protected, and only 14 out of 64 protected areas within their range have confirmed records. This is a cause of concern because climate change will make the area of suitable habitat smaller, although 85% of the area currently protected will remain effective in a future climate. Nevertheless, we recognize the incompleteness of the IUCN protected area database and the reality that protection is not actively implemented in some areas. Of particular concern is the level of habitat protection in Peru, where the impacts of climate change will render many protected areas inappropriate. On the opposite end of the distribution, the shifting distribution of Andean cats poleward, and towards lower elevations, opens new opportunities for conservation, with potential to preserve important genetic variability in areas previously considered marginal (by comparison with the cat populations at the centre of the range).

Among the options to enhance the protection of Andean cats in the face of climate change, it is arguably more efficient to build upon existing protected areas where they are predicted to remain suitable -than to create new ones- and to reinforce habitat protection and connectivity among protected areas, including international corridors at the centre of the species core range (triple frontier Argentina-Bolivia-Chile, and the frontier between Bolivia and Peru).

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7.6. Supplementary material

S.7.1.1. Andean cat Alliance database references

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Administración de Parques Nacionales, Argentina: Plan de vertebrados de la Patagonia

Administración de Parques Nacionales, Argentina: Avistajes de espcies de valor especial en áreas protegidas del noreste de Argentina

LSUMZ Mammals Collection

Natural History Museum of Los Angeles County: LACM Vertebrate Collection

California Academy of Sciences: CAS Mammalogy (MAM)

UMMZ Mammal Collection

Mammal Research Institute, Polish Academy of Sciences: Mammal Collection

Varied sources. Individual references may be obtained from website (paleodb.org)

iNaturalist.org: iNaturalist research-grade observations

Conservation International: Rapid Assessment Program (RAP) Biodiversity Survey Database

MMNH Mammal Collection

Yale Peabody Museum, (c) 2009. Specimen data records available through distributed digital resources.

MHP Mammal Collection

Museum of Vertebrate Zoology (MVZ), University of California, Berkeley

Yale Peabody Museum, (c) 2009. Specimen data records available through distributed digital resources.

Royal Ontario Museum: Mammalogy Collection - Royal Ontario Museum

ROM mammal collection

Royal Ontario Museum: Mammalogy Collection - Royal Ontario Museum

University of Wyoming Museum of Vertebrates

SBMNH Vertebrate Collection

Field Museum: Field Museum of Natural History (Zoology) Mammal Collection

Museo Argentino de Ciencias Naturales: Colección Nacional de Mastozoología - Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'

Natural History Museum, University of Oslo: Mammal collection, Natural History Museum, University of Oslo

TTU Mammal Collection

Ruedi M. Mammals housed at MHNG, Geneva. Muséum d'histoire naturelle de Genève

South Australian Museum: South Australian Museum Australia provider for OZCAM

University of Washington Burke Museum. Mammal Collection. Seattle, Washington.

Royal Belgian Institute of Natural Sciences: RBINS collections

Division of Mammals, Museum of Southwestern Biology (MSB)

Museum of Comparative Zoology, Harvard University

Administración de Parques Nacionales, Argentina: Registros biológicos en áreas protegidas obtenidos de documentos impresos

SNOMNH Mammal Collection

Yale Peabody Museum, (c) 2009. Specimen data records available through distributed digital resources.

MSU Vertebrate Collection

AMNH Mammal Collection

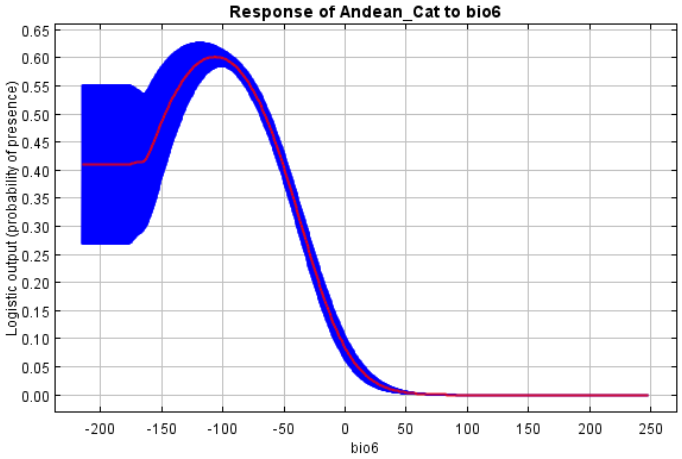
Museum of Vertebrate Zoology (MVZ), University of California, Berkeley

S.7.2. Maxent models results

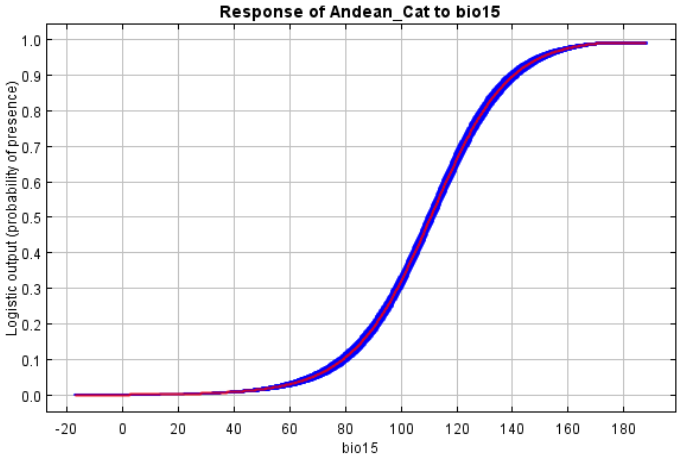
	Variable	Percent contribution	Permutation importance
Andean cat	Precipitation Seasonality	57.7	27.7
	Min Temperature of Coldest Month	27.1	37.5
	Temperature Seasonality	4.7	5.4
	Mean Diurnal Range	4.1	1.7
	Precipitation of Coldest Quarter	3.9	19.1
	Annual Precipitation	2.6	8.5
Vizcacha	Temperature Mean Diurnal Range	56.2	34.9
	Mean Temperature of Wettest Quarter	35.6	53.6
	Temperature Seasonality	5.3	9.9
	Min Temperature of Coldest Month	1.8	0.1
	Precipitation of the warmest quarter	1	1.5

Table S.7.2.1. Heuristic contribution of climatic predictors to Andean cat and mountain viscacha models.

Min Temperature of Coldest Month (bio6)



Precipitation Seasonality (bio15)



Precipitation of Coldest Quarter (bio19)

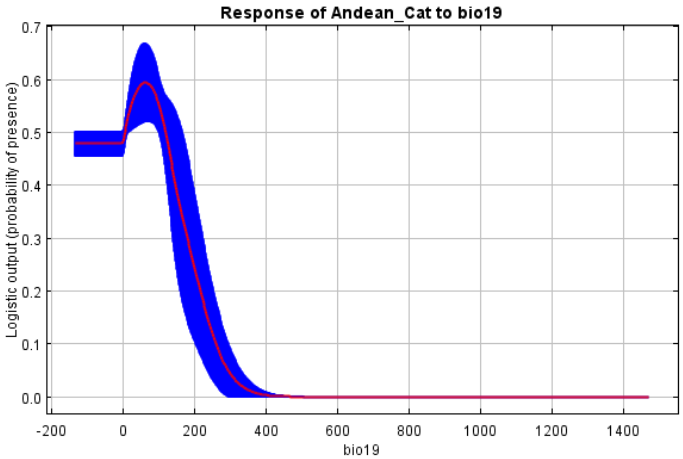


Figure S.7.2.1 Main response curves of the Andean cat model showing how the MaxEnt prediction varied as the main climatic variables change (maintaining the others at their average value).

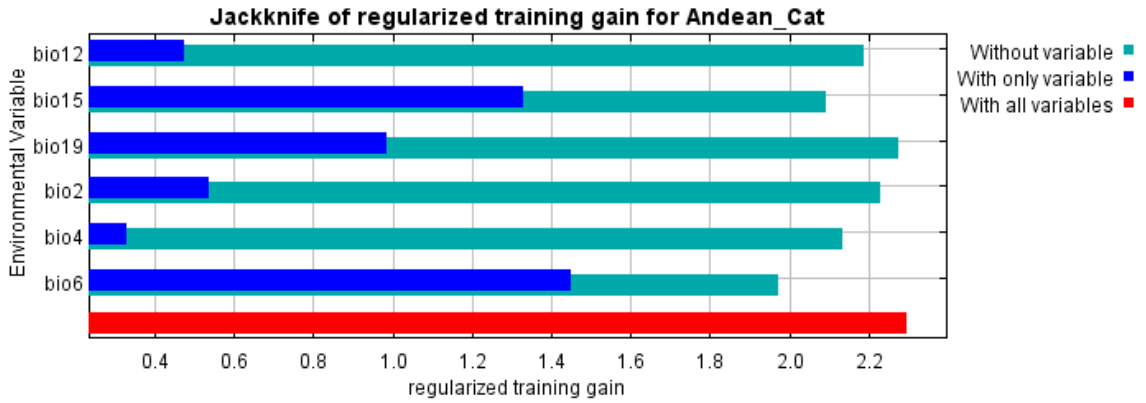


Figure S.7.2.2. Jacknife test for Andean cat model.

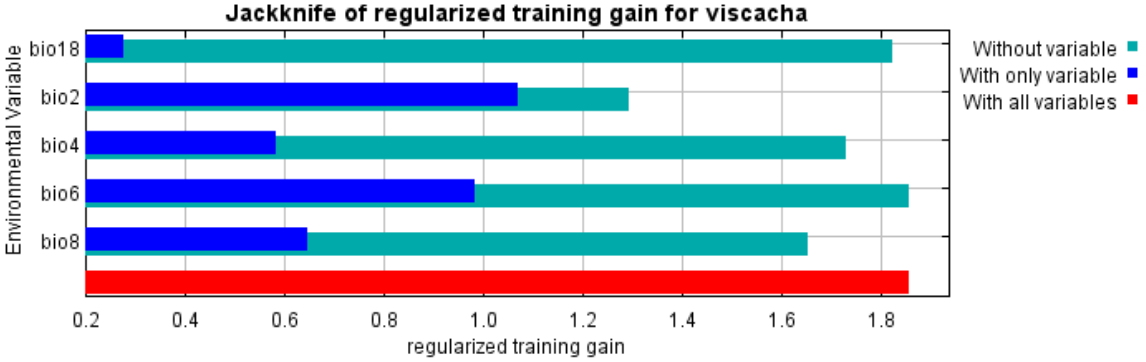
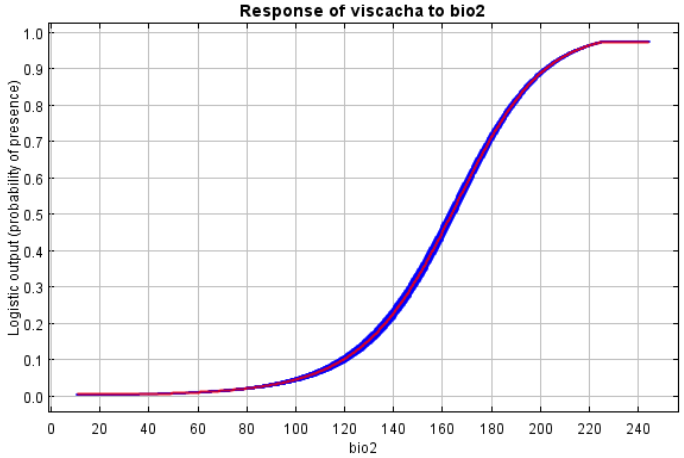
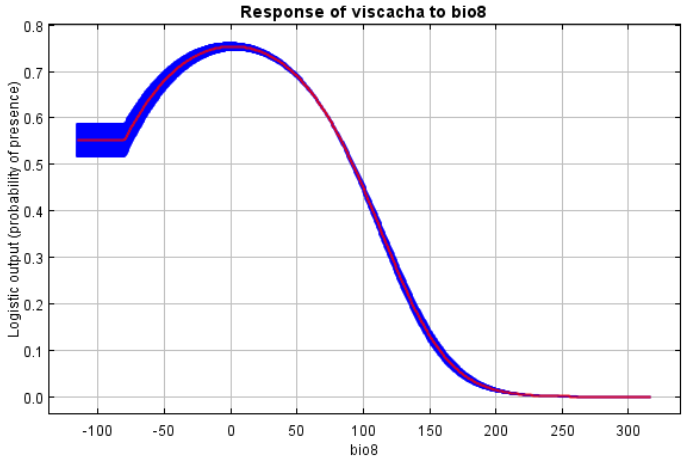


Figure S.7.2.3. Jacknife test for viscacha model.

Temperature Mean Diurnal Range (bio2)



Mean Temperature of Wettest Quarter (bio8)



Temperature Seasonality (bio4)

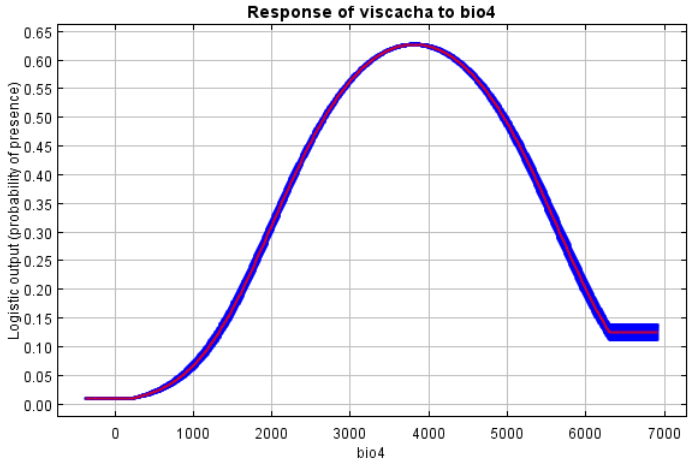


Figure S.7.2.4. Main response curves of the viscacha model showing how the MaxEnt prediction varied as the main climatic variables change (maintaining the others at their average value).

Chapter 8:

Discussion

The potential impacts of climate change on many ecosystems remain largely unknown, and this is particularly true for dry mountains which appear to be highly vulnerable to perturbations. In this thesis, I used a combination of climate data, remote sensing, direct field observations and modelling, to analyze the effects of climate variability and possible climate change on the Central Andean Dry Puna ecoregion.

The Dry Puna is a poorly studied high altitude ecoregion (Olson et al. 2001), and the driest area of the Andes. The triple frontier between Argentina, Bolivia and Chile is a key location to study climate variability due to the convergence there of tropical and extra-tropical atmospheric circulation (Messerli et al. 1997) and to the presence of the Andes as a major climatic barrier and imposing a strong elevation gradient (Garreaud et al. 2009). The Dry Puna is also an important system to study the effects of climate variability and trends on biodiversity due to three main factors: First, arid ecosystems can be severely affected by changes in climate (Melillo et al. 1993, Whitford 2002, Placzek et al. 2009); second, mountain areas have been suggested as one of the most vulnerable systems to climate change (Beniston 2003, Diaz et al. 2003); and third, the Dry Puna contains a high number of endemic species, being part of one of the most important hotspots of biodiversity in the planet (Myers et al. 2000), and as a result it is a global conservation priority area due to its biological distinctiveness and vulnerability (Dinerstein et al. 1995).

Considering this context, the main research aim of my thesis was to characterise the climate variability of the Dry Puna, and to understand the effects of this climate variability and possible long-term climate change on biological systems, focusing on a study area centred on the triple frontier of Argentina, Bolivia and Chile, between 3,000 to nearly 6,000m. This study is relevant to arid mountains in general, and to the fragile Dry Puna ecoregion in particular.

Here I summarise and discuss the key findings of my thesis, placing special emphasis on the vulnerability of Dry Puna ecosystems to future climate change and the implications for their conservation and future research.

8.1. Climate trends and patterns in the Dry Puna

The empirical evidence presented in this thesis confirmed that the climate of the Dry Puna is highly variable in space in response to the combined effects of topography and large-scale circulation systems (Chapter 3). The northeast part of the study area received a cooling elevation effect and a humid influence from the Amazon basin, resulting in more rainfall; the south-western portion was drier due to the barrier effect of the Andes and the dry influence of the Pacific anticyclone. The data also showed important climatic variation in relation to ENSO fluctuations, as it was expected for this region of South America (Vuille et al. 2000). Strong inter-annual variability in rainfall determined relative dry and hot conditions during El Niño events, and wet conditions during La Niña years.

In contrast with projections and observations of general warming in the Central Andes (Vuille and Bradley 2000, Vuille et al. 2003, Urrutia and Vuille 2009, Seiler et al. 2013), I found no consistent trends in precipitation or temperature across the study area over the last three decades. Rather than consistent temporal trends, the climate over this study period was dominated by strong inter-annual climate variability and by the interactive influences of tropical and subtropical systems. Data from four weather stations (out of eleven) were consistent with a significant temporal trend in annual temperatures: two decreasing and two increasing. This is likely the reflection of the complex topography, which by creating microclimates in mountains may well produce diverse climatic trends, due to differences in the amount of radiation received, changes in albedo, and differences between windward and sheltered slopes; therefore local measurements may not necessarily be representative of larger areas (Vuille 2011, Rangwala and Miller 2012).

Indeed, the lack of evidence of climate trends over the last 30 years should be considered with caution and in the context of the temporal scales at which these trends are investigated. For example, based on a tree-ring precipitation reconstruction Morales et al. (2012) revealed a clear drying trend for the Dry Puna since the 1930s. While the climatic data from high elevation in the study area showed no significant trend in rainfall such a drying process, operating over longer time scales, would probably strengthen the dry conditions associated to the ‘South American Arid Diagonal’ (Arroyo et al. 1988, Chacón et al. 2012), crossing the Andes south of the study area. The Arid Diagonal marks the transition between summer and winter rainfall regimes, at about 24ºS latitude. A strengthened Arid Diagonal could become a stronger barrier for the migration of many plants and animal species.

Besides assessing climate trends and variability in the Dry Puna, the climate dataset that I compiled from weather stations in the Dry Puna enabled me to demonstrate the low accuracy of global climate surfaces developed for mountains. Indeed, my empirical study with a dataset compiled from an extended network of 28 weather stations in the Dry Puna, revealed different behaviour in monthly precipitation and temperature than global climate surfaces in the Andes (Mosier et al. 2013), including a different magnitude and direction on long-term trends. Other authors have also pointed out to the poor representation of mountains in climate datasets, particularly for the Andes, with a spatially complex topography and few high altitude stations (Garreaud et al. 2009, Morales et al. 2012). My results highlight the relatively small scale at which climatic patterns are observed in high mountains, particularly where topographic changes are drastic like in my study area, where in a mere linear 100km the land rises from 2,400m in the Atacama Desert to the 5,920m in the Licancabur volcano.

Since the Central Andean Dry Puna is a poorly studied ecoregion, basic climatic data are urgently required to study climate change effects. As in most high altitude areas there is an urgent need to install weather stations in the triple frontier. It is necessary to study climate at local scales in mountains in order to detect how topography affect climate measures and trends and how this could be used to calibrate regional climatic models, making them more useful in mountain areas. At the same time, local measurement in mountains will allow to understand the effect of mountain weather in vegetation and ecosystems with accuracy. On the other hand, it is important to recognise that the poor precision of projected global climate datasets weakens the predictive performance of any model for mountains areas, so caution is needed when interpreting models in mountains using climate global databases.

8.2. Climate-linked impacts on primary productivity in the Dry Puna

Using NDVI as a proxy for green biomass, I studied how productivity responds to climate variability in the Dry Puna (Chapters 4 and 5). Primary productivity in the study area was generally low, as described for other high mountains with large areas devoid of vegetation and patchy and fragmented vegetation (Körner 2003). Productivity appeared to be driven by climatic processes operating both at regional and local scales. At the broader spatial scale, primary productivity increased with the proximity to the moisture source in the Amazon basin. At a more localized scale, primary productivity varied with altitude, slope and aspect, which combined create microclimatic conditions in mountains areas. At this high elevation

environment productivity decreased with altitude; it was higher in areas with a northern orientation, which received longer hours of sunlight, and thus also experienced higher temperatures, and were more exposed to the Amazonian humid influence. A similar phenomenon was described in the Andes at lower latitudes, where the dominance of drought deciduous species in northern orientations (with adaptations to maximize photosynthesis during the wet months) contrasted with the evergreen and semi evergreen vegetation in south facing slopes (Rundel et al. 2002). These results confirm the role of slope exposure in creating microclimates in high mountains, where there is a clear relationship between slope exposure and radiation, and heat (Körner 2003).

Like the climate, primary productivity showed no consistent trend over the last three decades, and a strong influence of ENSO oscillations –i.e. primary productivity was lower during El Niño years, relatively dry and hot. At a finer scale of resolution, I assessed the particular effect of low rainfall at the level of vegetation types, expecting that the responses of the dominant plant species will vary according to their adaptations to cope with the extreme weather of the Dry Puna. In agreement with my predictions, grasslands and mixed communities containing grasses were the most affected by reduced rainfall. The vegetation dominated by bushes, with longer root systems compared to grasses in this dry area (Arroyo et al. 1988, Schenk and Jackson 2002) and the vegetation associated to water sources (i.e. rivers, streams and underground sources) were the most resilience to dry years. Despite their restricted distribution, wetlands seem to be the centres of biodiversity in the Dry Puna even during dry years. For practical reasons, I could only compare satellite images from two years (one ‘normal’ and one ‘dry’ year). With additional sources of fine resolution data, it would be possible to assess the effects of consecutive dry years on the productivity of these ecosystems.

In view of the long-term decreasing rainfall and the predicted increasing frequency of extreme El Niño events (Cai et al. 2014), the productivity of the highlands might be critically affected in the future. Drier and warmer conditions will increase evapotranspiration, which diminishes water availability for plants and primary productivity. My research showed that the grasslands, which host important biodiversity and are the main source of food for diverse herbivores, will be particularly vulnerable, with additional social impacts through the effects upon the foraging grounds of llama herds (Patty et al. 2010). Even the wetland vegetation and scrublands, seemingly more resilient, can suffer from the accumulative effect of drier conditions upon the more permanent sources of water.

My study demonstrates the potential use of time series of NDVI data, derived from satellite images, to permanently monitor the responses of vegetation to climate change in high mountains. Moreover, in view of the scarcity of climatic records and the limited accessibility to mountain areas, the predictive relationships developed between NDVI and ENSO (Chapter 4) might help to better understand rainfall variability in the Dry Puna. Also, it would be good to test whether these relationships between NDVI and climate are maintained in other arid mountains. In addition, further studies should consider modelling NDVI values under future climate change scenarios. It is important to point out, however, that the implications derived from projections of changes in productivity, are based on the potential scenario in which current climate-NDVI relationships are maintained in the future, as well as the physiological vulnerability of certain vegetation or plant functional types to drier and warmer conditions.

8.3. Climate impacts on biodiversity: mountain carnivores as case studies

My study of the guild of medium-size carnivores inhabiting the Dry Puna revealed that coexistence of Andean cats (*Leopardus jacobita*), Pampas cats (*L. colocolo*) and culpeo foxes (*Lycalopex culpaeus*) was favoured by differences in habitat preference, including the spatial scales of habitat use, and access to key prey species such as southern mountain viscachas (*Lagidium viscacia*) and tucos (*Ctenomys* spp.) (Chapter 6). The Andean cat, the most specialized carnivore of the guild, is the rarest and with the most restricted distribution (Marino et al. 2010, Villalba et al. 2016), but my findings would indicate that it can coexist with the more abundant carnivores because it successfully exploits localized resources such as refuge and viscacha colonies. Both Andean cats and their main prey, the rocky specialist viscacha, selected areas close to wetlands and broken terrain, at fine scales. Other landscape characteristics associated to topography and directly influencing primary productivity (Chapter 5) were also selected by carnivores, including northern orientations. The generalist culpeo showed least preference, selected habitats at the broader scale, and was the more widely distributed, as expected from its larger body size and more diverse diet, which includes large herbivores such as llamas and vicuñas (Walker et al. 2007, Napolitano et al. 2008). A similar situation of high specialization in habitat use and trophic niche occurs with the Iberian Lynx (*Lynx pardinus*) and the generalists red fox (*Vulpes vulpes*) in the Mediterranean area (Soto and Palomares 2015). Moreover, an example of trophic

specialization in mountain carnivores is the Altai mountain weasel (*Mustela altaica*) which distribution followed that of its main prey the pika Ochotona spp. (Bischof et al. 2014).

This study is a good example of the mechanism facilitating carnivore coexistence in arid regions. In order to test the generalization of these results it is recommended to investigate carnivore coexistence in other areas of the High Andes, including spatial segregation and resource portioning in more humid areas, under less stringent environmental constrains.

The spatial ecology of medium size carnivores and their prey confirmed the critical role of wetlands in supporting the biological diversity of the Dry Puna, and how their resilience to periods of low rainfall can be crucial to sustain animal communities further up the food web. The relationship between wetlands and their water sources is however unclear (Squeo et al. 2006). This is an important gap of knowledge, as wetland dynamics and their dependence on underground water sources are clearly key to understand the resilience of the general system to climate change. Although this study found no significant trends in climate conditions, or in vegetation productivity, in the study area over the last three decades, other studies have reported changes in climate that may be having a long-term impact on wetlands, and through chain effects, on vegetation communities and mammal populations (Campbell et al. 2013, Owen-Smith and Ogutu 2013).

The long-term effect of climate change is a particular concern for high altitude animals. The evidence indicates that climate change is promoting an upwards shift in the range of mountain specialists (Parmesan 2006, Seimon et al. 2007, Lenoir et al. 2008, Raxworthy et al. 2008, Harsch et al. 2009, Luo et al. 2014). Given the lack of detailed information for many highland species, and their common adaptations, the model I developed to predict the response of the endangered Andean cat helps understand how other organisms living in similar climatic conditions may respond to climate change (Chapter 7). For example, the predicted distribution of suitable habitats for the Andean cat changed in different ways across the species range under future scenarios of climate change. The habitat predicted for Andean cats will be reduced by up to 30% by 2080 due to climate change, with the core of the Andean cat distribution in the central and northern population would move upwards, similar to what has been reported for other mountain species (Parmesan 2006, Seimon et al. 2007, Raxworthy et al. 2008) such as neotropical hummingbirds (Buermann et al. 2011) and Tibetan ungulates (Luo et al. 2014). Instead, the habitats in the southern range, seemingly less suitable, appeared to be less vulnerable, increasing polewards and into lower elevations. The implications are significant for the conservation of genetic diversity, as the Andean cat population has a strong

phylogenetic structure (Cossíos et al. 2012); our predictions indicate that biogeographical barriers between them will be reinforced under climate change. A strengthened Arid Diagonal would become a stronger barrier for dispersal, restricting even more the connectivity between the two main Andean cat lineages, in the northern and southern populations, which separated during the last post-glacial warming (Cossíos et al. 2012).

At the species level, the distribution of Andean cats reveals a close dependency with climates dominated by low temperatures, along the Andes and at lower elevation in Northern Patagonia (Marino et al. 2011). This thermal limitation underlies the predicted habitat loss and upwards shift under climate change. However, the predicted consequences were different in magnitude and direction at the northern and southern limits of the species range, and according to the future availability of viscachas, their main prey. This shows the importance of predict species-specific responses to climate change, as these may vary among species with different physiological tolerances and the capacity of adaptation to changes in climate (Guralnick and Pearman 2009). Similarly, our results suggest that it is not advisable to make generalizations from upwards shifts in mountain species under climate change, since suitable climatic conditions may also appear at lower elevations.

8.4. Implications for the conservation of Dry Puna biodiversity

My thesis illustrates the importance of including multiple spatial scales in the study of climate, vegetation and fauna in the Dry Puna and in arid mountains in general. In the triple frontier strong regional climate patterns overlapped with others driven by the rugged topography that creates microclimates with their local conditions of temperature, snow, water storage, precipitation, and wind, among others (Beniston 2003, Körner 2003). These microclimates are very important as create the relative high biological diversity of mountains (Körner 2003).

As other author have suggested for alpine species conservation it would be important to understand the several mechanisms and the complex factors and interactions that could affect them (as the use of microclimates caused by ruggedness) in order to suggest effective conservation strategies under climate change conditions (Ray et al. 2013). The relevance of spatial and temporal scales is clearly important for the conservation of the endangered Andean cat. At the broader spatial scale, the distribution of Andean cats is driven by cold climatic conditions and by the distribution of the prey, indicating that the species is vulnerable to

global warming. At the same time, at the local-scale Andean cat habitat associations are driven by the availability of wetlands and rocky formations, suggesting that the protection of these environments is a priority to meet conservation targets efficiently.

By taking a multi-scale and multi-species approach, this study provides a solid platform for conservation planning in this region of the Dry Puna. As an example, the dependence of viscachas on rocky outcrops in north facing slopes, which provide refuges from weather and predators and better conditions for thermal regulation, is fundamental to understand the species response to climate change.

The upslope shift experienced by mountain species under climate change reduces their chances of long-term survival, as populations become constrained into smaller areas and lose connectivity between them (Sekercioglu et al. 2008). As current networks of protected areas might not be useful to protect biodiversity in the future, it has been suggested that increasing connectivity between protected areas might become the best strategy for long-term conservation (Cross et al. 2013). One way to increase connectivity for Andean cats in the Dry Puna is through the protection of biological corridors based on the information about projected distribution under climate change (Soule et al. 2004). Corridors would facilitate animals tracking the changing climate conditions in space and time (Austin et al. 2013), for example the Andean cat corridors crossing environmental barriers such as the Arid Diagonal and Andean Knee (Figure 8.1), to maintain connections among populations.

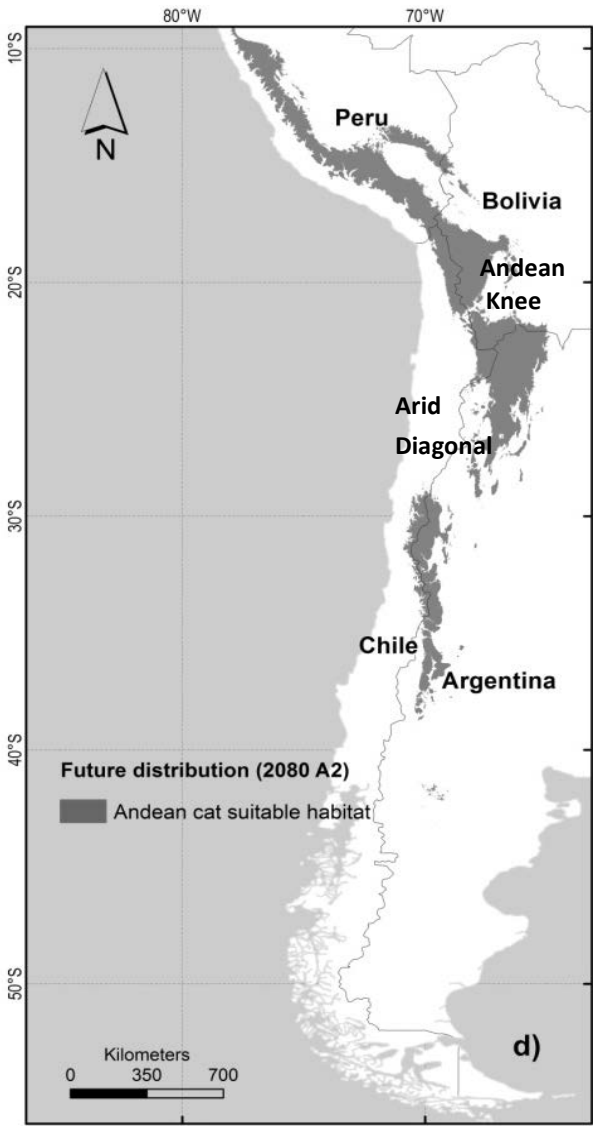


Figure 8.1. Maxent predictions of Andean cat habitat suitability under future climate conditions (2080 A2), using maximum sensitivity-specificity threshold (from Chapter 7). Map shows biogeographical barriers, Arid Diagonal and Andean Knee.

The triple frontier of Argentina, Bolivia and Chile is a clear stronghold for the conservation of Andean cats under climate change (Figure 8.2). In this area my models projects that favourable climatic conditions for the species and its prey will persist until 2080, when only 10 to 15% of the total habitat suitable for Andean cat will remain within the existing network or protected areas in South America.

In the triple frontier, habitat corridors for key species are associated to wetlands cross the international boundaries connecting the existing protected areas (Figure 8.2). For fine-scale habitat specialists, such as Andean cats and viscachas, these corridors are optimal locations to

ensure connectivity between populations and protected areas. The importance of wetlands for Dry Puna biodiversity in the study area, and for Andean cat population persistence in particular, highlight the urgency to protect them, given climate model projections and observations of climate change in the Andes.

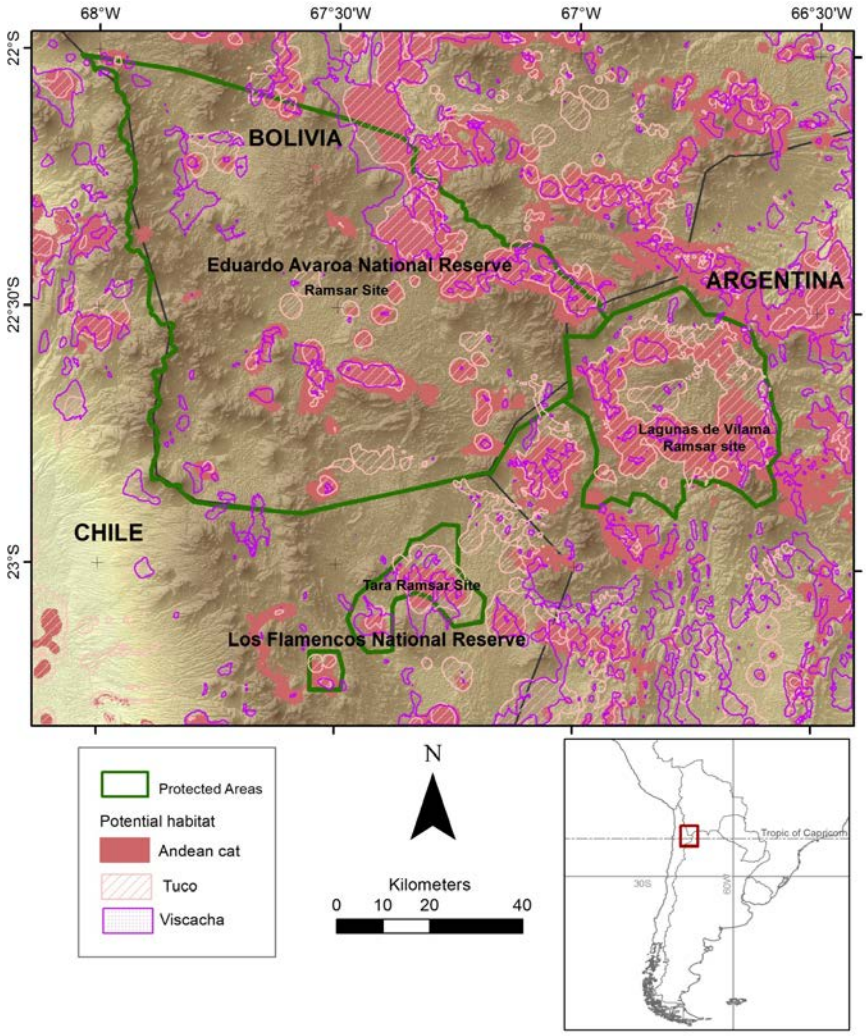


Figure 8.2. Protected areas in the triple frontier of Argentina, Bolivia and Chile, and the predicted distributions of Andean cats, viscachas and tucos (from Chapter 6).

Even though human density in the Dry Puna is low and with localized effects in the environment, there are emerging threats that could have significant impacts on biodiversity. Water extraction is an increasing concern, particularly in Chile and Bolivia, but there is not adequate data or systematic monitoring. Furthermore, land use changes can constrain the responses of species to climate change, so adequate monitoring and planning are needed to avoid detrimental consequences on biodiversity.

8.5. References

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Appendix 1. Peer-Reviewed Papers and Reports

Marino J, **M Bennett**, D Cossios, A Iriarte, M Lucherini, P Pliscoff, C Sillero-Zubiri, L Villalba and S Walker. 2011. *Bioclimatic constraints to Andean cat distribution: a modelling application for rare species.* Diversity and Distributions 17: 311–322

Villalba, L., Lucherini, M., Walker, S., Lagos, N., Cossios, D., Bennett, M. & Huaranca, J. 2016. *Leopardus jacobita*. The IUCN Red List of Threatened Species 2016: e.T15452A50657407.
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Diversity and Distributions

BIODIVERSITY RESEARCH

Bioclimatic constraints to Andean cat distribution: a modelling application for rare species

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ABSTRACT

Aim To identify the bioclimatic niche of the endangered Andean cat (*Leopardus jacobita*), one of the rarest and least known felids in the world, by developing a species distribution model.

Location South America, High Andes and Patagonian steppe. Peru, Bolivia, Chile, Argentina.

Methods We used 108 Andean cat records to build the models, and 27 to test them, applying the Maxent algorithm to sets of uncorrelated bioclimatic variables from global databases, including elevation. We based our biogeographical interpretations on the examination of the predicted geographic range, the modelled response curves and latitudinal variations in climatic variables associated with the locality data.

Results Simple bioclimatic models for Andean cats were highly predictive with only 3–4 explanatory variables. The climatic niche of the species was defined by extreme diurnal variations in temperature, cold minimum and moderate maximum temperatures, and aridity, characteristic not only of the Andean highlands but also of the Patagonian steppe. Argentina had the highest representation of suitable climates, and Chile the lowest. The most favourable conditions were centrally located and spanned across international boundaries. Discontinuities in suitable climatic conditions coincided with three biogeographical barriers associated with climatic or topographic transitions.

Main conclusions Simple bioclimatic models can produce useful predictions of suitable climatic conditions for rare species, including major biogeographical constraints. In our study case, these constraints are also known to affect the distribution of other Andean species and the genetic structure of Andean cat populations. We recommend surveys of areas with suitable climates and no Andean cat records, including the corridor connecting two core populations. The inclusion of landscape variables at finer scales, crucially the distribution of Andean cat prey, would contribute to refine our predictions for conservation applications.

Keywords

Andes, biogeographical barriers, biogeography, climatic niche, species distribution models.

INTRODUCTION

A central postulate in biogeography is that climate exerts a dominant control over the distribution of species, as evidenced by fossil records (Davis & Shaw, 2001) and recent observed trends (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003). Founded in the ecological niche theory (Hutchinson, 1957), climatic envelope models provide a suitable tool

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to test and advance the ecological and evolutionary theories underpinning the fields of biogeography and biological conservation (Araújo *et al.*, 2004; Munguía *et al.*, 2008; Makowsky *et al.*, 2010). Indeed, various modelling techniques developed over the last decades to study species' responses to the environment are now prominent in modern ecological theory (Heegaard, 2002; Guisan & Thuiller, 2005; Sagarin *et al.*, 2006; Austin, 2007; Elith & Leathwick, 2009).

Models based on bioclimatic variables at macro-scales are producing successful simulations of current distributions, and refined algorithms perform well with presence-only data and limited number of localities (Elith & Leathwick, 2009; Franklin *et al.*, 2009). These advances are particularly relevant for poorly known, rare and endangered species, and cryptic or nocturnal animals for which absence is difficult to define (Engler *et al.*, 2004; Papeş & Gaubert, 2007; Pearson *et al.*, 2007; Brito *et al.*, 2009; Thorn *et al.*, 2009; Wilting *et al.*, 2010). The Maxent algorithm, based on maximum entropy theory (Phillips *et al.*, 2006), is known to outperform alternative presence-only models when sample sizes are small (Hernandez *et al.*, 2006; Wisz *et al.*, 2008); it is also less sensible to the choice of calibration area for pseudo-absences (Giovanelli *et al.*, 2010) and performs particularly well for range-restricted or specialized organisms (Elith *et al.*, 2006; Phillips *et al.*, 2006).

We used Maxent to model the climatic niche of Andean cats (*Leopardus jacobita)* at the continental scale of South America. Andean cats are listed as endangered (Acosta *et al.*, 2008) and are considered one of the rarest and least known felids in the world (Villalba *et al.*, 2004; Brodie, 2009). Our poor understanding of the biology of Andean cats stems from their elusive behaviour and seemingly low population densities (Lucherini *et al.*, 2008; Marino *et al.*, 2010); and until recently there was only a small set of confirmed locations for the species (Yensen & Seymour, 2000; Villalba *et al.*, 2004). Thanks to the coordinated effort of members of the Andean Cat Alliance over the last decade, the number of confirmed localities has now increased to more than 200. The database compiled for this study includes published and unpublished records from Argentina, Bolivia, Chile and Peru (Sanderson, 1999; Perovic *et al.*, 2003; Barbry & Gallardo, 2006; Sorli *et al.*, 2006; Cossios *et al.*, 2007; Napolitano *et al.*, 2008; Viscarra, 2008; Torrico, 2009). Most records are confined to the Central Andes above 4000 m, but several recent findings also locate them at much lower elevation in arid regions of west Argentina (Di Martino *et al.*, 2008).

The newly extended database opens up the possibility of using statistical models with the following objectives: a) to explore the key dimensions of the climatic component of the Andean cat ecological niche (Pearson & Dawson, 2003), and b) to identify regions with environmental conditions similar to where the species is known to occur (Pearson *et al.*, 2007). While elevation clearly is a strong, albeit indirect, predictor of habitat suitability for Andean cats, the barrier effect of the Andes also creates asymmetric climatic conditions on each side of the cordillera (Garreaud, 2009), known to affect the distribution of species and their genetic variability (Chesser, 2000; Weigend, 2002; Marin *et al.*, 2007; Cossios *et al.*, 2009). To include these complex climatic patterns, we considered multiple climatic predictor variables at the level of South America, benefiting from Maxent's ability to handle complex functions and to produce easily interpretable response curves (Phillips *et al.*, 2006). In this paper, we also describe the process of variable selection, aimed at minimizing redundancy and to include factors related to the physiology of animals in harsh environments such as those of the High Andes. We discuss the scope for improvements and applications of these niche models, and elaborate on the implications of the species' dietary specialization upon Chinchillidae rodents - the chinchillas and viscachas of South America (Walker *et al.*, 2007; Napolitano *et al.*, 2008; Viscarra, 2008; Torrico, 2009).

METHODS

Location data

The authors compiled the Andean Cat Alliance database with reliable records spanning the period 1988–2009. These comprise the localities of 39 skins, three skulls, 19 sightings, 25 camera-trap captures, 99 DNA identifications (94 faecal samples, four hair samples and one skin sample), and 52 radio-tracking fixes from the only specimen ever trapped, an adult female captured in Bolivia (Delgado *et al.*, 2004).

To minimize the spatial dependences attributed to true biological origin or differential searching intensities across regions (Segurado *et al.*, 2006), we subsampled the data at a distance sufficient to reduce spatial autocorrelation. The spatial autocorrelation detected among some pairs of variables of the location data was dropped to levels depicted as insignificant by the Moran's I Test (Moran, 1950) after randomly selecting just one locality point per each 3 × 3 km cell of an over-imposed grid. As a result, the dataset was reduced from 237 to 135, of which 108 were used to run the models and 27 (20%) to test them.

Selection of variables

We selected predictor variables from the following: the WorldClim database of bioclimatic interpolated climate surfaces at 1-km resolution (derived from monthly temperature and rainfall values)(Hijmans *et al.*, 2005); the Global Land Cover GLC2000 at 1-km resolution (land cover types) (Bartholome & Belward, 2005); Shuttle Radar Topographic Mission (SRTM) at a resolution of 90 m (elevation, orientation and topography index) (Rabus *et al.*, 2003); and the Global Inventory Modelling and Mapping Studies (NDVI = Normalized Difference Vegetation Index at 250 m) (Tucker *et al.*, 2004). The latter two were resampled in ArcGIS 9.2 to a 1-km resolution. For area measurements, the layers were projected into UTM coordinates with the original datum WGS84.

We first summarized the climatic information associated with the locality data using principal component analysis

(PCA). The PCA helped to identify the sets of variables more strongly associated with the first and second axes of the ordination (with highest positive or negative loading scores), which together accounted for 79% of the variation among localities (Table 1). Between any two redundant variables (i.e. with Pearson correlation values > 0.70), those considered as surrogates for cold tolerance and moisture stress were preferred, because of the cold and dry climate of the High Andes (for example, minimum temperature of the coldest month rather than mean temperature of the cold quarter to represent absolute minimum temperatures). Because of redundancy in the climatic data, a few variables satisfied our correlation threshold. For this study, we ran models with all combinations of minimally correlated variables, both with and without elevation (Table 2).

Statistical model and validation

Maxent is a machine learning algorithm that estimates the most uniform distribution (maximum entropy) across the study area given the constraint that the expected value of each environmental predictor variable under this estimated distribution matches its empirical average (Phillips *et al.*, 2006). The modelled probability is a 'Gibbs' distribution (i.e. exponential in a weighted sum of the features) and the model logistic outputs have a natural probabilistic interpretation representing degrees of habitat suitability (0 = unsuitable to 0.99 = best habitat) (Pearson *et al.*, 2007). For a detailed explanation of modelling methodology using Maxent, refer the studies by Phillips *et al.* (2006) and Phillips & Dudik (2008). We applied version 3.2.19 of the Maxent software with default values, up to 1000 iterations and implementing linear, quadratic and product features types (Phillips & Dudik, 2008).

We partitioned the occurrence locations randomly into two subsamples, using 80% of the locations as the training dataset and the remaining 20% for testing the resulting (partitioned) models. The measure of fit implemented by Maxent is the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (ranging from 0.5 = random to 1 = perfect discrimination). Some studies have pointed to some limitations in the use of AUC as a measure of performance in presence-only models (Lobo *et al.*, 2010), but this is often used as a single threshold-independent measure of choice for model performance; it has been shown to be independent of prevalence and a highly effective measure of the performance of ordinal score models (Manel *et al.*, 2001; McPherson *et al.*, 2004; Thuiller *et al.*, 2005).

Table 1 Results of a principal component analysis (PCA) of bioclimatic and elevation variables associated with the Andean cat presence localities (n = 135).

	PCA loadings			
Variables	PC1	PC2	PC3	PC4
Elevation	**0.28**	0.17	0.05	0.01
Precipitation seasonality	**0.28**	−0.06	0.21	0.01
Temperature mean diurnal range	**0.24**	−0.13	0.02	0.64
Temperature annual range	0.13	**−0.31**	−0.15	0.42
Temperature seasonality	0.06	**−0.35**	−0.22	0.04
Precipitation of wettest month	0.04	**0.34**	0.24	0.12
Precipitation of warmest quarter	−0.10	**0.32**	0.14	0.29
Mean temperature of wettest quarter	−0.12	**−0.25**	0.38	0.06
Precipitation of wettest quarter	−0.16	**0.31**	0.11	0.31
Maximum temperature of warmest month	−0.18	**−0.31**	0.06	0.22
Annual precipitation	−0.20	**0.29**	0.04	0.26
Mean temperature of warmest quarter	−0.22	**−0.29**	0.10	0.06
Temperature annual mean	**−0.26**	−0.22	0.25	0.10
Precipitation of coldest quarter	**−0.26**	0.04	−0.43	0.08
Precipitation of driest month	**−0.28**	0.07	−0.37	0.10
Precipitation of driest quarter	**−0.28**	0.12	−0.30	0.12
Mean temperature of driest quarter	**−0.29**	−0.13	0.01	−0.12
Mean temperature of coldest quarter	**−0.31**	−0.01	0.33	0.06
Minimum temperature of coldest month	**−0.33**	−0.02	0.21	−0.19
Proportion of variance	0.43	0.36	0.10	0.05
Cumulative proportion	0.43	0.79	0.88	0.93

The columns show loading factors associated with the first four principal component factors or axes (PC), with the percentage of the variance explained by each of these factors at the bottom. In bold are highlighted the highest loading scores showing the two groups of variables associated with the first and second principal components.

Variable contribution and response curves

We considered Maxent's heuristic estimates of the relative contribution of environmental variables to the models and the results of jackknife analyses for each environmental layer (Phillips & Dudik, 2008). For the variables with highest predictive value, we examined the response curves showing how each of these environmental variables affects the Maxent prediction (Phillips & Dudik, 2008). The curves illustrate how the logistic prediction changes as each environmental variable is varied, while keeping all other environmental variables at their average sample value. The curves thus represent the marginal effect of changing exactly one variable.

RESULTS

Explanatory variables and model performance

The exploratory analyses of bioclimatic variables led to four combinations of minimally correlated variables, including elevation and various measures of temperature and precipitation (Table 2). Two combinations retained elevation as an explanatory variable plus measures of temperature variation, either the annual range (model A) or the mean diurnal range (model B) (themselves highly inter-correlated); all other temperature descriptors were closely correlated with elevation. The two other combinations were formed by the minimum and maximum temperatures of the coldest and warmest months (models C and D) as explanatory variables, or the

Table 2 Four complementary models of Andean cat habitat suitability, with and without elevation as explanatory variable.

	Complementary models			
	Percentage contribution of variables			
Variables	Model A	Model B	Model C	Model D
Elevation	49.7	47.4		
Temperature				
Annual mean temperature				62.4
Mean diurnal range temperature		50.0		35.8
Temperature annual range	49.4			
Minimum temperature of coldest month			57.3	
Maximum temperature of warmest month			37.1	
Precipitation				
Annual precipitation		1.2		0.8
Precipitation of driest quarter	0.8		5.6	
Precipitation of coldest quarter		1.5		1.8
Models' performance				
Training AUC	0.988	0.989	0.988	**0.990**
Test AUC	0.984	0.989	0.985	**0.993**

The values are Maxent's heuristic estimates of the relative contribution of environmental variables to the models (Phillips & Dudik, 2008). In grey are highlighted the variable/s in each model that contained the most useful information alone, and/or the most information that is not present in other variables (according to Jackknife tests of each environmental layer, not shown).
AUC, area under the curve.

annual mean temperature and mean diurnal range (models C and D). Minimally correlated variables describing precipitation contributed little to the models; among them, the amount of rainfall during the dry season was the more useful variable. The other environmental layers depicting productivity (NDVI), topography, orientation and land use type showed no predictive value (results not shown).

All four models based on these sets of uncorrelated variables provided good fit to the data and were successfully validated by the test dataset (Table 2). Model D provided the best fit, combining as predictor variables the annual mean and mean diurnal range temperature, with the amount of rainfall in the dry season (winter) and throughout the year. The variables that contributed the most information not present in other variables (from jackknife tests of each environmental layer, not shown) were elevation and a measure of temperature: mean diurnal range of temperature in model B; minimum temperature of the coldest month in model C; and mean annual and mean diurnal range temperature in model D.

Predicted range of suitable climates for Andean cats

We focused on model D - that with the highest AUC - to describe the geography of the areas climatically suitable for Andean cats (Fig. 1). All four models provided similar geographic predictions, with the main difference being the amount of area climatically suitable, albeit of low probability value, in Argentine Patagonia - the prediction from model D was intermediate in this regard. We chose the lowest predicted value associated with any one of the presence records to distinguish suitable from unsuitable conditions; this 'lowest presence threshold' identifies pixels predicted as being at least as suitable as those where a species' presence has been recorded (Hernandez *et al.*, 2006; Pearson *et al.*, 2007; Raxworthy *et al.*, 2007). The lowest predicted probability associated with a record was 0.028, corresponding to the southernmost locality (38.3° S, 69.9° W) and lowest elevation (650 m) (Di Martino *et al.*, 2008).

The areas predicted as suitable by the model covered 1,172,320 km^2, including: 326,720 km^2 (28%) in Perú, 233,270 km^2 (20%) in Bolivia, 127,560 km^2 (11%) in Chile, and 466, 260 km^2 (40%) in Argentina. Suitable climatic conditions for Andean cats were found along the High Andes and at lower elevations in the eastern slopes of the cordillera, towards the Argentine Patagonian steppes (Fig. 1). The most favourable climatic conditions were in the central portion of the predicted latitudinal range. The pixels with highest probabilities are concentrated around the region of the triple frontiers between Bolivia, Chile and Peru (18° S 69° W) and Argentina, Bolivia and Chile (23° S 67° W). These are connected by a band of highly suitable climates along the highest peaks. This bottleneck in optimal climatic conditions coincides with a climatic boundary at around 20° S in Bolivia, known as the 'Andean Knee', where the cordillera takes a sharp bend south (Fig. 1). The northern extreme of the climatically suitable range was predicted to be around 6.5° S and coincided with a climatic and biogeographic feature known as the 'Peruvian Low' or Huancabamba Depression; further north only small patches with suitable climatic conditions were predicted, in the highest peaks of the Ecuadorian Andes.

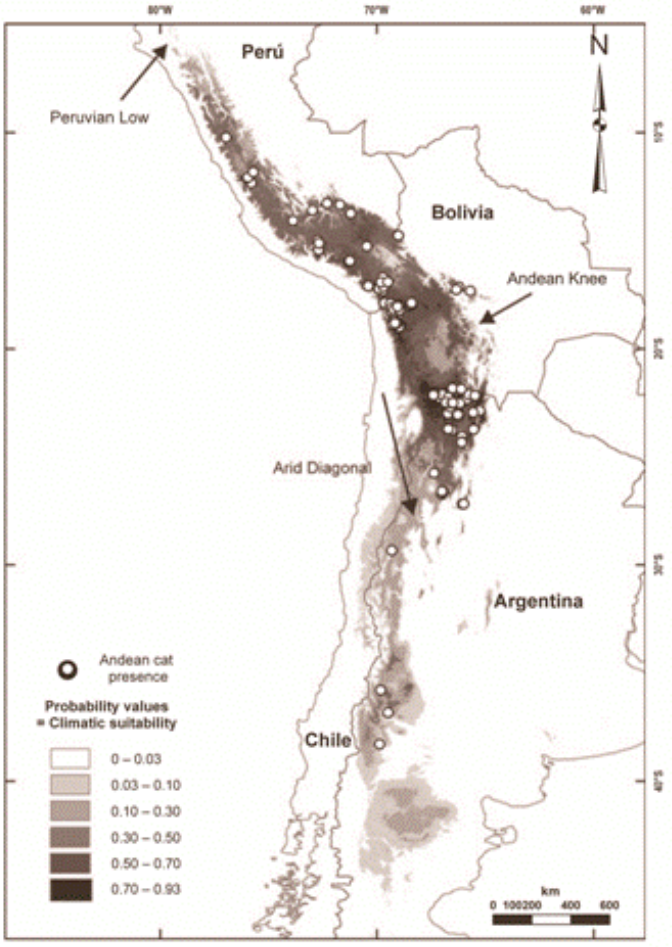

Figure 1 Andean cat suitability map (model D in Table 2). The lowest threshold for suitability (0.028) corresponds to the lowest probability of a known location and 0.93 to the highest.

Southwards, climatically suitable conditions narrowed markedly between 24° and 29° S along the Andes, where the 'Arid Diagonal' traverses the cordillera between Chile and Argentina (Fig. 1). While conditions improved further south, as latitude decreases below around 40° S the greater humidity and colder climate result in wet forests and glaciers seemingly unsuitable for Andean cats. A 'tail' of climatically suitable area, albeit of low suitability, descends into the Argentine Patagonia at the southern extreme of the predicted range, from where only a few records exist.

Climatic niche and response curves

The response curves in Fig. 2 illustrate how Maxent predictions of climatic suitability vary with elevation and key climatic variables across South America (only shown for those variables with highest predictive value, as shown in Table 2). Climatic suitability peaked around 4 °C of mean annual temperature, decreasing rapidly towards warmer climates (Fig. 2a); the empirical average from location data was 5.4 °C (SD 2.5, n = 135). With regard to the maximum temperature of the hottest month, the best climatic conditions were predicted around 20 °C, with an empirical average of 17.3 °C (SD 3.3) (Fig. 2b). All other curves showed more skewed responses, with optimal climatic conditions close to environmental extremes: around −13 °C of minimum temperature of the coldest month, and decreasing rapidly towards values just above zero (empirical average −9.0 °C, SD 3.2) (Fig. 2c); and around 12–20 °C of mean difference between the daily maximum and minimum temperatures (empirical average 17.6 °C, SD 1.6) (Fig. 2d). Most temperature-related aspects of the climatic niche of Andean cats were associated with variations in elevation. Suitable climatic conditions were mostly restricted to areas above 2000–3000 m, and incrementing

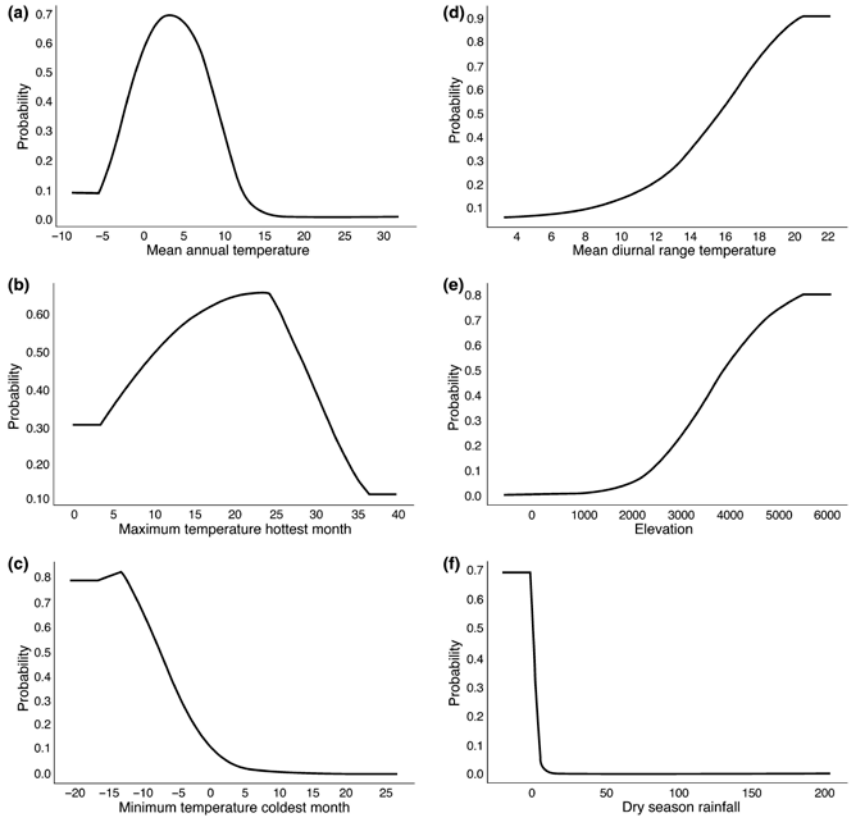

Figure 2 Marginal response curves showing how environmental variables affected the Maxent prediction of suitability (i.e. how the logistic prediction changes as each environmental predictor is varied, while keeping all others at their average sample value).

rapidly up to elevations above the empirical average of 4160 m (SD 620) (Fig. 2e). All Andean cat locations were in arid lands, with an empirical average of 268 mm of rainfall per year (SD 242), of which on average 185 mm (SD 139) fall in a relatively wet summer, and very little during winter. Climatic suitability decreased abruptly from areas with little or no rainfall during the dry season, towards areas with 50 mm or more (dry season empirical average 6.7 mm, SD 13.1) (Fig. 2f).

Three climatic variables were used to represent the environmental space of the Andean cat records along a north–south axis (Fig. 3). These environmental relationships notably change direction at around the latitude of the Andean Knee (20° S), where the Maxent model predicted a discontinuity in highly suitable climates. This is a region of extreme aridity, with cold weather and large diurnal temperature fluctuations (Fig. 3), conditions that become less harsh south and northwards, and seemingly less suitable for Andean cats towards the edges of the range. There is an apparent climatic gap that coincides with the latitudinal range of the Arid Diagonal, and the climatic conditions further south in the much lower lying Patagonian steppe tend to resemble those of the High Andes at the northern edge of the species range.

DISCUSSION

This study contributes relatively simple bioclimatic models for a rare species, which, despite a considerable increase in research and conservation efforts over the last 10 years, is still considered among 14 threatened and severely understudied felid species requiring more attention by conservation biologists (Brodie, 2009). The models provide valuable information on the climatic dimension of the Andean cat niche and on the effect of biogeographic barriers on its distribution, evidence of some bioclimatic constraints. We also discuss this fundamental source of uncertainty in climatic niche models, which is the assumption that climate limits species distributions (Parmesan & Yohe, 2003). Factors other than climate can prevent species from occupying areas that would otherwise be climatically

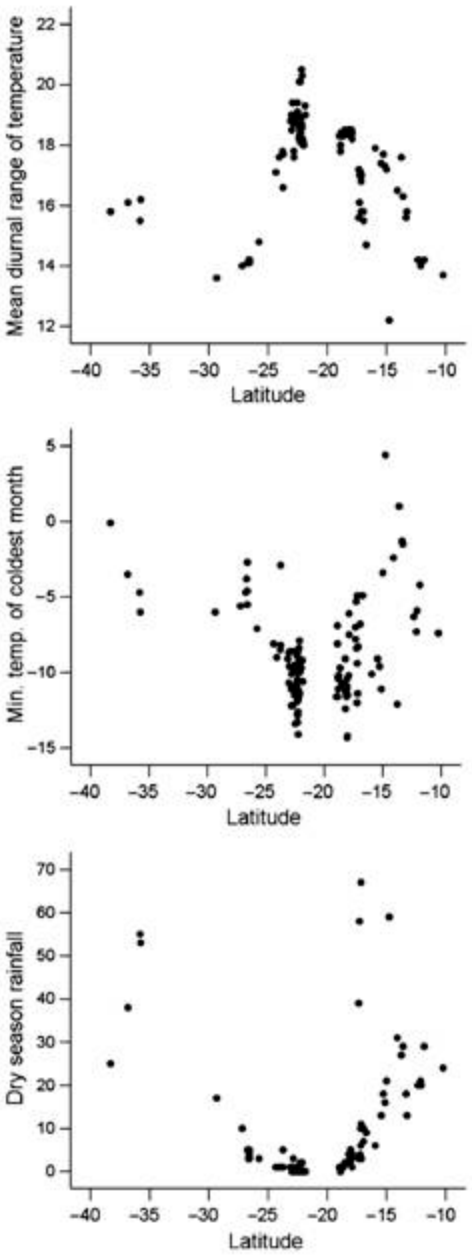

Figure 3 Variations in the climatic space determined by climatic variables associated with Andean cat records, along the latitudinal axis of its range. Notably, climatic relationships change direction in areas of climatic inversions along the Andes such as the Andean Knee around 20° S and the Arid Diagonal around 30° S, where the Maxent models predict lower climatic suitability.

suitable (Gaston, 2003) and in this case study these include the following: biotic interactions such as competition for prey and refuge with the Pampas cat and other carnivores; dispersal limitations created by geographic barriers (which the model successfully identified); and the distribution of the rodent prey.

The climatic characteristic associated with known Andean cat records – cold, dry, and with extreme diurnal variations in temperature – were present along the Andes in areas of montane grasslands, shrublands and steppes. These formations range from the Wet Puna ecoregion in Peru – with extensions into the Cordillera Central Paramo, through the Central Andean and Dry Punas, and descending into the Patagonian Steppe (Olson *et al.*, 2001). One of the strengths of the model was its ability to identify areas with environmental conditions similar to those where the species is known to occur. We acknowledge that caution should be exerted in the interpretation of these results, because of the possibility of models 'overpredicting'. On the one hand, the choice of the South American continent as calibration area for the pseudo-absences could lead to over-predictions (Lobo *et al.*, 2010); on the other, the Maxent algorithm tends to over-fit to the data and it performs well in species with restricted distributions (Phillips & Dudik, 2008). We therefore suggest prioritizing surveys of regions with suitable climatic conditions and no records of Andean cats to explore a highly suitable corridor connecting the two core areas, the possibility of unrecorded populations (for example in Patagonia), and to refine the models. It is possible that new records influence the shape of these predictions as more field studies are undertaken, particularly if data are provided from areas with environmental conditions poorly represented in this dataset such as the Patagonian steppe.

Within the predicted geographical range of the species, areas of relatively low suitability coincided with absences of, or few, Andean cat records, and major biogeographical barriers. The same climatic barriers are well-recognized boundaries for other plants and animals in South America (Chesser, 2000; Weigend, 2002; Marin *et al.*, 2007; Cossios *et al.*, 2009; Rex *et al.*, 2009), supporting our hypothesis of bioclimatic constraints on the distribution of Andean cats in present or past climatic conditions. These biogeographical barriers were: (1) marking the northern limit of the range, the *Peruvian Low* or *Huancabamba Depression*, an arid east–west valley dropping to about 500 m where the Marañón river, source of the Amazon River, originates (Weigend, 2002; Weigend *et al.*, 2010); (2) the *Andean Knee* in Bolivia, an hyper-arid transition zone between the Wet Puna with summer precipitations and the Dry Puna of extreme aridity (Cossios *et al.*, 2009), where suitable climates narrow at the core of the species' range – no Andean cat records exist for this region; and (3) the *South American Arid Diagonal*, another hyper-arid zone where precipitation patterns change on each side of the cordillera between Chile and Argentina (Garreaud, 2009), predicted as suboptimal for Andean cats and with a single record. The study by Cossios (2009) found out that these same biogeographic

barriers explain the observed genetic structure of Andean cat populations, with two northern haplotype groups separated at the location of the climatic transition in the Andean Knee, and the two main lineages separated at the Arid Diagonal some 200,000–300,000 years ago. It is apparent that limiting climatic conditions may have existed at least since then and that dispersal by Andean cats still is strongly constrained by post-glacial expansion (Cossios, 2009).

The bioclimatic envelope describing the Andean cat niche is amenable to interpretations of physiological limits to the species' climatic tolerance, although biotic interactions should also be considered (discussed further below). The shape of the relationship between predicted suitability and temperature is characteristic of species with a single optimum, where the species is most likely to occur, and decreasing likelihood of occurrence with distance from this optimum (Mueller-Dombois & Ellenberg, 1974). In contrast, the skewed relationships with minimum temperature and diurnal thermal amplitude indicate that the optimum for the species is near the extreme of a gradient (Oksanen & Minchin, 2002; Austin, 2007). The narrow environmental ranges of the Andean cat climatic niche indicate a stress-tolerant species (Thuiller *et al.*, 2004). Morphological and physiological adaptations to the extreme aridity, increased wind speeds, severe cold temperatures and decreased partial pressures of oxygen, that characterize the High Andes climate, could give Andean cats an adaptive advantage over their potential competitors. Examples are the Andean cat's large auditory bullae (a distinctive taxonomic character (Garcia-Perea, 2002; also apparent in sand cats *Felis margarita;* Huang *et al.*, 2002), and short legs and long hair with dense woolly under fur (as in snow leopards *Panthera uncial*) (McCarthy & Chapron, 2003). Physiological adaptations to life at high altitudes such as high blood oxygen affinities in chinchillas *Chinchilla brevicaudata* (Ostojic *et al.*,

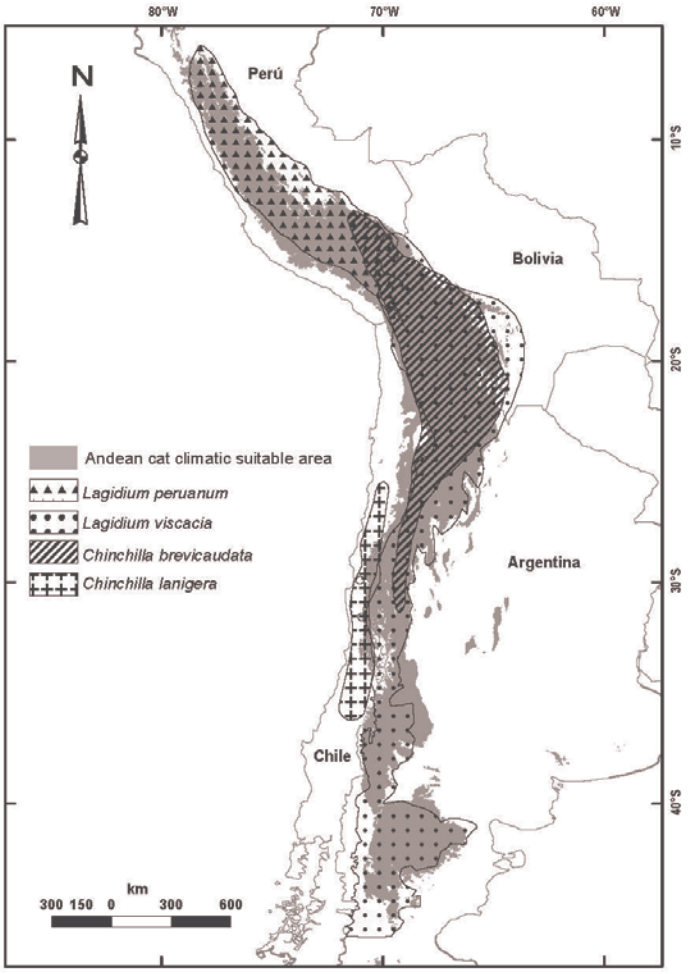

Figure 4 Map showing the overlying distributions of four Chinchillidae species (Patterson *et al.*, 2003; and updated from Parera, 2002 with unpublished data) and of suitable climates for Andean cats, as predicted by this paper's model. *Chinchilla lanigera* and *C. brevicaudata* are extinct and nearly extinct in the wild respectively (Iriarte & Jaksic, 1986 and Jiménez, 1996).

2002) and vicuñas *Vicugna vicugna* (Chiodi, 1970) have not been studied in Andean cats.

The habitat specificity of Andean cats also contrasts markedly with the generalized habits and ample distributions of sympatric carnivores in the Andes, such as, pumas (*Puma concolor*), culpeo foxes (*Pseudalopex culpaeus*) and Pampas cats (*Leopardus colocolo*) (Redford & Einsenberg, 1992; Nowell & Jackson, 1996; Rau *et al.*, 1998). Where they coexist in the High Andes, however, they share a limited pool of rodent prey (Marino *et al.*, 2010) and Andean cats depend more heavily on the mountain viscacha (Walker *et al.*, 2007; Napolitano *et al.*, 2008; Marino *et al.*, 2010). A likely explanation is that Andean cats are more efficient exploiters of the rock-specialist viscachas and chinchillas, conferring them a competitive advantage over sympatric carnivores. Notably, the areas predicted as suitable for Andean cats overlap closely with the approximate distributions of these Chinchillidae species (Fig. 4). These matching distributions, both present and historical, indicate similar climatic niches and potentially linked evolutionary histories. These Chinchillidae are large, rock-dwelling rodents, weighing 0.8–3 kg, and highly adapted to an extreme climate. The *Chinchilla* spp. have been driven to the edge of extinction owing to the demand for their thick, soft fur (Iriarte & Jaksic, 1986), and it is particularly important to explore the impacts of this extirpation of wild chinchillas *Chinchilla lanigera* and *C. brevicaudata* (Jiménez, 1996) on the current distribution of Andean cats.

Our recommendations to further improve the fit of Andean cat distribution models (Heikkinen *et al.*, 2006; Araújo & Luoto, 2007) are as follows: including landscape variables at finer spatial scales to account for more directly explanatory variables and resources (Hirzel & Le Lay, 2008) - crucially, the distribution of rocky outcrops used by the cat and its prey for refuge (Walker *et al.*, 2003) - and taking into account the spatial variations in the abundance of other carnivores. Very detailed data are also required to capture the characteristically patchy distribution of strong anthropogenic effects (Sagarin *et al.*, 2006), in our study case mining operations, hunting of prey species by people and killing of Andean cats for traditional ceremonies or by domestic dogs (Villalba *et al.*, 2004; Cossios *et al.*, 2007; Lucherini & Merino, 2008). Nevertheless, given serious concerns about species' responses to climate warming, the difficulty in detecting rare species and the speed of degradation of natural habitats, simple, large-scale bioclimatic models can be used to evaluate potential impacts of climate change on distribution, and identify populations, habitats and regions most at risk from climate change (Hannah *et al.*, 2007; Heller & Zavaleta, 2009; Mawdsley *et al.*, 2009).

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BIOSKETCH

Jorgelina Marino trained as an ecologist in Argentine Patagonia and has worked in wildlife ecology and conservation in Africa and South America since 1997. She completed her DPhil on the spatial ecology of Ethiopian wolves in 2003. Her academic interests are the biology of small populations; the ecology of rare species; niche modelling and the prediction of land use and climate change effects on mountain ecosystems.

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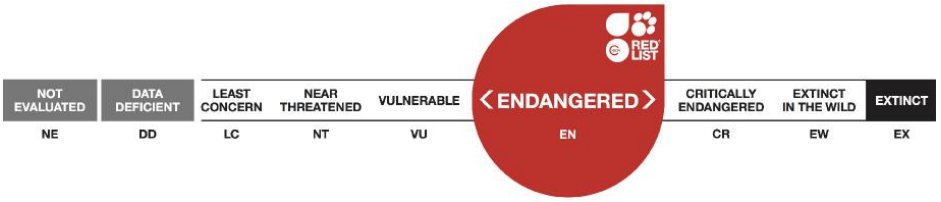
Leopardus jacobita, Andean Cat

Assessment by: Villalba, L., Lucherini, M., Walker, S., Lagos, N., Cossios, D., Bennett, M. & Huaranca, J.



View on www.iucnredlist.org

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Taxonomy

Kingdom	Phylum	Class	Order	Family
Animalia	Chordata	Mammalia	Carnivora	Felidae

Taxon Name: *Leopardus jacobita* (Cornalia, 1865) **Synonym(s):**

- *Felis jacobita* Cornalia, 1865
- *Oreailurus jacobita* (Cornalia, 1865)
- *Oreailurus jacobitus* (Cornalia, 1865) [orth. error]
- *Oreailurus jacobitus* (Cornalia, 1865)

Common Name(s):

- English: Andean Cat, Andean Mountain Cat, Mountain Cat
- French: Chat des Andes
- Spanish: Chinchay, Gato Andino, Gato Lince

Taxonomic Notes:

Taxonomy is currently under review by the IUCN SSC Cat Specialist Group. Previously recognized as belonging to a monotypic genus *Oreailurus* (Cabrera 1940, Wozencraft 1993, Nowell and Jackson 1996, Yensen and Seymour 2000), the Andean Cat is included in the genus *Leopardus*. The genus *Leopardus* includes most small Neotropical felids, and speciation within it has been relatively recent compared to other felid lineages (Johnson *et al.* 2006). While there is strong support for inclusion of the Andean Cat in this genus based on genetic analysis, how closely it is related to the Pampas Cat *L. colocolo* remains unclear. The classification of the Andean Cat as *Oreailurus* was based in part, from very few specimens, on the relative size difference in the skull's auditory chambers, but this trait is also found in other felid species (Johnson *et al.* 1998, Garcia-Perea 2002). The specific name, *jacobita*, is in honour of Jacobita Mantagazza (Cornalia 1865) and should not be declined to *jacobitus* (Yensen and Seymour 2000) as is sometimes seen in the literature. This is one of only two felids for which no subspecies have been classically described (Nowell and Jackson 1996).

Assessment Information

Red List Category & Criteria: Endangered C2a(i) ver 3.1
Year Published: 2016
Date Assessed: April 20, 2014
Justification:

The most recent information confirms that the Andean Cat is a rare species, occurring at low densities and with a patchy distribution due to a specialization for rocky habitats.

New records of the Andean Cat in Argentina extended its distribution range to the south and outside the Andes, into Patagonian steppe and shrub habitats, at elevations as low as 650 m (Novaro et al. 2010, Martinez et al. 2008). However, a study of the population genetics of the Andean Cat throughout most of its range (Cossios *et al.* 2012) indicated that the species has a very low mitochondrial and nuclear genetic diversity and identified two distinct Andean Cat populations that should be considered as two "Evolutionary Significant Units" (ESUs), the highland cats from the previously-known distribution and the newly-discovered population in the Patagonian steppe. Moreover, the northern ESU contains two genetically different groups, showing limited or no exchange of individuals between them, which should be considered as two "Management Units" (MUs).

Habitat loss and degradation is an increasing concern in most areas where the Andean Cat is present, due to the expansion of the agricultural frontier, inadequate livestock management

and water extraction, as well as water and soil contamination for a growing mining and petroleum industry activity in the South American highlands and the Patagonian steppe. The Andean Cat will be affected negatively by global climate change throughout most of its range by a decrease in the geographical distribution (Bennett *et al.* submitted) and more recently by rapid expansion of exploitation of shale oil and gas through hydraulic fracturing or fracking in northern Patagonia (Walker *et al.* 2013).

Additionally, Andean Cats are being killed by herders in Patagonia in retaliation for predation (Novaro *et al.* 2010) and in northwestern Argentina high mortality rates due to hunting by local people have also been inferred (Lucherini and Merino 2008). More recently, information gathered from monitoring Andean Cats and Pampas Cats with GPS collars in north-western Argentina suggests that competition between these two species may affect negatively Andean Cat populations and make them more susceptible to the mentioned threats (Tellaeche 2015).

Based on Andean Cat distribution records an extent of occurrence (EOO) of 1,530,818 km^2 was estimated. However, due to the specificity of Andean Cat to steep rocky environments, this area encompasses large areas between sites of records that are uninhabitable. In a preliminary estimation in a study area of 6,863 km^2 in Patagonia, only 1.4% of the total area was steep rocky areas. Additionally, in a study area of approximately 65,000 km^2 in Patagonia, only 3% of the cells in a grid size of 10x10 km were occupied, based on confirmed and unconfirmed Andean Cat records (Walker and Palacios, unpublished data).

This estimation can have more than one source of error (for example it uses still unconfirmed records) and was calculated for the Patagonian steppe, an environment that is different from that of the highland habitats in the northern and central part of the Andean cat distribution, where there is a greater proportion of rocky habitat. Therefore, to be conservative we estimated that 10% of the current EOO of the Andean Cat could actually be occupied.

Taking into account 10% of the EOO and the lowest density of 0.018 ind/km^2 (Huaranca *et al.* 2013), estimated for a region considered to have one of the most favourable climatic conditions for the Andean Cat (Marino *et al.* 2011), the total population of the Andean Cat is estimated at 2,755 individuals. Because no information about population structure is available, using a default value of 50% for the proportion of mature individuals within the Andean Cat population, only 1,378 would be mature individuals (see Table 1 in the Supplemental Material).

No information exists on trends with regard to habitat modification or destruction in the distribution area of the Andean Cat; but as early as 2002, the conservation status of the Patagonian Steppe and the Central Andean Puna were considered as Critically Endangered (CR) and Vulnerable (V), respectively, with habitat loss and fragmentation the most serious threats affecting their conservation status (Olson and Dinerstein 2002). There is no evidence that this situation has improved; an evaluation of the progress in the implementation of the Strategic Plan for Biodiversity 2011-2020 mentioned that most of the different habitats, including grasslands and wetlands, are still fragmenting and degrading (SCDB 2014).

Mining activities have increased and the associate use of water resources is impacting negatively most of the areas where the Andean cat presence has been confirmed; in the case of northern Argentinean Patagonia, fracking is an additional threat (Walker *et al.* 2013). In Bolivia, mining is a priority activity and mainly situated in the Andean mountain range; extractive mining without environmental precautions is increasing (Ribera 2013). In Chile, mining industry is an important part of the country´s economy and is mainly developed in the northern region, where the Andean cat is distributed and water is a scarce resource. There, the fragile high Andean ecosystems are being degraded and a reduction of the wetlands is predicted in Chile because of the effects of climate change (IEB, CASEB, CCG-UC - CONAMA 2010). In the Peruvian report to the Biodiversity Convention, it is mentioned that in recent years the transformation of natural ecosystems has increased due to changes in land use, particularly by extractive activities such as mining; a trend of transformation, desertification and erosion is mentioned for the fragile wetlands and grasslands in the Peruvian Andes (Ministerio del Ambiente 2014).

Considering the threats to the Andean Cat, the natural fragmentation of the habitat and the increasing trend in fragmentation due to habitat loss and degradation, a continued decline of the population number is inferred.
Based on the available data on Andean Cat distribution and genetic analysis of samples from most areas, 10 subpopulations were identified for the Andean Cat (see Table 2 and Figure 1 in the Supplemental Material). Three subpopulations in Peru (1=north, 2=west, 3=east); two in Bolivia (4=north, 5=centre east); one subpopulation shared among south Peru, centre west Bolivia and northern Chile (6); one subpopulation shared among south-western Bolivia, centre east Chile and north-western Argentina (7); and three subpopulations in Argentina (8=north centre, 9= centre west and 10=southern west). Although some of these could be connected, more studies and more samples for genetic studies are needed.In the meantime, as a precautionary measure these 10 subpopulations are identified.
The estimate of the number of mature individuals for each subpopulation was made in the same way as for the estimation of the total number of mature individuals of the whole Andean cat species. The area of each subpopulation polygon was estimated using the Minimum Bounding Geometry, Convex hull function in ArcGIS. As these polygons are all occupied areas within the EOO, we did not reduce the area to 10% as we did for the overall range. However, even within these occupied areas, occupancy and habitat use by Andean cats is patchy, and they are constrained to rocky places associated with wetlands and/or shrublands. Thus, considering new detailed information on space use (Lucherini *et al.* unpublished data, Huaranca unpublished data, Lagos unpublished data), we, estimated that only 40% of each subpopulation polygon is actually used by Andean Cats, and reduced the size of all polygons accordingly (see Table 2 and Figure 1 in the Supplemental Material). The largest subpopulation is estimated to contain 172 mature individuals.
A further reason for concern about the conservation of this cat species, and for adopting a precautionary approach to its categorization is climate change. According to Bennett et al. (submitted) the current bioclimatic distribution of the Andean Cat is clearly affected by climate change. By 2080, under the scenario A2 (medium to high emissions) the distribution area is expected to decrease between 15 and 30%, depending on the cut-off point used in the distribution model. Parallel to this, the model shows an increase in elevation in the north and central distribution, which puts the species even more at risk, because the environmental conditions at higher elevations do not provide the habitat requirements necessary for the Andean cat (Bennett *et al.* submitted).
More studies are needed to confirm the definition of the subpopulations presented here and to improve our estimates of the population size of each one of them, but considering the precautionary principle, the analysis described above supports the classification of the Andean Cat as Endangered.
For further information about this species, see Supplementary Material.

Previously Published Red List Assessments

2008 – Endangered (EN) – http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T15452A4586989.en
2002 – Endangered (EN)
1996 – Vulnerable (VU)
1994 – Insufficiently Known (K)
1990 – Rare (R)
1988 – Rare (R)
1986 – Rare (R)
1982 – Rare (R)

Geographic Range

Range Description:

The Andean Cat has a patchy distribution due to a specialization for naturally fragmented rocky habitats and most presence records are from the central Andes above 3,600 meters

in Argentina, Bolivia, Chile and Peru. However it has also been found at lower elevations in the southern Andes of Argentina at 1,800 m (Sorli *et al*. 2006) and more recent records of the Andean Cat in Argentina and Chile extend its distribution range to the south and outside the Andes, into Patagonian steppe and scrub habitats in Argentina, at elevations as low as 650 m (Novaro *et al*. 2010, Martinez *et al*. 2008), and at 2,200 m in Chile in the Atacama Region (Villalobos *et al*. in prep.).

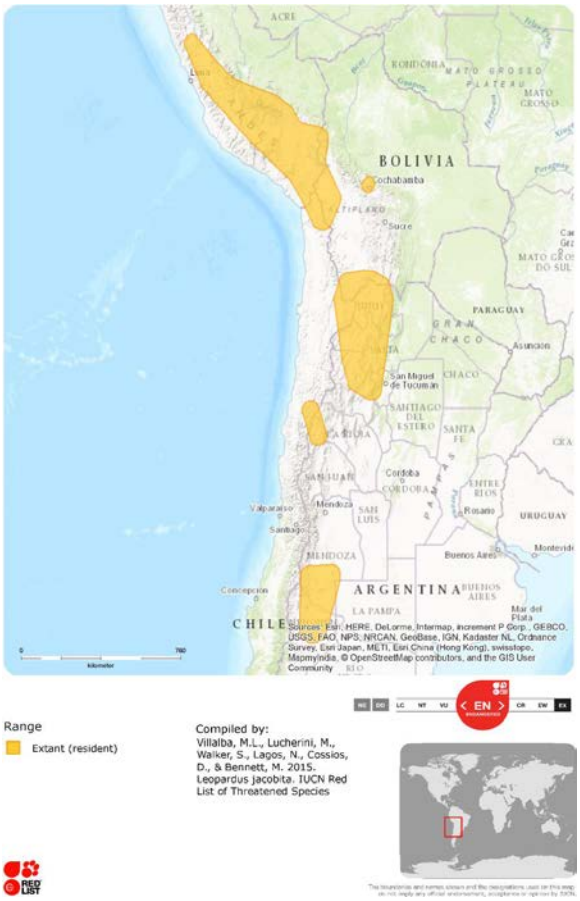
Within the high Andes the Andean Cat was recorded at an average elevation of 4,236 m in Argentina (Perovic *et al.* 2003), above 3,800 m in Bolivia (Villalba *et al*. 2012), between 3,714 and 4,414 m in Chile (Napolitano *et al*. 2008), and at 4,000 m or higher in Peru (Cossios *et al*. 2007).

Until the end of the nineties, Andean Cat records were scarce and restricted to southern Peru, southwest Bolivia, northwest Argentina and northern Chile (Yensen and Seymour 2000). Similarly, sightings of this species were very few (Scrocchi and Halloy 1986, Sanderson 1999), and museum specimens were equally few (Garcia-Perea 2002). However in the last two decades the number of distribution records has greatly increased due to the efforts of the Andean Cat Alliance (www.gatoandino.org), a network of specialist researchers.

Currently the known northern and southern limit for the Andean cat respectively is central Peru (10°13'S), and central Argentina (38°23'S) (Cossios *et al*. 2007, Novaro *et al*. 2010), but throughout this range the Andean Cat populations are patchily distributed. The results of modelling the Andean Cat distribution considering four bioclimatic variables (annual mean and mean diurnal range temperature, annual precipitation, and coldest season winter), shows the presence of three biogeographic barriers that affect the species' distribution: i) at the north in Peru that coincides with the Huancabamba depression, known as "Peruvian low" and defines the northern boundary of its distribution range, ii) at the centre in Bolivia, with the "Andean knee", an extremely arid transition zone between the wet and dry Puna and where there are no records of Andean cats, and iii) at the south with the "Arid Diagonal" in Chile and Argentina, that is also an hyper-arid zone and with very few records of Andean Cats (Marino *et al*. 2011).

According to this model and despite the differences in elevation over the current geographic range of the Andean Cat, there are common climatic conditions that favour for their presence, which are cold, dry and extreme diurnal variations in temperature (Marino *et al.* 2011).

Country Occurrence:



Native: Argentina; Bolivia, Chile; Peru.

Population

Until now three population estimates on Andean Cat were carried out. Napolitano *et al*. (2008), based on genetic sampling estimated five individuals to occur in a 25,000 ha area in northern Chile, around the Salar de Surire National Monument, resulting in a density of two Andean Cats in 100 km^2. More recent estimates based on systematic camera trapping resulted in 7-12 Andean Cats in 100 km^2 in northwestern Argentina (Reppucci *et al*. 2011) and in central western Bolivia, a preliminary estimate of 1.8 Andean cats in 100 km^2 was calculated by dividing the minimun number of identified Andean Cats by the area covered (164 km^2) (Huaranca *et al*. 2013). In the last two studies, densities of sympatric Pampas Cats were also estimated, resulting 74-79 Pampas Cats in 100 km^2 in Argentina and 4.9 Pampas Cats in 100 km^2 in Bolivia. Reppucci *et al*. (2011) also estimated the detection probabilities for both species, which were higher for Andean Cat (0.07) than Pampas Cat (0.02). Other studies based mainly on faecal sample collection have found records of the Pampas Cat much more frequently than the Andean Cat (Lucherini and Vidal 2003, Perovic *et al*. 2003, Cossios *et al*. 2007, Viscarra 2008, Torrico 2009, Novaro *et al*. 2010, Villalba *et al*. 2012). All this information confirms that the Andean Cat is much rarer than the Pampas Cat.

The three surveyed areas outlined above are located within the two regions that are considered to have the most favourable climatic conditions for Andean Cat, and that coincide with those places where a larger number of Andean Cat records have been obtained (Marino *et al*. 2011). In this context, it is expected that Andean Cat density in those areas with less favourable conditions will be much lower.

A study of the population genetics of the Andean cat throughout most of its range (Cossios *et al*. 2012) indicated that the species has a very low mitochondrial and nuclear genetic diversity and

two distinct Andean Cat subpopulations,which are latitudinally separated between 26 and 35° S, were identified that should be considered as two "Evolutionary Significant Units" (ESUs). Moreover, the northern ESU contains two genetically different groups, showing limited or no exchange of individuals between them, which should be considered as two "Management Units" (MUs).

The geographical separation between the northern and southern ESU concurs with the third biogeographic barrier, the South American Arid Diagonal and the separation between the two northern management units coincides with the transition zone between the wet and dry Puna (Cossíos *et al.* 2012); thus, the authors remark that these three groups of Andean Cat populations could have developed special adaptations because significant differences exist in rainfall patterns over this range.

Current Population Trend: Decreasing

Habitat and Ecology **(see Appendix for additional information)**

The Andean Cat is found primarily in rocky and steep terrains, in arid and sparsely vegetated areas of the high Andes above the timberline, and in scrub and steppe habitats within the Andean foothills of Central Argentina and the Patagonian steppe ecological region (Napolitano *et al*. 2008, Novaro *et al*. 2010). In general, climatic conditions are extreme with very low temperatures, large daily thermal variations and low precipitation that determine the presence of adapted plants such as bunchgrasses, cushion plants, and low shrubs with small or resinous leaves (Cabrera and Willink 1973). The presence of high Andean wetlands known as “bofedales” and “vegas” is characteristic in the high Andes and are an important resource for wildlife and domestic animals (Villalba *et al*. 2004).

The Andean Cat distribution is similar to the historic range of the Short-tailed Chinchilla (*Chinchilla chinchilla*) and current range of the mountain vizcacha (*Lagidium* spp.) (Yensen and Seymour 2000), which are its major prey (Walker *et al*. 2007, Napolitano *et al*. 2008). According to the results of diet studies in Argentina, Bolivia and Chile, and compared with that of other Andean carnivores, the Andean Cat occupies narrower niche with a wide overlap with the Pampas Cat diet (Walker *et al*. 2007, Marino *et al*. 2010). Rodents constitute the main prey item and the Mountain Vizcacha in three out of five diet studies was the more frequent prey: 52% and 43-53% in southern Bolivia and 44.1% in northern Chile (Viscarra 2008, Napolitano *et al*. 2008, Torrico 2009). In a diet study with samples mostly collected in northern Argentina, unidentified small rodents were the most frequent prey (37.3%), followed by the mountain vizcacha 28% (Walker *et al*. 2007); Tellaeche (2010) for a single locality in northern Argentina, also reported that small mammals were the item most frequently consumed by the Andean Cat (93.3% of the faeces), particularly rodents of the genus *Phyllotis* (found in 76.9% of the samples). Among the Andean Cat prey items, the mountain vizcacha has the greatest body mass by far; consequently it contributes significantly to the Andean Cat diet (Walker *et al*. 2007, Napolitano *et al*. 2008).

The Andean Cat is thought to be a solitary species, but may be seen in pairs or with kittens during the mating season and after the births of kittens respectively (Villalba *et al*. 2004). Mating season, according to local people in Bolivia, is between July and August (Villalba and Bernal 1999); however, it is possible that this period could be much longer, because small cubs have been observed in October and from April to September (Villalba 2002, Villalobos *et al*. In prep., Lucherini Unpublished data). Two kittens were seen by Villalba (2002), and what appears to be an older single cub by Sorli *et al.* (2006).

Most of the reported sightings of Andean Cats have been during daytime; however the radio-tracking of the first radio-collared Andean Cat in southern Bolivia recorded main activity peaks at dusk or at night, between 18:00 and 23:00 hours (Villalba *et al*. 2009); similarly the results of 1,596 camera-trap photos from different localities in Argentina, Bolivia and Chile showed the following proportions for Andean Cat activity: 37.6% at night, 34.4% crepuscular, and 28% during the day (Lucherini *et al*. 2009). Additionally, the results indicated that the Andean Cat activity

overlaps largely with that of the mountain vizcacha, a diurnal and crepuscular species (Galende *et al*. 1998).
Data on territoriality is absent, however, as occurs with most felids (Sunquist and Sunquist 2002), it is possible that male territories are larger than those of females and that there could be a certain degree of territory overlap between the sexes. Because the conditions of the Andean Cat habitat are severe and naturally fragmented, it is probable that territory and home ranges are very large; a radio-tracked female Andean Cat, between April and December 2004, had a home range of 65.5 km^2 (95% minimum convex polygon: Villalba *et al*. 2009).
The Andean Cat is a medium-sized felid; from measures of skins the total length in adults varies from 740 to 850 mm and in sub-adults varies from 577 to 600 mm; tail length is from 410 to 485 for adults and 330 to 420 mm for sub-adults. Only two records on the weight are available, the first from a sub-adult specimen from Peru, which weighed 4 kg (Pearson 1957, García-Perea 2002) and the second is from an adult female from Bolivia which weighed 4.5 kg (Delgado *et al.* 2004).
Andean Cat fur is mainly ash grey with brown-yellowish blotches that are distributed as vertical lines at both sides of the body, giving the appearance of continuous stripes. The tail of the Andean cat is very characteristic. It is very long (66 - 75% of the head and body length), thick and cylindrical, with a fluffy aspect and with 6 to 9 wide rings of dark brown to black colour (García-Perea 2002). The legs also have dark and narrower blotches or stripes, but they don't form complete rings.
Apparently the species is not sexually dimorphic in terms of fur colour, but comparisons among Andean Cat skulls carried out by García-Perea (2002) suggest that sexual dimorphism is present. Differences between juvenile and adult specimens were also found, with juveniles having a lighter coloration and more and smaller blotches (García-Perea 2002). Because of these features, sub-adult or juvenile Andean Cats can be confused much more easily with Pampas Cats (García-Perea 2002).
Systems: Terrestrial

Use and Trade

In Argentina, Bolivia, Chile and Perú people of Aymara origin, and in some cases Quechua, have similar beliefs regarding the Andean Cat and Pampas Cat (both known as titi or osqollo). A common tradition is the use of a skin or a stuffed cat during ceremonies that people perform for marking their domestic livestock, mainly llamas or alpacas; the titi is considered a sacred animal related with abundance and fertility of the livestock or quality of crops. It is important to note that both the Andean Cat and Pampas Cat are part of these traditions and beliefs, and in general, are used indiscriminately. There are some local variations within and between countries and in some cases the influence of western culture has resulted in a total or partial loss of the values of Andean cultures and the distortion of ancestral customs regarding the titi (Villalba *et al*. 2004).
Cossios *et al*. (2007) also reported the hunting of Andean and Pampas Cats for food and for traditional medicine in central Peru.

Threats **(see Appendix for additional information)**

In the early 2000s the Andean Cat Alliance considered traditional hunting the top threat, followed by prey reduction and habitat loss and fragmentation (Villalba *et al*. 2004), four years later a re-evaluation of the threats affecting the Andean Cat, established that habitat loss and habitat degradation are the main current threats; hunting (opportunistic/palliative or traditional) and reduction of prey populations are considered as the 3rd and 4th threats, in order of importance (ACA 2011: Andean Cat Alliance Strategic Plan).
Expansion of the agricultural frontier, inadequate livestock management and water extraction for a growing mining and petroleum industry activity in the South American highlands and the Patagonian steppe are altering the Andean Cat habitat. The Andean Cat will be affected negatively

by global climate change throughout most of its range by a decrease in the geographic distribution (Bennett *et al*. in progress) and more recently by rapid expansion of exploitation of shale oil and gas through hydraulic fracturing or fracking in northern Patagonia (Walker *et al*. 2013).

Hunting by local people who consider the Andean Cat a predator of their small domestic livestock has been frequently reported particularly in some regions of Argentina, Chile and Peru (Iriarte 1998, Cossíos and Madrid 2003, Lucherini and Merino 2008). Andean Cats are being killed by herders in Patagonia retaliation for predation (Novaro *et al*. 2010). These cats are also killed by dogs accompanying local shepherds and in north-western Argentina high mortality rates due to hunting by local people have also been inferred (C. Tellaeche and M. Lucherini unpub. data). Cossios *et al*. (2007) also reported the hunting of Andean and Pampas Cats for food and for traditional medicine in central Peru.

Particularly in Bolivia, Peru and northern Chile, the Andean Cat (as well as the Pampas Cat) is considered a sacred animal according to indigenous Aymara and Quechua traditions. Throughout much of its range, dried and stuffed specimens are kept by local people for use in harvest festivals (Iriarte 1999, Sanderson 1999, Villalba *et al*. 2004, Cossios *et al*. 2007, Villalba *et al*. 2012). Hunting for such cultural practices may represent a significant threat to the species.

The Short-tailed Chinchilla was likely to have been a major prey species for the Andean Cat, but the species was hunted nearly to extinction for the fur trade (Nowell and Jackson 1996). In most of its range, the main prey of the Andean Cat is now the Mountain Vizcacha (Walker *et al*. 2007, Viscarra 2008, Napolitano *et al.* 2008, Torrico 2009), which lives in patchily distributed small colonies and has also been reduced by hunting pressure. This may result in a highly fragmented distribution for the Andean Cat. Intra-guild competition, especially with the Pampas Cat, for Mountain Vizcacha prey, could negatively impact the Andean Cat (Lucherini and Luengos Vidal 2003, Walker *et al.* 2007, Reppucci 2012).

Conservation Actions **(see Appendix for additional information)**

Included on CITES Appendix I (as *Leopardus jacobitus*). The Andean Cat's conservation status in the range countries was also re-assessed. The species is listed as Critically Endangered in Bolivia, Endangered and Rare in Chile, Endangered in Peru and Vulnerable in Argentina; it also has full protection at the national level across its entire range, as described below. However, law enforcement is problematic, and hunted specimens are regularly observed in the field and for sale, although with less frequency than before, in special markets to be used in religious ceremonies.

After developing the actions outlined in the Andean Cat Conservation Action Plan (Villalba *et al*. 2004) and the information generated in the last 10 years, the Andean Cat Alliance elaborated the Strategic Plan for Andean Cat Conservation (AGA 2011) with the following objectives and maintaining the three main lines of action: Research, Education and Conservation:

a. To ensure long-term conservation of the Andean Cat and its natural environment, including the restoration or rehabilitation of the environments that have suffered degradation.

b. To integrate the conservation of the Andean Cat and its natural environment within local policies in the four countries where the species is present, working locally but with a global approach.

c. To strengthen activities of conservation and research in protected areas with Andean Cat populations, and to promote the creation or extension of existing protected areas to provide connectivity and/or protection of habitats and Andean cat populations.

d. To promote research on the conservation threats, ecological requirements of the species, its principal prey, and other sympatric carnivores.

e. To standardize the activities of working groups under common and more effective goals.

f. To train protected areas staff and local communities in activities in research, education and conservation, within and outside protected areas.

The Andean Cat is found in several protected areas across its range and some were prioritized for promoting effective conservation of the species as well as their habitats and others for the need to carry out surveys and promote effective conservation actions.
Mining and oil/gas extraction are a priority economic activity in South American countries, even in protected areas, therefore lobbying with authorities and the industry sector, as well as promoting and/or supporting the implementation of mitigation plans to minimize impacts are fundamental actions to be addressed (Walker *et al*. 2013).
Similarly, community-based conservation is an essential approach that is being implemented by promoting or supporting sustainable economic initiatives, favouring better practices in livestock management or other activities oriented to mitigate human-wildlife conflict. Community education and support for law enforcement are also important activities to minimize or stop Andean Cat hunting and encourage positive attitudes towards Andean cats and high Andean biodiversity.

National legislation

Argentina

The Andean Cat is protected by National Law 22421 of wildlife conservation and its Statutory Decree 666/97. Also, Resolution N°63/86 of the Secretary of Agriculture.

Bolivia

Along with other wild species of fauna and flora, the Andean cat is protected by the Supreme Decree N° 22641, promulgated in 1990, which establishes a general and undefined ban for the pursuit, capture, storing and conditioning of wild animals and its derivative products.

Chile

All felid species are fully protected since 1972 by Law N° 19473. The illegal hunting of felines in Chile is penalized with fines up to US$ 6.000 and imprisonment up to 3 years.

Peru

In 2014 a new regulation listed the Andean cat as Endangered and along with other wild species of fauna its hunting, commerce and hunting, capture, possession, trade, transport or export for commercial purposes is prohibited (Supreme Decree N°004-2014-MINAGRI).

Credits

Assessor(s): Villalba, L., Lucherini, M., Walker, S., Lagos, N., Cossios, D., Bennett, M. & Huaranca, J.

Reviewer(s): Nowell, K., Hunter, L., Schipper, J., Breitenmoser-Würsten, C., Lanz, T. & Breitenmoser, U.