Clouds on the Horizon:

Identifying global priorities for conservation marketing and planning the conservation of the Sunda clouded leopard on Borneo



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Ewan Macdonald

Oriel College, University of Oxford

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Abstract

Conservation effort and action is limited by resources. In response previous authors have sought to identify priorities for conservation and it has become clear that making decisions about conservation priorities necessitates encompassing the fields of human behaviour and psychology, politics, economics and fundamental ecology. In this thesis I bring together two novel strands of research in this arena, 'conservation marketing' and the identification of priority locations for conservation.

In the first part of this thesis I present an analysis of how a representative subset of mammalian species might be prioritised in the context of conservation marketing. I develop a novel collaboration with a market research firm to assess quantitatively which species a large sample of English-speaking people value for conservation, and analyse their choices to reveal the attributes that drive these preferences. Developing this idea, I extend this analysis to all terrestrial mammals to identify potential Ambassadors for conservation marketing campaigns. Felids perform well on metrics of charisma, and for many species of big cat their large biogeographical ranges encompassing many other threatened mammalian species make them good potential Ambassadors.

Despite its relative unfamiliarity to the public, the Sunda clouded leopard (*Neofelis diardi*) is among the species identified as a potentially good ambassador for conservation marketing and it is also one that faces severe threats from land use change across its range.

The second part of this thesis therefore provides insight into the threats faced by clouded leopards, how these threats impact them, and how they might be mitigated. I develop the first map of predicted deforestation across Borneo and use this to map the historic and future impacts of land-use change on clouded leopard populations (their demography and genetics), taking account of their favoured habitats and its fragmentation. Finally, I compare a number of contrasting policy scenarios to highlight how the existing network of protected areas provides poor coverage for clouded leopards and how new protected areas might improve this. These techniques demonstrate a toolset that can be usefully applied to a wide range of species and habitats in the future.

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List of Original Publications

Chapter 2

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Chapter 6

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Appendix 1

Dickman, A.J., Hinks, A.E., **Macdonald, E.A.**, Burnham, D. & Macdonald, D.W. 2015. Priorities for global felid conservation. Conservation Biology, 29, 854-864.

Appendix 2

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Author Affiliations

Macdonald, E.A. Environmental Change Institute, School of Geography and the Environment, University of Oxford, South Parks Road, Oxford OX1 3QY, UK.

and

Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, OX13 5QL, UK

Burnham, D., De Barros, A.E., Dickman, A.J., Hearn, A.J., Hinks, A.E., Macdonald, D.W., and Sandom, C.J. Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, OX13 5QL, UK

Cushman, S.A. Rocky Mountain Research Station, United States Forest Service, 2500 S. Pine Knoll Dr. Flagstaff, AZ 86001, USA

Malhi, Y. Environmental Change Institute, School of Geography and the Environment, University of Oxford, South Parks Road, Oxford OX1 3QY, UK

Matsumoto, M.H. The Nature Conservancy of Brazil, Curitiba, PR, Brazil

Landguth, E.L. Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA

Nijhawan, S. Panthera, 8 W. 40th St, 18th Floor, New York, NY 10018, U.S.A.

Paula, R.C. CENAP – National Research Center for Carnivore Conservation, Atibaia, SP, Brazil

Weiss, D. Malaria Atlas Project, Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, UK

Chapter 1

General Introduction

Introduction

Mounting evidence points to the world being on the verge of a biodiversity crisis, and the probability of averting it currently looks low: innovative, practical ideas, and their application, are urgently needed. Global extinction rates are estimated to be between one hundred and one thousand times above background rate in the fossil record (Pimm et al. 1995). Although coverage is too sparse to estimate the overall conservation status of many taxonomic groups with any useful precision, the number of threatened species for well-studied groups is ominous: among the vertebrates, 26% of mammals, 13% of birds and 41% of amphibians are classified as threatened by the IUCN Redlist (IUCN 2010). And these threats are not static; Hoffmann et al. (2010) estimate that each year 52 species of birds, mammals and amphibians teeter one category closer to extinction. In the face of such losses, and unless there is effective action to slow current rates of species erosion, an anthropogenic sixth mass extinction seems inevitable (Barnosky et al. 2011).

The losses of these species are a catastrophe, not just to those who consider that biodiversity has intrinsic value (Ghilarov 2000), but also because biodiversity, and functioning ecosystems underpin delivery of the ecosystem services on which humanity depends (Mace et al. 2012; Sukhdev et al. 2010). These services include provision of food, water and fuel, air quality and climate regulation, erosion prevention and maintenance of soil quality, pollination services, biological control, and cultural services (Kumar 2010). For example, the world's forests are an enormous sink for carbon dioxide, and their loss results in the emission of around 900 million tonnes of carbon per year, accounting for

about 10% of total anthropogenic carbon emissions globally (Ciais et al. 2013). The value of these ecosystem services has been estimated to be around $125 - 145 trillion per year (2007 US$)(Costanza et al. 2014), and while this has been called "a serious underestimate of infinity" (Pearce (2005) referring to Costanza et al. (1997)), it also serves as a benchmark against which we can compare global spending on conservation.

Global spending on conservation has been notoriously difficult to quantify accurately (Balmford et al. 2003; Halpern et al. 2006; James et al. 2001), however a recent study has estimated that the total annual expenditure on global biodiversity is approximately $21.5bn (Waldron et al. 2013). Despite this, it is estimated that conservation funding will need to increase by at least an order of magnitude in order to meet the Convention on Biological Diversity's targets for 2020 (CBD 2011; McCarthy et al. 2012). In the face of this funding gap it is vital that conservation biologists develop innovative mechanisms for increasing their revenue streams, as well as developing strategic approaches to ensure that the limited pool of resources is spent proportionately (Bottrill et al. 2009).

This thesis therefore sets out to explore different approaches to conservation prioritization and to do so from two different directions. In the first part of this thesis I consider the emerging field of conservation marketing to explore peoples' preferences for conservation, and how these preferences might be used to leverage public support for conservation and potentially increase revenue streams. In the second part of this thesis I will employ the case study of clouded leopard (*Neofelis Diardi*) conservation on Borneo to explore various approaches to conservation prioritization and show how these will impact on measures of clouded leopard genetic diversity.

Approaches to conservation prioritisation

Attempting to balance the mismatch between revenues and the costs (or aspirations) of conservation is not a new conundrum for conservation and many approaches have been suggested to aid the identification of species, areas or actions that should be prioritised.

The most commonly used approach to priority-setting is to focus on the perceived level of endangerment of the species, and several approaches have been developed for example Mace and Collar (1995), Master (1991), Millsap et al. (1990), and Reed (1992). The most established of these is probably the IUCN's Red List for endangered species, which uses a rule-based approach based on Mace and Lande (1991) in which a species is assigned to one of several categories (including Critically Endangered, Endangered, Vulnerable, Near Threatened and Least Concern) on the basis of five criteria relating to the population size and trends (IUCN 2016). In addition to endangerment, other "biological values" are sometimes considered when setting priorities such as endemism (e.g. Birdlife International's Endemic Bird Areas (Stattersfield et al. 1998)), irreplaceability and evolutionary distinctiveness (e.g. ZSL's EDGE of Existence (Isaac et al. 2007)), and surrogacy (e.g. Umbrella, Flagship and Keystone species (Caro 2010; Simberloff 1998)).

Since most conservation researchers and practitioners have traditionally had a background in the biological sciences, it is not surprising that many prominent approaches to prioritisation focus on the biological attributes of a species or ecosystem. However, "*conservation problems are social and economic, not scientific, yet biologists*

have traditionally been expected to solve them" (Schaller 1992). This large human dimension to most conservation problems mean that conservationists must look beyond pure biology to explicitly incorporate other criteria such as political, economic, societal considerations in the process of setting priorities (Jacobson & Duff 1998).

Mace et al. (2007) provide a non-exhaustive classification of variables other than risk that conservationists might consider for prioritisation. These are grouped into categories including biological values (discussed above), economic values, social and cultural values. Economic values could include the costs of management, the direct and indirect economic benefits of the species and ecosystem services which are becoming increasingly prominent (e.g. REDD+ (Venter & Koh 2012)). Social and cultural values could include scientific benefits, cultural and political status, popularity and the local, regional or international significance of the species. In addition to the values of species and ecosystems Mace et al. (2007) consider the urgency of conservation action as well as practical issues such as feasibility, recoverability and the impact of geopolitical factors that might influence conservation success (Dickman et al. 2015).

While it is possible to quantify many of the criteria that might contribute to a prioritisation exercise, deciding which criteria to consider is ultimately a subjective choice. Inevitably, many different organisations have followed their own inbuilt biases resulting in numerous competing prioritisations. Perhaps the most well known of these is Conservation International's Biodiversity Hotspots approach which identified 25 (now updated to 35) areas as priorities on the basis of vascular plant diversity, vertebrate endemism and threat of habitat loss (Myers et al. 2000). Other prominent global

prioritisation exercises include Endemic Bird Areas (Stattersfield et al. 1998), The Last of the Wild (Sanderson et al. 2002) and Topspots (Funk & Fa 2010) among others. Brooks et al. (2006) review and compare several prioritisation exercises revealing the divergent approaches towards vulnerability with some exercises being classified as reactive (prioritising high vulnerability), while others are classified as proactive (prioritising low vulnerability).

Designation of new protected areas is one of the primary tools that conservationists can employ for protecting land against alternative economic uses. In general, the conservation prioritisation exercises mentioned above tend to highlight broad geographic regions, however they do not delineate the precise locations of protected areas whose siting and configuration is vital to ensuring the efficient achievement of conservation objectives (Possingham et al. 2005; Venter et al. 2014). The development of sophisticated analytical tools has enabled the field of systematic conservation planning to emerge as a logical process for ensuring that protected areas are effective in conserving a comprehensive range of biological features, in adequate amounts, and in efficient locations and configurations for their long-term survival (Margules & Pressey 2000).

Surrogates for conservation

Among the "biological values" that might influence a species' conservation priority, is its ability to act as a surrogate for the conservation of other species. These surrogate species can be loosely grouped into three broad categories: those that help in locating areas of conservation significance, those that help in documenting effects of

environmental change on biological systems, and those employed in public-relations exercises (Caro 2010). In the first part of this thesis I focus primarily on this final category of surrogate species, those employed in public-relations exercises. Typically, these species are known as flagship species.

Terms like umbrella, indicator, keystone and flagship species have become well established labels in conservation (Heywood 1995; Simberloff 1998), however their usefulness has been limited by fuzzy and shifting definitions (Caro 2010). Barua (2011) found that these terms were frequently misused in science communication and news articles, and that 26% of references to "flagship species" were misrepresentations based on confusion with indicator, apex and umbrella species. As a result of the frequent confusion between flagship species and umbrellas, Verissimo et al. (2011) suggested a new definition for flagship species: "*a species used as the focus of a broader conservation marketing campaign based on its possession of one or more traits that appeal to the target audience*". This definition deliberately emphasizes the marketing potential of a species in an attempt to make clear that the flagship concept is not a biological or ecological phenomenon.

Conservation marketing

While some conservation NGOs and all advertising executives have always understood the marketing potential of certain species (WWF's panda, Jaguar cars, Lion chocolate bars etc.), the idea of conservation marketing appears to have received relatively little academic attention until the 1980s (Myers 1983; Western 1987). Despite some

conservation scientists feeling uneasy about the Strategic marketing of biodiversity (Schwartz 2006) the emerging field of conservation marketing is beginning to explore "*the systematic application of marketing along with other concepts and techniques to achieve specific behavioural goals for a social good*" (French et al. 2006) in (Smith et al. 2010). In 2015, conservation marketing's place in the mainstream of conservation was recognised with the Society for Conservation Biology holding it's first symposium dedicated to conservation marketing at the International Congress of Conservation Biology (Veríssimo & McKinley 2016).

Conservation inequality and the charismatic cat

Conservation marketing campaigns can be an important tool for raising funds and publicity (Smith et al. 2010). Flagship species (sensu Verissimo et al. (2011)) are often used to figurehead such campaigns.

Previous research in conservation marketing has explored the importance of selecting flagship species that are relevant to the issue (e.g. Barua et al. (2011)) and culturally appropriate (e.g. (Bowen-Jones & Entwistle 2002; Douglas & Veríssimo 2013; Linnell et al. 2000)). However little research exists on which species people prefer for conservation, and which attributes are associated with these preferences. In many cases this question may seem obvious – giant pandas (*Ailuropoda melanoleuca*), polar bears (*Ursus maritimus*) and African elephants (*Loxodonta Africana*) have all been used prominently in

conservation marketing campaigns, and jaguars (*Panthera onca)*, puma (*Puma concolor*) and lions (*Panthera leo*) are all figureheads of instantly recognisable private sector brands. However, while these public preferences may seem obvious, commercial companies invest fortunes in exploring the nuances of the choices made by their target audiences, and a matured conservation movement would be unwise to ignore that. The various attributes that are associated with high appeal have been discussed in an abstract sense by Lorimer (2007) and several papers have noted how species selected as flagships tend to be large, warm blooded, endangered and predatory with forward facing eyes (Caro & O'Doherty 1999; Clucas et al. 2008; Courchamp et al. 2006; Dietz et al. 1994; Johnson et al. 2010; Smith et al. 2012). However, most of these assertions are observational and the few broad scale attempts to quantify this analytically have been based on flagship species used on the covers of magazines (Caro & O'Doherty 1999) or on web searches (Smith et al. 2012). Other analyses have used choice experiments to investigate local scale preferences for bird conservation (Veríssimo et al. 2009) the preferences of children (Frew et al. 2016) and to explore the selection criteria for flagship species by conservation organizations in Switzerland (Home et al. 2009) however most of these have focussed on a narrow range of species.

In chapter 2 of this thesis I conducted a paired conjoint choice experiment to explore peoples' preferences for mammals in the context of conservation. This differs from previous work insofar as it is the first quantitative analysis of peoples' preferences towards a broad suite of mammals. In addition to simply providing a ranked list of 100 species ranked in terms of their relative preference scores, I was able to demonstrate a

useful tool that will allow conservation marketers to predict whether any mammal is likely to be appealing based on a few key attributes. The experiment was conducted online in 5 English-speaking nations, and the results also allow us to explore how differing cultures shape national preferences. The results of this analysis can provide a valuable 'off the shelf' guide that conservation marketers can use when selecting flagship species. However, as discussed in chapter 7 it is important question who the sample are representative of, and remember the importance of tailoring campaigns to specific stakeholders (Bowen-Jones & Entwistle 2002; Douglas & Veríssimo 2013; Linnell et al. 2000)). Furthermore, the survey design used in this analysis yielded high levels of positive engagement with respondents, which is seen as an important part of obtaining reliable data. This approach can therefore serve as a template for conservation marketers who want to take this research further either by extending it into new areas or by refining it to target a more specific group of stakeholders.

Identifying ambassadors for conservation marketing

In Chapter 2, I explored peoples' preferences for different species in the context of conservation. This enabled me to quantify and explore the great disparity in preferences for different species, and to explore how these preferences varied between different countries. However, in Chapter 3 I go on to argue that conservation marketers should go beyond the attributes of a particular species when selecting flagships for conservation,

and that they might find 'added value' in a species' ability to act as a marketing surrogate for a large number of high priority species.

This chapter builds on the existing concept of "flagship umbrella" species (Caro 2010), and the work of authors such as Di Minin and Moilanen (2014) and Di Minin et al. (2016) who have shown that inclusion of charismatic flagship species can improve surrogacy strategies, and explored the capacity of Carnivores to act as surrogates for a wide range of birds, mammals, amphibians, reptiles and ecoregions. A small number of papers has considered the usefulness of flagship umbrella species in the context of both forest and marine conservation (Dinerstein et al. 2010; Oviedo & Solís 2008) however I know of no other studies that apply the concept either to mammals or on such a large scale.

The underlying premise of Chapter 3 is that wide-ranging species have the potential to act as flagships for a wider range of issues and species under the appropriate circumstances. In this sense, a species' ability as a flagship may be judged both on the appeal to the target audience of its physical and or cultural characteristics, but it may also be judged on its ability to act as a marketing flagship for a wide range of other, less appealing, sympatric species. I describe a novel categorisation of species and coin the term "ambassador species" to describe those species that combine high flagship potential with the added benefit of being sympatric with a large number of high conservation priority species.

The Ambassador concept differs from the existing "flagship umbrella" concept in so far as it is entirely related to a species' usefulness as a focus for conservation marketing campaigns. This is in important contrast to "flagship umbrellas" which rely on the use of one high profile species (or group of species) to act as a surrogate for the conservation of other "background" species through their association with viable populations, protected areas or management actions (Caro 2010). This requirement to deliver tangible on-the-ground conservation benefits to other species potentially limits the applicability of flagship umbrellas since several analyses have questioned the practical use of umbrellas, either in identifying appropriate areas for conservation (Andelman & Fagan 2000; Williams et al. 2000) or in their requirement for a similar suite of management actions (Roberge & Angelstam 2004).

In addition to introducing a novel approach to identifying potential surrogates for conservation marketing, this paper presents the first attempt to quantify the relative appeal of all terrestrial mammals. Because it is important that conservation marketing campaigns are locally appropriate (Bowen-Jones & Entwistle 2002) I present these results separately for each of the 6 countries that were present in the original survey (see Chapter 1).

Spatial conservation prioritization

Human impacts on the natural environment have accelerated through the industrial revolution and into modern times. In the 1980s and 1990s 55% of new agricultural expansion in the tropics came from intact forests, while a further 28% came from already degraded forests (Gibbs et al. 2010). Between 2000 and 2012, approximately 230million ha of forest were lost due to disturbance globally (c.19million ha per year; (Hansen et al. 2013). It is easy to type out these strings of numbers without pausing to comprehend their enormity: the devastation of wilderness, and the biodiversity that populates it, is colossal; larger than the total area of Syria and nine times the area of Wales lost each year. This recent and rapid land use change has many ecological consequences and is overwhelmingly the primary threat to the world's vertebrates, driven primarily by expanding agriculture and logging (Baillie et al. 2010). Expanding agriculture threatens approximately 70% of mammals, 70% of reptiles and 75% of amphibians while logging threatens approximately 55% of mammals, 50% of reptiles and 65% of amphibians (Baillie et al. 2010).

Land use in Borneo has evolved in an *ad hoc* and opportunistic manner to meet various needs at different times; it has not been planned, designed or explicitly coordinated across different interests to achieve particular goals (Albrechts 2004). This has led to Borneo losing over 30% of its forest cover since 1973 (Gaveau et al. 2014). This loss is an enormous threat, not only for the Sunda clouded leopard and other Bornean fauna, but also, given the substantial reserves of forest carbon on Borneo (Saatchi et al. 2011). Current trends in land use and development trajectories are poised to place even greater

stress on this ecosystem. As these pressures escalate and evolve, decision-makers will face ever more difficult political choices about how to use limited resources to achieve different, often competing societal goals linked to the land.

Spatial conservation prioritization describes the use of quantitative techniques to generate spatial information about conservation priorities (Moilanen et al. 2009). Early examples of this approach were first applied in the 1980s as a simple iterative processes (e.g.(Cocks & Baird 1989; Kirkpatrick 1983)), and throughout the 1990s typical problems involved small datasets and simple complementarity models (Margules et al. 2002). Interest in the field of spatial conservation prioritization has grown exponentially since the 1990s (as measured by the number of papers published annually (Moilanen et al. 2009)), and combined with modern improvements in computing power has led to the development of reliable, user-friendly software designed to tackle conservation prioritization problems (e.g. Marxan (Ball et al. 2009), Zonation (Moilanen et al. 2009), and C-Plan (Pressey et al. 2009)).

For this research I used the site selection software Marxan (Ball et al. 2009). Marxan is designed to solve the minimum set reserve design problem in which conservation targets are set for a number of biodiversity features, Marxan then selects planning units that meet these targets for a minimum cost while allowing the user to provide weightings for the extent of spatial clustering in the reserve design. Marxan uses a process of simulated annealing to find multiple good solutions to enormous minimum set problems. This works by generating an initial set of sites, evaluating them, and then iteratively searching

for and accepting improvements to the set, while also stochastically accepting non-improving sites, this allows the model to avoid becoming trapped prematurely in a local optima that misses the global pattern – this approach is used because it is fast, simple, and robust to changes in the size and type of problem (Ball et al. 2009).

Marxan has become a widely used tool in spatial conservation prioritization, for example in the identification of no-take zones in the Great Barrier Reef (Fernandes et al. 2005), in the identification of a set of global priority areas for conservation that is based around balancing the opportunity costs of agriculture against threat (Carwardine et al. 2008), and in quantifying the relative irreplaceability of important bird and biodiversity areas (Marco et al. 2015).

Input data

Patterns and predictions of deforestation risk in Borneo

In order for conservationists to plan adequately to conserve the remaining forest areas, it is vital that they have reliable, spatially-explicit data on the areas that are likely to be most at risk.

The tools and techniques to collect and classify remotely sensed data on forest cover and deforestation have long been available (Congalton 1991), however computing power has historically restricted analyses to comparatively small, and then regional scales. As computing power has improved, substantial research effort has been dedicated to

improving our understanding of both global and regional patterns of deforestation. In terms of the scale of the analysis, Google's EarthEngine tool, based on Hansen et al. (2013) global map of forest cover is probably the most significant. However, this tool struggles to differentiate between areas of intensive forestry (such as palm oil) and natural forest (Hansen et al. 2013) and so regionally specific datasets are still necessary.

A wide range of statistical approaches has been applied to identify the correlates of past deforestation and predict these trends into the future. These include logistic regressions (Chowdhury 2006; Echeverria et al. 2008), genetic algorithms (Soares-Filho et al. 2013; Venema et al. 2005), weights of evidence (Maeda et al. 2011; Soares-Filho et al. 2010), cellular automata (Thapa et al. 2013) and Random Forests (Aide et al. 2013; Grinand et al. 2013).

Random Forests is a machine learning technique developed by Ho (1995) and updated by (Breiman 2001) that is based on constructing a 'forest' of multiple decision trees. The attributes considered at each node of each decision tree are subjected to some level of randomness, and trees are trained on a bootstrapped version of the original training data set. The classification decision is then based on the average answer across all decision trees.

In this study I use Random Forests because they frequently outperform other approaches (Rodriguez-Galiano et al. 2012; Schneider 2012) and because nonparametric procedures like RF are particularly effective at identifying complex multivariate associations, such as those that affect patterns of forest loss (Breiman 2001).

A key element of my approach is to use an explicitly multi scale approach to modelling the environmental correlates of forest loss. The idea that ecological patterns and processes interact across scales in space and time is well accepted. However a recent review of the landscape ecology literature found that most analyses failed to consider processes at multiple scales (McGarigal et al. 2016). The question of multi scale analysis is muddied in most land-use change modelling because many researchers allude to spatial scales by including distance to various landscape features (roads, rivers, population center, etc.) as a metric (e.g., (Rideout et al. 2013; Rosa et al. 2013; Vieilledent et al. 2013). However, by just including one or two scale dependent variables in their analysis they only consider the impact of scale in an implicit sense and fail to perform a full multi-scale optimisation. I know of no other studies that take an explicitly multi scale approach to land use change modelling.

Implications for rapid forest loss on population size, connectivity and genetic diversity of clouded leopards in Borneo.

The Sunda clouded leopard is native to the islands of Borneo and Sumatra, with a different subspecies occupying each island (*N. d. diardi* on Sumatra, and *N. d. borneensis* on Borneo; (Wilting et al. 2011)). The Sunda clouded leopard is currently listed as vulnerable and decreasing by the IUCN Redlist, and the Bornean subspecies (*Neofelis diardi ssp. borneensis*) is classified as endangered (Hearn et al. 2015). Very little is known about the ecology of the Sunda clouded leopard, apart from that they are thought to occur at low densities of 0.8 – 4.4 individuals per 100km^2 and are forest dependent

(Brodie & Giordano 2012; Cheyne & Macdonald 2011; Hearn et al. 2016; Wilting et al. 2012). The forests of Borneo are being lost rapidly, mainly through conversion to palm oil – a habitat that clouded leopards appear not to use regularly although they have been documented travelling through it (Najera et al. 2013; Ross et al. 2010). Although there appears to be some trade in clouded leopard skins (D'Cruze & Macdonald 2015), the conversion of habitat is overwhelmingly the most important threat, not just for clouded leopards but for the their many sympatric species that face similar threats (Hearn et al. 2015).

Loss of forests not only reduces the available habitat for clouded leopards, but it also breaks up larger blocks into smaller fragments interspersed with human dominated landscapes. In 1975, Jared Diamond was among the first scientists to notice a similarity between island biogeography and a fragmenting network of isolated protected areas. He concluded that the number of species that a reserve can support at equilibrium is a function of its area and its isolation (Diamond 1975). Larger reserves, and reserves located close to other reserves can hold more species, and when a block of habitat shrinks it may contain more species than it can support and will consequently experience a heightened extinction rate until equilibrium is achieved.

In his conclusion, Diamond discussed the possibility that "*connecting [disjunctive reserves] by strips of the protected habitat may significantly improve their conservation function at little further cost in land withdrawn from development*" (Diamond 1975). This concept of wildlife corridors has been hotly contested in the literature and empirical studies have has not provided unequivocal support for their effectiveness (see review by

Gilbert-Norton et al. (2010)). However, critics of wildlife corridors have often had an overly zealous focus on corridors as narrow strips of habitat between reserves and have failed to consider the wider context of stepping stones or landscape resistance (Bennett 1999)

A more inclusive approach defines landscape connectivity as "*the degree to which the landscape facilitates or impedes movement among resource patches*" (Taylor et al. 1993). Under this definition there are two components that influence the potential connectivity for a particular species: the structural component is determined by the spatial arrangement of habitat types in the landscape, and the behavioural component refers to factors such as scale at which a species perceives and moves within the environment, its habitat requirements and degree of habitat specialization, its tolerance of disturbed habitats and the life stage and timing of dispersal movements (Bennett 1999). Combining these two components allows scientists to conceptualise the landscape as a continuous resistance surface (typically represented as a Raster grid) in which the value of the cell represents the cost of some movement process (genes, dispersing individuals etc.) traversing that cell (Adriaensen et al. 2003; Wade et al. 2015). Habitat fragmentation and increased landscape resistance have been shown to decrease dispersal success, increase mortality, and reduce genetic diversity; additionally small isolated patches are mores prone to stochastic extinction events and are less likely to be recolonized (e.g. (Cushman et al. 2013b; Fahrig et al. 1995; Gibbs 1998; Harrison et al. 2015; Semlitsch & Bodie 2003; Wilson & Provan 2003)). Understanding the consequences of land use change, and developing effective strategies to maintain biodiversity in disturbed landscapes, is therefore a major challenge to both scientists and land managers (Bennett 1999)

Traditional approaches to connectivity modelling have been based on mapping least cost paths or corridors between a few "core" habitats or protected areas (Beier et al. 2011; Brodie et al. 2014), however this limits the generality and scope of inferences (Cushman & Landguth 2012). For many questions it is better to adopt spatially synoptic modelling in which connectivity is assessed continuously across space, from all locations to all others (Cushman et al. 2013a), however this approach very computationally demanding and is therefore not commonly applied.

Brodie et al. (2014) employ a circuit theory approach to identify clouded leopard corridors between a number of protected areas in Sarawak, however their analysis is limited in the spatial extent of the study and the use of a least cost path approach. The analysis presented in chapter 5 provides the first Borneo wide assessment of landscape connectivity for the clouded leopard and highlights the urgent practical need for effective strategies that will maintain connectivity in the landscape. In addition to the importance for applied conservation, this analysis presents the first attempt to model effects of ongoing deforestation on population decline and changes in population connectivity and genetic diversity of any species at this scale.

The impacts of future deforestation scenarios on clouded leopard population connectivity and gene flow

Chapters 3 and 4 of this thesis highlight the potential extent of forest loss on Borneo, and the impact that this is likely to have on clouded leopard population connectivity and gene

flow. Building on this work, and using the spatially explicit maps of forest-loss risk and clouded leopard core areas that I have already generated, Chapter 5 aims to explore the impact of different conservation scenarios on future clouded leopard populations.

Many of the forests occupied by clouded leopards contain extremely high levels of forest carbon (Saatchi et al. 2011). Carbon dioxide emitted as a result of land-use change is one of the major causes of anthropogenic CO_2 emissions (van der Werf et al. 2009), and so land use change in Borneo is a major threat not just to the forests' biodiversity but also in terms of potential CO_2 emissions. There is increasing interest in the congruence of benefits between biodiversity conservation and the forest carbon stocks (Collins et al. 2011; De Barros et al. 2014; Murray et al. 2015). In Chapter 6 of this thesis I bring these two ideas together to identify which areas of Borneo offer the optimal benefits for the conservation of clouded leopards and the carbon stored in the forests in which they live.

Historically the locations of protected areas have been biased towards remote and inaccessible areas with few competing demands for the land (Joppa & Pfaff 2009). Irrespective of their level of protection, many of these areas are so inhospitable that they are not at imminent risk of being lost or badly degraded as a result of human activity (Andam et al. 2008; Hoekstra et al. 2005). Investing scarce resources in parks that are not immediately threatened highlights inefficiency in the protected area network. Not only that, but the locations of many PAs leads to inefficiency in the network with some species being protected in multiple locations while others remain completely unprotected; thus

PA networks often fail to deliver optimal benefits for conservation leading to calls for underperforming protected areas to be replaced for better conservation outcomes(Fuller et al. 2010).

In this chapter I consider the impacts of several different conservation scenarios on the future of clouded leopards in Borneo. The scenarios that we tested involved exploring both “active" and “expedient” approaches to the allocation of new protected areas, as well as “business as usual’ scenarios involving no new protected areas but varying effectiveness of the existing network. The expedient scenarios follow the historical (although seldom explicit) practice of siting new protected areas in distant, remote locations by selecting sites with the lowest deforestation risk. In devising the active conservation scenarios I followed the opposite approach and sited new protected areas in the highest risk areas in the hope of slowing the immediate risks of deforestation. Several authors have suggested that an increased recognition of the hard trade offs in conservation, and an increased focus on prioritising high-risk areas for protection would improve conservation outcomes (Joppa & Pfaff 2010; McShane et al. 2011; Pfaff & Sanchez-Azofeifa 2004). I also considered the effectiveness of the existing protected area network by including scenarios that (a) retained the existing network and added to it and (b) started with a blank slate and designated a completely new set of protected areas irrespective of the existing network.

The designation of protected areas is a vital tool for conservation, however they have traditionally been thought of as permanent and immovable. Recent studies have challenged this perception by highlighting the extent of downgrading, downsizing and degazettement of existing PAs (known as PADDD) (Mascia & Pailler 2011; Mascia et al. 2014). Rather than being permanent fixtures of the landscape PAs are dynamic, socially defined and constructed governance regimes that can be manipulated (Mascia & Pailler 2011). Increasingly, there are calls to exploit this flexibility by reallocation conservation investment away from inefficient or under performing PAs, and directing it towards new protected areas that might deliver better conservation outcomes(Fuller et al. 2010).

I use MARXAN (Ball et al. 2009), the decision support tool described above, to evaluate seven different scenarios that seek to maximise the conservation outcomes for both clouded leopards on Borneo, and the conservation of forest carbon. Inspired by the debates around active or expedient approaches to conservation, and the idea of improving PA effectiveness by reallocating existing protected areas, I devised several scenarios that reflect these debates while seeking to maximise the conservation outcomes for both clouded leopards on Borneo, and the conservation of forest carbon. By way of comparison these scenarios are compared to both the 2010 baseline, and a *business as usual* approach that relies on the existing network of protected areas and assumes that these areas continue to be as effective as they were between 2000 and 2010 (Chapter 3).

Thesis structure

Against this background, I will explain the logical flow of this thesis. It is presented as a series of papers, either published or, at the time of writing submitted, or awaiting submission, for publication. Each of these papers begins with an introduction to its topic, and ends with a discussion of the wider context.

This thesis opens with two chapters that centre around the field of conservation marketing. In the first I explore which species people prefer for conservation and why.

Chapter 2 introduces themes of the emerging field of conservation marketing, and a pioneering collaboration with a market research company to investigate the relative appeal of 100 terrestrial mammal species, selected to be a representative panel of most mammal body morphs, in five countries on five continents. This enables me to rank each of the 100 species in terms of their appeal and explore differences between samples from the different countries. I then explore which attributes contribute to a species' appeal and use this to develop a method for reliably predicting the appeal of other mammals.

Chapter 3 builds on the themes of Chapter 2 to create a more generalised metric of 'appeal' for terrestrial mammals and considers how to use that metric to identify potential efficiencies in conservation marketing. I extend the analysis in Chapter 2 to provide national rankings of appeal for all terrestrial mammals and highlight the differences between countries. In addition I explore which species offer the best potential efficiencies for conservation marketing. Species with the highest appeal and the greatest opportunities for efficiencies are termed 'Ambassador' species.

Moving on to the second part of this thesis I take the case study of one potential ambassador species, the Sunda clouded leopard, to explore the consequences of land use change in Borneo on its conservation and its potential to act as an umbrella for carbon stored in Borneo's forests.

In Chapter 3 I begin by filling an important gap in understanding the drivers of deforestation risk across Borneo, and mapping the risk of deforestation by the year 2020. Using patterns of land use in the year 2000 I was able to predict areas of deforestation in 2010 with 91% accuracy and predict which cells would remain forested with 78% accuracy. These predictions compare favourably with other assessments of deforestation risk giving us confidence in our projections for the likely outcomes for Bornean forests in 2020.

Chapter 4 uses the predictions generated in the previous chapter as the basis for exploring the likely consequences of forest loss for the numbers and the genetic diversity of clouded leopards in Borneo under several scenarios. These scenarios reveal that between 2000 and 2010, forest loss drove substantial reductions in all metrics relating to clouded leopards including a projected 13% decline in population. Losses in all metrics are predicted to accelerate rapidly between 2010 and 2020, resulting in a predicted population decline of an additional 57%.

With these projected losses in mind, I turn to Chapter 6 where I model the impact of several different scenarios for future conservation on the demography and genetics of

clouded leopards, as well as for the levels of carbon stored in their forest habitats. The scenarios tested included a 'business as usual' scenario as well as two different approaches to the introduction of new protected areas. The "active" conservation scenarios targeted conservation effort in the areas under highest deforestation risk, while the "expedient" conservation scenarios targeted conservation effort in the areas of lowest risk.

While working on these chapters I have also been actively involved in research of related topics, of which two are presented as papers in the Appendix to this thesis. Developing the theme of Chapter 6, and the link between conserving wildlife and conserving carbon, Appendix 1 presents De Barros et al. (2014). Herein, we map the distributions of areas (Brazilian municipalities) known to be suitable for jaguars, for biodiversity more generally, and for forest carbon. In this way we identify municipalities that are important priorities for both Jaguars and forest carbon, naming these areas REDDspots. We identified 159 municipalities that qualified as REDDspots, and 135 municipalities that contained either current of planned REDD projects, however these two objectives coincided in only 40 municipalities (25%). We identified a further 95 municipalities that may have potential to develop additional REDD+ projects while also targeting biodiversity conservation.

These discussions led me a much broader view of the geopolitical context of conservation, and the differing socio-politics of different nations. The nation state is a relatively new innovation (Patten 2009) and may be one that is increasingly cumbersome as an operational unit in the globalized world. Nonetheless, it is still largely nations that determine, or at least implement, policies that affect conservation, and so in Appendix 2 I

present the paper by Dickman et al. (2015) in which we evaluated, nation by nation, their importance as priority locations for felid conservation. Facing the reality that nations differ in their capacity to deliver policy, and to function effectively, we then ranked each in terms of infra-structural capability. This reveals a quadrant of countries in terms of each country's capacity to deliver conservation and their priority. Countries that are both high priority and have a high likelihood of conservation success are postulated to offer better returns on conservation investment than countries that fall low on either metric. A readily made misinterpretation of these results would be that we suggest withdrawing support for countries that have less capacity to deliver conservation; on the contrary, our intention is to emphasise the importance of customizing conservation actions to local circumstances so that they are best fitted to their purpose.

Although I have not included them in the Appendices, on the grounds that while submitted to journals they are not yet accepted, two other pieces of research I have undertaken continue this trajectory towards global scale analyses. These papers are Sandom, C. J., Williams, J., Burnham, D., Dickman, A., Hinks, A., Macdonald, E.A. and Macdonald, D.W. (submitted) and Sandom C.J., Faurby, S., Burnham, D., Dickman, A., Hinks, A., Macdonald, E.A., Williams, J.,. & D.W. Macdonald (submitted). The first creates a new database on all the published papers on wild felid diet that we could find, and undertakes a meta-analysis to reveal, on 2 degree grid cells, the diversity of felid species, and their prey. Using this foundation, the second paper explores the number of felid species missing from each guild as the result of the Pleistocene extinctions of their prey base, and thus considers the options for reconstructing these guilds and for rewilding.

The papers presented in the thesis, and those in the appendices and submitted, comprise a body of work in which I have sought to understand how conservation science can best contribute to contemporary conservation. The journey started in a different place. Realising the potential of clouded leopards as both a deserving topic of fundamental research and as a potential ambassador, I began by undertaking camera-trapping and related fieldwork of these species in Cambodia, Sabah and Kalimantan. These experiences were rewarding, and the data will be used elsewhere, but I have included none of them in this thesis. Rather, the journey led me to conclude that the most promising opportunities for real progress currently lie in the field of conservation prioritization. Pragmatically, my attention has turned, for the first part of the thesis, to identifying good candidates for conservation marketing. For the second part of the thesis, I return to clouded leopards, but in the large scale context of forest loss, and with the hope of proving an evidence base for influencing policy. It remains to be seen whether these findings will gain traction, but my hope, for the next step, is to use the GIS-based models presented here, alongside targets for expanding agriculture, to work with national stakeholders to project the likely outcomes of alternative policies and to influence their choices between policy options.

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Chapter 2

Conservation inequality and the charismatic cat: Felis felicis

A modified version of this chapter has been published in *Global Ecology and Conservation*

Abstract

Conservation resources are limited, making it impossible to invest equally in all threatened species. One way to maximise conservation gains is to focus upon those species with particular public appeal, using them to generate funding and support that could also benefit less charismatic species. Although this approach is already used by many conservation organisations, no reliable metrics currently exist to determine the likely charisma of a given species, and therefore identify the most appropriate targets for such campaigns. Here we use market research techniques on over 1500 people from five continents to assess the relative charisma of different mammals, which factors appear to drive it, and how these patterns vary between countries. Felids and primates emerged as highly favoured species for conservation, with the tiger (*Panthera tigris*) the top species by a wide margin. Using an information theoretic approach we develop models that successfully predict respondents' preferences across the entire sample, suggesting global commonalities in the attributes that people prefer for conservation. However, by analysing each country separately we are able to improve our models, thus highlighting the importance of identifying locally specific flagships for conservation. The most important attributes were body size and IUCN status, although the extent of baldness, whether the species was a potential threat to humans and whether the eyes were forward or side facing were also widely important. Several of the key attributes revealed in this study could be extrapolated to nearly all terrestrial mammals, paving the way for a standardised global identification of species likely to prove effective for future conservation campaigns. The public preferred species with which they had affinity and familiarity, and we discuss how these aspects could be increased to promote the under-achievers, whilst maximising the funding potential of the highly charismatic mammals.

While the felids are widely regarded as a popular taxonomic group, the great extent to which they appealed to our respondents emphasises their potential as ambassadors for conservation. Indeed, the big cats were so highly rated that we might think of them as one, *Felis felicis:* a globally powerful flagship for conservation.

Introduction

While a sort of taxonomic egalitarianism might have it that all species are equal, it is clear that to most people some species are more equal than others. For example, while we might suspect that the man on the Clapham omnibus may value a gorilla (*Gorilla gorilla*) more highly than a house mouse (*Mus musculus*), it is less clear-cut, but still likely, that such differences are perceived even amongst closely related organisms, such as two species of felid. While such favouritism might be ethically inconsistent, it is likely to be highly relevant to practical conservation (Macdonald et al. 2006). This matters because, while Noah may have been determined to rescue at least one representative pair of everything, neither the public nor policy makers have the ability, let alone the inclination to be so even handed. In order to raise funds, and to have the best chance of influencing political decision making, it is arguably important for conservationists and policy makers to understand which species are most valued by the public and why.

Conservation organisations have a long history of focussing their campaigns around single charismatic species, but it wasn't until the 1990s that the term 'flagships' for conservation began to attract interest in the conservation literature. Since then it has been much discussed and has undergone many reinterpretations (Caro & O'Doherty 1999; Favreau et al. 2006; Heywood 1995; Meffe & Carroll 1997; Simberloff 1998a; Simberloff 1998b). A recent review of the concept defined flagship species as "*a species used as the focus of a broader conservation marketing campaign based on its possession of one or more traits that appeal to the target audience*" (Verissimo et al. 2011). The appropriateness and effectiveness of focusing conservation attention on a single species has been debated vigorously (Bowen-Jones & Entwistle 2002; Caro 2010; Favreau et al.

2006; Linnell et al. 2000; Small 2012a, b). On the critical side, some authors have preferred an emphasis on ecosystem management (Simberloff 1998b), and others have illustrated the dangers of selecting a flagship species that is locally inappropriate (Linnell et al. 2000) or found that focusing on single species does not necessarily confer the best protection of other locally occurring species (Lindenmayer et al. 2014). On the positive side, others have found that the presence of a charismatic flagship species increases the public's engagement with conservation issues (Smith & Sutton 2008) and their willingness to pay for conservation (Kontoleon & Swanson 2003; White et al. 2001). Governments and NGOs have also repeatedly and successfully used flagship species as marketing tools for leveraging political influence and funds for wider conservation (e.g. (Dietz et al. 1994; Loveridge 2014; Veríssimo et al. 2009). Much of the debate about flagship species stems from different interpretations of the term (Barua 2011), so in their definition, Verissimo *et al.* (2011) deliberately focus on their use as marketing tools. They avoid using the term 'charisma' because perceptions of charisma are likely to differ between stakeholder groups and because it is potentially susceptible to manipulation by marketers. However, charisma and attractiveness have been widely cited as being key traits that might contribute to public perceptions of a species (Lorimer 2007; Small 2012a), and indeed Veríssimo et al. (2014) found 'attractiveness' to be a significant determinant in identifying flagship bird species in Brazil.

In what some regard as the seminal paper on the subject, Lorimer (2007) identifies three facets of non-human charisma, namely ecological, aesthetic and corporeal charisma. Ecological charisma broadly relates to the 'detectability' of a species – in other words factors such as the size, circadian rhythm and elusiveness of species that are likely to

bring it to the attention of humans. Aesthetic charisma refers to the aesthetic characteristics of a species' appearance or behaviour, and corporeal charisma relates to a deeper emotional attachment that can be understood in terms of epiphanies (such as a childhood encounter) or the accumulation of expert knowledge of a species. In line with these ecological and aesthetic facets of charisma we can see that there appear to be some commonalities amongst the species that people find attractive - for instance, species chosen as flagships are typically large, warm blooded, endangered and predatory with forward facing eyes (Caro & O'Doherty 1999; Clucas et al. 2008; Courchamp et al. 2006; Dietz et al. 1994; Johnson et al. 2010; Smith et al. 2012). Further, zoological gardens trade on the ability of their collections to attract visitors, and consequently zoo species are likely to be large, attractive and even often of lower conservation priority than their close relatives not held in zoos (Frynta et al. 2013; Martin et al. 2014). However, despite the fact that there are obvious biases in people's attitudes, driven in part by the ecological and aesthetic components of charisma, there are currently no reliable metrics that objectively rate or predict which attributes might contribute to people's preferences. It is also important to note that a species' perceived attractiveness might also be affected, positively or negatively, by cultural or religious influences (Dunham 2006; Gosler et al. 2013; Richards 2000), or by positive or negative interactions with a species – one man's valued photo opportunity might just have eaten another man's livelihood.

Another key element of the flagship species debate is that any species selected as a flagship needs to be both relevant to the conservation issue and appropriate for to the intended recipients of the campaign (Bowen-Jones & Entwistle 2002; Douglas &

Veríssimo 2013; Linnell et al. 2000). Nevertheless, many large international NGOs (WWF, RSPB, Greenpeace etc.) continue to invest substantial funds on broad based campaigns aimed at improving general attitudes towards environmental issues, as well as attracting both funding and recruiting new members. These campaigns aim to reach as wide a selection of society as possible and can be seen in magazines, newspapers and on everything from the sides of buses to cans of cat food in cities around the world, and a single campaign can raise many hundreds of thousands of dollars (WWF 2014).

To some extent marketing firms already know which species people like: Jaguar cars, Tusker beer, Lynx aftershave, Camel cigarettes and Puma sports clothing are all powerful commercial icons, and the giant panda (*Ailuropoda melanoleuca*), polar bear (*Ursus maritimus*), lion (*Panthera leo*) and tiger (*Panthera tigris*) are all frequent stars of conservation marketing campaigns. However determining differences in peoples' preferences towards different species is not always intuitive and there are over 5000 species of terrestrial mammal, with astonishing variations in morphology, from Kitti's hog-nosed bat (*Craseonycteris thonglongyai*), at 2g to African elephants (*Loxodonta africana*) at 6,000kg, and from subterranean naked molerats (*Heterocephalus glaber*), to flying Malayan colugos (*Galeopterus variegatus*). Given that peoples' attitudes towards species are also likely to be heavily influenced by context and familiarity, we expect preferences to differ regionally and between people with different experiences of interacting with wildlife. These factors are likely to influence peoples' decision-making about conservation, arguably as much as technical evidence pertaining to particular conservation issues. Here, we define charisma as how attractive species are, relative to

each other for conservation, as perceived by our respondents and investigate which species have the highest appeal, and why.

To explore mammalian charisma we used photographs of terrestrial mammals to investigate whether our respondents preferred the conservation of certain species above others and assessed whether these preferences were regionally consistent. We then examined whether underlying factors, such as specific physical attributes, could be used to predict charisma, as well as which species were ranked as more or less charismatic than would be expected on the basis of those factors alone. By understanding which factors appear to determine our respondents' attitudes to conservation, we provide a method to predict charisma across all mammals, and therefore help identify which species are likely to be effective flagships for future conservation campaigns.

Methods

Following Verissimo et al. (2011) entreaty for greater collaboration between conservationists and market research professionals, we used industry standard, market research techniques usually employed for the exploration of human preferences of commercial products, to inform our study design and data collection protocols. The survey was designed in collaboration with, and conducted by market-research professionals (Touchstone Partners Limited) allowing us to make the most of their extensive professional experience in survey design. Touchstone Partners coordinated recruitment of respondents through proprietary market research panels.

100 photographs of terrestrial mammals representing 25 orders and 69 families were presented in pairs to over 1500 participants from 5 countries. For each pair of photographs, the respondents were asked the strength of their preference between the two species in the context of priorities for conservation. We used paired conjoint analysis (Green & Wind 1975; Green & Srinivasan 1978) to rank all 100 photographs in order of peoples' preferences. Each photograph was described by 15 descriptive attributes, which we analysed post hoc to explore if any could be identified as important in driving peoples' preferences.

Prior to final delivery, several naïve volunteers from both Touchstone Partners and the Wildlife Conservation Research Unit tested the survey for content and ease of use. Comments from these volunteers were fed back into the survey design and used to improve the clarity of the questions, as well as the overall accessibility of the survey.

Survey design and delivery

In order to reflect our interest in broad based international conservation campaigns, we targeted our survey at the people most likely to be targeted by such campaigns – in other words a subset of society focused around the moderately affluent middle classes, politically engaged, and who we felt were most likely to either donate to or be members of conservation organisations. In order to achieve this, the survey was presented online in 5 different countries (UK, USA, India, South Africa and Australia) with levels of internet penetration ranging from 41% (South Africa) to 81% (UK). Conducting the survey online, biases the respondents towards affluence but may also increase the likelihood that they

were politically engaged and have views and political leverage regarding environmental matters.

In total, the survey was taken by 1536 respondents aged 18-64 in 5 sub-samples (Australia: *n* = 303, India *n* = 310, South Africa *n* = 311, UK *n* = 305, USA: *n* = 307). Practical considerations meant that the survey was presented in English, and so we selected five English speaking countries with obvious differences in their mammalian fauna in order to test whether these biological differences influenced the attitudes of the respondents. While familiar with surveys, panellists are not contacted for surveys so frequently that they may be judged to have become unrepresentative of the wider population. Participants were asked to provide simple demographic information (age, sex, occupation) before viewing 25 pairs of images to establish their preferences between different mammals. Each participant was also asked to rate their familiarity with, and affinity for, a further selection of 25 photos. Across all regions the sex ratio of our respondents was 55.1% female with a mean age of 41.3 years for both sexes (♀ SD = 13.5, ♂ SD = 13.3). Demographics varied only slightly between countries however India was the only country where respondents were more likely to be male (24.8% ♀), the mean age of Indian respondents was also substantially lower than for other regions (35.0 for both sexes; Table 1). 28.1% of respondents were currently, or have been, members of a conservation organisation, 54.9% currently, or have previously donated to a wildlife conservation charity, 71.0% worry about conservation issues, and 75.8% believe that wildlife conservation should be a top priority for society (Table 1).

The total of 100 images was selected for practical reasons by trading-off the desire to include as many species as possible with factors such as cost, the amount of time people could be expected to devote without their attention waning, and the need for each image to be seen a sufficient number of times by members of each sub-population (300 from each of five countries) to deliver adequate analytical power. We designed our survey to take approximately 15 minutes, a duration that our market research partners have found to be optimal for online surveys (T. Baker pers comm) and comfortably within the 20 minutes advised by (Cape 2010), and in line with (Galesic & Bosnjak 2009) who found that both starting and completion rates were lower for surveys of 20 minutes and above. With a total of 100 images, and with each respondent viewing 25 pairings, we were able to ensure that each image would be seen on average 150 times in each sub sample of 300 participants.

Table 1. Demographics of survey respondents.

	Australia	India	South Africa	UK	USA	All regions
Total respondents	303	310	311	305	307	1536
n (♀)	188	77	194	198	190	847
n (♂)	115	233	117	107	117	689
% (♀)	62.0	24.8	62.4	64.9	61.9	55.1
Mean age (♀)	44.2	35.0	40.3	37.1	46.3	41.3
SD age (♀)	13.1	10.8	12.0	14.6	12.5	13.5
Mean age (♂)	46.1	35.0	41.6	46.1	44.6	41.3
SD age (♂)	12.7	11.6	12.2	13.9	13.1	13.3
% who have been a member of a conservation organisation	28.7	27.7	25.4	28.9	30.0	28.1
% who have donated to a wildlife conservation charity	56.8	49.0	63.0	55.4	50.5	54.9
% who worry about wildlife conservation issues	65.3	79.7	81.4	61.0	67.1	71.0
% who agree wildlife conservation should be a top priority for society	71.6	86.1	87.1	63.9	69.7	75.8

Paired Conjoint Test

The survey used a standard pair-wise trade-off technique which was analysed using conventional conjoint analysis (Orme 2005). Each respondent was shown 25 pairs of randomly selected mammalian species in a web-based presentation and asked to indicate their preference between them in the context of priorities for conservation, using a balanced five point semantic Likert scale that ran from left to right under the selected pair of pictures (Prefer completely / Prefer / Prefer Neither / Prefer / Prefer completely) (Malhotra 1996; Oppenheim 1992). Each image was shown only once, so that each respondent saw a randomly selected set of 50 of the 100 mammals.

Familiarity and Affinity Test

Having completed the 25 paired choices, each respondent was then shown a separate, random selection of 25 photos (viewed one at a time, as illustrated in Fig A.1 (appendix A)). For this exercise, each of the 100 mammal photos was randomly assigned to one of four sets of 25. One of these sets was then assigned, at random, to each respondent who was asked to record, for each photo a) how familiar they were with the subject (familiarity) and b) how much they liked the subject (affinity) (both on a 5 point semantic scale (Osgood et al. 1957)).

The entire survey took a median time of 14:28 minutes to complete. The pairwise comparisons took a mean of 6:50 minutes (standard deviation = $\pm$ 15:25 minutes). Decision times for each pair varied hugely, from 0.5 seconds for one pair to 3 hours 40 minutes. Surveys completed in <5 minutes (i.e. in less than 1/3 of the median time taken – termed by the market research industry as “speeders”), of which there were 10, were

excluded altogether. We did not exclude respondents taking an unusually long time to complete the survey as we could not distinguish the thoughtful from the distracted. Time to make a preference did not predict the score given to a species ($F_{1,\ 38398}$=0.001, P=0.971). Respondents who repeatedly clicked the same response option with no evidence they considered their responses each time ("flatliners") were also excluded, although these were all speeders and no further respondents needed to be removed. 71% of respondents reported that they enjoyed the survey "a lot" while only 4% reported negative feeling towards the survey, indicating that the vast majority of respondents were positively engaged.

Selection of species

We selected 100 photographs of terrestrial mammals for inclusion in our survey. Terrestrial mammals were selected for their taxonomic representativeness, at the level of the family, and to maximise the diversity of physical morphs. Following the taxonomy in Macdonald (2009) there are 132 families of terrestrial mammal (2 Monotremata, 20 Marsupialia and 110 Eutheria). Although taxonomically distinct, some families contain species of such similar appearance that they are unlikely to be viewed differently by the general public (for example, families within both the microchiropteran and megachiropteran bats). Consequently, we did not include families within orders that duplicated morphs, resulting in a sample of 69 families of distinct appearance. At least one species from each of these families was selected, choosing examples that illustrated the diversity of morphs within families and the whole class Mammalia. In some families this resulted in multiple representatives – for example in the Australian carnivorous marsupials (Dasyuromorphia) the Tasmanian devil (*Sarcophilus harrisii*), western quoll

(*Dasyurus geoffroii*), numbat (*Myrmecobius fasciatus*) and swamp antechinus (*Antechinus minimus*) were deemed so morphologically different to justify separate inclusion. Whereas in other cases the apparent evolutionary convergence on morphs within Mammalia led to species from different families representing each other. For example, the North American river otter (*Lontra canadensis*) was selected as one of the representatives of the family Mustelidae, but was also deemed a good morphological representative of the giant otter tenrec (*Potamogale velox*). The European hedgehog (*Erinaceus europaeus*) also provides a good morphological representation of the greater hedgehog tenrec (*Echinops telfairi*). Thus the order Tenrecidae was only represented by the highland streaked tenrec (*Hemicentetes nigriceps*), which was distinctive from the other mammals in the 100-strong sample.

In addition to one representative species per family, and building on our earlier analyses of felids and primates to function as umbrellas for each other (Burnham et al. 2012; Macdonald et al. 2012), we selected additional representatives from these two orders, which capture the attention of a wide public. Additionally while the primates selected displayed a wide range of morphologies, felids have a comparatively uniform body-type; thus allowing us to gain greater resolution into peoples attitudes towards distinctive body and facial markings by presenting respondents with a several species that have a similar body form except for their pelage. This brings the total number of Carnivora to 27 (including 9 felids (including both the melanistic and the common forms of the leopard (*Panthera pardus*), and 5 canids and 4 mustelids) and of primates to 13 (including 8 anthropoids (8 Haplorrhine, 4 Strepsirrhine and 1 Lorisidae). Appendix B gives a full list of species used in the 100 photographs.

Selection, labelling and categorisation of photos

Images were selected using the criterion of a clearly visible single adult, and wherever possible were shown in the most natural setting possible. Following (Takahashi et al. 2012) and to minimise possible biases due to differences in the photographs, we selected photos in which the mammal was positioned broadside to the camera, with its face visible but eyes not forcefully engaging the photographer. For species with sexual dimorphism, the more striking sex with the more exaggerated trait was selected on the assumption that these might be linked to charisma. For example, the male lion was selected for its mane and the male mandrill (*Mandrillus sphinx*) for its colourful facial markings. Each image incorporated the common English name of the species, an indication of its size (by comparison with a human silhouette or portion thereof), and its IUCN Red List status (see appendix A for annotated examples).

In order to minimise potential biases arising from the aesthetic qualities of the photos (composition, saturation contrast etc.) we endeavoured to select images that were as comparable as possible, however image quality was inevitably poorer for some of the less frequently photographed species. In order to account for these possible biases, an independent panel of 11 volunteers scored all images on their photographic qualities, and this value was included as an attribute in our analysis.

Species preference scores

During each paired test, each mammal was assigned a score: “Prefer completely” = 2, “Prefer” = 1, “No preference” = 0, “Prefer other” = -1, “Prefer other completely” = -2. If one photo in the pair was “Preferred completely” it was scored 2, and the other photo in

the pair would be scored -2, so for each pair the sum of scores given totalled 0. From this, the total preference score for each mammal was calculated by summing its scores across the whole sample. As each mammal was seen by a slightly different number of people, the scores were made proportional to the number of times it was seen. This average preference score was the basis of producing an overall rank for all 100 mammalian images. For example, the tiger was seen 774 times in total and the sum of all its pairwise scores was 870, thus it has a final preference score of 1.124 (870/774=1.124).

To test for position bias, each species' preference score was compared for the occasions when it was presented on the right or left of the pairing. The species preference scores generated from the right and left positions were highly and significantly correlated (r = 0.980, $t_{2, 98}$ = 48.9379, $p < 0.001$), indicating that there was no position bias.

Attribute scores

Each mammal image was classified according to a list of 15 attributes selected to reflect features known (e.g. eye position (Smith et al. 2012) or suspected (e.g. furriness or baldness) to affect peoples' reactions. To accommodate variation in peoples' perceptions of these attributes, each of the 100 images was independently scored by the authors and a further 6 participants (n = 11). The scores were tabulated, and the modal value for each attribute was accorded to each species, but not displayed to the survey participants. The purpose of these attributes was to identify any characteristics that might be associated with high or low preference scores. These attributes included some that were generally unambiguous (e.g. forward- or lateral-facing eyes, strident black-and-white patterning, bright colouration) and others that were more subjective (e.g. furriness or striking

physical appearance). In addition, each photo was rated for aesthetic quality to allow us to gauge the importance of the photography in influencing people's preferences. The list of these attributes is given in table 2. They were selected to cover all three of (Lorimer 2007)'s facets of non-human charisma, and reflected many of the character traits that have been mentioned as possible determinants of charisma in the literature (see table 2).

Model averaging

The survey respondents' overall preference score for each species (hereafter response) was normally distributed (Shapiro-Wilk normality test W = 0.978, p-value = 0.0981) and was analysed relative to the 15 attributes in linear models (lm). The full model included IUCN status, ED score, diet, body size, human threat, activity pattern, striking appearance, armour, facial markings, body markings, colouration, eye position, fluffiness, photo quality and baldness as categorical fixed effects. The levels within each attribute are detailed in Table 2. We used an information-theoretic approach to compare models that related the various attributes to the average preference scores each mammal accrued. The 'dredge' function of the 'MuMIn' function in R Version 3.0.3 was used to generate a set of candidate models with combinations of the terms in the full model.

Candidate models were evaluated by comparing differences in their second-order Akaike Information Criterion (AIC_C) values and Akaike weights (ω_i strength of evidence for each candidate model being best model of those fitted to the data). AIC considers both model fit and complexity, and finds models that most parsimoniously represent the strongest relationships. Models with the highest AIC weight identify the strongest relationships

between explanatory and response variables, and an Akaike weight > 0.9 indicates the presence of a single best model (Burnham and Anderson 2002).

Table 2. Full list of attributes and levels ascribed to each species.

Attribute	Levels	References
IUCN status *This survey was intended to explore attitudes towards species in the context of conservation marketing. We therefore included five IUCN Red List categories as a measure of conservation priority. Rarity also appears to be important in peoples' attitudes towards species with some studies finding that people ascribe increased value to rare species, while others found that zoos (which trade on animal charisma) often stock species of lower conservation priority.*	LC NT VU EN CR	(Courchamp et al. 2006; IUCN 2014; Martin et al. 2014)
ED score *As with IUCN score, Evolutionary Distinctiveness was included as a measure of conservation priority. These were divided into 3 levels to reflect species of high, medium and low evolutionary distinctiveness.*	<20 20-40 >40	(Isaac et al. 2007)
Diet *Traditionally flagship species have frequently been carnivorous, and so we test whether diet affects peoples' attitudes towards a species.*	Carnivore Carnivore/ Scavenger Herbivore Insectivore Omnivore	(Caro 2010; Clucas et al. 2008; Macdonald 2009; Myers et al. 2015)
Body Size *Size arguably affects the detectability of the species and thus it's ecological charisma. In addition traditional flagships have tended to be large species including the elephant, polar bear and tiger.*	<1 1-10 10-20 20-40 40-100 100-800 >800	(Lorimer 2007; Macdonald 2009)
Human threat *It has been proposed that humans may have an evolutionary predisposition to be attentive towards, and thus affected by species that may have been likely to harm them in their evolutionary history. By including this variable we test whether this has an impact on peoples' attitudes to species. Species were classified as being a potential threat to humans if they were either a member of the order Carnivora weighing >50kg, or if they weighed >100kg and had documented evidence of causing human fatalities.*	Not threat to humans Threat to humans	(Kruuk 2002; Mungall 2007; Woodroffe et al. 2005)
Activity pattern *Activity pattern arguably affects the detectability of the species and thus it's ecological charisma. People are more likely to be positively disposed to species that share a similar circadian rhythm.*	Crepuscular Crepuscular-Nocturnal Diurnal Nocturnal Variable	(Lorimer 2007; Macdonald 2009; Myers et al. 2015)

Striking appearance *This term was included to try and capture the 'je ne sais quoi' or 'oddness' that some species appear to posess (such as perhaps the aye-aye (Daubentonia madagascariensis)).*	Not striking Striking	Scored by 11 separate respondents prior to survey
Armour *Many species poses impressive ornamentation, tusks, horns or antlers, while others have distinctive defensive armour. This term was included to see if these distinctive characteristics influenced peoples' preferences.*	None Tusks Horns or antlers Scales or carapace Claws Spines or spikes	Scored by 11 separate respondents prior to survey.
Facial markings *Facial markings are often used to exaggerate facial traits such as large eyes, and may contribute to aesthetic charisma.*	None Some Extreme	Scored by 11 separate respondents prior to survey.
Body markings *Coat patterns can be eye catching and may contribute to aesthetic charisma.*	None Spots Stripes Spots and stripes Patches	Scored by 11 separate respondents prior to survey.
Colouration *High contrast colouration arguably affects the detectability of the species and thus it's ecological charisma, also likely to affect aesthetic charisma.*	Single plain coloured Single bright Multi-coloured low-contrast Multi coloured high-contrast Black and white	Scored by 11 separate respondents prior to survey.
Eye position *Several authors have suggested that people are attracted characteristics also found in human babies*	Forwards Lateral	Lorenz and Gould in (Sunquist 1992)
Fluffiness *This attribute was included because fluffiness often appears to be associated with a species' 'cuteness' and thus might be linked to peoples' perceptions.*	None Some Extreme	Scored by 11 separate respondents prior to survey.
Photo quality *In an attempt to avoid bias caused by aesthetic differences in the photographs, all photos were scored for their aesthetic quality, irrespective of their subject species.*	Poor Average Excellent	Scored by 11 separate respondents prior to survey.
Baldness *Many seemingly unpopular species appear to have regions of baldness, such as their tail. This variable was intended to assess whether these bald patches had an effect on peoples' attitudes.*	None Some Extreme	Scored by 11 separate respondents prior to survey.

However, when Akaike weights indicate there is no single best model, this was taken as an indication of uncertainty in model selection. Model averaging was used as a method of

multi-model inference to calculate relative variable importance values from model combinations within 2 AIC_C units of the highest ranked model(Burnham and Anderson 2002) and to provide model averaged parameter estimates of the strength of the relationship between each explanatory variable and the response.

Data collected from respondents in five countries in five continents (Australia, India, South Africa, UK, USA) were analysed collectively (all regions) and then separate full models were tested for each country's respondents in turn.

Many factors have the potential to influence peoples' perceptions of different species in addition to their physical attributes. For instance cultural biases may lead a species to be valued far more, or far less than we might expect from the physical characteristics alone. In order to gain an insight into these wider influences, we compared the predicted charisma scores for each species (calculated from the model averaged parameter estimates) with the actual preference scores from the survey to identify those species with the greatest residuals.

Results

When analysed across all regions, six of the ten top ranking species were members of the Felidae (with the jaguar (*Panthera onca*), black leopard (*P. pardus*) and puma (*Puma concolor*) coming in at 11th,13th and 18th respectively). Furthermore, while the intervals between the species preference scores for those ranked second to tenth ranged from 0.002 to 0.095, the first ranked species, the tiger, had a margin of 0.227 over the second choice (see Table 3). The two lowest ranked mammals were both commensal rodents;

the house mouse and the brown rat (*Rattus norvegicus*). The bottom ten animals also included various mammal morphs, including the striped skunk (*Mephitis mephitis*) and the star-nosed mole (*Condylura cristata*). Interestingly, there were three flying species in the list of ten lowest ranked mammals, two bats and the Malayan colugo, (appendix B). Exploring its extraordinary pre-eminence, the tiger was seen by respondents a total of 774 times, of which it received a negative preference score (-1 or -2) 94 times against 61 different mammal images. When compared against the tiger, the Iberian lynx and the leopard performed best, each beating the tiger in four instances. The tiger received a score of -2 (i.e. the other mammal was 'preferred completely') a total of 31 times, beaten by 30 different images. Only the jaguar was completely preferred to the tiger more than once. Summing the scores received by each species when presented against the tiger, the leopard had the highest preference score (5) and the bilby (*Macrotis lagotis*), Iberian lynx, jaguar, Lar gibbon (*Hylobates lar*) and the northern hairy-nosed wombat (*Lasiorhinus krefftii*) were all tied in second place with a preference score of 4.

Regional variation in preference scores

Although the tiger was the most favoured species in all five regions, and the African elephant was ranked second in three of the five, there were intercontinental differences in the rankings (Table 3). There were no statistically significant differences between nations in the actual preference scores (Friedman chi-squared = 0.44, df = 4, p= 0.9791) or ranked preferences (Friedman chi-squared = 0.5782, df = 4, p= 0.9655), but there were interesting anomalies amongst them.

Table 3. The ten top ranked mammal species for each region and across all regions.
A full list of species and their scores is provided in appendix B.

Rank	**Australia** (n = 303)			**India** (n =310)			**South Africa** (n = 311)			**UK** (n = 305)			**USA** (n = 307)			**All Regions** (n = 1536)		
	Species	All Regions Rank	Average score	Species	All Regions Rank	Average score	Species	All Regions Rank	Average score	Species	All Regions Rank	Average score	Species	All Regions Rank	Average score	Species	All Regions Rank	Average score
1	tiger	1	1.020	tiger	1	1.135	tiger	1	1.199	tiger	1	1.318	tiger	1	0.932	tiger	1	1.124
2	northern hairy-nosed wombat	16	0.993	lion	3	0.854	African elephant	2	1.072	African elephant	2	1.035	African elephant	2	0.881	African elephant	2	0.897
3	Bornean orang-utan	10	0.952	cheetah	4	0.819	jaguar	12	0.982	Iberian lynx	9	0.850	Grevy's zebra	8	0.845	lion	3	0.802
4	western gorilla	5	0.922	African elephant	2	0.733	cheetah	4	0.972	leopard	6	0.842	clouded leopard	7	0.830	cheetah	4	0.782
5	echidna	31	0.804	wild Bactrian camel	21	0.673	Sumatran rhinoceros	14	0.967	lion	3	0.833	cheetah	4	0.819	western gorilla	5	0.733
6	African elephant	2	0.779	red panda	11	0.657	lion	3	0.933	western gorilla	5	0.818	Iberian lynx	9	0.771	leopard	6	0.720
7	red shanked douc	17	0.648	Bornean orang-utan	10	0.600	leopard	6	0.894	cheetah	4	0.778	lion	3	0.765	clouded leopard	7	0.718
8	koala	22	0.646	jaguar	12	0.553	clouded leopard	7	0.882	clouded leopard	7	0.770	leopard	6	0.659	Grevy's zebra	8	0.684
9	red panda	11	0.639	leopard	6	0.553	Grevy's zebra	8	0.809	red panda	11	0.727	red wolf	15	0.659	Iberian Lynx	9	0.680
10	leopard	6	0.638	clouded leopard	7	0.543	western gorilla	5	0.790	black leopard	13	0.709	western gorilla	5	0.638	Bornean orang-utan	10	0.644

The ranking in Australia was markedly different to all others, with a notable preference for their native species. Aside from the unshakable pre-eminence of the tiger, Australians ranked the northern hairy-nosed wombat at the top of their list (15 places higher than its overall ranking). Indeed, the largest departure from the overall ranking for any species was the Australian respondents' ranking of the echidna (*Zaglossus attenboroughi*; an endemic of Australia and New Guinea) that they ranked 26 places above its overall rank. Australians, uniquely, ranked the red-shanked douc langur (*Pygathrix nemaeus*) in their top ten (this, along with their third choice, the orang-utan (*Pongo pygmaeus*), is a South East Asian species), and they, together with the Indian respondents, also ranked the red panda (*Ailurus fulgens*) highly. Indians, uniquely, ranked the Bactrian camel (*Camelus ferus*) very highly, at fifth place, while South Africans that ranked the South American jaguar most highly, and indeed more highly than their local analogue, the leopard. South Africans, uniquely, included the Sumatran rhino (*Dicerorhinus sumatrensis*) in their top ten, at fifth place. The UK was the most felid-oriented sub-population, with seven species in their top 10, and the only country to place the Iberian lynx in its top three. Americans ranked clouded leopards (*Neofelis nebulosa*) more highly (fourth) than did any other sub-population, and ranked the Grevy's zebra more highly (third) than did any other group (in its native South Africa it was ranked ninth).

Preferences for attributes

We used an information-theoretic approach to compare models that related the various attributes to the average preference scores each mammal. When analysed across all regions, 17 models fell within $2AIC_c$ of the top model. These models included 11 out of our 15 attributes, with baldness, human threat, IUCN status and body size featuring in 100% of the top models, while eye position was also important with a relative variable

importance of 0.86 (table 4). The top model for all regions included the variables Baldness + Body size + Colour + Eye position + Facial marking + Human threat + IUCN, however its low Akaike weight (ω_i = 0.1) indicates that this model was not greatly superior to the other top models (table 5). The evidence ratio indicates the top model was only 1.11 times better than the next highest ranked model, which does not include the terms for colouration or facial markings, but does include the variables ED score and diet. In addition, the top model was a less effective predictor of respondent preferences than the full model (Top model $\bar{R}^2$= 0.643, full model adjusted $\bar{R}^2$= 0.805). Across all regions respondents seemed to prefer species that had no baldness, that were in the largest size class, that were a single bright colour, had forward facing eyes, prominent facial markings, were potentially a threat to humans and were critically endangered. Species that had extensive baldness, were in the smallest size class, were black and white in colour, had lateral facing eyes, no facial markings, were not a human threat and were of least concern were the least favourable (full model averaged parameter estimates see appendix C).

When analysing each region separately, 4 models fell within $2AIC_c$ of the top model in Australia. The top models included 6 out of our 15 attributes with baldness, human threat, IUCN status and body size featuring in all of the top models. The top model for Australia included the variables baldness + body size + eye position + human threat + IUCN, and was reasonably well supported compared to the other top models with an Akaike weight of 0.36. The evidence ratio shows the top model was 1.5 times better at explaining the variation in the Australian participants' response scores than the next highest ranked model, which included ED score instead of eye position.

Table 4. The relative variable importance for each attribute in each region, and across all regions.

Attribute	Australia	India	South Africa	UK	USA	All Regions
Baldness	1	1	0.35	0.68	1	1
Body size	1	1	1	1	1	1
Human Threat	1	0.88	1	1	-	1
IUCN status	1	1	1	1	1	1
Eye position	0.58	0.88	-	1	1	0.86
Facial markings	-	0.41	1	0.49	-	0.47
ED score	0.46	0.77	-	0.2	1	0.47
Diet	-	-	-	0.09	1	0.29
Striking appearance	-	0.35	0.21	0.15	0.27	0.28
Photo quality	-	-	-	0.38	0.2	0.09
Activity pattern	-	1	-	-	-	0.04
Colour	-	1	1	-	-	-
Armour	-	-	-	-	-	-
Body markings	-	-	-	-	-	-
Fluffiness	-	-	-	-	-	-

The $\bar{R}^2$ values for Australia were comparatively low, however they still showed reasonably good predictive power for both the top model and the full model (Top model $\bar{R}^2$= 0.691, full model adjusted $\bar{R}^2$= 0.693. Australian respondents seemed to prefer species that had no baldness, forward facing eyes, were a potential threat to humans, were critically endangered, in the largest size class and had a high evolutionary distinctiveness. Species that had extensive baldness, lateral facing eyes, were not a potential threat to humans, were of least concern for conservation, weighed between 20 and 40kg and had an intermediate evolutionary distinctiveness were the least favourable.

Table 5. List of the strongest models produced by the model averaging analysis. Only models within 2 ΔAIC_C of the top model are presented.

Model rank	Variables in model	AIC_C	ΔAIC_C	ω_i	Evidence Ratio
Australia					
1	Baldness + Body Size + Eye position + Human threat + IUCN	47.64	0.00	0.36	1.00
2	Baldness + Body size + ED score + Human threat + IUCN	48.49	0.85	0.24	1.50
3	Baldness + Body size + ED score + Eye position + Human threat + IUCN	48.62	0.98	0.22	1.64
4	Baldness + Body size + Human threat + IUCN	49.00	1.36	0.18	2.00
India					
1	Activity pattern + Baldness + Body size + Colour + ED score + Eye position + Human threat + IUCN	-13.48	0.00	0.24	1.00
2	Activity pattern + Baldness + Body size + Colour + ED score + Eye position + Facial marking + Human threat + IUCN	-12.82	0.66	0.17	1.41
3	Activity pattern + Baldness + Body size + Colour + ED score + Eye position + Human threat + IUCN + Striking	-12.16	1.32	0.12	2.00
4	Activity pattern + Baldness + Body size + Colour + ED score + Facial marking + Human threat + IUCN	-12.16	1.32	0.12	2.00
5	Activity pattern + Baldness + Body size + Colour + ED score + Eye position + IUCN	-12.12	1.36	0.12	2.00
6	Activity pattern + Baldness + Body size + Colour + Eye position + Facial marking + Human threat + IUCN + Striking	-12.09	1.39	0.12	2.00
7	Activity pattern + Baldness + Body size + Colour + Eye position + Human threat + IUCN + Striking	-11.87	1.61	0.11	2.18
South Africa					
1	Body size + Colour + Facial marking + Human threat + IUCN	29.93	0.00	0.44	1.00
2	Baldness + Body size + Colour + Facial marking + Human threat + IUCN	30.36	0.43	0.35	1.26
3	Body size + Colour + Facial marking + Human threat + IUCN + Striking	31.45	1.52	0.21	2.10
UK					
1	Baldness + Body size + Eye position + Facial marking + Human threat + IUCN	42.71	0.00	0.12	1.00
2	Baldness + Body size + Eye position + Human threat + IUCN	42.86	1.00	0.11	1.09
3	Body size + Eye position + Facial marking + Human threat + IUCN + Photo quality	43.37	1.02	0.08	1.50
4	Body size + Eye position + Facial marking + Human threat + IUCN	43.39	1.02	0.08	1.50
5	Baldness + Body size + ED score + Eye position + Human threat + IUCN + Photo quality	43.43	1.02	0.08	1.50
6	Baldness + Body size + ED score + Eye position + Human threat + IUCN	43.67	1.02	0.07	1.71
7	Baldness + Body size + Eye position + Human threat + IUCN + Photo quality	43.75	1.02	0.07	1.71
8	Body size + Eye position + Facial marking + Human threat + IUCN + Striking	43.78	1.03	0.07	1.71
9	Baldness + Body size + Eye position + Facial marking + Human threat + IUCN + Photo quality	44.07	1.03	0.06	2.00

10	Body size + ED score + Eye position + Human threat + IUCN + Photo quality	44.49	1.04	0.05	2.40
11	Baldness + Body size + Diet + Eye position + Human threat + IUCN	44.55	1.04	0.05	2.40
12	Baldness + Body size + Diet + Eye position + Facial marking + Human threat + IUCN	44.66	1.05	0.04	3.00
13	Body size + Eye position + Human threat + IUCN + Photo quality	44.69	1.05	0.04	3.00
14	Baldness + Body size + Eye position + Human threat + IUCN + Striking	44.70	1.05	0.04	3.00
15	Baldness + Body size + Eye position + Facial marking + Human threat + IUCN + Striking	44.71	1.05	0.04	3.00
USA					
1	Baldness + Body size + Diet + ED score + Eye position + IUCN	38.11	0.00	0.53	1.00
2	Baldness + Body size + Diet + ED score + Eye position + IUCN + Striking	39.44	1.03	0.27	1.96
3	Baldness + Body size + Diet + ED score + Eye position + IUCN + Photo quality	40.01	1.05	0.20	2.65
All Regions					
1	Baldness + Body size + Colour + Eye position + Facial marking + Human threat + IUCN	3.29	0.00	0.10	1.00
2	Baldness + Body size + Diet + ED score + Eye position + Human threat + IUCN	3.48	1.06	0.09	1.11
3	Baldness + Body size + Colour + Facial marking + Human threat + IUCN	3.79	1.15	0.08	1.25
4	Baldness + Body size + Colour + Eye position + Facial marking + Human threat + IUCN + Striking	3.95	1.20	0.07	1.43
5	Baldness + Body size + Colour + Eye position + Human threat + IUCN + Striking	4.06	1.23	0.07	1.43
6	Baldness + Body size + Colour + ED score + Eye position + Human threat + IUCN	4.18	1.27	0.07	1.43
7	Baldness + Body size + Colour + Diet + Eye position + Facial marking + Human threat + IUCN	4.40	1.34	0.06	1.67
8	Baldness + Body size + Colour + Facial marking + Human threat + IUCN + Striking	4.46	1.36	0.06	1.67
9	Baldness + Body size + Colour + Diet + ED score + Eye position + Facial marking + Human threat + IUCN	4.50	1.37	0.06	1.67
10	Baldness + Body size + ED score + Eye position + Human threat + IUCN + Photo quality	4.62	1.40	0.05	2.00
11	Baldness + Body size + Colour + Eye position + Human threat + IUCN	4.86	1.48	0.05	2.00
12	Activity pattern + Baldness + Body size + Colour + Eye position + Human threat + IUCN + Striking	5.09	1.55	0.04	2.50
13	Baldness + Body size + Diet + ED score + Eye position + Human threat + IUCN + Photo quality	5.11	1.55	0.04	2.50
14	Baldness + Body size + Colour + Diet + ED score + Eye position + Human threat + IUCN	5.12	1.56	0.04	2.50
15	Baldness + Body size + Colour + ED score + Eye position + Human threat + IUCN + Striking	5.24	1.59	0.04	2.50
16	Baldness + Body size + ED score + Eye position + Human threat + IUCN	5.27	1.60	0.04	2.50
17	Baldness + Body size + Colour + ED score + Eye position + Facial marking + Human threat + IUCN	5.28	1.60	0.04	2.50

For India, 7 models fell within $2AIC_c$ of the top model and included 10 attributes, of which the most important appeared to be activity pattern, baldness, body size, colour and IUCN status, although both eye position and Human threat also had a high relative variable importance. The top model for India included the variables activity pattern + baldness + body size + colour + ED score + eye position + human threat + IUCN and was relatively well supported with an Akaike weight of 0.24 and having 1.4 times the support than the second highest ranked model, which included the facial markings variable, as well as all those in the top model. Both the full model and the top model performed well, and the difference between the $\bar{R}^2$for the two models was small (Top model $\bar{R}^2$= 0.764, full model adjusted $\bar{R}^2$= 0.801). Indian respondents seemed to prefer species that had a nocturnal/crepuscular activity pattern, no baldness, that were a single bright colour, that were not evolutionarily distinct, had forward facing eyes, were a human threat, were critically endangered, in the largest size class, had prominent facial markings and were not 'striking' in appearance. Species that had some partial baldness, were in the smallest size class, were least concern, were crepuscular and had a black and white body were the least favoured.

For South Africa, 3 models fell within $2AIC_c$ of the top model and included 7 attributes, of which the most important appeared to be body size, colour, facial markings, human threat and IUCN status. The top model for South Africa included the variables body size + colour + facial marking + human threat + IUCN status and was relatively well supported with an Akaike weight of 0.44, although the top model was only 1.26 times better supported than the second highest model, which had an Akaike weight of 0.35 and included the term for baldness in addition to the variables in the top model. Both the full model and the top model performed well, and the difference between the $\bar{R}^2$for the two

models was small (Top model $\bar{R}^2$= 0.775, full model adjusted $\bar{R}^2$= 0.820). South African respondents seemed to prefer species that were a single bright colour, had prominent facial markings, were a potential human threat, were critically endangered, in the largest size class, had no baldness, and did not have a 'striking' appearance. Species in the smallest size class, that were not a human threat, were of least conservation concern, had no facial markings and had a black and white body were the least favoured.

For the UK, 15 models fell within $2AIC_c$ of the top model and included 10 attributes, of which the most important appeared to be body size, eye position, human threat and IUCN status. The top model for the UK included the variables baldness + body size + eye position + facial marking + human threat + IUCN but had a low Akaike weight of 0.12 suggesting that the top model did not greatly out perform other candidate models. Indeed, the evidence ratio revealed that the second ranked model was almost equally supported by the data (evidence ratio = 1.09). The second highest model differed from the top model only in the omission of the facial marking variable. The $\bar{R}^2$ values for the UK were comparatively low, however still showed reasonably good predictive power for both the top model and the full model (Top model $\bar{R}^2$= 0.661, full model adjusted $\bar{R}^2$= 0.692). UK respondents seemed to prefer species that had no baldness, forward facing eyes, prominent facial markings, were a potential threat to humans, were critically endangered, were in the largest size class, had excellent photo quality, were not evolutionarily distinct, did not have a 'striking' appearance, and that were herbivorous. Species weighing between 20 and 40kg, that were not a human threat, were of least conservation concern and had lateral facing eyes were the least favoured.

Finally, 3 models were retained within $2AIC_c$ of the top model for the USA and included 8 attributes, of which the most important were baldness, body size, diet, ED score, eye position and IUCN status. The top model for the USA included the variables baldness + body size + diet + ED score + eye position + IUCN and was well supported with an Akaike weight of 0.53. The top model was almost twice as well supported as the second highest ranked model, which differed by the addition of the term of striking appearance. The difference between the $\bar{R}^2$for the top model and the full model was small (Top model $\bar{R}^2$= 0.686, full model adjusted $\bar{R}^2$= 0.710). Americans seemed to prefer species that had no baldness, were carnivorous, were not evolutionarily distinct, had forward facing eyes, were critically endangered, were in the largest size class, were not striking in appearance and had excellent quality photos. Species with extensively bald, in the smallest size class, of least conservation concern, with laterally positioned eyes, intermediate evolutionary distinctiveness and a carnivorous/scavenging diet were the least favoured.

Baldness, body size, human threat, IUCN status and eye position were included in a high proportion of top models for each country individually as well as for all regions and so can be considered to have the most influence on peoples attitudes. Armour, fluffiness and body markings did not feature in any of the top models and so appear to have very little effect on peoples' preferences.

Importantly photo quality was not retained in any of the top models for Australia, India and South Africa, and had consistently low relative variable importance in the regions where it was retained. This suggests that our attempts to standardise the photos used in the survey were successful and that photo quality did not exert an excessive influence on

peoples' preferences. Finally, although our models contained a large number of predictor variables, the low standard errors relative to parameter estimates show that the models were not overparameterised (appendix C).

The effects of affinity and familiarity

Across all regions, the correlation between the observed respondent rank and affinity is high ($t_{2, 98}$ = 15.535, p <0.001, r = 0.843), and indeed one might expect these two rankings to be very similar insofar as the question we posed to generate the respondent rankings was "how strong is your personal preference for conservation" of the particular species being contrasted, whereas for affinity we asked them to distinguish on a 5 point scale from "I like it a lot" to "I don't like it at all". Although the two judgments are closely linked they are clearly different: the common squirrel monkey (*Saimiri sciureus*), for example, came joint 19th on the affinity scale, but only 50th on the respondent ranking and the giraffe (*Giraffa camelopardalis*) came third in affinity, but only 20th in the respondent rank, whereas both the clouded leopard and the Iberian lynx were liked rather less than they were ranked by respondents.

Respondent rank was also significantly correlated to familiarity ($t_{2, 98}$ = 4.359, p <0.001, r = 0.403), although less strongly than to affinity. The red panda, for instance, is not very familiar to respondents yet they ranked it highly, whereas the red kangaroo (*Macropus rufus*) is very familiar but not ranked highly. Familiarity and affinity were also significantly and positively correlated, although again the strength of the correlation is much less than that between affinity and respondent rank ($t_{2, 98}$ = 6.449, p <0.001, r = 0.546). However, there is a big discrepancy between the familiarity and affinity for some species, such as

the red panda; respondents were not very familiar with this species, but liked it a great deal. The same applied markedly to the somewhat unfamiliar, but greatly liked clouded leopard and Iberian lynx.

Over and under performers

Across all regions, the koala, African elephant and red kangaroo were the top 'over performers' when comparing the results of the paired test than to the predicted charisma based on their physical attributes alone, while the African wild dog, aye-aye and African buffalo were the worst performers (table 6). This raises fascinating questions about the drivers of charisma that were not encapsulated by our attributes. For instance, Australians seemed to display a strong preference for native Australian species with the koala, parma wallaby and red kangaroo all performing far better than expected, while invasive species such as the red fox did far worse than expected. In contrast the red fox did far better than expected in both the USA and South Africa.

Table 6. Top 10 over and under performers for each region and all regions combined. Residuals are calculated from the difference between the predicted charisma score (calculated from the model averaged parameter estimates) and the actual survey response scores.

	Australia		India		South Africa		UK		USA		All Countries	
	Species	Residuals	Species	Residuals	Species	Residuals	Species	Residuals	Species	Residuals	Species	Residuals
1	Koala	0.85	Parma wallaby	0.4	Koala	0.82	European hedgehog	0.62	Red fox	0.47	Koala	0.54
2	Parma wallaby	0.52	Reeves's muntjac	0.36	Dik-dik	0.57	African elephant	0.51	African elephant	0.47	African elephant	0.41
3	Red kangeroo	0.48	Red panda	0.33	Red fox	0.38	Koala	0.51	Eurasian beaver	0.47	Red kangeroo	0.39
4	Caracal	0.4	African elephant	0.32	Grevys zebra	0.38	Parma wallaby	0.48	Koala	0.45	Parma wallaby	0.36
5	Common squirrel monkey	0.38	Koala	0.29	African elephant	0.32	Reindeer	0.45	Black-tailed jackrabbit	0.43	Grevys zebra	0.3
6	African elephant	0.37	Wild Bactrian camel	0.29	Common ringtail possum	0.29	Clouded leopard	0.4	Numbat	0.42	Dik-dik	0.28
7	Indian giant squirrel	0.33	Black-tailed jackrabbit	0.22	Clouded leopard	0.28	Eurasian beaver	0.31	Golden lion tamarin	0.36	Numbat	0.27
8	Clouded leopard	0.33	Sunda pangolin	0.2	Caracal	0.27	Dik-dik	0.31	Clouded leopard	0.34	Reindeer	0.27
9	Bornean orang-utan	0.32	Yellow mongoose	0.2	Patagonian mara	0.26	Bornean orang-utan	0.29	Red kangeroo	0.33	Eurasian beaver	0.21
10	Western gorilla	0.3	Tiger	0.19	Numbat	0.25	Red panda	0.29	Puma	0.32	Clouded leopard	0.2
91	Red fox	-0.37	East African oryx	-0.21	Brown rat	-0.3	Striped skunk	-0.33	African buffalo	-0.3	Sumatran rhinoceros	-0.26
92	Wild Bactrian camel	-0.37	Warthog	-0.24	Raccoon	-0.3	Raccoon	-0.34	Echidna	-0.32	Brown rat	-0.26
93	Raccoon	-0.39	North American river otter	-0.25	African buffalo	-0.35	Bilby	-0.35	Striped skunk	-0.32	Raccoon	-0.27
94	Fossa	-0.44	Aardvark	-0.26	Spotted hyena	-0.35	Sumatran rhinoceros	-0.36	Fossa	-0.32	Striped skunk	-0.27
95	Brown rat	-0.44	African wild dog	-0.27	European badger	-0.36	Malayan colugo	-0.43	Malayan tapir	-0.36	Malayan colugo	-0.33
96	Striped skunk	-0.46	Malayan tapir	-0.28	House mouse	-0.39	African wild dog	-0.43	Capybara	-0.38	Spotted hyena	-0.34
97	Aye-aye	-0.47	Maned sloth	-0.28	Mandrill	-0.42	Fossa	-0.45	African wild dog	-0.38	Fossa	-0.35
98	House mouse	-0.52	Aye-aye	-0.31	Striped skunk	-0.43	African buffalo	-0.45	Diademed sifaka	-0.41	African buffalo	-0.35
99	Warthog	-0.54	African buffalo	-0.32	Bilby	-0.43	Brown rat	-0.49	Asian palm civet	-0.42	Aye-aye	-0.36
100	Spotted hyena	-0.67	Bilby	-0.37	Malayan colugo	-0.52	Spotted hyena	-0.5	Common brushtail possum	-0.52	African wild dog	-0.37

Discussion

This study provides novel, valuable insights not only into which species people prefer for conservation, but also which attributes appear to influence those preferences. Cats – particularly large ones - appeared to have marked and striking appeal within our sample, with the tiger ranked as the most preferred species by a wide margin. Although the African elephant was ranked second overall, and 69 mammalian families were represented, six of the top ten selected species were from a single family, the Felidae. Following the tiger, these were the lion (3rd), cheetah (4th), leopard (6th), clouded leopard (7th) and Iberian lynx (9th). Furthermore, of the remaining four felids in the sample, all ranked highly, the jaguar 12th, black leopard 13th, puma 18th and caracal 39th. The appeal of felids to this sample of the public, in a conservation context, is overwhelming.

Despite our intention to focus our interest on the attitudes of a wide sample of society, the differences between each country taken individually, as well as compared to all regions combined illustrates how attitudes vary across the different societies. In particular, it is more than likely that close proximity and the conflict that this often generates will have a profound impact on the attitudes of the people who have to live alongside large carnivores (Douglas & Veríssimo 2013; Linnell et al. 2000). However, our sample is an interesting one because within each country it represents the perceptions of a computer literate middle class that increasingly dominates many societies and which, in particular, is likely to have opinions and a voice in societal choices about conservation. We will report on the sociological profile of these 1536 people elsewhere but suffice it to say that many reported that they were interested in nature, watched nature documentaries on TV and were members of environmental NGOs. In practice,

conservation action is the result of policy formulated through a political process, and the perceptions we report are those of a class whose members are a vital constituent of that political process.

Each image was tagged with a visual scale of conservation concern based on five levels of the IUCN Red List scores. This attribute proved to be of key importance occurring in all top models for each country as well as in all regions combined. In almost all cases respondents predictably preferred rarer species compared to species of lesser conservation concern, the only partial exception was the USA whose respondents showed the same general pattern as in other regions except for ranking vulnerable species fractionally above endangered species. Although we expected the choices to be made by respondents largely on the basis of the appearance of the species, by providing the IUCN score that became an element of the image, and clearly increasing rarity positively influenced preference for a mammal being selected. In a future experiment it would be revealing to compare ranks of the same species when the precariousness of its status was, or was not, disclosed.

In addition to IUCN status, body size was the only other variable to command such widespread influence, also occurring in all top models in all cases. Respondents unanimously had the strongest preference for species in the largest size class (>800kg) and most regions broadly ascribed to the notion that 'bigger is better' although there was also often a slight preference for small species left those species in the middle ground (20-40kg) as the least popular. Australia however bucked this trend, and although they

still had a strong preference for species in the largest size class, it was difficult to discern a clear pattern in their preferences towards the remaining size classes (appendix C).

Of the remaining attributes, several others appeared to have wide, if not universal appeal. For instance, in all areas apart from the USA, our respondents were strongly influenced by the attribute of human threat, with a preference for species that might potentially be threatening. Similarly baldness was an important attribute in all cases except South Africa, with respondents routinely preferring species that had no bald areas to species with either some or extensive baldness. The least important variables were armour, body markings and fluffiness, none of which featured in any of the top models for any country. The remaining attributes explained some, but not much, of the variation in charisma scores. Importantly, photo quality did not have an excessive influence on peoples' decisions.

In general, our models are able to predict the preferences of respondents with surprising effectiveness. Examining the data from all regions together yielded models with weaker predictive power than when analysing the data separately for each country, however, the $\bar{R}^2$ values for all regions remain high. This simultaneously highlights the fact that while there may be some commonalities in peoples' preferences across regions, it also supports studies that show important differences between disparate groups of stakeholders (Bowen-Jones & Entwistle 2002).

The similarities, and differences, amongst the five sub-populations of respondents raise intriguing puzzles. Why, for example, did the Indian survey respondents rank Parma

wallabies so highly? Similarly, why did South Africans rank jaguars higher than did any other nation, perhaps confusing it, or eliding it, with native leopards? And why did they so favour Sumatran rhinoceros (perhaps in resonance with the much publicized catastrophic poaching of Black and White Rhinos currently rampant in their region). As a generalisation, the tendency of Australians to rank highly endemics of Australia and South East Asia, but their distaste of the invasive red fox (*Vulpes vulpes*; ranked 90th in Australia Vs 48th across all regions) revealed a parochialism/localism not so conspicuously apparent in the other four sub-populations. However, the European badger (*Meles meles*) was ranked (lowly) with remarkable consistency in Australia (81st), South Africa (85th) and the USA (82nd), but much higher (57th) in the UK where it features in children's stories and is the emblem of a major conservation NGO. In this study we identified a range of attributes that we thought would be important drivers of peoples preferences, and the high $\bar{R}^2$ values achieved by our models is encouraging, however improving our understanding the cultural cues that lead to these differences may be useful to conservation organisations working in these areas and is an area of future research.

The mismatches between the observed and predicted rankings go to the heart of evaluating charisma and presumably are largely explained by the blight or boon of reputation. It may be unsurprising that the koala, or the African elephant performed better in the survey results than would have been predicted from their attributes – both are already popular icons and frequently portrayed favourably in both the fiction and news media. Similarly, the spotted hyena has an almost universally bad reputation and emerged as one of the worst performers across most regions. Understanding the cultural drivers of these over and under performers could be extremely valuable to conservation

organisations in their marketing campaigns. Another fascinating example is the red fox which performed extraordinarily badly in Australia where it is invasive, despite appearing to perform above expectation in most other regions. Perhaps the European hedgehog's success in the UK is a legacy of Beatrix Potter's Mrs Tiggy Winkle? Indeed this success is confirmed by the fact that the European hedgehog was recently voted BBC Wildlife Magazine's national icon (Hoare 2013).

A species' charisma is likely to influence greatly its capacity to engender public support or as a conservation icon, and for terrestrial mammals this influential capacity can be predicted with fair accuracy from a small set of attributes. However, there is extraordinary taxonomic inequality in the preferences of our respondents which reveals an almost complete pre-eminence of the big cats. While the popularity of these animals has always been obvious, the extent to which they are revealed to hold a wide subset of the public in their thrall emphasises their unequalled potential as ambassadors for conservation. Indeed, the big cats as a group scored so highly that we might think of them as one, *Felis felicis*, a globally powerful emblem and flagship for conservation. Our findings also identify species ripe for promotion to iconic roles. Amongst the felids, for example, while the clouded leopard was, unsurprisingly, not familiar to our respondents, they liked it greatly, and ranked it very highly in terms of their preferences. The link between familiarity and affinity suggests that public awareness campaigns might be an effective way of improving peoples' attitudes towards currently underrated species.

This preliminary exploration of the attributes that appear to drive peoples' preferences for terrestrial mammals raises questions with respect to both the species and the people

judging them. In the light of this triumph of the felids, what explains the variation in their charisma within the family? Indeed, since both families are seemingly attractive, agile, intelligent, adaptable predators (with forward facing eyes), why do the cats appear so much more charismatic than the dogs? To what extent, and how most effectively, can a species' appeal to relevant sections of the public be improved and utilised? And what aspects of the public's circumstances, experience and sociology affect the perceptions that shaped their choices? For example, the favourites of Australians differed markedly from those of the other respondents, with a possible tendency to localism – what are the consequences for conservation in that region? Finally, several studies (Hazzah et al. Under review; Veríssimo 2013; Zimmermann et al. 2014) have highlighted the importance of the disconnect between peoples' attitudes and their actions, and so understanding how conservation NGOs can best utilise the results presented here will be of critical importance. The answers to all these questions have the potential to be assembled into an ever-more holistic approach to conservation marketing. While we discovered that a suite of 15 attributes can reliably predict mammalian charisma within our sample, we hope that further exploration of these traits will allow us to identify a subset of readily available criteria that can be used to predict charisma beyond the 100 mammals in this analysis. This lays the groundwork for a powerful tool for quantifying and understanding mammalian charisma, and determining which species are really likely to be effective flagships for conservation.

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Appendix A

Examples of slides used during the online survey (Figs 1 and 2). The slides shown here did not form part of the actual survey but were used to illustrate the instructions given to each respondent prior to beginning the survey.

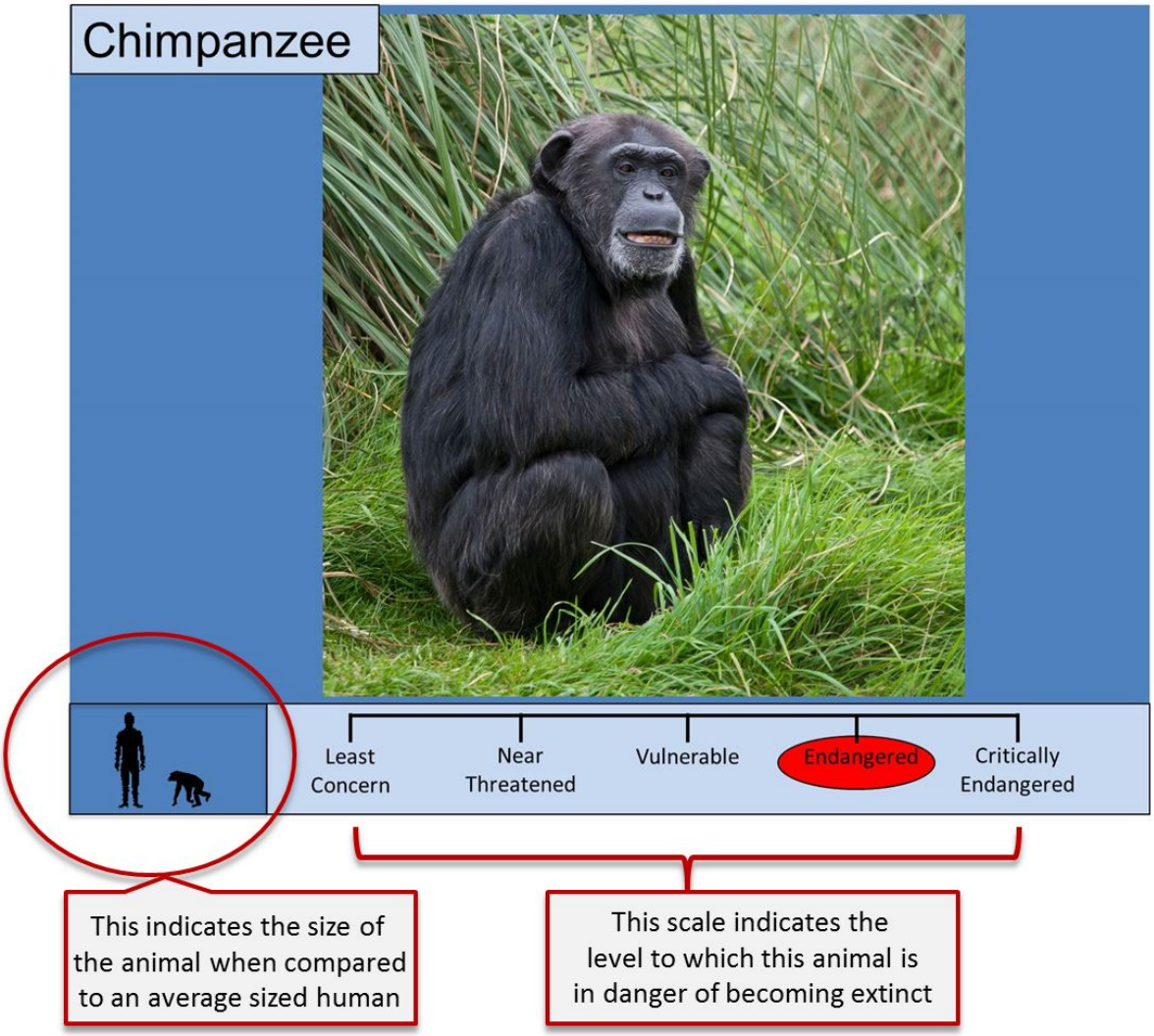

Figure 1. An example image, and associated information, of which 25 were displayed individually to each respondent in the survey of familiarity and affinity (see text), and 25 pairs (50 images) in the pairwise conjoint analysis.

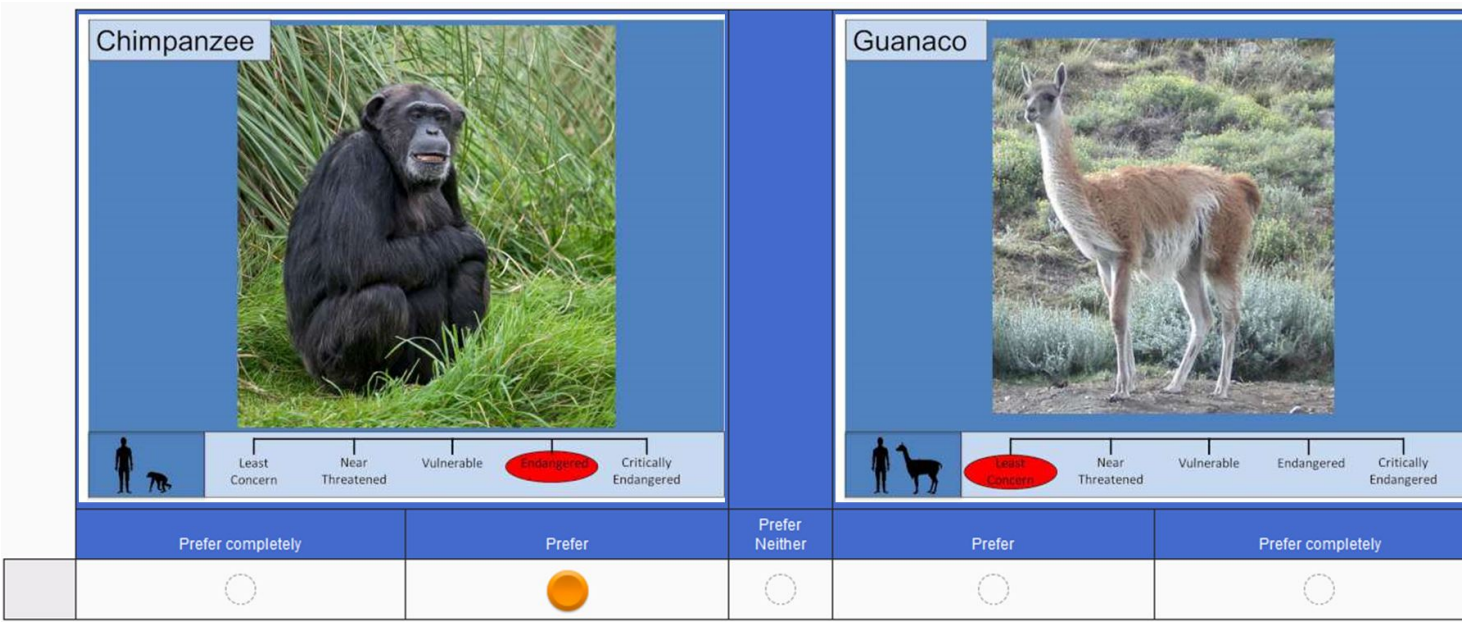

Figure 2. An example of the 25 choices presented to each respondent. The explanation, and question, presented to each respondent was: “We are exploring priorities for conservation and we are hoping you can help us discover which species appeal more to people. We are going to show you a number of pairs of animals and ask you, for each pair, how strong your personal preference is”. In this case the respondent preferred, although not completely, the chimpanzee over the guanaco.

Appendix B

Full results of the paired preference test for each country, and for all regions.

	Australia		India		South Africa		UK		USA		All regions	
Rank	**Species Binomial**	**Average score**	**Species**	**Average score**	**Species**	**Average score**	**Species**	**Average score**	**Species**	**Average score**	**Species**	**Average score**
1	Tiger *Panthera tigris*	1.02	Tiger	1.135	Tiger	1.199	Tiger	1.318	Tiger	0.932	Tiger	1.124
2	Northern hairy-nosed wombat *Lasiorhinus krefftii*	0.993	Lion	0.854	African elephant	1.072	African elephant	1.035	African elephant	0.881	African elephant	0.897
3	Bornean orang-utan *Pongo pygmaeus*	0.952	Cheetah	0.819	Jaguar	0.982	Iberian lynx	0.85	Grevys zebra	0.845	Lion	0.802
4	Western gorilla *Gorilla gorilla*	0.922	African elephant	0.733	Cheetah	0.972	Leopard	0.842	Clouded leopard	0.83	Cheetah	0.782
5	Echidna *Zaglossus attenboroughi*	0.804	Wild Bactrian camel	0.673	Sumatran rhinoceros	0.967	Lion	0.833	Cheetah	0.819	Western gorilla	0.733
6	African elephant *Loxodonta africana*	0.779	Red panda	0.657	Lion	0.933	Western gorilla	0.818	Iberian lynx	0.771	Leopard	0.72
7	Red-shanked douc *Pygathrix nemaeus*	0.648	Bornean orang-utan	0.6	Leopard	0.894	Cheetah	0.778	Lion	0.765	Clouded leopard	0.718
8	Koala *Phascolarctos cinereus*	0.646	Jaguar	0.553	Clouded leopard	0.882	Clouded leopard	0.77	Leopard	0.659	Grevys zebra	0.684
9	Red panda *Ailurus fulgens*	0.639	Leopard	0.553	Grevys zebra	0.809	Red panda	0.727	Red wolf	0.659	Iberian lynx	0.68
10	Leopard *Panthera pardus*	0.638	Clouded leopard	0.543	Western gorilla	0.79	Black leopard	0.709	Western gorilla	0.638	Bornean orang-utan	0.644
11	Grevys zebra *Equus grevyi*	0.614	Grevys zebra	0.533	Black leopard	0.727	Bornean orang-utan	0.673	Black leopard	0.636	Red panda	0.639
12	Lion *Panthera leo*	0.612	Iberian lynx	0.494	Iberian lynx	0.682	Northern hairy-nosed wombat	0.659	Puma	0.632	Jaguar	0.622
13	Tasmanian devil *Sarcophilus harrisii*	0.61	Western gorilla	0.479	Red wolf	0.676	Grevys zebra	0.586	Jaguar	0.56	Black leopard	0.606
14	Iberian lynx *Lynx pardinus*	0.609	Golden lion tamarin	0.416	Bornean orang-utan	0.662	Red wolf	0.532	Wild Bactrian camel	0.551	Sumatran rhinoceros	0.55
15	Clouded leopard *Neofelis nebulosa*	0.607	Black leopard	0.373	Giraffe	0.643	Jaguar	0.531	Red panda	0.534	Red wolf	0.532

16	Lar gibbon *Hylobates lar*	0.604	Sumatran rhinoceros	0.355	Red panda	0.628	Sumatran rhinoceros	0.529	Giraffe	0.483	Northern hairy-nosed wombat	0.524
17	Sumatran rhinoceros *Dicerorhinus sumatrensis*	0.598	Lar gibbon	0.354	Red-shanked douc	0.531	Giraffe	0.514	Short-tailed chinchilla	0.432	Red-shanked douc	0.481
18	Black leopard *Panthera pardus*	0.584	Red-shanked douc	0.319	Koala	0.528	Red-shanked douc	0.479	Red kangeroo	0.424	Puma	0.438
19	Red slender loris *Loris tardigradus*	0.565	Proboscis monkey	0.317	Northern hairy-nosed wombat	0.51	Puma	0.474	Red-shanked douc	0.422	Lar gibbon	0.433
20	Parma wallaby *Macropus parma*	0.564	Parma wallaby	0.314	Wild Bactrian camel	0.507	Lar gibbon	0.446	Parma wallaby	0.413	Giraffe	0.432
21	Numbat *Myrmecobius fasciatus*	0.559	Reindeer	0.301	Puma	0.5	Short-tailed chinchilla	0.442	Lar gibbon	0.397	Wild Bactrian camel	0.415
22	Cheetah *Acinonyx jubatus*	0.555	Saiga antelope	0.301	Hippopotamus	0.482	Red slender loris	0.39	Golden lion tamarin	0.392	Koala	0.39
23	Red wolf *Canis rufus*	0.532	Diademed sifaka	0.287	Dik-dik	0.457	Koala	0.362	Northern hairy-nosed wombat	0.377	Golden lion tamarin	0.382
24	Saiga antelope *Saiga tatarica*	0.51	Red wolf	0.25	Saiga antelope	0.454	Brown bear	0.344	Red fox	0.368	Saiga antelope	0.364
25	Golden lion tamarin *Leontopithecus rosalia*	0.474	Red kangeroo	0.248	Golden lion tamarin	0.42	Hippopotamus	0.309	Bornean orang-utan	0.351	Parma wallaby	0.318
26	Bilby *Macrotis lagotis*	0.466	Giraffe	0.247	Brown bear	0.396	Parma wallaby	0.305	Koala	0.338	Short-tailed chinchilla	0.28
27	Jaguar *Panthera onca*	0.463	Puma	0.247	East African oryx	0.394	European hedgehog	0.299	Saiga antelope	0.328	Hippopotamus	0.27
28	Short-tailed chinchilla *Chinchilla chinchilla*	0.429	Brown bear	0.194	Lar gibbon	0.367	Saiga antelope	0.232	Sumatran rhinoceros	0.321	Red slender loris	0.255
29	Diademed sifaka *Propithecus diadema*	0.37	Mandrill	0.194	Echidna	0.253	Reindeer	0.229	Brown bear	0.309	Brown bear	0.218
30	Puma *Puma concolor*	0.331	Hippopotamus	0.186	Diademed sifaka	0.248	Ring-tailed lemur	0.224	Black-tailed jackrabbit	0.304	Diademed sifaka	0.218
31	Giraffe *Giraffa camelopardalis*	0.299	Indian giant squirrel	0.185	Caracal	0.217	Numbat	0.21	Reindeer	0.286	Echidna	0.208
32	Maned sloth *Bradypus torquatus*	0.243	East African oryx	0.174	Red fox	0.196	Wild Bactrian camel	0.209	Numbat	0.235	Numbat	0.201
33	Proboscis monkey *Nasalis larvatus*	0.241	Sunda pangolin	0.136	Reindeer	0.182	Golden lion tamarin	0.204	Maned sloth	0.221	Reindeer	0.149
34	Red kangeroo *Macropus rufus*	0.198	Western quoll	0.129	African wild dog	0.123	Malayan tapir	0.188	East African oryx	0.216	Red kangeroo	0.142
35	Hippopotamus *Hippopotamus*	0.176	Dik-dik	0.128	Red slender loris	0.122	Echidna	0.149	Hippopotamus	0.181	East African oryx	0.131

	amphibius											
36	African wild dog *Lycaon pictus*	0.162	Wild goat	0.117	Sunda pangolin	0.115	Tasmanian devil	0.075	Dik-dik	0.166	Proboscis monkey	0.12
37	Wild Bactrian camel *Camelus ferus*	0.151	Northern hairy-nosed wombat	0.11	Patagonian mara	0.099	East African oryx	0.062	Diademed sifaka	0.153	Dik-dik	0.117
38	Mandrill *Mandrillus sphinx*	0.147	Yellow mongoose	0.097	Short-tailed chinchilla	0.096	Caracal	0.057	Red slender loris	0.139	Maned sloth	0.085
39	Ring-tailed lemur *Lemur catta*	0.141	Red slender loris	0.08	Maned sloth	0.094	Diademed sifaka	0.041	Proboscis monkey	0.095	Caracal	0.067
40	Golden-rumped elephant shrew *Rhynchocyon chrysopygus*	0.108	Numbat	0.073	Wild goat	0.067	Wild goat	0.027	Fennec fox	0.093	Ring-tailed lemur	0.064
41	Caracal *Caracal caracal*	0.067	Koala	0.069	African buffalo	0.063	Giant anteater	0.006	North American river otter	0.073	Mandrill	0.063
42	Sunda pangolin *Manis javanica*	0.027	Black-tailed jackrabbit	0.038	Malayan tapir	0.053	Common squirrel monkey	0	Wild goat	0.063	Wild goat	0.04
43	Gray-bellied shrew opossum *Caenolestes caniventer*	0.013	Ring-tailed lemur	0.019	Mandrill	0.038	Dik-dik	-0.006	Common spotted cuscus	0.058	Tasmanian devil	0.035
44	Malayan tapir *Tapirus indicus*	0.007	Raccoon	0.013	Proboscis monkey	-0.006	Fennec fox	-0.006	Mandrill	0.047	Malayan tapir	0.011
45	Indian giant squirrel *Ratufa indica*	0.007	Short-tailed chinchilla	0	Parma wallaby	-0.013	Red kangeroo	-0.02	Caracal	0.043	Sunda pangolin	-0.012
46	Western quoll *Dasyurus geoffroii*	0.006	Common spotted cuscus	-0.006	Numbat	-0.036	Maned sloth	-0.032	African wild dog	0.029	African wild dog	-0.012
47	Colocolo *Dromiciops gliroides*	-0.006	Giant anteater	-0.007	Indian giant squirrel	-0.04	Proboscis monkey	-0.04	Common squirrel monkey	0.013	Indian giant squirrel	-0.014
48	Eastern barred bandicoot *Perameles gunnii*	-0.013	Echidna	-0.019	Ring-tailed lemur	-0.048	Black-tailed jackrabbit	-0.049	Ring-tailed lemur	-0.006	Red fox	-0.015
49	Gunning's golden mole *Neamblysomus gunningi*	-0.019	Weasel	-0.019	Giant anteater	-0.068	Common spotted cuscus	-0.049	Weasel	-0.039	Giant anteater	-0.05
50	Giant anteater *Myrmecophaga tridactyla*	-0.045	African wild dog	-0.026	Southern long-nosed armadillo	-0.082	Giant golden-crowned flying fox	-0.082	Malayan tapir	-0.046	Common squirrel monkey	-0.056
51	Common squirrel monkey *Saimiri sciureus*	-0.046	Fossa	-0.026	Reeves's muntjac	-0.099	Red fox	-0.085	Reeves's muntjac	-0.072	Black-tailed jackrabbit	-0.059

52	Wild goat *Capra aegagrus*	-0.081	Fennec fox	-0.032	Warthog	-0.111	Mandrill	-0.094	Maned wolf	-0.093	Fennec fox	-0.077
53	Common spotted cuscus *Spilocuscus maculatus*	-0.137	African buffalo	-0.036	Tasmanian devil	-0.112	Indian giant squirrel	-0.11	Raccoon	-0.098	Common spotted cuscus	-0.079
54	Brown bear *Ursus arctos*	-0.14	Maned wolf	-0.044	Yellow mongoose	-0.122	Colocolo	-0.128	Indian giant squirrel	-0.118	European hedgehog	-0.131
55	Dik-dik *Madoqua kirkii*	-0.155	Red fox	-0.049	Common squirrel monkey	-0.122	Sunda pangolin	-0.153	Echidna	-0.119	Fossa	-0.146
56	Fossa *Cryptoprocta ferox*	-0.162	Reeves's muntjac	-0.054	Fossa	-0.136	Kinkajou	-0.156	Fossa	-0.123	Western quoll	-0.153
57	Sugar glider *Petaurus breviceps*	-0.167	Caracal	-0.057	Black-tailed jackrabbit	-0.147	European badger	-0.201	Giant anteater	-0.123	African buffalo	-0.158
58	Eastern tree hyrax *Dendrohyrax arboreus*	-0.168	Maned sloth	-0.075	Fennec fox	-0.166	African buffalo	-0.205	Tasmanian devil	-0.142	Colocolo	-0.162
59	East African oryx *Oryx beisa*	-0.172	Malayan tapir	-0.127	Red kangeroo	-0.169	Common brushtail possum	-0.205	European hedgehog	-0.156	Patagonian mara	-0.185
60	Southern long-nosed armadillo *Dasypus hybridus*	-0.174	Common squirrel monkey	-0.128	Common brushtail possum	-0.2	Patagonian mara	-0.217	Colocolo	-0.158	Golden-rumped elephant shrew	-0.186
61	Capybara *Hydrochoerus hydrochaeris*	-0.174	Colocolo	-0.132	European hedgehog	-0.201	Gray-bellied shrew opossum	-0.231	Swamp Antechinus	-0.176	Bilby	-0.189
62	Kinkajou *Potos flavus*	-0.185	European badger	-0.148	Aardvark	-0.209	Eurasian beaver	-0.235	African buffalo	-0.18	Weasel	-0.193
63	European hedgehog *Erinaceus europaeus*	-0.219	Gunning's golden mole	-0.156	Weasel	-0.211	Gunning's golden mole	-0.254	Sunda pangolin	-0.187	Reeves's muntjac	-0.193
64	Black-capped marmot *Marmota camtschatica*	-0.226	Asian palm civet	-0.159	Eurasian beaver	-0.225	Weasel	-0.255	Eurasian beaver	-0.189	Yellow mongoose	-0.203
65	North American river otter *Lontra canadensis*	-0.245	Giant golden-crowned flying fox	-0.164	Aye-aye	-0.226	Golden-rumped elephant shrew	-0.26	Yellow mongoose	-0.19	Maned wolf	-0.205
66	Reindeer *Rangifer tarandus*	-0.245	Golden-rumped elephant shrew	-0.177	Golden-rumped elephant shrew	-0.237	Common ringtail possum	-0.263	Giant golden-crowned flying fox	-0.193	Gunning's golden mole	-0.207
67	Patagonian mara *Dolichotis patagonum*	-0.28	Spotted hyena	-0.18	Common spotted cuscus	-0.264	Maned wolf	-0.264	Black-capped marmot	-0.199	Kinkajou	-0.219
68	Common brushtail possum *Trichosurus vulpecula*	-0.281	Southern long-nosed armadillo	-0.193	North American river otter	-0.288	Reeves's muntjac	-0.267	Patagonian mara	-0.199	North American river otter	-0.228
69	Fennec fox *Vulpes zerda*	-0.294	Black-capped marmot	-0.194	Kinkajou	-0.305	Aye-aye	-0.268	Gunning's golden mole	-0.2	Southern long-nosed armadillo	-0.234
70	Maned wolf *Chrysocyon*	-0.3	Tasmanian devil	-0.194	Maned wolf	-0.331	Raccoon	-0.268	Bilby	-0.217	Giant golden-crowned flying fox	-0.24

	brachyurus											
71	Woolly opossum *Caluromys lanatus*	-0.306	Kinkajou	-0.21	Raccoon	-0.346	Black-capped marmot	-0.282	Western quoll	-0.23	Black-capped marmot	-0.251
72	Aye-aye *Daubentonia madagascariensis*	-0.309	Eastern tree hyrax	-0.244	Asian palm civet	-0.349	Common vole	-0.284	Kinkajou	-0.24	Raccoon	-0.269
73	Swamp Antechinus *Antechinus minimus*	-0.313	Common brushtail possum	-0.268	Black-capped marmot	-0.349	Fossa	-0.289	Capybara	-0.288	Common brushtail possum	-0.281
74	Eurasian beaver *Castor fiber*	-0.346	Sugar glider	-0.292	Western quoll	-0.355	Bilby	-0.299	Aye-aye	-0.296	Eurasian beaver	-0.293
75	Aardvark *Orycteropus afer*	-0.348	Capybara	-0.294	Colocolo	-0.379	African wild dog	-0.303	Southern long-nosed armadillo	-0.3	Asian palm civet	-0.298
76	Giant golden-crowned flying fox *Acerodon jubatus*	-0.348	Striped skunk	-0.297	Common ringtail possum	-0.403	Western quoll	-0.304	Eastern tree hyrax	-0.327	Aye-aye	-0.304
77	Asian palm civet *Paradoxurus hermaphroditus*	-0.352	North American river otter	-0.298	Gunning's golden mole	-0.405	Asian palm civet	-0.307	Asian palm civet	-0.331	Eastern tree hyrax	-0.312
78	Common ringtail possum *Pseudocheirus peregrinus*	-0.375	Swamp Antechinus	-0.324	Giant golden-crowned flying fox	-0.409	North American porcupine	-0.333	Golden-rumped elephant shrew	-0.355	Capybara	-0.315
79	Yellow mongoose *Cynictis penicillata*	-0.397	Common ringtail possum	-0.336	Woolly opossum	-0.415	Sugar glider	-0.336	Aardvark	-0.378	Gray-bellied shrew opossum	-0.341
80	North American porcupine *Erethizon dorsatum*	-0.407	European hedgehog	-0.344	Capybara	-0.417	Aardvark	-0.343	Gray-bellied shrew opossum	-0.424	Eastern barred bandicoot	-0.353
81	European badger *Meles meles*	-0.417	Patagonian mara	-0.346	North American porcupine	-0.446	Eastern tree hyrax	-0.348	Sugar glider	-0.424	Sugar glider	-0.355
82	African buffalo *Syncerus caffer*	-0.426	Eastern barred bandicoot	-0.36	Bilby	-0.457	Woolly opossum	-0.351	Woolly opossum	-0.438	European badger	-0.364
83	Highland streaked tenrec *Hemicentetes nigriceps*	-0.453	Common pipistrelle	-0.365	Eastern tree hyrax	-0.486	Capybara	-0.377	Common brushtail possum	-0.447	Common ringtail possum	-0.368
84	Black-tailed jackrabbit *Lepus californicus*	-0.457	North American porcupine	-0.372	Spotted hyena	-0.497	North American river otter	-0.388	Spotted hyena	-0.453	Swamp Antechinus	-0.371
85	Weasel *Mustela nivalis*	-0.46	Malayan colugo	-0.403	European badger	-0.503	Yellow mongoose	-0.392	Eastern barred bandicoot	-0.463	Aardvark	-0.376
86	Star-nosed mole *Condylura cristata*	-0.464	Common treeshrew	-0.419	Swamp Antechinus	-0.507	Warthog	-0.403	Common treeshrew	-0.465	North American porcupine	-0.406
87	Reeves's muntjac *Muntiacus reevesi*	-0.477	Bilby	-0.432	Gray-bellied shrew opossum	-0.509	Southern long-nosed armadillo	-0.419	North American porcupine	-0.465	Woolly opossum	-0.414

88	Malayan colugo *Galeopterus variegatus*	-0.481	Aye-aye	-0.432	Eastern barred bandicoot	-0.527	Eastern barred bandicoot	-0.438	Common ringtail possum	-0.467	Warthog	-0.484
89	Common treeshrew *Tupaia glis*	-0.497	House mouse	-0.451	Common treeshrew	-0.561	Star-nosed mole	-0.478	European badger	-0.519	Common treeshrew	-0.496
90	Red fox *Vulpes vulpes*	-0.573	Brown rat	-0.469	Sugar glider	-0.569	Swamp Antechinus	-0.503	Malayan colugo	-0.526	Spotted hyena	-0.498
91	Raccoon *Procyon lotor*	-0.592	Eurasian beaver	-0.469	Malayan colugo	-0.707	Highland streaked tenrec	-0.506	Common pipistrelle	-0.594	Malayan colugo	-0.574
92	Common pipistrelle *Pipistrellus pipistrellus*	-0.69	Warthog	-0.484	Common pipistrelle	-0.712	Common treeshrew	-0.539	Striped skunk	-0.619	Common vole	-0.595
93	Common vole *Microtus arvalis*	-0.707	Gray-bellied shrew opossum	-0.534	Highland streaked tenrec	-0.729	Spotted hyena	-0.561	Common vole	-0.622	Common pipistrelle	-0.598
94	Striped skunk *Mephitis mephitis*	-0.781	Common vampire bat	-0.54	Common vole	-0.782	Common pipistrelle	-0.607	Warthog	-0.63	Highland streaked tenrec	-0.599
95	Warthog *Phacochoerus africanus*	-0.824	Woolly opossum	-0.542	Striped skunk	-0.783	Common vampire bat	-0.621	Highland streaked tenrec	-0.675	Star-nosed mole	-0.616
96	Etruscan shrew *Suncus etruscus*	-0.825	Star-nosed mole	-0.582	Etruscan shrew	-0.784	Striped skunk	-0.642	Star-nosed mole	-0.743	Striped skunk	-0.631
97	Spotted hyena *Crocuta crocuta*	-0.837	Common vole	-0.584	Star-nosed mole	-0.813	House mouse	-0.705	Etruscan shrew	-0.805	Common vampire bat	-0.767
98	Common vampire bat *Desmodus rotundus*	-0.934	Aardvark	-0.596	Common vampire bat	-0.846	Etruscan shrew	-0.711	House mouse	-0.831	Etruscan shrew	-0.78
99	Brown rat *Rattus norvegicus*	-1	Highland streaked tenrec	-0.641	Brown rat	-0.919	Malayan colugo	-0.743	Brown rat	-0.887	House mouse	-0.823
100	House mouse *Mus musculus*	-1.071	Etruscan shrew	-0.773	House mouse	-1.012	Brown rat	-1.007	Common vampire bat	-0.927	Brown rat	-0.849

Appendix C

Full model averaged parameter estimates for each country, and for all regions.

Australia	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)	
(Intercept)	0.1548	0.1669	0.1691	0.9160	0.3599	
Baldness: none	0.4365	0.1242	0.1259	3.4660	0.0005	***
Baldness: some	0.4006	0.1430	0.1449	2.7640	0.0057	**
Eye position: lateral	-0.1077	0.0616	0.0625	1.7240	0.0848	.
Human threat: threat	0.3268	0.1379	0.1397	2.3400	0.0193	*
IUCN status: EN	-0.1812	0.1198	0.1215	1.4910	0.1359	
IUCN status: LC	-1.0276	0.1087	0.1102	9.3260	< 2e-16	***
IUCN status: NT	-0.6508	0.1254	0.1272	5.1170	0.0000	***
IUCN status: VU	-0.3613	0.1331	0.1349	2.6780	0.0074	**
Body size: 1-10kg	0.2006	0.0842	0.0853	2.3520	0.0187	*
Body size: 10-20kg	0.0895	0.1100	0.1115	0.8020	0.4225	
Body size: 20-40kg	-0.1058	0.1308	0.1326	0.7980	0.4248	
Body size: 40-100kg	0.2495	0.1127	0.1143	2.1820	0.0291	*
Body size: 100-800kg	0.0318	0.1226	0.1244	0.2550	0.7985	
Body size: >800kg	0.7538	0.1793	0.1819	4.1450	0.0000	***
ED score: 20-40	-0.1590	0.0817	0.0829	1.9190	0.0550	.
ED score: >40	0.0752	0.1053	0.1069	0.7040	0.4813	

India	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)	
(Intercept)	-0.2375	0.2140	0.2171	1.0940	0.2740	
Activity pattern: crepuscular-nocturnal	0.4765	0.1409	0.1432	3.3290	0.0009	***
Activity Pattern: diurnal	0.3144	0.1103	0.1121	2.8050	0.0050	**
Activity Pattern: nocturnal	0.2345	0.1155	0.1173	1.9990	0.0456	*
Activity Pattern: variable	0.4002	0.1650	0.1677	2.3870	0.0170	*
Baldness: none	0.1029	0.1026	0.1041	0.9890	0.3228	
Baldness: some	-0.0909	0.1074	0.1090	0.8330	0.4046	
Colour: single bright coloured	0.4872	0.1627	0.1649	2.9550	0.0031	**
Colour: multi coloured high contrast	0.3377	0.0960	0.0975	3.4640	0.0005	***
Colour: multi coloured low contrast	0.0847	0.0858	0.0871	0.9730	0.3307	
Colour: single plain coloured	0.1517	0.0870	0.0882	1.7200	0.0854	.
ED score: 20-40	-0.1490	0.0622	0.0632	2.3600	0.0183	*
ED score: >40	-0.1624	0.0811	0.0824	1.9710	0.0487	*
Eye position: lateral	-0.1231	0.0522	0.0529	2.3260	0.0200	*
Human threat: threat	0.2123	0.0986	0.1001	2.1200	0.0340	*
IUCN status: EN	-0.0331	0.0906	0.0921	0.3590	0.7192	
IUCN status: LC	-0.4362	0.0752	0.0764	5.7100	< 2e-16	***

IUCN status: NT	-0.3636	0.0914	0.0928	3.9170	0.0001	***
IUCN status: VU	-0.1189	0.0974	0.0988	1.2040	0.2288	
Body size: 1-10kg	0.1899	0.0565	0.0574	3.3100	0.0009	***
Body size: 10-20kg	0.1945	0.0776	0.0788	2.4680	0.0136	*
Body size: 20-40kg	0.1304	0.0948	0.0962	1.3560	0.1752	
Body size: 40-100kg	0.1958	0.0848	0.0861	2.2750	0.0229	*
Body size: 100-800kg	0.3953	0.0914	0.0927	4.2650	0.0000	***
Body size: >800kg	0.6466	0.1350	0.1370	4.7210	0.0000	***
Facial markings: none	-0.1906	0.0812	0.0825	2.3090	0.0209	*
Facial markings: some	-0.0988	0.0797	0.0810	1.2200	0.2226	
Striking appearance: Striking	-0.0910	0.0517	0.0524	1.7360	0.0826	.

South Africa	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)	
(Intercept)	0.1643	0.1867	0.1892	0.8690	0.3851	
Colour: single bright coloured	0.8099	0.1894	0.1921	4.2150	0.0000	***
Colour: multi coloured high contrast	0.4231	0.1210	0.1228	3.4460	0.0006	***
Colour: multi coloured low contrast	0.1725	0.1082	0.1098	1.5710	0.1162	
Colour: single plain coloured	0.2578	0.1080	0.1095	2.3550	0.0185	*
Facial markings: none	-0.3173	0.1021	0.1037	3.0600	0.0022	**
Facial markings: some	-0.1477	0.1053	0.1069	1.3810	0.1672	
Human threat: threat	0.4571	0.1175	0.1192	3.8350	0.0001	***
IUCN status: EN	-0.3196	0.1120	0.1136	2.8130	0.0049	**
IUCN status: LC	-0.7419	0.0961	0.0975	7.6080	< 2e-16	***
IUCN status: NT	-0.6686	0.1147	0.1164	5.7430	< 2e-16	***
IUCN status: VU	-0.4034	0.1171	0.1189	3.3940	0.0007	***
Body size: 1-10kg	0.3144	0.0731	0.0741	4.2400	0.0000	***
Body size: 10-20kg	0.3805	0.0985	0.1000	3.8050	0.0001	***
Body size: 20-40kg	0.2477	0.1135	0.1152	2.1510	0.0315	*
Body size: 40-100kg	0.3554	0.1054	0.1069	3.3240	0.0009	***
Body size: 100-800kg	0.5478	0.1111	0.1127	4.8600	0.0000	***
Body size: >800kg	1.0540	0.1515	0.1537	6.8580	< 2e-16	***
Baldness: none	0.1369	0.1137	0.1155	1.1860	0.2357	
Baldness: some	-0.0166	0.1240	0.1259	0.1310	0.8955	
Striking appearance: Striking	-0.0675	0.0589	0.0598	1.1290	0.2591	

UK	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)	
(Intercept)	0.3296	0.2366	0.2382	1.3830	0.1666	
Baldness: none	0.2912	0.1231	0.1248	2.3330	0.0197	*
Baldness: some	0.2364	0.1390	0.1409	1.6780	0.0934	.
Eye position: lateral	-0.1771	0.0660	0.0669	2.6460	0.0081	**
Facial markings: none	-0.2238	0.0994	0.1008	2.2210	0.0264	*
Facial markings: some	-0.2067	0.1028	0.1043	1.9820	0.0475	*

Human threat: threat	0.4150	0.1415	0.1434	2.8950	0.0038	**
IUCN status: EN	-0.2637	0.1211	0.1227	2.1490	0.0317	*
IUCN status: LC	-0.7224	0.1052	0.1068	6.7680	< 2e-16	***
IUCN status: NT	-0.5715	0.1280	0.1297	4.4070	0.0000	***
IUCN status: VU	-0.3194	0.1331	0.1348	2.3690	0.0179	*
Body size: 1-10kg	0.1760	0.0809	0.0820	2.1460	0.0319	*
Body size: 10-20kg	0.1175	0.1123	0.1138	1.0330	0.3018	
Body size: 20-40kg	-0.0177	0.1276	0.1294	0.1360	0.8915	
Body size: 40-100kg	0.2846	0.1125	0.1140	2.4960	0.0126	*
Body size: 100-800kg	0.3214	0.1274	0.1291	2.4900	0.0128	*
Body size: >800kg	0.8789	0.1869	0.1892	4.6450	0.0000	***
Photo quality: excellent	0.2667	0.1241	0.1259	2.1190	0.0341	*
Photo quality: poor	-0.0681	0.3012	0.3056	0.2230	0.8237	
ED score: 20-40	-0.1732	0.0790	0.0802	2.1600	0.0308	*
ED score: >40	-0.0575	0.1018	0.1033	0.5570	0.5778	
Striking appearance: Striking	-0.0751	0.0661	0.0670	1.1210	0.2623	
Diet: carnivore and scavenger	-0.3918	0.1812	0.1839	2.1300	0.0332	*
Diet: herbivore	0.0223	0.1041	0.1057	0.2110	0.8329	
Diet: insectivore	-0.1175	0.1298	0.1318	0.8910	0.3727	
Diet: omnivore	-0.0963	0.1057	0.1073	0.8970	0.3695	

USA	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)	
(Intercept)	0.1706	0.1585	0.1609	1.0600	0.2892	
Baldness: none	0.3614	0.1176	0.1193	3.0280	0.0025	**
Baldness: some	0.1633	0.1375	0.1396	1.1700	0.2420	
Diet: carnivore and scavenger	-0.5001	0.1690	0.1716	2.9140	0.0036	**
Diet: herbivore	-0.0049	0.0953	0.0967	0.0500	0.9598	
Diet: insectivore	-0.1090	0.1263	0.1282	0.8500	0.3955	
Diet: omnivore	-0.1800	0.0964	0.0978	1.8400	0.0657	.
ED score: 20-40	-0.2856	0.0758	0.0770	3.7100	0.0002	***
ED score: >40	-0.1633	0.1070	0.1086	1.5030	0.1327	
Eye position: lateral	-0.1946	0.0646	0.0656	2.9670	0.0030	**
IUCN status: EN	-0.1196	0.1134	0.1151	1.0400	0.2986	
IUCN status: LC	-0.6072	0.0998	0.1013	5.9940	< 2e-16	***
IUCN status: NT	-0.3736	0.1143	0.1160	3.2210	0.0013	**
IUCN status: VU	-0.0829	0.1151	0.1169	0.7100	0.4779	
Body size: 1-10kg	0.1547	0.0790	0.0803	1.9270	0.0540	.
Body size: 10-20kg	0.0356	0.1060	0.1076	0.3310	0.7404	
Body size: 20-40kg	0.0047	0.1202	0.1220	0.0380	0.9694	
Body size: 40-100kg	0.3743	0.0991	0.1006	3.7210	0.0002	***
Body size: 100-800kg	0.3968	0.1101	0.1118	3.5490	0.0004	***
Body size: >800kg	0.8362	0.1732	0.1759	4.7540	0.0000	***
Striking appearance: Striking	-0.0870	0.0695	0.0706	1.2330	0.2177	
Photo quality: excellent	0.2167	0.1207	0.1226	1.7690	0.0770	.
Photo quality: poor	0.2015	0.2739	0.2782	0.7240	0.4690	

All Regions	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)	
(Intercept)	0.0922	0.1884	0.1906	0.4840	0.6284	
Baldness: none	0.2641	0.1047	0.1062	2.4870	0.0129	*
Baldness: some	0.1315	0.1176	0.1192	1.1020	0.2703	
Colour: single bright coloured	0.5385	0.1900	0.1922	2.8010	0.0051	**
Colour: multi coloured high contrast	0.2772	0.1124	0.1140	2.4320	0.0150	*
Colour: multi coloured low contrast	0.0899	0.0988	0.1002	0.8970	0.3695	
Colour: single plain coloured	0.1663	0.0978	0.0991	1.6780	0.0933	.
Eye position: lateral	-0.1384	0.0609	0.0617	2.2460	0.0247	*
Facial markings: none	-0.2365	0.0929	0.0943	2.5080	0.0121	*
Facial markings: some	-0.1522	0.0909	0.0923	1.6480	0.0993	.
Human threat: threat	0.2765	0.1153	0.1169	2.3660	0.0180	*
IUCN status: EN	-0.1939	0.0996	0.1010	1.9200	0.0549	.
IUCN status: LC	-0.7018	0.0848	0.0861	8.1500	< 2e-16	***
IUCN status: NT	-0.5390	0.1061	0.1075	5.0130	0.0000	***
IUCN status: VU	-0.2735	0.1130	0.1144	2.3910	0.0168	*
Body size: 1-10kg	0.2102	0.0649	0.0659	3.1900	0.0014	**
Body size: 10-20kg	0.1639	0.0961	0.0973	1.6840	0.0921	.
Body size: 20-40kg	0.0648	0.1083	0.1097	0.5900	0.5551	
Body size: 40-100kg	0.2547	0.1028	0.1040	2.4490	0.0143	*
Body size: 100-800kg	0.3471	0.0996	0.1011	3.4340	0.0006	***
Body size: >800kg	0.8555	0.1488	0.1509	5.6710	< 2e-16	***
Diet: carnivore and scavenger	-0.2986	0.1525	0.1548	1.9300	0.0537	.
Diet: herbivore	0.0519	0.0857	0.0870	0.5960	0.5510	
Diet: insectivore	0.0017	0.1147	0.1163	0.0150	0.9884	
Diet: omnivore	-0.0863	0.0876	0.0890	0.9700	0.3318	
ED score: 20-40	-0.1687	0.0696	0.0705	2.3940	0.0167	*
ED score: >40	-0.0767	0.0884	0.0897	0.8560	0.3921	
Striking appearance: Striking	-0.0854	0.0541	0.0549	1.5540	0.1201	
Photo quality: excellent	0.2200	0.1015	0.1031	2.1350	0.0328	*
Photo quality: poor	-0.0546	0.2478	0.2515	0.2170	0.8281	
Activity pattern: crepuscular-nocturnal	0.3797	0.1557	0.1582	2.4000	0.0164	*
Activity Pattern: diurnal	0.2678	0.1214	0.1233	2.1710	0.0299	*
Activity Pattern: nocturnal	0.2056	0.1222	0.1241	1.6560	0.0977	.
Activity Pattern: variable	0.4420	0.1804	0.1833	2.4110	0.0159	*

Chapter 3

Identifying ambassadors for conservation marketing

A modified version of this chapter has been submitted to *Global Ecology and Conservation*

Abstract

Conservation relies heavily on external funding, much of it from a supportive public. Therefore it is important to know which species are most likely to catalyse such funding and also the additional ecological value (such as offering co-benefits for the conservation of other species) of marketing these particular species. Whilst previous work has looked at the potential for appealing species to act as flagship species for marketing, or efficient umbrella species for co-occurring species, no previous studies have examined all terrestrial mammals for both these factors. Therefore, here we estimate 'efficiency' and 'appeal' scores for all terrestrial mammals (n=4320) and categorise them as ambassadors (highly appealing and efficient), celebrity species (highly appealing but relatively inefficient), worker species (highly efficient but relatively unappealing) or hitch-hikers (relatively unappealing and inefficient). Relatively few mammals (331, 7.7%) emerged as ambassadors, with carnivores featuring heavily in this group (representing 5% of terrestrial mammals but 39% of ambassadors). 'Top ambassadors' were defined as those with efficiency and appeal scores greater than 1 standard deviation above the mean - only 27 species, of which 18 were Carnivores, (0.6% of those examined) emerged as top ambassadors. Less than a quarter of the 20 most endangered and evolutionary distinct species in this study were classed as ambassadors, highlighting the need for surrogate species to catalyse conservation effort in areas with such priority species. As Carnivores are particularly good Ambassadors, there is a need to develop Carnivore conservation campaigns, not only for their own sake, but for the many other threatened mammals they co-occur with that are unlikely to generate similar levels of attention and funding. This is the first global analysis bringing together efficiency and appeal

for all terrestrial mammals, and demonstrates an approach for determining how best to market species in order to achieve maximal conservation gain in a world with urgent conservation need but limited resources.

Introduction

Conservation efforts are needed urgently, with ever-increasing threats posed to the world's biodiversity, largely due to anthropogenic factors (Butchart et al. 2010; Dirzo et al. 2014). Addressing threats of this scale will require significant global engagement and funding, running into billions of dollars annually (Lindsey et al. 2016). This will require commitments not only from governments but also from the general public, who exert increasing influence in conservation, not only through their philanthropy but also through the power and sometimes "viral" behaviour of the global internet forum (Macdonald et al. 2016a). Therefore, society's delivery of biodiversity conservation in the future hinges not only on the expertise and priorities of scientists and policymakers, but also on the support and engagement of numerous stakeholder groups, including the electronically-connected middle classes who tend to be most open to such engagement (Balmford & Cowling 2006; Macdonald et al. 2016a). In order to maximise the engagement of that public, and the impact of their support, conservation campaigns should carefully consider which species are likely to both be highly appealing to the public, and to offer maximum additional gains to other sympatric species.

Flagship species

The term 'flagships' for conservation has been widely discussed in the literature and undergone several reinterpretations (Caro & O'Doherty 1999; Favreau et al. 2006; Heywood 1995; Simberloff 1998). The review of the concept by Verissimo et al. (2011) focuses clearly on the concept's usefulness for conservation marketing. This focus on conservation

marketing can be applied at a range of scales, from raising awareness about a region's biodiversity among a local community (Veríssimo et al. 2014) to widespread national and international campaigns that can raise many hundreds of thousands of dollars. Being able to identify which species have the highest potential to act as flagship species is important for the success of these campaigns.

The effectiveness of campaigns depends largely upon public perceptions; from nematodes to gorillas, it is obvious that people do not view all animal species equally (Macdonald et al. 2006) and a growing number of studies are attempting to quantify their preferences. Frequently, the most high profile species are large mammals (Caro & O'Doherty 1999; Clucas et al. 2008; Johnson et al. 2010; Macdonald et al. 2006; Smith et al. 2012), however it is important to note that while these species may dominate the headlines in the western media, they may not be so highly regarded in other regions where peoples' perceptions and experiences may differ widely (Bowen-Jones & Entwistle 2002; Douglas & Veríssimo 2013; Macdonald et al. 2016b). In order for marketing campaigns to be successful it is important to consider both the target audience for the campaign as well as the stated use of the flagship species, for instance the polar bear (*Ursus maritimus*) might represent a good flagship to raise international awareness about the impacts of climate change, but a grey wolf (*Canis lupus*) might not be the optimal flagship amongst the shepherding community for species reintroduction campaigns in the Scottish highlands (Barua et al. 2011; Linnell et al. 2000; Sandom & Macdonald 2015) .

Accounting for stakeholder preferences and the purpose of the flagship, a species' appeal is an important dimension of its potential to lever public support for its conservation and, indeed, for conservation marketing more widely (Kontoleon & Swanson 2003; Veríssimo et al. 2009). It is possible that different species have certain characteristics that make them more or less likely to be successful flagships. For instance, Macdonald et al. (2015) explored the impact of characteristics such as size, rarity, orientation of eyes etc. on peoples' preferences for different species in the context of conservation prioritisation and found that these could be used to predict respondent preferences with high reliability.

Umbrella species

As with the term "flagships", there are many different interpretations of the term "umbrellas" (Caro 2010), and loose terminology has hindered debates about the efficacy of the concept. However a common theme among different definitions (and types of umbrella species) is the use of one species (or group of species) to act as a surrogate for the conservation of other "background" species through their association with viable populations, protected areas or management actions (Caro 2010). The efficacy of "umbrella" species is hotly debated in the conservation literature with some studies casting doubt on the ability of one species (or group of species) to act as surrogates for another (Roberge & Angelstam 2004) while others find support for the idea (Branton & Richardson 2011; Burnham et al. 2012; Fleishman et al. 2000). Recently, (Di Minin & Moilanen 2014; Di Minin et al. 2016) have shown that inclusion of charismatic flagship species can improve surrogacy strategies, and explored the capacity of Carnivores to act as surrogates for a wide range of

birds, mammals, amphibians, reptiles and ecoregions. These species that combine the marketing characteristics of flagship species, and the ecological benefits of umbrella species have been termed "flagship umbrella species" (Caro 2010) and have been considered in the context of both forest and marine conservation (e.g. (Dinerstein et al. ; Oviedo & Solís 2008)).

However, a species' ability to act as a surrogate for other species is not confined to its capacity to facilitate the delivery of effective conservation on the ground. Some species may be appropriate flagships for a wide range of conservation and environmental issues, while others may be effective only in certain circumstances. Similarly, some species may be range restricted and have very few sympatric species, such as the island dwelling Bryant's woodrat (*Neotoma bryanti*) which overlaps with only two other mammals, while others occur widely and are sympatric with many other species, such as the red fox *Vulpes vulpes*, whose range spans four continents and overlaps with more than 1200 mammalian species. Under the appropriate circumstances, these wide ranging species have the ability to act as flagships for a wider range of issues and species. In this sense, a species' ability as a flagship may be judged both on the appeal to the target audience of its physical and or cultural characteristics, but it may also be judged on its ability to act as a marketing flagship for a wide range of other less charismatic species.

Despite broad acceptance of the fact that ideal 'poster species' for conservation will be both appealing to the public and efficient in terms of their added conservation value, no previous studies have examined all terrestrial mammals for both these factors. Here, we estimate the

values of efficiency (representing the distinctiveness and level of threat of sympatric species) and appeal (extrapolated from published charisma scores (Macdonald et al. 2015)) and categorise all terrestrial mammals into one of four categories, in order to best inform conservation marketing.

Species which emerge as likely to be highly appealing and highly efficient are termed 'ambassador species', while highly appealing but relatively inefficient species are 'celebrity species'. Species which have high efficiency scores but which appear to be relatively unappealing to the public are termed 'worker' species, while those which are both relatively inefficient and unappealing are termed 'hitch-hiker' species. For each of these categories, we consider how they might be represented in the "shop window" of conservation, and how best their conservation could be achieved through marketing campaigns. All of these designations sit within the context of flagship species and reflect one element of a species' usefulness in the context of conservation marketing. This analysis is the first to suggest that a species' potential usefulness as a flagship for conservation campaign could be given added value by its ability to act as a marketing surrogate for a large number of high priority species. This analysis could inform future conservation marketing campaigns to fund conservation efforts in locations for which a charismatic species could be selected as the 'poster child' for the rest of the region's biodiversity. Such campaigns can rapidly spread through online sites and social media should they grab the attention of the general public, as evidenced by the Cecil the Lion phenomenon (Macdonald et al. 2016a).

We have selected terrestrial mammals for this first exploration of ambassador species, not only because mammals already feature conspicuously in the public's wider imagination but specifically because our earlier quantification of charisma (Macdonald et al. 2015) provides a unique opportunity to make a quantitative extrapolation to the entire taxon. The results of this study reveal not only which species are likely to generate most attention and added-value to a conservation campaign (ambassadors), but also how best to capitalise on the individual strengths of different species in the arena of conservation marketing.

Methods

Efficiency scores

In order to identify the extent to which a species might act as a flagship species for other mammals, we estimated an efficiency score for each species. This score was inspired by the External Threat Index developed by Cardillo et al. (2005), which represents the level of threat

$$E_{m1} = (\%RO_{m2} * EDGE_{m2}) + (\%RO_{m3} * EDGE_{m3}).....+ (\%RO_{mn} * EDGE_{mn})$$

within a species' distribution. The efficiency score is calculated for a given species *m1* as:

Where $\%RO_{m2}$, is the percentage of the range overlap (*%RO*) with other mammal species (m2, m3 etc.), multiplied by the EDGE (Evolutionarily Distinct and Globally Endangered; Isaac et al. 2007) score of each of those species. EDGE scores were used in order to account for both endangerment and phylogenetic diversity as measures of conservation value. Species

m1 may have a high efficiency either by overlapping with many less endangered and/or distinct species, or fewer more endangered and/or distinct species.

EDGE scores were obtained from EDGE of Existence (EDGE of Existence 2013; Isaac et al. 2007). Range maps were obtained from the IUCN Red List (IUCN 2010). Any part of a species range that was the result of a species introduction was removed, as were any parts of a range where the species was not believed to be extant (those classed by IUCN as extinct, possibly extinct, possibly extant and presence uncertain).

Range maps were rasterised at a cell size of 5 minutes (approximately 9 km x 9 km at the equator) using packages 'raster' and 'rgdal' in R (version 2.13.1). This resolution was selected to balance the twin goals of computational expediency, and the desire to use the finest resolution possible. The degree of overlap between each individual terrestrial mammal species was computed by building a matrix of presence/ absence counts for each terrestrial mammal species in every grid cell globally.

It is important to note that this metric of efficiency is designed to highlight the number and the EDGE scores of other species overlapped sympatrically across the entirety of a particular species' range. We selected this metric in the context of marketing for conservation, because a species that overlaps a great many other species across its range has the potential to act as an ambassador for all of those species. Obviously, species with large spatial distributions have a greater opportunity to overlap with a greater number of more endangered or phylogenetically distinct species, but we felt that this approach was justified

because these species have greater potential to act as ambassadors for a wide array of species than do range restricted species.

For the purposes of presenting the results, the efficiency scores were converted into standardised z-scores.

Appeal scores

Macdonald et al. (2015) employed a market research approach to identify which species, from a sample of 100 terrestrial mammals, people preferred for conservation. Over 1,500 participants from five English-speaking countries across five continents (Australia, India, South Africa, UK and the USA) were presented with photos of different species in a paired test, and asked to express their preference in the context of conservation. Respondents were surveyed using an online survey targeted towards moderately affluent, computer-literate individuals; this group of stakeholders was deliberately targeted to be representative of a politically engaged middle class who might also be the focal audience for broad based conservation marketing campaigns (full details of the survey and respondent demographics can be found in Macdonald et al. (2015)).

Here, we used the same dataset of survey responses and identified a core set of attributes that could be extrapolated to all mammal species, as they were either widely available from international databases or were readily generalised at a taxonomic level. These attributes were IUCN status, body size, eye position and human threat, all of which were shown to be

were important in influencing peoples' preferences (they had high relative variable importance values and featured in all or almost all top models) in Macdonald et al. (2015).

Following Macdonald et al. (2015) we used an information-theoretic approach to compare models that related the various attributes to the average preference scores for each mammal accrued. The full model included IUCN status, body size, eye position and human threat, and the 'dredge' function of the 'MuMIn' function in R Version 3.0.3 was used to generate a set of candidate models with combinations of the terms in the full model. Candidate models were evaluated by comparing differences in their second-order Akaike Information Criterion (AIC_C) values and Akaike weights (ω_i).

Data collected from respondents in five countries in five continents (Australia, India, South Africa, UK, USA) were analysed collectively (all countries) and then separate full models were tested for each country's respondents in turn, as Macdonald et al. (2015) found that preference for mammals varied between respondents of different nationalities.

For each country the best performing model was identified, and the model averaged parameter estimates for each attribute (IUCN status, body size, eye position and human threat) were summed to calculate an appeal score for each of the 4320 terrestrial mammals with sufficient available data.

For the purposes of presenting the results, the appeal scores were converted into standardised z-scores.

Ambassador scores

Taking the standardised z-scores for efficiency and appeal, we define 'ambassadors' as those species that had above-mean scores for both metrics. 'Top ambassadors' were defined as those species where both the standardised efficiency and appeal scores were more than 1 standard deviation above the mean.

In order to compare species that qualified as 'ambassador' species we summed the standardised appeal and efficiency scores for these species to give an ambassador score. Summing z-scores is a common method for producing composite scores, especially in medical studies (e.g. Diatchenko et al. (2005)), and previous published studies have used this method to determine conservation priority scores (Dickman et al. 2015). Ambassador scores were calculated for each of the five countries separately, and for all countries combined.

Results

Efficiency scores

The house mouse (*Mus musculus*) emerged as the species with the highest efficiency score, with its vast distribution overlapping at least part of the ranges of 1744 other mammal species (Table S1). The puma (*Puma concolor*) was the second most efficient species, overlapping 1422 species, followed by the common vampire bat (*Desmodus rotundus*) and the leopard (*Panthera pardus*). Interestingly, while having the 4th highest efficiency score, the leopard overlapped with the second largest number of other species (1701). Wide-

ranging bats were disproportionately represented in the 20 most efficient species, comprising 60% of those species despite bats representing only around 20% of mammals. Carnivores are also disproportionately represented among the most efficient species, making up 20% of the top 20 (including two of the top four) compared to only 5% in the overall sample. On average, species overlapped with 250 other mammals, and only around a quarter of species examined (n = 1140, 26.4%) had above-mean efficiency scores. 43 of the species we examined overlapped with no other species at the scale of our analysis so had efficiency scores of zero, while coincidentally 43 species overlapped at least 1000 species (Table S1 supplementary information). Range restricted species, with little opportunity to overlap with many species, perform poorly on our efficiency metric, as evidenced by the island-dwelling, endemic Hershkovitz's Grass Mouse (*Abrothrix hershkovitzi*), which was the lowest-scoring mammal amongst those which exhibited any degree of overlap with other species.

Appeal scores

In all cases the full model, containing all four variables, was the best performing model, we therefore consider the effect of all four variables across each country. In general, both within and across countries, survey respondents had a preference for large species, with a high threat level, forward facing eyes, and that were potentially threatening to humans. However, the specific pattern of these preferences varied in interesting ways between countries (Figure 1). For instance respondents in Australia, rather than simply preferring larger mammals, seemed to prefer species in the 1-20kg size classes over those in the 20-40kg class, and to prefer species in the 40-100kg size class over those weighing between 100

and 800kg. When we consider all countries combined, the trend was a preference for larger mammals, but species in the size range of a family pet (1-40kg) were favoured slightly more than the next largest size class. Similarly, while in general the survey respondents preferred more threatened mammals, in the USA respondents appeared not to differentiate strongly between vulnerable and endangered species, but did show a strong preference for critically endangered species.

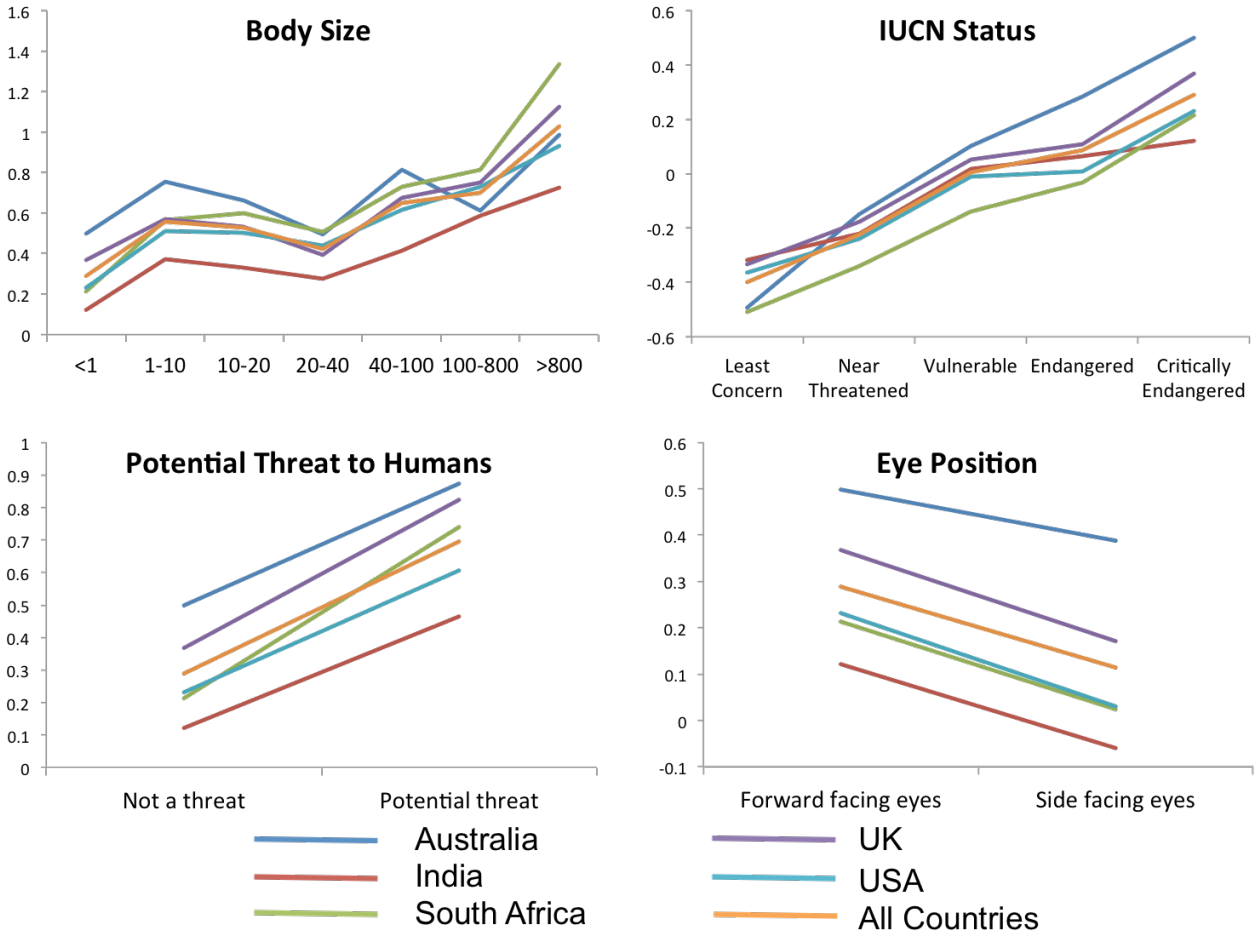

Figure 1 Model averaged parameter estimates for each variable. Appeal scores for each species are generated by summing the appropriate parameter estimates for each variable.

Combining the preference scores for each attribute of each species revealed that the Asian elephant (*Loxodonta maximus*) and the Indian water buffalo (*Bubalus arnee*) emerged as the joint highest scoring species in terms of appeal in Australia, South Africa, the UK, the USA, and all countries combined (Table S1), while the tiger (*Panthera tigris*) ranked top in India. Some species achieved consistently high appeal scores across countries – for example, 12 species occurred in the top 20 of all countries. Of these 12, eight were mega-mammals of the Cetardiodactyla, Proboscidea and Perissodactyla with their appeal primarily driven by their large size, while the remaining four were all large Carnivores (3 Asiatic bear species and the tiger). However, other species appeared much more variable in their appeal scores between countries: both the black bear (*Ursus americanus*) and brown bear (*Ursus arctos*) occurred in the top 20 in India and the USA, but were ranked joint 845th in Australia.

In general, approximately a third of mammal species were estimated to have above-mean appeal in each country (AUS= 36.4%, IND= 37.4%, RSA= 37.8%, GBR= 32.7%, USA= 37.8%, all= 37.4%; figure 4). When comparing the estimated appeal scores for each species with the actual survey responses from respondents, we found that the two measures showed strong agreement with R^2 values in excess of 60% in most countries (R^2: Aus: 60.7%, Ind 61.2%, RSA: 66.1%, UK: 58.2%, USA: 48.5%, All countries: 58.1%, Figure 2). While these relatively appealing species are likely to be more popular with the kind of people usually targeted by conservation campaigns than those species with lower scores, it is unlikely that the mean represents the tipping-point of public enthusiasm. The 'top ambassador' species, which have particularly high appeal scores, may represent a more likely subset of species with which to engage the public.

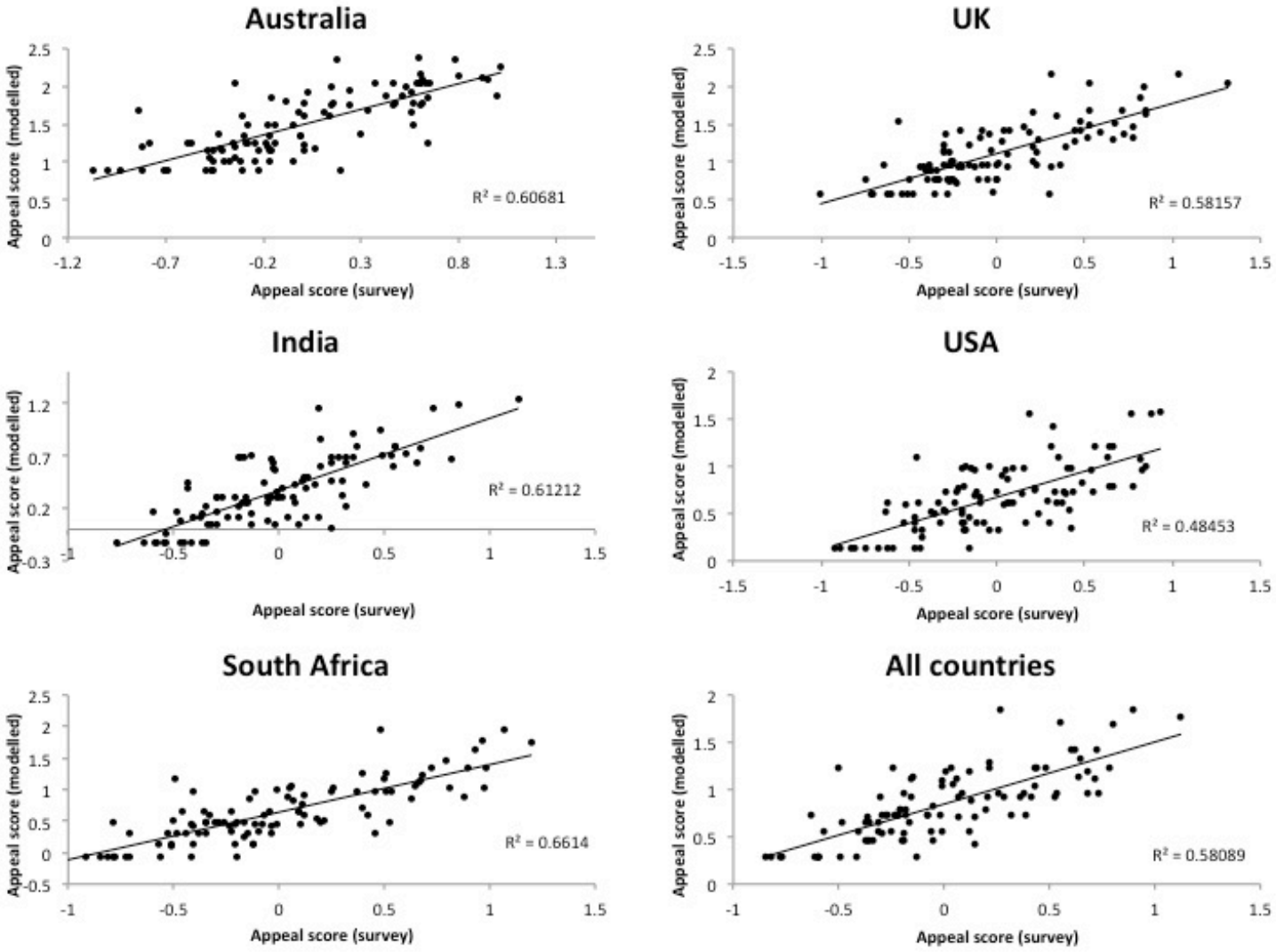

Figure 2. Plots of modelled appeal scores vs direct survey responses from (Macdonald et al. 2015).

Identifying ambassador and top ambassador species

Plotting efficiency and appeal scores revealed 331 potential ambassador species when using data from all respondents collectively. When we examined respondents from each country separately we found 256 'ambassador' species according to Australian respondents, 331 from respondents in India, 338 from South Africans, 240 from people in the UK, and 338

from those surveyed in the USA. In each country, only a very small group of species reached the criteria of being "top ambassadors", having both efficiency and appeal scores more than 1 standard deviation above the mean (Australia 23, India 32, South Africa 33, UK 26, USA 77, all countries 27; figure 3, figure 4).

Carnivores were also particularly well represented as top ambassadors. Over three-quarters (76.6%) of mammals categorised as top ambassadors using data from the USA survey were Carnivores, and the figure was close to 70% for Australia (69.6%) and UK (69.2%) and all countries combined (66.7%). Although the figure was lower for South African and Indian respondents (57.6% and 56.3% respectively), it is striking that in all countries, over half the 'top ambassador' species were Carnivores, despite them only representing 5% of the sample. The puma (*Puma concolor*) was the highest ranking ambassador species from the Indian, South African, UK and USA surveys, as well as across all countries combined. It was the second highest ranked species from the Australian survey, while the leopard (*Panthera pardus*) was the top ranking ambassador species from the Australian respondents and ranked 2nd across the remaining countries. Both species had high efficiency scores, with their wide ranges overlapping not only a large number of species (puma: 1442, leopard: 1701), but also a large overlap with species with high EDGE scores. Both species also showed high appeal scores, with the leopard ranked in the top 50 species by respondents from all countries apart from Australia: among USA respondents it was 16th, UK and South African respondents both ranked it 17th as did all respondents combined, while Indians ranked it 22nd and Australians 78th. Similarly, the puma was ranked in the top 100 species by respondents

from all countries apart from Australia (rankings were 26th in USA, 73rd in UK and South Africa, 82nd in South Africa and 490th in Australia, 29th in all countries; figure 3).

Ambassador species have the potential to be used as standard-bearers for the conservation of large numbers of other valuable species. Mammals identified as ambassadors from the UK survey overlapped with the highest number of other species on average (543.9), and even ambassadors identified by South African and USA respondents (which overlapped fewest species) overlapped with an average of 530 species. The z.'efficiency scores' for ambassadors ranged from 1.284 (in the South African and USA surveys) to a high of 1.357 from the UK survey.

Worker, celebrity and hitchhiker species

We divided the non-ambassador species into three alternative categories depending on their relative appeal and efficiency scores. Species with above-average efficiency scores but below-average appeal scores are termed "worker species". Approximately 20% of species examined (Aus: 20.5%, Ind: 18.7%, SA: 18.6%, UK: 20.8%, USA:18.6%, All countries:18.7%) fall into this category, which tends to be dominated by commensal rodents and bats with wide global distributions. On average worker species overlap around 500 species (Aus: 508.7, Ind: 504.1, SA: 504.5, UK: 503.7, USA: 504.5, All countries 504.1) species, and have average efficiency scores ranging from of 1.131 (UK) to 1.148 (AUS). These species currently have very little potential for conservation marketing, but if strategies can be found to raise their profile then their wide distributions and high efficiency scores might make them useful species for conservation marketing. An example is the Brazilian free-tailed bat (*Tadarida*

brasiliensis) that overlaps with an impressive 1376 species (the fourth highest of any terrestrial mammal examined, and more than double the average for ambassador species, Table 1), but has below average appeal across all regions considered.

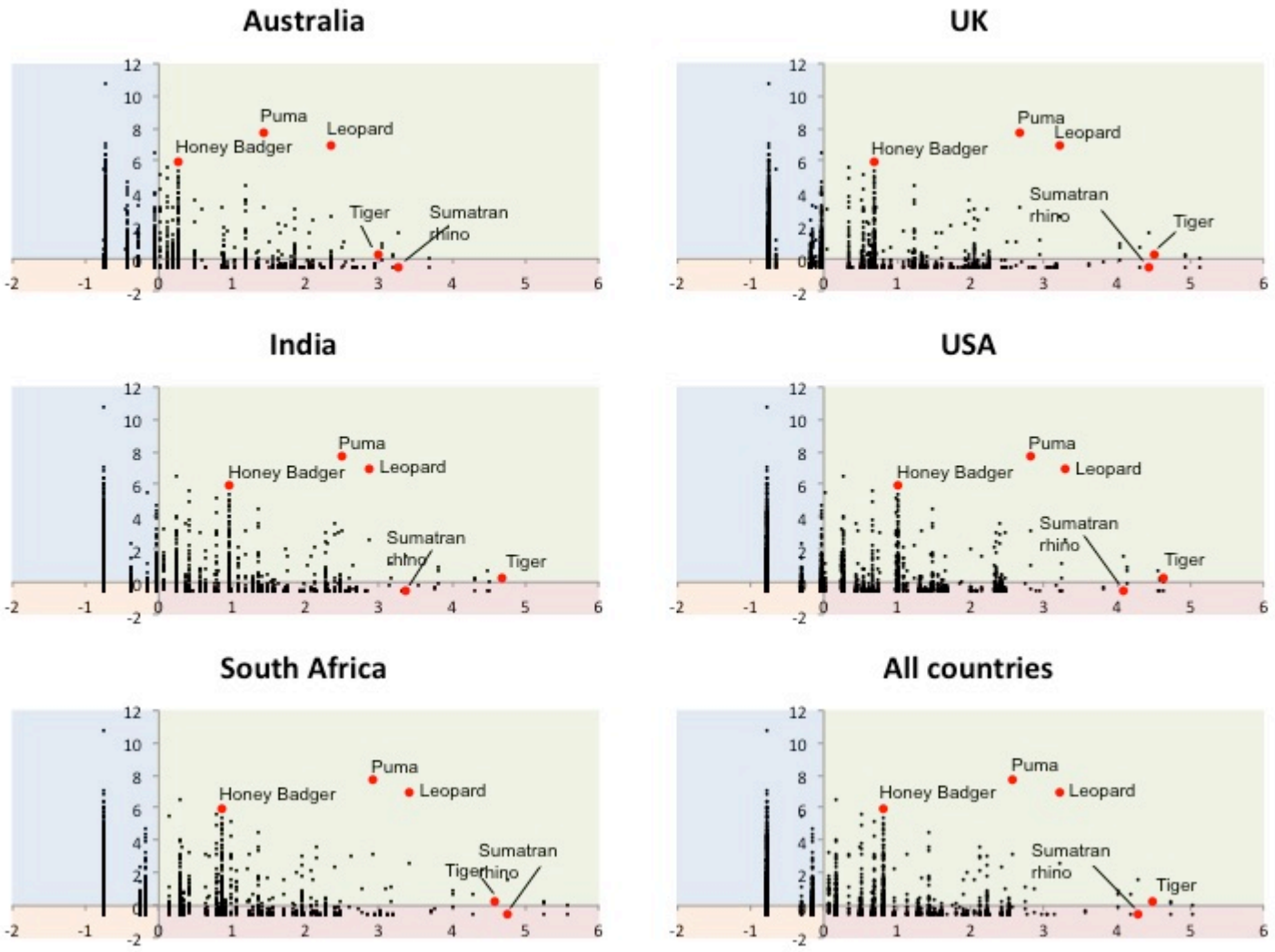

Figure 3. The distribution of species on the axes of standardised appeal and standardised efficiency scores for each country. Quadrants of the graphs are shaded in green to illustrate Ambassador (green), worker (blue), celebrity (orange) and hitchhiker (red) species.

At the other end of the spectrum, there are low-efficiency but highly appealing species that tend to be viewed very favourably by the public, but they are less likely to confer flagship benefits to a wide range of additional species, at least within the extent of their distribution. We describe these species, which have above-average appeal scores but below-average efficiency species as 'celebrity' species. Approximately 30% of species fall into this category (Aus: 30.5%, Ind: 29.7%, SA: 29.9%, UK: 27.2%, USA: 29.9%, All countries: 29.7%), and on average they overlap between 125 (UK) and 129 (Ind) species and have an average efficiency score between -0.478 (AUS) and -0.466 (SA and USA). These species currently have high potential for conservation marketing, but their applicability, as flagships for other species may be limited. These species are typified by the several rhino species including the Indian rhinoceros (*Rhinoceros unicornis*) that have very high appeal scores, but only overlaps with 173 other species, with similar patterns seen for the Sumatran rhinoceros (*Dicerorhinus sumatrensis*) and the Javan rhinoceros (*Rhinoceros sondaicus*). Similarly, the Iberian lynx (*Lynx pardinus*) receives significant attention as the only critically endangered cat, and has a high appeal score, however, it is extremely range-restricted and only overlaps 47 other species and has below average efficiency.

		Number of species	Proportion considered threatened by ICUN	Mean EDGE score	Proportion of species in the top quartile of EDGE scores	Mean number of species intersected	Mean z.efficiency score	Mean z.appeal score
Australia	Ambassador	256	21.9	2.89	28.9	524	1.286	0.677
	Celebrity	1316	73.2	3.74	70.7	126	-0.478	1.246
	Hitchiker	1864	0.0	2.21	2.1	178	-0.384	-0.671
	Worker	884	0.0	2.29	4.1	509	1.148	-0.637
India	Ambassador	331	16.9	2.76	23.3	532	1.288	0.960
	Celebrity	1283	75.1	3.70	70.3	129	-0.467	1.157
	Hitchiker	1897	0.0	2.26	3.6	175	-0.393	-0.667
	Worker	809	0.0	2.29	4.1	504	1.134	-0.663
South Africa	Ambassador	338	16.6	2.75	23.1	530	1.284	0.984
	Celebrity	1293	74.5	3.69	69.9	129	-0.466	1.120
	Hitchiker	1887	0.0	2.26	3.5	175	-0.393	-0.660
	Worker	802	0.0	2.29	4.0	504	1.134	-0.667
UK	Ambassador	240	23.3	2.84	26.7	544	1.357	1.055
	Celebrity	1173	82.1	3.83	76.5	125	-0.477	1.279
	Hitchiker	2007	0.0	2.26	3.6	175	-0.391	-0.610
	Worker	900	0.0	2.32	5.1	504	1.131	-0.589
USA	Ambassador	338	16.6	2.75	23.1	530	1.284	1.032
	Celebrity	1293	74.5	3.69	69.9	129	-0.466	1.136
	Hitchiker	1887	0.0	2.26	3.5	175	-0.393	-0.676
	Worker	802	0.0	2.29	4.0	504	1.134	-0.676
All countries	Ambassador	331	16.9	2.76	23.1	532	1.288	0.905
	Celebrity	1283	75.1	3.70	69.9	129	-0.467	1.190
	Hitchiker	1897	0.0	2.26	3.5	175	-0.393	-0.672
	Worker	809	0.0	2.29	4.0	504	1.134	-0.682

Table 1. Summary data for each category in each country

Nearly half (between 43.1% (Aus) and 46.5% (UK)) of the mammals examined scored below-average on both efficiency and appeal, and are typified by small species with limited spatial distributions. We refer to these low appeal, low efficiency species as hitchhiker species as they are likely to depend on the presence of other species for effective conservation campaigning. These species tend to overlap relatively few other species (from 175 (Ind and USA) to 178 (AUS)) and have average efficiency scores ranging from -0.393 (SA, USA and All countries) to -0.384 (AUS). As a group, these species tend to be of low conservation priority in themselves (with a mean EDGE score between 2.21 (AUS) and 2.26 in all other regions – below the mean EDGE score for all species of 2.73). These species are therefore unlikely to be chosen to front global conservation campaigns.

In general, the species identified as potential ambassador species were not necessarily high conservation value species in their own right. Only between 16.6% (SA and USA) and 23.3% (UK) of ambassador species were considered threatened by the IUCN in comparison to between 73.2% (AUS) to 82.1% (UK) of Celebrity species or 23.6% of all mammals in our sample. Similarly, between 23.1 (SA and USA) and 28.9% (IND) of ambassador species were in the top quartile of EDGE scores, compared to 69.9 (SA and USA) to 76.5% (UK) of celebrity species. A small proportion of hitch-hiker (2.1% (AUS) - 3.6% (UK and All countries) and worker species (4.0 (SA and USA) – 5.1% (UK)) were also identified as occurring in the top quartile of EDGE scores.

Summary data for each category in each country can be seen in Table 1, while full data for each of the 4320 species is available in the supplementary material.

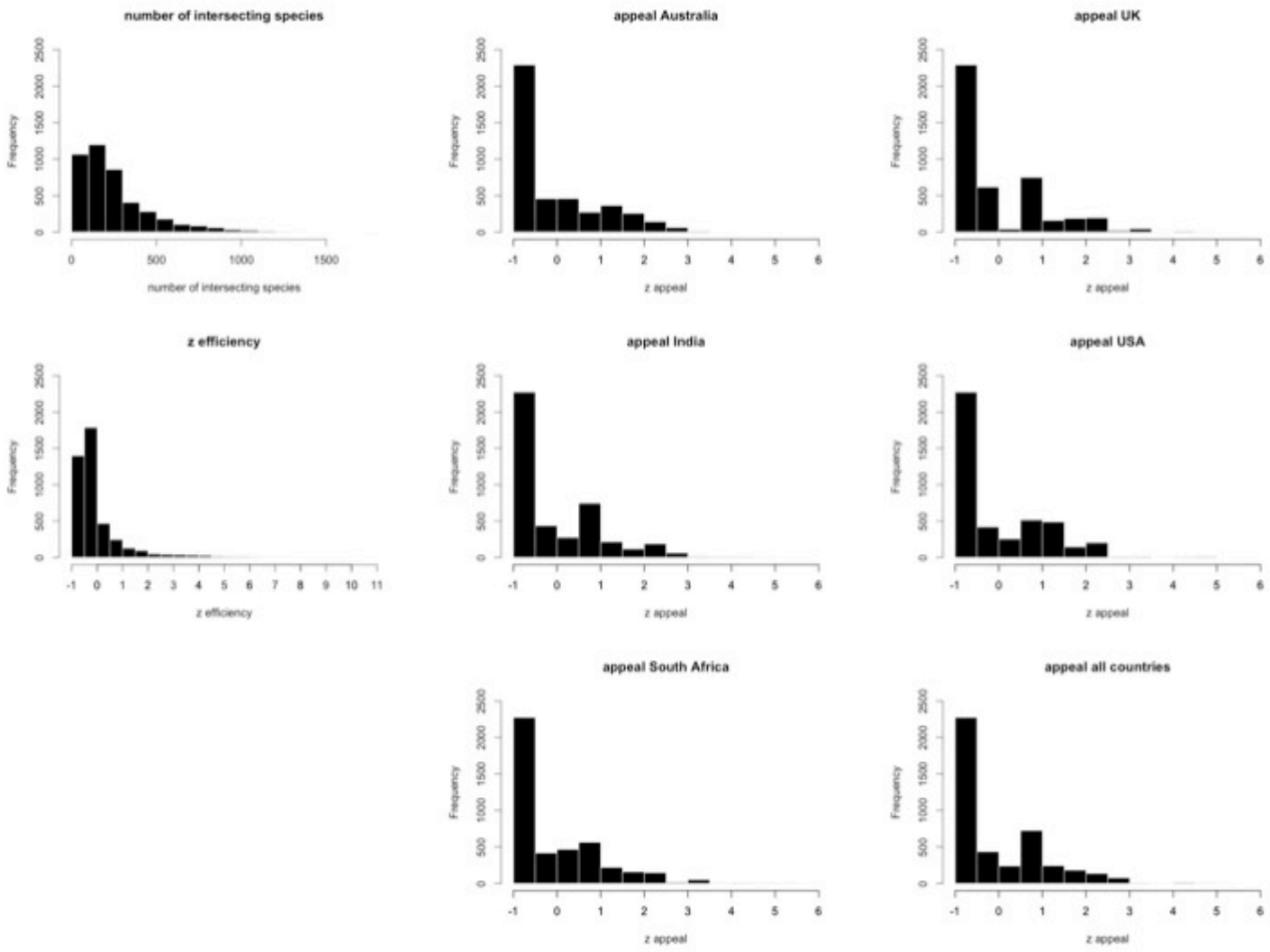

Figure 4. Frequency distributions showing the numbers of species with various efficiency and appeal scores for each country. These distributions demonstrate the skewed nature of appeal with very many species showing low appeal with very few species with high appeal scores.

Discussion

Worldwide, people are usually biased in terms of the species that they favour for conservation, and these biases are often influenced by both the attributes of the focal species (Macdonald et al. 2015; Veríssimo et al. 2009) as well as their cultural and experiential backgrounds (Bowen-Jones & Entwistle 2002; Takahashi et al. 2012). Conservation marketers should therefore seek to design targeted conservation campaigns tailored to the specific stakeholder group, and appropriate to the conservation issue at hand (Barua et al. 2011). However, only a tiny proportion of the world's species are sufficiently charismatic to catch the public's attention (in this context, by 'public' we specifically refer to the politically engaged middle class likely to respond to conservation campaigns, and targeted by the survey of (Macdonald et al. 2015)), and flagship species therefore need to act not only as emblems for particular issues, but also have the potential to act as flagships for other less appealing species. Under these circumstances it is reasonable to assume that a species would be better positioned to act as a flagship for its sympatriots than for distant species, additionally, it is reasonable to assume that species that exist in regions of high biodiversity might receive a small boost to their marketability from the high conservation priority of their environment. In this paper we propose that conservation marketers could increase the impact and flexibility of their flagship species by considering their ability to act as ambassadors for the wider community of sympatric species.

Our analysis allows us to plot 4320 terrestrial mammal species against two axes, their appeal, and their efficiency (a measure of the level of threat and endemism within a species' range;

Figure 3). This enabled us to quantify four broad categories of terrestrial mammals in terms of their flagship potential. Those with: high appeal and high efficiency (ambassadors); high appeal and low efficiency (celebrities); low appeal and low efficiency (hitch-hikers); low appeal and high efficiency (workers). The ambassador concept builds on the definition of "flagship umbrella" species (Caro 2010) to consider the potential of certain species to act as flagships for their wider community of sympatric species.

This study represents the first time so many mammals have been given comparable appeal scores based on systematic analysis of key attributes that make species attractive. We conducted our survey across 5 English-speaking countries, and here we present the results from each country separately in order to highlight how small differences in attitudes between stakeholder groups affects our results, we also present the results of all countries combined. Given the huge potential heterogeneity of attitudes found in a large political unit such as a country, we acknowledge it is unlikely that our country-level appeal scores are totally representative of all Australians, Indians etc., but our approach did target a broad section of society, and therefore can reveal species that could be used as emblems of broad based national conservation campaigns. Furthermore, despite the differences in appeal between the five countries we surveyed, there were still clear trends that held true when we considered the respondents' scores for all countries combined. As such, the ambassador species we identified, and particularly the top ambassadors, are strong candidates for international marketing campaigns to garner support for underfunded conservation efforts. Conducting the survey online may bias the respondents towards affluence but may also increase the likelihood that they were politically engaged and able to exert political leverage

regarding environmental matters (Macdonald et al. 2015). The results may not necessarily be representative of the attitudes of all potential stakeholders within each country, and they could certainly be improved with more detailed local analyses, but we feel that they are sufficiently robust to be a useful guide to conservation marketers.

In this study we used spatial data on species ranges from the IUCN (IUCN 2010), and their endangerment and evolutionary distinctiveness from the EDGE index (Isaac et al. 2007). Both of these databases attempt to offer global coverage, and consequently both have limitations. For example the IUCN database simply provides binary data about a species' supposed distribution and has been frequently criticised for introducing both omission and commission errors (Rondinini et al. 2006). These errors have important implications for conservation planning and prioritisation, however these maps remain widely used and these omission and commission errors do not have significant implications for this analysis where we are not highlighting the specific areas that should be prioritized for conservation but are simply attempting to highlight an additional consideration for conservation marketers who are using species as flagships for conservation at broad scales. Similarly, the EDGE database produces just one of many potential measures for assessing a species' conservation priority, referring to both their endangerment and their evolutionary distinctiveness. In their paper (Isaac et al. 2007) use the equation "*EDGE = ln(1+ED) + GE * ln(2)*" (where ED indicates a score for evolutionary distinctiveness and GE is a score for global endangerment based on IUCN redlist categories) and state that "*EDGE scores are therefore equivalent to a loge-transformation of the species-specific expected loss of evolutionary history in which each increment of Red List category represents a doubling (eln(2)) of extinction risk.*" We feel

that it is worth pointing out, that the EDGE equation as written by Isaac does not result in a doubling of extinction risk with each increment of red list category, rather each increment of red list category results in a uniform increase of (ln(2) =) 0.69 with each increment of red list category. This could be solved by either using the equation "*ln(EDGE) = ln(1+ED) + GE * ln(2)*" or by simply doubling the score given to each IUCN category (e.g. 1,2,4,8,16 as in (Dickman et al. 2015)). In any case, the specifics of the equation do not have significant implications for this paper and we chose to use EDGE scores as they remain a widely used and interesting approach to assessing conservation priority of species. Our approach is global and we hope to provide food for thought for readers considering what attributes might make a species a useful flagship for conservation, however we acknowledge that the scale of our analysis necessarily means that it cannot capture fine scale local intricacies, and cultural variations in peoples' preferences. Nevertheless we hope that the broad trends remain interesting and robust.

Efficiency

The efficiency score, calculated for each species, is a measure of how many other sympatric species fall within its range, the extent of that range overlap, and the significance of those sympatric species in terms of endangerment and phylogenetic distinctiveness. High-efficiency species tended to be wide ranging habitat generalists that are able to survive in a range of habitats. The house mouse (*Mus musculus*) had the highest efficiency score, living almost everywhere that people have transported it, but clearly the house mouse is far from a symbol of conservation (and no amount of "education" or marketing spin is likely to make it

one). This illustrates the point that to qualify as an ambassador species requires a combination of attributes, hence our combination of both efficiency and appeal.

Appeal

Using the same dataset of survey responses as Macdonald et al. (2015) we estimate appeal for all terrestrial mammals. Following previous studies that have highlighted cultural differences in stakeholder attitudes (Bowen-Jones & Entwistle 2002), Macdonald et al. (2015) found that analysing data from each country separately produced more robust results than treating all respondents as a single cohesive group. We therefore calculated appeal scores for all mammals from based on the separate models from each country.

Overall all countries showed a similar broad trend in terms of the parameter estimates for each attribute (figure 1). Large, rare species with forward facing eyes and that posed a potential threat to humans had the highest appeal across all countries, and thus some species ranked consistently highly (e.g. Indian elephant and tiger), while appeal for species such as the polar bear appeared much more variable – in this case driven by Australia's uniquely low preference for species weighing between 100-800kg. interestingly, species in the 20-40kg size range showed an unexpected dip in appeal across the all regions. R^2 values comparing the predicted appeal scores with those derived from actual survey responses were generally in the region of 60% (with only the USA exhibiting an R^2 below 50%) showing how a simple set of just 4 variables can provide robust broad scale predictions of species appeal. However, the remaining 40% of unexplained variability highlights the extent of fine

scale variability in stakeholder attitudes – readers should therefore be cautious of making predictions at too fine a scale on the basis of these data.

Ambassadors

Variation in appeal scores resulted in a different suite of mammals being identified as ambassador species in each country, however certain trends are apparent. Firstly wide-ranging Carnivores are disproportionately represented among top ambassador species – unsurprisingly this supports (Macdonald et al. 2015) who found felids to be particularly popular, but is also in line with the many private companies that use large Carnivores as an emblem (e.g. Jaguar cars, Puma sports apparel, Tiger beer etc). What is more interesting is that these species combine this high appeal with high efficiency scores, reflecting an unusually high degree of threat within their distributions.

Interestingly however, ambassador species do not necessarily have to be of high conservation priority themselves. Between 16 and 22% of ambassador species are considered threatened by the IUCN – this is similar to the IUCN 2015 Red List 'best estimate' that 26% of mammals globally are threatened. This was markedly different from 'celebrity' species with high appeal but low efficiency – around 70% of those were threatened, however these species may have less flexibility to act as flagships for other species within their range. Although conservation campaigns often focus on critically endangered species, such as the saola (*Pseudoryx ngehtinhensis*) or Western gorilla (*Gorilla gorilla*) and threat status is undoubtedly a strong component in a species' appeal, our results suggest that conservation marketers should not confine their efforts to these species alone.

Celebrities, Workers and Hitch-hikers

The mammals that do not meet our criteria of ambassador species are also interesting, and their ranking in both appeal and efficiency stimulates thinking about approaches to motivating their conservation. We refer to species with high appeal, but low efficiency, such as the Indian water buffalo, polar bear, Western gorilla and giant panda as 'celebrity species' since many of these species already receive intense attention focussed entirely, or almost entirely, on their particular plight. In many cases this attention may be justified where they are both culturally appropriate and focussed on a specific issue, however they may also have limited capacity to act as a flagship for wider biodiversity within their geographic extent. However, for some of these species, their appeal transcends considerations of efficiency and they have become icons representing broad international conservation issues, such as the ubiquitously known WWF panda, or the international symbolism of the polar bear as an emblem for climate change. Thus it is likely to be valuable to capitalise on the public appeal of celebrity species, both for their individual benefit and to generate and maintain public interest in wider conservation issues.

Worker species score highly on efficiency, but have low public appeal characterised by widely distributed rodents and bats, although Australians might also consider a species such as the grey wolf to fall into this category. Conservation campaigns are unlikely to use these species as flagships, due to their generally lower appeal. However their high efficiency scores suggest that if a positive media campaign could raise their appeal, or find a target audience

with whom they have particular resonance, then perhaps they could metamorphose into ambassador species in the future.

Finally, hitchhiker species neither keep interesting company nor attract attention, so their direct conservation marketing is likely to be difficult. None of the 1886 hitchhiker species are classed as threatened by the IUCN, however several have extremely high evolutionary distinctiveness, e.g. the common mole rat (*Cryptomys hottentotus*) which has one of the highest EDGE scores while being considered a hitchhiker in all countries. These species are good candidates for those that might benefit most from the marketability of ambassador species.

Conclusions

This study is a first attempt to highlight a link between a species' appeal, and their ability to act as flagship species for the potentially diverse species with which they co-occur. Many authors have discussed the emerging importance of conservation marketing (e.g. Veríssimo and McKinley (2016)), and several have attempted to identify suites of characteristics that influence a species' charisma (e.g. (Lorimer 2007; Macdonald et al. 2015)). In this paper we hope to build on these concepts and propose that species that occur in areas of high conservation priority may present added value in terms of their potential for conservation marketing. In addition to their native appeal, these species may be more marketable as a result of them living in diverse and biologically important regions.

We attempt to capture this relationship by plotting 4320 terrestrial mammal species on two axes, of appeal and efficiency. This is the first study to attempt to estimate an index of species appeal for all terrestrial mammals, and efficiency scores were calculated to reflect the level of threat within a species' distribution. We develop a unique categorisation for mammals on the basis of these two metrics such that species with high appeal and high efficiency scores are termed ambassador species to reflect the idea that these species may be effective at generating attention for wider biodiversity within their distribution. Species with high appeal scores but low efficiency scores are termed celebrities, species with high efficiency but low appeal are termed worker species, and finally species with low appeal and low efficiency scores are termed hitchhiker species. How conservationists choose to market each species may be influenced by their relative categorisation.

When planning conservation marketing campaigns it is vital that the campaign is both targeted at a particular issue (Barua et al. 2011) and is locally appropriate (Bowen-Jones & Entwistle 2002). We have therefore presented appeal scores separately for each country surveyed in addition to a more general index that considers all countries combined. Appeal scores were extrapolated from surveys conducted by Macdonald et al. (2015) considering the appeal of 100 terrestrial mammals among respondents from Australia, India, South Africa, the UK and USA. These surveys were conducted online and were targeted to access a wide subset of society and hopefully reflect broad national trends, however online surveys may bias the results towards younger and more affluent respondents.

Efficiency scores were calculated to reflect the level of threat across a species' distribution. A species could therefore have a high efficiency score either by overlapping with a few high priority species, or alternatively by overlapping many low priority species. For example the nine banded armadillo (*Dasypus novemcinctus*) and the leopard have very similar efficiency scores despite the leopard overlapping with 453 fewer species. This approach was used to reflect the potential ability of wide ranging species to act as flagships for a large number of sympatric species across their range, however future studies might also consider more localised metrics of efficiency. Similarly, not all species with high appeal scores will be obvious immediate candidates for conservation marketing campaigns - these scores are broad scale extrapolations based on just 4 broad attributes. However, they show good agreement with actual survey responses (figure 2), and the high appeal species that are not currently being used as flagships could be seen as "Cinderella species" or species with unutilised potential (Smith et al. 2012).

We find that Carnivores are disproportionally likely to be classified as ambassador species, but that ambassador species are not necessarily high value conservation species themselves. While rarity is frequently a contributor to a species' appeal (Courchamp et al. 2006; Macdonald et al. 2015), this result highlights how conservation marketers could widen their net in order to identify a wider variety of potential flagship species. In contrast, celebrity species were disproportionately likely to be classified as threatened by the IUCN. This is potentially a result of the fact that range restricted species are more vulnerable to exogenous threats while at the same time they are less likely to occur with a large number of sympatric species. These species are therefore more likely to be useful emblems for

conservation marketing campaigns targeting broader global issues and highlights how different approaches to conservation marketing might apply to the different categories of species.

We hope that in a world that is increasingly interconnected and influenced by viral marketing campaigns, that this new approach sheds fresh light on considering how species might best be marketed for conservation.

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Chapter 4

Patterns and predictions of deforestation risk in Borneo

A modified version of this chapter is under review at *Landscape Ecology*

Abstract

Context. The forests of Borneo are among the most biodiverse on the planet, however, recent studies show that 30% of those forests have been lost since 1973.

Objectives. In order for conservationists to plan adequately to conserve the remaining forest areas, it is vital that they have reliable, spatially-explicit data on the areas that are likely to be most at risk. Our objective was to identify the multiple-scale drivers of recent deforestation and predict future deforestation risk across Borneo.

Methods. We used Random Forest machine learning in a multi-scale approach to assess topographical and landscape composition correlates of forest loss in Borneo between the years 2000 and 2010, and applied the model to predict the spatial pattern of deforestation risk in 2020. This analysis is the first model of forest loss to explicitly model the impact of landscape composition and configuration at multiple spatial scales.

Results. We are able to predict areas of forest loss across Borneo with an overall accuracy of > 86%. We predict that 37% of the remaining forest in Borneo will have a greater than 25% risk of being cleared by 2020 and that approximately 13% (an area of 11,167 km^2) will have a greater than 50% chance of being lost in that time frame.

Conclusions. These results suggest immense immanent risk to Borneo's forests, but we hope that our predictions will inform conservation policy with regard to the rates, patterns, drivers and future risk of forest loss, as well as provide a framework for similar deforestation studies and assessments.

Keywords: Borneo, forest cover, land-use change, forest loss, deforestation risk, Random Forests

Introduction

Forests are a vital part of the global ecosystem, and changes in forest cover affect the delivery of important ecosystem services, including biodiversity richness (Barlow *et al.*, 2007, Myers *et al.*, 2000, Pimm & Raven, 2000, Wilcove *et al.*, 2013), climate regulation (Nepstad *et al.*, 2008, Pan *et al.*, 2011, Pielke *et al.*, 2002), carbon storage (Asner *et al.*, 2010, Ciais *et al.*, 2013, van der Werf *et al.*, 2009), and water supplies (Foley *et al.*, 2005). Recent analysis of earth observation satellite data suggest that approximately 230 million ha of forest were lost due to disturbance globally in the period 2000-2012 (c.19million ha per year) with the greatest loss occurring in the tropics (Hansen *et al.*, 2013). Rates of deforestation in South East Asia are high and accelerating, with Indonesia showing the largest recent increase in the rate of forest loss globally, while Malaysia has the highest level of forest loss in relation to land area (Hansen *et al.*, 2013). Harris *et al.* (2012) estimate that 32% of emissions from land-use change in the tropics arose in South and South-east Asia, and Indonesia was the second highest emitter, accounting for 13% of total emissions from deforestation. In the light of these impacts and international commitments to reduce carbon emissions from deforestation and degradation (REDD+) in developing countries it is important to understand the dynamics of land-use change and predict which areas are at highest risk in the future.

Multiple studies have attempted to quantify and predict future deforestation, most notably in the Amazon basin (Rosa *et al.*, 2013, Soares-Filho *et al.*, 2006), and in other forests around the world (Rideout *et al.*, 2013, Vieilledent *et al.*, 2013); however, to date we know of no analyses that predict future forest loss in Borneo.

Analyses of forest loss published to date employ a range of statistical techniques to identify the correlates of past deforestation and predict these trends into the future, including logistic regressions (Chowdhury, 2006, Echeverria *et al.*, 2008), genetic algorithms (Soares-Filho *et al.*, 2013, Venema *et al.*, 2005), weights of evidence (Maeda *et al.*, 2011, Soares-Filho *et al.*, 2010) and cellular automata (Thapa *et al.*, 2013). These models are based on a number of environmental and anthropogenic landscape features that are thought to drive deforestation rates. Commonly, these include distance to important features, as well as measures of slope and elevation.

In this study, we use Random Forests machine learning in a multi-scale framework to predict future risk of forest loss in Borneo. Random Forests (RF; (Breiman, 2001a) is increasingly used in a range of applications including digital soil mapping (Grimm *et al.*, 2008), forest biomass mapping (Baccini *et al.*, 2012), and others given its often superior performance compared to other methods (Evans *et al.*, 2011). RF is also gaining prominence in land-use classification (e.g., (Aide *et al.*, 2013, Grinand *et al.*, 2013), where it outperforms Classification and Regression Trees (CART; (Rodriguez-Galiano *et al.*, 2012) and maximum likelihood classifiers (Schneider, 2012). Nonparametric procedures like RF are particularly effective at identifying complex multivariate associations, such as those that affect patterns of forest loss. In addition, (Breiman, 2001b) argues that assumptions in parametric models, such as independence and multivariate-normality, are frequently violated in ecological data sets, whereas algorithmic approaches are not affected by these violations and provide more reliable results in the context of complex, non-linear relationships, autocorrelation, and variable interaction across temporal and spatial scales (Evans *et al.*, 2011).

The idea that ecological patterns and processes interact across scales in space and time is now widely recognised (McGarigal *et al.*, 2016). Despite this widespread recognition, a review of the current literature found that most habitat ecology papers fail to address multiple spatial pattern-process relationships (McGarigal *et al.*, 2016). While many recent studies of land-use change allude to spatial scales, they do so implicitly by including distance to various landscape features (roads, rivers, population center, etc.) as a metric (e.g., (Rideout *et al.*, 2013, Rosa *et al.*, 2013, Vieilledent *et al.*, 2013). Additionally, while several analyses consider some element of landscape composition (e.g., Rosa *et al.* (2013), Vieilledent *et al.* (2013), Rideout *et al.* (2013)), few studies consider the composition and configuration of the multi-scale neighbourhood around a point as a predictor variable. This analysis is the first model of forest loss to explicitly model the impact of landscape composition and configuration at multiple spatial scales.

The goal of this study is to identify the multiple-scale drivers of forest loss across the full extent of Borneo between 2000 and 2010, and to then apply the model to predict risk of forest loss between 2010 and 2020. We had several hypotheses. First, we expected that risk of forest loss would be related to landscape variables similarly in each country. Second, we expected that topography would be a strong predictor of the risk of forest loss, with high risk at low elevations and flat areas, and low risk at higher elevations and steep terrain. Third, we expected that the extent of past forest loss in the surrounding region would be strongly associated with risk of future loss. Fourth, we predicted that protected area status would be a strong predictor of the risk of forest loss, with protected areas experiencing low loss, regardless of their landscape context. Fifth, we

predicted that human population parameters such as distance to large settlements and local population density would have weaker but important contributions to the risk of forest loss. Sixth, we predicted that topographical factors would be most influential at broad spatial scales, while land cover and past forest loss would predict risk at finer scales.

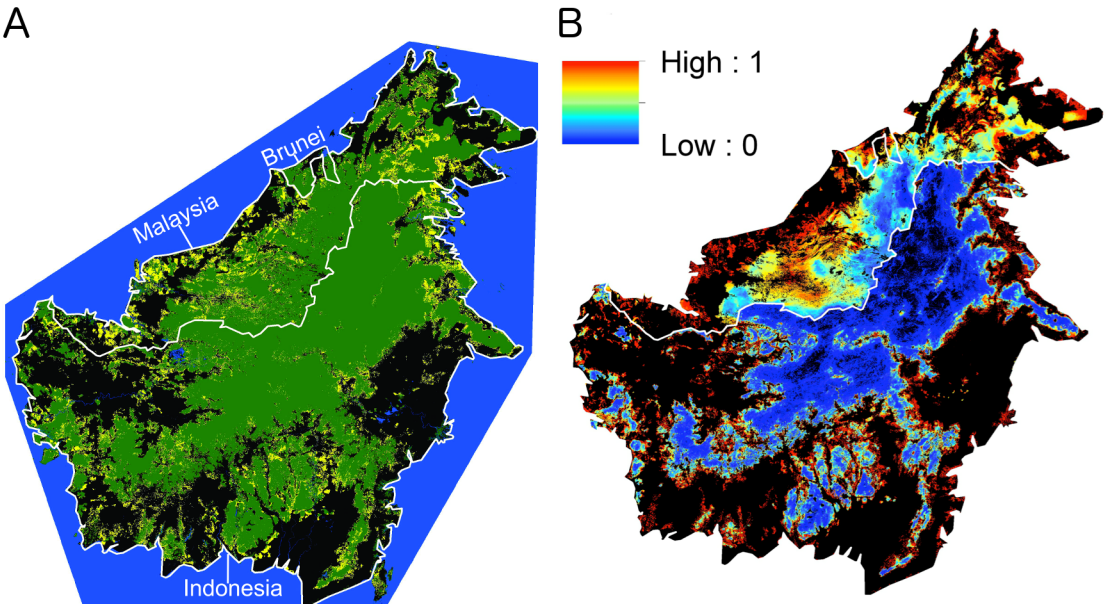

Figure 1. (A) Map of Borneo showing (1) areas deforested between 2000 and 2010 in yellow, (2) areas that were forest in both dates in green, (3) areas that were disturbed by human land use change prior to 2000 in black. (B) Map of Borneo showing risk deforestation risk in 2020. Red represents areas that are at highest risk while blue represents areas that are at lowest risk.

Methods

Study Area

This analysis covers the entire island of Borneo, consisting of Brunei, the Indonesian provinces of Kalimantan and Malaysian provinces of Sabah and Sarawak (Figure 1A). The extent is 731,058 km^2.

Land Cover Change Data for 2000-2010

We utilised the land cover maps produced for the years 2000 and 2010 by the Centre for Remote Imaging, Sensing and Processing (CRISP;(Miettinen *et al.*, 2011, Miettinen *et al.*, 2012); Figure 1A). These maps were based on MODIS Surface Reflectance Product images (NASA, 2010), Shuttle Radar Topography Mission (SRTM) 90 m version 4 digital elevation information (Jarvis *et al.*, 2006) and several peatland distribution maps (Selvaradjou *et al.*, 2005, Wahyunto *et al.*, 2006, Wahyunto *et al.*, 2003, Wahyunto *et al.*, 2004). A three step classification process was used to classify the landscape into the following 13 categories: water, mangrove, peat swamp forest, lowland forest, lower montane forest, upper montane forest, plantation/regrowth, lowland mosaic, montane mosaic, lowland open, montane open, urban and large scale palm plantation (Miettinen *et al.*, 2011, Miettinen *et al.*, 2012). Accuracy assessment for these maps, conducted by the authors, found overall accuracies of 83% for 2000 and 85% for 2010, with class accuracies between 75% and 85% for the non-forest classes and up to 97% for the forest classes (Miettinen *et al.*, 2011, Miettinen *et al.*, 2012). The authors report that largest confusion

in the classification took place between the plantation/regrowth, lowland mosaic and lowland open classes; this was not surprising given the similarity between these classes and the fact that they often occur in close proximity to one another leading to misclassifications at the class boundaries. Because all three of these classes would later be reclassified as not-forest for our analyses, this confusion was judged to be acceptable. Overall, the accuracy assessment of these maps compares favourably to other studies (e.g., Rodriguez-Galiano *et al.* (2012): 92%, Rozenstein and Karnieli (2011): 81%, Clark *et al.* (2010): 79.3%), Friedl *et al.* (2010): 75%) and the map provides reliable regional-level information on the status of land cover in Borneo (Miettinen *et al.*, 2012).

Response Variable for Analysis

Mangrove, peat swamp forest, lowland forest, lower montane forest and upper montane forest were reclassified to forest, while all other areas were considered to be non-forest for our analysis.

The response variable in our analysis was a binary GIS layer depicting areas of the study area that were forest in 2000 and became non-forest or regenerating forest in 2010 (value of 1 or "loss"), and areas that were forest in 2000 and remained forest in 2010 (value of 0 or "not-loss") (Figure 1A). We drew a spatially random sample of points from each of the "loss" and "not-loss" classes, resulting in a total sample of 279,809 points in the loss class, and 1,296,311 points in the not-loss class. This sample was drawn from the whole of Borneo and thus the proportion of loss to not-loss cells reflects the overall proportion of these land uses on Borneo.

Predictor Variables for Analysis

A priori, we proposed several environmental and anthropogenic variables as possible correlates of recent forest loss in the study area (Table 1). Anthropogenic variables included: distance to large population centres, defined as areas with greater than 100 people/km^2; regional population density, defined as the focal mean of population density within a 100 km radius; local population density defined as the point population density at the pixel scale of 250 m; and a map of designated protected areas.

Topographical variables included elevation from the ASTER DEM and several terrain complexity measures produced using the Geomorphometry and Gradient Metrics Toolbox (ArcGIS 10.0; (Evans & Oakleaf, 2012). These included: topographical roughness, which measures the topographical complexity of the landscape within a defined focal extent (Blaszczynski, 1997, Riley *et al.*, 1999), and relative slope position, which measures the relative position of the focal pixel within a defined extent on a gradient from valley bottom to ridge top (Evans *et al.*, 2014). Given that topographical factors may be related to deforestation at a range of spatial scales (Wiens, 1989), we calculated topographical roughness and relative slope position at six spatial extents including focal radii of 1 km, 10 km, 20 km, 30 km, 40 km and 50 km. These were chosen because 1km is represents a single pixel and its very near neighbours, 10, 20, 30, 40, 50 km span a range from local to regional neighbourhoods.

Table 1. Predictor Variables Used in the Analysis

Anthropogenic Variables			
Variable name	Description	Rational	Source
Local Population Density	Local population density calculated as the point population density at the pixel scale of 250m	Risk of forest loss hypothesised to be greater with increased local population due to increased demand and infrastructure (Carr, 2004, Vieilledent *et al.*, 2013)	CIESIN, CIAT (2005): Gridded Population of the World, Version 3
Regional Population Density	Regional population density calculated as the focal mean of local population density within a 100km radius	Risk of forest loss hypothesised to be greater with increased regional population due to increased demand and infrastructure (Carr, 2004, Vieilledent *et al.*, 2013)	CIESIN, CIAT (2005): Gridded Population of the World, Version 3
Distance to large population centre	Distance to large population centre, defined as areas with more than 100 people per square kilometre	Risk of forest loss hypothesised to be greater with proximity to large population centres population due to increased demand and infrastructure (Carr, 2004, Mon *et al.*, 2012, Vieilledent *et al.*, 2013)	CIESIN, CIAT (2005): Gridded Population of the World, Version 3
Protected Areas	Protected areas. A binary map with protected areas classified as 1 and other areas classified as 0.	Risk of forest loss hypothesised to be lower within protected areas (although some studies have reported no statistical difference in deforestation between timber concessions and protected areas (Gaveau *et al.*, 2013))	IUCN, UNEP-WCMC (2014), The World Database on Protected Areas
Topographical variables			
Variable name	Description	Rational	Source
Elevation	Point elevation from Aster DEM	Risk of forest loss hypothesised to decrease with elevation (Mon *et al.*, 2012)	NASA LPDAAC (2011) Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model Version 2 (GDEM V2)

Roughness[x]	Focal topographical roughness within radius x km. Values for x are: 1,10, 20, 30, 40, 50.	Risk of forest loss hypothesised to decrease with increased topographic roughness at a moderate scale of 10-20km	Geomorphology and Gradient Metrics Toolbox, http://evansmurphy.wix.com/evansspatial#!arcgis-gradient-metrics-toolbox/crro
Slope[x[	Focal relative slope position within radius x km. Values for x are: 1,10, 20, 30, 40, 50.	Risk of forest loss hypothesised to decrease with increased slope at a moderate scale of 10-20km (Gaveau *et al.*, 2013)	Geomorphology and Gradient Metrics Toolbox, http://evansmurphy.wix.com/evansspatial#!arcgis-gradient-metrics-toolbox/crro
Landscape Metrics			
Variable name	Description	Rational	Source
landuse[x] (e.g. water[10])	Percentage of the landscape class within radius x km. Landuse classes are: water, mangrove, peatswamp forest, lowland forest, lower montane forest, upper montane forest, plantation/regrowth, lowland mosaic, montane mosaic, lowland open, montane open, urban. Values for x are: 1,10, 20, 30, 40, 50.	Risk of forest loss hypothesised to increases with extent of previously deforested (not forest) cells area in the region surrounding the pixel. We expect that extremely local effects are probably minimal so the impact of previously deforested cells expected to be greatest at the scale of 10-30km.	FRAGSTATS analysis of reclassified Meittenen et al. (2011) land cover map
Aggregation[x]	Aggregation Index for the full landscape mosaic within radius x km. Values for x are: 1,10, 20, 30, 40, 50.	Risk of forest loss hypothesised to decrease with increased aggregation. Low aggregation index represents a highly fragmented landscape that is potentially more susceptible to forest loss.	FRAGSTATS analysis of reclassified Meittenen et al. (2011) land cover map

Edge[x]	Edge density for the full landscape mosaic within radius x km. Values for x are: 1,10, 20, 30, 40, 50.	Risk of forest loss hypothesised to increase with increased edge density. High edge density represents a highly fragmented landscape that is potentially more susceptible to forest loss.	FRAGSTATS analysis of reclassified Meittenen et al. (2011) land cover map
Patch[x]	Patch Density for the full landscape mosaic within radius x km. Values for x are: 1,10, 20, 30, 40, 50.	Risk of forest loss hypothesised to increase with increased patch density. High patch density represents a highly fragmented landscape that is potentially more susceptible to forest loss.	FRAGSTATS analysis of reclassified Meittenen et al. (2011) land cover map
Shannon[x]	Shannon's Diversity Index for the full landscape mosaic within radius x km. Values for x are: 1,10, 20, 30, 40, 50.	Risk of forest loss hypothesised to increase with increased Shannon's Diversity. High Shannon's Diversity represents a highly fragmented landscape that is potentially more susceptible to forest loss.	FRAGSTATS analysis of reclassified Meittenen et al. (2011) land cover map

We also included FRAGSTATS metrics quantifying the extent and configuration of different land cover classes across a range of focal extents as predictor variables. The classes used in the analysis include: (1) Water, (2) Mangrove, (3) Peatswamp Forest, (4) Lowland Forest, (5) Lower Montane Forest, (6) Upper Montane Forest, (7) Plantation or Regrowth, (8) Lowland Mosaic, (9) Montane Mosaic, (10) Lowland Open, (11) Montane Open, (12) Urban (Miettinen *et al.*, 2011, Miettinen *et al.*, 2012). For each of these classes we used FRAGSTATS 4.0 (McGarigal *et al.*, 2012) to calculate the percentage of the focal landscape covered by each class within the six focal window extents (1 km, 10 km, 20 km, 30 km, 40 km and 50 km). In addition to class-level percentage of the landscape in each cover class, we calculated four landscape-level metrics quantifying the structure of the full multi-class mosaic to assess how landscape complexity was related to deforestation risk. These landscape metrics were edge density (Edge[x]), patch density (Patch[x]), aggregation index (Aggregation[x]; which measures the compaction or aggregation of cover types), and Shannon's diversity index (Shannon[x]; which measures the diversity of the landscape mosaic within a window in terms of the richness and evenness of the cover types present). Each of these four metrics was also calculated for focal windows at the six spatial extents (1 km, 10 km, 20 km, 30 km, 40 km and 50 km). All spatial layers were resampled to a 500 m pixel size and projected to an Albers conformal conic projection for analysis.

Predictive Modelling with Random Forest

We used Random Forest machine learning to predict deforestation in 2010 from the 2000 landscape variables separately for each country within the study area (Brunei, Malaysia,

Indonesia), to assess how the drivers of deforestation may differ between nations. In theory it would have been possible to treat country as an explanatory variable within RF; however, since RF is a partitioning approach, the results would be the same as running the nations separately, countries were therefore treated separately to facilitate computation with a large dataset and facilitate interpretation.

Random Forests is a classification and regression tree (CART; (De'ath & Fabricius, 2000) based bootstrap method that corrects many of the known issues in CART, such as over-fitting (Breiman, 2001a, Cutler *et al.*, 2007), and provides very well-supported predictions with large numbers of independent variables (Cutler *et al.*, 2007). The model fit was assessed using the out-of-bag (OOB) error estimate (De'ath & Fabricius, 2000). The OOB involves withholding about one third of the sample from the bootstrapping process and then comparing the classification of these cells with the predictions generated by Random Forests. The OOB error is the median taken from an error distribution across the randomized trees.

We used a modelling approach developed by Evans and Cushman (2009) to predict occurrence probabilities of deforestation for each nation using the Random Forests method (Breiman, 2001a, Cutler *et al.*, 2007) as implemented in the package 'randomForest' (Liaw & Wiener, 2002) with R (R Development Core Team, 2008). We conducted the analysis in two steps. First, we evaluated the performance of each predictor variable across the multiple scales analysed to identify the scale at which each variable had the strongest ability to predict deforestation in 2010 from the landscape condition in 2000. To accomplish this, we ran a single Random Forest analysis for each

variable in each nation in which we used the Model Improvement Ratio (MIR; (Murphy *et al.*, 2010) to measure the relative predictive strength of each scale of the variable. The MIR calculates the permuted variable importance, represented by the mean decrease in OOB error, standardized from zero to one. We compared the MIR scores for all scales for each variable, and retained the scale that had the highest MIR score for further multivariate modelling.

In the second step we used Random Forest to develop multivariate models predicting probability of deforestation in each nation in 2010 as a function of landscape condition across the suite of scale-optimized variables. Previous studies (Chawla *et al.*, 2003, Chen *et al.*, 2004) demonstrated that imbalance between the proportion of presence and absence classes can cause bias in the prediction and model-fit. When an imbalanced sample is present the bootstrap of the data is biased towards the majority class, thus over-predicting the majority-class and under-predicting the minority. The resulting model fit can be deceptive, exhibiting very small overall OOB error due to very small errors in the majority as a result of extremely high cross-classification error from the minority class (Evans *et al.*, 2011). In the case of our analysis we had a total sample of 279,809 points in the deforested class, and 1,296,311 points in the not-deforested class. To correct for this imbalance between number of deforested and not-deforested cells, and with the purpose of balancing omission and commission errors, we took a larger random sample of deforested points than forested points to result in a ratio of 2 not-deforested points to 1 deforested point in each of the three nations with territories on Borneo (Evans & Cushman, 2009).

To identify the most parsimonious model we applied the Model Improvement Ratio (MIR; (Murphy *et al.*, 2010). The MIR uses the permuted variable importance, represented by the mean decrease in OOB error, standardized from zero to one. The variables are subset using 0.10 threshold increments, with all variables above the threshold retained for each model. This subset is always performed on the original model's variable importance to avoid over-fitting (Svetnik *et al.*, 2004). We compared each subset model and select the model that exhibits the lowest total OOB and lowest maximum within-class error.

Model predictions were created by using a ratio of the Random Forests majority votes-matrix to create a probability distribution. Random Forests makes predictions based on the plurality of votes across all bootstrap trees and not on a single rule set. This votes matrix can be scaled and treated as a probability given the error distribution of the model. We used the function that (Evans & Cushman, 2009) added to GridAsciiPredect (Crookston & Finley, 2008) which uses the votes-probability function to write the probabilities to ASCII grid(s).

Once Random Forest models had been produced predicting deforestation in 2010 from the landscape variables in 2000 for each nation (Brunei, Malaysia, Indonesia), we applied these models to the 2010 landscape variables to predict deforestation risk for the period between 2010 and 2020. We analysed these predictions of future deforestation with FRAGSTATS to assess how much of each national territory in Borneo had deforestation risk greater than 25%, 50%, and 75% probability of being deforested between 2010 and 2020. These thresholds were used to provide comparative benchmarks between analyses at levels that are intuitive.

Results

Model accuracy

We are able to predict areas of deforestation with 91% accuracy and predict which cells would remain forested with about 78% accuracy across the whole of Borneo (Table 2). Our model showed high Overall Accuracy (OA) in all countries (> 86%; Table 2), indicating a high probability of correctly predicting forest loss or absence of forest loss. The Specificity (Spe) was also high in all countries (> 89%; Table 2) suggesting a high probability of correctly predicting the areas that remained forest. However, Vieilledent *et al.* (2013) point out that OA and Spe can be unreliable metrics because a model that predicts no forest loss would also produce high scores where the number of forested cells greatly outnumbered the number of forest loss cells. We therefore followed Vieilledent *et al.* (2013) and also computed the Figure Of Merit (FOM), Sensitivity (Sen), the True Skill Statistic (TSS), and Cohen's Kappa (K) for each country (Table 2). Our model performed as well or better based on each of these measures than other published deforestation models. There were no major differences in the accuracy assessment metrics between each country suggesting that our models performed well across the whole of Borneo.

Table 2. Accuracy assessment for the random forests model showing the Classification Confusion Matrix, and accuracy indices for the deforestation models in each country on Borneo.

observed / predicted	Brunei			Malaysia			Indonesia		
	0 (forest)	1 (forest loss)	Total	0 (forest)	1 (forest loss)	Total	0 (forest)	1 (forest loss)	Total
0 (forest)	n_{00} 1423	n_{01} 159	n_{0+} 1582	27233	3393	30626	27225	3145	30370
1 (forest loss)	n_{10} 177	n_{11} 641	n_{10} 818	2767	11607	14374	2775	11855	14630
Total	n_{+0} 1600	n_{+1} 800	n 2400	30000	15000	45000	30000	15000	45000
Class Error (*number of mis-classified cells divided by the total number of cells in that class*)	0.111	0.199		0.092	0.226		0.093	0.210	
Overall Accuracy ($=(n_{11}+n_{00})/n$)	0.86			0.86			0.87		
Figure Of Merit ($=n_{11}/(n_{11}+n_{10}+n_{01})$)	0.66			0.65			0.67		
Sensitivity ($=n_{11}/(n_{11}+n_{01})$)	0.80			0.77			0.79		
Specificity ($=n_{00}/(n_{00}+n_{10})$)	0.89			0.91			0.91		
True Skill Statistic *(=Sensitivity+Specificity−1)*	0.69			0.68			0.70		
Cohen's Kappa ($=(OA-\alpha)/(1-\alpha)$) Where $\alpha = (n_{1+}n_{+1} + n_{0+}n_{+0})/n^2$	0.69			0.69			0.71		

Correlates of deforestation between 2000 and 2010

Although the specific correlates of deforestation vary between the three countries with territories on Borneo, the overall trend is for deforestation to be driven by landscape features such as elevation, patch density (both particularly important in Indonesian Borneo) and topographic roughness, as well as previous land-use at a range of scales (Figure 2). In both Malaysian and Indonesian Borneo the most important past land uses were the presence of plantation/regrowth and the presence lowland mosaics although the scales at which these land uses exerted an influence was smaller in Malaysia. In Brunei, the most important land uses were the proportion of water within a 50 km radius and the proportion of lowland open habitat within 40 km. In Brunei's case, the effect of the presence of water can be interpreted as an effect of distance to the coast. Interestingly the most important anthropogenic feature was population density within a focal mean of 100 km which was an important variable in both Malaysian and Indonesian Borneo although it was not retained by the MIR model selection in Brunei. Similarly, presence of protected areas was retained by the MIR model selection in only Malaysian and Indonesian Borneo, however, in both cases it was one of the least important variables. This suggests that while many protected areas in Borneo may still be in relatively good condition, this is likely due to other factors such as their relative remoteness and presence in high and inaccessible areas than the effectiveness of their protection.

Local population density, and Aggregation index were the only two variables not to be retained by any of the models.

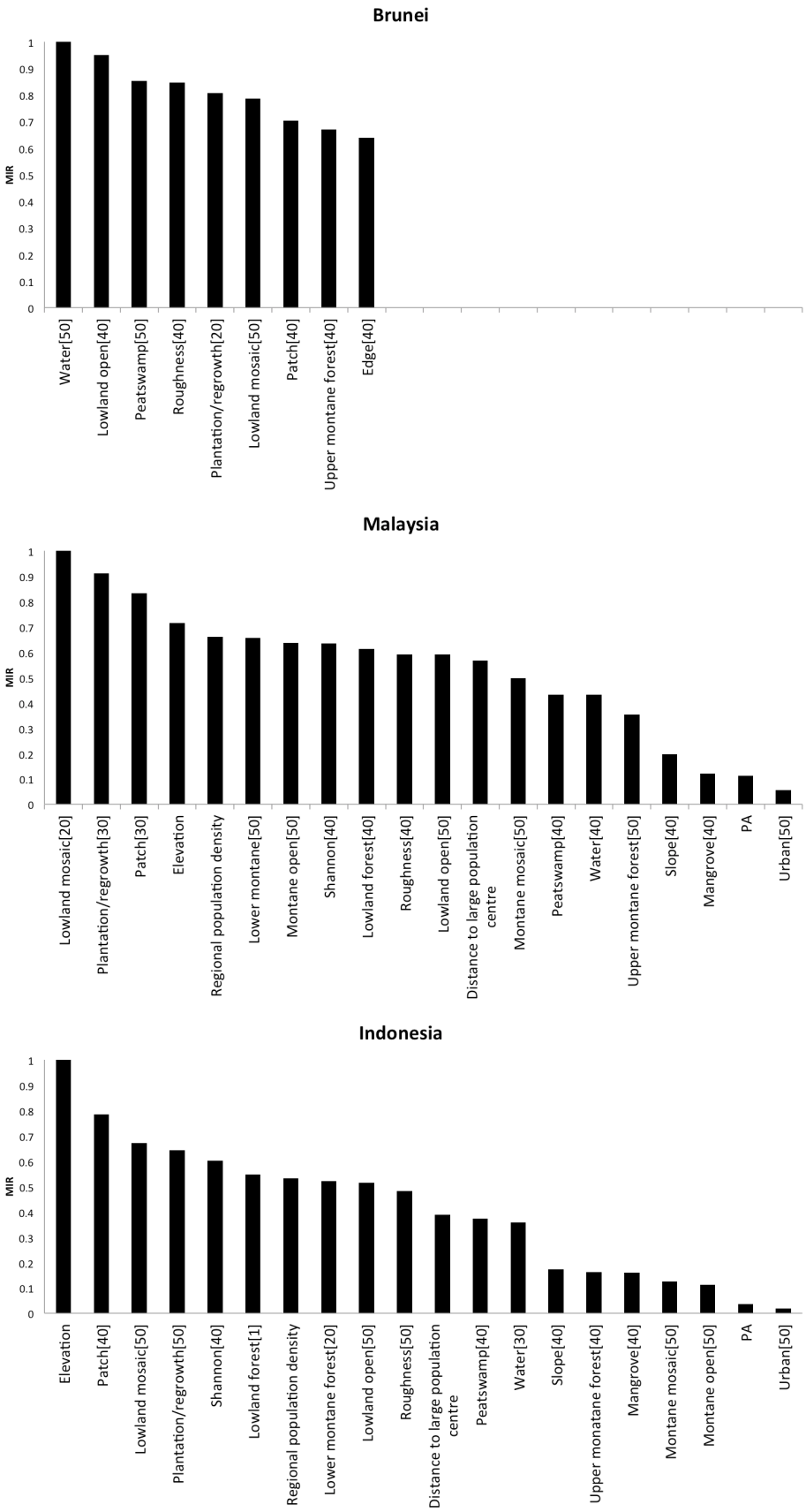

Figure 2. Model Improvement Ratio (MIR) results for the Random Forest model in each country. (see box for legend)

Figure 2 legend (prev. page)

Model Improvement Ratio (MIR) results for the Random Forest model in each country. Variable names along the x-axis are those retained by the MIR model selection procedure, only 9 variables were retained by the model in Brunei while 20 variables were retained in each of Malaysian and Indonesian Borneo. The height of the bar indicates the variable importance, with the most important variable having value of 1 and subsequent variables indicating the relative improvement of model performance as each variable is added to the model.

Figure 3 legend (next page)

LOWESS splines depicting the relationship between each of the ten most important variables. (see box for legend) in predicting deforestation in each country on Borneo. Values of each pixel (0/1) are represented as dots, while the LOWESS splines show the general shape of the relationship between each variable and the risk of forest

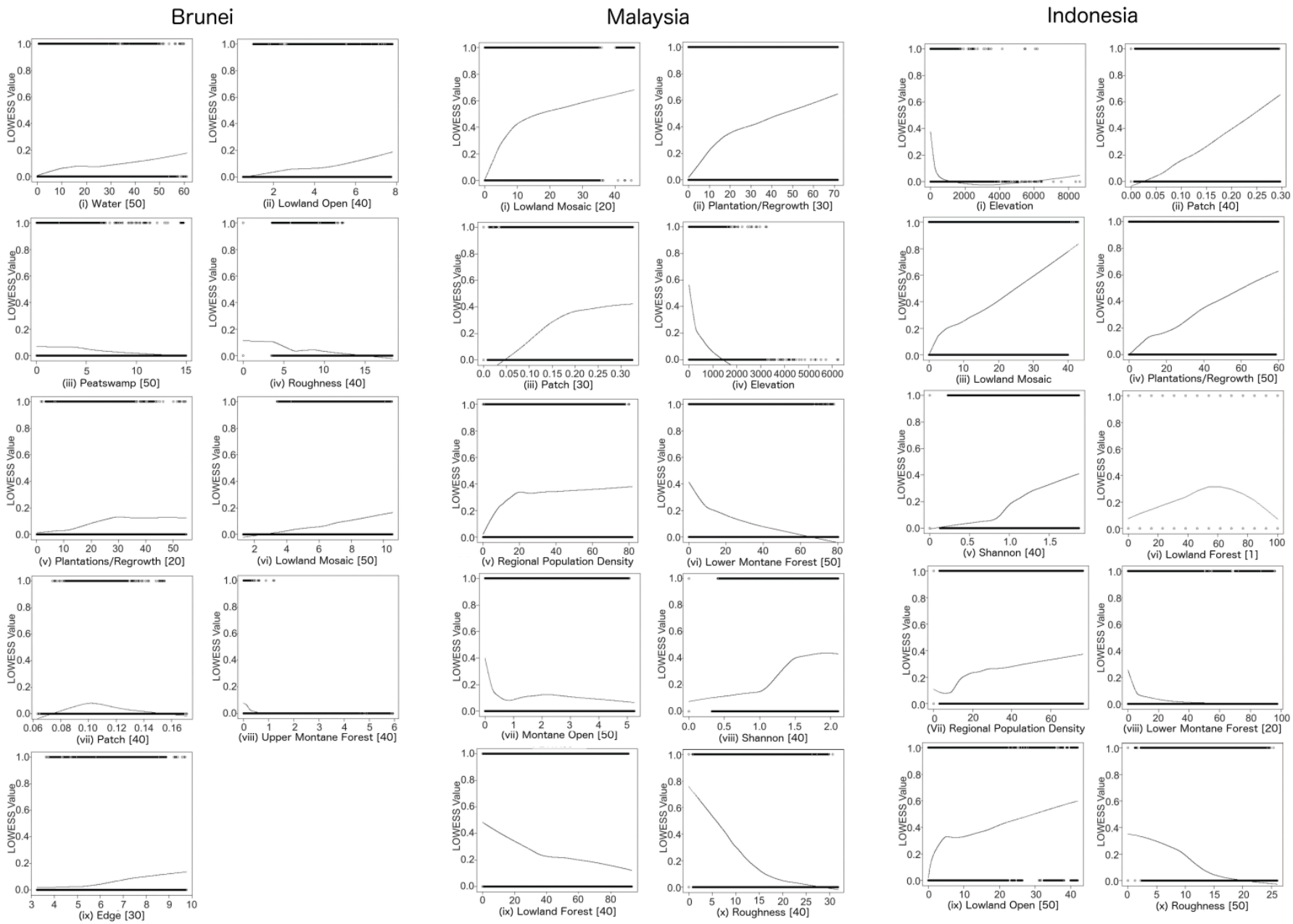

Figure 3 LOWESS splines depicting the relationship between each of the ten most important variables. (see box for legend)

Prediction of future deforestation risk

By 2020, we predict approximately 37% of the remaining forest in Borneo will have a greater than 25% risk of being deforested, and that approximately 13% (an area of 11,167 km^2) will have a greater than 50% chance of being lost, given conditions observed in 2000 (Table 3). Figure 1B shows the spatial distribution of deforestation risk across Borneo. Although particularly remote regions such as the central highlands seem to be at relatively low risk, vast areas of more accessible lowland forest appear to face a highly uncertain future.

Comparing the three nations of Borneo, the first thing to note is the comparatively vast proportion of remaining forest in Indonesian Borneo; 70% of all remaining Bornean forest occurs within Indonesian provinces in comparison with 29% in Malaysia and 1% in Brunei. The majority of forest in Indonesian Borneo is classified as being of low risk (71% in the 0-25% risk category), however, the huge size of these forests means that 8,475 km^2 were classified as having a greater than 50% risk of deforestation risk by 2020. The most important predictors of deforestation in Indonesian Borneo were elevation, landscape heterogeneity (Patch[40]), the proportion of lowland mosaic and the proportion of plantation/regrowth both within a focal radius of 50 km (Table 2). The strong effect of elevation suggests that highland areas of Indonesian Borneo remain relatively low risk, while lowland areas are considerably more vulnerable, especially areas along “fronts” and “fragment edges” of past deforestation events.

The risk profiles of Malaysian Borneo and Brunei appear very similar to one another with just over 40% of forest being classified as low risk (0-25%) and around 10% being classified as high risk (> 50%)(Table 3). As with Indonesian Borneo, deforestation risk in Malaysian Borneo and Brunei is positively associated with landscape heterogeneity and the extent of human dominated landscapes at medium spatial scales, however, visual inspection of Figure 1B reveals very different patterns of risk between the Indonesian and Malaysian provinces of Borneo.

Table 3. Extent of each territory predicted to have 0-25%, 25-50%, 50-75% or greater than 75% probability of deforestation between 2010 and 2020.

		Area (km^2)	Percentage of territory	Percentage of forest area within territory
Brunei	0-25	435.6	29	42
	25-50	536.4	36	51
	50-75	71.4	5	7
	75-100	0	0	0
Malaysia	0-25	10697.0	22	44
	25-50	11200.1	23	46
	50-75	2598.3	5	11
	75-100	21.5	0	0
Indonesia	0-25	41708.2	22	71
	25-50	8545.7	23	15
	50-75	5977.5	5	10
	75-100	2497.9	0	4

Discussion

The goal of this study was to identify the multi-scale drivers of forest loss across Borneo, and then to apply this model to predict the risk of forest loss between 2010 and 2020. We identified several hypotheses to help us explore these relationships.

First, we expected that the risk of forest loss would be related to landscape variables similarly in each country. Comparing countries, there are many similarities between the correlates of forest loss in Malaysian and Indonesian Borneo, with nine of the 10 most important variables being shared by the two countries. In particular, the same suite of four predictor variables (Lowland Mosaic, Plantations/Regrowth, Patch Density and Elevation) appear to be highly important both countries, however the differing importance of these variables highlights interesting differences. In Malaysian Borneo the most important predictor variables were Lowland Mosaic and Plantation/Regrowth emphasising the importance of human dominated landscapes and past deforestation on predicting future deforestation. In Indonesian Borneo, Elevation emerged as the strongest predictor of forest loss. This highlights the extent of lowland forest loss in Indonesia in comparison to Malaysia where many upland areas had already experienced clearance before the year 2000. The variables associated with forest loss in Brunei differed from those in Malaysian and Indonesian Borneo with the most important variable being the proportion of water within a 50 km focal radius. Water itself is unlikely to be directly associated with forest loss, the importance of this variable suggests a strong link with land-use change in more developed coastal areas. While the variables associated with forest loss in Brunei appear to diverge slightly from those in Malaysian and Indonesian Borneo, we find that the landscape variables associated with forest loss

are similar across these two nations and thus across the majority of the land area of Borneo.

Second, we expected that topography would be a strong predictor of the risk of forest loss, with high risk at low elevations and flat areas, and low risk at higher elevations and steep terrain. In all countries, the relationship with the topographic variables largely matched this hypothesis. In Brunei, Roughness was the only topographical variable to be retained by the model, and showed a negative relationship with the risk of forest loss at a medium scale (40km). In Malaysia, both Elevation and topographic roughness at a medium scale (40km) showed a strong negative relationship with forest loss. In Indonesia, elevation was the strongest predictor variable in the model, and along with topographic roughness it showed a negative relationship with forest loss indicating that the central highlands are of comparatively lower risk.

Third, we expected that the extent of past forest loss in the surrounding region would be strongly associated with risk of future loss. In all countries, the proportion of human dominated land-use classes in the neighbourhood showed a positive relationship with the risk of forest loss. In Brunei, the presence of lowland open, plantations/regrowth and lowland mosaic were all retained in the model and increased the risk of forest loss. In Malaysia, the proportion of lowland mosaic, plantations/regrowth and regional population, were all important variables in the model and had a positive association with forest loss. Similarly, in Indonesian Borneo the proportion of lowland mosaic, plantations/regrowth, regional population, and lowland open all had a positive association with forest loss. This link between human dominated landscapes and land-

use change fits with our hypothesis, however the optimal scale for considering composition of human dominated landscapes was often higher than expected with variables being included at scales above 20km and frequently as high as 50km (the largest scale considered in this analysis). This is much larger than the scales considered in other studies that include some measure of landscape composition (e.g., Rosa *et al.* (2013) included the proportion of previously deforested cells within a 25x25 km focal grid, and Vieilledent *et al.* (2013) use a 9x9 km focal grid to assess forest fragmentation) and highlights the importance of scale optimization.

Conversely, where the model included landscapes that were not considered human dominated, they showed a negative association with forest loss. For instance in Brunei, the neighbourhood proportion of peatswamp, and upper montane forest were retained in the model, in Malaysian Borneo the proportion of lower montane and lowland forests was retained and in Indonesian Borneo lower montane forest was retained. Interestingly, the presence of the Lowland Forest class in Indonesia exhibited slightly more complex relationship. The risk of forest loss was lowest when the lowland forest class was either completely absent, or completely dominant in the neighbourhood, while the risk of forest loss was highest when the neighbourhood comprised approximately 60% lowland forest. The optimal scale for this variable was very small (1 km), considering only the immediate vicinity of the cell. This hints at the local scale selection of patches of lowland forest for clearance.

Of the landscape fragmentation indices, Patch Density appeared to be the most important with a high MIR in all countries. In Brunei, Patch Density showed a curvilinear

relationship with the highest risk of forest loss occurring with a patch density of approximately 0.1 at a 40 km scale, while risk also increased with increasing Edge Density. In both Malaysian and Indonesian Borneo, forest loss increased with increasing Patch Density (at 30 and 40 km scales respectively) and increasing Shannon's Diversity (at 40 km) suggesting that landscape fragmentation is an important correlate of forest loss.

This conjunction of high risk of forest loss in areas that are both highly fragmented, and contain a large proportion of human dominated land at a regional scale support our hypothesis that the extent of past forest loss in the surrounding region would be strongly associated with risk of future loss.

Fourth, we predicted that protected area status would be a strong predictor of the risk of forest loss, with protected areas experiencing low loss, regardless of their landscape context. While protected areas may not provide complete protection from forest loss, the models also retained the presence of PAs as a variable for both Malaysian and Indonesian Borneo with a lower risk of forest loss within PAs than outside. While this is an encouraging start, the low MIR shows that the wider landscape composition and topography are more important predictors of forest loss.

Fifth, we predicted that human population parameters such as distance to large settlements and local/regional population density would have weaker but important contributions to the risk of forest loss. Both Regional Population Density and Distance to Large Population Centre were retained in the models for both Indonesia and Malaysia, as was the proportion of urban landscape within 50km. This supports other studies that

show a link between forest loss and population (Carr, 2004, Vieilledent *et al.*, 2013), but these variables appear to be important at a regional rather than a local level indicating that risk of forest loss is more closely associated with regional development than local scale populations (DeFries *et al.*, 2010).

Sixth, we predicted that topographical factors would be most influential at broad spatial scales, while land cover and past forest loss would predict risk at finer scales. Across all regions of Borneo, we found that the majority of variables (67%) retained in the models were optimized to the scale of 40-50km, and that this applied equally to both topographic factors as well as land cover factors and the pattern of previous forest loss. This is interesting as because 50km was the largest spatial extent considered in this model and is far larger than equivalent variables in other studies. This points strongly to regional scale correlates of forest loss, rather than more local scale associations.

Novelty of approach

Random Forest is a powerful tool for classification and regression analysis and has been widely used in land-use classifications from remotely sensed images (e.g., (Aide *et al.*, 2013, Grinand *et al.*, 2013, Rodriguez-Galiano *et al.*, 2012), and increasingly in the wider field of ecology where it often outperforms other statistical approaches (e.g., (Armitage & Ober, 2010, Cutler *et al.*, 2007, D. Rosa *et al.*, 2016, Elith & Graham, 2009, Evans & Cushman, 2009, Kampichler *et al.*, 2010, Prasad *et al.*, 2006). Compared to other statistical tools, RF provides high classification accuracy, the ability to analyse complex non-linear and non-parametric relationships between predictor variables, and runs

efficiently on large and otherwise intractable datasets. This makes it particularly well suited to exploring the complex socio-geographic system that drives land-use change, however to our knowledge no other studies have attempted to use RF in this context.

This study is the first to explicitly evaluate multiple-scale landscape drivers of deforestation. Despite the wide recognition of scale dependence in ecology (Levin, 1992, Wiens, 1989), very few ecological papers explicitly address scale-dependence in pattern process relationships (McGarigal *et al.*, 2016), and to our knowledge no models of forest loss have used a multi-scale optimization approach, like used here, that McGarigal *et al.* (2016) argue is the most robust way to evaluate scale dependence. Several existing papers on land-use change do include some scale dependent variables in their analysis (such as distance to roads or rivers e.g. (Rideout *et al.*, 2013, Soares-Filho *et al.*, 2006) or distance to population centre e.g. (Vieilledent *et al.*, 2013) however they do so implicitly and they retain other variables (such as number of roads, or landscape fragmentation) which are constrained to a single scale. Additionally, while some studies include some measure of landscape composition (e.g. proportion of deforested cells within a neighbourhood, or landscape fragmentation (Rosa *et al.*, 2013, Vieilledent *et al.*, 2013), our study is the first to use optimized relationships with both landscape composition and configuration across a range of spatial scales. Our use of an explicitly multiscale approach that optimises the scales at which landscape features and landscape composition are included in the model is novel to studies of land-use change.

Comparison with other approaches

By applying our model to data from the year 2000 and using it to predict deforestation in 2010, and then comparing these predictions to known deforestation in 2010, we demonstrate that we are able to predict areas of deforestation with both high Overall Accuracy (>86%) and Specificity (>89%) in all countries. This level of accuracy compares well with similar studies (e.g., (Vieilledent *et al.*, 2013); however, these measures are sometimes misleading due to the low proportion of forest-loss cells (1) compared to forested cells (0). Our model also performed impressively across all countries for the remaining accuracy indices (FOM: >65%, Sen: >77%, TSS: >68%, K: >69%). By comparison Vieilledent *et al.* (2013) reported FOM scores of 10-14% for spiny dry, and humid forests respectively in Madagascar while Pontius *et al.* (2008) analysed 13 models of land-use change and reported that only one model achieved a FOM above 50%. Our remaining accuracy indices also outperform those from other studies using other approaches such as Vieilledent *et al.* (2013), who used a 3 step approach combining dynamic population changes and logistic regression (Sen: 18-41%, TSS: 16-35%, K: 16-32%), Kim (2010) comparing GEOMOD Modeling (GM) and Land Change Modeler (LCM) tools (FOM: <8%), and Guerrero *et al.* (2008) using GEOMOD Modeling (K: -0.03 – 0.29). These comparisons indicate that our model performs well, especially given the complexity of the socio-political drivers of forest loss at the scale of Borneo.

The very high performance of our model suggests that multi-scale analysis of landscape structure is critical to strong predictions of land-use change in general, and demonstrates that RF is an effective tool for predicting land-use change. The high performance of our model in predicting the 2010 change from the 2000 landscape gives us confidence in our predictions for 2020. However, one weakness of our model is that it predicts based on

correlations with landscape features rather than predicting based on socio-economic processes. It is possible that changes in local, regional, national and global economic conditions could change these relationships, leading to a weaker prediction. However, given our prediction is only made 10 years into the future we have confidence that the underlying processes governing the relationships are likely to remain relevant. The drivers of forest loss are incredibly complex, and total rates will be influenced by many more factors than we have included here (such as governance and economics and a dynamically changing population); however, the high importance of topographic and landscape composition in our models give us confidence that our relative predictions will remain robust even if the absolute risks of forest loss fluctuate.

Several other studies have found that distance to roads and the density of the road network within the neighbourhood of the cell have proven important predictors of land-use change in other systems (e.g. (Barber *et al.*, 2014, Soares-Filho *et al.*, 2006, Vieilledent *et al.*, 2013)). However in this study we were not able to source a Borneo wide map of roads with a consistent level of accuracy across regions. For this reason we decided to exclude roads from our analysis, however development of improved road data in Borneo may facilitate their inclusion in the future.

Patterns of deforestation risk in 2020

Deforestation in Indonesian Borneo appears to act along fronts of destruction (Figure 1B), contagiously spreading into the forest and leaving very few patches behind. Conversely, deforestation in Malaysian Borneo appears to be spread much more diffusely throughout

the landscape. This is reflected by the higher importance of elevation in predicting deforestation risk in Indonesian Borneo, and may be driven in part by the fact that Malaysian forests already appear to be far more "peppered" with small scale patches of human land classes than those in Indonesia. This may in turn reflect different trajectories of land-use change in these two countries.

Policy implications

Funding for conservation is scarce and conservationists must make tough decisions about which areas to prioritize. Therefore, understanding the risk of future deforestation is vital for conservation planning, particularly in the context of the UNFCCC's programme of Reduced Emissions from Deforestation and Degradation (known as REDD+).

Borneo was almost completely forested, but has lost 30% of its forests since 1973 (Gaveau *et al.*, 2014). The remaining forests are some of the most biologically diverse in the world and are home to an estimated 15,000 flowering plant species and 3,000 tree species (MacKinnon *et al.*, 1997) as well as hundreds of bird and mammal species, including charismatic Clouded Leopards, *Neofelis diardi*, and Orang-utans, *Pongo pongo*. Most of these species are already threatened and further habitat loss could imperil their long-term survival. Furthermore, forests provide a range of ecosystem services at both a local scale (such as watershed management) and a global scale (through the storage and sequestration of Carbon). Reliable understanding of the risk of forest loss is an important tool in identifying which areas should be prioritised for future conservation action.

This study aims to provide a first step in identifying the factors associated with forest loss in Borneo and to predict the areas that are most at risk of future forest loss. We used a novel combination of multiple-scale modelling with Random Forest, using both landscape composition and configuration as predictors. The very high performance of our models suggests that multiple-scale modelling using Random Forest and a combination of landscape composition and configuration greatly improves accuracy of predictions about the drivers and future patterns of deforestation.

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Chapter 5

Implications for rapid forest loss on population size, connectivity and genetic diversity of clouded leopards in Borneo.

Abstract

Habitat loss is the greatest threat to biodiversity in Borneo, and to anticipate and combat its effects it is important to predict the pattern of loss and its consequences. Technical advances, such as resistant kernel and factorial least-cost path connectivity modelling and improved computational power, combined to enable us to model the effects of landscape fragmentation on population connectivity in a spatially synoptic framework for the Sunda clouded leopard (*Neofelis diardi*) across the full extent of Borneo. This is both relevant and urgent because Borneo is not only a region of great biodiversity, from which forest is being lost faster than in any other, but also because the little-known Sunda clouded leopard is the top predator in Borneo and is likely to depend critically on habitat connectivity that is currently being rapidly fragmented. To develop conservation strategies, we assessed impacts of rapid landscape change, addressing uncertainties in landscape resistance by convening a panel of experts on the species, and species distribution by estimating distribution and density across space as proportional to local habitat suitability as defined by the expert panel. We modelled the impacts of land use change between the years 2000, 2010 and projected forwards to 2020. We found substantial reductions across all metrics between 2000 and 2010: the proportion of landscape connected by dispersal fell by approximately 24% and the largest patch size declined by around 30%, leading to a 13% decline in clouded leopard numbers. We also predict that these trends will accelerate towards 2020, with the percentage of the landscape being connected by dispersal falling by about 63%, the largest patch size falling by around 68% and the clouded leopard population falling by around 57% between 2010 and 2020. We predicted that these large declines in clouded leopard

population size and connectivity will also have a major impact on the genetic diversity of the clouded leopard population.

Introduction

Prediction of how changes in the landscape affect the size and connectivity of populations is essential to assess the impacts of habitat loss and fragmentation and to develop effective conservation responses to these changes. However, it is difficult to predict population connectivity reliably (Cushman et al. 2013c; Rudnick et al. 2012) given that connectivity is scale, species and system dependent (Cushman 2006). For a particular species in a particular system, population connectivity is the result of the combined effects of the distribution and density of the population, composition and configuration of the landscape, and species-specific dispersal characteristics (including effects of different landscape features on movement, sex and age differences in dispersal), and how these combine to shape the dispersal kernel (Cushman & Landguth 2012b). In most populations there is substantial uncertainty about species distributions and densities (Cushman 2006), how different landscape features affect movement (Zeller et al. 2012), and limited understanding of species dispersal abilities (Elliot et al. 2014). These compounding uncertainties limit the confidence that can be placed in the results of many connectivity analyses.

In addition to major gaps in knowledge about the ecology of organisms and their responses to landscape conditions, there are significant technical challenges in producing fine-scale, spatially explicit predictions of population connectivity across large areas. Traditional approaches to connectivity modelling have been based on mapping least cost paths or corridors between a few “core” habitats or protected areas (Beier et al. 2011; Brodie et al. 2014), which limits the generality and scope of inferences (Cushman & Landguth 2012b). For

many questions it is better to adopt spatially synoptic modelling in which connectivity is assessed continuously across space, from all locations to all others (Cushman et al. 2013b). The challenge arises because the tools commonly available for least cost path and corridor analysis have not enabled such synoptic analysis (Cushman et al. 2014); however, recent technical advances and improved computational power combine to enable scientists to predict more robustly the effects of landscape structure and fragmentation on population connectivity in a spatially synoptic framework. For example, resistant kernel (Compton et al. 2007; Cushman et al. 2010a; Landguth et al. 2012) and factorial least-cost path approaches (Cushman et al. 2010b; Cushman et al. 2009; Landguth & Cushman 2010), coupled with landscape pattern analysis (Cushman et al. 2012a; McGarigal et al. 2012; Wasserman et al. 2012), provide a framework within which to predict the location of core habitats, barriers, and movement corridors for a range of dispersal abilities across vast landscapes (Cushman & Landguth 2012a; Cushman & Landguth 2012b; Cushman et al. 2013a; Hand et al. 2014).

Tropical forests are among the most biodiverse habitats on earth, and provide a myriad of environmental services (Foley et al. 2005; Pielke et al. 2002; Pimm & Raven 2000; van der Werf et al. 2009). However these habitats are being lost at a devastating rate with Hansen et al. (2013) estimating that approximately 230million ha of forest were destroyed globally between 2000-2012. Of all countries, Hansen et al. (2013) found that Indonesia had experienced the largest increase in the rate of forest loss, and Gaveau et al. (2014) estimated that Borneo lost 30.2% of it's forest area between 1973 and 2010.

The Sunda clouded leopard (*Neofelis diardi*) is the largest obligate carnivore in Borneo, an ecologically important role that adds urgency to remedying the currently minimal knowledge of its ecology, which is based largely on observations in captivity (Selous & Banks 1935), anecdotal reports (Rabinowitz et al. 1987; Santiapillai & Ashby 1988) and a few recent field studies (Brodie & Giordano 2012; Hearn et al. 2013). However, despite this lack of ecological knowledge, the clouded leopard is charismatic and attractive to a global public (Macdonald et al. 2015) and has considerable potential to act as an ambassador *sensu* Macdonald et al. (submitted) for wider biodiversity conservation on Borneo.

Brodie et al. (2014) investigated clouded leopard corridors as part of a multi-species conservation approach for Sarawak. However, they employed least cost path and circuit theory to identify the optimal corridors between chosen pairs of protected areas rather than the spatially synoptic approaches we adopt (resistant kernel and factorial least cost path analysis; Cushman et al. (2014)). Specifically, we address uncertainties in landscape resistance by convening a panel of experts on the species and combining their opinions. The use of expert opinion is increasing in conservation, in part due to the increasing urgency of conservation decision-making, and in particular in situations where empirically derived field data is limited (Kuhnert 2011). We address uncertainties in dispersal ability by modelling across two levels of dispersal (supplementary material). We address uncertainty in species distribution by estimating distribution and density across space as proportional to local habitat suitability as defined by the expert panel we convened. Finally, we use spatially

synoptic approaches to evaluate patterns and change in Borneo-wide connectivity for clouded leopards.

Methods

We produced resistance maps for the years 2000 and 2010 for the island of Borneo based on the application of expert opinion regarding the relative habitat suitability for clouded leopards of different land cover classes. The land cover classes were taken from (Miettinen et al. 2012) and included: water, peat swamp forest, lowland forest, lower montane forest, plantations/regrowth, lowland mosaic, montane mosaic, lowland open, montane open, urban and large scale plantation.

Expert elicitation

Experts are commonly defined as individuals who hold information about a given topic and are deferred to in it's interpretation (Martin et al. 2012). This knowledge can be acquired in a variety of ways including training, research, skills and personal experience (Burgman et al. 2011). We convened a panel of 13 experts selected on the basis of them being directly involved in field research relating to the ecology and conservation of clouded leopards.

Group approaches to expert elicitation can result in dilution of the full diversity of opinions through the dominance of one or more members of the group, polarization among subsets of members, and groupthink (Martin et al. 2012). Panel members were therefore contacted individually and asked to provide a relative habitat suitability value estimate for each land

cover class. Respondents were provided with a short questionnaire that included some brief background questions regarding the duration, type and geographic location of their experience. They were then presented with a map of land uses in Borneo, along with a list of land use classes (the map, as well as the full descriptions for each class were taken from Miettinen et al. (2011), the descriptions are reproduced in Table 1). For each land use class participants were asked (i) whether they had any direct experience working in that habitat, (ii) to estimate the population density of *N. diardi* per 100km^2 in that land use class, (iii) the relative habitat suitability of that land use class for *N. diardi* on an interval scale of 1 – 5 with 5 representing the best quality habitat and 1 representing the lowest quality habitat (iv) for any additional information that they thought might be relevant including the sources drawn upon to produce the estimates. Respondents were asked to only provide answers for those land use classes for which they felt comfortable and were invited to contact the authors in the event that they felt any elements of the survey were unclear. Additionally a pilot version of the survey was sent to a subset of respondents for comment prior to the deployment of the final survey.

The number of respondents who felt confident to assess habitat suitability varied between each land use class ranging from a low of 7 (Peatswamp forest, Lowland open, Large scale plantation) to a high of 12 (Lowland forest, Lower Montane forest). The frequency distributions of scores allocated to each habitat class are presented in figure 1. The Intraclass Correlation Coefficient (ICC) was high ($ICC_{(3,1)}$: 0.66, $ICC_{(3,k)}$: 0.96) and in excess frequently quoted guidelines for interpretation of inter-rater agreement measures (>0.60

good, >0.75 excellent) (Cicchetti 1994; Shrout & Fleiss 1979) this provides confidence in the level of agreement between experts in assessing habitat suitability.

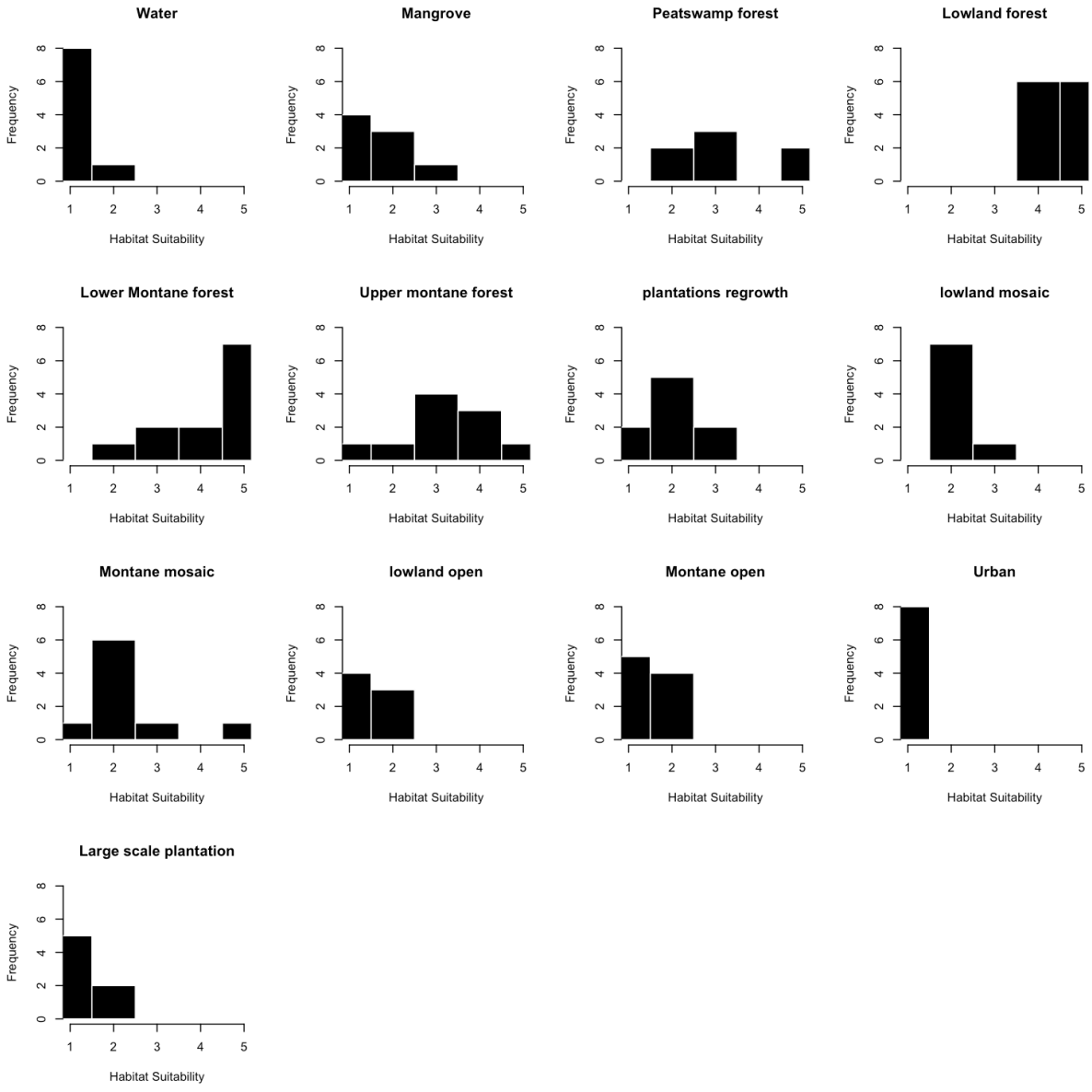

Figure 1. Frequency distributions of survey responses for each land use class on Borneo.

The habitat suitability score for each land use class was calculated from the mean of the habitat suitability scores provided by each respondent, this is appropriate because responses were provided in an interval scale (Table 1)(Siegel & Castellan Jr. 1988). The mean habitat suitability scores showed a very tight relationship with the mean predicted population density for each land use class (R^2= 0.905, supplementary material) providing further support for the use of the use of the habitat suitability scores.

Resistance mapping in 2000 and 2010

The habitat suitability scores were translated into relative resistances by inverting and scaling from a minimum of 1 to a maximum of 100. This translation assumes that landscape resistance is directly and inversely proportional to habitat suitability, and has a minimum of 1 in the highest quality habitat and a maximum of 100 in the lowest quality habitat. This is a very common approach that is widely used in connectivity modelling, and habitat suitability is the most common proxy adopted for landscape resistance (Mateo-Sánchez et al. 2015; Zeller et al. 2012). We applied this landscape resistance classification to the (Miettinen et al. 2011; Miettinen et al. 2012) land cover maps for the years 2000 and 2010 and then resampled to a 1000m pixel size with bilinear interpolation. The resampling was done to facilitate connectivity analysis that is extremely computationally demanding and becomes intractable at fine pixel size over large areas. Cushman and Landguth (2010a) found that resampling resistance maps to coarser pixel size with bilinear interpolation has relatively little effect on predicted gene flow and thus is appropriate in this case to enable connectivity modeling.

Resistance mapping for 2020

(Macdonald et al. in review) used a multi-scale random forest machine learning modelling approach developed by (Evans & Cushman 2009) to predict deforestation risk in 2020 from observed patterns of deforestation in relation to topographical, landcover, human population density, and conservation status of lands between 2000 and 2010. This deforestation risk map provided the probability that a pixel that was forested in 2010 would be deforested by 2020. We used this deforestation risk map to translate the resistance map described above for 2010 to one predicted for 2020. This was done by multiplying the probability of deforestation by the resistance value for that location if it were plantations/regrowth and adding this net predicted change in resistance to the resistance value for that pixel in 2010. We did this because forest pixels lost to deforestation were most likely to transition either to plantations or regrowth.

Table 1. Table of expert derived habitat suitability scores. The experts showed a high level of agreement in rating habitat suitability with $ICC_{(3,1)}$: 0.66 and $ICC_{(3,k)}$: 0.96. Descriptions of land use classes from (Miettinen et al. 2011)

Description	Number of responses	Min score	Max score	Standard deviation	Mean score
Water In addition to natural waterbodies, this class also includes, for example, large-scale fisheries and prawn farming areas.	9	1	2	0.314	1.111
Mangrove Mangrove area masks were created using visual image interpretation. Pixels classified as forest within these areas were labeled as mangrove.	8	1	3	0.696	1.625
Peatswamp forest Forest growing on peat soil. The term 'forest' refers to all forests that could not be distinguished from primary forest in visual image interpretation. Therefore, this class may include also selectively logged forests and secondary forests that have reached structural characteristics (height, canopy structure, etc.) similar to primary forest.	7	2	5	1.161	3.286
Lowland forest Forest growing on mineral soil in elevation up to 750 m above sea level.	12	4	5	0.500	4.500
Lower montane forest Forest growing on mineral soil in elevation above 750 m, up to 1500 m above sea level.	12	2	5	1.010	4.250
Upper montane forest Forest growing on mineral soil in elevation above 1500 m above sea level.	10	1	5	1.077	3.200
Plantations / regrowth Plantations and natural regrowth. This class includes areas from large-scale industrial plantations and small-holder plantations to dense shrublands and young secondary forests.	9	1	3	0.667	2.000
Lowland mosaic Sub-pixel size (250 x 250 m) mosaic of closed canopy vegetation and open areas in elevation up to 750 m above sea level. Typically consists of small plantations, agricultural fields, urban areas, patches of forest and secondary forest. Note that sparse/patchy shrub vegetation, most notably in peatland areas, falls into this class.	8	2	3	0.331	2.125
Montane mosaic Same as lowland mosaic, but occurring in elevation above 750 m above sea level.	9	1	5	1.054	2.333
Lowland open Clearances and other open areas covered by seasonal crops, remnants of original vegetation, sparse ferns/grass or low shrub. Typically agricultural areas, areas undergoing land cover change or extremely degraded areas.	7	1	2	0.495	1.429
Montane open Same as lowland open, but occurring in elevation above 750 m above sea level. In addition, this class includes some naturally bare areas in high elevation.	9	1	2	0.497	1.444
Urban Major urban areas.	8	1	1	0.000	1.000
Large scale plantation Contiguous closed canopy palm plantations larger than 2 km^2. Great majority of these areas are expected to be oil palm, but in some parts of the region (e.g. in Mindanao and in the coastal peatlands of Sumatra), small-holder coconut plantations cover extensive contiguous areas and are classified into this class. Note that newly established and young open canopy plantations are classified into the mosaic or open classes because of mixture of soil and vegetation reflectance.	7	1	2	0.452	1.286

Defining source points for dispersers in connectivity modelling

We used the resistance layers for 2000, 2010 and 2020 to seed locations for dispersing clouded leopards. Given that the resistance surface is an inverted and scaled version of the habitat suitability map, using the resistance surface is equivalent to seeding dispersers based on estimated habitat suitability. This was done by creating a grid of random values between 0 and 1 of the same dimension and cell size as the resistance grids and then multiplying this random grid by the inverse of the resistance value and selecting all resulting pixels with values larger than a given threshold and using them as source points. We chose a threshold value for year 2000 that produced 2,869 source points. This number was selected because it plausibly approximates the effective population size of clouded leopards on Borneo (Hearn et al. 2015); however, for the purposes of this analysis the actual number is not strictly important as we report the relative changes in connectivity and gene flow rather than the absolute values. We used this same threshold for 2010 and 2020, producing 2,555 and 1,197 source points for these years, respectively.

Connectivity modelling

Resistant kernel approach – The resistant kernel approach to connectivity modelling is based on all-directional least-cost dispersal from a defined set of sources (Compton et al. 2007), selected as described in the section above. The resistance maps for the three dates provide resistances for all locations in the study area, in the form of the increased cost of crossing each pixel relative to the least-cost condition. These costs are used as weights in the dispersal function, such that the expected density of dispersing individuals in a pixel is down-

weighted by the cumulative cost from the source, following the least-cost route (Compton et al. 2007). The initial expected density was set to 1 in each cell containing a source point. The model calculates the expected relative density of dispersers in each pixel around the source, given the dispersal ability of the species, the nature of the dispersal function, and the resistance of the landscape (Compton et al. 2007; Cushman et al. 2010a). We used UNICOR (Landguth et al. 2012) to calculate the cumulative resistant kernel density for each resistance map at 125,000 cost units (125kcu), reflecting a maximum dispersal ability of 125km in ideal habitat, and proportionately less through higher resistance landscape conditions.

Data on maximum dispersal distances are scarce for any species and dispersal distances are not known for clouded leopards. However, a number of studies have attempted to describe allometric relationships between maximum dispersal distances and a range of physiological and life history traits for mammals in general (Bowman et al. 2002; Whitmee & Orme 2013). Bowman estimates that maximum dispersal distance is equal to 40*(home range size$^{0.5}$) and since clouded leopards are thought to have home ranges in the region of 16km^2 (*N. diardi*) - 40km^2 (*N. nebulosa*) we therefore estimate that a likely range of dispersal distances from 160 -252km (Austin et al. 2007; Bowman et al. 2002; Grassman et al. 2005; Hearn et al. 2013). For this study we therefore selected 125km as a plausible conservative estimate of dispersal in clouded leopards. Additionally, to test the sensitivity of our model to dispersal distance we ran all analyses with a plausible upper limit of 250kcu (representing 250km in ideal habitat) and the results are presented in the supplementary material.

Least-cost path approach – In the second form of the connectivity modelling approach we used UNICOR (Landguth et al. 2012) to produce predicted least-cost path routes from each source point to each destination point. In this factorial least cost path analysis the source points, described above, define starting and ending nodes of the least-cost paths between pairs of individuals (e.g. Cushman et al. (2009), Cushman et al. (2013c)). The least-cost paths were then combined through summation (as in Cushman et al. (2009)) to produce maps of connectivity networks among all pairs of sources and destinations. This predicted least-cost density network was buffered by calculating the focal mean of the least cost path network with a 10,000m radius (e.g. Cushman et al. (2009)).

Analysis of resistant kernel maps

In their raw form the resistant kernel density maps depict the expected density of dispersing individuals for each year. These densities indicate the distribution of connected populations. It is necessary to define a threshold kernel density for delineating connected populations. We defined connected populations as those areas greater than the 10th percentile of the 2000 kernel surface for all three dates. Given any particular threshold is arbitrary, we decided to explore how patterns of predicted connectivity varied across various thresholds. We therefore also tested the impact of using both the 5th and 20th percentile of the 2000 kernel surface as thresholds in our analysis; the results of this are presented in the supplementary material. We reclassified the six kernel density maps into binary form of value 1 where the kernel density probability of dispersal is greater than the percentile threshold and 0 where it is less.

We used FRAGSTATS (McGarigal et al. 2012) to calculate the percentage of the landscape, largest patch index, and number of patches that are predicted to be connected habitat for each year. The percentage of the landscape is the simplest metric of landscape composition, and quantifies how much of the study area is predicted to be connected habitat for each kernel map. The largest patch index (McGarigal et al. 2012) reports the extent, as a proportion of the size of the study area, of the largest patch of connected habitat. Lastly, we calculated the number of patches of internally connected habitat for each map.

Analysis of factorial least cost path maps

In their raw form the three least cost path density maps (one for each year 2000, 2010, 2020) depict the location and strength of connections uniting all pairs of source points in a least cost network. Similarly to the kernel analysis, it is necessary to define a threshold least cost path density for defining meaningful connections. We chose the same threshold of the 10th percentile of the least cost path network value distribution for year 2000 and reclassified the six least cost path density maps into binary form of value 1 where the least cost path density is greater than the threshold and 0 where it is less (threshold values of 5th and 20th percentile were also tested and are presented in the supplementary material). We used FRAGSTATS (McGarigal et al. 2012) to calculate the correlation length for the least cost path density maps. Correlation length provides a measure of the average distance an organism can move within a patch before encountering the patch boundary from a random starting point (McGarigal et al. 2012). The correlation length gives a global measure of the connectivity of the landscape and is a more relevant functional measure of network

connectivity than more basic measures such as patch size, nearest neighbor distance, and percentage of the landscape in occupied habitat (Cushman et al. 2012b). We chose to omit the other metrics since the least cost path network is a measure of connectivity among a network of points, such that correlation length is the logical measure of the extensiveness of this network, and areal measures such as percentage of the landscape and largest patch index are less well matched to this data structure (Short Bull et al. 2011).

CDPOP Simulations

Simulation modelling provides explicit control over pattern-process relationships (Epperson et al. 2010) and enables rigorous attribution of the causes of observed patterns genetic differentiation and diversity (e.g. (Castillo et al. 2014; Shirk & Cushman 2011; Wasserman et al. 2010)). By varying functional parameters, environmental characterization, and organism attributes, simulation enables scientists to investigate hypotheses about the relative influence of different factors, their interactions, and ranges of organism characteristics, such as gradients of landscape resistance, population size or dispersal ability. This provides a means for thorough evaluation of complexes of factors that would be impossible to investigate directly in the field. In addition, simulations are particularly important in evaluating scenarios of future landscape change, such as predicted patterns of deforestation, on landscape resistance and its effects on future population genetic structure.

We used CDPOP 1.0 (Landguth & Cushman 2010) to simulate the processes of mating and dispersal as functions of the spatial patterns of resistance across the three resistance maps

corresponding to the 2000, 2010 and 2020 dates at the dispersal distance of 125kcu. CDPOP is an individual based, spatially explicit, landscape genetic program that simulates birth, death, mating and dispersal of individuals in complex landscapes as probabilistic functions of movement cost among them. In each of the three landscape resistance maps, we used the same source cells described above in the resistant kernel analysis as locations of individual clouded leopards. We stipulated the population to have 30 loci, with 10 alleles per locus, initially randomly assigned among individuals and a mutation rate of 0.0005, which are standard parameters widely used in landscape genetics simulation modelling (e.g. Cushman and Landguth (2010b)). As with the resistant kernel analysis above we used an inverse square mating and dispersal probability function, with maximum dispersal cost-weighted distance of 125kcu. Reproduction was sexual with non-overlapping generations, and the number of offspring was based on a Poisson probability draw with mean of 2. For each of the six resistance scenarios, we ran 10 Monte Carlo runs in CDPOP to assess stochastic variability. We simulated gene flow among these locations for 200 non-overlapping generations. Past studies have shown that this is sufficient time to ensure spatial genetic equilibrium (Landguth et al. 2010). We extracted several global measures of population genetic structure for the full study area at generation 200. These include total number of alleles in the population, observed and expected heterozygosity. We analyzed the differences in these global measures of genetic structure between 2000, 2010, and 2020.

sGD mapping of local genetic diversity

We also assessed local population genetic structure across all CDPOP scenarios. We utilized the sGD program (Shirk & Cushman 2011) to map local total number of alleles and observed heterozygosity. sGD uses a variable radius focal window to calculate locally centered values of a number of population genetic parameters, such as allelic richness, expected and observed heterozygosity, across spatially structured populations. We calculated the local number of alleles, observed heterozygosity and expected heterozygosity within local windows with width equal to 1/2 of the range of significant spatial genetic autocorrelation of the Mantel correlogram across the average of the 10 runs of CDPOP for each scenario (Shirk & Cushman 2014; Wasserman et al. 2012).

Several of the approaches used in this study are computationally demanding (e.g the spatially synoptic analysis of least cost paths, and the individual based population genetics models) and may not be practical for many conservation practitioners. We therefore tested whether it was possible to take a pragmatic shortcut in estimating landscape scale changes in allelic richness and heterozygosity by simply using the maps of landscape resistance, path density and kernel density. In order to do this we used linear regression in library lm in R to construct linear models relating these measures of genetic structure to cumulative resistant kernel value, factorial least cost path density and local average landscape resistance within a focal window of 10,000m radius to explore the relationship between these genetic attributes and landscape patterns of population connectivity.

Results

Landscape resistance change between 2000 and 2010 was driven by loss of forest cover along the edges of forested patches in Kalimantan and by a more diffuse pattern of perforation and attrition of forest patches in Sarawak and Sabah (Fig. 1). The change in landscape resistance predicted between 2010 and 2020 extended and accelerated the pattern observed between 2000 and 2010. Specifically, in Kalimantan additional forest loss was predicted primarily along the edges of existing forest patches while in Malaysian Borneo we predicted large changes in regional resistance as a result of predicted extensive and diffuse forest loss across broad areas (Fig. 2).

Analysis of resistant kernel maps

Figure 2 shows cumulative resistant kernel density of predicted frequency of dispersal given a 125kcu dispersal threshold for the years 2000, 2010, and 2020.

The extent of the landscape connected by dispersal changed markedly between 2000 and 2020 (Fig. 3). The percentage of connected landscape declined by 24.6% between 2000 and 2010, however this loss accelerated and there was a 63.4% decrease in the connected landscape between 2010 and 2020 (Table 2). The relative effect of the different percentile thresholds and dispersal abilities was much less than that due to landscape change between dates (Supplementary material).

Table 2. Relative change in Fragstats metrics between 2000-2010 and 2010-2020.

	Change between 2000 and 2010	Change between 2010 to 2020
Proportion of landscape connected by dispersal	-24.6%	-63.4%
Largest patch index	-36.5%	-69.2%
Number of patches	+20%	-11.1%
Correlation Length	-6.7%	-40.6%

Largest patch index followed a similar pattern (Figure 3) with the extent of the largest patch of connected habitat as percentage of the landscape falling by 36.5% between 2000 and 2010, and then 62.9% between 2010 and 2020 (Table 2). As with percentage of the landscape connected by dispersal, the change in largest patch index between years had a much greater effect than choice of dispersal threshold or percentile threshold on largest patch index (Supplementary material).

The number of isolated patches of internally connected habitat followed a different pattern to the other FRAGSTATS metrics (Fig. 3). Specifically, the number of patches increased from 2000 to 2010 and then decreased from 2010 to 2020 as large connected patches were broken up by fragmentation and then progressively lost through attrition. Selecting different kernel percentile thresholds, and dispersal distances did affect the trend in the number of isolated patches, highlighting the complexity of the impacts of forest fragmentation (supplementary material).

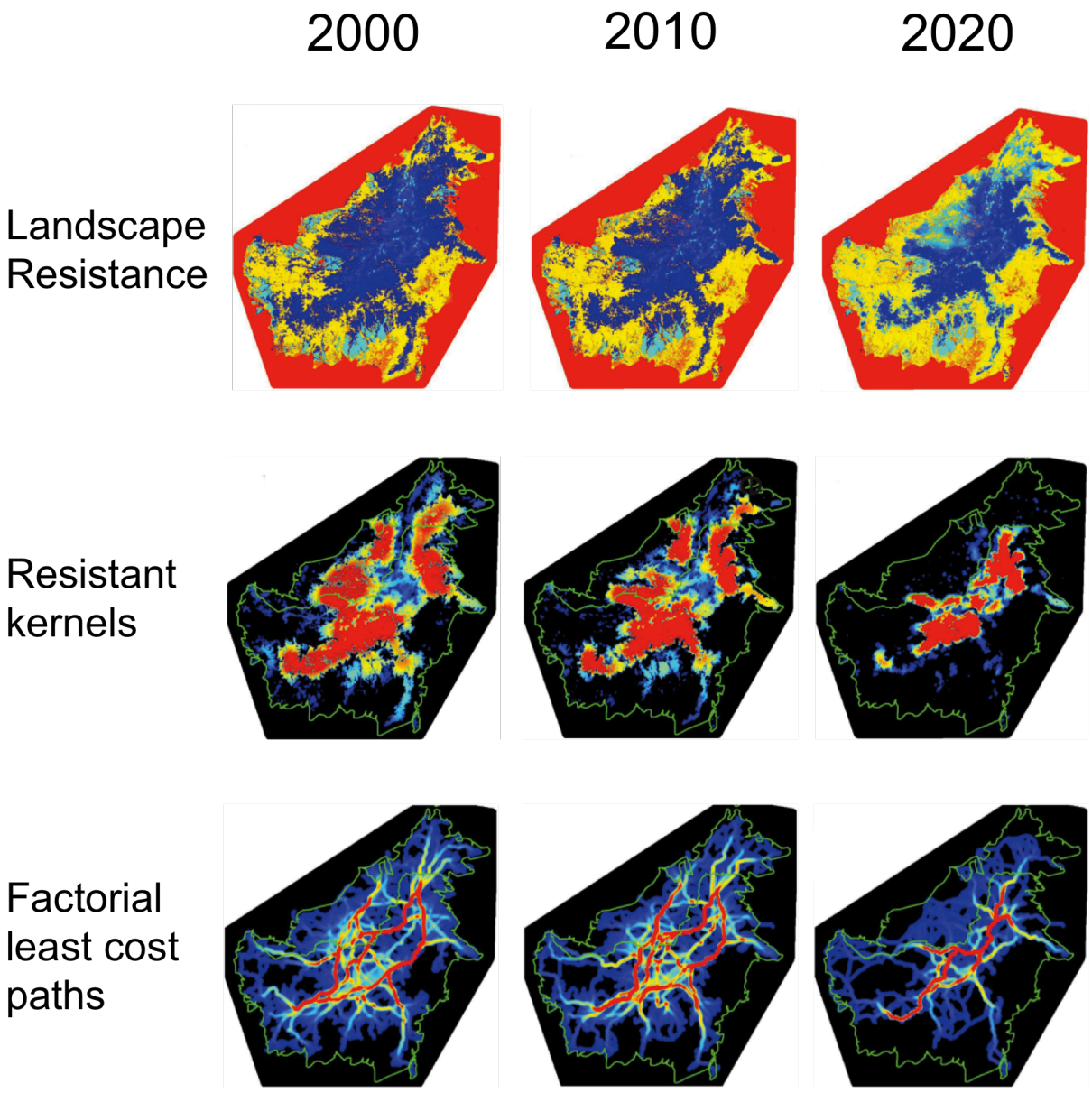

Figure 2. Resistance maps and cumulative resistant kernel surfaces and factorial least cost paths for 2000, 2010, 2020. Landscape resistance maps scaled from 1 in blue to 100 in red, cumulative resistant kernel maps and factorial least cost path density maps scaled from low density in blue to high density in red.

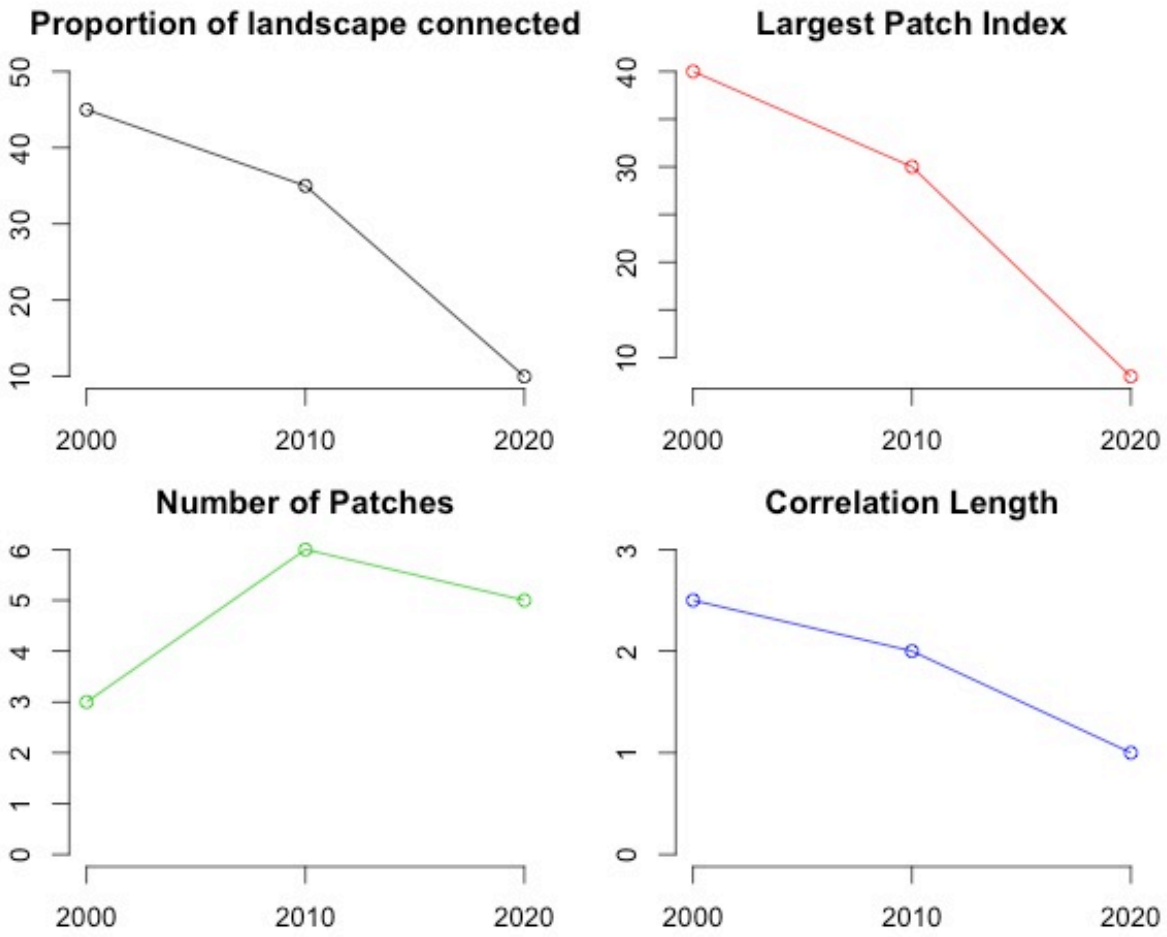

Figure 3. Change in the percentage of the landscape connected by dispersal, the extent of the largest patch of connected habitat as percentage of the landscape, the number of isolated patches of connected habitat, and the correlation length of the factorial least cost path network for the years 2000, 2010, and 2020 at a dispersal of 125kcu.

Analysis of factorial least cost path maps

Figure 2 shows least cost path density for the years 2000, 2010, and 2020. The correlation length of the connected least cost path network decreased by 6.7% between 2000 and 2010. In contrast, between 2010 and 2020 correlation length decreased more than 40% (Figure 3,

Table 2). Correlation length was also highly sensitive to choice of percentile threshold, declining 13.8% as the threshold was moved from 5th to 10th percentile, and another 36.7% when moved from 10th to 20th percentile (Supplementary material).

CDPOP Simulation Results

Over the three CDPOP scenarios (2000, 2010, 2020) there was considerable variation in simulated population size, expected heterozygosity, observed heterozygosity, average mating distance and average dispersal distance (Figure 3, Table 4). There was relatively little difference between the 125kcu and 250kcu dispersal scenarios in these population characteristics (supplementary material). In contrast, there was a large difference between the years for each of these parameters. For example, the simulations predicted that after 200 generations of breeding the population supported by the 2010 landscape was 13% smaller than that supported by the landscape in 2000, and that the 2020 landscape was predicted to be 57% smaller than in 2010. After 200 genereations, there was relatively little predicted change in the equilibrium values for observed and expected heterozygosity between 2000 and 2010 landscapes, but the simulations predicted that the 2020 landscape would lead to a 28% reduction in observed heterozygosity compared to 2010 (Figure 4, Table 4).

Figure 4 shows the relative difference between observed and expected heterozygosity for each scenario, averaged across the 10 model runs. Expected heterozygosity is the

heterozygosity that would be achieved in the population given the distribution in allele frequency if breeding and dispersal were entirely random. The difference between observed

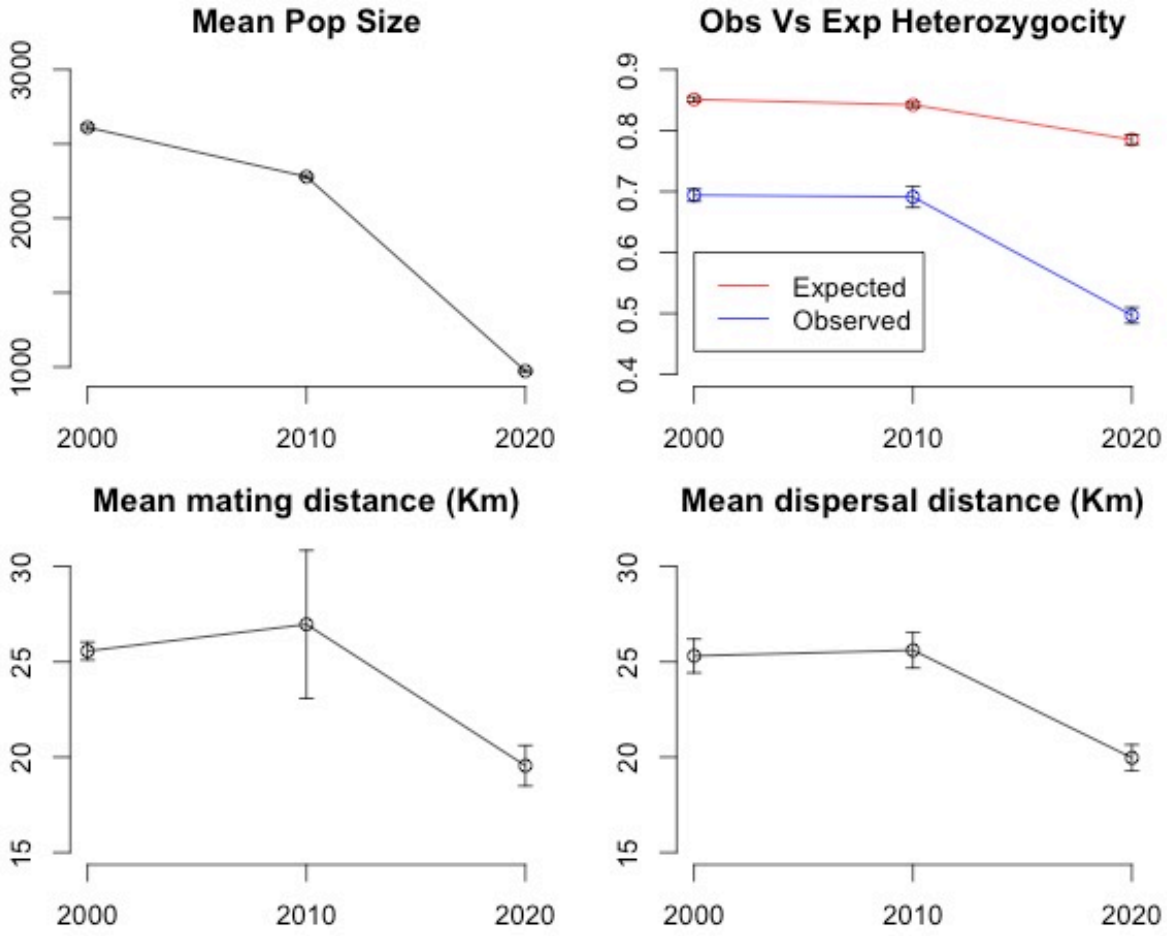

Figure 4. Changes in the mean population size, observed and expected heterozygocity, mean mating distance and mean dispersal distance for the years 2000, 2010, and 2020 at a dispersal of 125kcu. All values represent the equilibrium position after a simulated 200 generations of mating under each landscape condition. Each simulation was run 10times and the points indicate the mean result and the bars indicate the standard deviation.

and expected heterozygosity is a measure of how strongly spatial limitations in breeding reduce observed heterozygosity (Landguth & Cushman 2010). The simulations indicated that

spatial limitations to random mating reduce heterozygosity differently for the 125kcu and 250kcu dispersal distance scenarios, with an ~18% relative reduction in heterozygosity due to spatially limited mating and dispersal for the 2000 and 2010 simulations for the 125kcu scenario and an ~13% relative reduction for the 250kcu scenario (Supplementary material). In contrast to the similarity between 2000 and 2010 landscapes, there was a very large predicted decrease in relative heterozygosity due to spatially limited breeding and dispersal in the simulations of the 2020 landscape (36.7%). This indicates that habitat fragmentation in the 2020 landscape substantially limits breeding and dispersal, such that there is a large reduction in the observed heterozygosity relative to expected heterozygosity.

Table 4. Population characteristics at generation 200 from CDPOP simulations, averages and standard deviations across 10 CDPOP runs for each scenario.

Year		Population size	Expected Heterozygosity	Observed Heterozygosity	Reduction in observed vs expected heterozygocity (%)	Average Mating Distance (km)	Average Dispersal Distance (km)
2000	mean	2611	0.851	0.694	18.45	25.6	25.3
	stdev	15	0.004	0.010		0.5	0.9
2010	mean	2279	0.842	0.691	17.93	27.0	25.6
	stdev	11	0.004	0.017		3.9	0.9
2020	mean	973	0.785	0.497	36.69	19.6	20.0
	stdev	10	0.008	0.013		1.0	0.7

sGD mapping of local genetic diversity

The simulations produced marked patterns of allelic richness (Fig. 5) and observed heterozygosity (Fig. 6) across the population. The average number of alleles varied

consistently with cumulative resistant kernel density, with relatively high allelic richness in areas predicted by the kernel modelling to have high density of dispersers and low allelic richness in isolated, peninsular and edge locations of the population with lower cumulative resistant kernel value (Fig. 5). Observed heterozygosity showed a similar pattern with high heterozygosity predicted in the centre of large patches of high cumulative kernel value, and low heterozygosity in isolated, peninsular and peripheral parts of the population (Fig. 6). Patterns of observed deforestation from 2000 and 2010 and predicted deforestation between 2010 and 2020 resulted in marked changes in simulated allelic richness and heterozygosity, with particularly large declines in both variables in portions of the population that become smaller and more isolated, especially those on the periphery and peninsular patches.

We explored the relationships between local average number of alleles per locus (Fig. 7) and local heterozygosity (Fig. 8) and focal mean landscape resistance, cumulative density of least cost paths, and cumulative resistant kernel density. Visual inspection of the scatterplots suggested little relationship between allelic richness or heterozygosity and average landscape resistance within a 10km radius focal window. Cumulative density of least cost paths and cumulative resistant kernel value evinced curvilinear relationships with both allelic richness and heterozygosity in local genetic neighborhoods.

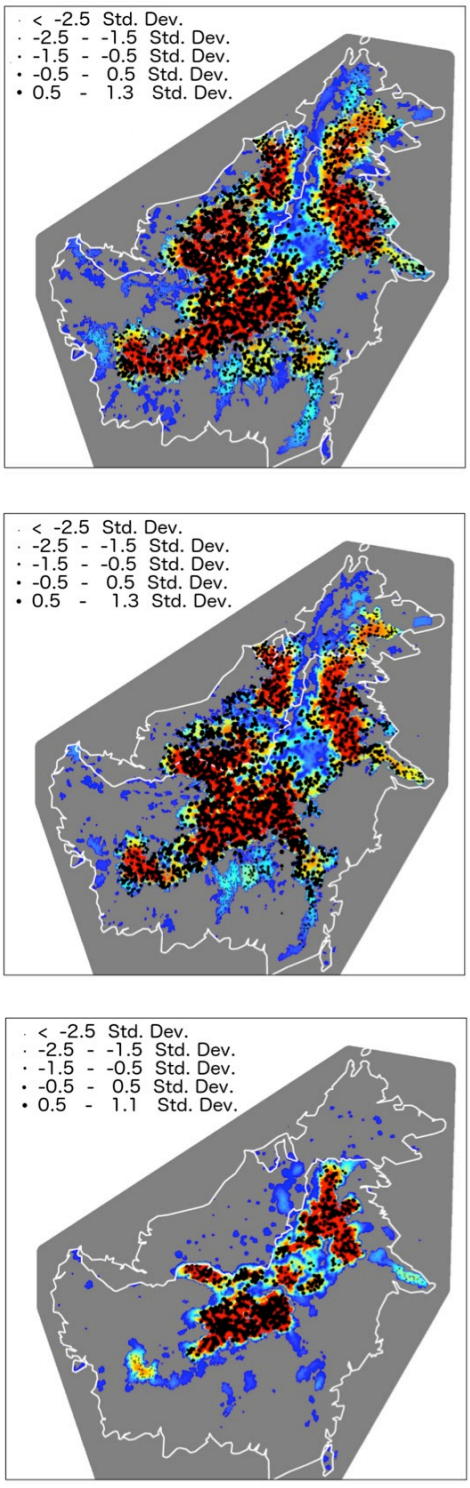

Figure 5. Mapping of sGD predictions of local average number of alleles per locus for the three years (top 2000, middle 2010, bottom 2020). Black marker size indicates the relative number of alleles per locus for the genetic neighborhood surrounding that point.

Our regression analysis indicated that cumulative resistant kernel density was the dominant predictor, with an inverse transformation to linearize the relationship for number of alleles and the heterozygocity at 125kcu dispersal distance. We evaluated all combinations of local resistance, cumulative least cost path density and cumulative resistant kernel value for both the average alleles per locus and observed heterozygosity. We selected the single variable model with cumulative resistant kernel value as the only predictor variable, based on the observation that the single variable resistant kernel model was within 1% of the total deviance explained by the global model, and that none of the other variables' single variable models explained more than about 15% of the deviance (Table 5). This indicates that neither local landscape resistance nor cumulative least cost path density are good predictors of genetic diversity in a population. On the other hand, the resistant kernel models were remarkably good, explaining over 52% of deviance for both alleles and heterozygosity in the 125kcu dispersal scenario (Fig 9; this rose to excess of 80% of the deviance for both variables in the 250kcu dispersal distance scenario supplementary material).

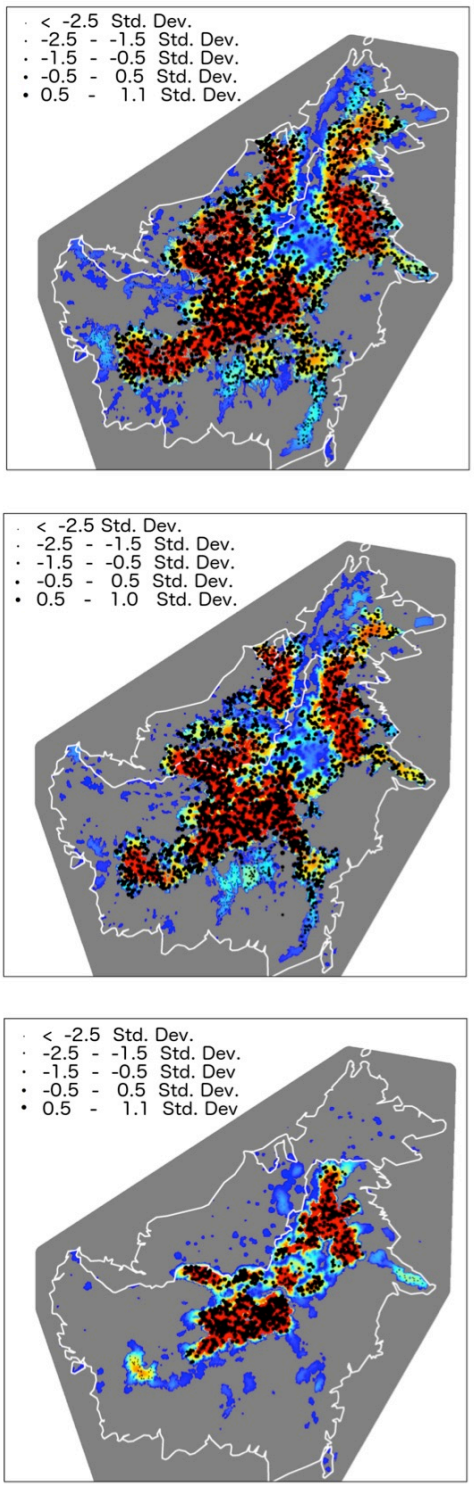

Figure 6. Mapping of sGD predictions of local observed heterozygosity for the three years (top 2000, middle 2010, bottom 2020). Black marker size indicates the observed heterozygosity for the genetic neighborhood surrounding that point.

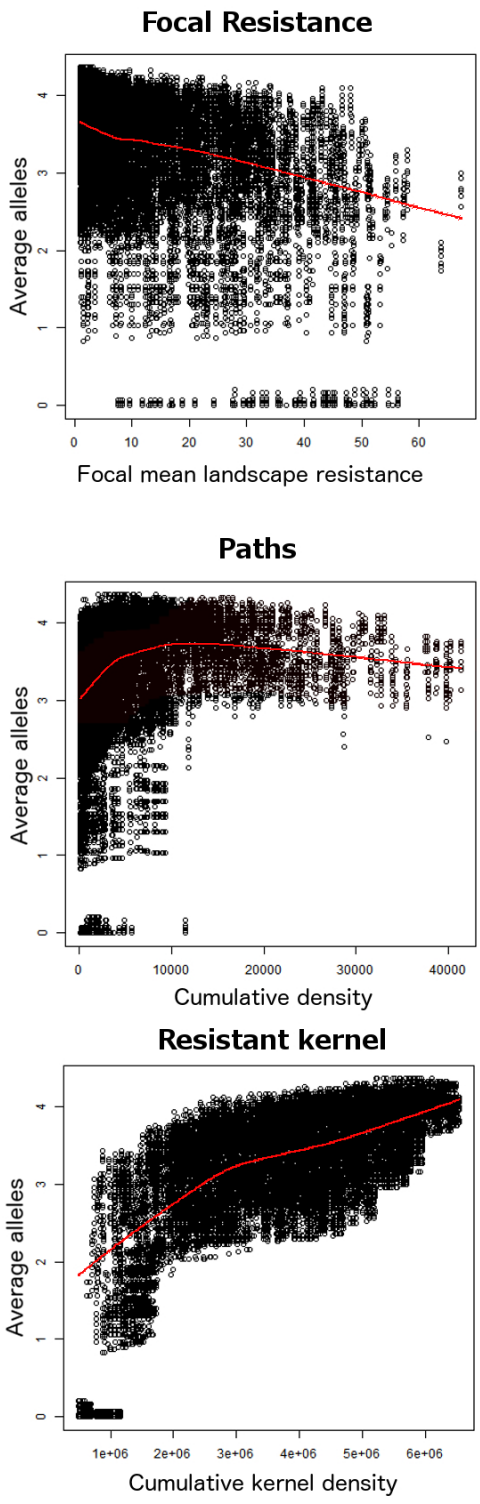

Figure 7. Scatterplots and fitted lowest splines for relationship between average number of alleles per locus and focal mean landscape resistance within a 10km radius, cumulative density of least cost paths, and cumulative resistant kernel density.

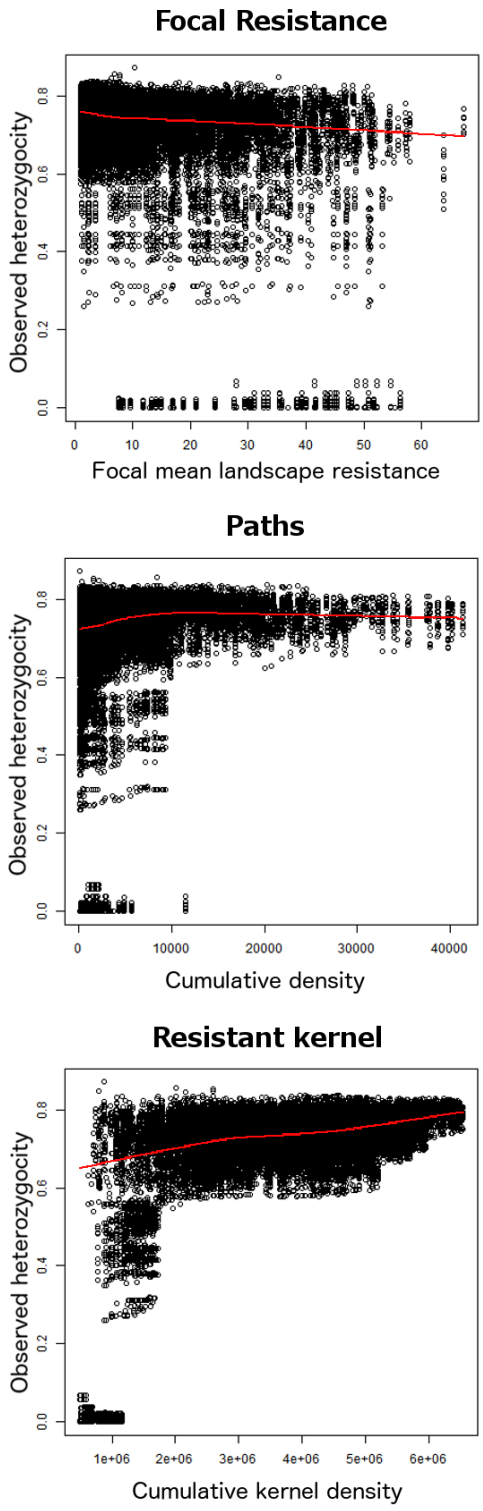

Figure 8. Scatterplots and fitted lowest splines for relationship between observed heterozygosity and focal mean landscape resistance within a 10km radius, cumulative density of least cost paths, and cumulative resistant kernel density.

Table 5. Candidate models predicting average alleles per locus (Axxxx) and observed heterozygosity (Hoxxx) as a function of cumulative resistant kernel value (K), cumulative density of least cost paths (P), and focal average landscape resistance within 10km (R), for the 125kcu (125) dispersal scenarios.

Model	aic	delta	deviance	residual deviance	deviance explained
A125KPR	34843		14826.2	6058.4	0.591
A125KP	34852	9	14826.2	6061.1	0.591
A125KR	35135	292	14826.2	6134.6	0.586
A125k	35229	386	14826.2	6159.7	0.585
A125PR	50714	15871	14826	11905	0.197
A125R	51891	17048	14826	12518	0.156
A125P	52558	17715	14826	12878	0.131
Ho125KPR	-47814		380.73	179.73	0.528
Ho125KP	-47804	10	380.73	179.81	0.528
Ho125KR	-47786	28	380.73	179.95	0.527
Ho125k	-47760	54	380.73	180.17	0.527
Ho125PR	-32943	14871	380.73	338.46	0.111
Ho125R	-32700	15114	380.73	342	0.102
Ho125P	-31363	16451	380.73	362.03	0.049

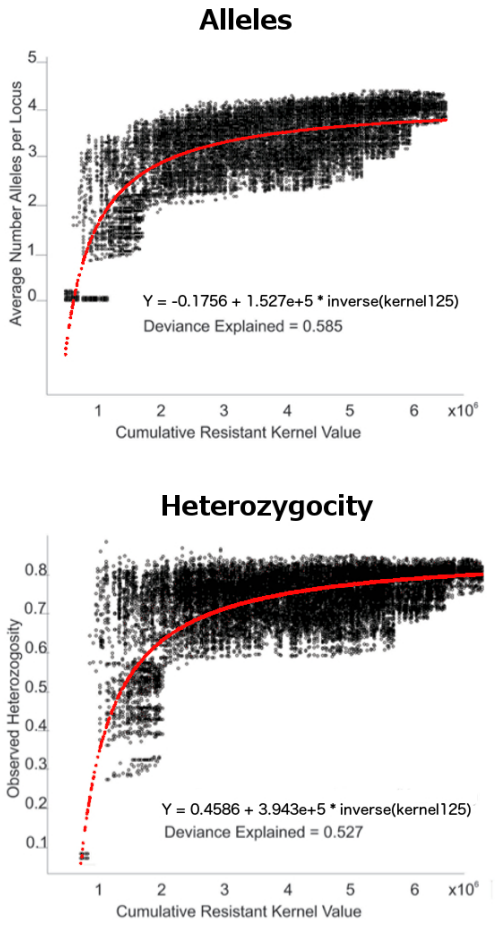

Figure 9. Scatterplots of average number of alleles per locus in a local neighborhood relative to resistant kernel value for a) the 125kcu scenaro and b) the 250kcu scenario, and heterozygosity of the local neighborhood relative to resistant kernel value for c) the 125kcu scenario and d) the 250kcu scenario. The fitted regression equation is shown in red overlay, and the equation and deviance explained are displayed below each scatterplot.

Discussion

Ongoing rapid landscape change on Borneo is likely to reduce the extent and increase the fragmentation of habitat of clouded leopards with important repercussions for both their genetic diversity and their projected population sizes. Our simulation of clouded leopard population dynamics predicted that the 2010 landscape would support 13% fewer clouded leopards than the 2000 landscape. Mirroring the accelerating rate of change exhibited by the landscape metrics, we predicted that the 2020 landscape would support approximately 57% fewer clouded leopards than the 2010 landscape and 63% fewer than the 2000 landscape. Similar trends were found for heterozygocity and allelic richness, suggesting that shrinkage and fragmentation of habitat across Borneo will not only result in smaller clouded leopard populations, but also populations that are potentially more vulnerable to demographic stochasticity and inbreeding depression as well as being less able to adapt to future challenges (Frankham et al. 2002). These risks of reduced heterozygosity and allelic richness are most pronounced in small, isolated and peripheral populations of clouded leopards.

We demonstrated that, in the face of probable continuing forest loss and fragmentation, the prospects for the Sunda clouded leopard on Borneo are likely to deteriorate both in terms of the overall population numbers and genetic diversity. We found that between 2000 and 2010 the percentage of land area connected by dispersal and the extent of the largest interconnected patch both fell steeply (by approximately 25% and 37% respectively); however, for both metrics the rate of loss is predicted to accelerate, with losses of around 63% and 69% respectively between 2010 and 2020. These trends were robust across

dispersal distances (125km and 250km) and across different percentile thresholds for clouded leopard core areas. The number of patches exhibited a slightly more complicated pattern related to the loss of small marginal patches between 2000 and 2010 and then the subsequent break up of larger patches between 2010 and 2020.

Some parts of our model are populated by data derived from expert opinion, and although our team includes researchers with many years of experience conducting field research on clouded leopards, maps of habitat suitability derived from expert opinion have been shown to be less reliable than empirically derived data (Seoane et al. 2005; Shirk et al. 2015; Shirk et al. 2010). In this study, the ICC suggests that survey respondents showed a high level of agreement, however inevitably the results for some land uses were certain than others. Frequency distributions for the survey responses are shown in figure 1, and these show that while reviewers were reasonably unanimous in their view that lowland forests represented high quality habitat, they were less consistent in their view towards peat swamp forest. The comparative uncertainty in these areas could influence the reliability of our model and highlights the need for greater research in these less understood habitat types. Reassuringly however, the estimated population density provided by the survey respondents (1.12 ind. per 100km^2) falls within the empirically estimated range of population density for clouded leopards in the peat swamp forest of Sabangau (0.72 to 4.41 ind. per 100km^2)(Cheyne et al. 2013). For this reason it will be important to collect empirical data on population distribution, abundance, genetic diversity and gene flow to verify and improve our predictions.

Additionally, our method for estimating the landscape resistance in 2020 has inherent uncertainty. Our method involves multiplying pixel values by the probability of deforestation in each cell, and thus if we have two pixels that both have a 50% probability of deforestation by 2020, then both cells will be multiplied by 50% whereas in reality we might expect that one cell might be completely deforested and the other might remain intact. One potential solution to this inaccuracy would have been to allocate a number of cells for deforestation based on their probability of loss, however, under this approach we would still have no objective way of knowing which pixel would be deforested. Our approach cannot therefore be used to interpret fine scale impacts of local land use changes, although the impacts at a wider landscape scale remain robust. Nonetheless, the present urgency of guiding conservation in Borneo requires prompt action to address an unfolding biodiversity crisis. Therefore, we believe the governments of Borneo should work with conservationists, scientists and economists to utilize the best information currently available to develop proactive strategies to slow the dramatic pace of forest loss and biodiversity impacts. It was our goal in this paper to help provide some information for this effort.

In addition to our findings about the plight of the clouded leopard on Borneo it is important to note that this is the first study to attempt to model effects of ongoing deforestation on population decline and changes in population connectivity and genetic diversity of any species at this scale. The spatially synoptic analysis of least cost paths across Borneo in particular was incredibly computationally demanding requiring the calculation of all least cost paths between all source points (between 715,806 and 4,114,146 least cost paths for

each scenario). In addition, parameterizing and running an individual based population genetics model such as CDPOP across such a vast scale and large population size represents a considerable challenge for most practitioners. Therefore, we tested whether it was possible to take a pragmatic shortcut in estimating landscape scale changes in allelic richness and heterozygosity by simply using the maps of landscape resistance, path density and kernel density that we had already computed. Our regression analysis showed that the full model (using all three predictor variables) allowed us to explain about 60% of the deviance for both allelic richness and heterozygosity. However in all cases, the single variable model (including only kernel density) was the most parsimonious solution and explained an almost identical proportion of the deviance. Future studies that are limited by time or computational power might therefore be able to rely on cumulative resistant kernel density as a proxy for changes in measures of genetic diversity.

Despite a recent increase in research effort, the Sunda clouded leopard on Borneo remains elusive and one of the world's least known felids, and this hampers the development of coherent conservation actions (Hearn et al. 2015). Nonetheless, this study highlights the severe impacts of ongoing fragmentation and loss of forest habitats on Borneo. Our analyses predicted a marked decline in both the overall area of clouded leopard core areas and a marked reduction in patch sizes with several patches being lost all together, coupled with dramatic declines in allelic richness and heterozygosity. Future conservation effort should focus effort on slowing the rate of land use change in Borneo, while prioritizing conservation in areas that maintain the extent of core populations and the connectivity between them.

Additionally, while a small number of studies have successfully made local estimates of clouded leopard density (Brodie & Giordano 2012; Cheyne et al. 2013; Hearn et al. 2013), future research should focus on better estimates of clouded leopard abundance and density across Borneo as well as improving our knowledge of the species' basic ecology (particularly it's dispersal) and how it responds to anthropogenic changes in it's environment. This would improve our ability to reliably map both habitat suitability and landscape resistance. We are currently in the process of refining the models presented in this paper using empirical field data from the relatively well-studied region of Sabah, however Borneo wide initiatives are also required.

The implications of this study extend beyond the conservation of the clouded leopard. Firstly, while our models were parameterized specifically for clouded leopards based on expert opinion, who assigned suitability values based on their understanding of the species' dependence on natural lowland forest ecosystems. Consequently our model is likely to have relevance to any other medium sized forest dependent mammals on Borneo (such as the sun bear (*Helarctos malayanus*) that may have similar dispersal distances and habitat associations.

Macdonald et al. (2012) have highlighted the fact that many species (for example felids and primates) face the same threats in the same locations and may benefit from many of the same solutions. Building on this notion, (Macdonald et al. submitted) and (Macdonald et al. 2015) have shown that the clouded leopard is not only regarded as charismatic by the

general public but that it has strong potential to act as an Ambassador for conservation marketing campaigns. This supports the widespread approach of protecting patches or corridors that support one or several wide-ranging, often large-bodied, species on the assumption that conservation of these umbrella species will also facilitate conservation of smaller or less mobile organisms (e.g. (Baguette et al. 2013; Noon et al. 2009) but see (Cushman & Landguth 2012b; Cushman et al. 2013a)). As a generalization, (Beier et al. 2008) argued that habitat corridors may more effectively protect regional biodiversity if they are developed to support the movement of multiple species simultaneously, because so many species are threatened by fragmentation, a proposition which underlies the analyses presented by (Brodie et al. 2014) for a basket of SE Asian species including clouded leopards.

Deforestation is on-going and accelerating across Borneo with immense implications for biodiversity. Our analysis is the first to use robust predictions of future landscape change at such a broad scale to simulate changes in population size, connectivity, gene flow and genetic diversity. Our results suggest large recent declines in clouded leopard population size and genetic diversity and predict much larger imminent declines as deforestation continues across Borneo, particularly in Sabah and Sarawak, where the pattern of forest loss is much more damaging due to its widespread, diffusive nature. Our analyses provide plausible inferences about how recent and future landscape change may affect clouded leopard populations across Borneo. Additional work using extensive occurrence, genetic and movement data is needed to verify and improve our predictions. However, given the immediate and urgent need for effective conservation action in the part of the world

experiencing the most rapid loss of tropical forest, we hope our analyses could be of immediate utility in identifying (1) population core areas for priority conservation, (2) linkages between these core areas, (3) relationships between habitat extent, landscape resistance, population size, dispersal ability and genetic diversity to help managers and planners anticipate the effects of a range of alternative conservation scenarios. The tools we have presented here could be of use in developing and evaluating the specific impacts of alternative scenarios on population size, connectivity and genetic diversity.

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Zeller, K. A., K. McGarigal, and A. R. Whiteley. 2012. Estimating landscape resistance to movement: a review. Landscape Ecology **27**:777-797.

Supplementary material

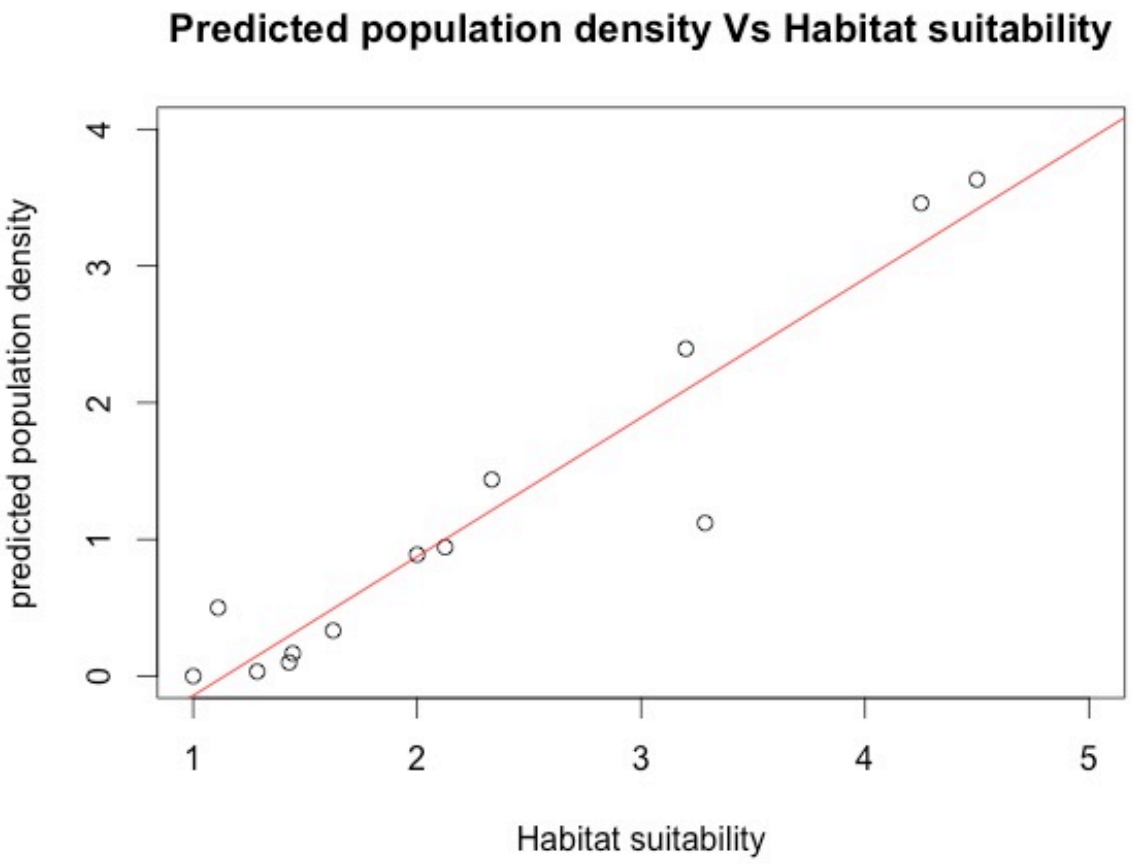

Figure A1. Plot of the mean respondent scores for habitat suitability vs the mean estimated population density for clouded leopards. The high of R^2= 0.905 shows high consistency in the estimates provided by the panel of experts.

In the main body of this paper we state that "*Data on maximum dispersal distances are scarce for any species and dispersal distances are not known for clouded leopards. However, a number of studies have attempted to describe allometric relationships between maximum dispersal distances and a range of physiological and life history traits for mammals in general (Bowman et al. 2002; Whitmee & Orme 2013). Bowman estimates that maximum dispersal*

distance is equal to 40(home range size$^{0.5}$) and since clouded leopards are thought to have home ranges in the region of 16km^2 (N. diardi) - 40km^2 (N. nebulosa) we therefore estimate that a likely range of dispersal distances from 160 -252km (Austin et al. 2007; Bowman et al. 2002; Grassman et al. 2005; Hearn et al. 2013). For this study we therefore selected 125km as a plausible conservative estimate of dispersal in clouded leopards*". In order to test the sensitivity of our results to this estimate we also ran all analyses under an alternative dispersal scenario of 250km. This figure was selected to represent a plausible upper boundary for the maximum dispersal distance for clouded leopards. A comparison of resistant kernel maps for the 125kcu and 250kcu scenarios can be seen in Figure A2. As expected, the landscape shows higher levels of connectivity between populations under the 250kcu dispersal scenario.

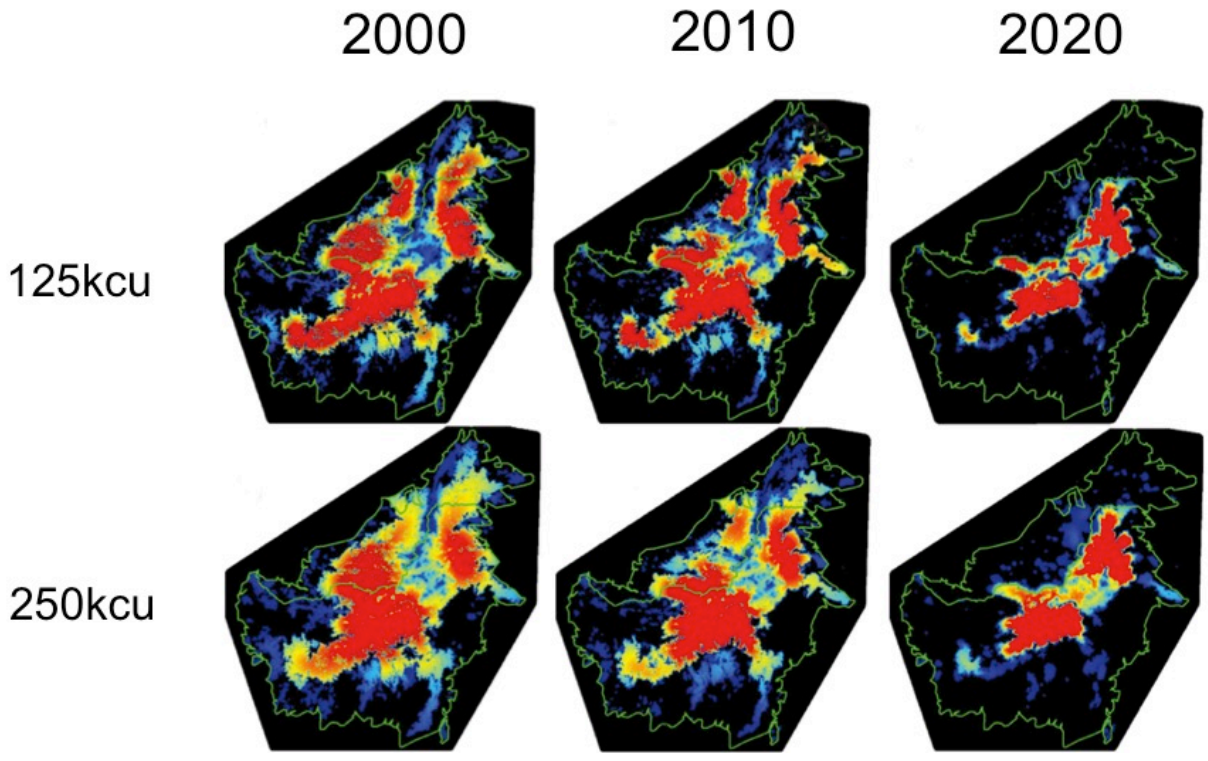

Figure A2. Comparison of resistant kernel maps for two potential dispersal distances. 125kcu (as shown in Figure 2, and 250kcu.

In addition to testing the sensitivity of our analyses to differences in dispersal distance, it was necessary for us to adopt a threshold for clouded leopard priority areas. In the main analysis we defined connected populations as those areas greater than the 10th percentile of the 2000 kernel surface for all three dates. Given any particular threshold is arbitrary, we decided to explore how patterns of predicted connectivity varied across various thresholds. We therefore also tested the impact of using both the 5th and 20th percentile of the 2000 kernel surface as thresholds in our analysis.

All analyses were conducted at both dispersal distances and across all thresholds and the results of those analyses are presented below.

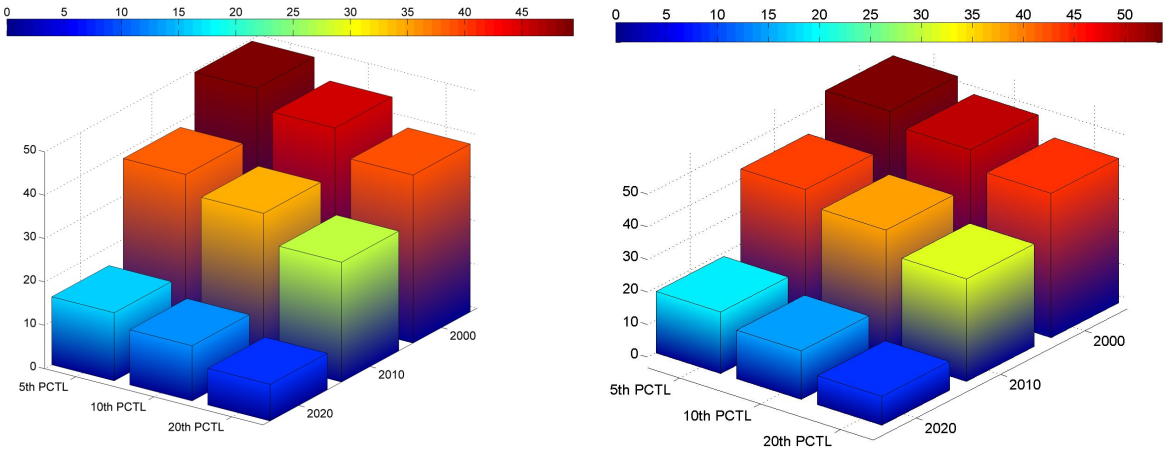

Figure A3. Change in the percentage of the landscape connected by dispersal for 2000, 2010, and 2020 across varying thresholds for selection and dispersal distance.

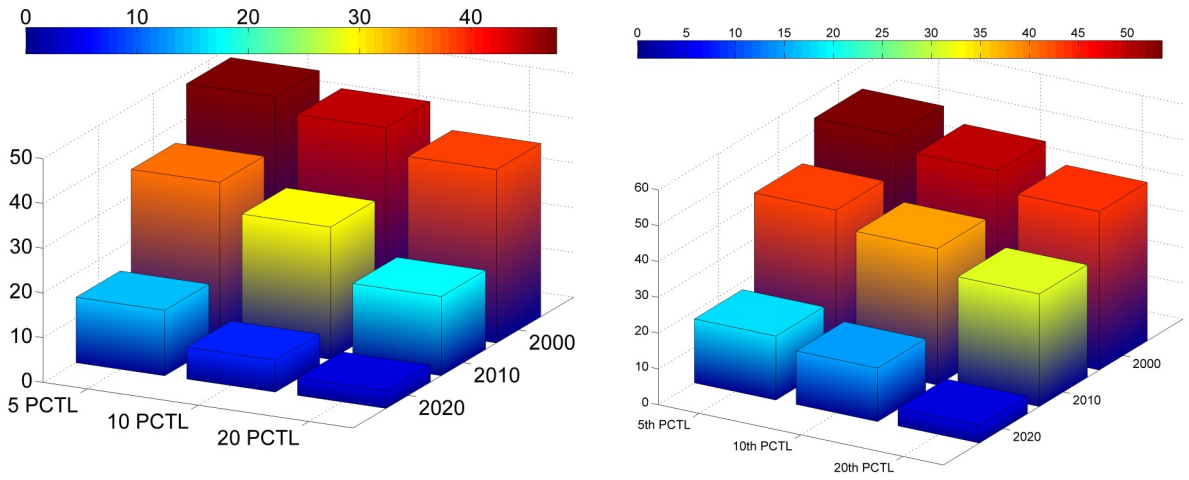

Figure A4. Change in the extent of the largest patch of connected habitat as percentage of the landscape across the 5th, 10th and 20th percentiles of the cumulative kernel surface in year 2000 for 2000, 2010, and 2020 at (a) 125kcu and (b) 250kcu dispersal thresholds.

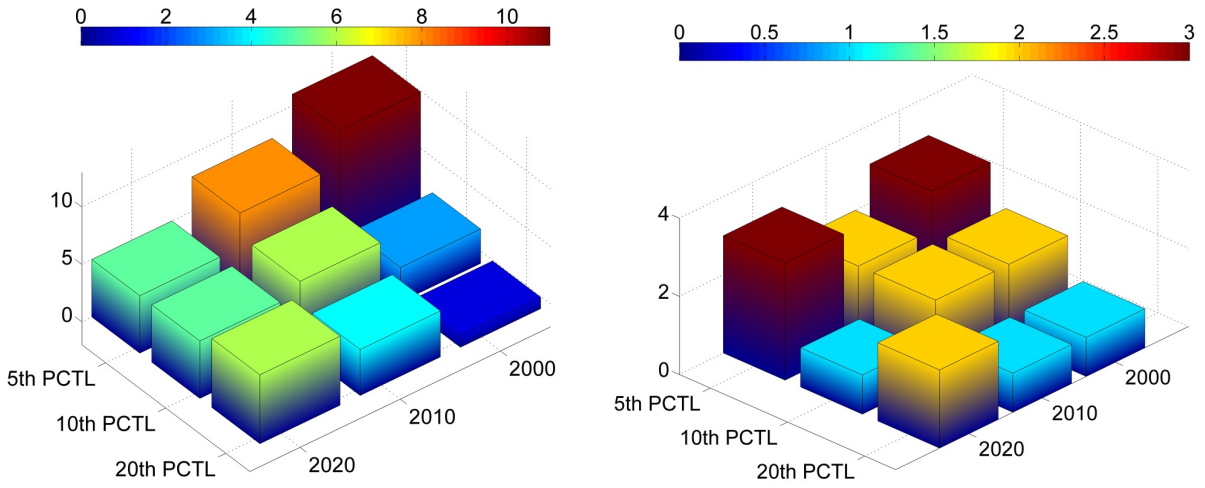

Figure A5. Change in the number of isolated patches of connected habitat across the 5th, 10th and 20th percentiles of the cumulative kernel surface in year 2000 for years 2000, 2010, and 2020 at (a) 125kcu and (b) 250kcu dispersal thresholds.

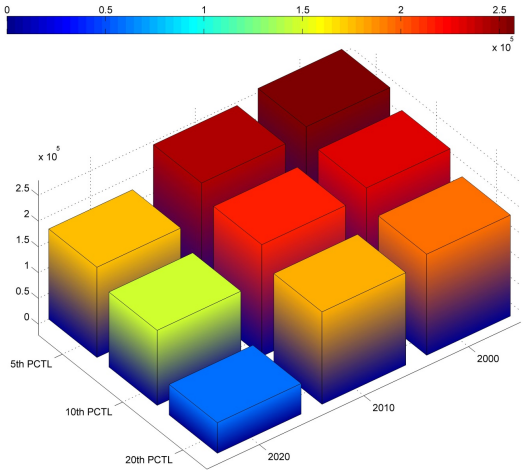

Figure A6. Changes in the correlation length of the factorial least cost path network across three density thresholds (5th percentile, 10th percentile and 20th percentile of the least cost path density in 2000), and across the three dates (2000, 2010, 2020).

Table A1. Relative change in Fragstats metrics between 2000-2010 and 2010-2020 for dispersal abilities 125 and 250kcu and percentile thresholds 5th, 10th and 20th percentile.

	125		250		125		250	
	5 to 10	10 to 20	5 to 10	10 to 20	2000 to 2010	2010 to 2020	2000 to 2010	2010 to 2020
Proportion of landscape connected by dispersal	-0.107	-0.161	-0.174	-0.212	-0.246	-0.634	-0.235	-0.623
Largest patch index	-0.174	-0.212	-0.101	-0.193	-0.365	-0.692	-0.238	-0.665
Number of patches	-0.714	-0.273	-0.6	-0.25	0.2	-0.11111	-0.16667	0.2

Table A2. Relative change in correlation length of connected least cost path network between 2000-2010 and 2010-2020 for dispersal abilities 125 and 250kcu.

	5 to 10	10 to 20	2000 to 2010	2010 to 2020
Correlation Length	-0.138061264	-0.366897158	-0.067002253	-0.405899178

The above figures and tables show that across all landscape metrics, the impact of landscape change through time is far higher than the impact of either dispersal distance or threshold value. The only exception to this is in the number of isolated patches, which displays a complicated pattern that balances the increase in the number of patches from the fracturing of large areas against the decrease in number, as smaller patches are lost completely.

A similar pattern could be seen when we examined the impact of dispersal distance on the genetic metrics in this study. Changes through time dwarfed the effect of dispersal distance on changes in heterozygocity and local scale measures of genetic diversity.

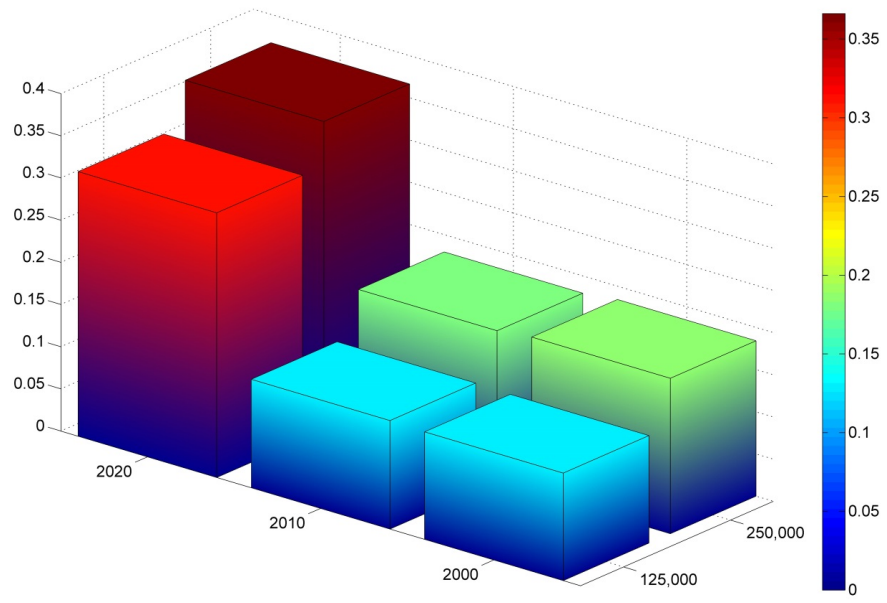

Figure A7. Proportional reduction in heterozygosity between Expected and Observed heterozygosity in each simulation scenario, indicating the relative effect of population connectivity on heterozygosity.

Table A3. Population characteristics at generation 200 from CDPOP simulations, averages and standard deviations across 10 CDPOP runs for each scenario.

Year	Dispersal Ability (kcu)		Population size	Expected Heterozygosity	Observed Heterozygosity	Reduction in observed vs expected heterozygocity (%)	Average Mating Distance (km)	Average Dispersal Distance (km)
2000	125	mean	2610.7	0.851	0.694	18.45	25.569	25.315
		stdev	14.7	0.004	0.010		0.469	0.887
2000	250	mean	2623.3	0.844	0.737	12.68	36.938	26.031
		stdev	10.6	0.005	0.008		0.614	0.596
2010	125	mean	2279.0	0.842	0.691	17.93	26.967	25.610
		stdev	11.2	0.004	0.017		3.884	0.925
2010	250	mean	2280.1	0.840	0.732	12.86	36.933	25.935
		stdev	6.4	0.005	0.009		1.321	1.250
2020	125	mean	972.9	0.785	0.497	36.69	19.553	19.967
		stdev	10.0	0.008	0.013		1.060	0.689
2020	250	mean	971.3	0.766	0.526	31.33	27.344	20.094
		stdev	9.7	0.015	0.017		1.336	0.779

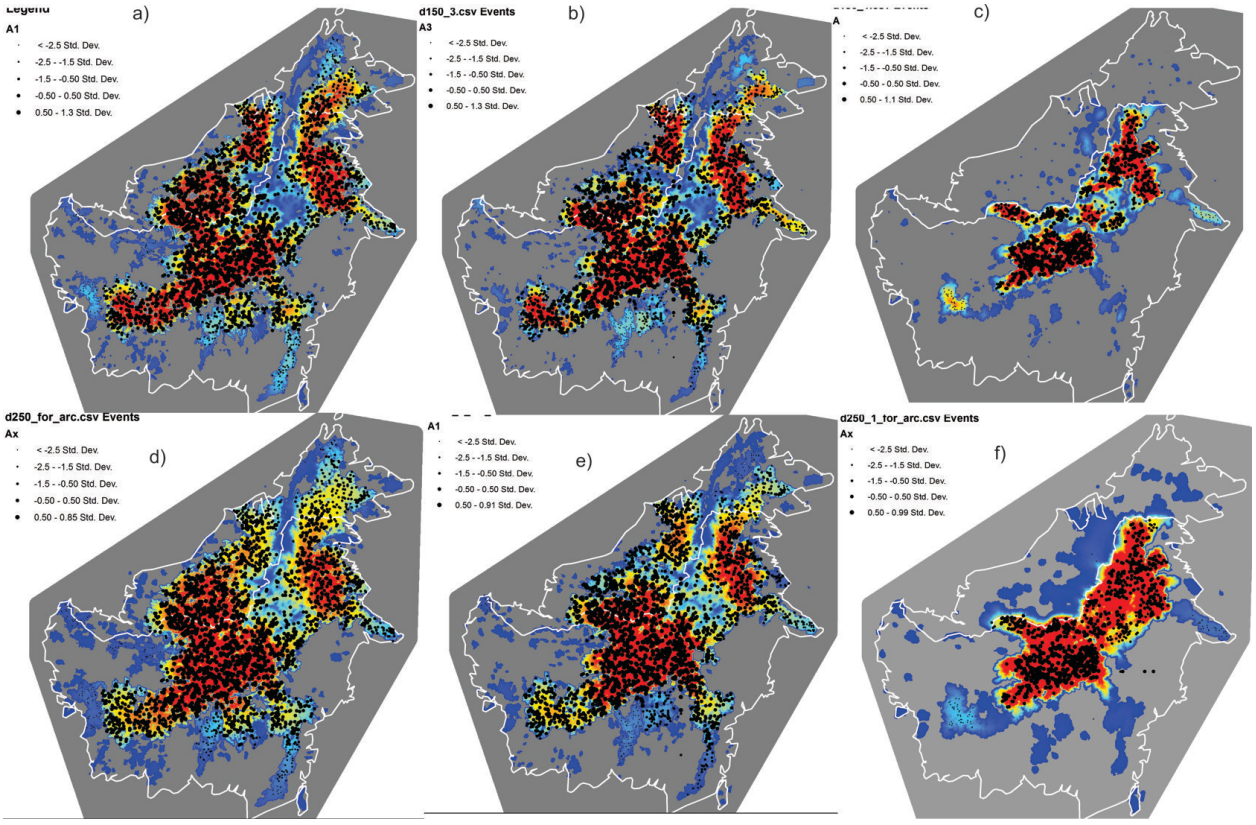

Figure A8. Mapping of sGD predictions of local average number of alleles per locus for the two dispersal ability thresholds (125kcu a), b),c); 250kcu d), e), f), for the three years (2000 a), d); 2010, b),e); 2020, c),f)). Black marker size indicates the relative number of alleles per locus for the genetic neighborhood surrounding that point.

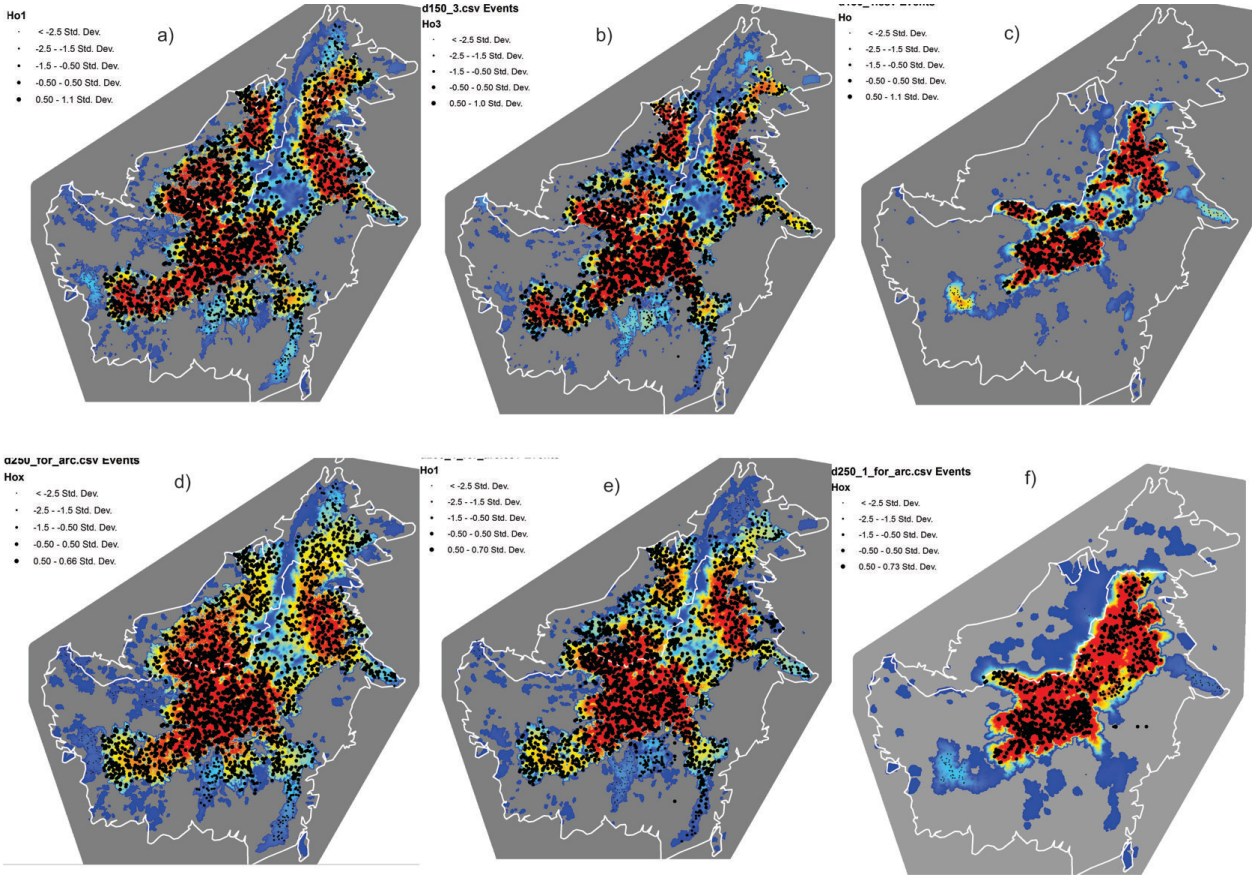

Figure A9. Mapping of sGD predictions of local observed heterozygosity for the two dispersal ability thresholds (125kcu a), b),c); 250kcu d), e), f), for the three years (2000 a), d); 2010, b),e); 2020, c),f)). Black marker size indicates the observed heterozygosity for the genetic neighborhood surrounding that point.

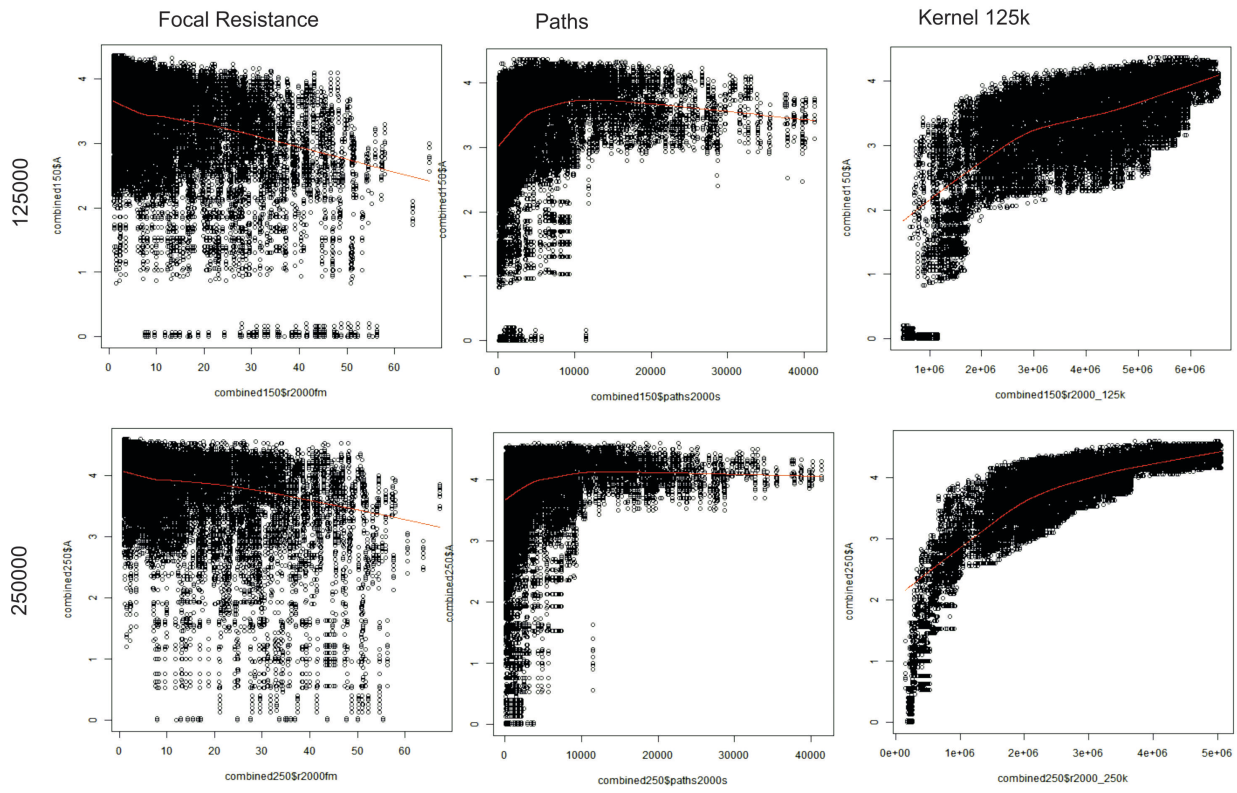

Figure A10. Scatterplots and fitted lowest splines for relationship between average number of alleles per locus and focal mean landscape resistance within a 10km radius (column 1), cumulative density of least cost paths (column 2), and cumulative resistant kernel density (column 3), across the two dispersal distance scenarios (125kcu, row 1; 250kcu, row 2).

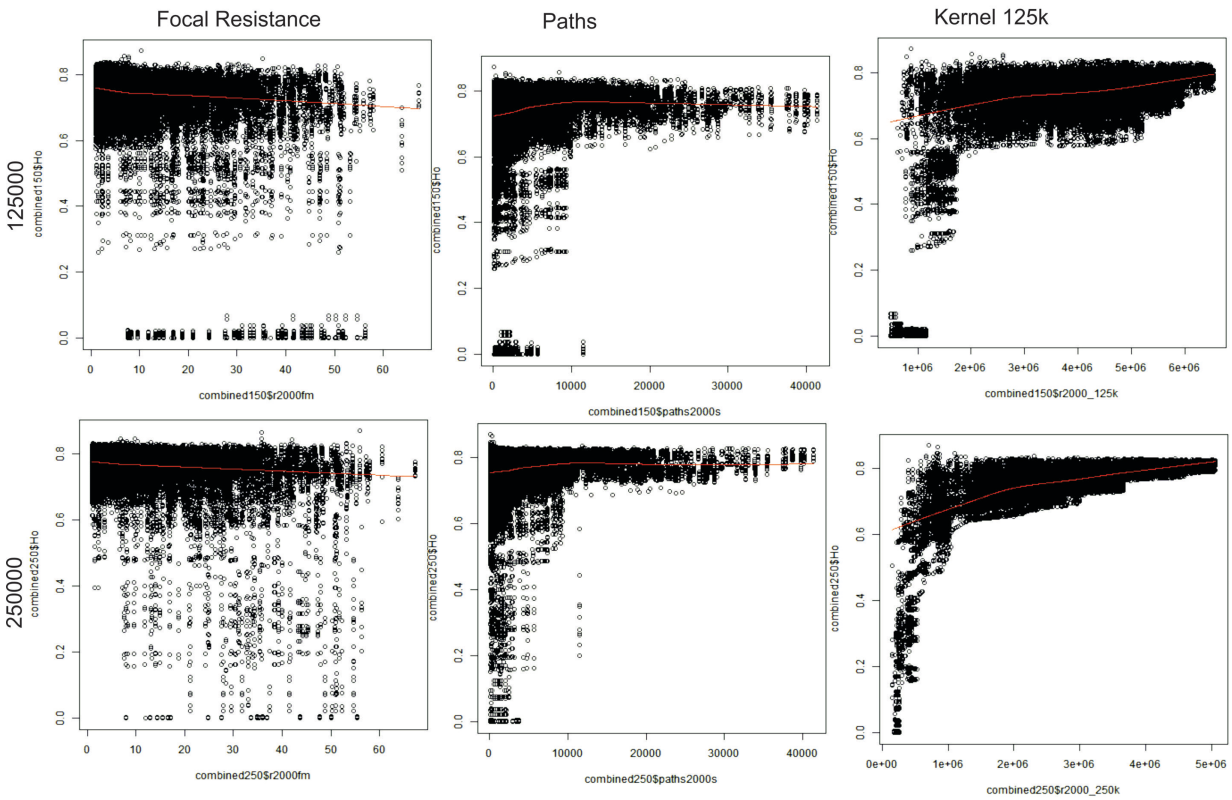

Figure A11. Scatterplots and fitted lowest splines for relationship between observed heterozygosity and focal mean landscape resistance within a 10km radius (column 1), cumulative density of least cost paths (column 2), and cumulative resistant kernel density (column 3), across the two dispersal distance scenarios (125kcu, row 1; 250kcu , row 2).

Table A4. Candidate models predicting average alleles per locus (Axxxx) and observed heterozygosity (Hoxxx) as a function of cumulative resistant kernel value (K), cumulative density of least cost paths (P), and focal average landscape resistance within 10km (R), for the 125kcu (125) and 250kcu (250) cost unit dispersal scenarios.

Model	aic	delta	deviance	residual deviance	deviance explained
A125KPR	34843		14826.2	6058.4	0.591372
A125KP	34852	9	14826.2	6061.1	0.59119
A125KR	35135	292	14826.2	6134.6	0.586232
A125k	35229	386	14826.2	6159.7	0.58454
A125PR	50714	15871	14826	11905	0.197019
A125R	51891	17048	14826	12518	0.155672
A125P	52558	17715	14826	12878	0.131391
A250KPR	12826		14639.3	2466.6	0.831258
A250KP	12901	75	14639.3	2474	0.831003
A250KR	13728	902	14639.3	2555.7	0.825422
A250k	14103	1277	14639.3	2593.8	0.822819
A250PR	52922	40096	14639	11906	0.186693
A250R	53834	41008	14639	12341	0.156978
A250P	55026	42200	14639	12933	0.116538
Ho125KPR	-47814		380.73	179.73	0.527933
Ho125KP	-47804	10	380.73	179.81	0.527723
Ho125KR	-47786	28	380.73	179.95	0.527355
Ho125k	-47760	54	380.73	180.17	0.526778
Ho125PR	-32943	14871	380.73	338.46	0.111024
Ho125R	-32700	15114	380.73	342	0.101726
Ho125P	-31363	16451	380.73	362.03	0.049116
Ho250KPR	-81268		313.74	61.338	0.804494
Ho250KP	-81125	118	313.74	61.628	0.80357
Ho250KR	-80922	346	313.74	62.184	0.801798
Ho250k	-80520	748	313.74	63.176	0.798636
Ho250PR	-42578	38690	313.74	280.2	0.106904
Ho250R	-42448	38820	313.74	281.65	0.102282
Ho250P	-40884	40384	313.74	299.48	0.045452

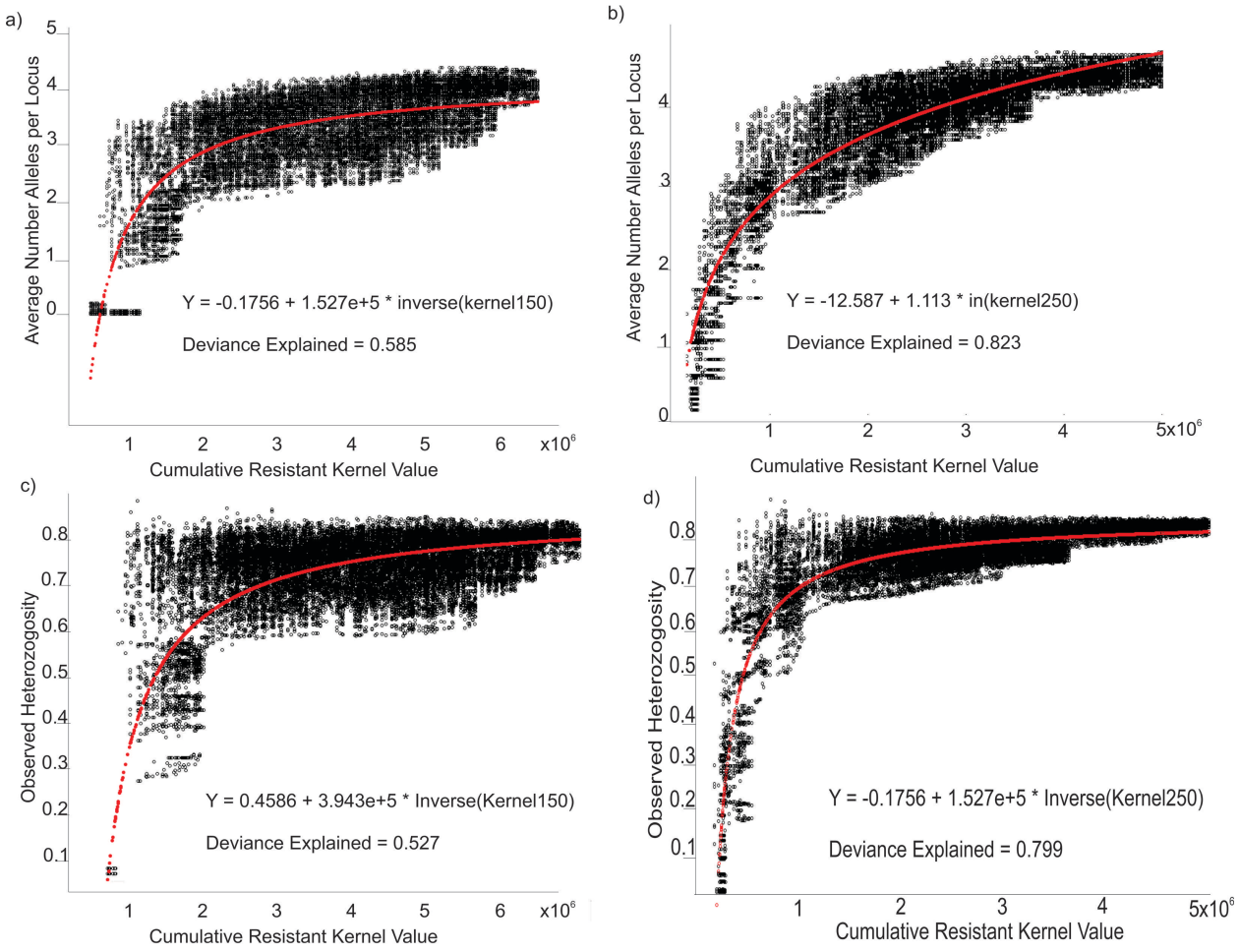

Figure A12. Scatterplots of average number of alleles per locus in a local neighborhood relative to resistant kernel value for a) the 125kcu scenario and b) the 250kcu scenario, and heterozygosity of the local neighborhood relative to resistant kernel value for c) the 125kcu scenario and d) the 250kcu scenario. The fitted regression equation is shown in red overlay, and the equation and deviance explained are displayed below each scatterplot.

Chapter 6

Clouds on the horizon: The impacts of future deforestation on clouded leopard population connectivity and gene flow across Borneo under contrasting scenarios for conservation

Abstract

Predictive modelling, using multi-scale random forest machine learning, indicates that 37% of the remaining forest in Borneo will have a greater than 25% risk of being deforested by 2020, with the consequence that habitat connectivity and corridors for the dispersal of clouded leopard are likely to deteriorate. As these changes unfold, they may be mitigated, or worsened, by a variety of contrasting forest conservation scenarios. We modelled seven such scenarios including a 2010 baseline condition, a 2020 business as usual scenario as well as variants on both "active" and "expedient" approaches to conservation. The "active" conservation scenarios targeted conservation effort in the areas under highest deforestation risk, while the "expedient" conservation scenarios targeted conservation effort in the areas of lowest risk. We used the decision support tool MARXAN to identify the optimal placement of the protected areas under each scenario and modelled the impacts of each scenario on clouded leopard population size and habitat connectivity over a period of 200 generations.

In 2010 29% of the landscape was connected by dispersal but this fell to just 15% in 2020 under the business as usual scenario. We predict that this loss of habitat will have profound implications for clouded leopard populations, with the business as usual landscape able to support 51% fewer clouded leopards in 2020 than the 2010 baseline. Scenarios that permitted the reallocation of protected areas typically performed best suggesting that existing protected areas are situated in areas whose inaccessibility and risk profile means they are unlikely to have a significant impact on reducing rates of habitat loss in the near future. These active approaches to conservation planning would result in a 53% increase in the area connected by dispersal, a 70% increase in the largest

patch size and a 30% increase in the average distance a clouded leopard can travel within a patch relative to the BAU scenario. Comparing the impact of different scenarios on the storage of above ground biomass carbon revealed that the best performing active scenario retained 94 million tons more carbon than under business as usual scenario.

Introduction

Forest loss is a global crisis, and one that appears to be worsening in S.E. Asia. Currently Indonesia has the most rapidly accelerating rate of forest loss in the world, experiencing losses over 20,000km^2/yr in 2011 and 2012, while Malaysia experienced the highest total gross loss of forest in relation to its land area (14.4% of its total land area between 2000-2012; Hansen et al. (2013)). On Borneo, 30% of forest area was lost between 1973 and 2010 (Gaveau et al. 2014). These forests are also among the most globally important carbon stores/sinks with approximately 60% more Above Ground Biomass per unit area than the Amazon (Slik et al. 2010).

This loss and fragmentation of Borneo's forest ecosystems is a major threat to biodiversity in one of the world's most important hotspots (Myers et al. 2000). The island of Borneo is home to in excess of 14,000 plant species and 1,600 vertebrate species, among which there are 196 mammals including the elusive and enigmatic Sunda clouded leopard, *Neofelis diardi* a species about which little is known, but which depends on threatened forests for habitat ((Corbet & Hill 1992; Inger & Voris 2001; Kottelat 1989; Myers 2009; Roos et al. 2004; Uetz & Hošek 2013) in (Runting et al. 2015)). Top predators like the clouded leopard have a particularly important role in ecosystems (Ripple et al. 2014), and they are also highly charismatic (Macdonald et al. 2015) giving them the ability to act as ambassadors for wider conservation efforts (Macdonald et al. submitted). Previously, having predicted forest loss in Borneo using multi-scale random forest machine learning (Macdonald et al. in review) and having shown how these projected losses are likely to impact the population dynamics and genetic health of

Borneo's clouded leopards (Macdonald et al. In Prep-a), we now raise the question of what policy might mitigate, or even reverse, these losses.

Habitat loss is among the most significant threats to the clouded leopard (Hearn et al. 2015), and so policies to reduce the rate of deforestation, such as the introduction of new protected areas are an important tool for their conservation. However scarce resources and the competing demands on undeveloped land make it important for any new protected areas to be planned and located systematically for the greatest benefit (Ferrier & Wintle 2009; Pressey et al. 2007). Systematic spatial conservation prioritisation has consequently become an increasingly popular tool among both conservation practitioners and researchers (Ferrier & Wintle 2009). A common approach to systematic conservation prioritisation is for researchers to quantify the efficiency of the existing protected area network before going on to identify new areas whose conservation would fill any gaps (Rodrigues et al. 2004; Underwood et al. 2009). Increasingly sophisticated approaches allow researchers to consider the impact of reserve design on diverse conservation features, and to seek a network of complementary reserves that minimise the cost of conservation while ensuring all the targets receive some level of conservation investment (Wilson et al. 2009). In addition to biodiversity features, researchers are increasingly seeking benefits between biodiversity conservation and the delivery of wider ecosystem services (Chan et al. 2006) most notably the conservation of forest carbon stocks (Chan et al. 2006; De Barros et al. 2014; Murray et al. 2015; Runting et al. 2015; Venter et al. 2013).

While systematically adding new protected areas to an existing network has the potential to improve overall coverage, it is also increasingly accepted that the existing global protected area network is inefficient. Historically the placement of protected areas has been driven more by expediency than contribution to conservation goals (Ando et al. 1998). Consequently, the locations of protected areas are biased towards "high and far" locations that are that are unlikely to be lost even in the absence of protection, and that such protected areas can do little to prevent land conversion (Hoekstra et al. 2005; Joppa & Pfaff 2009). Considering vulnerability is therefore a vital step in identifying priorities for conservation, and has been popularized by Conservation International's now famous biodiversity hotspots (Brooks et al. 2006; Myers et al. 2000). In order to be an effective tool for conservation protected areas must change land use outcomes and must therefore be located in areas that are most at risk from land conversion (Joppa & Pfaff 2009).

While a vital tool in conservation practice, protected areas have traditionally been thought of as permanent and immovable. However, recent studies have challenged this perception by highlighting the extent of downgrading, downsizing and degazettement of existing PAs (known as PADDD) (Mascia & Pailler 2011; Mascia et al. 2014). Rather than being permanent fixtures of the landscape PAs are dynamic, socially defined and constructed governance regimes that can be manipulated (Mascia & Pailler 2011). Frequently this process has been controversial (Dearden et al. 1998; Mascia & Pailler 2011; Vandergeest 1996, 1999) however it has also been proposed that reallocating conservation investment from inefficient, or under performing protected areas towards

new areas that improve the overall effectiveness of the network could be an economical strategy for improving conservation effectiveness (Fuller et al. 2010).

Influenced by these debates, we use MARXAN (Ball et al. 2009), a widely used decision support tool, to evaluate seven different scenarios that seek to maximise the conservation outcomes for both clouded leopards on Borneo, and the conservation of forest carbon. The scenarios are discussed in detail in the methods below, but include variants that rely on adding new protected areas to the existing network, as well as hypothetical variants that consider which areas should be prioritised under the hypothetical conditions of redesigning protected areas from scratch. We also explore two different approaches to locating protected areas – one that actively focuses effort on the areas of highest threat, while the other expediently focuses effort on areas of lowest threat. These contrast with a *business as usual* approach that relies on the existing network of protected areas and assumes that these areas continue to be as effective as they were between 2000 and 2010 (Macdonald et al. in prep-c).

The impact that each of these scenarios will then be assessed using connectivity modelling (UNICOR; Landguth et al. (2012)) and individual-based landscape genetic simulation (CDPOP; Landguth and Cushman (2010) to evaluate the impacts of each scenario on conservation outcomes for clouded leopards. The use of prospective scenarios is an important approach for conservation planning, not least to exclude unfeasible or catastrophic options at an early stage (Kass et al. 2011).

Methods

Data Layers (Fig. 1)

Clouded leopard core areas: Macdonald et al. (In Prep-a) used a resistant kernel approach (Compton et al. 2007) to identify areas of Borneo that are likely to be core areas for clouded leopard populations in the years 2000, 2010 and 2020. The resistant kernel approach predicts the relative density of dispersing individuals in each pixel across the analysis area given the dispersal ability of the species, the nature of the dispersal function, and the resistance of the landscape (Cushman et al. 2012). Areas with a high cumulative resistant kernel score can be interpreted as core areas for clouded leopards or corridors for dispersal; areas with a lower score are likely to be less frequently utilized by clouded leopards. Because little is known about clouded leopard dispersal, Macdonald et al. (In Prep-a) calculated resistant kernel values for two dispersal distances representing the plausible upper (250km) and lower (125km) bounds for maximum dispersal distance.

In this analysis we used the Macdonald et al. (In Prep-a) cumulative resistant kernel map for the year 2010, with a dispersal distance of 125km. We selected the year 2010 as the best representation of the 'current' state of clouded leopard core areas in Borneo. We selected the 125km dispersal distance, because it was the best fit with estimated dispersal distances based on empirically derived home range data for clouded leopards on Borneo (Bowman et al. 2002; Hearn et al. 2013). In addition, we compared the effect

of dispersal distance on several of our metrics and these results are presented in the supplementary material.

Deforestation risk: Estimates of future deforestation risk were obtained from Macdonald et al. (in review). This analysis used a multi-scale random forest machine learning modelling approach (Evans & Cushman 2009) to predict deforestation risk in 2020 from observed patterns of deforestation in relation to topographical, landcover, human population density, and conservation status of lands between 2000 and 2010. This deforestation risk map provided the probability that a pixel that was forested in 2010 would be deforested by 2020.

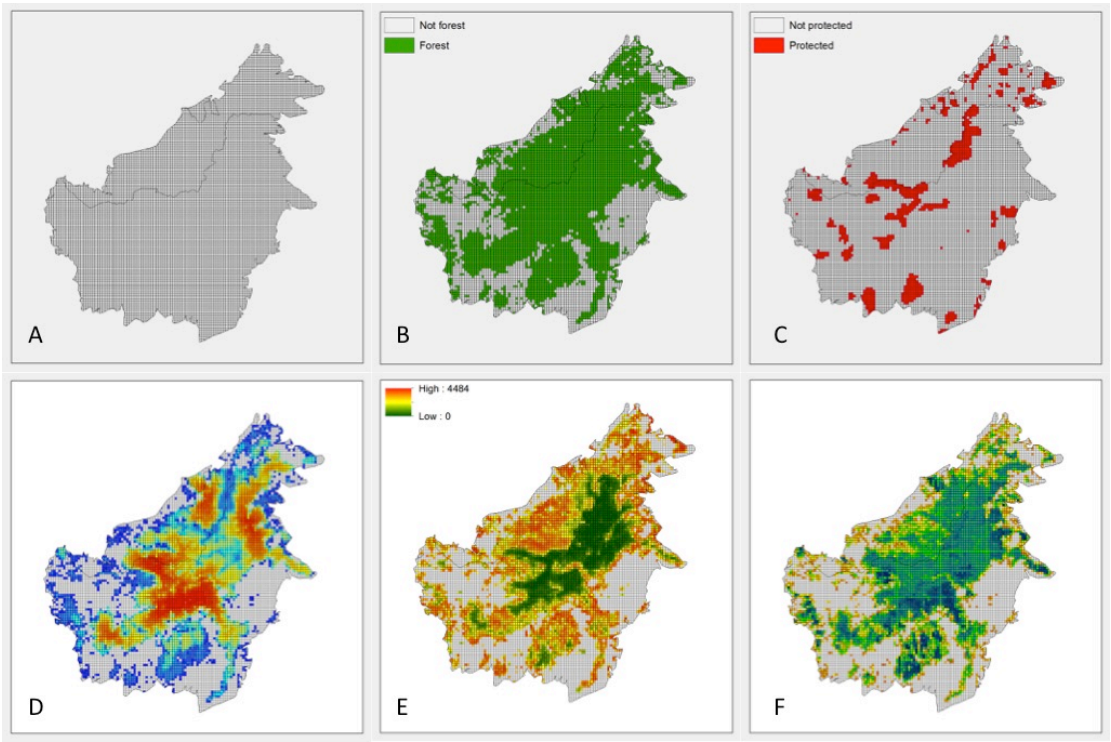

Figure 1. Data layers used in analysis. (A) Map of planning units across Borneo, (B) Planning units classified as Forest, (C) Planning units classified as protected, (D) Sum

kernel value in each planning unit, (E) Mean risk of deforestation in each planning unit, (F) Sum carbon value in each planning unit.

Forest carbon stocks: Estimates of forest carbon stocks were obtained from Saatchi et al. (2011) who provide a benchmark map of forest carbon stocks in the tropics. Saatchi et al. (2011) provide estimates for above and below ground biomass as well as total biomass carbon at a 1km resolution. Because most current carbon finance schemes exclude below-ground biomass from their calculations, we restricted our analysis to Above Ground Biomass (AGB).

Protected areas: A map of protected areas was obtained from the World Database on Protected Areas (IUCN & UNEP-WCMC 2014). Only IUCN category I-VI protected areas with associated shape files were included in the analysis.

Forest vs not forested areas: Because clouded leopards are strongly associated with forest habitats (Macdonald et al. In Prep-a), we locked areas that were predominantly non-forest out of our MARXAN analysis because they were not considered 'habitat'. Forest and not forest areas were identified from Miettinen et al. (2012), with mangrove, peatswamp forest, lowland forest, lower montane forest, upper montane forest being classified as forest, while the remaining habitat types (water, plantation/regrowth, lowland mosaic, mountain mosaic, lowland open, montane open, urban, and large scale palm plantations) were considered to be suboptimal habitat types for clouded leopards (Macdonald et al. In Prep-a) and were classed as not forest.

All data layers were resampled to a resolution of 500m, and divided by their maximum value to scale them from 0 to 1. MARXAN analyses were conducted at the scale of a 10x10km grid of planning units across the island of Borneo. In total there were 7,675 planning units, the vast majority of which encompassed an area of 100km^2 (89.8%), however the remaining 10.2% occurred in coastal areas and were therefore covered a smaller land area.

For each planning unit, we calculated the area classified as forest, the area covered by PAs, the sum resistant kernel score, the sum above ground biomass, and the mean deforestation risk.

Little is known about the spatial ecology of clouded leopards, however, one radio-collared female was estimated to have a home range of 16.1km^2 (Hearn et al. 2013), and so any planning units that did not contain a minimum of 16km^2 of forested habitat were locked-out of any reserve design solutions. Similarly, only planning units that contained more than 16km^2 of existing protected areas were considered to be protected.

Scenarios

We considered several contrasting scenarios for clouded leopard conservation. Scenario 1 represented the baseline 2010 condition, scenarios 2 and 3 represented an 'active' approach to conservation in which new protected areas are placed in areas of imminent high risk while scenarios 4 and 5 represented an 'expedient' approach to conservation in which new protected areas are located in the areas with the lowest risk of deforestation and thus presumably have the lowest cost of conservation. Within these 'active' and 'expedient' scenarios we also considered the impact of the existing protected area

network on the reserve design – scenarios 2 and 4 ignored the existing protected areas and 'started from scratch', while scenarios 3 and 5 were forced to include the existing protected area network in the future reserve design. Finally scenarios 6 and 7 retained the existing protected area network but assumed that no new protected areas were added. Of these, scenario 6 assumed that the existing PA network will be effective and that these areas will be invulnerable to deforestation, while scenario 7 assumed that these PAs will be subject to the deforestation risks predicted by (Macdonald et al. in review), which includes protection status as one of the predictor variables.

Under the expedient scenarios (4 and 5), we asked "which areas provide optimal conservation benefits for both clouded leopards and carbon at the lowest risk?" We expected that these scenarios would suggest conservation actions in central Borneo but that high risk lowland areas are likely to be lost to other land uses. Under the active conservation scenarios (2 and 3) we asked "which areas provide optimal conservation benefits for both clouded leopards and carbon stocks while minimising likely forest losses?" We expected that the active scenarios would suggest conservation actions in the most vulnerable areas of Sabah and Sarawak. The central Bornean highlands are unlikely to be prioritised under this scenario; however, these areas are also classified as being low risk (predominantly because they are high in elevation, topographically rough and far from existing deforested areas; Macdonald et al. in review) and are therefore unlikely to be lost within the timescale of this analysis.

MARXAN parameterisation

We used the decision support tool MARXAN (Ball et al. 2009), running in Zonae Cogito (Segan et al. 2011) to identify the optimal placement of the protected areas used in scenarios 2, 3, 4 and 5.

All forested planning units were available for selection, while all 'not forest' planning units were locked out of the reserve design. For all scenarios that included the existing protected area network (scenarios 3 and 5), all planning units containing greater than 16km^2 protected areas were locked into the reserve design. Clouded leopard resistant kernel density and forest carbon stocks were included as 'conservation features'. Under the active conservation scenarios (scenarios 2 and 3) deforestation risk was also included as a 'conservation feature' while the 'cost' of conserving each planning unit was proportional to the area of the planning unit. Under the expedient conservation scenarios (scenarios 4 and 5) the 'cost' of conserving each planning unit was deemed to be proportional to its deforestation risk.

To ensure comparability between scenarios, the same MARXAN parameters were used throughout. In all instances the Species Protection Factor (SPF) was set to 2, and the Boundary Length Modifier (BLM) was set to 0.0015. These values were identified through several calibration runs and were deemed to provide the most realistic conservation scenarios (e.g, Ardron et al. (2010)). The SPF represents the penalty imposed by MARXAN if a scenario fails to meet the conservation target for that species, a value of 2 meant that all targets were met in >99% of the scenarios. The BLM is a weighting that adjusts the 'clumpiness' of the solution. Because MARXAN was able to identify a large number of similar scenarios, a small BLM was sufficient to yield a realistic level of clumping in the

reserve design, while avoiding either a 'salt and pepper' reserve design, or a single clumped reserve. To maintain an equal weighting between them, the target for all conservation features was set to 30%. Each MARXAN Scenario involved 1,000,000 iterations and 10,000 runs.

In the scenarios where we added additional protected areas our goal was to protect 17% of Borneo's land area, consistent with the Convention on Biological Diversity's Aichi Target 11, and so the final reserve selection was designed to include 1305 of the total 7675 planning units. In scenarios 2 and 3, MARXAN was forced to include the 944 planning units that contained existing reserves and was free to allocate an additional 311 units to the reserve design before reaching our area target of 17%. In scenarios 4 and 5, MARXAN was free to allocate all 1305 units to the optimal reserve design.

Comparison of scenario Solutions

Following Macdonald et al. (In Prep-a) we used the deforestation risk map to project changes in landscape resistance from 2010 to 2020, and then applied the resistant kernel model to infer the effect of these changes on clouded leopard core areas. This was done by multiplying the probability of deforestation for each cell by the resistance value for the "plantations and regrowth" land use class (creating the expected mean increase in resistance) and then adding this value to the existing resistance value in 2010. This was done since forest pixels lost to deforestation were most likely to transition either to plantations or regrowth. All areas included within our reserve networks were considered to be effectively protected (excluding scenario 7) and retained the same resistance values as in 2010, while all other areas were adjusted to account for their deforestation risk.

This conversation assumes that there was no leakage, and that the protection of forest in one area didn't result in the commensurate loss of forest in another.

In their raw form the four 2020 resistant kernel density maps depict the expected density of dispersing individuals. These densities indicate the distribution of connected populations. It is necessary to define a threshold kernel density for delineating connected populations. We used a threshold value of the 10th percentile to reflect clouded leopard core areas (all areas above the 10th percentile in resistant kernel density) and reclassified the six kernel density maps into binary form of value 1 where the kernel density probability of dispersal is greater than each percentile threshold and 0 where it is less.
We used FRAGSTATS (McGarigal et al. 2012) to calculate the percentage of the landscape, number of patches, largest patch index, area weighted mean patch size and correlation length of the landscape connected by dispersal for clouded leopards. The percentage of the landscape is the simplest metric of landscape composition, and quantifies how much of the study area is predicted to be connected habitat for each kernel map. The largest patch index (McGarigal et al. 2012) reports the extent, as a proportion of the size of the study area, of the largest patch of connected habitat. The area weighted mean patch size (McGarigal et al. 2012) calculates the average size of each patch of connected habitat in which large patches are weighted more heavily than small patches to reflect the greater ecological importance. Lastly, correlation length is the average distance an organism can move within a patch from a random starting point before encountering the edge of the patch.

Following (Macdonald et al. In Prep-a) we used CDPOP 1.0 (Landguth & Cushman 2010) to simulate the processes of clouded leopard mating and dispersal as functions of the spatial patterns of resistance across the seven scenarios. We extracted several global measures of population genetic structure for the full study area after 200 generations of CDPOP simulation time. These include observed heterozygosity, total number of alleles in the population, and population size. We analyzed the differences in these global measures of population size and genetic structure between the scenarios.

Finally, we considered the impact of all seven scenarios on the above ground biomass carbon stocks in Borneo's forests (i.e. in all areas classified as forest). For each of the 2020 scenarios we calculated the carbon values in each cell by reducing the current (2010) carbon values by the product of current carbon and the inverse probability of that cell being deforested. In scenario 7 we assumed that existing protected areas were subject to the level of risk predicted by the risk surface (which includes protected area status as a predictor variable; Macdonald et al. (in review)). In all other scenarios, protected areas were assumed to be effective and retained their 2010 carbon values.

Results

Distribution of new protected areas

We evaluated the impact of seven different scenarios on the conservation of clouded leopards. Four of these scenarios involved the addition of new areas to the protected area network. Figure 2 shows the proposed reserve design network under these scenarios: (2) Active conservation reallocating protected areas, (3) Active conservation

including existing protected areas, (4) Expedient conservation reallocating protected areas. (5) Expedient conservation including existing protected areas.

The spatial distribution of protected areas varied markedly under each scenario, with the two active scenarios (2 and 3) largely prioritising high-risk areas around the periphery of Borneo's forested areas while the expedient scenarios (4 and 5) prioritised low risk areas in Borneo's Central Highlands region. Additionally, there were marked differences between the scenarios that included the existing protected area network and the scenarios that reallocated existing protected areas. Comparing scenarios 2 and 4 with scenarios 3 and 5 respectively we can see that very few existing protected areas are retained when the prioritisation is allowed to start from scratch, implying that the existing protected area network is poorly suited to delivering optimal conservation of both clouded leopards and forest carbon.

Comparing the two active scenarios (2 and 3), the scenario that retained existing PAs, primarily focussed new PAs around Indonesia's Betung Kerihun National Park along the Indonesian Sarawak border, as well as in Sabah where they improve connectivity between multiple smaller protected areas. By contrast, the scenario that reallocated the existing protected area network focussed attention in the high-risk areas of Sarawak's Hulu Rajang region and Sabah, in the high carbon areas around Sabangau and north of Palangkaraya, and along the border between South and East Kalimantan.

The two expedient scenarios (4 and 5) both concentrated allocation of protected areas to the central regions of Borneo where risk of deforestation is lowest, however scenario 5

was constrained to retain the existing PA network, while scenario 4 was free to reallocate most conservation effort away from peripheral areas to create a large contiguous protected area in the centre of the island reminiscent of the Heart of Borneo proposal (Wulffraat & Morrison 2013).

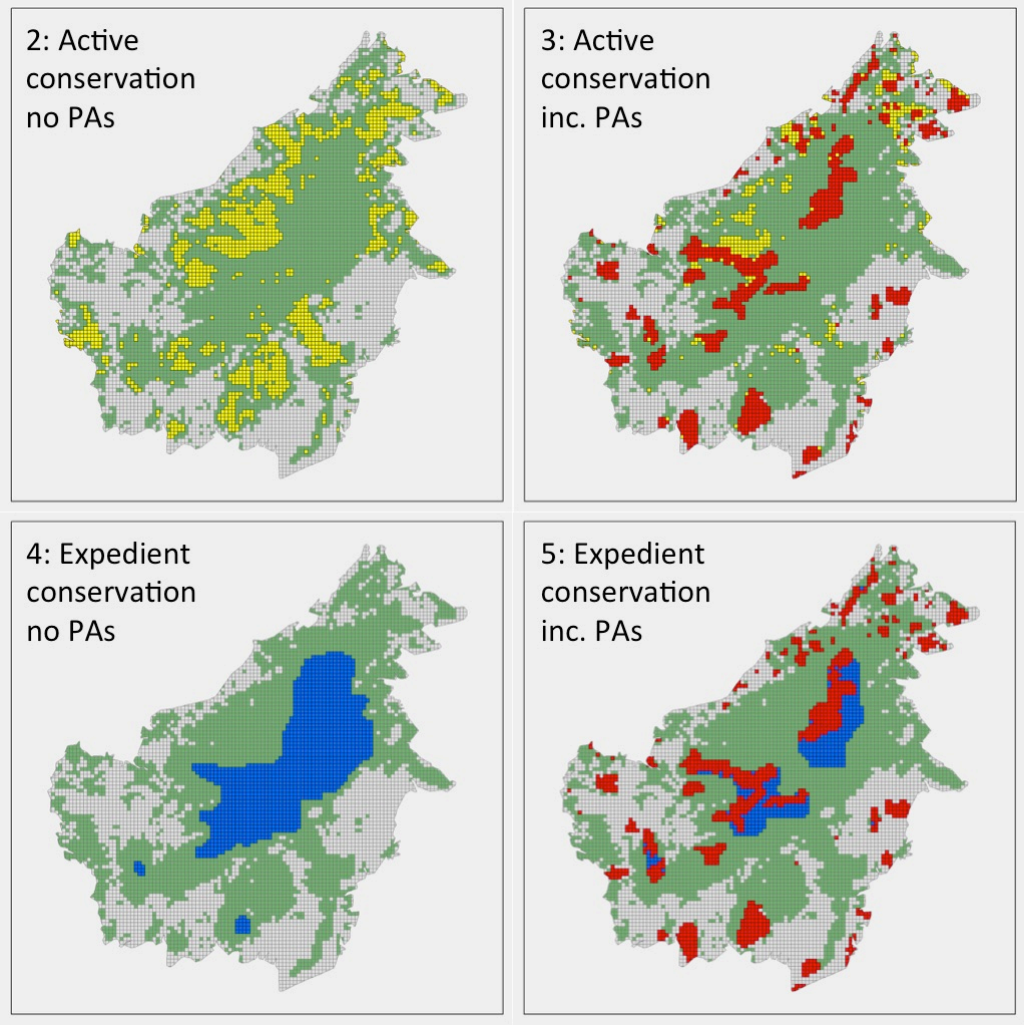

Figure 2. Four of our scenarios involved designating additional areas for protection under different scenarios. Scenario 2: Active conservation no PAs, 3: Active conservation including PAs, 4: Expedient conservation no PAs, 5: Expedient conservation including PAs. The remaining scenarios (1, 6 and 7) all relied exclusively on the existing PA network and are not shown here.

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Impact of solutions of clouded leopard core areas

In 2010, 29.09% of the Borneo's extent was predicted to be connected by clouded leopard dispersal (Fig. 3) This was predicted to fall in all scenarios, with the greatest losses occurring in the business as usual scenario (7) where no new protected areas were added and in which current protected areas were affected by deforestation at the rate predicted by Macdonald et al. (in review)(15.18% of the landscape connected). Improving enforcement such that the existing network were effectively protected (scenario 6) resulted in only a small improvement in the percentage of landscape connected by dispersal relative to business as usual (16.6% of the landscape connected) (Table 1; Fig. 3).

Overall, the active conservation scenarios (2 and 3) tended to perform best by maintaining the largest areas of connected landscape (23.15% and 19.37% of the landscape, an improvement of 53% and 28% respectively relative to the BAU scenario). In particular scenario 2 (active conservation reallocating protected areas) was effective at retaining connectivity with the largest patch of connected habitat covering 20.45% of the landscape compared to 12-14% for the other 2020 scenarios. This widespread connectivity was enabled by the flexibility to reallocate conservation investment away from small isolated patches in the existing PA network and towards areas that contributed to wider connectivity; this can be seen in the relatively small number of patches retained by scenario 2 (38 patches). The 'expedient' scenarios performed comparatively poorly, and were only slightly better than scenarios in which no new protected areas were added: 17.02% of the landscape was connected under scenario 5 (expedient conservation including existing PAs) and 15.97% of the landscape was

connected under scenario 4 (expedient conservation reallocating PAs; Fig. 3). Neither of these outcomes are substantially different to scenario 6 in which no new protected areas are added, but the existing network is assumed to be effective (16.54%).

The number of isolated patches of clouded leopard core habitat fell in all scenarios relative to the 2010 baseline due to the loss of small peripheral patches (Fig. 4). In all cases, the scenarios with the highest number of patches were the scenarios that assume effective conservation of the existing protected area network. This is because the existing network 'locks in' many small isolated PAs that have a high risk of being lost without protection.

	Landscape connected by dispersal (%)	Number of patches connected habitat	Largest patch index for connected habitat (%)	Area weighted mean patch size (000 km2)	Correlation length within connected habitat (km)	Million tonnes of forest carbon
1. 2010 baseline	29.09	86	26.92	290.22	238.55	1321.54
2. 2020 Active conservation no PAs	23.15	38	20.45	210.70	208.94	1159.88
3. 2020 Active conservation inc. PAs	19.37	61	13.88	117.70	157.56	1122.51
4. 2020 Expedient conservation no PAs	15.97	30	13.59	135.26	168.57	1077.89
5. 2020 Expedient conservation inc. PAs	17.02	50	12.51	108.62	150.44	1093.11
6. 2020 existing PAs effective	16.54	48	12.32	108.33	152.18	1084.38
7. 2020 (BAU) existing PAs not effective	15.18	34	12.03	112.19	157.81	1065.42

Table 1. Impact of different scenarios on different landscape metrics for clouded leopards.

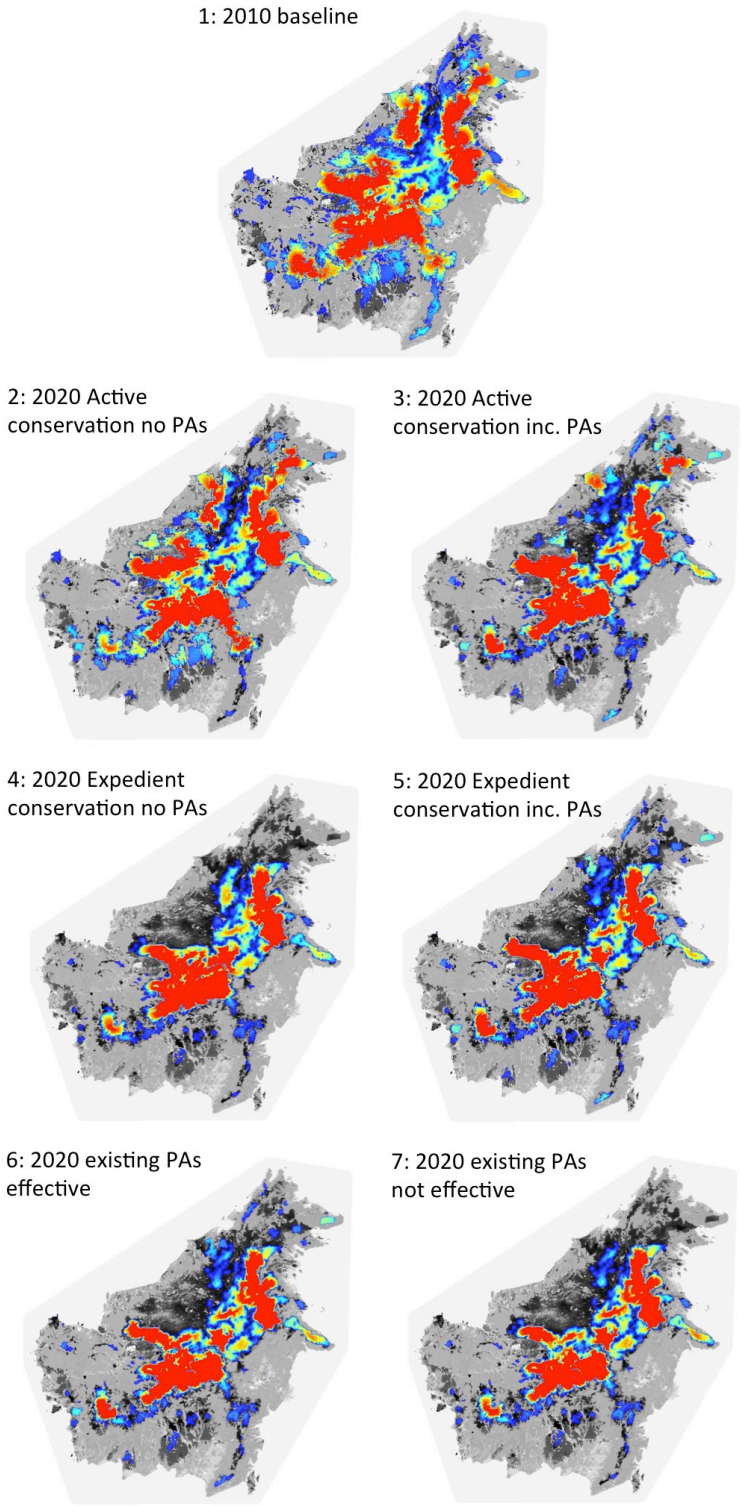

Figure 3. Clouded leopard kernel densities under a number of different scenarios. 1: 2010, 2: Active conservation no PAs, 3: Active conservation including PAs, 4: Expedient conservation no PAs, 5: Expedient conservation including PAs, 6: 2020 existing PAs effective, 7: 2020 existing PAs not effective.

The area weighted mean patch size (in which large patches are weighted more heavily than small patches to reflect the greater ecological importance of these areas) was 290,220km^2 in 2010 and fell substantially in all scenarios (Table 1; Fig. 4). Both scenarios that excluded the existing protected area network (2 and 4) had a higher area weighted mean patch size than their counterpart scenarios that included the existing protected area network (3 and 5) – reflecting the large number of small protected areas in the present network.

The correlation length of clouded leopard core habitat (the average distance an organism can move within a patch from a random starting point) was 238,545m in 2010, and fell by 12.4% in scenario 2 (active conservation redistributing PAs; Fig. 4). In all other scenarios, correlation length fell by 29% or more. The worst performing scenario was scenario 5 (expedient conservation including PAs) with a correlation length of 150,443m. This was likely the worst performing scenario because it focused conservation effort in low risk areas and thus failed to protect high risk peripheral areas of the network, furthermore the inclusion of the existing PA network increased the number of small isolated patches.

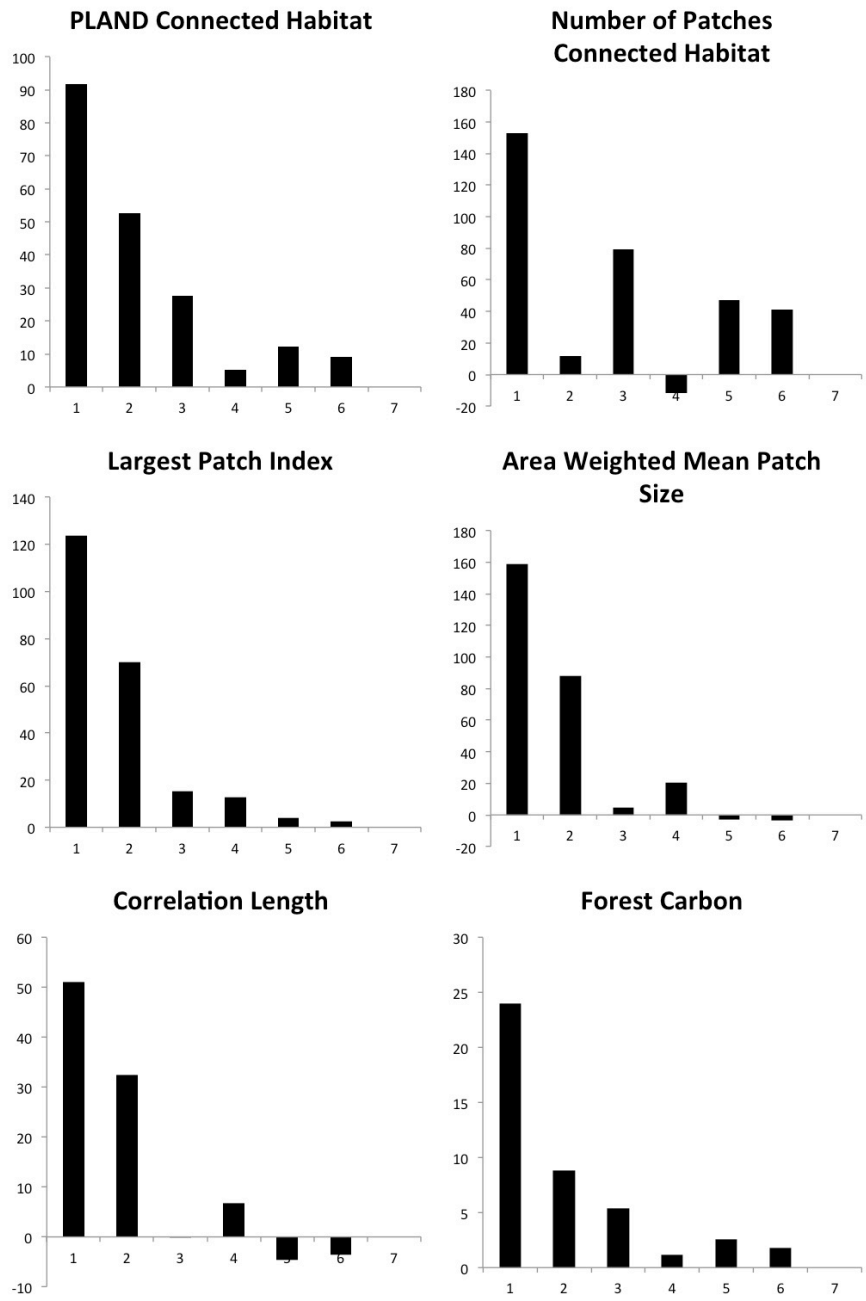

Figure 4. Comparison of landscape metrics, and forest carbon stocks for each of the different scenarios. In each case the percentage improvement relative to the BAU scenario 7 is shown. Scenarios listed on the x axis: 1: 2010, 2: Active conservation no PAs, 3: Active conservation including PAs, 4: Expedient conservation no PAs, 5: Expedient conservation including PAs, 6: 2020 existing PAs effective, 7: 2020 existing parks not effective.

CDPOP simulations

Over the seven CDPOP scenarios there was considerable variation in simulated population size, heterozygosity, and number of alleles (Fig. 5). After 200 generations our simulation projected a total population size of about 1100 clouded leopards under the 2010 landscape condition. The simulated population size was predicted to decrease dramatically by 2020 under all scenarios due to predicted landscape change. Scenario 2 (active conservation reallocating PAs) had by far the smallest decline in population when compared to the other 2020 scenarios, and resulted in a simulated population size of approximately 850 individuals. Scenario 3, active conservation including PAs, was the next best performing scenario, projecting a simulated population size of about 625 individuals. Scenario 4, expedient conservation redistributing PAs, was the next most effective, with a simulated population size of about 600 individuals. Scenario 5 (expedient conservation including PAs) was only marginally more effective than scenario 6 (protecting current protected areas), resulting in simulated population sizes of 575 and 560 clouded leopards, respectively. These scenarios were also not substantially different than scenario 7, in which existing PAs succumb to their projected deforestation risk and in which no new PAs are added (predicted population size of 545; Fig. 5).

After 200 generations, all future scenarios are also predicted to result in large reductions in observed heterozygosity. Scenario 2, active conservation reallocating PAs, and scenario 4, expedient conservation reallocating PAs resulted in the smallest losses in observed heterozygosity. The two scenarios that forced in existing protected areas both resulted in lower projected heterozygosity, similar to those in scenarios 6 and 7 where no new

protected areas were added. This indicates that forcing in existing protected areas results in lower overall population-wide heterozygosity, likely because it results in a more dispersed and fragmented network of protected areas which each experience a higher loss of genetic diversity due to isolation effects and genetic drift.

Scenario 2, active conservation reallocating PAs, resulted in substantially higher allelic richness than any other scenario, amounting to a reduction of approximately 10% from the 2010 scenario. Scenarios 3 and 4 (active conservation including PAs, and expedient conservation reallocating PAs) had roughly equivalent simulated allelic richness (approximately 18% reduction from the 2010 scenario). Scenarios 5, 6, and 7 had similar reductions of allelic richness (~74%), indicating the that expedient conservation including PAs (5) did not result in improved total allelic diversity in the population over the scenarios that did not protect any additional protected areas.

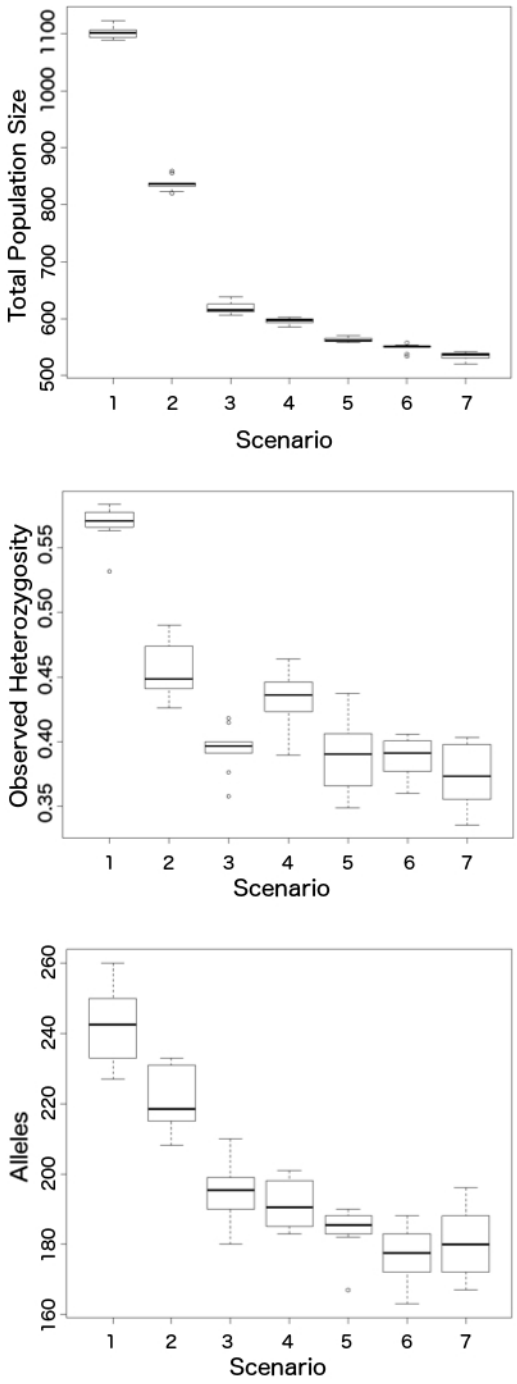

Figure 5. Comparison of genetic metrics for each of the different scenarios. 1: 2010, 2: Active conservation no PAs, 3: Active conservation including PAs, 4: Expedient conservation no PAs, 5: Expedient conservation including PAs, 6: 2020 existing PAs effective, 7: 2020 existing parks not effective.

Impact of solutions of forest carbon stocks

In 2010, areas classified as forest contained 1321.54 million tons of carbon in above ground biomass (Fig 4.). This was predicted to fall in all 2020 scenarios; however scenario 2 (Active conservation reallocating existing protected areas) performed best, with a predicted loss of 161.66 million tons of carbon (12.2%). The two least effective scenarios were scenario 4 (Expedient conservation reallocating PAs) and scenario 7 (2020 existing parks not effective) which experienced 18.4% and 19.4% losses respectively. Scenario 4 performed badly because the majority of protected areas were sited in central, low risk regions of Borneo. Scenario 7 lost 18.96 million tons of carbon more than scenario 6 which assumed that existing protected areas would be effective (Table 1, Fig. 4).

Discussion

Impact of the different scenarios

The foregoing results make clear that predicted forest loss in Borneo by 2020 is highly likely to be associated with deteriorating conditions for Sunda clouded leopards, which we consider an ambassador species (*sensu* Macdonald et al., submitted) for the island and it's wider biodiversity. While the six scenarios explored here vary in the outcomes they predict, all are variously bad outcomes for clouded leopard conservation.

As expected, the business as usual scenario was the worst performing scenario and will result in widespread reductions in all landscape composition metrics, indicative of a widespread loss and fragmentation of habitat, alongside the loss of 256.12million tons of carbon currently stored as above ground biomass, relative to the 2010 baseline.

Modelling the impact of this fragmentation on the genetic diversity of the clouded leopard populations reveals that a business as usual scenario will likely precipitate a widespread decline in clouded leopard numbers that is further compounded by dramatic declines in genetic diversity.

The business as usual scenario presented in this analysis recognises the existence of Borneo's protected area network, but assumes that these areas will suffer from deforestation at a rate commensurate with that predicted within protected areas by Macdonald et al. (in review). If these protected areas were to be secured (as they are in scenario 6) then we predict that this would result in a 10% increase in the extent of connected landscape relative to the business as usual scenario. While the enforcement of existing PAs is of course a laudable ambition, the results of our genetic modelling suggest that under this scenario clouded leopards will still be likely to see widespread population declines and decreases in genetic diversity. This is important because it highlights the fact that the existing protected area network is insufficient to deliver adequate protection of clouded leopards in the face of widespread forest loss.

Comparing the remaining scenarios reveals that the only scenario likely to have a major benefit for clouded leopards is scenario 2, active conservation reallocating protected areas. Adopting this scenario would see a 90% improvement in the percentage of the landscape connected by dispersal relative to the baseline, and would substantially reduce habitat fragmentation with fewer, larger discreet patches of habitat than many other scenarios. Of all the scenarios scenario 2 also performed best in terms of the measures of simulated genetic diversity, resulting in a landscape that would likely support 50%

more clouded leopards, and almost 10% more forest carbon than the business as usual scenario.

Limitations and assumptions

It is important to note that our analysis comes with several caveats. Firstly our model is seeded with a starting population of 2,869 clouded leopards, and results in predicted populations of 1100 clouded leopards under the 2010 baseline scenario, 850 clouded leopards under scenario 2 and 545 clouded leopards under scenario 7. These numbers do not represent actual predictions of future clouded leopard populations, rather, they represent the equilibrium population after 200 generations of simulated breeding in that particular landscape, this is a standard approach e.g. (Cushman & Landguth 2010; Landguth et al. 2010; Macdonald et al. in prep-b). In other words, we predict that if the 2010 landscape were to remain static for 200 generations, then we would expect that the landscape resistance would result in 62% decline in the clouded leopard population relative to the starting condition. Rather than accurate predictions of population decline, these numbers are more representative of the relative number of clouded leopards that any particular landscape would be able to support. Additionally, this analysis included only internationally recognised IUCN category I-VI protected areas. However many areas of Borneo may retain at least part of their forest cover under other legal statuses (from national and state level protection to different categories of extraction forest). The extent to which these areas may add to the conservation of clouded leopards, either by providing further habitat, or by increasing connectivity, requires further study. Finally, this model is unable to account for leakage in the system and therefore assumes that a reduction in the risk of forest loss in one location (i.e. through protection) will not drive

an increase in risk in another location. There is a lack of current research showing how leakage develops from an intervention, and the factors influencing this process (Atmadja & Verchot 2012) however this was beyond the scope of this analysis. Even so it is worth noting that the risk map developed by Macdonald et al. (in review) provides the relative probabilities of forest loss based on a range of topographic and landscape features considered at multiple scales, and so we predict that the spatial pattern of relative risk will remain robust under changing political and economic circumstances.

Impacts for clouded leopards

Our analysis, importantly, took a large step beyond simply measuring the differences among scenarios in terms of hectares lost by addressing the population level effects of these losses in terms of changes in population size, observed heterozygosity, and allelic richness, which are directly linked to species viability (Soule 1984). Our results indicate that the active scenario reallocating existing protected areas vastly outperforms all other scenarios based on total simulated clouded leopard population size.

These changes in population size across scenarios interact with the spatial pattern and connectivity of the reserve network to affect heterozygosity and allelic richness in different ways. Consistent with Wasserman et al. (2012) and Macdonald et al. (In Prep-a) we found that heterozygosity is highly influenced by population connectivity, and is lower in scenarios where the population is most fragmented, as well as being affected by overall population size. The active scenario reallocating protected areas resulted in the highest predicted heterozygosity, while the expedient scenario including protected areas offered no benefit relative to the business as usual scenario. Also, consistent with

(Macdonald et al. In Prep-a; Wasserman et al. 2012), we found that allelic richness is primarily a function of population size and is relatively insensitive to habitat fragmentation. The active scenario reallocating existing protected areas again vastly outperformed other scenarios in maintaining allelic richness in the population, and the expedient scenarios again performed no better than the *laisses faire* business as usual scenario.

Conservation implications

This analysis suggests that the existing network of protected areas in Borneo tends to be biased towards remote and inaccessible locations that are unlikely to be threatened in the near future as well as comparatively small patches that have already been isolated by historical forest loss. This network is insufficient to deliver effective conservation of the clouded leopards, and its impact on reducing the loss of above ground biomass is likely to minimal over the next decade. This bias in the locations of protected areas has been noted elsewhere (Hoekstra et al. 2005), however if protected areas hope to deliver effective conservation in the future then their allocation must differ from historic protection strategies (Joppa & Pfaff 2009).

If the purpose of protected areas is to thwart the avoidable loss of habitat and biodiversity, then a more proactive approach would be to position the network of protected areas, or at least new elements added to it, in the places that are most threatened.

We do not propose dissolving Borneo's existing protected area networks, as widespread downgrading and de-gazetting of protected areas might threaten the perceived legal permanence of protected areas (Forrest et al. 2015). Additionally, although we know of no studies that test this empirically, there may be arguments that long established PAs might have a better-established infrastructure and may have developed more effective coexistence with local communities and therefore are more effective and less controversial than new PAs. However we do highlight current inadequacies in the network and suggest that in future conservation planners should balance the strategic placement of new protected areas alongside the cautious reallocation of conservation investment from underperforming areas towards higher priority areas.

This supports a growing body of literature that a redistribution of conservation investment away from underperforming protected areas could yield improvements in the efficiency of the entire network (Fuller et al. 2010). The expedient scenarios which avoid protecting areas with high deforestation risk resulted in very little marginal improvement in expected clouded leopard population size compared with the *laissez-faire* business as usual scenario.

The need to target areas of high risk is not a new idea for conservation biology, and has been popularised by Conservation International's biodiversity hotspots among others (Myers et al. 2000). However, expanding the protected area network to meet meaningful targets for species conservation is likely to be considerably more expensive than the lowest cost scenarios (Venter et al. 2014). Many of the areas identified as being of highest risk by Macdonald et al. (in review) are at risk because they face the greatest

competing demands from alternative land uses such as oil palm plantations and industrial timber plantations which both deliver substantial economic revenue. There is therefore a substantial need to coordinate both economic development and conservation planning, and doing so could result in substantial efficiencies (Runting et al. 2015).

Conclusions

Our analysis leads us to three main conclusions. First, the trajectory of landscape change in Borneo under the business as usual scenario without additional conservation action will likely result in very large declines in the extent of clouded leopard habitat and large increases in fragmentation, which combine to drive large declines in population size, heterozygosity, and allelic richness, potentially resulting in extinction vortex dynamics in many parts of Borneo with small and isolated populations (Fagan & Holmes 2006).

Second, the existing protected area network is not optimal for protecting the parts of the landscape that are most important for maintaining clouded leopard populations, given that large protected areas are concentrated in high elevation areas that are not at risk of deforestation, and the low elevation protected areas are often small and isolated remnants that have limited population-level function in clouded leopard viability (Fuller et al. 2010; Joppa & Pfaff 2009).

Third, active scenarios that prioritize conservation areas in areas that are currently at high risk of forest loss would be vastly more effective at conserving clouded leopard population size, population connectivity, genetic diversity, and the quantity of forest carbon. Conservation planners need to recognise this fact and work with governments to

develop strategies that balance the legitimate desire to develop land for economic growth with need for more effective conservation. Doing so will probably require a greater recognition of the many benefits that intact habitats provide, both in terms of intangible cultural and social values as well the provision of ecosystem services.

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Chapter 7

Discussion

In the face a large gap between conservation costs and revenues, it is vital that conservation biologists develop innovative mechanisms for increasing their revenue streams, as well as developing strategic approaches to ensure that the limited pool of resources is spent proportionately (Bottrill et al. 2009). In this thesis, I therefore set out to explore different approaches to conservation prioritization and to do so from two different directions. In the first part of this thesis I considered the emerging field of conservation marketing to explore peoples' preferences for conservation, and how these preferences might be used to leverage public support for conservation and potentially increase revenue streams. In the second part of this thesis I examined the case study of clouded leopard conservation on Borneo to explore various approaches to spatial conservation prioritization and discover how these will impact on measures of genetic diversity in the Sunda Clouded Leopard (*Neofelis diardi*).

Key contributions and findings

1. This study conducted the first broad scale analysis of which mammalian species people prefer in the context of conservation, and then went on to use this information to build models of predicted appeal for each of the different countries surveyed. I found that, from the sample of 100 mammals included in the survey the tiger was unanimously the most popular across all countries. The specific attributes associated with high-ranking species varied between different countries revealing cultural differences, although baldness, body size, IUCN status were important variables in all countries (Chapter 2). I

used these attributes to create the first estimate of the relative appeal of all terrestrial mammal species (Chapter 3). This provides a useful tool for conservationists looking to identify potential flagships for future marketing campaigns.

2. Building on the existing concept of flagship-umbrella species (Caro 2010) and propose that species that occur in areas of high conservation priority may present added value in terms of their potential for conservation marketing. In addition to their native appeal, these species may be more marketable as a result of them living in diverse and biologically important regions. I develop a novel categorisation, and introduce the term "Ambassadors" to describe species with high appeal and high efficiency scores to reflect the idea that these species may be effective at generating attention for wider biodiversity within their distribution (Chapter 3).

3. Random Forest machine learning was used in a multi-scale approach to assess topographical and landscape composition correlates of forest loss in Borneo between the years 2000 and 2010, and applied the model to predict the spatial pattern of deforestation risk in 2020. This analysis is the first model of forest loss to model the impact of landscape composition and configuration explicitly at multiple spatial scales (Chapter 4). The model predicts areas of deforestation with both high Overall Accuracy (>86%) and

Specificity (>89%) in all countries on Borneo. The very high performance of the models suggests that multiple-scale modelling using Random Forest and a combination of landscape composition and configuration greatly improves accuracy of predictions about the drivers and future patterns of deforestation. This finding has wide implications for future landscape modelling.

4. A spatially synoptic approache was used to evaluate the impact of forest loss on the patterns of Borneo-wide connectivity for the Sunda clouded leopard (*Neofelis diardi*)(Chapter 5). This analysis is the first to apply a spatially synoptic approach to clouded leopard population connectivity, and is also the first paper to examine the impact of past and future forest loss on Borneo's clouded leopards. As such it also provides the first blueprint for such work that can now be generalized to, and customized for, other species. The model predicts substantial reductions across all connectivity metrics between 2000, 2010 and 2020. These will lead to large declines in clouded leopard population size and reductions in connectivity will also have a major impact on the genetic diversity of the clouded leopard population.

5. The existing protected area network on Borneo is insufficient to safeguard the long-term conservation of clouded leopards. I therefore used the decision support tool MARXAN to model the impact of several scenarios for

future clouded leopard conservation. The scenarios explored two divergent paradigms referred to as “active” and “expedient” approaches to conservation. Active conservation scenarios out-perform expedient scenarios with the best performing scenario resulting in a 53% increase in the area connected by dispersal, a 70% increase in the largest patch size and the retention of 94 million tons of forest carbon relative to business-as-usual scenario.

The findings in context – why do they matter?

Conservation marketing

A major challenge in conservation is influencing people’s behaviour, whether this takes the form of mitigating human wildlife conflict, lobbying governments or raising funds for conservation organisations. Commercial companies have a long understood this, and have developed sophisticated techniques to increase their revenues influencing the behaviour of their customers (Kotler & Armstrong 2010). The application of these techniques to conservation can be an important tool both for raising funds and for publicising issues that might otherwise be ignored. In recognition of this, and as part of conservation maturing on the global stage, the field of conservation marketing is now growing rapidly and gaining in acceptance, and in 2015, I was fortunate to attend the International Congress of Conservation Biology’s first symposium dedicated to conservation marketing (Veríssimo & McKinley 2016).

Several studies have attempted to describe the various attributes that are associated with high appeal (e.g. (Caro & O'Doherty 1999; Clucas et al. 2008; Courchamp et al. 2006; Dietz et al. 1994; Johnson et al. 2010; Lorimer 2007; Smith et al. 2012). In general these studies have reported that the species selected as flagships tend to be large, warm blooded, endangered and predatory with forward facing eyes. Unfortunately these conclusions are of little empirical value having been based on a combination of speculation and small scale analyses of the flagship species used on magazine covers (Caro & O'Doherty 1999) or on web searches (Smith et al. 2012).

As the field of conservation marketing grows, there are an increasing number of empirical choice experiments for example Veríssimo et al. (2014) investigated local preferences for bird conservation in Brazil, Frew et al. (2016) asked children about their preferences towards different species, and Home et al. (2009) explored the selection criteria for flagship species by conservation organizations in Switzerland.

In chapter 2 of this thesis I conducted a paired conjoint choice experiment to explore peoples' preferences for mammals in the context of conservation. This is the first quantitative analysis of peoples' attitudes to a broad suite of mammals and revealed the large appeal of the big cats. In addition to simply providing a list of 100 species ranked in terms of their relative preference scores, I was able to provide a useful tool that will allow conservation marketers to predict whether any mammal is likely to be appealing based on a

few key attributes. In general most respondents preferred larger, rarer species that had no bald areas and were classified as a potential threat to humans. These results can provide a valuable guide that conservation marketers can use when selecting flagship species. Furthermore, the survey design used in this analysis yielded high levels of positive engagement with respondents, which is an important indicator of reliable survey data. This approach can therefore serve as a template for conservation marketers who want to take this research further, either by extending it into new areas or by refining it to target a more specific group of stakeholders.

In general most respondents preferred larger, rarer species that had no bald areas and were classified as a potential threat to humans, however the precise mix of attributes and their weightings varied by country and is available in the chapter.

Among the most interesting findings of this paper were the cultural differences that emerged between countries, for instance Australian respondents showed an unusually strong preference for regionally native species, and against species that are invasive in Australia. The strength and direction of this preference came as a surprise when we discussed these results with conservation biologists in Australia and is an opportunity for future research (Dickman pers. comm.). Another pleasing example of regional differences is the unexpectedly strong preference of the UK respondents for the European hedgehog (*Erinaceus europaeus*), a species that is firmly embedded in British culture in the guise of Beatrix Potter's Mrs. Tiggy-Winkle. These regional differences support existing research on

the importance of local contexts and cultures in identifying flagship species (Bowen-Jones & Entwistle 2002; Douglas & Veríssimo 2013).

Our survey was conducted on 1,500 respondents from 5 countries, selected because of their global distribution but constrained to countries where English was widely spoken to minimise the costs of translation. Respondents were approached online by a 3rd party market research firm that specialises in contacting people for surveys. The use of such companies is standard practice in commercial market research and these companies trade on their ability to reach a broad section of society with customers typically offered a wide variety of criteria that they can use to focus their survey on the desired demographic. In the case of our survey, we deliberately specified the widest possible criteria such that the respondents should be drawn from a pool that is as broadly representative of the country's internet users as possible. Rates of internet penetration (% individuals who have used the Internet in the last 12 months) vary between the different countries in our sample from 41% (South Africa) to 81% (UK), and it is likely that stakeholders with limited or no access to internet might exhibit different preferences. When generalising the results of this study it is important to note that the sample is therefore biased towards predominantly middle class internet users from English speaking countries with a strong Anglo-Saxon cultural influence.

Identifying ambassadors for conservation marketing

In Chapter 2, I explored peoples' preferences for different species in the context of conservation. This enabled me to quantify and explore the great disparity in preferences for

different species, and to explore how these preferences varied between different countries. However, in Chapter 3 I go on to argue that conservation marketers should go beyond the attributes of a particular species when selecting flagships for conservation, and that they might find 'added value' in a species' ability to act as a marketing surrogate for a large number of high priority species.

In Chapter 3 I introduce a novel categorisation of species in terms of their usefulness for conservation marketing. This approach is called the Ambassador Species concept and is based on the premise that under appropriate circumstances, wide ranging species have the potential to act as flagships for the wide range of issues and species encountered across their range. In this sense, a species' ability as a flagship may be judged both on the appeal to the target audience of its physical and or cultural characteristics, but it may also be judged on its ability to act as a marketing flagship for a wide range of other, less appealing, sympatric species. Ambassador species are consequently defined as those species with an above average appeal score and an above average efficiency score. In addition to coining the term "ambassador species" I describe 3 other categories on the basis of a species' potential ability to act as a marketing flagship for it's sympatriots.

The Ambassador concept differs from the existing "flagship umbrella" concept in so far as "flagship umbrellas" rely on the use of one species (or group of species) to act as a surrogate for the conservation of other "background" species through their association with viable populations, protected areas or management actions (Caro 2010).

In addition to introducing a novel approach to identifying potential surrogates for conservation marketing, this paper presents the first attempt to quantify the relative appeal of all terrestrial mammals. Because it is important that conservation marketing campaigns are to their target stakeholder group (Bowen-Jones & Entwistle 2002) I present these results separately for each of the 6 countries that were present in the original survey. While the results of this study retain the bias towards predominantly middle-class internet-users from English-speaking countries with a strong Anglo-Saxon cultural influence, the results can still be a useful guide to conservation marketers looking to identify flagship species to use in these countries.

This study also highlights the fact that while high-resolution data on species attributes is preferable when identifying flagships, it is also possible to generate broad brush, but reliable estimates of species appeal form a reduced set of key attributes. These attributes (Body size, IUCN status, potential threat to humans, and eye position) are easily obtained for all species or generalizable at a taxonomic level.

Spatial conservation prioritization

Patterns and predictions of deforestation risk in Borneo

The forests of Borneo are among the most biodiverse on the planet, however, recent studies show that 30% of those forests have been lost since 1973 (Gaveau et al. 2014). In order for conservationists to plan adequately to conserve the remaining forest areas, it is

vital that they have reliable, spatially-explicit data on the areas that are likely to be most at risk. My objective was to identify the multiple-scale drivers of recent deforestation and predict future deforestation risk across Borneo.

Recent analysis suggests that approximately c.19million ha of forest is lost to disturbance each year (Hansen et al. 2013). It is therefore not a surprise that significant academic effort has been invested in studying correlates of deforestation risk in different parts of the world. Most of this work has been conducted in the Amazon basin (Rosa et al. 2013; Soares-Filho et al. 2006), although numerous examples exist from other parts of the world (Rideout et al. 2013; Vieilledent et al. 2013). Multiple statistical approaches are employed in these analyses and include techniques such as logistic regressions (Chowdhury 2006; Echeverria et al. 2008), genetic algorithms (Soares-Filho et al. 2013; Venema et al. 2005), weights of evidence (Maeda et al. 2011; Soares-Filho et al. 2010) and cellular automata (Thapa et al. 2013).

Despite widespread recognition of scale dependence in ecology (Levin 1992; Wiens 1989), very few ecological papers explicitly address scale-dependence in pattern process relationships (McGarigal et al. 2016). Several studies do include some scale-dependent variables in their analysis (such as distance to roads or rivers e.g. (Rideout et al. 2013; Soares-Filho et al. 2006) or distance to population centre e.g. (Vieilledent et al. 2013) however they do so implicitly and they retain other variables (such as number of roads, or landscape fragmentation) which are constrained to a single scale. This analysis uses

Random Forests machine learning in the first application of a multi-scale framework to the prediction of future deforestation risk.

This analysis uses random forest machine learning to provide the first explicitly multi scale framework for the prediction of future deforestation risk. The results from this analysis show that the model is able to predict areas of deforestation with 91% accuracy and predict which cells would remain forested with about 78% accuracy across the whole of Borneo. The model performed well in terms of accuracy assessment with both high Overall Accuracy (>86%) and high Specificity (>89%) across all countries on Borneo. This out performs other studies (e.g. (Grinand et al. 2013)) and the high model performance was consistent across multiple methods of accuracy assessment.

These spatially explicit map of deforestation risk produced by this analysis will be of interest to both researchers and conservation planners working in Borneo who can use to inform future conservation planning initiatives. However I hope that this research will also have a wider reach. This analysis demonstrates that an explicitly multi scale approach to land use change modelling is both computationally feasible and produces accurate results; I therefore call on land use change modellers in general to consider this approach in their future analyses.

I*mplications for rapid forest loss on population size, connectivity and genetic diversity of clouded leopards in Borneo*

In the face of rapid land use change, it is important that conservation decisions are based on the best possible available information, and it is important to understand both the status of clouded leopard populations and the risks that they face. In Chapter 5 met the need to quantify the risks faced by clouded leopards by develop an accurate and spatially explicit map of deforestation risk across Borneo. However while empirical ecological data about the clouded leopard's distribution, it's population status and trends exist, they are sparse (Brodie & Giordano 2012; Cheyne & Macdonald 2011; Cheyne et al. 2014; Hearn et al. 2015; Hearn et al. 2016; Wilting et al. 2012). This is in part because clouded leopards are notoriously difficult to study and it is not unusual for experienced field biologists to capture insufficient high quality photos to produce reliable population estimates and some studies have failed to detect clouded leopards at all, even in supposedly good habitat (Hearn, Ross and Macdonald, unpublished data; (Cheyne et al. in prep)). The difficulty of collecting data on this species constrains the opportunities for reliably modelling clouded leopard habitat associations across Borneo. However, while the quantity of published data is sparse, there is a cadre of people working hard on the species and with considerable experience of them. To draw on this knowledge, I conducted a survey of expert opinion to assess the habitat suitability for clouded leopards of different land classes across Borneo. Maps of habitat suitability derived from expert opinion have been shown to be less reliable than empirically derived data (Seoane et al. 2005; Shirk et al. 2015; Shirk et al. 2010), however in the light of the rapid land use change in Borneo, and the difficulty of collecting empirical data, this represents the best data available.

Many studies have discussed the importance of landscape connectivity in delivering effective conservation in a fragmented habitat (Diamond 1975; Gilbert-Norton et al. 2010; Taylor et al. 1993), as habitat fragmentation and increased landscape resistance have been shown to decrease dispersal success, increase mortality, and reduce genetic diversity; additionally small isolated patches are mores prone to stochastic extinction events and are less likely to be recolonized (e.g. (Cushman et al. 2013; Fahrig et al. 1995; Gibbs 1998; Harrison et al. 2015; Semlitsch & Bodie 2003; Wilson & Provan 2003)).

Against this context I explored the impact of habitat fragmentation and population connectivity on the population and genetic diversity of clouded leopards on Borneo. This isn't the first analysis to explore landscape connectivity for clouded leopards, Brodie et al. (2014) explored the cost of movement across the landscape for a suite of Bornean species in Sarawak, however the analysis presented in Chapter 5 represents a large step forward in terms of the scale, scope and the use of a spatially synoptic approach.

The results raise a stark warning with severe declines in all metrics of landscape connectivity. If these models are correct, and I argue there is strong evidence that they provide insights at least as reliable as any others available, then the loss and fragmentation of their habitat could be far more extreme than has currently been supposed with severe impacts on the forecast population size and levels of genetic diversity in the population.

Even worse, while our models were parameterized specifically for clouded leopards based on expert opinion, who assigned suitability values based on their understanding of the

species' dependence on natural lowland forest ecosystems. Consequently our model is likely to have relevance to any other medium sized forest dependent mammals on Borneo (such as the sun bear (*Helarctos malayanus*) and perhaps the orang utan (*Pongo pygmaeus*) that may have similar or even more sensitive responses to landscape resistance.

The conservation implication of this chapter is therefore clear, the need to slow land use change in core areas of clouded leopard habitat to mitigate losses in connectivity is even more urgent than previously thought. In addition to the importance for applied conservation, this analysis presents the first attempt to model effects of on-going deforestation on population decline and changes in population connectivity and genetic diversity of any species at this scale, and the unexpectedly stark future of the clouded leopard suggests the importance of extending this approach to a wider number of species and areas.

The impacts of future deforestation on clouded leopard population connectivity and gene flow across Borneo under contrasting scenarios for conservation

In Chapter 6 of this thesis I attempt to explore several scenarios for the potential future of clouded leopard conservation. These scenarios are intended to balance the needs of maintaining both clouded leopard core areas as well as recognising the increasing interest in the congruence of benefits between biodiversity conservation and forest carbon stocks (Collins et al. 2011; De Barros et al. 2014; Murray et al. 2015). I bring these two ideas together in the context of two controversial debates in conservation science: the idea that

an increased focus on prioritising high-risk areas for protection would improve conservation outcomes (Joppa & Pfaff 2010; McShane et al. 2011; Pfaff & Sanchez-Azofeifa 2004), and the idea of Protected Area Downgrading, Downsizing and Degazettement to improve the efficiency of the reserve network (Fuller et al. 2010; Mascia & Pailler 2011; Mascia et al. 2014).

I devised several scenarios that reflect these debates while seeking to maximise the conservation outcomes for both clouded leopards on Borneo, and the conservation of forest carbon. By way of comparison these scenarios are compared to both the 2010 baseline, and a *business as usual* approach that relies on the existing network of protected areas and assumes that these areas continue to be as effective as they were between 2000 and 2010.

The results of this analysis reiterate the findings in Chaprer 5 in making clear that predicted forest loss in Borneo by 2020 is highly likely to be associated with deteriorating conditions for the Sunda clouded leopard. While the scenarios explored here vary in the outcomes they predict, all are variously bad outcomes for clouded leopard conservation.

In almost all cases, the active conservation strategies that focussed conservation attention in areas of high risk performed better than their analogous expedient conservation strategies that focussed on areas of lowest risk. This is inline with existing studies that suggest conservation efforts are more likely to have an impact when we prioritise high risk locations (e.g. Joppa and Pfaff (2009) and (Pfaff & Sanchez-Azofeifa 2004)). Additionally the scenarios in which were free to reallocate investment away from the existing PAs

outperformed those that were constrained to include existing PAs. This suggests that not only is the existing network of PAs on Borneo insufficient to deliver significant conservation benefits for clouded leopards (Chapter 5), but also that its impact on reducing the loss of above ground biomass is likely to minimal over the next decade.

Importantly, this analysis took a large step beyond simply measuring the differences among scenarios in terms of area of habitat saved by addressing the population level effects of these land use change in terms of changes in population size, observed heterozygosity, and allelic richness, which are directly linked to species viability (Soule 1984).

Consistent with Wasserman et al. (2012) and Chapter 5, we found that heterozygosity is highly influenced by population connectivity, and is lower in scenarios where the population is most fragmented, while allelic richness is primarily a function of population size and is relatively insensitive to habitat fragmentation.

If the purpose of protected areas is to thwart the avoidable loss of habitat and biodiversity, then a more proactive approach would be to position the network of protected areas, or at least new elements added to it, in the places that are most threatened. We do not propose the wholesale dissolution of Borneo's existing protected area network because this is politically unrealistic, because the network may provide benefits for other species not tested in this analysis and because widespread downgrading and de-gazetting of protected areas might threaten the perceived legal permanence of protected areas (Forrest et al. 2015). However we do highlight current inadequacies in the network and suggest that in

future planners should acknowledge the difficult trade offs that need to be made in conservation and consider directing new conservation investment towards areas currently experiencing high risk of deforestation. In addition these same planners should endeavour to balance the strategic placement of new protected areas alongside the cautious reallocation of conservation investment from underperforming areas towards higher priority areas.

Conclusions and future research

My principal aim in this thesis has been to explore innovative approaches to conservation prioritisation, both in terms of conservation marketing and spatial conservation prioritisation. Of course conservation is about biology, and the inter-disciplinary network of approaches to understanding the relationships between nature and people. However, and no less urgently, conservation is about societal choices and thus, ultimately people, politics and economics (Adams & Hutton 2007; Jacobson & Duff 1998; Schaller 1992). That is why, in Chapters 2 and 3, I sought to provide an empirical basis for understanding which species are most likely to appeal to one section of the public (predominantly middle class internet users from English speaking countries with a strong Anglo-Saxon cultural influence) as flagships for conservation marketing campaigns. Chapter 3 builds on this to suggest an innovative way of classifying a large number of species in terms of their potential usefulness for conservation marketing. These Ambassador species provide a novel way of thinking about conservation marketing and represent the first attempt to quantify the relative appeal of all terrestrial mammal species.

The two species of clouded leopards (*N. diardi* and *N. nebulosa*), which are probably interchangeable in this context (insofar as their appearances are so similar as to be indistinguishable to most laymen), appear to be particularly valued by the general public; they scored highly in terms of appeal and routinely received higher preference scores in the surveys than would have been predicted by their traits alone suggesting a surprising level of affinity given their unfamiliarity. Both species of clouded leopards were identified as potentially potent ambassadors for conservation. Due to its precarious status in the threatened forests of Borneo, the Sunda clouded leopard on Borneo makes it a compelling subject for conservation attention, and one that I propose should be adopted to sit alongside the Orang utan as an ambassador for wider conservation on Borneo.

Land use change is the most substantial threat to clouded leopards on Borneo, and this thesis highlights the impact that current rates of deforestation may have on clouded leopard populations. These impacts are severe and, insofar as my analyses are right, calls for urgent action to slow the rate of forest loss. Furthermore, while the models in Chapter 5 were parameterised specifically for clouded leopards, the impacts to extend to other forest dependent species that with a similar, or more sensitive response to landscape resistance.

Throughout this thesis I present novel approaches that range from innovative partnerships with market research firms to sophisticated and computationally demanding spatial modelling tools. I highlight the importance of an explicitly multi scale approach to land change modelling and show how considering the impact of habitat fragmentation can

extend far beyond simple spatial measures of habitat loss. I hope that these approaches prove useful to conservation researchers and practitioners alike and I hope that they find some interest in the practical conservation conclusions I draw from their use. In particular I encourage conservation biologists to embrace the field of conservation marketing, both in terms of identifying flagship species but also in improving the communication and dissemination of their findings. With regard to conservation planning in Borneo I call for conservation planners to be open about making hard decisions. It is likely that the high risk areas in Borneo that are identified in my models are high risk because they are not only important areas for biodiversity but they are also prime locations for economic development. Countries such as Indonesia, Malaysia and Brunei depend on industries such as the cultivation of rice and palm to feed their citizens and progress along their development pathways. This inevitably brings them into conflict with conservation objectives, and solution will usually be decided in government offices rather than academic papers. It may not always be possible to deliver conservation and development side by side but conservation biologists can only hope to influence these decisions if they are open and transparent about the hard choices that need to be made, and are clear about the outcomes of such choices.

Future research

Part 1 of this thesis is about understanding people's perceptions towards wildlife and how this can be leveraged to maximise the engagement of the general public with conservation issues. The "general public" that we deliberately target in Chapter 2 are the relatively affluent middle classes who influence policy though their political engagement and who

direct the conservation agenda through their membership of, and donations to, conservation organisations such as WWF or RSPB. However we can dissect the term "general public" into many different constituencies, and while the western middle classes may be important drivers of the conservation agenda, their opinions are no more valid than those of the people who have to live alongside wildlife on a daily basis. Among the respondents to our survey, big cats and carnivores were overwhelmingly supported and the death of Cecil the lion lead to uproar in the western press; however it is not hard to imagine a village on the periphery of Hwange National Park (Cecil's former home) that feel quite the opposite attitude towards big cats and who express a similar outrage towards persistent loss of livestock to lions.

Conservation marketing is a growing field, but if it is to have any hope of influencing people's attitudes, campaigns must be specifically tailored to their target audience. The novel approach outlined in Chapter 1 can be easily translated into the field and has the potential to be deployed all over the world, from Borneo to Zimbabwe, to better understand the attitudes of the people who suffer human wildlife conflict on a daily basis.

Further, while Chapter 2 revealed fascinating insights into peoples' reported preferences for wildlife; we have no idea how these preferences translate into actions in conservation campaigns. To explore this in more detail I am currently planning collaboration with the RSPB (Europe's largest conservation NGO), and my collaborators Touchstone where we will repeat the survey in Chapter 1 with a focus on UK species. This will then be followed up by a series of fundraising campaigns each championed by different species. Comparing the

revenues received from each campaign will allow us to investigate how well peoples' preferences translate into actions.

Part 2 of this thesis highlights both the extreme threats faced by clouded leopards, and the limits of our knowledge about their basic ecology. The habitat suitability maps in Chapter 5 were based on surveys of expert opinion, and while these are currently the best available data, surveys of expert opinion have been shown to be less reliable than empirical data. I am therefore working with the wider clouded leopard team at WildCRU to generate improved, empirically derived habitat suitability and landscape resistance maps based on our extensive camera trapping surveys and emerging GPS collar data. These maps will enable us to estimate the impacts of deforestation on clouded leopard genetics with increased precision.

While the approach used in Chapter 5 of this study have been shown to provide robust estimates of landscape mediated gene flow in the wild, these numbers remain estimates. However, it is possible to empirically test these predictions using landscape scale genetic analyses. Previous studies have already collected genetic samples from clouded leopard scats and so while this may be difficult it should be feasible to collect clouded leopard scats across a wide study area. These could be used to measure the current genetic diversity of the population, and more importantly to test the impact of various landscape features on clouded leopard gene flow.

Finally, in chapter 6 I identify areas that offer the best co-benefits for both clouded leopard conservation and forest carbon, and show that the best performing scenarios will result in substantially better outcomes for both clouded leopard conservation and the conservation of carbon stocks relative to the business as usual scenario. However, at present our models fail to account for leakage. Furthermore, if conservation policy is going to be taken seriously at a national level, it needs to take account of the many competing demands on the land. Expanding the approach used in Chapter 7 it would be possible to tackle both of these problems by setting targets for other land uses (such as conversion for palm oil) within the model.

Final thoughts

My hope, as the research reported in this thesis has unfolded, has been to contribute new understanding of how conservation science can contribute to conservation practice. Of course, that ambition is a big one, and to the extent that it is fulfilled the journey will doubtless be one of small nudges forward. Nonetheless, I hope that the foregoing chapters provide not only scholarly insights into the academic field of conservation, but also that they are a step towards delivering conservation outcomes that would not previously have been possible.

Although the quests for originality and usefulness are both dauntingly challenging, my aim at the outset was to make a contribution to the understanding and usefulness of various metrics of conservation prioritisation, both at the general level of which species make good

emblems of conservation marketing campaigns and at the more specific level of identifying which areas should be prioritised for clouded leopard conservation in Borneo.

While I have developed an approach for a particular felid on a particular island, my aim has been to demonstrate an approach that could be applied to any species in any landscape. These insights demonstrate the urgency of conservation action to slow the rate of deforestation loss on Borneo. My hope is that my comparison of scenarios provides the basis for informed debate among conservation biologists and politicians about how best to locate protected areas, and a basis for conservation planners in Borneo to build effective conservation action plans for the clouded leopard, and associated wildlife, into the future.



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Appendix 1

Identification of areas in Brazil that optimize conservation of forest carbon, jaguars, and biodiversity

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Contributed Paper

Identification of Areas in Brazil that Optimize Conservation of Forest Carbon, Jaguars, and Biodiversity

ALAN E. DE BARROS,* †† EWAN A. MACDONALD,† MARCELO H. MATSUMOTO,‡ ROGÉRIO C. PAULA,§ SAHIL NIJHAWAN,** Y. MALHI,† AND DAVID W. MACDONALD*

*Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, The Recanati-Kaplan Centre, Tubney House, Tubney, Oxford OX13 5QL, United Kingdom
†School of Geography and Environment, University of Oxford, Oxford, United Kingdom
‡The Nature Conservancy of Brazil, Curitiba, PR, Brazil
§CENAP – National Research Center for Carnivore Conservation, Atibaia, SP, Brazil
**Panthera, 8 W. 40th St, 18th Floor, New York, NY 10018, U.S.A.

Abstract: *A major question in global environmental policy is whether schemes to reduce carbon pollution through forest management, such as Reducing Emissions from Deforestation and Degradation (REDD+), can also benefit biodiversity conservation in tropical countries. We identified municipalities in Brazil that are priorities for reducing rates of deforestation and thus preserving carbon stocks that are also conservation targets for the endangered jaguar (*Panthera onca*) and biodiversity in general. Preliminary statistical analysis showed that municipalities with high biodiversity were positively associated with high forest carbon stocks. We used a multicriteria decision analysis to identify municipalities that offered the best opportunities for the conservation of forest carbon stocks and biodiversity conservation under a range of scenarios with different rates of deforestation and carbon values. We further categorized these areas by their representativeness of the entire country (through measures such as percent forest cover) and an indirect measure of cost (number of municipalities). The municipalities that offered optimal co-benefits for forest carbon stocks and conservation were termed REDDspots (n = 159), and their spatial distribution was compared with the distribution of current and proposed REDD projects (n = 135). We defined REDDspots as the municipalities that offer the best opportunities for co-benefits between the conservation of forest carbon stocks, jaguars, and other wildlife. These areas coincided in 25% (n = 40) of municipalities. We identified a further 95 municipalities that may have the greatest potential to develop additional REDD+ projects while also targeting biodiversity conservation. We concluded that REDD+ strategies could be an efficient tool for biodiversity conservation in key locations, especially in Amazonian and Atlantic Forest biomes.*

Keywords: corridors, multicriteria decision, prioritization, PROMETHEE, REDD+

Identificación de Áreas en Brasil que Optimizan la Conservación del Carbono del Bosque, Jaguares y la Biodiversidad

Resumen: *Una gran pregunta en la política ambiental global es si los esquemas para reducir la contaminación de carbono por medio del manejo forestal, como la Reducción de Emisiones de la Deforestación y la Degradación (REDD+), también pueden beneficiar la conservación de la biodiversidad en países tropicales. Identificamos municipalidades en Brasil que son prioridades para la reducción de tasas de deforestación y así preservan cantidades de carbono que también son objetivos de conservación para el jaguar (Panthera onca), que se encuentra en peligro de extinción, y la biodiversidad en general. El análisis estadístico preliminar mostró que las municipalidades con alta biodiversidad estuvieron asociadas positivamente con cantidades altas de carbono forestal. Usamos una decisión multi-criterio para identificar a las municipalidades que ofrecían las mejores oportunidades para la conservación del carbono forestal y la biodiversidad bajo un*

††*email alanbiology@gmail.com*
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rango de escenarios con diferentes tasas de deforestación y valores de carbono. Categorizamos estas áreas por su representatividad de todo el país (por medio de medidas como el porcentaje de cobertura forestal) y una medida indirecta del costo (número de municipalidades). Las municipalidades que ofrecían co-beneficios óptimos por el carbono forestal y la conservación se denominaron puntos REDD (n =159) y su distribución espacial se comparó con la distribución de proyectos REDD actuales o propuestos (n = 135). Definimos los puntos REDD como las municipalidades que ofrecen las mejores oportunidades para co-beneficios entre la conservación del carbono forestal, jaguares y otra vida silvestre. Estas áreas coincidieron en un 25% (n = 40) de las municipalidades. Identificamos además 95 municipalidades que pueden tener el mayor potencial para desarrollar proyectos REDD+ adicionales a la par de enfocarse en la conservación de la biodiversidad. Concluimos que las estrategias de REDD+ pueden ser una herramienta eficiente para la conservación de la biodiversidad en localidades clave, especialmente en los biomas del Amazonas y el Bosque Atlántico.

Palabras Clave: Corredores, decisión multi-criterio, priorización, PROMETHEE, REDD+

Introduction

Tropical forest biomass contains an estimated 323 billion ton of carbon (Gibbs et al. 2007) and approximately two-thirds of the world's terrestrial biodiversity (Gardner et al. 2010). Deforestation contributes around 12% to global annual CO_2 emissions, the second largest emitter by sector (Van der Werf et al. 2009) and causes habitat fragmentation and biodiversity loss (Gardner et al. 2010). Reducing Emissions from Deforestation and Degradation (REDD) is topical and it is hoped that REDD+ might benefit biodiversity conservation (Laurance 2008) (the + in REDD+ refers to strategies that also consider the role that conservation, sustainable forest management, and enhancement of forest carbon stocks have in reducing emissions). Furthermore, the addition of a biodiversity component to REDD+ may offer mechanisms to conserve key species (Venter et al. 2009). A major policy question is whether this mechanism can be adapted to deliver these diverse goals.

We explored whether a REDD+ like scheme has the potential to deliver protection of forest carbon and the conservation of a top predator, the jaguar, *Panthera onca*, and associated other biodiversity. Although we acknowledge that REDD+ offers many diverse opportunities for conservation, in this analysis we were primarily concerned with preserving existing jaguar habitat and thus we focused on the avoided deforestation aspect of REDD+.

Jaguars are listed as near threatened on the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species (Caso et al. 2008), but their numbers are decreasing and their regional status varies in the different Brazilian biomes (Paula et al. 2010; Desbiez & Paula 2012). Jaguars occupy about 46% of their historical range (Sanderson et al. 2002), and in past decades Brazil has lost more jaguar habitat than any other country (Cavalcanti et al. 2010). Although jaguars are not obligate forest dwellers, they rely on vegetation cover (Crawshaw & Quigley 1991), so deforestation poses a major threat (Haag et al. 2010) and increases their vulnerability to human persecution (Nowell & Jackson 1996). Additionally, because of their large home range sizes (34.1–262.9 km^2) (Cavalcanti & Gese 2009) jaguars are potential umbrellas for wider biodiversity conservation, whereas their absence might indicate simplification of the ecosystem and trigger trophic cascades (Estes et al. 2011). Finally, jaguars are charismatic but controversial; consequently, they exert disproportionate leverage in international and local communities (Cavalcanti et al. 2010).

Jaguar conservation units (JCUs) are a network of priority areas for jaguar conservation, defined by Sanderson et al. (2002) and subsequently refined to include a network of corridors (Rabinowitz & Zeller 2010; Nijhawan 2012). The Brazilian Jaguar Action Plan (PAN: Plano de Ação Nacional para Onça-pintada) promotes the concept of JCUs connected by dispersal corridors as the basis of jaguar conservation in the country (Nijhawan et al. 2010; Paula et al. 2010; Desbiez & Paula 2012). The PAN assigned levels of conservation priority to JCUs: urgent protection, conservation and research, conservation, and exploratory research. In addition, it included 2 models of corridors, one taking account of natural and human-made barriers (barrier corridors) and another, hypothetical, assuming these barriers do not influence jaguar dispersal (no barrier corridors).

As a stronghold of carbon and biodiversity with a high deforestation risk, Brazil has been at the forefront of the international REDD debate (Kapos et al. 2008; Laurance 2008; Parker et al. 2009). Consequently, REDD initiatives are flourishing in Brazil (May & Millikan 2010). The locations of REDD+ programs might be based on a range of factors including high carbon stocks and deforestation risk (Harris et al. 2008), opportunity costs (Olsen & Bishop 2009), and the congruence of high carbon stocks and biodiversity (Kapos et al. 2008; Venter et al. 2009). We used a multicriteria decision analysis to identify municipalities where REDD+ projects might yield protection against deforestation and the combined conservation of carbon stocks, jaguars, and overall biodiversity. We are the first to suggest prioritization schemes considering optimal areas based on carbon stocks and deforestation risk (ideal areas for REDD), conservation initiatives for jaguars, and overall biodiversity. We called these co-benefit areas REDDspots (REDDspots are defined as the municipalities that offer the best opportunities for

co-benefits between the conservation of forest carbon stocks, jaguars and wider wildlife conservation).

We identified municipalities in Brazil that represented REDDspots (i.e., priority areas for REDD+ that simultaneously deliver the greatest benefits for the conservation of jaguars and wider biodiversity and reduce deforestation and consequently conserve carbon stocks) and municipalities where current or proposed REDD projects overlapped REDDspots and where new REDD+ could be initiated to target jaguar and biodiversity conservation.

Methods

First, we quantified how carbon stocks and annual deforestation rates (ADefR) relate to the importance of each municipality for jaguars and for biodiversity conservation. We tested the hypothesis that municipalities with high carbon stocks have greater potential for jaguar and biodiversity conservation than municipalities with low carbon stocks.

Second, we analyzed key variables (carbon stocks, ADefR, and importance for jaguars and biodiversity) and measures of their representativeness (in relation to Brazilian totals) and cost (number of municipalities [NM]) in the context of a number of different scenarios of varying forest carbon stocks and deforestation rates. These scenarios were generated by applying varyingly inclusive threshold criteria to all municipalities for both forest carbon stocks and ADefR, which we then compared in a decision matrix to identify which municipalities delivered the greatest benefits for jaguar and wider biodiversity conservation for any carbon and deforestation risk targets. Having identified candidate scenarios for our REDDspots, we tested their sensitivity to the NM involved (as a proxy for cost) and recent deforestation rates (surrogate for deforestation risk). Because each scenario identified a number of municipalities, the sensitivity analysis was preferred to the alternative approach of simply selecting the top few municipalities in each group (i.e., top 100, 200, etc; Olson & Dinerstein 2002). The least sensitive scenario was chosen to represent our REDDspot priorities. The final areas identified as REDDspots were then compared with current and planned REDD-related activities to identify areas where prospective REDD+ projects could best target jaguar and biodiversity conservation as collateral benefits.

Data Sets

Detailed information on all data sources is in Supporting Information. Data sets were analyzed at the scale of Brazilian municipalities ($n = 5565$) (IBGE 2008) (Supporting Information) in a single nation-wide database (Fig. 1). Municipalities are the functional administrative

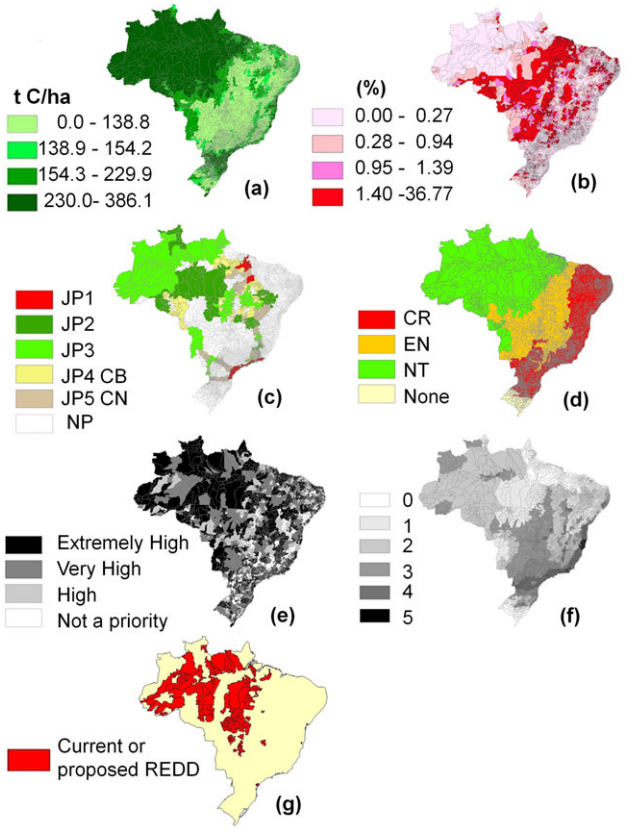

Figure 1. Maps showing, at the municipality level ($n = 5565$) (IBGE 2008), (a) forest carbon stock, (b) annual deforestation rate (2002–2008), (c) Jaguar conservation units and corridors (JCUs) (JP1, urgent action; JP2, research and conservation; JP3, research or conservation; JP4CB, barrier corridors; JP5CN, no barrier corridors; NP, no priority), (d) jaguar status in the biome (CR, critically endangered; EN, endangered; NT, near threatened; none, jaguars absent or extirpated), (e) Brazilian Ministry of Environment (MMA) biodiversity priorities, (f) international biodiversity priorities (IBPs) (absence of priority areas [0] to overlap of 5 distinct biodiversity priority areas [5]), (g) current or proposed REDD projects in Brazil. Scale values of carbon storage and annual deforestation rate correspond to the thresholds used for the analysis (Fig. 2). More details about data sets are in Table 1 and Supporting Information.

units in Brazil and compatible with available information on REDD projects.

The original carbon storage layer from UNEP/WCMC (Kapos et al. 2008; Ruesch & Gibbs 2008) (Supporting Information) was combined with a remnant vegetation layer from 2008 (National Institute for Space Research: INPE 2009; Brazilian Ministry of Environment: MMA/IBAMA 2010) (Supporting Information). The resultant grid file provided an estimate of total carbon stock

per hectare within forest remnants. Forest carbon values varied from 0 to 386.13 tC/ha per municipality (Fig. 1a). Whenever we refer to carbon or a derived term in the context of our analysis, we are always referring to this value of forest carbon stock per municipality. To validate our use of Ruesch and Gibbs (2008) data set, we compared it with Saatchi et al. (2011).

We used recent deforestation data as a surrogate for deforestation risk. Recent deforestation (INPE 2009; MMA/IBAMA 2010) (Supporting Information) was calculated as the difference in forest remnants between 2002 and 2008, converted into a raster layer (1-ha resolution), and expressed as an ADefR (%) (Puyravaud 2003) for each municipality. The ADefR varied from 0% to 36.77% per municipality (2002–2008) (Fig. 1b).

To identify areas of importance for Jaguars, we followed the PAN and used the JCU priority classifications and the IUCN jaguar extinction risk categories for jaguars in different biomes (Nijhawan et al. 2010; Paula et al. 2010; Desbiez & Paula 2012). In Amazonia and the Pantanal, jaguars are near threatened, in the Cerrado they are endangered, whereas in the highly fragmented Atlantic Forest and Caatinga biomes jaguars are critically endangered. JCUs are designed to identify priority areas for jaguar conservation that consider factors such as density, prey availability, vegetation cover, and threats. Corridors are the routes that a jaguar is most likely to use for dispersal between populations.

We assigned scores to each municipality based on their JCU priority and status. In cases where municipalities contained more than one JCU category, we assigned the higher score to the whole municipality (Table 1). Because this analysis aimed to highlight areas that benefit both jaguar and carbon conservation, we focused on the most important areas for jaguars and excluded those municipalities without JCUs or corridors (NP in Table 1). The JCUs include 2 classes of corridor: those that account for natural and human-made barriers (barrier corridors) and a hypothetical class based on the assumption that these barriers do not influence jaguar dispersal (no barrier corridors). We included both models of corridor in our analysis, but because barrier corridors were deemed to be more realistic, we assigned these a higher score.

This municipality scale data set was then assessed on how the binary presence or absence of JCUs correlated with deforestation and carbon values (generating probabilities of occurrence); how carbon and deforestation varied across different JCU priorities; and how carbon and deforestation values correlated with the jaguar index (I), which combined JCU priority and jaguar status calculated as (Table 1 & Figs. 1c–d):

$$I = \frac{(J + S)}{2} \times O, \quad (1)$$

where J is JCU priority score, S is jaguar status, and O is proportion of a municipality occupied by JCUs (calculated by dividing the JCU area within a municipality by the area of the municipality). The jaguar index controlled for area and varied from 0 to 4.5.

We used 2 data sets of biodiversity priority areas (Supporting Information). First, Kapos et al.'s (2008) synthesis of international biodiversity priorities (IBPs) and, second, a Brazilian Ministry of Environment's map of biological priority areas based on research and expert opinion (MMA 2007). The original scale of the IBP data was retained in our analysis, whereas the categorical biodiversity MMA data (scaled from not important to extremely important) were converted into an ordinal scale (Table 1 & Fig. 1). Where a municipality included more than one category, it was assigned to the category that occupied the largest area. Biodiversity data were analyzed at municipality level to understand how the presence or absence of biodiversity spots correlated with deforestation and carbon values, how carbon and deforestation varied across different biodiversity priorities, and how carbon and deforestation values correlated with the biodiversity indices, which were generated by multiplying the value of the ordinal scale (for each of the biodiversity maps) by the proportion of a municipality designated as a priority site. The IBP index varied from 0 to 5, and MMA index varied from 0 to 3.7. These ranking differences were subsequently accounted for with the Promethee method (Brans & Mareschal 2005).

Data on current or proposed REDD projects were gathered from CIFOR (May & Millikan 2010), the Brazilian Forestry Services (SFB-MMA 2009), and IDESAM (Cenamo et al. 2010) (Supporting Information). We identified 35 REDD-related initiatives at varying stages of implementation distributed across 135 municipalities (Fig. 1g). The initiatives varied considerably in size from small private areas <100 ha, to a proposed project covering more than 20 municipalities representing indigenous territories in Brazil. Spatially explicit information was unavailable for most REDD sites so we used presence or absence within municipalities. We used Ministry of Environment data sets on Brazilian Biomes (MMA 2005) and Protected Areas and Indigenous Territories (MMA&FUNAI 2010) (Supporting Information).

Data Analyses

We used binomial logistic regression to investigate whether the presence or absence of jaguar or biodiversity priority areas was related to forest carbon stocks (Ruesch & Gibbs 2008) or ADefR.

We also investigated whether forest carbon or ADefR were related to a specific JCU priority and biodiversity category using box-plots and Kruskal-Wallis tests (Supporting Information).

To identify the municipalities that offered the greatest opportunities for co-benefits, we applied thresholds for JCU priority, amounts of carbon, ADefR, and forest cover

Table 1. Data sets used in the statistical and multicriteria decision analyses which defined the REDDspots. References and categories are included.

	REDD	*Jaguar Conservation Units & Corridors (JCUs)*		Criterion[a] *International Biodiversity Priorities (IBPs)*	*MMA Biodiversity Priorities*		*IBP, MMA, and Jaguar Indices*[c]
	current or proposed (occurrence in municipality)	priority for action	jaguar status	(number of priorities overlapping municipality)	(biological priority categories)	Occurrence of JCUS, IBPS, and MMA (biodiversity priorities in municipality)	priority categories and% area occupied in municipality
	Reference[a]						
Score[b]	*SFB, CIFOR, Idesam, Supporting Information*	*CENAP/ ICMbio Supporting Information*		*UNEP-WCMC, Supporting Information*	*MMA, Supporting Information*	*CENAP, MMA, IBGE, Supporting Information*	*UNEP-WCMC, Supporting Information*
0	absent	Other municipalities (NP)	least concern	0	insufficient data or not important	absent	calculated[c]
1	present	No barrier corridors (JP5CN)	not threatened	1	high	present	calculated[c]
2	-	Barrier corridors (JP4CB)[d]	vulnerable	2	very high	-	calculated[c]
3	-	Exploratory Research or conservation (JP3)[e]	endangered	3	extremely high	-	calculated[c]
4	-	Research and conservation (JP2)	critically endangered	4	-	-	calculated[c]
5	-	Urgent (JP1)	-	5	-	-	calculated[c]

[a]*Abbreviations: MMA, Brazilian Ministry of Environment; SFB, Brazilian Forestry Service; CIFOR, Center for International Forestry Research; Idesam, Institute for the Conservation and Sustainable Development of Amazonas; CENAP/ICMbio, National Research Center for the Conservation of Natural Predators/Chico Mendes Institute; UNEP-WCMC, United Nations Environment Programme's World Conservation Monitoring Centre; IBGE, Brazilian Institute of Geography and Statistics.*

[b]*In cases where the original data were presented in a categorical format (e.g., JCUs or the presence or absence of current or proposed REDD projects), we converted each category into an ordinal score as shown here.*

[c]*Jaguar index was calculated by adding the score for priority for action and jaguar status. This value was divided by 2 and the quotient was multiplied by the proportion of area occupied in the municipality (see Methods). Biodiversity priority indices were calculated independently for IBPS and MMA biodiversity priorities in each municipality by multiplying the ordinal scores by the proportion of area occupied.*

[d]*The category barrier corridors (JP4B) was judged to be more realistic than the no barrier corridors category (JP5CN) and was therefore assigned a higher score.*

[e]*The category exploratory research or conservation (JP3) includes 2 of the original priority categories for jaguars (Nijhawan et al. 2010): exploratory research and conservation.*

within municipalities. Only municipalities that met the relevant threshold criteria were included in subsequent steps of the analyses.

For jaguars, we considered only municipalities that contained JCUs or corridors (Fig. 1c). JCUs occurred in 23% (1281) of Brazilian municipalities. Of these, 96% (1229) contained IBP sites and 82% contained (1052) MMA biodiversity sites.

We took the 1281 municipalities where JCUs occurred and examined them in the context of varyingly inclusive scenarios generated by applying threshold criteria for forest carbon (Ruesch & Gibbs 2008) and ADefR. The threshold values were no threshold and median, mean, and high threshold. All municipalities that failed to meet the relevant threshold criteria for either forest carbon or ADefR were excluded from that scenario. Median and mean values were calculated for all Brazilian municipalities including those that were not priority areas for jaguars (forest carbon: median = 138.86 tC/ha, mean = 154.26 tC/ha; ADefR: median = 0.28%, mean = 0.95%). For the high carbon threshold, we used a carbon density above 230.00 tC/ha (Harris et al. 2008). The threshold for high ADefR was set at 1.4% because it was between the high-rate intervals obtained by Griscom et al. (2009) (0.8% to 1.5%) and above the 0.22% global average used by da Fonseca et al. (2007). Thus, 16 scenarios were created encompassing all combinations of these thresholds (Fig. 2).

We used the following forest cover thresholds for our classification: >60% forest cover (Oliveira Filho &

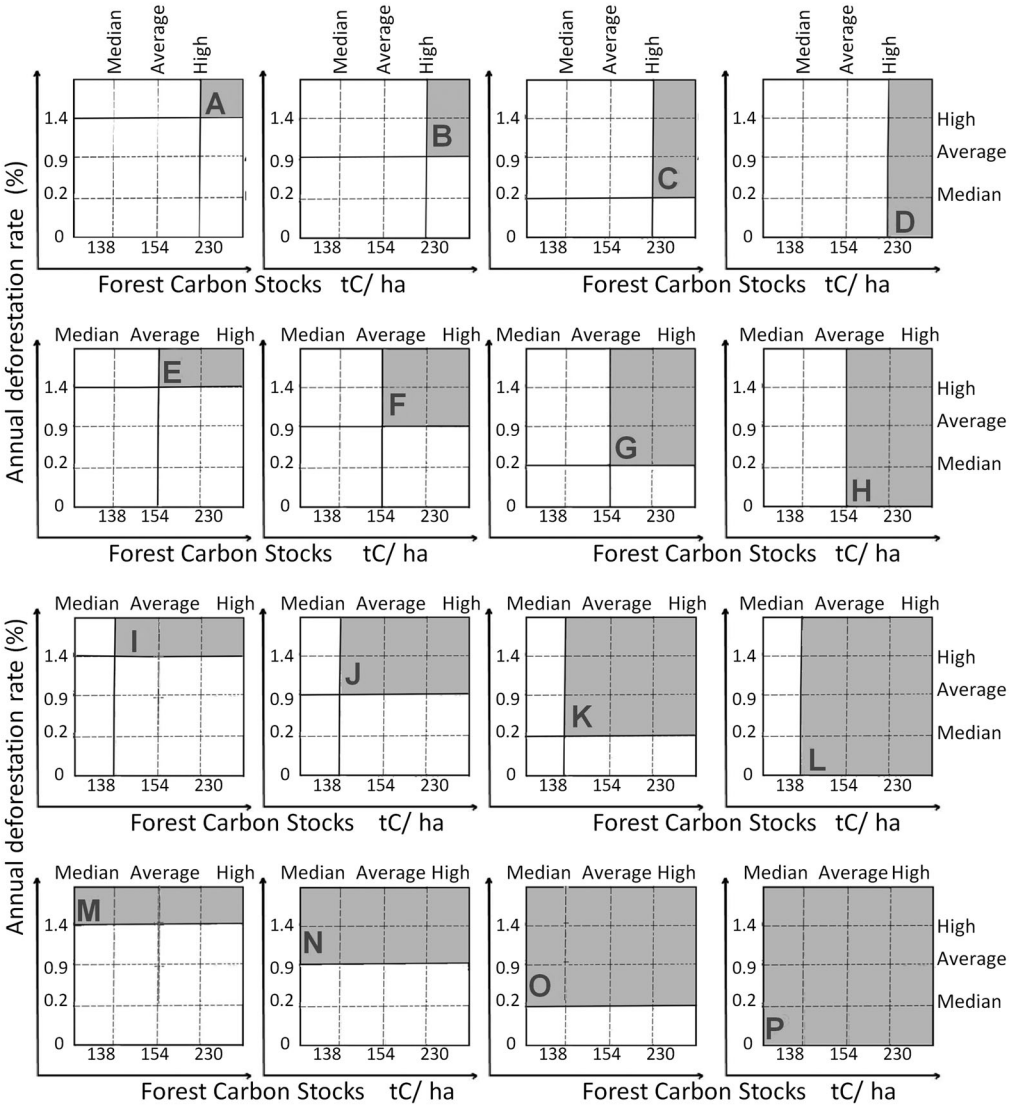

Figure 2. Sixteen scenarios (A–P) generated by combining threshold values (no threshold, median, average, and high threshold values) for forest carbon stocks and annual rate of deforestation 2002–2008. The most restrictive scenario included only municipalities that contained both high carbon stocks and high deforestation rate (scenario A, n = 86), whereas the least restrictive scenario imposed no threshold for either carbon stock or deforestation rate and thus included all municipalities (scenario P, n = 1281). Descriptions of threshold values used are in Methods. These scenarios were compared in the Promethee analyses.

Metzger 2006), >30–60%, >20–30% (Pardini et al. 2010), ≤20% but >10000 ha, and <5000 ha (approximately the size of a single jaguar home range, below which jaguar conservation may be ineffective due to insufficient habitat to support viable populations).

Decision Matrix Criteria

The 16 scenarios for varying forest carbon and deforestation thresholds were compared in a multicriteria decision analysis against 17 criteria (Table 2) in a 2-step comparison. Scenarios that scored highest for all criteria were defined as the preferred options for decision making. First, we compared all scenarios against 6 fundamental criteria (directly associated with carbon, deforestation, and amounts of vegetation cover or to probabilities of occurrence of jaguars and biodiversity priority areas). We then selected the top 4 scenarios and compared them with reference to another 11 representativeness criteria (Table 2). To consider their representativeness, each scenario was compared to the total value of a criterion for the whole country (e.g., percent total forest cover in Brazil) as well as the cost (NM, used on the assumption that more municipalities would

Table 2. Criteria used in the PROMETHEE program for comparing 16 scenarios of varying forest carbon stocks and annual deforestation rate.

*Criterion**	*Criteria type*	*Used as a threshold*	*Data type compared*	*Preference factor*
Forest carbon stocks (tC/ha)	FC	Yes	Median	0.25
Annual deforestation rate 2002–2008 (%)	FC	Yes	Median	1.00
Probability of JCU occurrence	FC	Yes	Median	0.30
Probability of IBP occurrence	FC	No	Median	0.10
Probability of MMA Biodiversity occurrence	FC	No	Median	0.10
Proportion of Forest Remnant	FC	Yes	Median	0.20
Jaguar index	RC	No	Median	0.30
IBP index	RC	No	Median	0.25
MMA index	RC	No	Median	0.30
Proportion of protected areas within JCUs (km^2)	RC	No	Median	0.50
Total annual deforestation rate (2002–2008) in Brazil (%)	RC	No	Total	2.00
Total forest cover in Brazil (%)	RC	No	Total	2.00
Total carbon in Brazil (%)	RC	No	Total	2.00
Total JCU and corridors area in Brazil (%)	RC	No	Total	2.00
Total IBP biodiversity area in Brazil (%)	RC	No	Total	2.00
Total MMA biodiversity area in Brazil (%)	RC	No	Total	2.00
Number of municipalities	Cost	No	Total	2.00

**Abbreviations: FC, fundamental criteria (eliminatory and classificatory use); RC, representativeness criteria (classificatory use); cost, number of municipalities as a proxy for cost (classificatory use); median (median values of a criterion for all municipalities within a scenario); total (sum of values of a criterion for all municipalities within a scenario expressed as a percentage of the sum of that criterion for all Brazilian municipalities); preference factors, relative preference factors (proportions) used in the Promethee matrices. Methodologically, these preference factors should be smaller than maximum and minimum values (Mareschal 2011) and were adjusted accordingly. A v-shape preference function (Brans & Mareschal 2005; Mareschal 2011) and equal weights were adopted. All criteria were maximized, with exception of number of municipalities, which were minimized.*

increase the cost of conservation strategies targeting that scenario). The highest scoring scenarios for most criteria were ultimately submitted to a sensitivity analyses with respect to the NM and representativeness to give a balanced selection of the least sensitive scenario for REDDspots.

PROMETHEE Outranking

We used the Visual PROMETHEE-GAIA (Preference Ranking Organisation Method for Enrichment Evaluations and Geometrical Analysis for Interactive decision Aid) software for multicriteria decision analysis (Mareschal 2011). This creates a matrix for each criterion in which all the alternative scenarios are compared against each other, highlighting the relative strengths of each scenario for a given criterion, and then combines the results in a final decision matrix (Drechsler 2004; Brans & Mareschal 2005).

For all the criteria, except NM, the maximum values were favored, and the software allocated a score of 1 for the highest value in each pairwise comparison between scenarios. To be considered significantly different, the value for one scenario must exceed its pair by an amount known as the preference factor (PF) (Table 2). Preference factors and the mathematical functions that best fit each criterion are determined by the user. This enables the comparison of criteria with different ranking categories or types of data because the PF and function are adjusted according to the inherent characteristics of the data corresponding to each criterion. If the difference between 2 compared scenarios is smaller to the PF, then the program automatically flags these as being estimates of weak preference. A score of zero is assigned to scenarios that are either equal or lower than their pair during the pairwise comparisons. For the criteria NM, the model favored smaller values to reflect our preference for scenarios that encompassed fewer municipalities.

After completing pairwise comparisons between the scenarios for each criterion, the scores are summed in a final matrix providing outfluxes (Φ^+; how much better one scenario is than others in relation to the overall criteria) and influxes (Φ^-; how much worse a scenario is than others in relation to the overall criteria). The difference of outfluxes and influxes provides a final net outranking flow: $\Phi = (\Phi^+)-(\Phi^-)$. The scenarios that have the highest net flow (Φ) are the scenarios that perform best with respect to all criteria (PROMETHEE II, with complete rank procedure) (Brans & Mareschal 2005). In this particular analysis, we kept equal weights among criteria but we attached greatest importance to the fundamental criteria (Table 2) and used them as a basis for eliminating less satisfactory scenarios. We applied the complete rank procedure in 2 phases: comparison of all scenarios against the 6 fundamental criteria to determine only the top 4 REDDspot scenarios and comparison of the top 4 scenarios against all the fundamental, representativeness, and cost criteria. For both phases, the final matrices provided outfluxes (Φ^+), influxes (Φ^-), and a final net outranking flow (Φ) for each scenario.

Assessment of the Decision Matrix Results and Suitable REDDspots

We varied the weightings for the cost (NM) and deforestation risk (ADefR) criteria to examine their effect on the final net outranking flow results. From the top 4 REDDspot scenarios (based on equal weights for all the co-benefits), we selected the scenario that was least sensitive to varying weights of cost (NM) and deforestation risk (ADefR). This scenario represented an optimal solution for jaguar and forest carbon conservation, balancing the co-benefits and the NM.

REDDspots versus Current or Proposed REDD Projects

Chi-square tests were used to compare the overlap between municipalities with current and/or proposed REDD projects and the REDDspots derived from the analysis above.

REDDspots and Use of Alternative Carbon Data Sets

We compared the carbon data set used here (Ruesch & Gibbs 2008) with another empirically derived data set (Saatchi et al 2011). Method and result details regarding this comparison are in Supporting Information.

Results

Forest Carbon and Deforestation

Presence of JCUs was positively associated with carbon and negatively associated with deforestation. The odds of a municipality including a JCU or corridor increased by 0.8% for each unit increase of carbon ($z = 13.89$, $p < 0.0001$) and decreased by 16% for each unit increase in deforestation ($z = -2.33$, $p < 0.05$).

Jaguar index varied positively with carbon stocks and negatively with deforestation. The highest jaguar conservation priority areas were mostly above 230 t C/ha of carbon storage and with an ADefR under 5% (Fig. 3a).

Municipalities containing urgent priority JCUs had higher carbon stocks ($\chi^2 = 397.03$, df = 5, $p < 0.0001$) and lower deforestation rates ($\chi^2 = 157.53$, df = 5, $p < 0.0001$) compared with municipalities containing other categories (Supporting Information).

The probability of biodiversity priorities occurring in a municipality was influenced by the negative interaction between carbon and deforestation. Consequently, when both deforestation and carbon values increased, the likelihood of a municipality containing MMA or IBPs decreased by 0.1% and 0.3%, respectively ($z = 2.66$, $p < 0.01$ and $z = -7.59$, $p < 0.0001$).

When considered separately, each unit increase in carbon increased the likelihood of occurrence of both MMA biodiversity priorities (by 0.7%, $z = 11.73$, $p < 0.0001$) and IBPs (by 0.2%, $z = 2.58$, $p < 0.01$). And for each unit increase in ADefR, the likelihood of a municipality including an IBP increased by 46% ($z = 4.72$, $p < 0.0001$); however, there was no significant relationship with MMA biodiversity priorities ($z = -1.687$, $p = 0.09$).

Municipalities with the highest IBP index were typified by either high carbon and low deforestation or by low carbon and high deforestation (Fig. 3b). Municipalities with the highest MMA indices were more evenly distributed (Fig. 3c), but still exhibited positive association with carbon stocks.

The highest IBP biodiversity categories (4 and 5) were positively associated with forest carbon stocks ($\chi^2 = 316.58$, df = 5, $p < 0.0001$, Supporting Information) and negatively associated with deforestation ($\chi^2 = 578.03$, df = 5, $p < 0.0001$, Supporting Information), whereas lower scores (0 and 1) exhibited the opposite trend. The MMA biodiversity medians differed significantly for carbon ($\chi^2 = 214.31$, df = 3, $p < 0.0001$, Supporting Information) and deforestation ($\chi^2 = 54.29$, df = 3, $p < 0.0001$, Supporting Information), but only category 0 differed significantly from the others.

Multicriteria Decision Matrix Analyses (PROMETHEE)

The values used to compare the 16 scenarios (Fig. 2) in the fundamental criteria matrix are summarized in Table 2 and Supporting Information. The length of the criterion axes indicated the strength of the discriminating criteria (Fig. 4a). All fundamental criteria presented a similar length, but the deforestation ADefR criterion exhibited the longest axis and thus the most influence on the overall decision.

Scenarios C and D were ranked highest, appearing close to the decision axis for all fundamental criteria π (Fig. 4a) and in particular for carbon storage, probability of JCU occurrence, probability of MMA occurrence, and proportion of forest remnant.

Probability of IBP occurrence and proportion of forest remnant showed similar orientations, but they were opposite to ADefR (indicating conflicting preferences between these criteria).

Scenarios I and E performed best in relation to the criteria for deforestation (in agreement with the thresholds for deforestation in both scenarios), and scenarios L and H performed best in relation to IBP occurrence. Overall scenarios M, N, O, and P were the least preferred scenarios (opposite to the decision axis π [Fig. 4a]). The long length of π implies that the decision axis had a strong decision power and that the preferred solutions will be oriented in that direction. Scenarios A, B, C, and D were selected as the preferred candidates considering the pairwise comparison for all fundamental criteria.

The final net outranking flow (Φ) for the top 4 scenarios in the PROMETHEE II analysis corresponded to Φ = D > C > B > A. Scenarios D and C exhibited the highest scores for net flow (Φ), which is the difference between

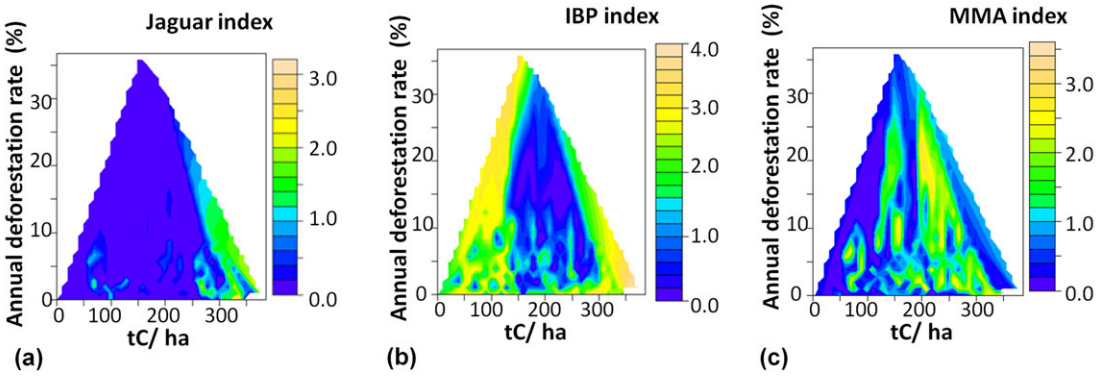

Figure 3. Relations among the variables forest carbon (0–386 t C/ha) and annual deforestation rate 2002–2008 (0–36%) and (a) priorities for jaguar conservation (jaguar index), (b) international biodiversity priorities (IBP index), and (c) Brazilian Ministry of Environment (MMA index) (the higher the index value, the higher the conservation priority of the index).

outfluxes (Φ^+; how much a scenario is preferred to all other scenarios) and influxes (Φ^-; how much all other scenarios are preferred to a given scenario). However, scenario D had the highest outfluxes whereas C had the highest score for influxes. Thus one should not assume D is better than C. We therefore compared the top 4 scenarios in another decision matrix including additional criteria (Table 2 & Supporting Information).

The top 4 scenarios compared against all 17 fundamental, representativeness, and cost criteria (Supporting Information) obtained an equivalent final net flow Φ result (D>C>B>A). These 4 scenarios had a high carbon threshold (≥230 tC/ha), but different thresholds for deforestation (Figs. 2 & 4b).

Assessment of Decision Matrix Results and Suitable REDDspots

The criteria we used as proxies for cost and deforestation risk favored scenarios A and B, which had fewer municipalities (A = 86, B = 95) and higher deforestation thresholds (Fig. 4b), whereas most of the representativeness criteria (e.g., percent total forest cover and percent total forest carbon) were maximized in scenario D (371 municipalities). Subsequent PROMETHEE-GAIA analysis confirmed this relationship but indicated the choice between C or D depended upon the weighting attributed to each criteria, with changes of 10% affecting the direction of the decision axis toward selecting either D or C. Varying the weightings by more than 65% could push the outcome toward B or A.

We explored the sensitivity of the top 4 scenarios to variations in the weights of cost and deforestation risk (Figs. 4c & d). Increasing the weighting of cost favored scenarios with fewer municipalities. Under equal weights (6%), D was the preferred scenario; however, when weights were >57% for cost and >33% for deforestation risk, scenario D became the least favorable scenario.

Scenario C was revealed as the least susceptible to weightings variations in both cost and deforestation risk (Figs. 4c & d). Scenario D was the preferred option when cost and risk were not taken into account, whereas C was a reasonable solution considering these factors, remembering that all municipalities contained in C were also contained in D (Figs. 2 & 4b). We therefore selected the municipalities highlighted in scenario C as our REDDspots.

REDDspots (scenario C) (Fig. 4b) were distributed in 3 biomes and 10 states: 5 states from Amazonia, 3 from Amazonia/Cerrado, and 2 from Atlantic Forest. The general trend was the selection of municipalities from Amazonian arc of deforestation and the Atlantic rainforest because these are the 2 high-carbon regions most affected by large scale deforestation.

A threshold for forest cover was applied to the REDDspots identified under scenario C (Figs. 5a & 5b) concerned specifically with potential jaguar conservation. From 159 REDDspot municipalities, 12 (7%) contained <5000 ha of forest cover, and these occurred in the Atlantic forest and Amazonia biomes in the states of Santa Catarina (4), Parana (6), and Maranhão (2). Of these, 8 corresponded to Jaguar corridors, 7 of which were of the less realistic no barrier corridors category. In municipalities with less than 5000 ha of forest cover, there may be fewer opportunities for successful interventions focused on jaguar conservation.

REDDspot (n = 159) and current or proposed REDD projects (n = 135) coincided in 25% (n = 40) of municipalities (Fig. 5d), a significantly greater level of overlap than expected by chance (χ^2 = 357.30, df = 1, p << 0.0001). All REDD projects in Amazonia (n = 39) occurred in REDDspot municipalities, whereas only 1 did so in the Cerrado. Of the 119 municipalities that were identified as REDDspots but for which we were unaware of any REDD projects, 84 occurred in Amazonia and 35 in Atlantic Forest. There were 95 municipalities that contained

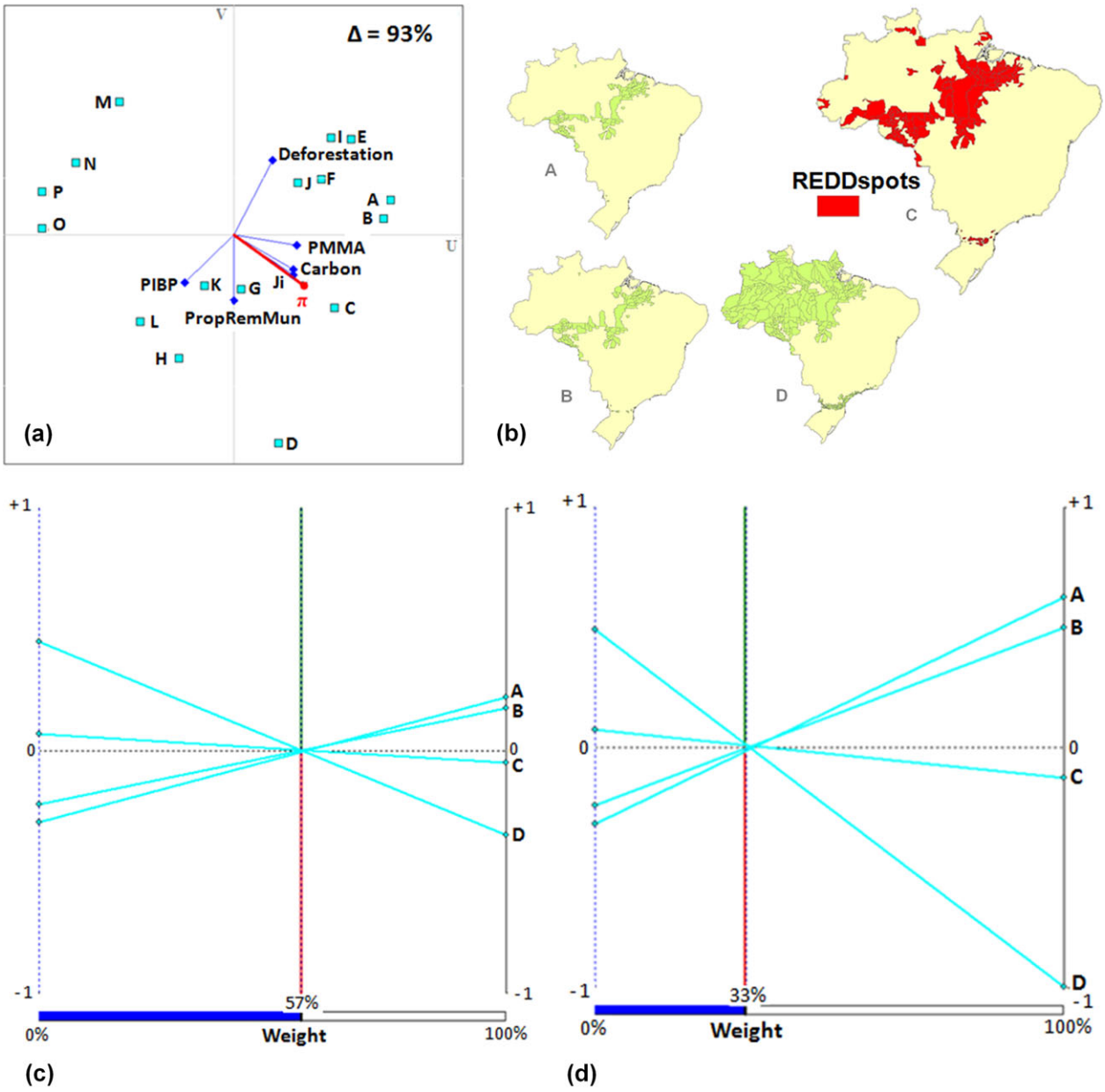

Figure 4. (a) Results of PROMETHEE-GAIA visual analyses that show how the 16 scenarios (squares A to P) (see Fig. 2) performed relative to the 6 fundamental criteria (carbon, carbon stocks in tons of C per hectare; deforestation, percent annual deforestation rate in 2002–2008; PropRemMun, median proportion of forest remnant in 2008; Pj, probabilities of occurrence for jaguar conservation priorities; PMMA, probabilities of occurrence for Brazilian Ministry of Environment biodiversity priorities; PIBP, probabilities of occurrence for international biodiversity priorities; π, optimal decision [all criteria decision axis]; Δ, amount of information explained in the GAIA projection). (b) Suitable scenarios for REDDSpots (A, B, C, and D) and their corresponding municipalities (A, n = 86; B, n = 95; C, n = 159; D, n = 371). Municipalities shown in scenario C were selected as REDDspots. (c) Stability intervals show effect of different weights on municipalities in the final net outranking flow (Φ) (scenario C is least sensitive to weight variation in the municipality criteria and D is the most sensitive to differences in cost). (d) Stability intervals showing the effect of different weights of annual percent deforestation rate (2002–2008) on the top 4 scenarios (scenario D is the lowest ranked scenario when weights are >33% and includes municipalities with no recent deforestation, which explains the low performance of scenario D relative to the deforestation risk criteria).

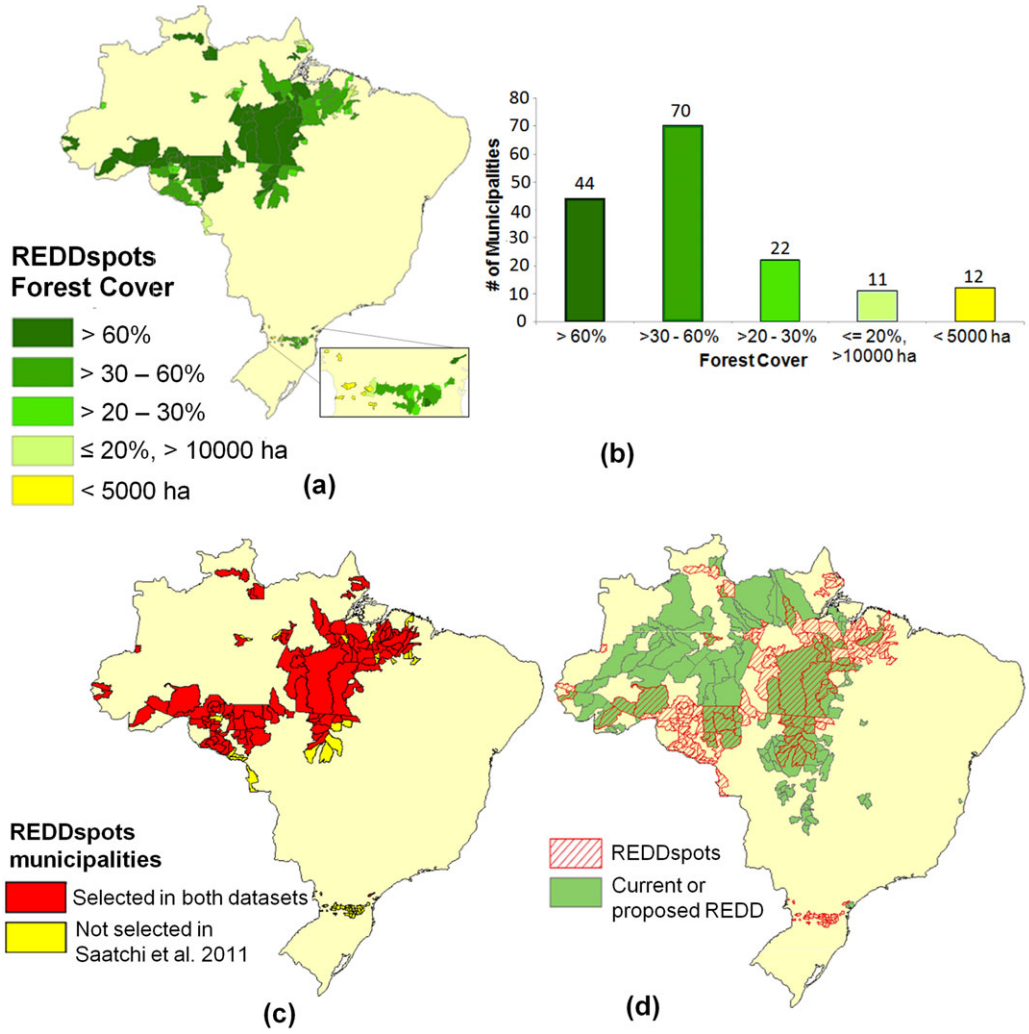

Figure 5. (a) Area of forest cover in municipalities selected as REDDspots (i.e., areas that offer the greatest opportunity for co-benefits between the conservation of forest carbon and biodiversity). Expanded region shows where most of the municipalities with <5000 ha of forest cover occur. (b) Number of municipalities associated with each class of forest cover in REDDspot municipalities. (c) Areas selected as REDDspots either in both data sets or not selected in Saatchi et al. (2011). (d) Overlap of REDDspot municipalities and municipalities containing current or proposed REDD projects (see Supporting Information for details).

current or planned REDD projects (61 in Amazonia, 31 in Cerrado, and 3 in Atlantic Forest) but which did not meet all the criteria or thresholds we used to select REDDspots. Of these, 41 failed to meet the threshold value for forest carbon, 37 failed to meet the threshold value for ADefR, 3 failed to meet the thresholds for both forest carbon and ADefR, and 14 occurred outside JCUs.

The carbon data sets used were correlated for all Brazilian municipalities (Pearson's correlation $r = 0.75$, $p << 0.0001$, df = 5563, 95% CI = 0.74–0.76) (Supporting Information); however, estimated total forest carbon per municipality was lower in Saatchi et al's (2011) data (M = 91.7 tC/ha) than in the Ruesch and Gibbs (2008) data (M = 154.3 tC/ha). The correlation and the differences between the means of the 2 data sets were variable between biomes. This is possibly related to the degree of uncertainty in Saatchi et al. (2011) or the differing NM per biome. In practice, the use of Saatchi et al. (2011) data (considering our >230 tC/ha threshold for high carbon) reduced the number of REDDspot municipalities from 159 to 103 (Fig. 5c), mainly due to Saatchi et al.'s (2011) lower carbon estimates (Supporting Information).

Discussion

REDDspots highlight areas that offer the greatest opportunity for combining the conservation of forest carbon, jaguars, and wider biodiversity. We propose that the

concept of REDDspots as a useful tool for decision makers in optimizing reduced deforestation risk while targeting carbon and biodiversity conservation. Opportunity costs (Olsen & Bishop 2009) may drive REDD+ initiatives to areas of low deforestation risk; however, the greatest benefits would be to reduce deforestation risk where it is high (Harris et al. 2008). REDD+ includes biodiversity conservation only incidentally (Collins et al. 2011*b*); however, there are frameworks within which biodiversity gains could be bundled into REDD+ programs (Collins et al. 2011*a*). Furthermore, the REDDspot concept may be technically adapted with use of different scales or data sets.

High jaguar indices, the probability of a JCU occurring in a municipality, and a JCU's priority level (Fig. 3 & Supporting Information) were all positively associated with forest carbon stocks and negatively associated with deforestation. This was expected because JCUs and corridors were developed based on possible stable jaguar populations, protected areas, and indigenous territories (Nijhawan 2012). Although high-priority JCUs were associated with high forest carbon stocks and protected or indigenous areas, corridors often lay in unprotected and agricultural landscapes that are generally associated with high deforestation rates (Supporting Information).

Both measures of biodiversity priority were positively associated with forest carbon. However, although MMA biodiversity categories were more evenly distributed among biomes, IBP areas were predominantly associated with the Atlantic Forest and Cerrado (Fig. 1). The congruence between both measures of biodiversity and forest carbon stocks illustrates the potential for REDDspots to provide co-benefits, but should not diminish attention to biodiversity conservation in low carbon areas.

REDDspots balance several criteria selected alongside carbon and deforestation thresholds. The opportunity to explore combinations of cause and effect is a strength of the scenario approach (Soares Filho et al. 2006; Kass et al. 2011), and the PROMETHEE-GAIA analysis aided the selection of optimal scenarios. For fundamental criteria (Table 2) high carbon municipalities achieved the best results, in particular for jaguars and MMA biodiversity priorities (Fig. 4). Comparing the 4 high carbon scenarios, deforestation thresholds limited the selection of municipalities. Scenario D was preferred in terms of representativeness criteria, whereas scenario A was the least costly. Scenario C was the most balanced in relation to fundamental and representativeness criteria and the least sensitive to weighting changes for cost and deforestation (Fig. 4). The PROMETHEE method is a valuable tool for conservation decision making, but the final decision depends on stakeholders' goals and limitations and ultimately on discussion and judgment (Drechsler 2004).

Among the 159 municipalities highlighted as REDDspots, 12 had <5000 ha of forest (8 corresponding to potential jaguar corridors in the Atlantic Forest). Jaguar populations may not exist in such municipalities, but corridors could promote connectivity with other municipalities with small effective populations and enhance their survival (Rabinowitz & Zeller 2010). Limited forest cover, fragmentation, and road barriers could particularly affect female jaguars' mobility and dispersal (Conde el al. 2010). In addition, reduction in forest cover thresholds may negatively impact populations of forest dependent species (Oliveira Filho & Metzger 2006; Pardini et al. 2010).

The threshold values that were selected (i.e., high carbon) as well as the data set used may have major implications on the results of prioritization schemes or multicriteria decision analyses. They should therefore be considered carefully. For example, the 2 carbon data sets used here were significantly correlated; however, shifting from Ruesch and Gibbs (2008) to Saatchi et al. (2011) while maintaining the same thresholds for carbon (>230 tC/ha) would have resulted in 56 fewer municipalities being selected as REDDspots. However, because this stems from our choice of threshold value, it does not radically alter our underlying message.

REDD projects in Brazil may occur inside and outside protected areas and involve diverse stakeholders. Current or planned REDD projects ($n = 135$) overlap with REDDspots ($n = 159$) in 40 municipalities. Ninety-five municipalities contained REDD projects, but did not overlap with REDDspots. Of these, 85% were not selected as REDDspots because they did not reach the thresholds for forest carbon or ADefR, which suggests that a focus on high carbon and on deforestation risk may not have been the predominant driver of project location. The remaining 15% were sited outside JCUs and represented a potential missed opportunity for conservation.

We identified a further 119 municipalities which may have potential to develop additional REDD+ projects. These represent the areas with greatest potential for a portfolio of REDD+ projects to sensitively balance benefits to existing conservation strategies, such as the PAN, with areas of simultaneously high carbon stocks and high deforestation risk, such as the Amazon arc of deforestation. REDDspots could also be used to identify areas where avoided deforestation and reforestation projects could be combined to maintain and improve jaguar corridors. For example, in the Atlantic rainforest of southeastern Brazil, jaguar populations are perilously isolated (Haag et al. 2010). Given low forest cover and road-induced habitat fragmentation, reforestation strategies could be a useful tool in this region. Although REDDspots are a powerful tool, they are not a panacea. In the Caatinga and Cerrado the jaguar is endangered but carbon stocks are low, so REDD+ projects offer little scope for combining co-benefits for carbon and jaguar conservation.

We see great potential rewards for integrating biodiversity conservation with carbon protection and avoided

deforestation, especially in the case of the jaguar which may also deliver umbrella and flagship benefits.

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Supporting Information

Additional references (Appendix S7), data sets used for GIS analysis (Appendix S1) and to compile REDD strategies in Brazil (Appendix S2), information relevant to quantitative analyses and parameters used in the Promethee analysis (Appendix S3), a list of municipalities elected as REDDspots (Appendix S4), additional spatial analyses (Appendix S5), and the results of the comparison among the quoted carbon data sets (Appendix S6) are available online. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Appendix 2

Priorities for global felid conservation

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Contributed Paper

Priorities for global felid conservation

Amy J. Dickman,* Amy E. Hinks,*¶ Ewan A. Macdonald,† Dawn Burnham,* and David W. Macdonald*

*Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, The Recanati-Kaplan Centre, Tubney House, Tubney, Oxford OX13 5QL, United Kingdom

†Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford OX1 3QY, United Kingdom

Abstract: *Conservation resources are limited, necessitating prioritization of species and locations for action. Most prioritization approaches are based solely on biologically relevant characteristics of taxa or areas and ignore geopolitical realities. Doing so risks a poor return on conservation investment due to nonbiological factors, such as economic or political instability. We considered felids, a taxon which attracts intense conservation attention, to demonstrate a new approach that incorporates both intrinsic species traits and geopolitical characteristics of countries. We developed conservation priority scores for wild felids based on their International Union for Conservation of Nature status, body mass, habitat, range within protected area, evolutionary distinctiveness, and conservation umbrella potential. We used published data on governance, economics and welfare, human population pressures, and conservation policy to assign conservation-likelihood scores to 142 felid-hosting countries. We identified 71 countries as high priorities (above median) for felid conservation. These countries collectively encompassed all 36 felid species and supported an average of 96% of each species' range. Of these countries, 60.6% had below-average conservation-likelihood scores, which indicated these countries are relatively risky conservation investments. Governance was the most common factor limiting conservation likelihood. It was the major contributor to below-median likelihood scores for 62.5% of the 32 felid species occurring in lower-likelihood countries. Governance was followed by economics for which scores were below median for 25% of these species. An average of 58% of species' ranges occurred in 43 higher-priority lower-likelihood countries. Human population pressure was second to governance as a limiting factor when accounting for percentage of species' ranges in each country. As conservation likelihood decreases, it will be increasingly important to identify relevant geopolitical limitations and tailor conservation strategies accordingly. Our analysis provides an objective framework for biodiversity conservation action planning. Our results highlight not only which species most urgently require conservation action and which countries should be prioritized for such action, but also the diverse constraints which must be overcome to maximize long-term success.*

Keywords: conservation likelihood, conservation limitations, geopolitics, priority setting

Prioridades para la Conservación Global de Félidos

Resumen: *Los recursos para la conservación son limitados, por lo que necesitan de la priorización de especies y localidades para actuar. La mayoría de las estrategias de priorización están basadas solamente en las características biológicamente relevantes de los taxones o áreas e ignoran la realidad geopolítica. Hacer esto lleva consigo el riesgo de un pobre retorno de la inversión en la conservación debido a factores no-biológicos, como la inestabilidad económica o política. Consideramos a los félidos, un taxón que atrae una atención intensa de conservación, para demostrar una estrategia nueva que incorpora tanto los rasgos intrínsecos de la especie como las características geopolíticas de los países. Desarrollamos puntajes de prioridad de conservación para los félidos salvajes con base en su estado de acuerdo a la Unión Internacional para la Conservación de la Naturaleza, su masa corporal, hábitat, extensión dentro de un área protegida, peculiaridad evolutiva, y potencial como paraguas de conservación. Utilizamos datos publicados sobre el gobierno, economía y bienestar, presiones de la población humana, y políticas de conservación para asignar puntajes de probabilidad de conservación a 142 países con poblaciones de félidos. Identificamos a 71 países*

¶*Address correspondence to A.E. Hinks, email amy.hinks@zoo.ox.ac.uk*
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como prioridades altas (por encima de la media) para la conservación de los félidos. Estos países englobaron colectivamente a las 36 especies de félidos y mantuvieron a un promedio de 96% de la extensión de cada especie. De estos países, 60.6% tuvo un puntaje de probabilidad de conservación por debajo del promedio, lo que indica que estos países son potencialmente riesgos de inversión para la conservación. El gobierno fue el factor limitante más común para la probabilidad de la conservación. También fue el principal contribuyente para los puntajes por debajo del promedio del 62.5% de las 32 especies de félidos que se presentaron en países de menor probabilidad de conservación. Al gobierno lo siguió la economía, para la cual los puntajes estuvieron por debajo de la media para el 25% de las especies. Un promedio de 58% de la extensión de las especies se presentó en 43 países de prioridad alta con probabilidad baja. La presión de la población humana fue segunda al gobierno como factor limitante al tomarse en cuenta el porcentaje de extensión de las especies en cada país. Conforme disminuya la probabilidad de conservación, será cada vez más importante identificar las limitaciones geopolíticas y confeccionar estrategias de conservación acordes a ellas. Nuestro análisis proporciona un marco de trabajo objetivo para la planeación de acciones para la conservación de la biodiversidad. Nuestros resultados resaltan no sólo cuáles especies requieren más urgentemente de acciones de conservación y cuáles países deberían ser prioridad para dichas acciones, sino también las restricciones diversas que se deben superar para maximizar el éxito a largo plazo.

Palabras Clave: establecimiento de prioridades, geopolítica, limitantes de la conservación

Introduction

Biodiversity loss is occurring at a rate that constitutes a sixth great extinction period, with species extinction rates thousands of times greater than the background level (Ceballos et al. 2010). Furthermore, mammal range contractions are on average 68% (Ceballos & Ehrlich 2002). This global biodiversity crisis requires urgent action, but deciding what and where to prioritize is difficult for both conservation biologists and wider society (Macdonald et al. 2006). Prioritization exercises range from broad-scale location-based approaches, such as biodiversity hotspots and ecoregions (Olson & Dinerstein 1998; Myers et al. 2000), to priority-setting methods for individual taxa, such as mammals (Isaac et al. 2007). One approach is to select areas which offer the greatest rewards, in terms of endangered species, as illustrated for North American carnivores (Valenzuela-Galvan et al. 2008) or for groups of threatened felids and primates (Macdonald et al. 2012).

In practice, however, conservation effectiveness is driven not only by biological characteristics of the species or their habitats, but also by practicalities, such as politics, infrastructure, and logistics. Most prioritization efforts fail to incorporate issues such as the cost and likelihood of conservation success; thus, misallocation of scarce resources and failure of the conservation action could result (Joseph et al. 2009). We examined potential conservation priorities for Felidae, one of the most high-profile mammal families. We used a species-level approach followed by a country-level approach. We incorporated not only the biological aspects of the species concerned, but also socio-economic factors such as a country's wealth, purchasing power, and level of corruption, which are likely to affect conservation success on the ground. We sought to determine which wild felids are of higher conservation priority than other felids and to determine the countries where an investment in them is most likely to yield realistic conservation gains. Recent collaborative efforts aimed at wild cat conservation (Panthera 2014) could result in substantial policy and conservation impacts, but only if effort and funds are targeted effectively. Therefore, we aimed to garner information that would be useful to people who make such resource allocation decisions.

Determining which felid species to invest in over others and where specifically to target that investment is a substantial problem, one that has not been systematically analyzed previously. Some felids—particularly big cats, such as lion (*Panthera leo*), tiger (*Panthera tigris*), and cheetah (*Acinonyx jubatus*)—are both familiar and charismatic, and as such they attract huge support (Brodie 2009). However, Felidae is a diverse taxon, ranging from the diminutive rusty-spotted cat (*Prionailurus rubiginosus*), which can weigh around 1 kg, to the tiger, which can exceed 300 kg (Macdonald et al. 2010). Despite the intense attention paid to charismatic cats, many of the smaller felids are elusive and poorly known (Brodie 2009); thus, they may appear as low priorities on the conservation agenda, even if they are highly threatened. To provide a practical framework for decision makers to prioritize felids and countries for conservation action, we sought to identify which felid species are most in need of conservation, to determine which countries support concentrations of these higher priority felids, and to determine the likelihood of conducting effective, long-term felid conservation in countries where conservation dollars might be spent. This conservation likelihood can be affected by many factors such as amount of habitat, ability of a country to invest in conservation and enact relevant policies, and intensity of other pressures likely to divert attention from conservation (e.g., conflict or political instability) (Kanyamibwa 1998; Smith et al. 2003).

Protected areas are fundamentally important for many conservation efforts (Bruner et al. 2001), both at a species and national level (Walston et al. 2010; Henschel et al. 2014), so protected area size was included in our metrics

for species priority scores and conservation likelihood. However, in reality, such protected areas may be poorly governed and fail to effectively secure biodiversity (Bonham et al. 2008). Several factors affect how effective protected areas are, including a country's level of corruption, poverty (measured as Gross Domestic Product per capita), conflict intensity, and instability; human development index (HDI); and governance effectiveness (Wright et al. 2007; Irland 2008). We therefore used these metrics to provide some insight into likely protected area effectiveness. Although gaining insights into effectiveness of protected areas is informative, even relatively ineffective protected areas offer some protection (Bruner et al. 2001). Thus, we retained percentage of range protected in the felid priority and nation-wide conservation likelihood scores because we believe it is a valid index of future conservation need.

Methods

We based our analyses on range maps of 36 felids from IUCN's (2013) Red List of Threatened Species. Protected area shapefiles were obtained from the World Database on Protected Areas (IUCN [International Union for Conservation of Nature] and UNEP [United Nations Environment Programme] 2014). Country shapefiles were obtained from Natural Earth (2013). Evolutionary distinctiveness (ED) data were obtained from EDGE of Existence (2013). Sources for data used to calculate country national conservation likelihood (NCL) scores are in Supporting Information.

We calculated felid conservation priority (FCP) scores for each species and national conservation priority (NCP) and NCL scores for those countries that support populations of wild felids.

FCP Scores

We used a 2-step process to develop an FCP score for each wild felid species. First, we calculated standardized scores for each felid for IUCN red-list category, mean body size, habitat association, protected area coverage, and ED.

The IUCN (2013) bases categorization of a species' extinction risk on population size, range area, and rate of population decline (Joseph & Possingham 2008). To maintain a proportionate change in score between categories and assuming that each additional rank achieved represented a doubling of conservation need for the species, we scored felids according to their red-list category: 1, least concern; 2, near threatened; 4, vulnerable; 8, endangered; 16, critically endangered. A higher score indicated higher conservation priority.

Large mammals tend to be more extinction prone than small ones (Cardillo & Bromham 2001). For example, large cats range over wider areas and elicit greater conflict with humans than small cats (Inskip & Zimmerman 2009), and these traits are conservation risk factors (Woodroffe & Ginsberg 1998). For each species, we used average body mass across sexes (Inskip & Zimmerman 2009). A higher score denoted higher body mass and higher conservation priority.

Felids associated with a narrow spectrum of habitats are considered at greater risk of extinction than felids with a broad spectrum of habitats (Nowell & Jackson 1996), so we used the habitat association scores in the IUCN Wild Cats Action Plan. We calculated inverse scores, so that a higher value represented a narrower habitat association and therefore greater conservation priority.

Wild felids are usually most threatened in human-dominated landscapes (Nowell & Jackson 1996), so we examined the percentage of each felid's geographic range covered by an existing protected area network. Inverse scores were calculated, so that higher values denoted less protection and higher conservation priority.

ED is a measure of how much each species contributes toward overall phylogenetic diversity (Isaac et al. 2007). Felids which are genetically more distant from other species have high ED. More genetically distinct felids were deemed a priority for conservation, meaning a higher score represented greater ED and higher priority. A separate ED score was not available for the recently described Sunda clouded leopard (*Neofelis diardi*), so we used the ED score for *Neofelis nebulosa* for both clouded leopard species.

The 5 standardized variables were summed per species and the most negative score plus 0.01 added to the sum to generate a positive preliminary FCP (pFCP) score for each species. This summed score is a composite measure of individual conservation priority factors and reveals where each species emerges relative to others in terms of overall conservation priority. Combining factors can provide a more informative picture than examining factors individually (Andersen et al. 2003), and summing z scores is an established method for producing composite measures (Andersen et al. 2006; Tanha et al. 2011). There are arguments for giving some factors (such as endangerment) more weight than others. However, we believe equal weighting introduces the least subjective bias. Despite some correlation ($-0.45 \leq r_s \leq 0.67$), we retained the variables individually because each contributed additional value (e.g., endangered species restricted to particular habitats merit more attention than those that are just endangered, even if the 2 processes are related).

Umbrella Score

Felids face multiple common threats, so conservation strategies aimed at 1 species are likely to benefit others as well (Macdonald et al. 2012). Thus, we calculated a

score that measured how many other felids a conservation effort for a given felid could additionally benefit (hereafter umbrella score). We created a raster of felid range distributions (cell size of 5 min or approximately 9×9 km at the equator) with packages raster and rgdal in R (version 2.13.1) to extract the degree of interspecific overlap in pairwise comparisons. The most valuable umbrella species were those which overlapped the most with multiple higher priority felids. The umbrella score for each species was calculated as

$$U_{f1} = (\%RO_{f2} * pFCP_{f2}) + (\%RO_{f3} * pFCP_{f3}) \ldots\ldots\ldots\ldots + (\%RO_{fn} * pFCP_{fn}), \quad (1)$$

where f is the focal species; %RO is percentage of the range of other felid species (f2, f3, etc.) that the focal species' range encompasses; and pFCP is the preliminary FCP score of those species. The sum of all 6 standardized variables (IUCN ranking, body mass, habitat association, protected area coverage, ED, and umbrella score) was made positive and used as the final FCP score for each species.

NCP Scores

The NCP scores were calculated as

$$NCP_{c1} = (FCP_{f1} * \%R_{f1}) + FCP_{f2} * \%R_{f2} \ldots\ldots\ldots\ldots + FCP_{fn} * \%R_{fn}, \quad (2)$$

where c1 is the target country, f1 . . . . . fn the felid species which occur in that country, FCP is the FCP score for the species concerned, and $\%R_f$ is the percentage of that species' range falling within the country's borders.

NCL Scores

We considered 16 variables (Supporting Information) important indicators of likely conservation effectiveness in a country. These are not the only factors which affect conservation; rather, they are an initial indicator of conservation likelihood and were derived from national-level data which were uniformly available for all countries. Six countries with incomplete data on felids were excluded (Andorra, French Guiana, North Korea, Somalia, Western Sahara, and Zimbabwe), and East Timor and South Sudan were excluded because data were not available for these countries independently. Sudan was included as a single country, to provide some insight into its value for felids and likely conservation effectiveness.

The variables were standardized and the resulting z scores inversed when a lower value of a given measure was deemed better for conservation likelihood, such as for population density and conflict intensity. As before, no additional weighting was imposed, and despite some correlation ($0.04 \leq r_s \leq 0.60$), we retained metrics individually because poor, corrupt countries were deemed a riskier conservation investment than merely poor countries, even if underlying mechanisms are linked. Each standardized value was allocated to 1 of 4 categories (governance, economics and welfare, habitat and environment, and conservation policy), such that each category had from 3 to 5 contributing variables (Supporting Information). The mean values of the variables in each category were summed to produce an overall NCL score for each felid range country that would show where each country was relative to others in terms of overall conservation likelihood.

EFFECTIVENESS OF PROTECTED AREAS

The 6 national-level variables in our NCL score identified as likely factors in the effectiveness of protected areas (corruption, GDP per capita, conflict intensity, political stability, government effectiveness, and HDI) (Wright et al. 2007; Irland 2008) were standardized and summed to derive a protected-area effectiveness score for each country. A high score indicates a country is likely to have more effective protected areas. For each felid species, the percentage of protected range in each country was multiplied by that country's effectiveness score, with the summed value providing an index of protected-area effectiveness at a species level.

Results

Preliminary FCP, Umbrella, and Final Conservation Priority Scores

Just under half of wild felid species (44%, $n = 16$) had an IUCN ranking of vulnerable or above, and a significantly greater proportion of felid range occurred in protected areas ($t = 3.40$, df 35, $p = 0.002$). Protected areas encompassed 17.8% of felid ranges on average. Because protected areas are an important conservation strategy for felids, we prioritized those species with less representation in current protected areas. There was no significant relationship between the percentage of range protected and felid body mass ($r_s = 0.321$, df = 34, $p = 0.056$), IUCN ranking (KW $\chi^2 = 7.328$, df = 4, $p = 0.120$), or ED score ($r_s = 0.240$, $n = 36$, $p = 0.159$).

The pFCP score (all pFCP scores in Supporting Information) (without umbrella scores) ranked the tiger as the felid most in need of conservation action; the wild cat (*Felis silvestris*) was the least in need of conservation. Felids differed markedly in terms of the umbrella effect they offered one another. On average, species overlapped with 8.81 other felid species in total across their ranges (range 1–20). The Iberian lynx (*Lynx pardinus*) had the lowest umbrella score and the leopard (*Panthera pardus*) the highest (Supporting Information). The average pFCP score of other cats under a felid's umbrella was

highest for the Sunda clouded leopard and lowest for the Iberian lynx (Supporting Information). Contrary to what might have been expected, larger-bodied felids were not significantly more effective umbrella species for other felids ($r_s = 0.042$, $n = 36$, $p = 0.809$).

Species with a wide geographic distribution were better umbrella species because they have the opportunity to overlap with more felids globally ($r = 0.576$, $n = 36$, $p < 0.001$). When the umbrella score was calculated per 100,000 km^2, the most efficient umbrella species was the Sunda clouded leopard, and the Iberian lynx was the least efficient (Supporting Information). The species most negatively affected by calculating the umbrella score per unit area was the Eurasian lynx (*Lynx lynx*), which emerged as fractionally above average according to the initial umbrella score, but was a very inefficient umbrella per unit area due to its restricted range. In contrast, the flat-headed cat (*Prionailurus planiceps*) was in the lowest quartile for umbrella score, but its umbrella score per 100,000 km^2 was the fourth highest of all felids (Supporting Information). This is because the distribution of the flat-headed cat overlaps with many other species, despite its relatively small range.

When umbrella z scores were incorporated to produce the final FCP scores, the 6 highest priority (highest conservation need) species were tiger, flat-headed cat, cheetah, leopard, puma (*Puma concolor*) and marbled cat (*Pardofelis marmorata*). These felids had FCP scores more than 1 SD greater than the mean. The leopard and leopard cat (*Prionailurus bengalensis*) were most positively affected by including umbrella score in the final FCP rankings; both rose 23 places after inclusion, whereas the kodkod (*Leopardus guigna*) was most negatively affected (it fell 11 places) (Supporting Information). Including umbrella score in the final FCP rankings did not alter the position of the 3 highest ranked felids.

NCP and Likelihood Scores

The NCP and NCL scores for the 142 countries with extant or probably extant felid populations varied markedly within and among the 5 continents examined (Fig. 1). India supported the highest number of felid species (15 known felids) followed by China (11 felids) and Argentina, Malaysia, Myanmar, Nepal, and Pakistan (each with 10 felids [Supporting Information]). China, Indonesia, and India had the highest NCP scores, whereas Luxembourg, Japan, and the Czech Republic had the lowest scores for felid priority (Supporting Information).

We defined as higher priority the 71 countries with above-median NCP scores (Supporting Information). These countries collectively represented all 36 felid species and covered a mean of 96% (81–100%) of each species' range (Supporting Information). Ten of the highest priority countries collectively provided some representation of all 36 species, together averaging nearly half (48.0%, range 12.7–100%) of those species' ranges (Supporting Information).

Germany had the highest NCL score with good governance, economics, and conservation policy (Supporting Information). India had the lowest NCL score, mainly due to poor governance and intense human pressure. Iraq had the second lowest NCL score; poor governance and conservation policy were the key limiting factors (Supporting Information).

These results highlight that countries lie on spectra of conservation priority and likelihood, so we combined NCP and NCL scores in a quadrant-based framework to better understand where different conservation planning strategies might be most advisable (Fig. 2). Twenty-eight (39%) higher priority countries had above-median NCL scores and thus were in the higher priority, higher likelihood quadrant (Supporting Information). These 28 countries represented all but 1 of the 36 felid species (Canada lynx [*Lynx canadensis*] occurs only in the United States and Canada, both higher priority, lower likelihood countries), but collectively they averaged less than half (44%, range 2.8–100%) of those 35 species' ranges. The remaining 43 higher priority countries (which supported 32 felid species and averaged 58% [0.4–99.9%] of species' ranges) scored below average for conservation likelihood (lower likelihood [Supporting Information]). There was marked variation between countries in both the degree of conservation likelihood and its drivers (Fig. 3). For instance, China and Indonesia were ranked the highest 2 countries for FCP. However, Indonesia had an above-median conservation likelihood score, whereas China was a low-likelihood country (Supporting Information). Both human pressure and governance were limiting factors in China, but human pressure was by far the greater issue, contributing over 60 times more negative value than governance. In contrast, only governance, not human pressure, was a limitation in Indonesia (Supporting Information). Other countries such as the United States and Canada scored very high on governance and economics, but they were limited by relatively low engagement with international conservation agreements.

Impact and Drivers of Low Conservation Likelihood

Felid distributions spanned between 1 and 95 countries (Supporting Information). Thirty-two felids, including 5 of the 6 top priority species, occurred to varying extents in lower-likelihood countries. Only the Bornean bay cat (*Pardofelis badia*), flat-headed cat, Iberian lynx, and Sunda clouded leopard occurred exclusively in higher likelihood countries (Supporting Information). Dependence upon lower-likelihood areas varied substantially between cats; thus, the degree of risk of any investment in their conservation would also vary. The tiger (the top priority species) was affected by lower likelihood in 46% of countries in which it occurred and in 69% of its range,

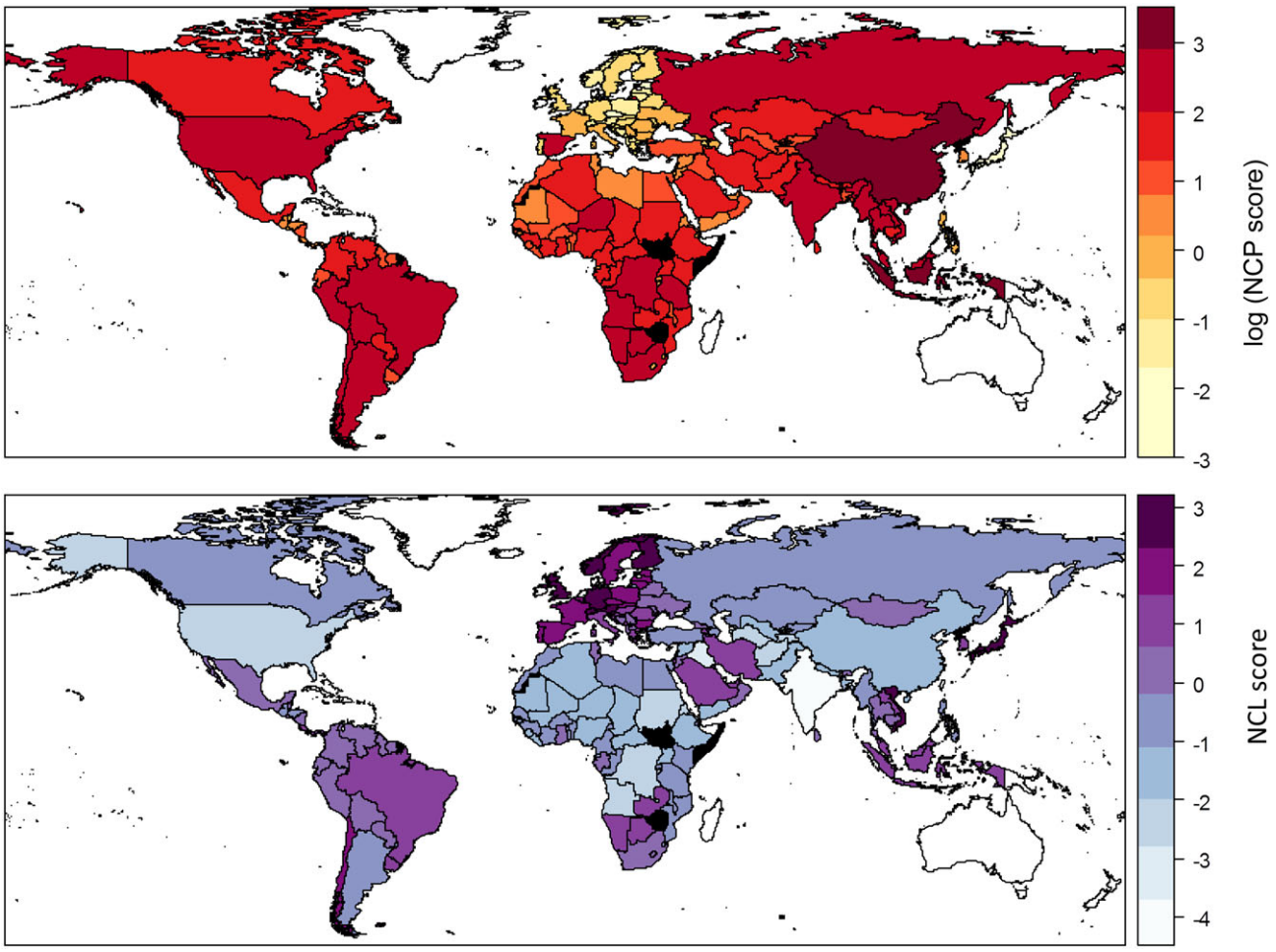

Figure 1. Map of (a) log national conservation priority (NCP) scores (darker shades, countries which support felid populations that are higher priority for conservation) and (b) national conservation likelihood (NCL) scores (darker shades, countries where conservation investment is more likely to produce long-term success). Countries in black have felids but insufficient data for analysis, whereas countries in white have no wild felid populations according to International Union for Conservation of Nature range maps.

whereas the flat-headed cat (second highest priority) was relatively unaffected by geopolitical pressures because it occurred in 1 higher likelihood country (Supporting Information).

Of the 32 felid species that occurred in lower likelihood countries, governance was the major contributor to below-average NCL values for 62.5% of them; poor economics was the major factor for 25%, whereas human pressure and conservation policy were each major factors for 6.25% at the country scale (Supporting Information). The impact of poor governance declined slightly when we considered the percentage of species' ranges in each country, although it remained a key limitation for 59.4% of felids. The influence of human pressure increased substantially relative to the country scale and was the major limiting factor for 21.9% of felid species. Poor economics and conservation policy were each major limiting factors for 9.4% of species when range was considered, meaning that the importance of economics decreased and policy increased relative to the country scale.

Effectiveness of Protected Areas

Protected area extent (KS = 5.35, $p < 0.001$) and the likely effectiveness of those areas (KS = 3.45, $p < 0.001$) varied significantly between countries, although there was no significant relationship between these 2 variables ($r_s = -0.100$, $n = 142$, $p = 0.236$). India, which had below-average scores for conflict intensity, corruption, government stability, and HDI, had the highest risk of ineffective protected areas, followed by Afghanistan and Sudan (Supporting Information). Conversely, protected areas in the United States, Japan, and Germany were the most likely to be effective (due to relatively great wealth and good governance) (Supporting

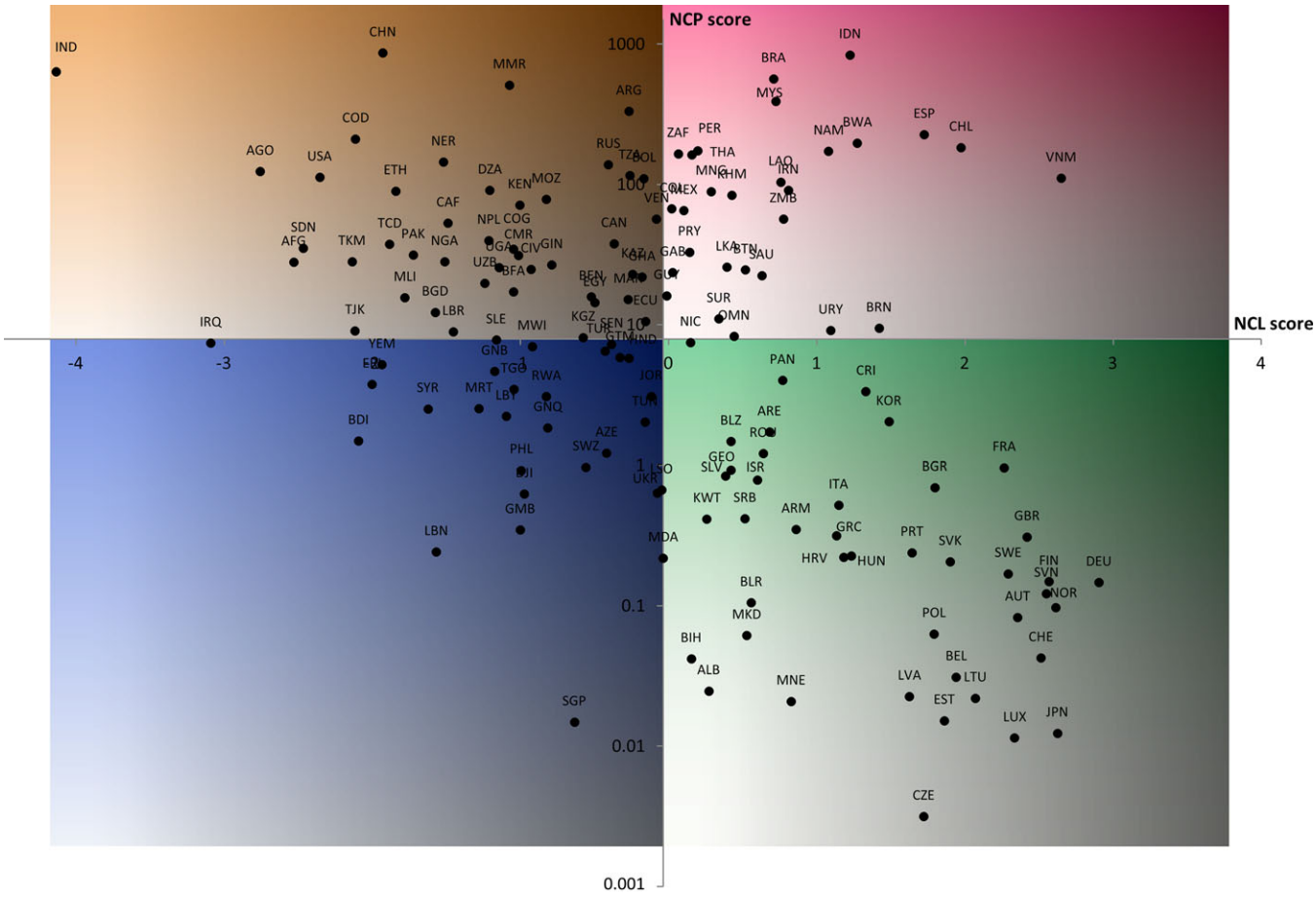

Figure 2. Country classifications according to their national conservation likelihood (NCL) scores and log national conservation priority (NCP) scores. Axes are positioned at median values, and country codes are provided in Supporting Information. The more intense the color, the higher the NCP score, whereas the darker the grey shading, the higher the NCL score.

Information). This international variation influenced the threat to individual species of ineffective protected areas; we examined a mean of 98.7% (range 92.0–100%) of felid species' protected area range (Supporting Information). The rusty-spotted cat was at the highest risk from protected area ineffectiveness. It is the only species where 100% of its examined protected area range occurred in countries with above-average risk of ineffective protected areas (Supporting Information). Ninety-four percent of tiger protected area range was in countries with above-average risk of ineffective protected areas (Supporting Information). At the other end of the scale, Canada lynx, bobcat (*Lynx rufus*), and Iberian lynx were likely to receive more than just token protection in protected areas because 100% of their ranges occurred in countries with low (below-average) risk of ineffective protected areas. Overall, there was a marginally positive significant relationship between a species' FCP score and likelihood of ineffective protected areas ($r_s = 0.334$, $n = 142$, $p = 0.046$).

Discussion

There is often a disconnect between conservation planners and people making resource allocation decisions (Game et al. 2013), but increasingly, major funders of wild cat conservation are partnering with academic institutions whose research can help inform resource allocation. Our results may help those decision makers identify species in most need of conservation action, although we are not suggesting that lower priority species do not also deserve attention. We acknowledge that prioritization results depend on which metrics are selected for inclusion and on the data, methods, and scales used to derive scores (Wolman 2006; Game et al. 2013). We restricted our analyses to publicly available data from reliable sources such as the World Bank, rather than creating arbitrary scales, and used only data where a single source provided comparable data for all species or countries. These decisions affected the results generated, and alternative choices or methods could have

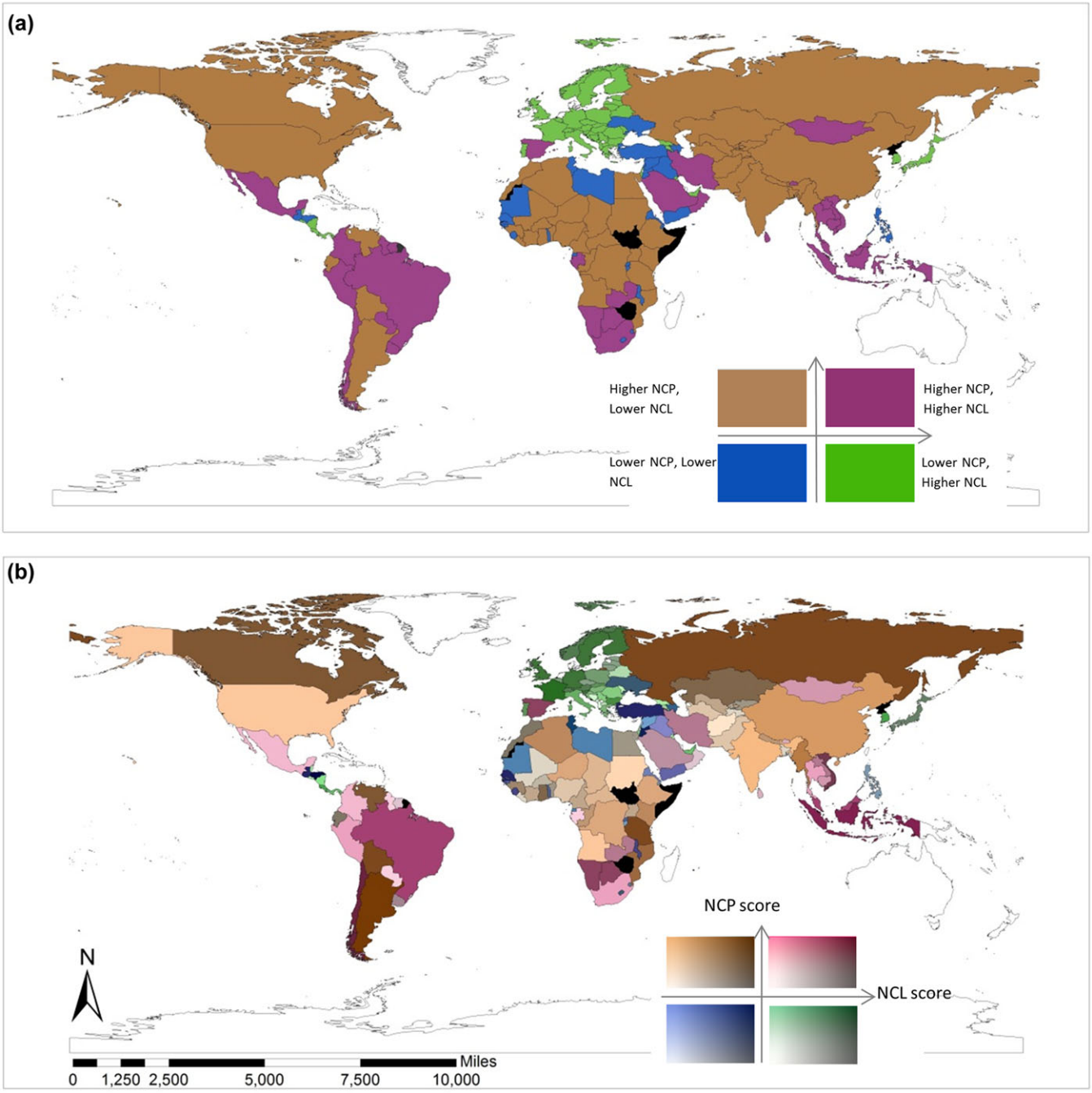

Figure 3. Global patterns of national conservation priority (NCP) and national conservation likelihood (NCL) scores (a) classified into 4 broad groups based on whether a country had above-median (higher) or below-median (lower) NCP and NCL scores and (b) as in (a) but with more detail on variation within the 4 categories (e.g., Brazil, Columbia, and Saudi Arabia are pink because they are higher priority, higher likelihood countries). There is variation in where countries score within each category, shown in (b) as different shades of pink for the high-NCP, high-NCL category. Columbia's NCL score is much closer to the median than that of Brazil, so it is lighter pink. Saudi Arabia's NCP score is closer to the median than either of the 2 South American countries, so it is a more grey-tinted pink. Countries in black have felids but insufficient data for analysis, whereas countries in white have no wild felid populations according to International Union for Conservation of Nature range maps.

produced markedly different results. Furthermore, the metrics we used to develop FCP scores were intrinsically dynamic, so factors such as conservation endeavors would affect species' rankings over time. Nonetheless, we believe the species rankings we determined are valuable, particularly because they reveal where investment in 1 species could generate efficient conservation for other felids under the target species' umbrella. Although the extent of efficiency depends upon the commonalities of threats faced by overlapping species, a comprehensive analysis of all available felid conservation action plans shows that threats to wild cats are often similar and occur in the same place (Macdonald et al. 2012), strengthening our argument for this umbrella-based approach.

Prioritizing species also helps determine which countries most urgently require conservation investment in their wild cat populations, which will help decision makers develop both immediate and long-term conservation plans. Nearly two-thirds of the higher conservation priority countries (61%) we identified had below average NCL scores, suggesting that in the majority of countries where felid conservation should be prioritized, effective conservation may be harder to achieve given the prevailing geopolitical backdrop. Funding bodies are sensitive to the risk of wasting money (Ferraro & Pattanayak 2006), so our NCL scores also provide a valuable estimate of how risky a conservation investment might be. Based on our results, we suggest the safest strategy would be to focus on the 28 higher priority, higher likelihood countries—effective conservation there would secure the majority of geographic ranges for 39% of felid species. However, this would neglect at least 114 countries with felids and over half of all felid ranges. Therefore, it is equally urgent to support the 43 countries in the higher priority, lower likelihood quadrant, but these countries are likely to require different strategies to achieve the same conservation gain as in higher likelihood countries. For instance, our results highlight the importance of considering the risk of ineffective protected areas. Although such areas likely offer some protection (Bruner et al. 2001), improving their management could have important consequences for species that rely heavily upon protected areas, especially in politically unstable or poor countries.

Lower likelihood does not preclude conservation success—countries such as India have maintained a wide diversity of wild felids despite daunting geopolitical challenges which hinder the likelihood of long-term conservation effectiveness. Future conservation success in such countries necessitates tailor-made approaches that focus on wider issues such as development and policy and may require greater funding over a longer period. Specific strategies depend upon the limiting factors relevant to that country. For example, in the United States conservation likelihood could most easily be improved by focusing on policy, whereas in India human pressure is unlikely to be resolved, so conservation action plans should focus upon securing effective protected areas. Because the relative importance of geopolitical pressures can very according to the scale of an analysis, be that national, range wide, or local, decision makers and practitioners must evaluate these pressures at the correct scale to best understand the threats to likelihood of success of their conservation efforts. For example, conservation policy was the major driver of lower likelihood for the North American bobcat, whereas for the South American kodkod, human pressure was the major driver (Supporting Information). As with prioritizing felids, national conservation prioritization is dynamic and will change with circumstances.

Our analysis represents only 1 stage of felid prioritization. Ultimately, decisions about resource allocation will depend upon a finer-scale examination of specific actions that need to be taken and their costs (Joseph et al. 2009; Game et al. 2013). Although these factors are not specifically examined here for reasons of brevity, our results highlight tactics for species-focused conservation in general. For instance, long-term lion conservation necessitates improving governance and economics, whereas Iberian lynx programs might focus on more traditional conservation, such as improving prey populations and habitat. However, individual actions can be very context specific, even within a species. For instance, in Nigeria recommendations for lion conservation involve protecting and linking remaining habitat patches (Henschel et al. 2010), while in Tanzania strategies for the same species prioritize reducing retaliatory killing and improving trophy hunting management (TAWIRI 2007). The NCL scores and drivers presented here are particularly valuable because they highlight likely limitations affecting different countries, which can inform decision makers of the likely costs, benefits, and chances of success of implementing conservation strategies. We provide an initial, broad prioritization of felid species and range countries, laying the groundwork for more detailed studies at the scale of individual species and countries.

Economic cost is clearly a key concern for decision makers and conservationists because failing to consider the financial constraints associated with different species or locations can reduce conservation efficiency, hinder effective management, and increase the risk of extinction (Joseph et al. 2009). We did not examine specific costs because the global scale of our analysis precluded recommending individual actions for species and countries and assigning a realistic cost. Although lower management costs in a country may be attractive, lower economic costs are often associated with limiting factors such as political instability (McCreless et al. 2013). Although we included a national-scale economic metric in our NCL calculations, which included factors such as a country's wealth and its purchasing power parity, we gave this equivalent weight to other factors such as corruption and the pressures of human population density and growth,

because they all play a substantial role in affecting conservation likelihood (McKee et al. 2004; Smith & Walpole 2005). We hope our work will stimulate further studies focused upon a subset of countries or species that examine the specific actions required for conservation and their associated economic costs, as has been done for threatened species in New Zealand (Joseph et al. 2009).

Ultimately, our results emphasize the need for conservationists to take an interdisciplinary approach to maximize chances of long-term success for felid conservation, considering both ecological priorities and geopolitical pressures. This pragmatic approach to prioritization could be applied to many different taxa, at varying spatial scales, to inform which conservation strategies are likely to produce effective outcomes in an increasingly human-dominated world.

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Supporting Information

Sources of the data used to calculate national conservation likelihood (NCL) scores (Appendix S1), the felid conservation priority (FCP) scores for all felid species (Appendix S2), the NCL and national conservation priority (NCP) scores for all felid range countries (Appendix S3), species distributions in NCL and NCP countries (Appendix S4), list of the 10 highest-priority felid range countries (Appendix S5), factors that limit NCL scores for felid range countries (Appendix S6), and the extent and effectiveness of protected areas in felid ranges (Appendix S7) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Appendix 3

Identifying ambassadors for conservation marketing:

Supplementary material

Full electronic dataset available on request from

ewan.macdonald@zoo.ox.ac.uk