EFFECTIVENESS OF PROTECTED AREAS AND IMPLICATIONS FOR CONSERVATION OF BIODIVERSITY AND ECOSYSTEM SERVICES

Submitted by

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to

THE UNIVERSITY OF EXETER

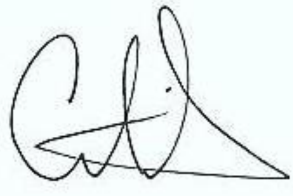
as a thesis for the degree of

DOCTOR OF PHILOSOPHY IN BIOLOGICAL SCIENCES

in

JULY 2014

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signature: …  …………………………

To Elida and Moisés.

ABSTRACT

Protected areas (PAs) are considered a key strategy to ensure the *in situ* persistence of biodiversity and the ecosystem services (ES) that this provides. The coverage of PAs has exponentially expanded in the last 25 years, and they now account for approximately 13% of the Earth's surface. Alongside this expansion, PA research literature has also increased seeking to identify and assess the main factors that influence the effectiveness of PAs in sheltering biodiversity and ES from anthropogenic pressures. Spatial distribution, spatial design, management strategy and threats, have been widely acknowledged as key factors. However, despite significant progress, several aspects of these factors remain poorly explored. This thesis aims to identify and address some of the gaps, which I detail below.

The second chapter contributes to understanding of how the distribution of PAs affects the representation of biodiversity and ES. To this end, the Chilean PA system was used as a case study as this has never been previously assessed in terms of ES. I found that the strong bias in Chilean PAs distribution toward southern areas, which contain mainly ice and bare rock, hampers the PA system in achieving effective representativeness.

The third and fourth chapters address some gaps in PA spatial design. The third assesses for the first time the spatial design of the global PA system and provides new methodologies to achieve this at such a large scale. Focusing on the size, shape, level of fragmentation, occurrence of buffer zones and proximity to the closest PA, I demonstrate that PAs tend to be small, irregularly shaped and fragmented. However, they are often close to one another and generally have buffer zones. Using the methodology generated on third chapter, I explicitly test in the fourth chapter the combined and interactive effects of PA spatial features on their ability to represent biodiversity, which has never been tested before. Using South America as a model for study I show that the spatial design largely explains biodiversity representation and that the interaction between spatial features affects the latter.

The fifth chapter focuses on threats to PAs, assessing the extent to which metal mining activities represent an actual conflict with the global PA system. Evidence suggests that the global terrestrial PA system has been effective at displacing metal mining activities from within its bounds. However, given the high proportion of mines found in the close surroundings of PAs, and the distances over which mining activities can have influences, it

is highly likely that the conservation performance of a significant proportion of PAs is being affected.

So far I have demonstrated that PAs are not always optimally distributed and they can compete with other land uses, which can undermine their functionality. In this regard, in the final analytical chapter I explore how using spatial conservation prioritization (SCP) tools it is possible to optimize the representation of conservation features by minimizing competition with other land uses. Specifically, I assess the consequences for biodiversity and ES representation of incorporating land use trade-offs in SCP analyses. I show that the dichotomist decision of treating a land use as a trade-off or not can have enormous consequences on biodiversity and ES representation, and the implications of such decisions have to be considered before policy recommendations.

This thesis shows that distribution, spatial design and threats play an important role in PA representativeness, and that SCP techniques can make a significant contribution to balancing biodiversity and ES conservation with human activities, when trade-offs are treated comprehensively. Finally, I discuss the importance of prioritising the interactions between, rather than just individual effects of, factors in order to optimise PA effectiveness and the distribution of scarce conservation resources.

ACKNOWLEDGMENTS

Doing a PhD as an international student implies two main things: to write a very complex document in a foreign language and to rely in some people more than you would normally do back home. It is that why these Acknowledgments have a special meaning to me: I am writing for the first time a text for my thesis that will not go through proof reading and, I have a deep gratitude to put in words.

Kevin, thank you for your vocation to teach how to do research. Thank you for your patience, your critical and sharp mind, your constant support, and for giving me the space to learn from my mistakes even if that meant more time and effort to you. I'm very grateful for all those unexpected *5 minutes question* chats that allowed moments of inspiration to settle as paragraphs and then as a PhD thesis. Gracias!

I would like to thank to Richatron: my PhD down here in Cornwall would not have been the same without you Rich. Thanks for being **SO** supportive, for all the academic and life chats, for the countless edits… and for the daily laughs, oh thanks for that.

A special big thank you to Andrew Beckerman who supervises me during a period of my PhD in Sheffield, in particular through my first year upgrade. Also, thanks Andrew to convince me to come down to Cornwall, it definitely was the best thing to do.

I am enormously grateful to all the critical minds that provided me priceless help giving me a hand, reading my manuscripts or helping me with a brief advice in the coffee break. Thanks to Jonathan Bennie, Barbara Goettsch, Ilya McDonald, Malu Avila, Maru Correra, Andy Suggitt, Mauricio Carter, Rodrigo Ramos, Lisette Cantu, Stefano Casalegno, Iain Sttot, Tom Davies, Jill Edmonson and Nicola McHugh. I would like to give a particular thanks to James Duffy, my Neighb, for his huge patience, help, time and willingness to always contribute. Thanks for being so special Neighb.

I also need to thanks to Isabel Noon for the proof-reading support and for being particularly keen in understanding the complexity behind *protected area effectiveness*. Thanks for your punctiliousness Isabel!

Out of the academic circle there are countless people who indirectly contribute to this work and to whom I also own part of this thesis.

The four years in UK would not have been so special without my friends. All my crew up in Sheffield made my days in the Middle-land very unique. Thanks to Xime, Claudio, Marcita, Jeshu, Aldo, Hector, Imara, Jose, Herman, Anna K., Iñigo, Kat, Laura , Miko, Carmen, Juan, Nago, Bernardo, Andrew and Sophie. A deep thank you to Molly, for looking after me, loving me, listening to me and opening the doors of her family, her house and her life. Also, I can't be more grateful to Berna and Ester for being my *parents* in this faraway island.

A special thank you to Mauricio Carter for his priceless support and for helping to convince me I was able to do this.

Coming now to the South, to my beloved Cornwall, I am so grateful of the beautiful people I have met here. So grateful for their friendship, for sharing their love for life and nature with me. Emma, thank you for always being there. Thank you Leti and Rich for your love, all the fun, van trips and for being so wonderful. Devi, Nadja, Maru, Caro, Sasita, Ade, Robyn, Elly, Sally, thanks girls for being as you are and your friendship. Kieron, thank you for all the good moments, meals, conversations and extra beers. Thank you to the Dunvegan crew, Andy, Amy, Chris and Ed for being so cool housemates and making *our* house feel as a home. And thanks to all the amazing people that have recently populated my life and have made this last period of my PhD unforgettable. YABAILY.

Going further South I land now in Chile, where my roots and my heart are. All this effort, work, perseverance would haven't been possible without the unconditional love and support of my family. To my parents, Marcia and Alejandro, my siblings Alejandro, Luciano and Susana... this achievement is because of you. All the rest of my family has been so important as well: Vivi, Ricardo, Emilia, Flavia, Alonso, Moi, Mocho, Mathias, Pablo, Aida, Lauramanda, Ma. Luisa...I am so thankful to all of you. And to all my friends mariposas, OnlyShiquillas, Sambucucu and Orumsireses that always were with me from the other side of the Atlantic.

Finally, a *romantic thanks* to Oscar Peterson: the long hours of concentration wouldn't have been possible without his music and inspiration.

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INTRODUCTION

A fundamental aim in conservation biology is to provide principles and tools for preserving biological diversity perturbed by anthropogenic activities or other agents (Soulé 1985). The relevance of protecting biological diversity (hereafter biodiversity) at all its levels - genes, species, habitats, ecosystems, biomes - resides not only in its intrinsic value (Oksanen 1997; Ghilarov 2000), but also in its instrumental value, better known as ecosystem services (ES) (Daily 1997). Defined as the services and goods derived from ecosystems, ES contribute directly (through provisioning, regulating, and cultural services), and indirectly (through supporting services) to human well-being (MA 2005). After approximately two decades of experimental research, the role of biodiversity in regulating and modulating ecosystem properties that underpin the delivery of ES is well acknowledged (Naeem *et al.* 1995; Tilman 1996; Balvanera *et al.* 2006; Reich *et al.* 2012). Thereby, the preservation of both biodiversity and ES has become increasingly important not only for the scientific community, but also for stakeholders and policy-makers (MA 2005; Daily *et al.* 2009; Rio+20 2012).

Particular concern has arisen from the continuous biodiversity decline and the consequent threat to delivering ES in the Anthropocene (i.e. the geological epoch in which human impacts on the Earth are comparable to those of geological forces) (Dobson *et al.* 2006; Steffen *et al.* 2011; Cardinale *et al.* 2012). Direct drivers of this decline (e.g., climate change, habitat transformation, overexploitation, pollution and alien species), which in turn have indirect drivers (e.g., socio-politics, economics, cultural factors), have changed some natural systems to such an extent that they can no longer recover and return to their original states (MA 2005). Species extinction rates (Pimm *et al.* 1995), land degradation (Reynolds *et al.* 2007), deforestation (Achard *et al.* 2002), reduction in water availability (Vörösmarty *et al.* 2010), and increase in Earth's surface temperature (Levitus *et al.* 2000; Ramanathan *et al.* 2001), have been identified as the main processes under which natural systems are shifting to more anthropogenic based systems (Foley *et al.* 2005; Ellis *et al.* 2010). Finding effective ways of promoting biodiversity and ES persistence in the light of anthropogenic pressures has therefore become more urgent than ever (Balmford & Bond 2005; Rio+20 2012).

Protected areas (PAs) are probably the most common and well-accepted strategy for sheltering biodiversity and ES from anthropogenic pressures (Bruner *et al.* 2001; Naughton-Treves *et al.* 2005; Andam *et al.* 2008; Tang *et al.* 2011). Since the creation of

Yellowstone National Park in 1872, the extent of PA coverage has rapidly expanded, and PAs nowadays account for 12.7% of terrestrial global land. The concept of PA as a conservation strategy has also changed. PAs were originally seen as isolated islands reserved to maintain the *status quo,* with no major social aspects considered in the conservation approach. However, in the 1990s PAs came to be regarded as functional networks and their connectivity (i.e. ecological corridors) became a management focus as it fosters species movement (Bennett 1990). Management processes to benefit local communities were also promoted, and PAs began to acquire a more active role in society (West *et al.* 2006). Since the mid-2000s, PAs have come to be recognized as spatial units within the landscape, with surrounding environments directly and indirectly influencing their internal socio-ecological conditions (Laurance *et al.* 2012). This evolution of the concept of PAs has grown to acknowledge the complexity of factors influencing their performance (Hansen & DeFries 2007; Palomo *et al.* 2014) and fostered a broad research literature on PAs, which aims to enhance the understanding of these factors (Williams *et al*. 2005; Nebbia & Zalba 2007; Cerdeira *et al*. 2010; Lasky & Keitt 2013). Spatial distribution, spatial design, management strategy and threats have been recognised as key factors driving the effectiveness of PAs (Williams *et al*. 2005). However, despite significant progress, several aspects of these factors remain poorly explored. Identifying and addressing some of these gaps will significantly contribute to understanding of the effectiveness of PAs and their new acknowledged role in society (Palomo *et al*. 2014).

The spatial distribution of PAs is a key factor in the ability to represent biodiversity and associated ES. The representation of PAs is commonly evaluated through a 'gap analysis' (Scott *et al.* 1993; Jennings 2000), in which the proportion of biodiversity elements (e.g. species, habitats, biomes) or the relative extent of their distribution ranges under protection is calculated (Rodrigues *et al.* 2004; Chape *et al.* 2005; Maiorano *et al.* 2006; Araújo *et al.* 2007; Tognelli *et al.* 2008). Based on criteria that distinguish a biodiversity element as protected or not protected, these can be considered covered, partially covered or completely uncovered, which is then considered as a 'gap element'. Evidence indicates that PAs tend to over represent certain groups of species over others (Rodrigues *et al*. 2004), as well as types of habitats (Chape *et al*. 2005). Nevertheless, existing PAs present a high conservation value and despite the constant increase of anthropogenic pressures they still maintain biodiversity elements better than if these were not protected (Gaston *et al*. 2008; Laurance *et al.* 2012). However, while the representation of different biodiversity elements has been evaluated, the extent to which

ES are captured by existing PAs remains poorly explored (Scharlemann *et al.* 2010; Tang *et al.* 2011). A lack of appropriate data and methodologies explicitly to map ES distribution have hampered progress on ES research (Eigenbrod *et al*. 2010). Thus, efforts to map ES in order to evaluate their representation within existing PAs are critical effectively to promote appropriate protection (Daily *et al*. 2009).

Understanding how the spatial design of PAs influences the representation and persistence of biodiversity has also been a strong focus of research (Kunin 1997; Schwartz 1999; Cabeza & Moilanen 2001; Williams *et al.* 2005; Edgar *et al.* 2014). Research based on island biogeography and metapopulation theories has shown that spatial design features play a key role in PA effectiveness (Diamond 1975; Margules *et al.* 1982). Probably the most studied spatial features have been size, shape, proximity, connectivity, buffer zones and fragmentation levels (Williams *et al.* 2005). These are often tested independently through mathematical modelling. The best geometrical configuration is tested in order to optimize the representation of biodiversity elements, or their persistence when facing a threat (e.g., fire events) (Possingham *et al.* 2000; McDonnell *et al.* 2002; Williams 2008; Jafari & Hearne 2013).These optimization tests have resulted in design guidelines and have informed policy, such as the World Conservation Strategy (IUCN 1980). However, while design guidelines have been incorporated into conservation strategies and acknowledged by decision makers, it is unknown to what extent existing PAs have followed such guidelines. In addition, given that the individual effect of PA spatial attributes has been well described, it seems logical to expect combined and interactive effects of PA spatial attributes on their effectiveness, which surprisingly have also been overlooked. Assessment of the actual design of existing PAs and of spatial attribute interactions can certainly inform and improve conservation actions regarding best PA responses to external pressures.

Anthropogenic threats are another key factor affecting PA effectiveness (Woodroffe & Ginsberg 1998). The impacts of threats are often evaluated using a 'before and after' approach, in which the condition of a protected feature that is apparently affected by a threat is assessed through time (Butchart *et al.* 2010; Pimm *et al.* 2014). According to where the threat originates, these can be differentiated into direct and indirect threats. Direct threats are those that arise within PA boundaries, while indirect threats refer to pressures from outside but which harm conservation values within, i.e. edge-effects (Lockwood 2006). Habitat degradation through human land use expansion is considered one of the major threats to PAs (Lindenmayer & Possingham 2013; Mascia *et al*. 2014).

Anthropogenic land use such as agriculture, deforestation and urbanization can have a direct impact when occurring (legal or illegally) within PAs mainly by overexploiting and deteriorating the internal habitat. Indirect effects can occur when intensive land use surrounds PAs thus increasing their isolation and exposure to edge-effects (Woodroffe & Ginsberg 1998; Hansen & DeFries 2007). In particular, extractive activities are increasingly imposing political pressures to acquire legal exploitation rights within PAs, also described as 'Protected area downgrading, downsizing and degazettement (PADDD)' (Mascia & Pailler 2011). While the impact on PAs from extractive activities, such as agriculture and deforestation have been well described (Andam *et al*. 2010; Dobrovolski *et al*. 2011; Tang *et al*. 2011; Laurence *et al*. 2012), other extractive activities remain to be assessed.

A useful way to minimize potential threats to PAs is using spatial conservation prioritization (SCP) techniques to inform decision-making (Margules & Pressey 2000; Moilanen 2009). By using quantitative approaches, SCP optimizes the representation of conservation elements in the landscape taking into account economically productive areas (e.g. agriculture, industry) (Moilanen 2009). This results in the effective and efficient selection of PAs, where conflict with non-compatible alternative land uses has been minimized. Several approaches and software packages have been developed for SCP in the last decade, allowing important progress in the alleviation of conservation trade-offs (Moilanen *et al.* 2011; Thomas *et al.* 2013). However, like other progress in conservation biology so far, these developments have been targeted mostly at biodiversity rather than ES. Given the continuous reduction in land and resources for conservation, the simultaneous consideration of biodiversity and ES within one strategy is becoming a priority (Mace *et al.* 2012; Thomas *et al.* 2013) that can be addressed by SCP techniques.

This thesis aims to address the identified gaps concerning the main factors that drive the ability of PAs to protect both biodiversity and ES. Each chapter is a standalone paper written during my PhD study, five of which have been submitted to peer reviewed journals. Here, the order of the chapters was determined according to the chronological steps in which a PA is established, often the same sequence in which the driving factors influence PAs. Thus, the chapters variously focus, in the following order, on PA distribution, spatial design, threats, SCP techniques, and, aspects of PA management are mentioned within each. Given each chapter uses spatial statistics as the main methodological approach, the analyses carried out in this thesis relied on the best available spatial dataset, therefore variably focusing on biodiversity, ES or both, and the scale of analysis.

The second chapter uses Chile as a case study to assess how the spatial distribution of terrestrial PAs can affect the representation of different ES and biodiversity. Chile is currently expanding its PA system and it is unknown the extent to which existing and suggested new PAs represent ES. Therefore, this study is an important contribution to the improvement of the Chilean protected area system, and based on the main findings recommendations are made.

The third and fourth chapters address the gaps in PA spatial design. The third evaluates for the first time the spatial design of existing PAs and how well they follow historical design recommendations in regard to size, shape, proximity, buffer zone and fragmentation levels, and the consequences for conservation. Using an unprecedented data set of biodiversity representation in the New World PA system, the fourth chapter explores the combined and interactive effects of PA spatial features on species richness representation.

The fifth chapter assesses the potential impact of metal mining activities on the global PA system. This is the first study assessing the extent to which metal mining activities represent a real threat to existing PAs on a global scale.

The sixth chapter explores the consequences for biodiversity and ES representation of incorporating agricultural lands as a trade-off in SCP analyses. It discusses the effects that trade-offs in SCP can have on representation, and how they can predetermine the spectrum of management approaches to be applied to priority areas.

Based on the individual discussions in each of the five chapters, the general discussion of this thesis focuses on a new perspective on PA effectiveness. Specifically, it argues for the distribution, spatial design, management and threats to be considered as the core factors comprising and driving PA effectiveness. I encourage the conservation community to shift attention to the interactive effects of these core factors, rather than their individual effects.

CHAPTER 2

The first step in establishing a protected area is to decide its geographical location, which will directly determine the representation of conservation features. Understanding the extent to which existing protected areas represent such features is essential in order strategically to expand a protected system and to allocate conservation resources most effectively. While several studies have evaluated the representativeness of existing protected areas, most have focused on biodiversity elements rather than ecosystem services, which are currently regarded as key features to promote. Chapter 1 tests how the distribution of protected areas affects their ability to represent ecosystem services.

Chapter 2:

Durán AP, Casalegno S, Marquet PA, Gaston KJ (2013) Representation of ecosystem services by terrestrial protected areas: Chile as a case of study. *PLoS One*, 8(12):e82643.

doi:10.1371/journal.pone.0082643

Author contributions:

Conceived and designed the experiments: APD, SC.

Analysed the data: APD, SC.

Wrote the paper: APD, PAM, KJG.

REPRESENTATION OF ECOSYSTEM SERVICES BY TERRESTRIAL PROTECTED AREAS: CHILE AS A CASE STUDY

ABSTRACT

Protected areas are increasingly considered to play a key role in the global maintenance of ecosystem processes and the ecosystem services they provide. It is thus vital to assess the extent to which existing protected area systems represent those services. Here, for the first time, we document the effectiveness of the current Chilean protected area system and its planned extensions in representing both ecosystem services (plant productivity, carbon storage and agricultural production) and biodiversity. Additionally, we evaluate the effectiveness of protected areas based on their respective management objectives. Our results show that existing protected areas in Chile do not contain an unusually high proportion of carbon storage (14.9%), agricultural production (0.2%) or biodiversity (11.8%), and also represent a low level of plant productivity (Normalized Difference Vegetation Index of 0.38). Proposed additional priority sites enhance the representation of ecosystem services and biodiversity, but not sufficiently to attain levels of representation higher than would be expected for their area of coverage. Moreover, when the species groups were assessed separately, amphibians was the only one well represented. Suggested priority sites for biodiversity conservation, without formal protection yet, was the only protected area category that over-represents carbon storage, agricultural production and biodiversity. The low representation of ecosystem services and species' distribution ranges by the current protected area system is because these protected areas are heavily biased toward southern Chile, and contain large extents of ice and bare rock. The designation and management of proposed priority sites needs to be addressed in order to increase the representation of ecosystem services within the Chilean protected area system.

INTRODUCTION

Ecosystem services, the benefits that humans derive from ecosystems, are vital for sustaining human well-being (Daily 1997; De Groot *et al.* 2002; MA 2005). However, these services are also increasingly threatened by human activities (MA 2005). It is thus critical to evaluate to what extent current conservation strategies capture ecosystem services, and therefore might ensure their provision in the future (Pimm 2001; Daily & Matson 2008). Due to their vast terrestrial coverage and historical success in conserving natural ecosystems, protected areas are increasingly considered to play a key role in the maintenance of the ecosystem processes that promote ecosystem service provision (MA 2005; Turner & Daily 2008; Perrings *et al.* 2010). However, most existing protected areas have not been designated, established or managed to meet this specific objective, and might reasonably be expected in some instances to be inappropriate for doing so (e.g. agricultural and timber production). Indeed, whilst the representation of biodiversity within protected areas has been widely assessed (Bruner *et al.* 2001; Brooks *et al.* 2004; Rodrigues *et al.* 2004; Chape *et al.* 2005; Cantú-Salazar & Gaston 2010; Klorvuttimontara *et al.* 2011), only a few studies have evaluated to what extent these are capturing ecosystem services (Naidoo *et al.* 2008; Eigenbrod *et al.* 2010a; Tang *et al.* 2011). Moreover, those studies that have been conducted have tended to focus on the representation of a single ecosystem service (Tang *et al.* 2011), or have been carried out at a rather coarse spatial resolution (Naidoo *et al.* 2008). Assessments considering multiple services at a finer resolution are limited to developed countries (i.e. highly human-dominated regions) (Eigenbrod *et al.* 2009). A broader range of studies are required to help understand the nature of the gaps in ecosystem service conservation and where they occur, and thus to aid systematic planning to designate and establish future protected areas to redress these gaps.

The provision of key ecosystem services can present trade-offs (e.g. carbon storage vs agricultural production) making their conservation within the same areas challenging (Anderson *et al.* 2009; Eigenbrod *et al.* 2010b). Ecosystem services that involve active management practices can influence the potential for "disservices", often harming biodiversity and reducing the production of other services. For example, agriculture is a highly valuable provisioning service (MA 2005), providing food, forage, fibre, bioenergy and pharmaceuticals, but due to the often intensive form of associated land management, it is commonly considered a negative pressure on biological conservation (Power 2010; Mascia & Pailler 2011). How well protected area systems represent ecosystem services will depend, therefore, on what services are considered valuable to include or exclude, and this threshold is generally determined by the socioeconomic conditions and climatic region in which the protected area system is located. For instance, in a highly human-dominated region, where a higher proportion of land has been converted and species assemblages may have long been shaped by human activities, agriculture might be promoted, or at least tolerated, as an ecosystem service within protected areas (Eigenbrod *et al.* 2009). In contrast, in a less developed region with relatively pristine ecosystems, this activity might be excluded from protected areas (Soares-Filho *et al.* 2010).

There is a particular paucity of data for appropriate evaluation of protected area effectiveness in capturing ecosystem services in poor and developing countries (Tallis *et al.* 2008). These are often also countries that are particularly rich in natural resources (renewable and non-renewable) and whose economies depend on their extraction, which makes the establishment of protected areas, strict management objectives and the assessment of their performance particularly challenging. Chile provides one such example (Pauchard & Villarroel 2002; Asmüessen & Simonetti 2007). Its economy depends strongly on extractive activities such as wood pulp production, agricultural production and mining, and the establishment and performance of strict environmental management strategies has been poor (Asmüessen & Simonetti 2007; Armesto *et al.* 2010). Indeed, the Chilean National System of Protected Areas (SNASPE) is known to be inefficient in providing adequate coverage of the country's biodiversity (Armesto *et al.* 1998; Tognelli *et al.* 2008; Tognelli *et al.* 2009; Squeo *et al.* 2012) and is underfunded, receiving only 0.03% of the national budget [CONAF 2005, unpublished data]. In response, the Chilean Ministry of Environment has made an urgent call to assess and improve the current protected area system (CONAMA-PNUD 2006) and to increase the protection of the country's non-transformed ecosystems. Thus, in collaboration with the Global Environment Facility (GEF) and the United Nations Development Program (UNDP), the Ministry of Environment aims to create an integrated public and private protected area system in order to increase protected area coverage and share responsibilities and costs among the different governmental and private bodies (CONAMA-PNUD 2006). Private protected areas and priority sites for biodiversity conservation have been identified and suggested to be incorporated into a new integrated protected area system, however the extent to which these locations are valuable for ecosystem service provision is unknown.

This study analyses for the first time to what extent the current and suggested integrated protected area system represent selected ecosystem services of Chile. Specifically, the representation of three ecosystem services - plant productivity, carbon storage, agricultural production - and biodiversity is assessed under three protection scenarios. These scenarios capture the current status and medium-term projections for the protected area system. Given the large extent of pristine forest ecosystem remaining, we would expect that Chilean protected areas tend to represent high levels of net primary production, carbon storage, and biodiversity, but tend to exclude agricultural production. We address three main questions: 1) How are the three ecosystem services and biodiversity distributed across Chile?; 2) To what extent do the three protection scenarios represent the chosen ecosystem services and biodiversity?; and 3) How effective are Chilean protected area categories in representing ecosystem services and biodiversity?

DATA AND METHODS

PROTECTED AREA SYSTEM COVERAGE

In order to assess the effectiveness of the current Chilean protection system we considered all areas with statutory protection. These are the protected areas belonging to SNASPE, which comprises 33 national parks, 49 national reserves, and 16 natural monuments. We also included nature sanctuaries (n= 31), and lands protected by the Chilean Ministry of National Heritage (n=18) (Table A2.1). SNASPE makes up the majority of traditional public protected areas in Chile and is administered by the National Forestry Corporation (CONAF) created by the Chilean government in 1984. Nature sanctuaries include both public and private lands that obtained statutory protection under the Chilean National Environmental Law in 1994 and law No. 17 288 relating to National Monuments in 1970. Those lands administered by the Ministry of National Heritage are public protected areas managed exclusively for conservation and established by decree in 1977. To assess the potential effectiveness of the new suggested sites we considered protected priority sites for biodiversity conservation (PSBC) identified by the National Environmental Commission (CONAMA) in 2011 (n=68), and private protected areas (n=295). PSBC identified by the Chilean Ministry of Environment are part of the country´s National Biodiversity Strategy [CONAMA 2003, unpublished data], which aims to improve the representation of biodiversity within the Chilean protected area system. Private protected areas were also defined by the National Environmental Law (Article 35), and these are portions of private land which the owners have voluntarily set aside for conservation objectives. Both PSBC and private protected areas have not received statutory protection yet, but they are suggested as protected areas to be incorporated into the current protected area system and thus create the new *integrated protected area system*. Current protected areas, PSBC and private protected areas datasets were obtained from the Chilean Ministry of Environment in vector format. Current protected areas datasets are freely available at the Chilean Ministry of Environment web site (ide.mma.gob.cl). Considering the entire set used in this study (n=510), the average size of protected areas was 40,218 ha, varying from a minimum of 0.64 ha to a maximum of 3,677,849 ha. All of the seven protected area groups, except PSBC and private protected areas, are listed under an IUCN category (IUCN 1994). These management categories differ in the level of human activity allowed, from strict protection where no extractive activity is allowed (IUCN Ia-III) to a more permissive approach where human habitation and sustainable extractive use are accepted (IUCN IV-VI) (see Table A2.1 for details).

Following a similar approach to that of Pliscoff and Fuentes-Castillo (2011), we created three protection scenarios in order to evaluate the effectiveness of the existing protection system and the potential contribution of

PSBC and private protected areas to the new integrated protected area system. The three scenarios were (Fig. 1):

- Scenario 1 (current protection system, Fig. 1-A): SNASPE + National Sanctuary + Ministry of Heritage lands.

- Scenario 2 (Fig. 1-B): Scenario 1 + Priority sites for biodiversity conservation (PSBC).

- Scenario 3 (Fig. 1-C): Scenario 2 + Private protected areas.

DISTRIBUTION OF ECOSYSTEM SERVICES

CARBON STORAGE

We calculated carbon storage by combining an estimate of above and below ground vegetation biomass and a soil organic carbon (SOC) dataset (in kg C). Aboveground vegetation data were obtained following the IPCC GPG Tier-1 method for estimating vegetation carbon stocks using the global default values provided for above ground biomass (Aalde *et al.* 2006). Below ground vegetative biomass (root) carbon stock was added using the root-to-shoot ratios for each vegetation type (i.e. shrubland, forest, grassland, steppe) obtained from the same IPCC (Aalde *et al.* 2006) document, and then total living vegetation biomass was converted to carbon stock using the carbon fraction for each vegetation type. All estimates and conversions were specific to each of the nine ecofloristic zones (FAO 2000) in Chile, and vegetation type obtained from the Chilean land use cover at 1.56 km^2 resolution (CONAMA). Thus, a total of 246 carbon zones with unique carbon stock values were compiled based on the IPCC Tier-1 methods.

Soil carbon density data were obtained from the most recent soil carbon database, the Harmonized World Soil Database (HWSD) version 1.1 (FAO/IIASA/ISRIC/ISSCAS/JRC 2012), at 1 x 1 km resolution.

We used these datasets to create a final carbon storage estimation at 1.25 x 1.25 km resolution.

PLANT PRODUCTIVITY

Plant productivity (PP) patterns were determined using the Normalized Difference Vegetation Index (NDVI), which has been widely used for this purpose (Paruelo *et al.* 1997; Running *et al.* 2000; Turner *et al.* 2003; Tang *et al.* 2011; Pettorelli *et al.* 2012). NDVI is a linear estimator of the fraction of photosynthetically active radiation intercepted by vegetation (fAPAR) (Di Bellat *et al.* 2004; Garbulsky & Paruelo 2004; Roldan *et al.* 2010), which is the main control of carbon gain (Monteith, 1981) and hence a good estimator of PP. NDVI is derived from the red:near-infrared reflectance ratio [NDVI=(NIR-RED)/(NIR+RED), where NIR and RED are the amount of near-infrared and red light, respectively, reflected by the vegetation and captured by the sensor of the satellite]. The formula is based on the fact that chlorophyll absorbs RED (fAPAR as mentioned above), whereas the mesophyll leaf structure scatters NIR. NDVI values range from -1 to +1, where negative values correspond to an absence of vegetation (e.g. water bodies) and values closer to +1 correspond to abundant and dense vegetation (e.g. evergreen forest).

Monthly NDVI composites were obtained from the 1km^2 resolution Global MODIS (TERRA) (Moderate Resolution Imaging Spectroradiometer - LPDAAC, NASA) dataset, available for 2000-2010. For each pixel we calculated the average of the annual NDVI mean for the 10 year period.

AGRICULTURAL PRODUCTION

Agricultural production was calculated as the sum of gross production (USA dollar) for 2000. In order to generate a fine resolution layer, a spatial disaggregation process was carried out, in which a coarse resolution dataset is 'disaggregated' in a finer and related resolution dataset. Specifically, the agricultural production layer was calculated as follows (i) We multiplied the harvested area of 32 major crops (i.e. proportion of a grid cell that has been harvested for a specific type of crop) at 10 km x 10 km resolution (Monfreda *et al.* 2008) by crop land cover at 1 km x 1 km resolution (i.e. spatial distribution of agricultural lands) (European Commission Joint Research Centre 2003). Thus, through the disaggregation process, we obtained a second 1 km resolution layer showing the area per pixel (i.e. ha) that was harvested for each major crop; (ii) The resultant layers for each major crop were then multiplied by their respective yields (tonnes/ha) (Ramankutty *et al.* 2008), obtaining tonnes of crops produced per pixel; and (iii) Finally, tonnes per pixel of each major crop were then multiplied by prices (USD/tonnes) for 2000 (FAOStat, http://faostat3.fao.org/home/index.html; Table A2.2), thus obtaining USD of agricultural production per pixel.

DISTRIBUTION OF BIODIVERSITY

The Chilean biodiversity dataset comprised four taxonomic groups: mammals (n= 113), birds (n= 364), amphibians (n= 58) and vascular plants (n=1,061). Distribution maps for mammals, birds and amphibians that occur in Chile were obtained from the IUCN Global Mammal Assessment, BirdLife International and the Global Amphibian Assessment, respectively. All these are freely available at the IUCN Red List web site (IUCN 2012), and released as polygon vector files. The dataset for plant distributions was obtained from work carried out by the Ministry of the Environment (Marquet *et al.* 2011). Plant distributions were generated using the Maximum Entropy Model (MaxEnt), which was based on a dataset comprising georeferenced records from the largest plant collection in Chile (Museum of Concepción) complemented with records derived from available literature. Only species with more than 10 records entered into the analysis. MaxEnt models were developed using the meteorological database for Chile (1961-1990) developed by the Department of Geophysics of the University of Chile (DFG-CONAMA 2006). Plant species distributions were modelled using the variables temperature (max., min. and average), precipitation (max., min. and total), altitude, slope and aspect. The area under the curve (AUC), a criterion used to assess fit in distribution models such as MaxEnt (see (Elith *et al.* 2006), was on average 0.978.

Each taxonomic group was analysed separately, using a 1 km x 1 km grid resolution.

DATA ANALYSES

QUANTIFICATION OF ECOSYSTEM SERVICES AND BIODIVERSITY WITHIN PROTECTED AREAS

A spatial overlap analysis was used to calculate the representation of each ecosystem service and of biodiversity within the Chilean protected area system. The three protection scenario covers were overlapped with each ecosystem service and biodiversity layer, and the spatially coincident coverage extracted. However, as ecosystem service layers and biodiversity were mapped in different units, their representation was calculated in distinct ways as follows:

(i) The units of carbon storage and agricultural production layers are the total amount of carbon (kg) and USD production, respectively, per pixel. Thus, the representation of these two ecosystem services was calculated as the sum of all those pixels that fell within protected areas.

(ii) The PP captured was estimated from the average of the NDVI values of those pixels that fell within protected areas. As NDVI varies according to vegetation type, we calculated a weighted average in accordance with the proportion of total area of each vegetation type found within the protected area system. Thus, the resulting NDVI average is representative of the extents of different vegetation types within the protected area system. Vegetation types found within protected areas were Forest, Shrubland, Steppe, Wetland, Crop, Peatland and Bare areas (Table A2.5). For comparison purposes, a weighted NDVI average was also calculated for the entire country (Table A2.3).

(iii) The representation of biodiversity was calculated as the summed proportion of species' ranges that fell within the protected area coverage. This was calculated per taxon and for all species together.

ASSESSING EFFECTIVENESS OF PROTECTION SCENARIOS AND PROTECTED AREA CATEGORIES

We divided the percentage of each of the measures of ecosystem services and biodiversity contained within each scenario and protected area category by the percentage land area covered by that particular scenario and category (Eigenbrod *et al.* 2009). This approach will indicate whether the amount of a given ecosystem service or biodiversity is more or less than would be expected for the protected coverage area. A value greater than one thus indicates that a particular scenario or category contains a disproportionately large amount of a specific ecosystem service or biodiversity group relative to the area that it covers. Our measure of biodiversity within each of the three protection scenario and seven management categories was the summed proportion of the ranges of all species. NDVI is an index and it is thus meaningless to use the same approach, so we calculated a weighted average of NDVI values that fall within each of the seven protected area categories in the same way as indicated above (as an example see Table A2.3).

RESULTS

The bulk of carbon storage, net primary production and agricultural production were located in the south-central zone of Chile (Fig. 2). Areas with the highest density of stored carbon were located between 36° - 41° S, mainly concentrated in the eastern forest (Fig. 2B). Areas with the highest values of NDVI were located between 35° - 43° S, particularly in the southern-central coastal range (Fig. 2A). Croplands were grouped in the central valley of Chile between 32° - 41° S, and the highest production crops were in the region of Bernardo O'Higgins (32° - 34° S) (Fig. 2C). The latitudinal region with the highest species richness was between 31° - 40° S (Fig. 2D, Fig. A2.1).

The proportion of stored carbon varied from a low of 14.9% in Scenario 1, which increased to 19.0% and 19.9% in Scenario 2 and Scenario 3, respectively (Table 1). In the three scenarios carbon was underrepresented as would be expected for their coverage area (i.e. ratio less than 1, Table 1). An NDVI value of 0.38 was represented within the current protected area system (Scenario 1), 0.04 units higher than the whole country average (Table A2.3). This increased to 0.39 in Scenario 3 when private protected areas were added to the total coverage (Table 1). Only 0.2% of the total agricultural production was captured within the current protected area system (Table 1). However, this representation increased to 2.2% in Scenario 2 and 2.7% with Scenario 3

(Table 1). Again, none of the three representations was as much as would be expected for the area covered by the scenarios (Table 1).

The current protected areas capture 13.9%, 18.2%, 20.7% and 8.9% of mammal, bird, amphibian and plant ranges respectively. Amphibians was the only group well represented, with a ratio slightly higher than one (1.03). All species' representation levels increased substantially in Scenario 2 (i.e. when PSBC sites were included), capturing this time 18.9%, 23.0%, 27.1% and 14.7% of mammal, bird, amphibian and plant species' ranges respectively. In Scenario 2 only amphibian representation ratio was above one (1.07). When Private Protected Areas were included in Scenario 3, representation levels increased by approximately 1% for all species groups, with only that of amphibians' being well represented (Table 1). When species groups were assessed all together, its level of representation was 11.8%, 17.3% and 18.0% in scenario 1, 2 and 3 respectively. In all scenarios biodiversity was underrepresented (Table 1).

Carbon storage was well represented only by PSBC (4.08 times as much as would be expected for the area). The other protected area categories, except private protected areas, had values slightly below 1 (Table 2). All protected area categories together under-represented carbon stock with a value below 1 (Table 2). Private protected areas had the highest NDVI average value (0.54), followed by National Reserves (0.48), Nature Sanctuaries (0.47), and Ministry of Heritage lands (0.45). PSBC, National Parks and Natural Monuments had NDVI values below 0.4, Natural Monuments having the lowest average (Table 2). All categories had an NDVI value (0.39) slightly higher than the national average (0.38). Agricultural production was also well represented only by PSBC (2.09). This time the rest of the categories, including all categories together, had ratios below 1 (Table 2). Finally, biodiversity, the summed proportion of ranges of all species, was under-represented in all categories together, but was over-represented by Natural Monuments and PSBC categories (Table 2). When the species groups were assessed separately, amphibians were best represented by different protected area categories: Ministry of Heritage lands (2.36), National Parks (1.06), Nature Sanctuaries (2.92), and PSBC (5.46). Amphibians were the only group well represented by all categories together (Table A2.4). Mammals were well represented by Natural Monuments (1.36), Nature

Sanctuaries (1.22), and PSBC (4.05). Birds and plants were over-represented only by PSBC (4.16 and 4.69 respectively), this being the most successful category in the representation of biodiversity (Table A2.4).

DISCUSSION

Previous assessments of the effectiveness of the Chilean protected area system have focused exclusively on biodiversity (Arroyo 1997; Armesto *et al.* 1998; Luebert 1998; Turner & Daily 2008; Pliscoff & Fuentes-Castillo 2011). Here, we document for the first time the effectiveness of the system in capturing both ecosystem services and biodiversity relative to its area of coverage (Table 1). We found that existing protected areas in Chile do not contain an unusually high proportion of the total national carbon storage (14.9%), agricultural production (0.2%) or species' ranges (11.8%). Also, PP representation (0.38) was low with regard to the maximum value range (-1 to +1) and with respect to the national forest cover PP (0.63, Table A2.3). This was, however, slightly higher than the national average (0.34). When the levels of representation were assessed relative to the percentage of land area covered by existing protected areas, we found that amphibians was the only conservation feature overrepresented. The underrepresentation by existing protected areas seems to result from the strong spatial bias of current protected areas toward southern Chile (Fig. 1A), which raises three key points regarding the resulting representation of ecosystem services and because of their relatively small geographic ranges.

First, as forest coverage, as well as protected areas, is concentrated in southern Chile, we would have expected a higher representation of carbon storage (Table 1). The c. 15% of carbon storage represented reflects, therefore, that southern protected areas are mainly protecting lands devoid of vegetation, such as ice and rock (Table A2.5). This is also reflected in the level of PP represented within protected areas, which despite being slightly higher than the national average, is closer to zero than to one, indicating a predominance of poorly vegetated lands within the Chilean protected area system.

Second, the underrepresented crop production found within the existing protected areas suggests that these are displacing or avoiding areas of agricultural production, which could reasonably be argued as reflecting their effectiveness. Chilean protected areas conserve a significant proportion of untransformed landscape, facing the challenge of displacing human activities beyond their boundaries. What is not clear however is whether the low agricultural activity within protected areas is due to the management strategy of conserving these lands intact, or because the spatial bias of protected areas towards southern regions renders them unsuitable for agriculture.

Third, while the largest coverage by protected areas is concentrated in the Austral Chilean zone (44° - 56° S), our results show that the highest species richness areas are located in the central (28°- 36° S) and south-central (36°- 43° S) zones of Chile (Fig. A2.1, see (Samaniego & Marquet 2009)), which is reflected in the underrepresentation of biodiversity within the current protected area system. In fact, central and south-central zones include a hotspot of global biodiversity (Myers *et al.* 2000), which is characterized by a large number of endemic plants and vertebrate species (Arroyo 1997; Tognelli *et al.* 2008). However, amphibians is the only group overrepresented, likely because a relatively high proportion of their distribution ranges covers southern areas.

Adding PSBC and private protected areas to the current protected area system (i.e. Scenarios 2 and 3) enhances the representation of ecosystem services and total biodiversity (Table 1). This increase, however, was not sufficient to attain a representation higher than would be expected for their respective areas of coverage. (Table 1). Interestingly, PSBC increase the representation of both carbon storage and crop production, suggesting that current croplands are located in rich organic carbon soil areas, an important proportion of the total calculated carbon storage (see methods). Given that PSBC represent multiple ecosystem services and biodiversity, a multi-goal management strategy will be required in order to optimize the supply of carbon storage and biodiversity as much as agriculture. Thus, conservation planning exercises that include both biodiversity and ecosystem services (Chan *et al.* 2006) may be required to improve the Chilean PA network.

When protected areas were evaluated based on their management objective categories, our results showed that no existing protected area category with statutory protection represents the level of ecosystem services and biodiversity one would have expected based on their coverage, except the Natural Monument category that over-represented biodiversity (Table 2). This over-representation is likely related to the small coverage of the Natural Monument category, the smallest of all categories (Table A2.6). PSBC was the only category with no statutory protection that over-represented carbon storage (4.08 times as much as would be expected for their area), agricultural production (2.09 times) and biodiversity (4.51 times) (Table 2). Despite the under-representation of existing protected area categories together, our results show that National Parks, the strictest protection category (IUCN, Ia), represent a carbon ratio close to one (0.75), and a very low representation value for agriculture (0.006), which is also reflected in the proportion of land use cover within this category (Table A2.6). This is consistent with the strict and single land use management aim of this category, which is apparently mainly promoting carbon storage. By contrast, Nature Sanctuary sites, the more permissive category (IUCN, VI), represent exactly the same ratio of carbon storage as National Parks, but also 20 times more crop production, indicating the multi-use landscape nature of this category (Table A2.6). Only Natural Monument and PSBC categories over-represent biodiversity, indicating that these protected area categories are well placed with regard to species' range distributions (Table 2), however around 20% of amphibian are gap species, not yet represented in protected areas (Marquet *et al.* 2011). When species groups were assessed separately, amphibians was the only one overrepresented by all protected area categories (1.06), although the bird representation ratio was very close to one (0.92) (Table A2.4).

The existing Chilean protected area network does not perform well in representing all biodiversity groups together, but achieves a good representation of amphibians. Also, its provision of ecosystem services is poor. It is highly likely that this gap would need to be addressed principally by the expansion of the coverage of the protected area system. In this regard we suggest two measures. First, a re-evaluation of the already suggested new sites for the integrated protected area system, as these do not significantly increase ecosystem service representation. Second, a systematic assessment plan of current conservation management objectives and strategies, in order to enhance ecosystem service supply by existing protected areas.

TABLES

Table 1 Provision of ecosystem services and biodiversity under three protection scenarios. A ratio of > 1 (in bold) indicates that an ecosystem service is over-represented compared with what would be expected for the area; values < 1 indicate under-representation. The percentage of the total ecosystem services and biodiversity (summed proportion of ranges) in each of the three scenarios is given. Scenario 1: current protection system; Scenario 2: scenario 1 + suggested priority sites for biodiversity conservation; Scenario 3: scenario 2 + suggested private protected areas.

	Scenario 1		Scenario 2		Scenario 3	
	% of total	ratio	% of total	ratio	% of total	ratio
PP[a]		0.38		0.38		0.39
Carbon	14.9	0.73	19.0	0.75	19.9	0.76
Agriculture	0.2	0.01	2.2	0.9	2.7	0.1
Biodiversity	11.8	0.59	17.3	0.68	18.0	0.69
Mammals	13.9	0.69	18.9	0.74	19.7	0.75
Birds	18.2	0.91	23.0	0.91	24.0	0.92
Amphibians	20.7	**1.03**	27.1	**1.07**	27.8	**1.06**
Plants	8.9	0.44	14.7	0.58	15.4	0.59

Table 2 Provision of ecosystem services and biodiversity under seven protected area categories. A ratio of > 1 (in bold) indicates that an ecosystem service is over-represented compared with what would be expected for the area; values < 1 indicate under-representation. The percentage of the total amount of biodiversity (summed proportion of ranges) and other ecosystem services in Chile is given for each protected area category. PSBC: Priority sites for biodiversity conservation; PAs: protected areas; 'All PA categories' refers to the area covered by all seven categories.

Protected area categories	Carbon storage	PP*	Agriculture	Biodiversity
Natural Monument	0.88	0.17	0.06	**1.13**
National Parks	0.75	0.33	0.006	0.55
National Reserve	0.97	0.48	0.02	0.59
Nature Sanctuary	0.75	0.47	0.12	0.88
Ministry of Heritage lands	0.84	0.45	0.0003	0.67
PSBC	**4.08**	0.39	**2.09**	**4.51**
Private PAs	0.37	0.54	0.22	0.21
All PA categories	0.76	0.39	0.10	0.69

(*) Weighted average of NDVI values that fall within each of the seven protected area categories (see methods for details).

FIGURES

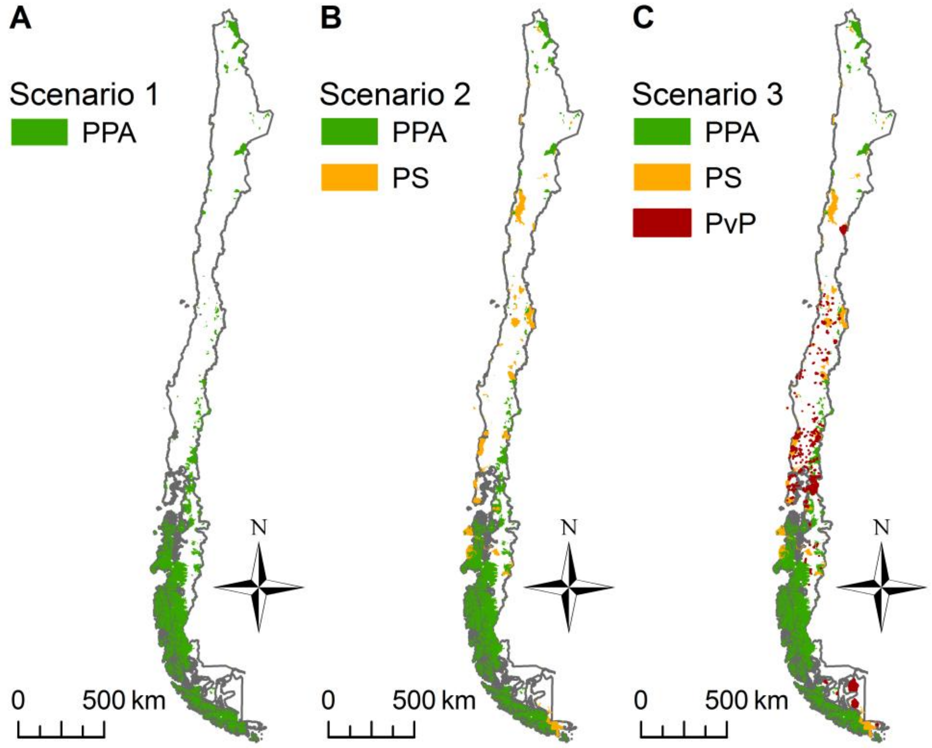

Figure 1: Distribution of three protection scenarios. The scenarios represent alternative conservation approaches. (A) Scenario 1, (B) Scenario 2, (C) Scenario 3. PPA: Public Protected Areas (current PA system in Chile); PS: Priority Sites for Biodiversity; PvP: Private Protected Areas.

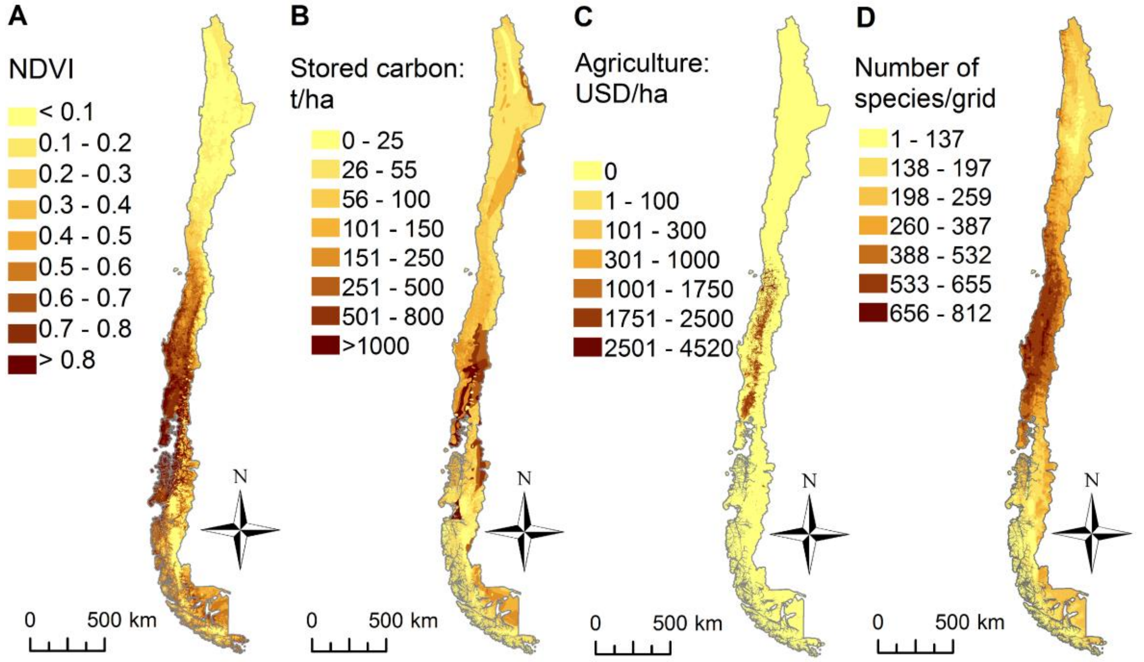

Figure 2: Ecosystem service and biodiversity distribution in Chile. Distribution of (A) net primary production, (B) carbon storage, (C) agricultural production and (D) biodiversity.

CHAPTER 3

Once the location of a protected area has been defined, an appropriate spatial design can be planned in order to maximize the representation and persistence of the features to be conserved. Design guidelines have been derived from a broad literature based principally on island biogeography and metapopulation theories. However, in practice, socio-economic pressures often place strong constraints on how a protected area should be appropriately designed. Therefore, the extent to which existing protected areas follow these design recommendations is largely unknown. Chapter 2, is the first study to evaluate the spatial design of terrestrial protected areas globally and discusses the implications for conservation.

Chapter 3:
Durán AP, Gaston KJ. Existing protected areas, historical design guidelines and the implications for conservation. *In prep*.

Author contributions:
Conceived and designed the experiments: APD, KJG.
Analysed the data: APD.
Wrote the paper: APD, KJG.

EXISTING PROTECTED AREAS, HISTORICAL DESIGN GUIDELINES AND THE IMPLICATIONS FOR CONSERVATION

ABSTRACT

Over the last 30 years the optimal spatial design of individual protected areas to maximize the representation and persistence of biodiversity has been widely discussed. As a result guidelines have been developed and incorporated in global conservation strategies. However, socio-economic factors are often key constraints, and how well existing protected areas follow these recommendations is poorly understood. Here we evaluate to what extent the global terrestrial protected area system follows spatial design guidelines for the size, shape, and fragmentation attributes of individual areas, and for the occurrence of buffer zones and proximity to other protected areas. The results show that some guidelines have been better met than others. Contrary to recommendations, protected areas tend to be small (<1 km^2), non-compact in shape, and highly fragmented. However, they do tend to be close to other protected areas and to have buffer zones (planned or otherwise) that increase the effective area available for species thus mitigating some of the inadequacies of other design features. Although there are clear opportunities, the weaknesses in the design of existing protected areas are in many cases challenging retrospectively to resolve, emphasizing the importance of paying greater attention to these issues when new protected areas are established.

INTRODUCTION

How best to design individual protected areas (PAs) in order to maximize the representation and persistence of biodiversity has been discussed for more than 30 years (Diamond 1975; Margules *et al.* 1982; Williams *et al.* 2005; Cerdeira *et al.* 2010). These recommendations have mainly been derived from the theory of island biogeography, in which a PA system is envisaged to resemble a set of islands of remnant habitat surrounded by a 'sea' of anthropogenically altered habitat. The local survival and extinction rates of species are then determined foremost by the quantities of natural habitat found within the PAs and their spatial distribution (Schwartz 1999). Whilst doubtless a marked simplification, the resultant recommendations are useful, in as much as many PAs have already effectively become discrete habitat islands (DeFries *et al.* 2005; Seiferling *et al.* 2012), and many more are likely to do so. Indeed, design guidelines are available for the spatial attributes of individual PAs, such as their size, shape and fragmentation, and for the occurrence of buffer zones and proximity to other protected areas (Williams *et al.* 2005). Several of these have attracted policy attention and were, for example, incorporated into the World Conservation Strategy (IUCN 1980). However, in practice, socio-economic pressures often place strong constraints on how PAs are actually designed (Knight *et al.* 2011), and the extent to which existing PAs follow these historical design recommendations is largely unknown. Here, using novel spatial approaches, we address this gap in understanding for the global protected area system.

Size has been the most debated spatial attribute of individual PAs (Diamond 1975; Soulé & Simberloff 1986; Fahrig 2001), in particular in the context of whether PA systems should consist of a few large PAs or several smaller ones (i.e., the single large or several small, SLOSS, debate) (Simberloff & Abele 1976). In terms of the number of species that a network can represent, empirical studies have suggested that dispersed, small PAs usually contain at least as many species as a single PA of equal area does (Soulé & Simberloff 1986). Nevertheless, given that a key goal, particularly as PAs become increasingly isolated and the challenges of managing sets of PAs as metapopulations become apparent, is to ensure the persistence of represented species, PAs should ideally be large enough to support minimum viable populations (MVP) of focal species (i.e. the minimum number of individuals needed to guarantee a high probability of population survival in the long term; (Shaffer 1981)).

In addition to size, the shape of a PA - whether it is compact or not - is also important for species representation and persistence (Kunin 1997). All else being equal, less compact PAs capture greater species richness because they sample more environmental variation (Williams *et al.* 2005; Heegaard *et al.* 2007). However, less compact PAs also have higher edge-to-area ratios, increasing the proportion of their extent that is exposed to anthropogenic pressures from outside their bounds, known as edge effects (Kunin 1997). Hence, in general, PAs are recommended to be designed to be more compact (Williams *et al.* 2005). As the proportion of area subject to edge effects declines with size, departure from this recommendation is more detrimental to small PAs than to larger ones (Heegaard *et al.* 2007).

However compact they are, PAs will suffer from edge effects. Buffer zones seem the most appropriate approach to counter these (Carvalheiro *et al.* 2011). Often established as areas immediately surrounding a PA in which extractive human activities are regulated, buffer zones particularly seek to mitigate the impact of adjacent land use activities. The most appropriate design of buffer zones will reflect what is being protected and the particular threats (Carvalheiro *et al.* 2011). For instance, a PA located near an urban area is likely to require a wider buffer zone than a PA already isolated from any immediate human activity. Although buffer zone design is species and threat specific (Schwartz 1999), the general guideline is that any buffer zone is better than none (Diamond 1975).

The proximity of PAs to each other affects species representation and persistence in opposing ways. While greater separation between PAs may result in higher net representation through capturing more spatial turnover in species occurrences (Margules *et al.* 1982), greater proximity facilitates the dispersal of individuals between PAs, and therefore, their existence as a metapopulation, and reduces the likelihood of the loss of genetic diversity due to inbreeding (Hanski 1998). Given the rapid expansion of anthropogenic land use worldwide, it is critical to maintain species dispersal within PA systems, and therefore ensuring the proximity of PAs is important (Williams *et al.* 2005). Fragmentation due to habitat loss is one of the major threats to the persistence of species populations (Fischer & Lindenmayer 2007). Habitat fragmentation increases patch isolation, exposure to edge effects, and the likelihood of stochastic population extinction (see (Fahrig 2003)). Unsurprisingly, habitat extent and loss are important criteria in the International Union for Conservation of Nature's (IUCN) determination of a species' risk of extinction (IUCN 2001). A low level of habitat fragmentation within individual PAs is therefore typically the optimum spatial attribute for species population persistence.

In this study we evaluate to what extent the global PA system follows the historical design guidelines for the size, shape, buffer zone, proximity and fragmentation attributes of individual PAs. Using geographic information system (GIS) tools we calculated, for all 166,109 PAs for which boundaries are available, their size, shape index and proximity to the closest PAs. In addition, we evaluate whether PAs effectively have buffer zones (whether planned or otherwise) by comparing the similarity of plant productivity within a PA's boundary and in the immediately adjacent 1 km band of land. We use the Normalized Difference Vegetation Index (NDVI) to estimate plant productivity as they are linearly related (Monteith 1981; Pettorelli *et al.* 2005). Assessing the level of variation of plant productivity within PAs we also infer their level of fragmentation. Finally, we also assess how the four continuous spatial attributes covary and what are the implications for biodiversity conservation.

MATERIAL AND METHODS

DATA

Analyses were based on the 2012 version of the World Database on Protected Areas. PAs were only included if records (i) were provided as polygon vectors (i.e. not points) thereby presenting actual spatial attributes (e.g. shape, proximity), (ii) had the *Status* of "Designated" or "Adopted"; and (iii) were terrestrial. Selected records were clipped to land coastline and duplicate records were deleted.

NDVI composites were used to measure buffer zone and fragmentation spatial attributes of PAs. NDVI is a linear estimator of the fraction of photosynthetically active radiation intercepted by vegetation (fAPAR), which is the main control of carbon gain (Monteith 1981) and hence a good estimator of plant productivity. NDVI maps have been widely used to characterize landscape properties (Turner *et al.* 2003; Paruelo *et al.* 2005; Pettorelli *et al.* 2005), and these were obtained from the 1 km^2 resolution Global MODIS (TERRA) (Moderate Resolution Imaging Spectroradiometer - LPDAAC, NASA) dataset. For each pixel we calculated the average of the annual NDVI for the 2008-2012 period. Negative NDVI pixel values (i.e. water bodies) were removed.

SPATIAL ATTRIBUTE MEASUREMENT

(i) The **size** of each PA was measured in ArcGIS 10 (ESRI 2004, www.esri.com) using the default function 'calculate geometry' from the attribute table. **(ii) Shape** was derived as the ratio of a PA's perimeter to the perimeter of a circle of the same area, also known as the circularity index (Rc). Rc indicates the extent of a shape's departure from a perfect circle, which is the most compact shape. While a perfect circle has an Rc equal to one, the Rc of a shape that departs markedly from circularity approaches zero. The advantage of Rc over alternative measures, is that it is unaffected by the shape's size. PA perimeter was also measured in ArcGIS 10 using the 'calculate geometry' function. **(iii)** The presence of a **buffer zone** was established by comparing the plant productivity inside (pp-PA) and within 1 km of the PA (pp-Buffer). Plant productivity was estimated as the average of the NDVI pixel values for each PA and of its associated surrounding zone. As the two variables, pp-Buffer and pp-PA, contain error, we carried out a Major Axis Regression (MAR). For the intercept and the slope of each regression, a 95% confidence interval was calculated. MAR analyses were conducted using 'lmodel2' (Legendre 2008) package in R (www.r-project.org). **(iv) Proximity** was measured as the shortest linear distance between two PAs. PAs were treated as independent units of protection for analytical purposes. Therefore PAs that are adjacent or completely or partially overlap have a proximity distance equal to zero. Proximity was calculated in the statistical software R (www.r-project.org) using the 'gDistance' function from the 'rgeos' package (Bivand 2012). **(v)**

Fragmentation effects on species survival can be assessed in terms of habitat degradation, habitat isolation, landscape connectivity and the sizes of patches, among others (Fischer & Lindenmayer 2007). We focused on land-cover type heterogeneity given we are typically working with small fixed spaces (i.e. PAs), where any increase in environmental heterogeneity caused by fragmentation must lead to a reduction in the average amount of effective area available for individual species (Allouche *et al.* 2012), which has significant negative effects on mean species abundance and positive effects on species extinction rate (Allouche *et al.* 2012). We estimated landscape heterogeneity using the variation in plant productivity within a PA, calculated using the coefficient of variation (CV) [CV = σ/μ; σ: standard deviation, μ: average] of the NDVI pixel values extracted for each PA. We carried out a comparison of CV values, the NDVI pixel map and the satellite imagery for several studies in which the fragmentation level within PAs was evaluated (see Table A3.1 and Fig. A3.1). The association found between CV and fragmentation level was classified as follows: CV [0 - 0.03] *low fragmentation*, CV [0.031 - 0.06] *medium fragmentation*, and CV [> 0.06] *high fragmentation*.

RESULTS

SIZE

A high percentage of the global system of PAs (hereafter 'global PAs') was small in size (Fig. 1A). 55.7% of them were smaller than 1 km^2, only 7.9 % larger than 100 km^2, and 2.1% exceeded 1,000 km^2 (Fig. 1A). Comparing regions, European, Oceanian, N. American and Australian systems had the highest percentage of small PAs (Fig. A3.2-A). For each of these regions at least 85% of the PAs were smaller than 50 km^2. In contrast, African, Asian and S. American systems had a higher percentage of large PAs, with c. 50% larger than 50 km^2 (Fig. A3.2-A). We compared global PA size against the areas required to maintain the estimated MVPs of samples of small, medium and large sized, herbivorous and carnivorous mammal species (Table A3.2); mammals are one of the most endangered taxonomic groups (Jenkins *et al.* 2013). These areas were calculated from species' ecological densities and a rule-of-thumb approach to the minimum number of individuals required to maintain a MVP (Reed *et al.* 2003). For small, medium and large herbivores, 25.1%, 11.6% and 2.0% of global PAs, respectively, were sufficiently large to maintain a viable population (Fig. 1A). For small, medium and large carnivores, 29.8%, 0.5% and 0.03% of global PAs, respectively, were sufficiently large to maintain a viable population (Fig. 1A).

SHAPE

The circularity ratio (Rc) calculated for each PA revealed that most are not compact in shape (Fig. 1B). 81.4% of PAs had a ratio below 0.6 (0 being the least compact), and only 2.9% of between 0.8 and 1 (1 being the most compact). When we evaluated PA shape by region, Australian and Oceanian systems had the highest percentage of non-compact PAs (Fig. A3.2-B), with c. 59% and 40% of their PAs, respectively, with Rc between 0 and 0.2. In contrast, African and Asian systems had the highest percentage of compact PAs (i.e. close to circularity), both regions having c. 8% of their PAs with an Rc between 0.8 and 1 (Fig. A3.2-B). About 50% of European, North American and South American PAs had an Rc between 0.2 and 0.6 (Fig. A3.2-B).

BUFFER ZONE

We considered a minimal condition for buffer zones effectively to be present was when plant productivity in a 1 km zone surrounding a PA (pp-Buffer) was similar to the productivity within the PA (pp-PA), acknowledging that this may not reflect the reduction or absence of all anthropogenic pressures (many of which are difficult to evaluate using remote imagery). In order to determine the level of similarity, we tested whether pp-PA and pp-Buffer were strongly correlated with a slope equal or close to one, for both the global and the regional PA systems (see methods, Fig. A3.3). This was the case for the global system (Table 1, Fig. A3.3), suggesting that a high proportion of PA have buffer zones. This was also the case for all the regional systems, except Europe, for which, although significant, the correlation was weaker and the slope departed from unity (Table 1, Fig. A3.3). Indeed, omitting the European data increased the strength of the correlation considerably (from r^2 = 0.44 to r^2 = 0.92). Differences between pp-Buffer and pp-PA were biased toward higher values of the former relative to the latter in the European, Oceanian and global systems, evidenced by a tendency for residuals about a slope of unity to be positive (Table 1, Fig. A3.4). However, if we once again omitted the European PAs from the global system, residuals were biased toward negative values (mean= -0.008, Fig. A3.4-I).

PROXIMITY

Globally, PAs tended to be close to one another (Fig. 1C). 47.0% of PAs were adjacent to or partially overlapped the boundaries of another PA (i.e. proximity zero), and approximately 15%, 24% and 12% of PAs were located respectively within a distance of 0-1 km, 1-10 km and 10-100 km of another PA (Fig. 1C). Only 0.7% of PAs were located more than 1,000 km from others. Europe was the system in which PAs were closest to one another, with 86.0% adjacent or closer than 1km to one another (Fig. A3.2-C). In contrast, the Asian system had the greatest distances between its PAs, with c. 40% adjacent or closer than 1 km, and c. 4% further than 100 km from another PA (Fig. A3.2-C). The rest of the regional systems had similar proximity distances, with c. 50% of their PAs adjacent or closer than 1 km to one another (Fig. A3.2-C).

We compared PA proximity against the dispersal abilities of small, medium and large sized, herbivorous and carnivorous mammal species (Table A3.3). In terms of distance, small, medium and large mammal herbivores would be able to move between 55.3%, 80.4% and 97.5% of PAs in the global system, respectively (Fig. 1C, Table A3.3). Small, medium and large mammal carnivores would be able to move between 49.3%, 99.1% and 89.3% of global PAs, respectively (Fig. 1C, Table A3.3).

FRAGMENTATION

To estimate their level of fragmentation, we calculated the coefficient of variation (CV) of the NDVI pixel values for each PA. By comparison of these estimates (Table A3.1) and remote sensing images for exemplar PAs (Fig. A3.1), we distinguished three coarse levels of fragmentation: *low* - CV [0 - 0.03], *medium* - CV [0.031 - 0.06], and *high* - CV [>0.06]. About 20%, 34% and 46% of global PAs had low, medium and high levels of fragmentation, respectively. Comparing regions, Oceanian (46.6%), Australian (28.4%) and European

(23.4%) systems had the highest percentage of PAs with low levels of fragmentation (Fig. A3.2-D). The African system had a high percentage of PAs (39.6%) with a medium level of fragmentation, while Asian (64.4%), and North (54.1%) and South American (56.9%) systems had the highest percentage of PAs with high fragmentation levels.

COVARIANCE OF SPATIAL ATTRIBUTES

Covariances between spatial attributes were calculated using Spearman's rank correlations. Size had weak negative correlations with shape (ρ= -0.05, $p<0.01$) and proximity (ρ= -0.04, $p<0.01$), but a stronger and positive correlation with fragmentation (ρ= 0.36, $p<0.01$) (Table 2, Fig. A3.5-A). Shape was positively correlated with proximity (ρ= 0.24, $p<0.01$) (Fig. A3.5-B) and negatively with fragmentation (ρ= -0.11, $p<0.01$) (Fig. A3.5-C), such that less compact PAs were more fragmented and more distant from one another. Proximity had a weak negative correlation with fragmentation (ρ= -0.04, $p<0.01$).

DISCUSSION

Our results demonstrate that the global protected area system only partially follows the widely recommended design guidelines for individual PAs. Contrary to these recommendations, a large proportion of PAs tend to be small, non-compact and have high levels of fragmentation. However, globally, PAs are close to each other and tend to have buffer zones. These various attributes influence the effectiveness of the global PA system in achieving the representation and persistence of biodiversity.

That approximately 56% of PAs are smaller than 1 km^2 suggests that many are too small to maintain MVPs of species, such as medium-sized and large mammals (Fig. 1A). While in this study we focused on mammals given their critical conservation status, mammals can be used in this context as ‘umbrella species’; it is likely that if a PA is large enough to maintain large carnivorous mammal species this area will also be able to maintain MVPs of other smaller species. In addition, given the key position that carnivorous mammals have in trophic cascades, a PA that is able to maintain them might also promote an appropriate ecological functioning, facilitating the persistence of the ecological community.

Our results suggest that a high proportion of PAs have medium to high levels of fragmentation, as reflected in their spatial patterns of plant productivity. In some cases this is doubtless a consequence of the natural structure of their landscapes (e.g. savanna, alpine). However, in the main it is likely to be detrimental. This is particularly so within small PAs as fragmentation further reduces the effective habitat available for species survival. Nevertheless, the close proximity between PAs and the positive correlation between PA size and fragmentation could mitigate any negative effects. Small but proximate PAs can provide adequate connectivity, working as a 'protected network'. In fact, the proximity distances between a high proportion of existing PAs seem suitable for the dispersion of species such as small, medium and large herbivorous and carnivorous mammals (Fig. 1C). Fragmentation is positively correlated with PA size and negatively correlated with shape, suggesting that higher landscape heterogeneity levels are present in large, less compact PAs. Although highly heterogeneous, a large PA would provide a greater effective area available for species.

PAs tend not to be compact in shape, which will increase the edge effects that are experienced (Fig. 1B). However, our results suggest that a high proportion of PAs have buffer zones (Table 1), in terms of similarity of vegetation productivity, which could ameliorate these edge effects. For global, European and Oceanian PA systems, those PAs that do not have buffer zones (i.e. depart markedly from a pp-Buffer versus pp-PA slope equal to 1) typically have higher plant productivity in the surrounding areas than within the PA. This could occur for a variety of reasons, including the biased establishment of protected areas in regions with low plant productivity (Hoekstra *et al.* 2005; Joppa & Pfaff 2009), the decrease of plant productivity within PAs given the well documented land cover transformation in recent decades (Mascia & Pailler 2011), and the increase of plant productivity in the surroundings caused by irrigation and fertilization or overgrazing induced woody encroachment (Bradford *et al.* 2005; Van Auken 2009; Tang *et al.* 2011). However, omitting the European data reverses this tendency (i.e. higher plant productivity within PAs than in their surroundings) (Fig. A3.3). This contrasting pattern is likely to reflect the disproportionate demand on resources and human population growth that can occur around PAs (Wittemyer *et al.* 2008; Seiferling *et al.* 2012; Mackenzie & Hartter 2013).

Reducing the design limitations of individual PAs once they have been established is challenging. In some cases it may be possible to increase their size, but this often cannot be done, and where it can it is costly and/or time consuming (requiring habitat restoration). Likewise, as PAs become progressively more like islands in seas of transformed landscapes, improving their shape so as to reduce edge effects becomes difficult, short of reducing their area to achieve this outcome. Where appropriate, and this will not always be the case, reducing the internal fragmentation of PAs may be more readily achievable through suitable management actions. Limitations in the size, shape and fragmentation of PAs will not always be helpfully addressed by the use of buffer zones and improving the connectivity between them, because these are the design goals that are already better attained. Of course, this is not uniformly the case, so there are undoubted opportunities in these regards, and these should often be taken when they arise. This can partly be achieved through the careful choice of placement of new protected areas, which will themselves be more effective in the maintenance of biodiversity if, unlike many of their forebears, they are better designed.

TABLES

Table 1 Parameters of reduced major axis regression assessing the relation between mean NDVI within PAs (pp-PA) and mean NDVI of their respective buffers (pp-Buffer).

Region	Correlation coefficient (r)	Intercept [95% C.I.]	Slope [95% C.I.]	Mean residual
Africa	0.956***	0.0105 [0.006, 0.015]	0.95 [0.945, 0.961]	-0.010
Asia	0.954***	-0.001 [-0.006, 0.004]	0.95 [0.948, 0.966]	-0.017
Australia	0.973***	0.0002 [-0.002, 0.003]	0.98 [0.979, 0.988]	-0.006
Europe	0.211***	0.236 [0.224, 0.246]	0.61 [0.592, 0.630]	0.008
North America	0.96***	0.012 [0.010, 0.014]	0.96 [0.958, 0.965]	-0.006
Oceania	0.913***	0.074 [0.065, 0.084]	0.89 [0.885, 0.910]	0.001
South America	0.915***	-0.004 [-0.016, 0.007]	0.96 [0.944, 0.979]	-0.021
Global	**0.66*** **	**0.047 [0.043, 0.050]**	**0.92 [0.918, 0.929]**	**0.003**

FIGURES

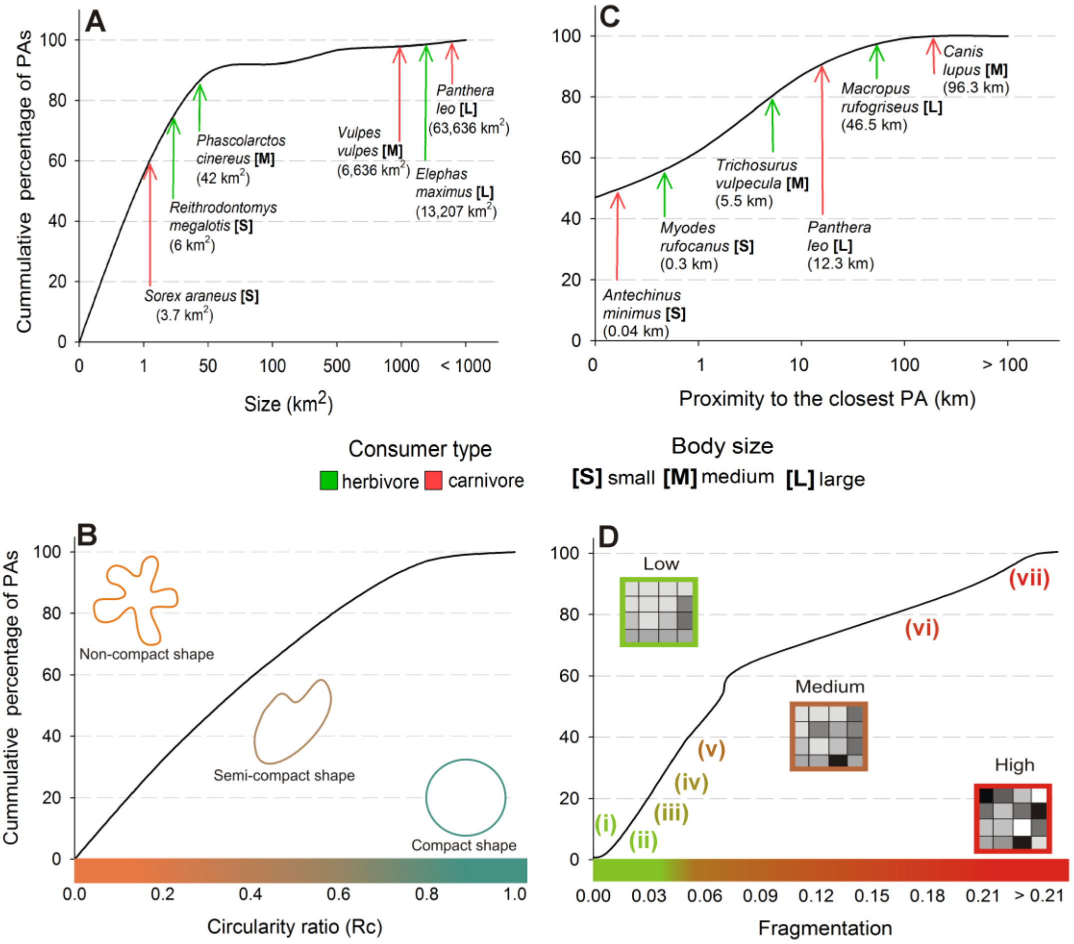

Figure 1: Cumulative percentage distribution of protected areas (PAs) for six spatial attributes: size, shape, proximity and fragmentation. **A)** Size of PAs with examples of areas required to maintain MVPs for four mammal species, **B)** Shape of PAs expressed by circularity ratio (Rc), **C)** Proximity among PAs with examples of dispersal ability for four mammal species, **D)** Fragmentation level within PAs estimated from coefficient of variation (CV) calculated from NDVI pixel values extracted for PAs. These results are compared against studies that evaluated and described the fragmentation level of the following PAs (Fig. A3.1; Table A3.1): (i) Monarch Butterfly Biosphere Reserve (Navarrete *et al.* 2011), (ii) Tinkal National Park (Nagendra 2008), (iii) Gunung Palung National Park (Curran *et al.* 2004), (iv) Tambopata National Reserve (Vuohelainen *et al.* 2012), (v) Blue Mountains National Park (Chai *et al.* 2009), (vi) Caroni Swamp Reserve Forest Reserve (Gibbes *et al.* 2009), and (vii) Xochimilco World Heritage Site (Merlín-Uribe *et al.* 2013). Examples species in **A)** and **C)** are small, medium and large sized, herbivorous and carnivorous mammals (Table A2.1 and A2.2).

CHAPTER 4

The spatial design of protected areas is a key factor affecting their ability to represent and maintain conservation features. However, given that protected area effectiveness is influenced by multiple spatial attributes, knowledge of their combined and interactive effects is essential to understanding the actual role of these attributes. While several studies have evaluated the effect of individual spatial attributes on protected area effectiveness, there is a lack of research considering their multiple and interactive effects. Chapter 3 makes use of the information generated in Chapter 2, determines these effects on biodiversity representation.

Chapter 4:

Durán AP, Inger R, Cantú-Salazar L, Gaston KJ. Biodiversity representation within protected areas is affected by multiple interacting spatial design features. *Conservation Letters*. Under review.

Author contributions:
Conceived and designed the experiments: APD, RI.
Analysed the data: APD, RI.
Wrote the paper: APD, RI, LCS, KJG.

BIODIVERSITY REPRESENTATION WITHIN PROTECTED AREAS IS ASSOCIATED WITH MULTIPLE INTERACTING SPATIAL DESIGN FEATURES

ABSTRACT

The spatial design of protected areas (e.g. size, shape, level of fragmentation) plays a key role in their ability to represent and maintain biodiversity. However, while several studies have evaluated the effects of individual design features, there is a lack of research considering their combined and interactive effects. Here, we assess the extent to which size, shape, fragmentation and proximity to the closest protected area, and their interactions, predict species richness representation. Overall, variation in spatial design explained about 40% of species representation, with the magnitude of the effect varying between spatial features and among taxonomic groups. Additionally, we show that the effect of one feature can be amplified or buffered by that of another. These findings have important implications for the design of existing and future protected areas, for how design is addressed according to target taxonomic group, and how conservation resources are targeted.

INTRODUCTION

The spatial design of terrestrial protected areas (PAs) can significantly influence how effective they are in representing and maintaining biodiversity (Williams *et al.* 2005; Lasky & Keitt 2013). Since the 1970s, several ecological theories dealing with the relation between biodiversity and the geographical and spatial distribution of species, such as island biogeography and metapopulation dynamics (Diamond 1975; Margules *et al.* 1982) have provided useful insights to plan and develop practical conservation strategies including spatial design features (e.g. considering the size, shape, fragmentation level of PAs and their proximity to other PAs). In fact, several of these recommendations have attracted policy attention and were, for example, incorporated into the World Conservation Strategy (IUCN 1980). The recommendations regarding the optimal design of PAs have been often based on studies evaluating the effect of specific and isolated spatial features, however, multiple spatial features are likely to interact and influence PA effectiveness simultaneously (Lemes *et al.* 2014). Some spatial features may influence biodiversity more strongly than others, and two or more features may interact in synergistic or antagonistic ways. For instance, the size of a PA may have a strong effect on biodiversity representation and persistence, a beneficial effect which could be buffered by high levels of fragmentation within the PA. Understanding the relative effects of different spatial features, and how they interact, can provide new insights into how to design PAs to best deliver their conservation goals, and also to ensure that conservation efforts are optimally deployed.

The size of a PA is a key feature influencing the quantity of biodiversity represented (Margules *et al.* 1982; Williams *et al.* 2005). Larger-sized PAs typically capture a greater range of environmental variation, and hence larger number of species. In addition, larger PAs are more likely to support 'viable' populations (i.e. the minimum number of individuals needed to guarantee the survival of a population in the long term; (Reed *et al.* 2003).

The shape of a PA – whether it is compact (e.g. perfect circle) or non-compact (e.g. 'starfish') – can influence the level of biodiversity to be represented in opposite ways. Less compact PAs (i.e. shapes that depart from circularity) increase representation because they sample more environmental variation (the linear distance between the two closest points within a geometric shape is always larger for less compact ones; (Yamaura *et al.* 2008), however, they negatively influence species survival by increasing the edge-to-area ratios, known to increase the extent of the area exposed to anthropogenic pressures (known as edge effects; (Kunin 1997; Hansen & DeFries 2007). In the long term, this will reduce the level of biodiversity represented within the PA boundaries, and therefore, PAs are generally recommended to have compact shapes (Kunin 1997).

High levels of fragmentation of a PA can strongly undermine the number of species found within its boundaries (Lasky & Keitt 2013). Fragmentation leads to a reduction in biodiversity representation as only more tolerant species can persist in a modified and degraded habitat, thus leading to a reduction of local biological diversity (Fahrig 2003). Also, it reduces species survival by increasing patch isolation, exposure to edge effects and the likelihood of stochastic extinction (Fahrig 2003). Hence low levels of habitat fragmentation within PAs are encouraged.

High proximity between PAs promotes species dispersal and recolonization of areas locally extinct, which increases species representation and survival within individual PAs (Kitzes & Merenlender 2013). Therefore, a distance between PAs that fosters the interaction between spatially separated populations has been recommended (Williams *et al.* 2005).

Most of the studies evaluating the effects of spatial features on PA effectiveness are based on theoretical approaches (e.g. mathematical optimization models) (Possingham *et al.* 2000; McDonnell *et al.* 2002; Williams 2008), or on empirical cases restricted to small geographical scales. While these studies have made significant progress on this topic, there is still a lack of research testing the theoretical predictions using empirical data that encompass a wider variety of biodiversity, across substantial areas of conservation potential. Such studies will facilitate a more comprehensive understanding of the actual role of design in existing PAs.

A lack of appropriate field data on actual levels of species representation within PAs is perhaps the greatest obstacle to testing theoretical predictions of spatial feature effects. This has led to many studies being based on the distribution ranges of species (Brooks *et al.* 2004; Rodrigues *et al.* 2004; Araújo *et al.* 2007; Cantú-Salazar & Gaston 2010). Although distribution range datasets are the most appropriate available to date, they overestimate species presence in PAs and can introduce significant biases into analyses (Hurlbert & Jetz 2007). Species distribution maps based on habitat suitability models increase the certainty of species presence. However, this has only been carried out for terrestrial mammals on a large scale (Rondinini *et al.* 2011), mainly because of limitations on data and computational processing capacity (Rondinini *et al.* 2011). Recently a new dataset has been published, which compiles species sampling inventories within more than 400 protected areas in the New World for amphibians, birds and mammals (Cantu-Salazar & Gaston 2013). Although not without their own problems (likely suffering more from omission than commission errors), these data provide an excellent opportunity to test the relative effect size of PA spatial features and some of their interactive effects based on empirical data.

In this study, we investigated the extent to which multiple PA spatial features and some of their interactions predict species representation. We calculated the size, shape index, fragmentation level and proximity of more than 400 PAs in the Western hemisphere. The representation levels, measured as species richness, were taken from Cantu-Salazar and Gaston (2013) dataset. The direction and strength with which spatial features predict the represented species richness within the PAs was then analysed. We discuss the implications of the findings on PA effectiveness, contributions for the appropriate design of future PAs, and potential mitigation actions for inadequate design of existing PAs.

METHODS

DATA

A species richness dataset for amphibians, birds and mammals of more than 400 PAs in the Western hemisphere was obtained from Cantu-Salazar and Gaston (2013). Their study compiled species numbers reported for PAs based on inventories (i.e. observed species richness), which are openly available from Internet sources. Searches were focused on management plans from national agencies, technical reports, environmental assessments, official PA websites, biodiversity databases and conservation agencies. The compiled inventory species checklist (> 115,600 records) was standardized with nomenclature according to the IUCN and Nature Serve databases and only native species were retained (see (Cantu-Salazar & Gaston 2013) for details).

Distribution of the PAs was obtained from the World Database on Protected Areas (UNEP 2012); http://www.wdpa.org). The final dataset included PA polygons of which 337 had associated amphibian species richness data, 456 had data for birds, 380 had data for mammals, and 405 had data for all three taxa (hereafter 'all taxa'). 'All taxa' data is made up only by those PAs with species richness records for all three taxa.

SPATIAL FEATURES

Using geographic information system (GIS) tools and remote sensing images for each PA polygon we measured four spatial design features: size, shape, fragmentation level and proximity to the closest PA. (i) The size of each PA was measured in ArcGIS 10 (ESRI 2004, www.esri.com) using the default function 'calculate geometry' from the attribute table. (ii) Shape was derived as the ratio of a PA’s perimeter to the perimeter of a circle of the same area, also known as the circularity index (Rc) (Bogaert *et al.* 2000). Rc indicates the extent of a shape’s departure from a perfect circle, which is the most compact shape. While a perfect circle has an Rc equal to one, the Rc of a shape that departs markedly from circularity approaches zero. (iii) Among many methods, fragmentation can be assessed in terms of habitat degradation, habitat isolation, landscape connectivity and the size of patches. In order to estimate fragmentation levels, we focused on land-cover type heterogeneity using variation in plant productivity. This was calculated using the coefficient of variation (CV) [CV = σ/μ; σ: standard deviation, μ: average] of the Normalized Difference Vegetation Index (NDVI) pixel values extracted for each PA. NDVI is a widely used estimator of plant productivity as they are linearly related (Monteith 1981). (iv) Proximity was measured as the shortest linear distance between two PAs. Given we are using a subset of PAs, we measured proximity of the PAs used in this study against the total number of existing PA polygons. Proximity was calculated in R v2.14.1 statistical language (R Development Core Team 2011) using the 'gDistance' function from the 'rgeos' package (Bivand & Rundel 2012). Finally, the latitude of each PA was extracted based on their centroid to account for the dominant positional influence of species richness (Gaston 2000).

STATISTICAL ANALYSIS

To assess the relative effect size of PA spatial features on species representation and how they interact, we utilised generalised linear mixed effect models with a Poisson error structure using the package 'lme4' (Bates & Maechler 2009) in the R statistical language. Different analyses were carried out for amphibians, birds, mammals separately and for a combination of all three (all taxa, see Data above). Species richness was used as the dependant variable in all models, with size, shape index, fragmentation level and proximity being incorporated as fixed factors, and latitude as a covariate. In all models we assessed the interactions between area*fragmentation, area*shape, fragmentation*shape and fragmentation*latitude (Table 1). Given that the subset of PAs is taken from many different countries, each of which will have spatial designs resulting from a different mix of drivers (e.g. socio-economics, topographic, geographic), we included 'country' as a random (intercept) factor to control for this variation. Also, in order to account for the habitat effect on species richness within PAs, we included as a second random factor the terrestrial 'ecoregion' (i.e. a biogeographic regionalization of the Earth's terrestrial biodiversity) with which each PA overlapped (see details in Appendix 4.1). In order to set the fixed effects on a common scale and make them comparable, we standardised all using the 'arm' package (Gelman *et al*. 2009).

We performed a multi-model inference approach in order to select and simplify the generated models. All subsets of models were produced based on the global model and ranked according to their AICc (package 'MuMIn', (Bartoń 2009). Following Richards (2008) we retained all models where Δ AIC <6 in order to chose with 95% of confidence the set of most parsimonious models. Using the function 'model.avg' from the MuMIn package, we averaged the sets of best-supported models producing the average parameter estimates and relative importance of each parameter. Conditional r^2 (variance explained by fixed + random effects) and marginal r^2 (variance explained only by the fixed effect) were calculated for the top model (i.e., ΔAIC= 0) using the methods described in Nakagawa and Schielzeth (2013).

RESULTS

The conditional r2 (variance explained by the whole model) of top models for amphibians, birds, mammals and all taxa were 0.80, 0.42, 0.35, 0.60, respectively. The marginal r2 (variance explained by the fixed effects) of global models for amphibians, birds, mammals and all taxa were 0.13, 0.25, 0.28 and 0.38, respectively. After considering only those models within Δ6 AICc units, there were 10 models for amphibians, 8 for birds, 5 for mammals and 4 for all taxa (Table 2).

The direction (i.e. how PA spatial features affect the species richness represented) and strength (i.e. relative size effect of the spatial features on represented species richness) of the predictors' effects from the average models are shown in Fig. 1. Bars above zero indicate a positive effect of a predictor, while bars below zero indicate a negative effect. The size of the bar indicates the magnitude of the effect. The direction of the predictors of the averaged models was the same across all the taxonomic groups, except for proximity, which was positive in amphibians and mammals and negative in the rest of taxa (Fig. 1).

PA size showed a positive effect, indicating that species representation is favoured by larger areas. In contrast, they showed negative effects for shape, fragmentation level and latitude (Fig. 1). This indicates that less compact shapes, low fragmentation levels and low latitude locations benefit species richness representation. However, the effect of shape was not significant on mammal representation, nor was the effect of proximity on amphibians, birds and mammals, although it was significant for all taxa combined (Fig. 1).

Only the interactions of area with fragmentation and fragmentation with latitude were significant for all groups, other than for mammals where the area by shape interaction was significant (Fig. 1). Fragmentation showed a negative interaction with area, but a positive interaction with latitude (Fig. 1). The negative interaction suggests that the positive effect of area in species richness representation is reduced with an increase in fragmentation. The positive interaction indicates that the rate of increase in species richness toward lower latitudes is reduced with fragmentation.

Unlike the direction, the relative strength of predictor effects greatly differs across taxa (Fig. 1). PA spatial features better explain variation in bird representation than variation in mammal and amphibian richness, in decreasing order (Fig. 1). The relative importance of predictors (i.e. proportion of time it appears in the top model) and 95% confidence interval of estimates are indicated in Table A4.1.

DISCUSSION

Our results represent the first evidence for the combined and interactive effects of PA spatial features and their impacts on the ability of PAs to represent biodiversity. These findings contribute to the fixing of existing design inadequacies and to optimizing the planning of future designs. While there has been considerable progress in understanding the importance of the spatial features of PAs and how these affects biodiversity representation, spatial features have mostly been tested independently. This has hampered a more comprehensive understanding of the actual role that PA design plays on their effectiveness, and subsequent conservation goals.

Our results show that size, shape, fragmentation, and proximity to the nearest PA explain about 40% of the variance observed in amphibian, bird and mammal species richness within PAs. The results empirically support findings on the direction of the effects from previous studies which assessed features independently or through mathematical models (Table 1). However, examining the relative effect sizes of these features revealed that the influence of each is not equal, and differs with different taxonomic groups (Fig. 1).

The spatial features (i.e. fixed effect- marginal r2) explained about 40% of the variance in species richness within PAs, and an additional 20% was explained by habitat and country, totalling 60% of the variance for the whole model (i.e. fixed + random effect - conditional r2). Given the empirical and large scale nature of the data used in this study, our results suggest that there are other local factors that explain the remaining 40% of the variance in species richness representation. These factors are likely related to the management within PAs (Leverington *et al.* 2010; Lawson *et al.* 2014), the internal threats (e.g. poaching, habitat transformation), and the anthropogenic pressures from the surrounding landscape (Hansen & DeFries 2007). All of these influence species survival and as a consequence their representation. Environmental variables also play an important role in predicting species richness, and these were indirectly incorporated into our model by considering latitude as a co-vary.

The variable strengths of the effects of the different spatial features indicate that some have a stronger influence on the number of species within PAs than others. Area and fragmentation were the features that better predicted biodiversity representation across the three taxa, with fragmentation strongly minimizing the positive effect of area (i.e. negative interaction between fragmentation and area) (Fig. 1). Given that the fragmentation measurement was based on land-cover heterogeneity, the observed negative interaction between area and fragmentation might result from a 'area-heterogeneity trade-off', in which any increase in environmental heterogeneity within a fixed space leads to a reduction in the average amount of effective area available for individual species, thereby affecting species survival (Allouche *et al.* 2012). This negative interaction suggests that conservation efforts applied to the design of PAs (e.g. making PAs bigger) may be ineffective if the type of management approach (i.e. extent of land use transformation allowed within PAs leading to fragmentation) is not taken into account.

The overall effects of the spatial features also differed between taxa, suggesting that amphibians, birds and mammals respond differently to PA design. Different responses might be explained by the inherent ecological attributes of each group. That bird representation is better predicted than mammals and that mammals is better predicted than amphibians (Fig. 1), suggests that the importance associated with PA design should reflect the taxa to be targeted for conservation. Also, when all taxonomic groups were considered PA design had the highest effect, suggesting that multiple and interactive effects of spatial features on all three groups should be taken into account. Mammals were the only group on which shape did not have a significant effect (Fig. 1). Large bodied mammals often have large home ranges

(Jetz *et al.* 2004; Ottaviani *et al.* 2006), which may encompasses or go beyond PA boundaries, thus eliminating the greater spatial turnover normally captured by non-compact shapes. Indeed the positive interaction between area and shape was only significant for mammals (Fig. 1), suggesting that non-compact shapes capture higher spatial turnover of mammal species only with large PAs.

Our findings have direct implications for conservation strategies and policy. First, understanding how PA spatial features affect representation in the real world provides opportunities to ameliorate the inadequacies in existing PA designs through mitigation measures, such as minimization (e.g. ecological corridors or buffer zones) or restoration (e.g. reforestation actions to restore connectivity between PAs). Second, identifying the variability of spatial design effects on different taxonomic groups will aid the design of future PAs for target species. Finally, that the positive effect of a spatial feature (i.e. size) can be buffered by another (i.e. fragmentation) highlights the importance of considering the interrelation between spatial features during PA planning in order to optimize conservation efforts and avoid wastage of resource.

TABLES

Table 1 Predictors that compose the global model which investigates the effects of PA spatial features on species representation.

Model Predictors	**Prediction**
Area	Larger areas are expected to cover higher β -diversity, and counting higher species richness.
Shape	Less compact shapes are expected to cover higher β -diversity and counting higher species richness.
Fragmentation	High habitat fragmentation within a fix area is expected to decrease species survival and only more tolerant species would persist, thus representing less species richness.
Proximity	Closer PAs are expected to allow higher rate of species dispersion and recolonization, and counting higher species richness.
Latitude [*covariate*]	Protected areas closer to low latitudes should predict higher species richness
Area * Fragmentation	The slope of the relationship between area and species richness changes depending on the level of fragmentation. A high level of fragmentation is excepted to buffer the positive effect of area on species representation.
Area*Shape	The slope of the relationship between area and species richness changes depending on the compactness of a PA shape. A less compact shape is expected to amplify the positive effect of area on species representation.
Fragmentation* Latitude	The slope of the relationship between fragmentation and species richness changes depending on the latitude. PAs toward low latitude are expected to predict lower species richness in presence of high fragmentation levels.
Fragmentation*Shape	The slope of the relationship between fragmentation and species richness changes depending on the compactness of PA shape. A high level of fragmentation is excepted to buffer the positive effect of shape on species representation.
(1|Country) [*random effect*]	National PA systems have different histories resulted from a mix of motivations for conservation and socio-economic factors. Thereby *Country* is considered a driver of the design of PAs which is included as random effect.
(1|Habitat) [*random effect*]	Habitat type is an important determinant of species richness and was therefore included as a random effect in the model.

Table 2 Four different sets of top models investigating spatial features that predict variation of PA representation of amphibians, birds, mammals and all taxa species richness together, ranked by AICc. Int. intercept; A: area; Sh: shape index; Prox: proximity; Fr: fragmentation; Lat: latitude; A*Fr: area*fragmentation interaction; A*Sh: area*shape interaction; Fr*Sh: fragmentation*shape interaction; Fr*Lat: fragmentation*latitude interaction; Weight: Akaike weight.

	Int.	A	Sh	Prox	Frag	Lat	A*Frag	A*Sh	Frag*Sh	Frag*Lat	ΔAICc	Weight
Amphibian	17.96	6.89	-3.39		-9.69	-10.02	-10.63			16.30	0.00	0.274
	17.51	7.16	-3.30	2.09	-9.61	-10.8	-10.75			16.13	0.63	0.200
	18.11	6.75	-3.24		-9.39	-9.99	-10.29		2.12	16.15	1.66	0.119
	17.96	6.96	-3.32		-9.69	-10.03	-10.55	0.65		16.27	2.12	0.095
	17.67	7.01	-3.14	2.13	-9.28	-10.78	-10.40		2.19	15.96	2.26	0.089
	17.51	7.18	-3.27	2.09	-9.61	-10.81	-10.72	0.27		16.11	2.78	0.068
	17.81	7.29			-8.75	-10.27	-11.03			15.99	3.62	0.045
	18.11	6.75	-3.24	2.24	-9.39	-9.99	-10.29	0.001	2.12	16.15	3.81	0.041
	17.32	7.58		2.13	-8.67	-11.11	-11.16			15.80	4.04	0.036
	17.66	6.97	-3.18		-9.28	-10.77	-10.44	-0.42	2.23	15.98	4.42	0.030
Bird	193.4	63.14	-62.13		-46.88	-95.05	-83.38		32.44	90.39	0.00	0.223
	192.4	64.88	-63.92		-48.76	-96.13	-85.34			82.23	0.12	0.209
	194.0	63.50	-61.73	-12.88	-48.07	-94.87	-84.04		34.34	93.70	0.60	0.166
	192.9	65.29	-63.66	-11.70	-49.94	-96.02	-86.04			84.80	0.97	0.137
	193.4	63.38	-62.00		-46.87	-95.10	-83.31	1.42	32.33	90.36	2.11	0.078
	192.7	66.92	-62.75		-48.63	-96.53	-84.69	12.39		82.21	2.15	0.076
	194.1	64.22	-61.35	-12.93	-48.04	-95.01	-83.84	4.25	34.02	93.62	2.71	0.058
	193.3	67.86	-62.18	-11.92	-49.80	-96.53	-85.24	15.53		84.82	2.97	0.051

Mammal	48.75	24.89	-1.69	5.19	-13.53	-25.60	-27.53	31.83	7.53	32.93	0.00	0.521
	48.73	25.30	-1.71		-13.47	-25.18	-27.81	31.12	8.53	32.82	0.93	0.327
	48.15	20.80	-4.58		-13.47	-24.15	-29.72		11.28	34.16	4.63	0.052
	48.16	24.41	-1.66	5.18	-14.22	-24.23	-27.12	33.29		32.47	4.82	0.047
	47.18	24.92	-1.77		-14.28	-23.84	-27.42	32.96		31.96	5.72	0.030
All taxa	284.3	75.31	-71.07	-47.14	-78.77	-179.4	-88.04		48.04	146.4	0.00	0.384
	283.7	76.17	-74.01	-47.66	-83.40	-145.5	-94.03			142.7	0.48	0.302
	283.4	75.00	-73.83	-46.44	-79.06	-181.0	-94.42	-31.01	50.59	149.1	1.72	0.163
	283.1	76.00	-75.92	-47.23	-83.76	-176.3	-98.41	-20.30		144.3	2.43	0.114

FIGURES

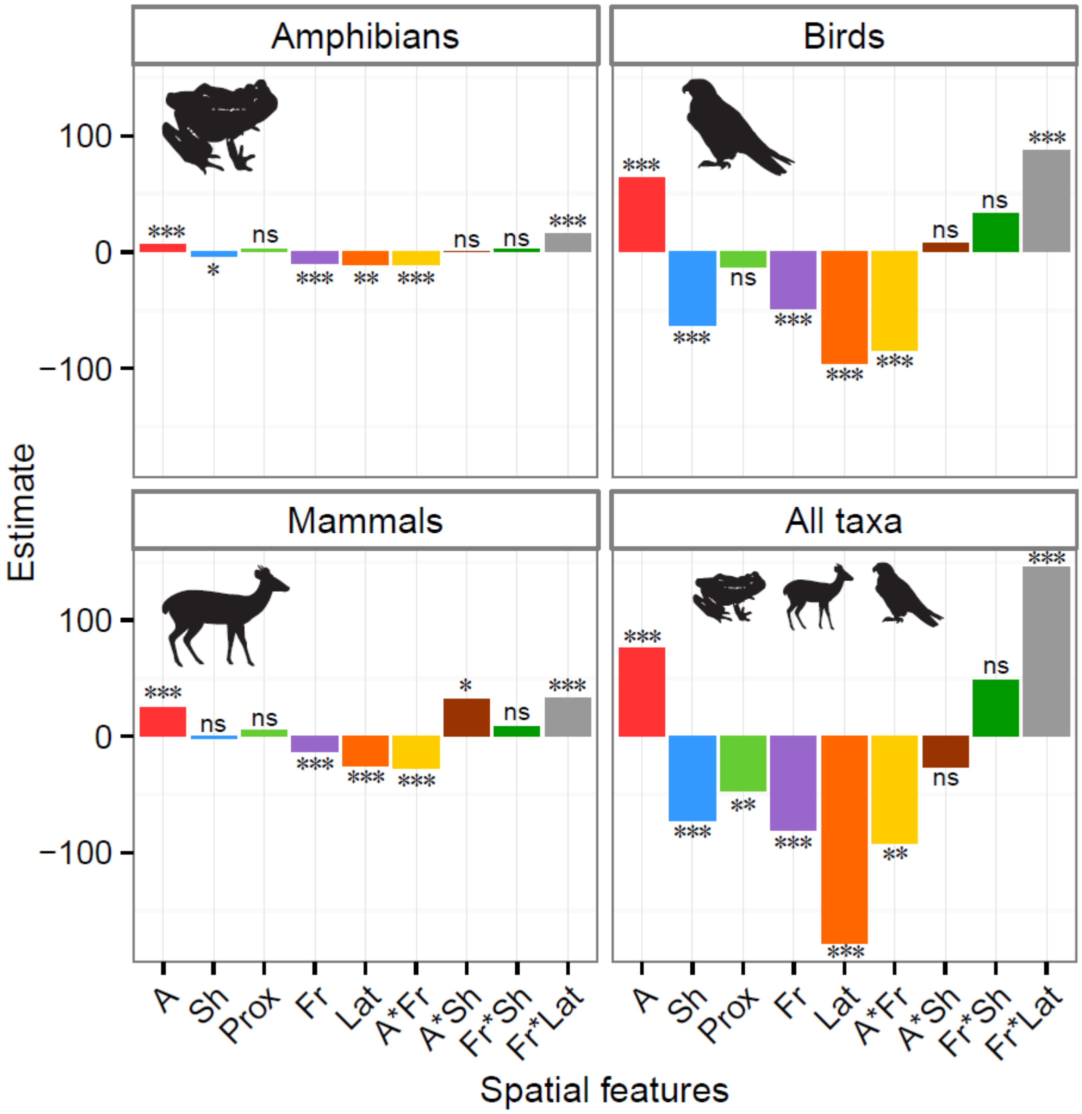

Figure 1: Estimates of averaged models for amphibians, birds, mammals and all taxa together. Size of the bar indicates relative strength of each predictor on species richness representation, and sign (above or below zero line) indicates direction of the effect. A positive effect (above zero line) indicates that species richness representation is favoured with high values of the predictor, while a negative effect (below zero line) indicates that low predictor values lead to higher species richness representation. A: area; Sh: shape index; Prox: proximity; Fr: fragmentation; Lat: latitude; A*Fr: area*fragmentation interaction; A*Sh: area*shape interaction; Fr*Sh: fragmentation*shape interaction; Fr*Lat: fragmentation*latitude interaction. Significance of the effect, *** p <0.001; ** p<0.01; * p<0.05; "ns" not significant.

CHAPTER 5

The benefits arising from selecting an appropriate location and spatial design for a protected area can be seriously undermined by potential threats, especially if these are not considered during the planning stage. It is therefore crucial to have knowledge of the different threats that can affect protected areas, and the extent to which these pressures are currently affecting them. Chapter 4 contributes to this understanding by assessing the extent to which metal mining activities spatially compete with the global protected area system.

Chapter 5:

Durán AP, Rauch J, Gaston KJ (2013) Global spatial coincidence between protected areas and metal mining activities. *Biological Conservation*, 160:272-278.
doi: 10.1016/j.biocon.2013.02.003

Author contributions:
Conceived and designed the experiments: APD, KJG.
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Wrote the paper: APD, RJ, KJG.

GLOBAL SPATIAL COINCIDENCE BETWEEN PROTECTED AREAS AND METAL MINING ACTIVITIES

ABSTRACT

The global protected area (PA) system has a key role to play in biological conservation, and it is thus vital to understand the factors that are likely to limit this potential. Attention to date has focused foremost on the consequences of biases in the spatial distribution of PAs for their effectiveness and efficiency in representing biodiversity. What is less clear is the extent to which these biases may also have affected the likelihood with which PAs coincide with or are influenced by particular kinds of threatening processes, further undermining their role. An obvious candidate for such concerns is metal mining activities. Here we demonstrate that approximately 7% of mines for four key metals directly overlap with PAs and a further 27% lie within 10 km of a PA boundary. Moreover, those PAs with mining activity within their boundaries constitute around 6% of the total areal coverage of the global terrestrial PA system, and those with mining activity within or up to 10 km from their boundary constitute nearly 14% of the total area. Given the distances over which mining activities can have influences, the persistence of their effects (often long after actual operations have closed down), and the rapidly growing demand for metals, there is an urgent need to limit or mitigate such conflicts, and for effective dialogue between biological conservation and the mining industry.

INTRODUCTION

Terrestrial protected areas (PAs) are widely regarded as key elements of in situ conservation strategies at local, regional and global scales (Margules & Pressey 2000; MA 2005; Gaston *et al.* 2008). This reflects evidence of their historical success, when compared with areas that are not so protected, in holding significant components of biodiversity within their bounds (Andam *et al.* 2008; Gaston *et al.* 2008; Jackson & Gaston 2008), and in buffering those components from external pressures (Chape *et al.* 2005). Nonetheless, numerous ways have been identified in which PAs could be improved, including individually in terms of their structure and management (Lockwood 2006) and collectively in terms of their distribution and extent (Brooks *et al.* 2004; Rodrigues *et al.* 2004; Fuller *et al.* 2010). Particular attention has been focused on the frequent tendency for PAs to be biased towards lands at higher elevations, with steeper slopes, lower primary productivity, and/or lower economic worth (Hoekstra *et al.* 2005; Joppa & Pfaff 2009). In other words, the tendency for PAs to be designated and established in parts of the landscape in which many (although not necessarily all) potentially competing uses are a priori minimized.

Such existing spatial biases in the distribution of terrestrial PAs are well known to have had important consequences. In particular, they have, often markedly, reduced their effectiveness and efficiency in representing biodiversity (Rodrigues *et al.* 2004; Chape *et al.* 2005; Gorenflo & Brandon 2006; Barr *et al.* 2011). What is less clear is the extent to which these biases may also have affected the likelihood with which PAs coincide with or are influenced by particular kinds of threatening processes, yet further undermining their role. One obvious candidate for such concerns is metal mining activities, due to their location and environmental impact. For some key metals a high proportion of potentially accessible ore deposits tends, like protected areas, also to be located in topographically more complex areas and at higher altitudes (e.g. (Edwards & Atkinson 1986; Evans 1993). Moreover, increasing demand (Fig. 1a) and prices (Fig. A5.1) are extending these activities into more remote and previously unmined regions (Pulgar-Vidal 2010). Consequently, metal mining activities have become of major export significance to several countries with notably high biodiversity (e.g. Chile, Peru, Zambia, Papua New Guinea; MA 2005). Indeed, mining activities have proven a threat to a number of PAs, and such proposed activities are one driver of the downgrading, downsizing, and degazettement of PAs (Phillips 2001; Earthworks & Oxfam 2004; Farrington 2005; Mascia & Pailler 2011).

Metal mining activities are potentially of major concern for biological conservation because they can be extensive and physically destructive of natural habitats, require infrastructure (e.g. for transport) that can extend over yet larger areas (e.g. access roads, rail networks), and can cause both chronic and acute pollution that can persist for many decades (Lefcort *et al.* 2010). Moreover, this pollution can extend considerable distances from the mine workings themselves, with a new collation of the results of a set of published empirical studies showing effects on the scale of tens of kilometers (Fig. 1b). This raises the potential for PAs to be influenced by metal mine workings that lie well beyond their immediate boundaries.

In this paper, we determine the spatial overlap between terrestrial PAs and mining activities for ore deposits for four metals (aluminium (Al), copper (Cu), iron (Fe) and zinc (Zn)). We determine the variation across the globe both in direct overlaps and in the proximity of mining activities to the boundaries of PAs, which given the 'long reach' of these activities may be just as significant as is the occurrence of active mine workings within PAs.

DATA AND METHODS

Global maps of the locations of bauxite (for production of Al), Cu, Fe and Zn mines were developed using Rauch (2009) as the baseline dataset. This was updated using information on mining activities obtained from the Raw Material Group (RMG), the world's most extensive mining industry database, containing information on a broad range of legal mining industry entities. The latitude and longitude of mines were determined using company reports, company websites and other available sources. Every updated location was verified using images from Google Earth. The final dataset comprised information on a total of 1418 mines.

Data on the global distribution of PAs were obtained from the World Database on Protected Areas (WDPA 2010). These data comprise both polygons and point records with associated extents. Following Rodrigues *et al.* (2004), (i) records were eliminated for marine PAs, and for PAs for which *Status* was indicated as "Proposed", "Recommended" or "Not reported"; (ii) point records were converted into circles of the stated area; (iii) point record circular areas were subsequently merged with those for which original polygon data were provided to generate a common polygon shapefile with a total of 129,422 records; and (iv) for the purposes of overlap analysis, but not for counting numbers and areas of PAs, the polygons that shared a common boundary or overlapped were dissolved.

To determine the proximity of mines to PAs we overlapped the point locality data for mines and the final merged polygon data for PAs. Those mines that were located within PAs, or within distances of 1 km, 1-5 km and 5-10 km from the boundary of the PAs were accounted. We selected a maximum buffer distance of 10 km to capture potential local to mesoscale effects of mining activities on PAs, whilst acknowledging that longer distance effects can also exist. The coincidence of mine activity within PAs or the buffer distances defined (1 km, 1-5 km and 5-10 km) were compared with a null model in which the same numbers of mines as observed were randomly distributed across the global land masses (including islands but excluding Antarctica), without overlap. This exercise was repeated 100 times, and each individual run was compared to the actual data. This procedure was then carried out separately for each of the six geographic regions of Africa, Asia, Europe, North America, Oceania and South America.

RESULTS

Mining activities for Al, Cu, Fe and Zn were widely distributed across the Earth’s surface, but with notable concentrations in the Andes range, west North America, eastern Europe, southern Africa, East Asia and Australia (Fig. 2a). The distribution of PAs was less clumped, but with particularly high coverage in north-east South America, western North America, northern and central Europe, southern-central Australia and East Asia (Fig. 2b).

Approximately 6.7% of mines were located within the boundaries of PAs, which although substantial, was less than expected by chance (Table 1). These overlaps mainly occurred in Europe, followed by Asia, South America and North America (Fig. 2c). Approximately 2.9%, 10.5% and 13.8% of mines respectively, were located within 1 km, 1-5 km and 5-10 km distance bands from the PA boundaries, leading to a total of 27.2% lying within 10 km of a PA. In all cases this was greater than expected by chance (Table 1). Focusing on individual geographic regions, only Europe had a higher percentage of mines within PA boundaries (16.4%) than expected by chance (Table 1). Similarly, only Asia had a higher percentage of mines within 1 km of a PA boundary (1.7%) than expected by chance (Table 1). However, in all six geographic regions there was a higher percentage of mines within 1-5 km and 5-10 km of a PA boundary than expected by chance (Table 1).

Considering mines separated by their metal production type (i.e. Al, Cu, Fe and Zn), at a global scale the percentages of mines lying within PAs were lower than expected by chance for all metals (Table A5.1). However, the percentages lying within 1 km, 1-5 km, and 5-10 km of a PA boundary were higher than expected for Cu, Fe and Zn (Table A5.1). These co-occurrences were distributed mainly in Africa, Asia and North America (Fig. A5.2-A.5.5). In Africa the percentage of mines within PAs was higher than expected for Al, and within 1 km, 1-5 km and 5-10 km of a PA boundary for Cu. In Asia, the percentage of mines within PAs was higher than expected for Zn, and within 5-10 km of a PA boundary in all cases except for Al. In Europe the percentage of mines within PAs was higher than expected by chance for Zn, and within 1 km, 1-5 km, and 5-10 km of a PA boundary in all cases except for Al within the 1 km distance band. For neither North nor South America were the percentages of mines lying within PAs higher than expected by chance for any of the metals, although percentages within the 5-10 km distance band were higher than expected by chance in all cases, except for Fe in North America and Al in South America.

Addressing the coincidence of mines and PAs from an alternative perspective, those PAs with mining activity within their boundaries constitute

6.1% of the total areal coverage of the global terrestrial protected area system (Table A5.2). Those with mining activity within 1 km, 1-5 km, and 5-10 km of their boundary constitute 0.1%, 5.9%, and 1.9% of worldwide PA land cover, and those with mining activity within or up to 10 km from their boundary constitute 14% of the total area. South America, followed by Asia and North America, exhibited the highest areal land cover of PAs that overlapped with mining activities within the four distance buffers (Table A5.2).

DISCUSSION

Studies of the threats to terrestrial PAs arising from human resource exploitation have focused heavily on potentially 'renewable' ecosystem goods and services (e.g. forestry, harvesting of wildlife; e.g. (Gaveau *et al.* 2007; Andam *et al.* 2008; Gaston *et al.* 2008; Craigie *et al.* 2010). Here the key issues are the degree to which such areas serve effectively to attract, limit or displace these activities by virtue of their being protected. For non-renewable resources some of the challenges are similar and others somewhat different. Moreover, for the metal mining activities considered here those challenges need to be evaluated carefully because, as we have shown, they can influence a substantial proportion of the terrestrial PA estate: approximately 7% of mines for the four key metals directly overlap with PAs, a further 27% lie within 10 km of a PA boundary, those protected areas with mining activity within their boundaries constitute about 6% of the total areal coverage of the global terrestrial protected area system, and those with mining activity within or up to 10km from their boundary constitute 14% of the total area.

First, in the main, any overlap between the distribution of the resource and that of PAs is typically much less likely to be a consequence of the designation of the PA per se (as can, for example, be the case when this results in the increase or maintenance of the numbers of a particular species of organism) for metal mining activities than for many renewable resources. Nonetheless, as demonstrated by metal mining activities, this coincidence can be marked. There is less mining activity within the bounds of PAs than expected by chance, which likely follows from a combination of a reduced likelihood of

PAs being established in areas where mining activity is already present and also of mining activities being established in areas where PAs are already present. Nonetheless, there remains some substantial overlap between mining activities and PAs (Table 1, A4.2), which is reflected in the pressures both for altering the status of some existing PAs and for licensing mining activities within them (Farrington 2005; Mascia & Pailler 2011). This almost certainly follows from PAs being established in areas in which the demands for many other forms of land use such as urbanization, agriculture and logging, are often substantially reduced (Hoekstra *et al.* 2005; Joppa & Pfaff 2009). Not surprisingly, subsequent analyses show that the occurrence of mining activities within PAs depends on their IUCN conservation category (IUCN, I-IV) (χ^2= 33.9091, df=5, p< 0.001). PAs in more permissive categories (IUCN, IV-VI) contained a higher than expected frequency of mines within their bounds than those in more strict categories (IUCN, I-III). This dependence was not explained by the geographic region in which PAs were located (χ^2= 26.6377, p=0.15) [Fisher's exact test with simulated p-value by a Monte Carlo test by 2000 iterations]. Second, because of the nature of practically and economically accessible metal deposits, there are arguably limited opportunities for the substantial displacement of mining activities away from the regions in which many PAs have been established. This results in the greater than expected occurrence of mining activities within relatively short distances of the boundaries of PAs (Table 1). Not surprisingly, the aggregated distribution of mining activities (Fig. 2a) coincides with metal-rich zones that resulted from geologic processes such as plate convergence, collision tectonics and extensional tectonics (Edwards & Atkinson 1986). These high density ore deposit regions have been named Metallogenic Provinces (Parker 1984), which offer good opportunities for exploration of new ore deposits and thus allocation of mining activities.

There have been repeated calls to redesign the global PA system (or, more realistically, its regional and national constituent parts) so that it better reflects conservation needs (Rodrigues *et al.* 2004; Fuller *et al.* 2010). However, whilst some have proposed that this should be done by a combination of degazettement of existing areas that contribute too little (particularly relative to their cost) and establishment of entirely new areas (Fuller *et al.* 2010), it seems likely that changes will occur principally by the latter expansion. There seems little prospect of degazettement of large numbers of PAs in close proximity to mining activities being motivated principally by conservation considerations. This places a high priority on limiting the environmental impacts of mining activities both within and beyond the immediate bounds of operations, and particularly the atmospheric and water-borne spread of pollutants.

Third, the threats to PAs from mining activities operate on spatial scales that are seldom considered in the context of the impacts of exploitation of renewable resources. Habitat changes beyond PA boundaries can have important influences through effects on overall patch sizes and on ecosystem functioning (through, for example, changes in rainfall; (Webb *et al.* 2006), and the killing of individuals of more wide-ranging species when outside PAs can have important effects on their population sizes within those areas (Woodroffe & Ginsberg 1998). However, it is clear with regard to mining activities both that influences can routinely occur over distances of tens of kilometers (Fig. 1b), and that many PAs and much of the PA estate occur within such proximity of those activities. Of course, the magnitudes of the impacts of metal mining activities and the distances at which these impacts act vary depending on a range of factors (method of extraction, topography, presence or not of refinery). Equally, the potential impacts of mining highlighted by the analyses reported here are based solely on legal activities, operating under regulated standards. There are likely to be additional threats from illegal and artisanal mining (Collen *et al.* 2011; Laurance *et al.* 2012).

Fourth, the difficulties that the non-random co-occurrence of mining activities and PAs may present are undoubtedly heightened by the combination of rising metal prices, increasing scarcity of some kinds of metal deposits, and the economic potential now held in previously non-viable deposits. Given these pressures, it is more urgent than ever to generate effective approaches which promote mitigation measures to minimize the impacts of mining activities. Indeed, within the mitigation hierarchy of avoidance, minimization, restoration and offset there are a variety of different measures that should be considered during the planning of mining projects (Quintero & Mathur 2011) (see Table 3 for examples). Avoidance measures are taken to prevent adverse effects on biological diversity. Minimization measures reduce the duration, intensity or spatial extent of effects which cannot be avoided. Restoration refers to the rehabilitation of ecosystems adversely affected by mining activities. Offsets are measures taken to compensate any negative effect on biological diversity that cannot be avoided, minimized, or restored (BBOP & UNEP 2010). A successful initiative that has utilized these mitigation measures is the Smart Green Infrastructure (SGI) project led by the World Bank in Tiger Range Countries. This large international project has identified the infrastructure of mining activities as one of the major contributors to the degradation of tiger habitat (Quintero *et al.* 2010). Several mitigation measures have been promoted in order to avoid, minimize, restore and compensate any negative effects of previous and future extractive activities. Other similar initiatives are the Mining, Minerals and Sustainable Development (MMSD) and the Sustainable Energy, Oil, Gas and Mining Unit (SEGOM) programs of the World Bank. These initiatives provide evidence that mitigation measures for mining projects are feasible, although more political will and resources are required to ensure implementation worldwide.

Finally, the present study, based on four key metal mine distributions, strongly suggests that metal mining activities are a potential threat to the global PA network, and that it is likely that the overlap between PAs and mines will increase in the future. The incorporation of mines for other key metals and illegal activities would almost certainly increase the frequency of overlaps between mines and PAs, amplifying the magnitude of this important land use trade-off.

CONCLUSION

Studies to date have highlighted two important consequences of biases in the spatial distribution of PAs for their ecological performance. The first, and negative, consequence is the typically lower capture of biodiversity features, that is lower representation, than might have been achieved by alternative distributions (Scott *et al.* 2001; Brooks *et al.* 2004; Rodrigues *et al.* 2004; Araújo *et al.* 2007). The second, and positive, consequence is the often lower threat, or greater persistence, faced by biodiversity features within PAs than beyond their bounds (Andam *et al.* 2008; Gaston *et al.* 2008; Joppa & Pfaff 2010). By contrast, our analyses identify an example where the spatial distribution of PAs has served to increase the threat to their biodiversity. The global terrestrial PA system has been effective at displacing metal mining activities from within its bounds, either because PAs or mines have been established such that overlap between the two has been reduced. However, given the higher than expected proportion of mines in the close surroundings of PAs, and the distances over which mining activities can have influences, it is highly likely that the conservation performance of a significant proportion of PAs is being affected.

TABLES

Table 1 Percentage of total metal mines observed within different levels of proximity (buffers) from protected areas (PAs) in different geographic regions, compared with a null model. Column 'Randomization larger than observed' indicates how many times the percentage of mines within PAs and buffers as determined from a null model was higher than the percentage observed.

Geographic Region	PAs buffer	Percentage of mines within PAs and buffers (cumulative percentage)	Percentage of mines within PAs and buffers by null model (mean ± SD)	Percentage of randomization larger than observed (%)
Global	Within	6.7	12.15 ± 1.07	100
	1 km	2.89 (9.59)	1.82 ± 0.56	0
	1 km - 5 km	10.51 (20.1)	6.71 ± 0.59	0
	5 km - 10 km	13.75 (33.85)	7.71 ± 0.63	0
Africa	Within	3.81	11.5 ± 2.7	100
	1 km	0.76 (4.57)	0.87 ± 0.74	34
	1 km - 5 km	22.9 (27.47)	3.86 ± 1.65	0
	5 km - 10 km	16.03 (43.5)	4.47 ± 1.88	0
Asia	Within	7.71	11.44 ± 1.54	99
	1 km	1.74 (9.45)	1.01 ± 0.49	5
	1 km - 5 km	4.72 (14.17)	4.36 ± 0.99	31
	5 km - 10 km	10.45 (24.62)	5.82 ± 1.28	0
Europe	Within	16.35	12.09 ± 2.31	3
	1 km	10.28 (16.63)	3.03 ± 1.19	0
	1 km - 5 km	17.75 (44.38)	12.05 ± 2.13	0
	5 km - 10 km	18.22 (62.6)	11.77 ± 2.66	0
N. America	Within	3.04	7.68 ± 1.62	99
	1 km	1.14 (4.18)	2.61 ± 0.87	91
	1 km - 5 km	12.93 (17.11)	9.7 ± 1.86	7
	5 km - 10 km	15.97 (33.08)	11.28 ± 1.77	3
Oceania	Within	0	10.52 ± 2.46	100
	1 km	2.52 (2.52)	2.26 ± 1.13	31
	1 km - 5 km	9.43 (11.95)	7.52 ± 2.11	19
	5 km - 10 km	13.21 (25.16)	7.03 ± 2.13	0
S. America	Within	6.42	21.13 ± 3.29	100
	1 km	1.61 (8.03)	1.39 ± 0.75	25
	1 km - 5 km	5.22 (13.25)	5.05 ± 1.47	42
	5 km - 10 km	12.05 (25.3)	6.21 ± 1.50	0

Table 2 Summary of examples of published studies that evaluate the extent of impact of mining activities on various ecological and environmental variables.

Authors	**Mine type**	**Ecological/Environmental effect**	**Maximum distance impact from mining source**
Hernandez *et al.* 1999	Pyrite	Bird mortality	25 km
Vasquez *et al.* 1999	Copper	Macroalgae abundance	3 km
Razo *et al.* 2004	Copper-Gold, Lead-Zinc-Silver	Heavy metal concentration	5 km
Telmer *et al.* 2006	Copper	Heavy metal concentration in lake sediments	50 km
Yakolev *et al.* 2008	Nickel	Soil quality	25 km
Kodirov & Shukurov 2009	Copper and Zinc	Heavy metal concentration in soil	4 km
Kuznetsova 2009	Copper	Collembola communities in coniferous forests	7 km
Lafabrie *et al.* 2009	Cobalt	Heavy metal concentration in seagrass	5 km
Taylor *et al.* 2009	Copper, Zinc and Lead	Downstream water quality	30 km
Bonifait & Villard 2010	Peat	Odonate abundance	1 km
Chauhan 2010	Zinc	Deforestation	11 km [a]
Huang *et al.* 2010	Copper and Zinc	Water acidity and heavy metal concentration	10 km
Katpatal & Patil 2010	Coal	Flooding	15 km
Lefcort *et al.* 2010	Copper and Zinc	Stream insect diversity and abundance	2.5 km [a]
Vodyanitskii *et al.* 2011	Copper	Decrease of soil quality	30 km

[a] Distance impact was calculated as the perimeter of a circle with stated area mining impact.

Table 3 Measures from mitigation hierarchy and example of potential actions to be taken.

Mitigation measure	Example of action
Avoidance	To avoid infrastructure in priority areas for biodiversity using spatial planning methods.
Minimization	Establishment of ecological corridor and buffer zones.
Restoration	To restore connectivity between patches of habitats within landscapes. Reforestation
Offset	Environmental compensation policies and payment of ecosystem services schemes.

FIGURES

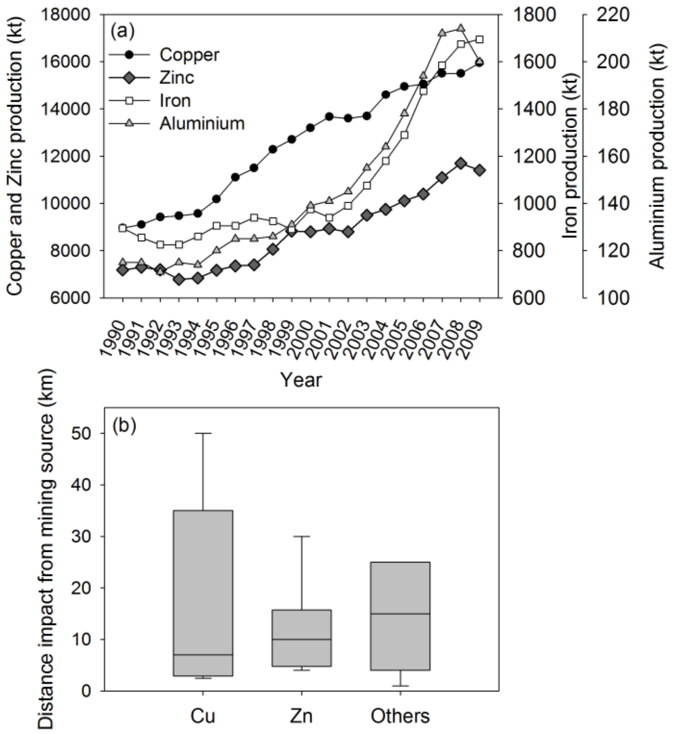


Figure 1: A) Annual variation in global production of aluminium, copper, zinc and iron from 1992 to 2010. (Information source: Raw Material Group). B) Average maximum distance of ecological impacts from mining sources for three different mine types: copper, zinc and others. Fifteen papers that evaluate mining activity impact zones were reviewed (Table 2). Boxes show the median, upper value, lower value, 25th and 75th percentile.

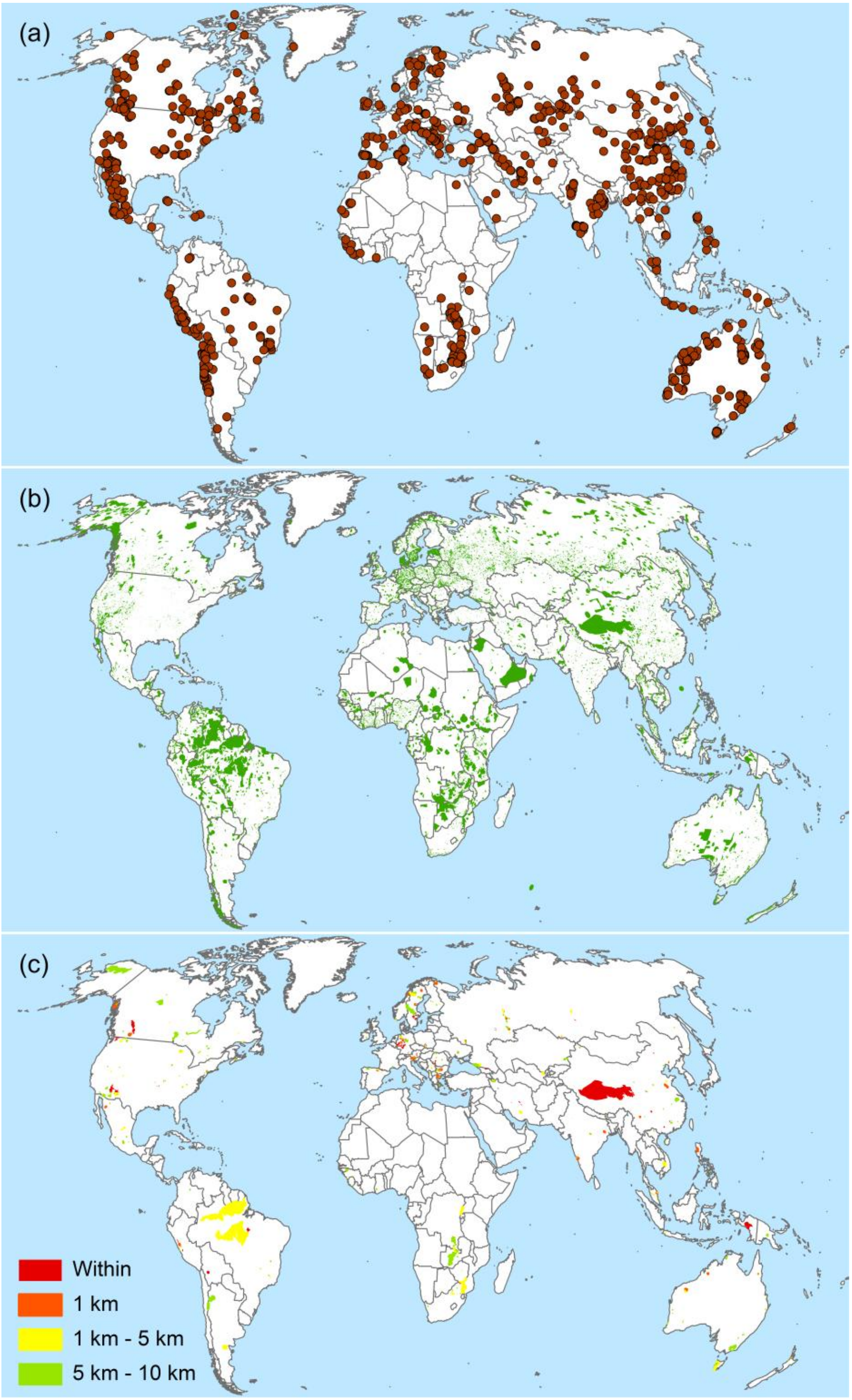


Figure 2: Global distributions of A) Bauxite, Copper, Iron and Zinc mines, B) Protected Areas, and C) Protected Areas having mining activities at different levels of proximity [Within: protected areas that completely contain at least one mining activity. 1km: protected areas located at 1km distance from at least one mining activity. 1-5 km: protected areas having at least one mining activity at 1-5 km distance. 5-10 km: protected areas having at least one mining activity at 5-10 km distance].

CHAPTER 6

Given that available land for new protected areas has become increasingly scarce due to the continuous expansion of anthropogenic land uses, selecting locations that optimize the representation of conservation features while minimizing land use conflicts is vital. An effective way of achieving this is through the use of Spatial Conservation Prioritization (SCP) tools. Using quantitative approaches, SCP identifies those locations that optimize the representation of a conservation feature and also do not overlap (i.e. compete) with conflicting land use. However, arguably, considering a particular land use as incompatible with conservation purposes is an arbitrary decision that can have important consequences in the final set of identified locations. Chapter 5 addresses this issue by exploring the consequences for biodiversity and ecosystem services representation when agricultural land is considered compatible (hence incorporated) or incompatible (hence excluded) in SCP analyses for South America.

Chapter 6:

Durán AP, Duffy JP, Gaston KJ (2014) Exclusion of agricultural lands in spatial conservation prioritization strategies: consequences for biodiversity and ecosystem service representation. *Proceedings of the Royal Society B*. 281(1792), 20141529.

Author contributions:

Conceived and designed the experiments: APD, KJG.

Analysed the data: APD, JPD.

Wrote the paper: APD, JPD, KJG.

EXCLUSION OF AGRICULTURAL LANDS IN SPATIAL CONSERVATION PRIORITIZATION STRATEGIES: CONSEQUENCES FOR BIODIVERSITY AND ECOSYSTEM SERVICE REPRESENTATION

ABSTRACT

Agroecosystems have traditionally been considered incompatible with biological conservation goals, and often been excluded from spatial conservation prioritization strategies. The consequences for the representativeness of identified priority areas have been little explored. Here, we evaluate these for biodiversity and carbon storage representation when agricultural land areas are excluded from a spatial prioritization strategy for South America. Comparing different prioritization approaches, we also assess how the spatial overlap of priority areas changes. The exclusion of agricultural lands was detrimental to biodiversity representation, indicating that priority areas for agricultural production overlap with areas of relatively high occurrence of species. In contrast, exclusion of agricultural lands benefits representation of carbon storage within priority areas, as lands of high value for agriculture and carbon storage overlap little. When agricultural lands were included and equally weighted with biodiversity and carbon storage, a balanced representation resulted. Our findings suggest that with appropriate management South American agroecosystems can significantly contribute to biodiversity conservation.

INTRODUCTION

Conservation strategies increasingly face the challenge of combining the consideration of biodiversity and of ecosystem service distributions within a single planning framework (Turner *et al.* 2007; Goldman *et al.* 2008; Perrings *et al.* 2010; Cardinale *et al.* 2012). Spatial conservation prioritization (SCP) techniques have been an important tool in this regard, as they allow for the identification of sets of priority sites which optimize the representation of both, taking into account levels of complementarity (Chan *et al.* 2006; Moilanen *et al.* 2011; Thomas *et al.* 2013). SCP techniques also allow for the explicit incorporation of potential trade-offs between biodiversity and ecosystem services, enhancing the suitability of the priority sites identified by decreasing *a priori* land use conflicts. The consequences, however, for biodiversity and ecosystem service representation when incorporating these trade-offs within prioritization strategies has not been well studied.

Most examples of where biodiversity and ecosystem service trade-offs arise concern provisioning services (MA 2005; Reyers *et al.* 2012). The Millennium Ecosystem Assessment (MA 2005) defined provisioning services as 'products obtained from ecosystems', and found that trade-offs between these services and biodiversity have been the largest driver of biodiversity loss over the last 50 years (MA 2005). This is due to the dramatic land transformation that provisioning services normally imply (Power 2010; Reyers *et al.* 2012).

Agriculture is a vital provisioning service for human well-being and a key component of the global economy (McCouch *et al.* 2013). Nearly 40% of the Earth's terrestrial surface is covered by agroecosystems (FAO 2012), and since agricultural practices can decrease biodiversity through multiple pathways (Green *et al.* 2005; Potts *et al.* 2010; Balmford *et al.* 2012), agricultural land use and biodiversity conservation have traditionally been viewed as incompatible (Green *et al.* 2005). Given however the current scale of agricultural land use, an increasing number of studies are considering agriculture's contribution to biodiversity and to related ecosystem services critical for successful conservation in the future (Scherr & McNeely 2008; Carvalheiro *et al.* 2011; Fischer *et al.* 2011; Pywell *et al.* 2012).

The divergent approaches within the conservation community of considering agriculture as either compatible or incompatible with conservation goals are reflected in the SCP literature. SCP studies strictly focused on biodiversity conservation tend to include agriculture as a trade-off in prioritization strategies (i.e. a negatively weighted feature; e.g. (Moilanen *et al.* 2011)), hence forcing its exclusion from priority areas even though these areas could host significant levels of biodiversity and ecosystem services (Pywell *et al.* 2012; Bommarco *et al.* 2013; Sokos *et al.* 2013; Mouysset *et al.* 2014; Vrdoljak & Samways 2014; Werling *et al.* 2014). This results in the selection of locations with two main characteristics (i) areas which over-represent biodiversity components that are found outside agroecosystems, while penalizing those that fall within agricultural lands, and (ii) areas which tend to promote exclusive conservation use, and are suitable for proactive approach strategies (i.e. priority areas with low vulnerability; (Brooks *et al.* 2006)). In contrast, SCP studies focused on both biodiversity and ecosystem service conservation tend to include agriculture as a ‘conservation feature’ (i.e. a positively weighted feature; e.g. (Chan *et al.* 2006)), thus promoting the inclusion of agroecosystems within priority sites. This leads to solutions that select a set of locations that can: (i) over-represent biodiversity and ecosystem services, or agriculture, or represent intermediate levels of all three, and (ii) promote multi-use lands, which require appropriate extractive practices compatible with conservation aims, and are suitable for reactive approach strategies (i.e. priority areas with high vulnerability; (Brooks *et al.* 2006)). While both SCP approaches might address similar conservation issues and interests, their results are likely to differ significantly. To what extent and with what consequences for conservation decisions has yet to be assessed.

Here we evaluate the consequences for biodiversity and carbon storage representation when agricultural production is considered as either a trade-off or conservation feature in SCPs for South America. Using three different prioritization strategies, in which agriculture is weighted as positive, negative or neutral, we assess how the distribution, representativeness and extent of spatial overlap of priority areas change for biodiversity, carbon storage and agriculture. We also evaluate the benefits and penalties for biodiversity under different biodiversity-carbon-agriculture conservation strategies. Finally, we discuss the implications of these different strategies for conservation strategy recommendations.

MATERIAL AND METHODS

PRIORITY AREA

A 'Priority area' can be defined as a location or zone that optimizes the representation of a particular variable in the landscape. This variable can be relevant either for conservation or productive purposes. While a *biodiversity priority area* can represent relatively high species richness or endemism, a *productive priority area* can represent relatively high economic production or specific environmental conditions to generate a particular kind of product (i.e. Altiplanic climate for Quinoa production). For both conservation and producer parties, the identification of biological and productive priority areas is critical in order to assess potential synergies and trade-offs between these, thereby promoting both practices. Promoting different practices can be done by exclusively protecting some biodiversity priority areas and exploiting others, or by making compatible the co-existence of both practices when possible. Here a priority area is considered as an area with relatively high value of a feature in the landscape, and not only an area with high conservation value for protection.

DATA

Data were processed and analysed using the South American Albers Equal Area Conic projection.

Following a similar approach to Durán *et al.* (2013), agricultural production was calculated as the sum of the averaged gross production (US dollars) between 2000-2010. Specifically, the agricultural production layer was calculated as follows: (i) The harvested area of 95 major crops (i.e. proportion of a grid cell that has been harvested for a specific type of crop) in 2000 (Monfreda *et al.* 2008) was multiplied by crop land cover (i.e. spatial distribution of agricultural lands) (European Commission Joint Research Centre 2003). From this we obtained a second layer showing the area per grid (i.e ha) that was harvested for each major crop; (ii) The resultant layers for each major crop were then multiplied by their respective yields (tonnes/ha) for the year 2000 (Ramankutty *et al.* 2008), obtaining tonnes of crops produced per grid; finally, (iii) tonnes per grid of each major crop were then multiplied by the average price (USD/tonnes) for 2000-2010 (FAOStat), to enable the resultant layers to be sensibly combined, and to obtain USD of agricultural production per grid (Fig. A5.1-d).

The carbon storage data set was obtained from (Saatchi *et al.* 2011). Their above- and below-ground live biomass carbon stock map was produced using a combination of data from 4,079 in situ inventory plots, satellite light detection, ranging (LiDAR) samples of forest structure to estimate carbon storage, plus optical and microwave imagery (1-km resolution) to extrapolate over the landscape. This data set is at 1 x 1 km resolution and cells were aggregated by calculating their average in order to attain the same resolution as other layers (Fig. A5.1-c).

We used global data sets on the distributions of amphibian (compiled by the IUCN Global Amphibian Assessment), bird (BirdLife 2000) and mammal (compiled by the IUCN Global Mammal Assessment) species downloaded from the International Union for Conservation of Nature (IUCN) Red List of Threatened Species website (http://www.iucnredlist.org/) in January 2014. For comparative purposes we used two groups of biodiversity data for analysis: all of the species that occur in South America ('all species', hereafter) and just the threatened species. Threatened species were selected based on their conservation status - critically endangered, endangered and vulnerable - published on the IUCN website. For both all and threatened species, distribution shapefiles were clipped to a South American continent boundary shapefile, thus maintaining only South American native ranges. They were then rasterized to presence/absence grids. For the all species group, 6,606 species were included (2,308 amphibians, 3,090 birds and 1,208 mammals) (Fig. A5.1-a), whereas a subset of 1,120 species (573 amphibians, 360 birds, 187 mammals) were in the threatened group (Fig. A5.1-b).

Given our biodiversity dataset is based on species extent-of-occurrence range maps, for which there is increasing uncertainty in species presence at high spatial resolutions, we processed and analysed all our maps at three different resolutions - 10 km, 0.5° (~56 km) and 2° (~224 km) - and compared the results. Given that there were no substantial differences in the key findings reported here (Table A6.1; Fig. A5.2, A5.3), the results for the finest resolution are presented in the text.

ZONATION FRAMEWORK

The analyses were carried out using Zonation (Moilanen *et al.* 2005), a spatial conservation planning tool that produces a hierarchical prioritization of the representation value of a gridded landscape. 'Hierarchical' here implies that the most valuable 5% of the landscape is within the most valuable 10%, the top 2% is in the top 5% and so on. The Zonation algorithm operates by successively removing those cells whose loss results in the smallest reduction in the value of a feature in the remaining landscape, thereby producing a ranking of the contribution of each cell. The removal order of cells depends on the *cell removal rule*, which determines which cell leads to the smallest marginal loss of a feature value (Moilanen *et al.* 2005). In our analyses we used the core-area cell removal rule, in which each species distribution is considered separately, securing locations that gather a high proportion of a species' geographical distribution, thus favouring the rarest species in the resulting priority area. We used this rule in order to generate complementary priority sites that contain high-priority features (i.e. rare species), which is considered a better approach to target conservation efforts in comparison to species richness (i.e. 'additive benefit function' cell removal rule in Zonation).

Using only one feature the strategy exclusively benefits cells that include that unique variable ('single-criterion strategy' hereafter), while using more than one feature the strategy optimizes the representation of all the variables at the same time ('multi-criterion strategy' hereafter). Features can be given numeric weights making it harder to remove cells that contain features with greater weightings. Thus, features that have been assigned with greater weightings will dominate within the top percentage of the landscape that has been prioritised. The latest version of Zonation has been expanded in order to consider simultaneously both positively and negatively weighted features from the perspective of conservation (Moilanen *et al.* 2011). Areas with positive conservation features are retained in the top fraction of the priority ranking whereas areas with negative features (e.g. industrial areas) are removed early in the prioritization, thereby receiving a low priority ranking. This variant of Zonation produces a spatial priority ranking that reduces the interference between competing land uses.

SPATIAL PRIORITIZATION ANALYSES

We evaluated the performance of different prioritization strategies, in which the solution units were: (i) averaged proportion of the range of each species contained within the priority area for biodiversity (applies for both all and threatened species analyses); (ii) tons of carbon biomass for carbon storage, and (iii) USD dollars for agricultural production. We first evaluated the performance of single-criterion strategies - 'biodiversity-only', 'carbon-only' and 'agriculture-only' - in order to calculate to what extent these would represent one another. In order to evaluate the consequences for biodiversity and carbon representation when agriculture is considered either as a trade-off (i.e. negatively weighted hence excluded from conservation priority areas) or as a conservation feature (i.e. positively weighted hence included within conservation priority areas), we assessed the performance of three multi-criterion strategies in which agriculture was respectively weighted for each of the three cases: 0 (hence ignored), -1.0 and +1.0. All species were weighted equally (w = 1/6,606 all species; w = 1/1,120 threatened species) and carbon was weighted 1.0. This implies that species were jointly equal to the carbon and the agriculture values (when agriculture = ±1.0). Following the Strategic Plan 2011-2020 of the Convention on Biological Diversity (CBD 2010), we used a cutoff of 17% to define the spatial extent of our high priority areas (Dobrovolski *et al.* 2013). Using the resulting prioritization maps from the single and multi-criterion strategies, we evaluated the extent of their spatial overlap by calculating the percentage of overlapping grid squares for the highest priority (hereafter 'top') 17% of the landscape (Moilanen *et al.* 2011).

Following a similar approach to Thomas et al. (Thomas *et al.* 2013), we assessed the variation in biodiversity representation in combined biodiversity-carbon-agriculture prioritization strategies. Relative priority weightings were assigned to carbon and agriculture, but the weight for each species was kept equal to 1.0. Agriculture was also weighted both positively and negatively. Thus, by assigning relative weightings to carbon and agriculture, it is possible to evaluate the extra carbon value gained for a given percentage of agriculture loss, and *vice versa*, and how much representation of biodiversity is achieved within these combined strategies. The relative weightings ascribed to carbon and to agriculture were defined in units of *n*; where *n* was the total number of biological species in the analysis (*n* = 6,606 all species; *n* = 1,120 threatened species). Similar weightings were assigned as for Thomas et al. (Thomas *et al.* 2013): 64*n*, 32*n*, 16*n*, 8*n*, 4*n*, 2*n*, *n*, 0.5*n*, 0.25*n*, 0.125*n*, 0.0625*n*, 0.0312*n*, and 0.0155n.

For the combined strategies in which agriculture was considered as a conservation feature, both carbon and agriculture were assigned positive relative weights, and thereby both variables were retained in the top percentage of the landscape for conservation priority sites. For those combined strategies in which agriculture was considered as a trade-off, carbon was assigned positive weights and agriculture negative weights. This results in the retention of carbon in the top percentage of the landscape, but in the early removal of areas that contain agricultural lands, hence its exclusion from priority sites.

For both combined strategy approaches, agriculture positive and negative, relative weightings were ascribed *reciprocally*. This means that when carbon received the maximum weight (64*n*) agriculture received the minimum (0.0155*n*), and all combinations were tested through to agriculture receiving the maximum (64*n*) weight and carbon the minimum (0.0155*n*) (Table A6.2). Thus, when agriculture is positive, as carbon loses priority agriculture gains priority. However, when agriculture is negative, as carbon loses priority agriculture loses priority too, due to agriculture's weights becoming increasingly more negative (e.g -64*n*), resulting in its earlier removal from the landscape.

RESULTS

Priority areas for biodiversity, carbon and agriculture differ in their locations (Fig. 1). High-priority biodiversity areas (i.e. areas that represent a relatively high species occurrence) for both all and threatened species, are concentrated to the west of South America, south east of Brazil and south of Chile (Fig. 1a, d). Carbon priority areas are highly aggregated in the north-west and north-east of the Amazon forest (Fig. 1b), and high-priority agriculture areas occur in northern, and southern South America (Fig. 1c). Using all species (n= 6,606), the 'biodiversity-only' strategy represents 56.2% of biodiversity, 18.4% of carbon stock and 28.7% of agricultural production within the top 17% of the landscape. For the 'carbon-only' strategy the top 17% of land captures 19.0% of biodiversity, 42.0% of carbon and only 8.1% of agricultural production. Alternatively, an 'agriculture-only' strategy would maintain within the top 17% of the landscape 27.1% of biodiversity, 12.0% of carbon stock and 88.0% of total agricultural production. For threatened species, 'biodiversity-only' represents in the top 17% of the landscape 86.4% of biodiversity, 16.3% of carbon and 27.2% of agricultural production. Single-carbon and single-agriculture strategies represent 13.0% and 36.7% of threatened biodiversity, respectively.

The multi-criterion strategy in which agriculture was considered neutral (i.e. weighted zero hence ignored) maintains 33.6% of biodiversity, 40.0% of carbon stock and 10.9% of agricultural production considering all species, and 63.1% of biodiversity, 38.4% of carbon and 13.5% of agriculture considering threatened species. High-priority areas for this strategy, for both all and threatened species, are located mainly in the Amazon forest where high levels of carbon also occur (Fig. 2a, d). When agriculture was weighted negatively the representation of biodiversity and agricultural production fell to 13.3% and 0.1% respectively in the top 17% of the landscape for all species, but carbon representation remained similar at 39.8%. The drop in biodiversity and agriculture representation was more dramatic using threatened species, falling to 7.9% and 0%, respectively. Carbon representation remained high at 38.4%. This strategy has the characteristic that the bottom 17% of the landscape (i.e. lowest priority) has the high-priority areas for biodiversity and agricultural production, while the top 17% has high-priority areas for carbon storage (Fig. 2b, e). Assigning positive weight to agriculture increases the representation of the three variables with 38.9% of biodiversity, 31.8% of carbon stock and 64.3% of agricultural production using all species, and 65.2% of biodiversity, 30.3% of carbon and 64.2% of agricultural production using threatened species. This strategy combines areas from the far north and south of South America, and from west Amazon forest, achieving a balanced representation of the three features (Fig. 2c, f).

25.9% of biodiversity-only areas overlap with agriculture-only areas in the top 17% of the landscape, while only 16.7% overlap with carbon-only areas (Table 1). This is consistent with cells that contain high proportions of species' distribution ranges tending to co-occur with agricultural lands. The corresponding overlap between carbon-only and agriculture-only areas is low, overlapping only 7.3% of the top 17% of the landscape. Multi-criterion strategies that weight agriculture 0 and -1.0, present the highest overlap with carbon-only sites. This indicates that combined prioritization strategies in South America that ignore or exclude agricultural lands would strongly promote carbon storage representation (Table 1). However, the resulting priority areas from the strategy in which agriculture was weighted equal +1.0, showed a 58.4% overlap with carbon-only areas, suggesting that the inclusion of agriculture in prioritization strategies still balances a set of areas that represent high-priority carbon areas. Moreover, this multi-criterion strategy where agriculture is weighted positively overlaps 28.7% with biodiversity-only sites, supporting once again that the inclusion of agricultural lands in prioritization strategies captures areas that represent a high relative proportion of species' distribution ranges. For threatened species the same overlap relation was observed (Table 1).

Potential conflicts and synergies between land uses are also apparent from performance curves (Fig. 3). Prioritizing for 'carbon only' (Fig. 3b, e) carries a slightly higher penalty for biodiversity representation than prioritizing for 'agriculture only' (Fig. 3c, f), and this penalty is higher for all species than threatened species. Threatened species are more effectively represented than all species when a low proportion of the landscape is allocated for conservation ('biodiversity only' strategy), although this carries a slightly higher cost for agricultural production (Fig. 3a, d). Excluding agricultural lands ('All, agr. x -1'; Fig. 3h, k) carries a higher cost for biodiversity representation than when these are included ('All, agr. x +1'; Fig. 3i, l). In contrast, when agricultural lands are excluded, there is not a high cost for carbon representation (Fig. 3h, k, i, l). Threatened species can be relatively better represented than all species when agricultural lands are included in the strategy (Fig. 3i, l).

Figure 4 shows how biodiversity representation varies with relative priority weightings for carbon and agriculture, for the top 17% of the landscape. By weighting agriculture positively, the relative proportion of species' ranges is better represented when prioritization benefits agriculture over carbon, using both, all and threatened species (Fig. 4a, c). Adding positive weight to agriculture in the prioritization strategies results in a rapid increase of biodiversity and decrease of carbon representation, with the increase in biodiversity being higher for threatened species (Fig. 4c). Considering all species, biodiversity representation reaches a maximum of 38.9% when agriculture is weighted *n,* and a 66.5% for threatened species when agriculture is weighted *2n*. However, as agriculture positive weight keeps increasing, biodiversity representation starts to decrease ending in a representation of 27.1% for all species and 42.4% for threatened species when agriculture equals 64*n* (Fig. 4a, c). Assigning the same positive weight to carbon and agriculture (*n*), priority sites in the top 17% of the landscape represent 38.9% of biodiversity, 31.8% of carbon stock and 64.3% of agricultural production when all species were considered, and 65.2 % of biodiversity, 30.3% of carbon and 64.2% of agricultural production when threatened species were considered (Fig. 4a, c). Alternatively, when agriculture is weighted negatively, as its negative weight increases in magnitude (hence its priority decreases), biodiversity representation remains roughly the same, starting with a maximum representation of 19.0% and ending with 13.1% when agriculture weight equals -64*n* (Fig. 4b). The variation of threatened species representation is larger, starting with 12.9%, reaching a maximum of 22.9%, and ending with 8.7% (Fig. 4d). The variation of agriculture representation among negative weighted strategies is small using either biodiversity group, with variation of no more than 8% between the highest priority (-0.0155*n*) and the lowest (-64*n*) for agriculture (Fig. 4b, d). The reduction rate of carbon representation is smaller when agriculture is weighted negatively (Fig. 4b, d). Finally, assigning the same magnitude weight to carbon and agriculture (negative), priority areas represent 13.3% of biodiversity, 39.8% of carbon and 0.1% of agriculture for all species, and 7.9% of biodiversity, 39.1% of carbon and 0% of agriculture for threatened biodiversity.

DISCUSSION

In the present study, we evaluated for the first time what the consequences for biodiversity and carbon storage representation are when agricultural lands are both incorporated and excluded from a prioritization strategy in South America. Our results show that the incorporation of agricultural lands in the prioritization strategy increases biodiversity representation (i.e. relative proportion of species' ranges), although it does not promote carbon storage representation (Fig. 4a, c). Also, assigning a relatively high weighting to carbon decreases biodiversity representation in the resulting priority areas (Fig. 4a, c). In contrast, when agricultural lands are excluded from priority sites, biodiversity representation decreases while carbon storage increases (Fig. 4b, d). We consider the basic and applied implications of these results.

DISTRIBUTION AND REPRESENTATIVENESS OF PRIORITY SITES

Priority areas identified by the three single-criterion strategies - biodiversity, carbon and agriculture - differ in their distribution and level of representation (Fig. 1). The agriculture-only strategy represents 8.1% (all species) and 36% (threatened species) more biodiversity than the carbon-only strategy, and a high positive weighting on agriculture results in a dramatic increase in biodiversity representation (Fig. 4a, c). This indicates that the highest carbon environments in South America do not host a relatively high occurrence of species, but that agricultural lands co-occur with a high proportion of species' range distributions. A similar result was obtained by (Dobrovolski *et al.* 2013), where excluding forecasted agricultural lands for the 21st century from prioritization strategies (*agrosolution*), resulted in a significant reduction of carnivorous mammal representation, compared to strategies in which agricultural lands were included (*biosolution*). Like our study, this suggests that the benefits of this conflict alleviation (by excluding agricultural lands from SCP) come at a biological cost (Dobrovolski *et al.* 2013). While (Dobrovolski *et al.* 2013) also used species extent-of-occurrence data, they carried out the analyses at a coarser resolution (e.g. 0.5°) hence decreasing the overestimation of species presence within their distribution ranges, and therefore within agricultural lands. However, that we did not find significant variation in our key findings among analyses at three spatial resolutions (10 km, 0.5° and 2.0°, see Methods), suggests that these results are quite robust to such concerns. Thus, that these two studies indicate a relatively high overlap between biodiversity and both current and forecasted agricultural lands, reinforces how critical it is to identify existing agricultural lands that co-occur with a high proportion of species distributions (by including agricultural lands in SCP), and thereby targeting these lands with appropriate farming management actions.

Multi-criterion strategies that consider agriculture as a neutral or negative feature also indicate that areas with relatively high occurrence of species and with high crop production levels often overlap. This can be observed in the reduction in biodiversity representation when agricultural lands are excluded (Fig. 4b, d), and in the high penalty to biodiversity representation that is carried by the negative weighting of agricultural lands (Fig. 3h, k). Contrastingly, carbon representation increases with these strategies, which indicates that high priority carbon areas tend not to co-occur with high priority biodiversity and agricultural lands (Fig. 1). The multi-criterion strategy that includes agricultural lands presents a good balance among the three variables, covering 38.9% of biodiversity, 31.8% of carbon and 64.3% of agriculture using all species, and 65.2% of biodiversity, 30.3% of carbon and 64.3% of agriculture using threatened species. This suggests that, if systematic protection is applied to carbon and biodiversity highest priority areas, together with biodiversity-friendly farming in those agroecosystems that overlap with priority biodiversity areas, simultaneous and effective representation of carbon, biodiversity and agricultural production could take place in South America.

While our results show a high proportion of agricultural areas overlapping with biodiversity priority areas, the actual proportion of species occurring within agrosystems is likely an overestimation, mainly because the analysis assumes that all agricultural land is suitable for every species for which this falls within their distribution bounds. For conservation purposes such overestimation is in some senses significantly less costly, as missing the opportunity of promoting appropriate farming management in agricultural areas that could potentially host a high number of species (given the disproportionally high overlap with species' ranges) hampers the ongoing efforts of balancing agriculture with conservation.

SPATIAL OVERLAP, WEIGHTINGS AND TRADE-OFFS

In an extraction *vs.* conservation competing scenario two approaches have been suggested (Green *et al.* 2005; Fischer *et al.* 2008): (i) *land sparing* - protect some land very strictly and exploit the rest intensively, and (ii) *land sharing* - protect less land but exploit the remainder with friendly practices. Given that an increasing number of empirical studies show that friendly farming practices can support high biodiversity while achieving moderately high yields (Gordon *et al.* 2007; Duncan & Dorrough 2009; Clough *et al.* 2011), a land sharing approach seems a potential solution for those locations where high extraction and biodiversity priority areas overlap. This could be the case for the 25.9% of overlap between biodiversity-only and agriculture-only priority sites in the top 17% of the South American landscape (Table 1). In contrast, a land sparing approach seems more suitable for the low 7.3% overlap between carbon-only and agriculture-only priority areas, as the outputs of these two activities are rather incompatible.

The strong conflict between agricultural lands and carbon storage can be seen in the penalty for carbon when an agriculture-only strategy is carried out (Fig. 3c, f) and in the rapid decrease in carbon storage as agriculture gains higher positive weighting (Fig. 4a, c). However, as agriculture receives higher negative weighting (Fig. 4b, d), carbon representation also decreases, suggesting that some carbon priority sites co-occur with agricultural lands. This co-occurrence is supported by the 58.4% overlap between carbon-only priority areas and the multi-criterion priority sites that include agricultural lands in the top 17% of the landscape (Table 1).

Moreover, our results show that for all species, 28.7% of biodiversity-only and 58.4% of carbon-only priority areas overlap with the multi-criterion strategy that includes agricultural lands (Table 1), and which represents 64.3% of South American crop production. This shows that some areas identified by this multi-criterion strategy prioritize biodiversity, carbon and agriculture separately, while others prioritize both biodiversity and agriculture. While biodiversity representation increases rapidly as agriculture receives higher positive weighting, it starts to decrease when agriculture's weight approaches its maximum (Fig. 4a, c). This indicates that a proportion of agriculture priority areas do not co-occur with high priority biodiversity areas. In this regard, neither land sparing nor land sharing seems the appropriate strategy for this set of priority sites, rather a mix of both. Balancing both strategies also applies to those agricultural lands that co-occur with biodiversity priority areas. While for some of them promoting biodiversity conservation may be particularly feasible and lands sharing can be applied (e.g., multiple cropping or polycropping, (Bommarco *et al.* 2013)), for others, given viability constraints, promoting a more suitable habitat for biodiversity conservation may be economically unfeasible and a land sparing strategy more appropriate. Thus, depending on the extent of overlap between 'competing' priority sites, how compatible the overlapping activities are (i.e. biodiversity vs. farming), and how many priority sites without overlap are identified, would indicate the type of approach to adopt.

IMPLICATIONS FOR CONSERVATION

Excluding agricultural lands (and any other form of land use) from SCP analyses is an arbitrary decision that arises from the conceptual framework on which a study is based. This exclusion predetermines what type of management approach (proactive *vs.* reactive) can be applied on identified priority areas, as excluding lands from the prioritization process modifies *a priori* the nature, extent and number of variables represented. If agricultural lands are excluded, the identified priority areas will more likely be suitable for a single management approach, where only strict conservation activities are promoted (i.e. single land use). In contrast, if agricultural lands are included, the spectrum of management approaches widens. More biodiversity-friendly management approaches need to be included in agricultural regions in order to promote the representation of competing activities simultaneously (e.g. conservation agriculture; (Baudron *et al.* 2009)). In this regard, our study suggests that using trade-offs comprehensively in SCP aids in the identification of appropriate strategies required for the different types of priority areas (i.e. single or multi use). This corresponds with other studies (Dobson *et al.* 2001; Luck 2007; Dobrovolski *et al.* 2011), which suggest that different areas need different conservation strategies. For instance, reactive approaches require the identification and protection of remnant natural areas in landscapes dominated by agriculture and other human uses (Dobrovolski *et al.* 2011). Reactive approaches also often need strategies of coexistence of agriculture and biodiversity conservation. Proactive approaches might need strategies that protect large areas as these lands are available and tend to be cheaper (Peres 2005).

Combining agricultural practices with biodiversity conservation is particularly relevant in the light of agricultural expansion, which is expected to impact about 1 billion hectares of land if current trends of agricultural intensification continue (Tilman *et al.* 2011). Promoting strategic agricultural intensification on existing agricultural land can not only reduce the extent of agricultural expansion, hence the new conflicts with biodiversity priority areas, but can also foster the re-colonization of intensively exploited land that currently co-occurs with a high relative proportion of species' ranges but likely does not contain many species given the inadequate conditions.

Finally, even though our results highlight the increase of biodiversity representation when agricultural lands are included, we are not suggesting that all conservation strategies should be adopted within agricultural lands. Rather this study aims to raise awareness about the important effects that trade-offs in SCP can have on the representation of conservation features, and predetermines the spectrum of management approaches applied on the priority areas identified. Thus, when an SCP analysis is carried out, the consequences of excluding a particular land use, and the resulting implications for policy recommendation, should be considered.

TABLES

Table 1 Spatial overlap between multiple features (biodiversity, carbon and agriculture) in South America. Percentage of overlapping grid squares for the top 17% of the landscape using all species (below-white) and threatened species (above-grey). 'Feature-only': prioritization with each variable alone; 'All, agri. x': all species weighted equally, carbon 1.0 and agriculture 0, -1.0 and +1.0 respectively.

Variable	Bio. only	Carbon only	Agri. only	All, agri. x 0	All, agri. x -1	All, agri. x 1
Biodiversity only	*******	13.4	23.8	26.5	11.0	30.4
Carbon only	16.7	*******	7.3	84.6	71.3	54.0
Agriculture only	25.9	7.3	*******	11.8	0.2	44.7
All, agri. x 0	23.5	91.9	9.7	*******	62.9	65.2
All, agri. x -1	11.4	71.6	0.2	67.1	*******	39.4
All, agri. x 1	28.7	58.4	44.6	63.5	41.9	*******

FIGURES

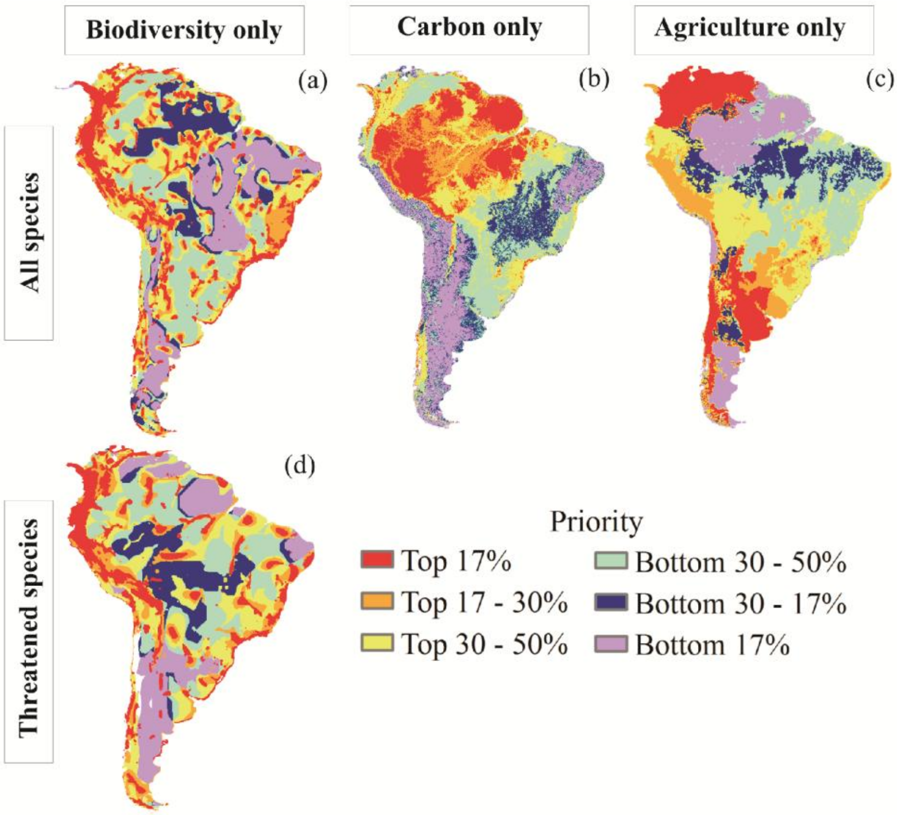


Figure 1: Priority maps for South America based on single-criterion Zonation analyses: (a) biodiversity only using all species (6,606 species of mammal, amphibian and bird); (b) carbon storage only; (c) agricultural production only; and (d) biodiversity only using threatened species (1,120 species of mammal, amphibian and bird).

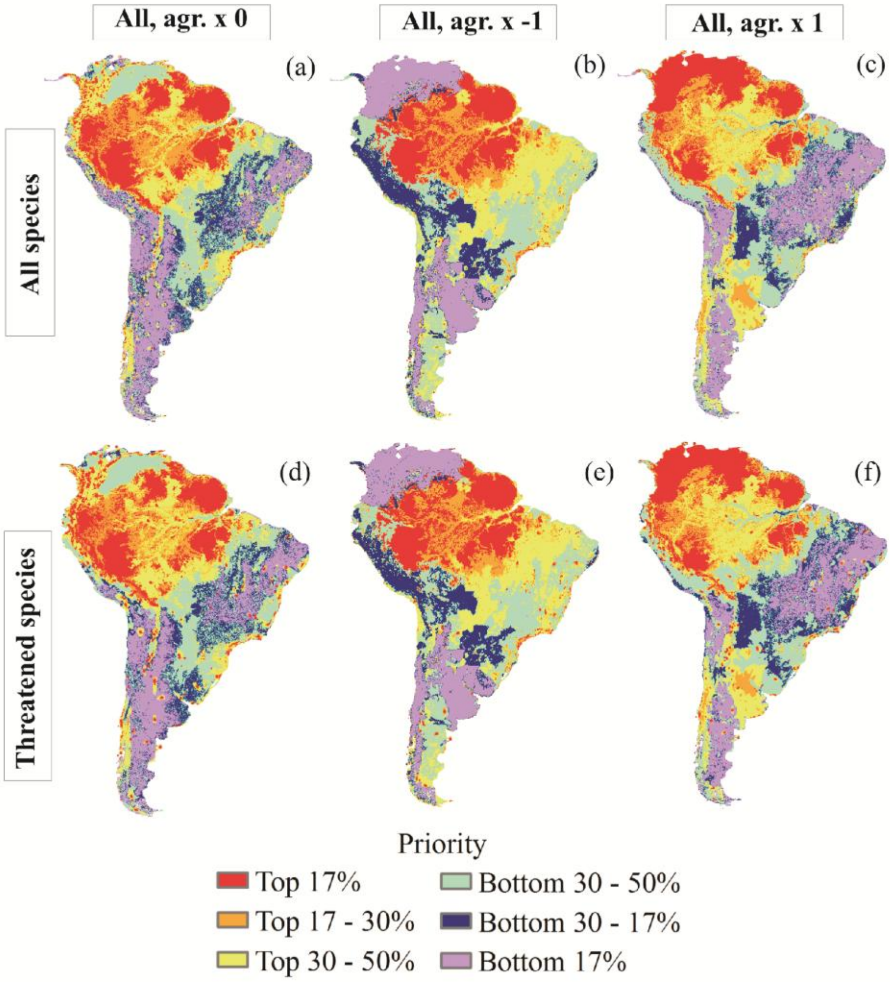


Figure 2: Priority maps for South America based on multi-criterion Zonation analyses. For six maps 'All': all species weighted equally and carbon 1.0. 'All, agr. x 0': All and agriculture weighted 0; 'All, agr. x -1': All and agriculture weighted -1.0; 'All, agr. x +1.0': All and agriculture weighted +1.0. a-c: All species; d-f: Threatened species.

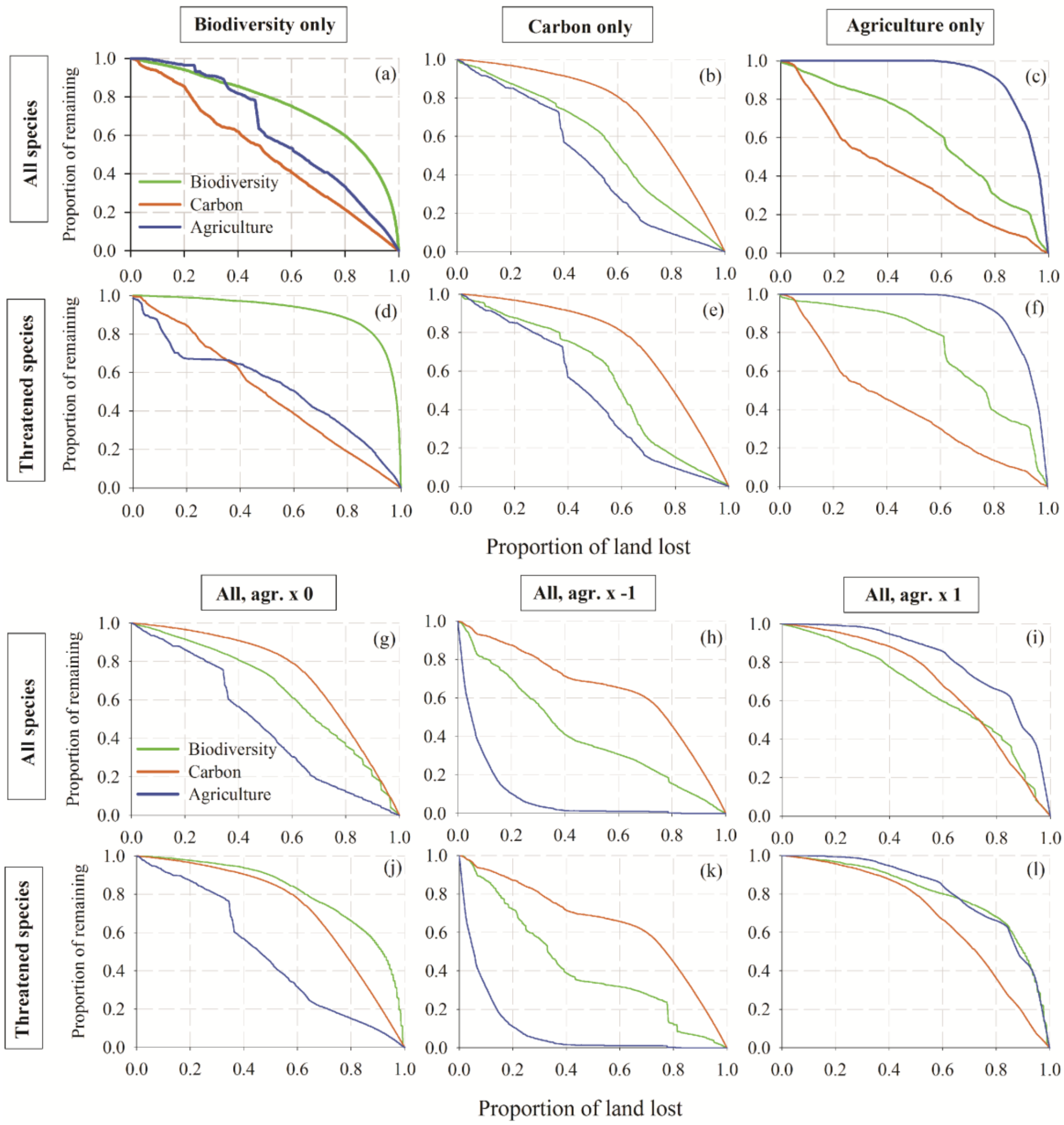


Figure 3: Performance curves for different prioritization strategies using all species and threatened species separately as biodiversity features. The x-axis represents the proportion of land that has been removed from the entire landscape, and y-axis represents the proportion that remains for that particular feature (when x=0 everything remains in the landscape). For biodiversity, the performance curve is an average across individual species curves. 'Feature-only': prioritization with each variable alone, where (a-c) All species, and (d-f) Threatened species. 'All, agri. x': all species weighted equally, carbon 1.0 and agriculture 0, -1.0 and +1.0 respectively. (g-i) All species, and (j-l) Threatened species.

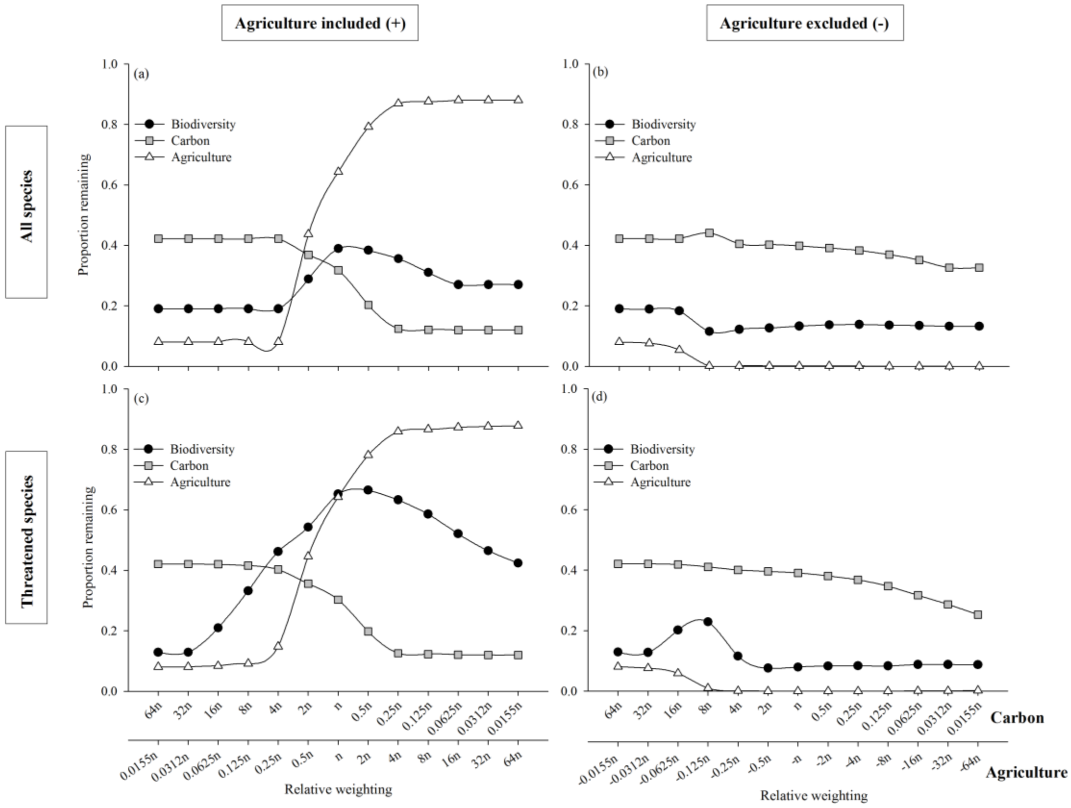


Figure 4: Relative weightings given to carbon *vs.* agriculture whilst biodiversity weight was kept constant at 1.0. Y-*axis* represents what proportion remains for that feature within the top 17% of the landscape. (a-b) Using all species, agriculture is weighted positively and negatively, respectively; (c-d) Using threatened species, agriculture is weighted positively and negatively, respectively.

DISCUSSION

So far, this thesis has assessed the individual effects of location, spatial design and threats on the ability of protected areas to represent and maintain conservation features. It has also explored the role of SCP tools in promoting protected area effectiveness, and the influence of management strategies has been discussed within each of the five chapters. While it is crucial to understand the individual effects of each of these factors, in practice, protected areas are affected simultaneously by all of them. Therefore, knowledge of the interactive effects on protected area effectiveness of location, spatial design, management and threats is fundamental. The general discussion of this thesis presents a framework that assesses these interactive effects. At the very least, I hope that this framework provides a platform to foster new research.

PROTECTED AREA EFFECTIVENESS: DRIVING FACTORS AND THEIR INTERACTIONS

ABSTRACT

Establishing and maintaining effective protected areas is challenging in the Anthropocene. Substantial efforts have been made to understand the main factors that drive this effectiveness, and therefore promote the conservation goals of protected areas. Location, spatial design, management strategy and threats, have been widely acknowledged as key factors. These, have, however, typically been evaluated independently, and there is limited understanding of how they interact and the resulting effects on protected area effectiveness. Here, I develop a framework that brings these four factors together and addresses their combined and interactive effects. This has important implications for how conservation actions are planned and resources are targeted.

INTRODUCTION

WHAT DRIVES THE EFFECTIVENESS OF PROTECTED AREAS?

The establishment and maintenance of protected areas is widely recognized as a key strategy to sustain biodiversity and the ecosystem services that it can provide, both of which can be considered as 'conservation features' (Glossary 1). Given the continuous expansion of human activities and their associated environmental impacts, important efforts have been made to identify and assess the main factors that influence the ability of protected areas to shelter conservation features from anthropogenic pressures (Palomo *et al.* 2014). Location (Rodrigues *et al.* 2004; Thomas *et al.* 2012), spatial design (Williams *et al.* 2005; Edgar *et al.* 2014), management strategy (Leverington *et al.* 2010; Le Saout *et al.* 2013), and threats (Laurance *et al.* 2012b) have been widely assessed as important in driving protected area performance. However, these factors have typically been evaluated independently, and a coherent framework is lacking that brings them together and addresses their combined and interactive effects. This is particularly significant because the effect of one factor can be amplified or buffered by that of another, with important implications for how conservation actions are planned and resources are targeted.

Here, I present such a framework, focusing on location, spatial design, management strategy and threats, which arguably constitute the core of protected area effectiveness. Location refers to the geographic place in the landscape where a protected area is established. Spatial design is the geometric configuration of a protected area, which is determined by its size, shape, connectivity and buffer zone, among others. Management strategy refers to the actions and activities that deal with the land/sea and conservation features under protection. Threats are adverse pressures, often arising from anthropogenic activities, which can be detrimental to the persistence of conservation features. I assess the individual effects of these factors on protected area effectiveness, how they interact, their potential implications for conservation, and the future research needed to address gaps in knowledge.

THE MAIN FACTORS IN ISOLATION

The key aim of protected areas is to separate conservation features from activities that threaten their existence in the natural habitat (Gaston *et al.* 2008). To achieve this they should ideally meet two main objectives. The first is *representation* - sampling biodiversity features and ecological processes. The second is *persistence* – promoting the long-term survival of those conservation features sampled (Gaston *et al.* 2008). It is important first to consider the individual effects of location, design, management and threat on both representation and persistence, as sometimes a factor promoting representation will not necessarily benefit persistence, and vice versa (Table 1).

Location is probably the most influential factor in representation as it determines the nature and extent of the conservation features to be captured within a protected area (Fig. 1). The extent to which an individual protected area captures the biodiversity, the proportion of abundance and distribution ranges of conservation features from a region will determine its representativeness (Gaston *et al.* 2008). This is often tested by comparing the level of occurrence of conservation features within and outside a protected area. While most studies have found that occurrence is greater within protected areas than equivalent sized areas outside, others have found no significant difference, or the converse (Gaston *et al.* 2008). This variation depends mainly on (i) where the protected area is relative to the local distributions of conservation features when it was originally designated; (ii) the extent to which the protected area reduces threatening processes hence promoting the recovery of features; or (iii) the rate of land use change and threatening processes affecting the surrounding area and its associated features.

The location of a protected area also influences the persistence of features captured within it as location largely determines the potential presence of threats taking place within the protected area boundary and those in the surrounding matrix (Hansen & DeFries 2007; Davis & Hansen 2011); added complexity is provided when such threats are escalated by the establishment of the protected area. Persistence can be assessed with respect to how conservation features have changed through time within a protected area boundary. Contrasting this change within and outside individual protected areas will indicate how the status of protection is affecting the persistence of features, enhancing or maintaining them. Studies have shown that, in general, protected areas effectively promote conservation feature persistence by reducing anthropogenic impacts within their bounds (Andam *et al.* 2008; Tang *et al.* 2011; Durán *et al.* 2013a; Durán *et al.* 2013b).

Design directly influences the representation of conservation features within a protected area, and how well they can be maintained (Fig. 1). The individual effects of spatial attributes on protected areas have mainly been assessed through quantitative modelling, however limited studies have empirically evaluated these (Edgar *et al.* 2014). While theoretical studies commonly test *what should be the best spatial design* in order to optimize biodiversity representation, or its persistence when facing threats (e.g. fire events) (Possingham *et al.* 2000; Williams *et al.* 2005), empirical studies test *the observed effect of the spatial design* on representation and persistence from existing protected areas. They achieve this by measuring, often individually, spatial attributes and the sampling and condition of conservation features within its boundary. The most studied spatial attributes have been size, shape, proximity to other protected areas, connectivity and buffer zones (Williams *et al.* 2005). Larger, non-compact and distant protected areas from each other increase representation because they sample more environmental variation (Yamaura *et al.* 2008). However, non-compact protected areas also have higher edge-to-area ratios, increasing the proportion of protected land exposed to edge effects, therefore undermining persistence (Kunin 1997). In addition, isolated protected areas hamper species dispersal between protected areas and re-colonization rates (Newmark 2008; Seiferling *et al.* 2012). In compensation, buffer zones can reduce edge-effects and ecological corridors can promote species dispersal (Watson *et al.* 2013; Wegmann *et al.* 2014). However, how the combined effects of the different spatial attributes can simultaneously balance representation and persistence within individual protected areas is not fully understood.

Management strategies can strongly influence the persistence of conservation features as they define the type of land use and the level of human activities legally permitted within protected areas (Fig. 1). Management strategies range from a very strict conservation approach where human activities are rigorously controlled and limited (e.g. IUCN Management categories Ia-Ib, (IUCN 1994)), to a more permissive approach in which low-impact natural resource management is promoted (e.g. IUCN Management category VI, (IUCN 1994)). However, while there is a broad literature on best practice management, there are limited studies on the extent to which these are actually promoting the persistence of conservation features. Management actions such as anti-poaching patrols (de Merode *et al.* 2007; Briceno *et al.* 2013), wildfire prevention (van Wilgen *et al.* 2010;

Shive *et al.* 2013) and habitat management (Lawson *et al.* 2014) have been commonly assessed, and both effective and ineffective performance have been documented. This suggests that management strategies are very context specific, making it particularly challenging to set out general recommendations.

Threats can strongly influence the survival of conservation features, and consequently their representation. The impacts of threats are often evaluated using a 'before and after' approach, in which the condition of a protected feature that is apparently affected by a threat is assessed through time (Butchart *et al.* 2010; Pimm *et al.* 2014). According to where the threat originates, it is possible to differentiate direct and indirect threats. Direct threats are those that arise within protected area boundaries, while indirect threats refer to pressures from outside but which harm conservation values within (e.g. edge-effects) (Graeme L. Worboys 2006). Direct threats such as illegal hunting, deforestation and harvesting (Graeme L. Worboys 2006) are often a result of the displacement of indigenous communities from their traditional lands fostered by the imposition of a protected area (West *et al.* 2006). They can also be stimulated by the relatively good condition of conservation features within protected areas. Indirect threats are broadly driven by four processes: habitat transformation, over-exploitation, biotic exchange and pollution (MA 2005).

A more comprehensive understanding of the socio-ecological effects of the establishment of an individual protected area on local communities is required in order to prevent and mitigate direct threats. How conservation features are understood to respond to external pressures is also key for successful management strategies.

INTERACTIVE EFFECTS THAT DRIVE PROTECTED AREA EFFECTIVENESS

Location, design, management and threats directly affect protected area effectiveness and, thus, knowledge of their interactive effects is essential for achieving the best representation and persistence of conservation features. Many interactive effects are indirect, in that one factor modifies the magnitude (amplifies or buffers) or direction (positive or negative) of the effect of another. Several studies have demonstrated, although often not as the main aim of their research, pair-wise interactions between the four factors affecting protected area effectiveness (Table 2).

Given that I have previously described the individual effects of each of the factors on representation and persistence, in the following section I focus on the interactions between location, design, management and threats, from which the effects on protected area effectiveness (Box 1) can then be deduced.

Location-Design: location can influence the spatial design of protected areas in different ways (Fig. 1). First, by determining the nature and extent of what is being represented, location influences the type of spatial design required to achieve an effective protection. For instance, depending on ecological requirements, such as the home range extent and the minimum viable population size of conservation features, the area of a protected area should vary accordingly (Simberloff & Abele 1976). Also, supporting ecosystem services (e.g. primary production) are considered to require large protected areas in order to be appropriately promoted, relative to other ecosystem services such as cultural (i.e. recreation) for which small size areas can be adequate (Peres 2005; Palomo *et al.* 2014). Second, the topography of the location will influence protected area spatial features, such as the shape, which in turn determines the extent to which a protected area is exposed to the edge-effects generated by the threats associated with the surrounding matrix (Hansen & DeFries 2007). Such exposure to external pressures can promote the establishment of a buffer zone, a common mitigation measure to minimize edge-effects (Carvalho Perello *et al.* 2012).

Location-Threats: the location of a protected area also determines the characteristics of the surrounding system or matrix and its associated threats (Hansen & DeFries 2007; Davis & Hansen 2011), which, according to the threat, can directly or indirectly undermine the persistence of conservation features (Fig. 1). The surrounding matrix may be dominated by a continuous area of unmodified and unsettled habitat, which is less prone to generating anthropogenic threats. Alternatively, the matrix may be highly fragmented with patches of different anthropogenic land use, for example, urban, agricultural, industrial or any type of extractive activity.

Location-Management: a protected area management strategy is usually applied based on the conservation aims, which in turn are determined by the local conservation features to be protected (Fig. 1). The level of vulnerability of such conservation features (also determined by threats from the surrounding matrix) is often an important criterion in deciding the management approach (Lockwood 2010). For example, while a *proactive* approach is oriented to areas with low levels of vulnerability, a *reactive* approach focuses on highly vulnerable areas exposed to strong pressures (Brooks *et al.* 2006).

Design-Management: design and management can interact in both directions (Fig. 1). Depending on the extent to which design promotes conservation features persistence, this will influence the cost of management actions (Fig. 1). For instance, if the size or shape of a protected area are not appropriate for maintaining species (e.g. too small for population size, high edge-effects), management actions will need to be applied to mitigate these design inadequacies. Such management actions can, in turn, modify the design (Fig. 1), by widening a buffer zone or increasing connectivity through ecological corridors (Jantz *et al.* 2014).

Design-Threats: similar to the design-management interaction, design and threats interact in both directions (Fig. 1). Design influences the impact of threats by determining the ability of species to cope with the harmful effects of those pressures. The persistence of species populations will commonly be boosted through the provision of sufficient area, connectivity for dispersal and shelter from edge-effects(Treves 2009). In addition, threats can foster modifications to the design of protected areas, such as establishing a buffer zone or ecological corridors. Equally, the expansion of surrounding competing land-uses can also alter spatial design by contracting a protected area boundary (e.g. *downsizing,* (Mascia & Pailler 2011)).

Management-Threats: the extent to which potential threats are identified during management planning will largely affect how readily they can be later mitigated (Fig. 1). The success of a mitigation measure will then determine the impact of a threat on persistence (Lockwood 2010; Hayward 2011; Le Saout *et al.* 2013). A lack of or failure to deliver appropriate management (the former known as the 'paper park' phenomenon) can become a threat itself. Management procedures can, however, be dynamic, and by continuous monitoring of the performance of protected areas and risk assessment, they can be readdressed in order to better mitigate emerging pressures. Equally, political pressure to promote human extractive activities within protected areas can also influence management and decrease its stringency (e.g. *downgrading,* (Mascia & Pailler 2011)).

Multiple-Interactions on Threats: the type and magnitude of a threat arises from the synergistic effects of location, design and management factors. In other words, the combined effects resulting from: (i) the susceptibility of conservation features to potential pressures in the surrounding matrix, (ii) the extent to which the design aggravates and/or mitigates these potential pressures, and (iii) the ability of management actions to foresee and/or tackle the adverse effects. All three determine the net impact on the persistence of conservation features, and as consequence, on their representation (Laurance *et al.* 2012b).

CONCLUDING REMARKS AND FUTURE DIRECTIONS

Despite progress in understanding the individual effects of the factors driving the effectiveness of protected areas, studies considering multiple factors and evaluating their interactions remain scarce. I believe that such an advance is particularly hampered by the lack of a more comprehensive framework highlighting the relevance of these interactions in protected area research.

The effects of pair-wise interactions between threats and the other three factors, location, design and management, are probably the best assessed. The persistence of features within a protected area whose surrounding matrix does not contribute to its conservation goals will constantly be threatened (Hansen & DeFries 2007; DeFries *et al.* 2010). A surrounding matrix dominated by intensive human activities, such as agriculture, mining or urbanization, enhances the isolation of a protected area, which can be particularly detrimental for species dispersal, population source-sink dynamics and trophic structure (Hansen & DeFries 2007). In such situations, the spatial design of a protected area plays a vital role in mitigating impacts of the external pressures. Thus, depending on the effective area available for species survival and ecosystem functions, the connectivity with other protected areas and the proportion of protected land exposed to the adjacent matrix will determine the degree of such impacts. In this regard, understanding the interactions between spatial attributes becomes critical as their synergistic or antagonistic effects will certainly influence the benefits to persistence promoted by mitigation actions.

There has also been research into the pair-wise interaction between location and management. Management actions have been often recommended based on threats derived from a specific location (Table 2). However, such actions commonly do not account for the interaction between the spatial design of the protected area and the threats. Thus, the extent to which the spatial design can buffer the benefits of management actions on conservation features remains poorly explored.

Progress in understanding other interactions between factors remains limited. In particular, and essential, are the interactive effects between location and design. In the light of limited land and resources for the designation of new protected areas, optimizing the spatial design according to what conservation features are to be protected is crucial. For instance, basic knowledge on the minimum area required to maintain viable populations of target species is still very limited (Flather *et al.* 2011). Similarly, the minimum proximity to allow species movement or successful migration has not been well documented. Given that this knowledge is species-habitat specific, providing general advice becomes highly challenging.

In summary, the main challenges are to generate empirical evidence of the interactive effects between location, design, management and threats on the persistence of conservation features in protected areas. Ideally, this evidence should be generated through field work in order to explicitly evaluate pair-wise and multiple interactions (Box 1). Equally important is for such field work to be long-term, in order to analyse how adverse effects on persistence can change the representativeness of the features captured by existing protected areas. For this purpose, research is required at an individual protected area scale in order to track the effects of specific interactions on persistence at population and community levels. It is also required at a protected area system scale, in order to extrapolate the effects at a metapopulation level and the overall representation of conservation features. Such an approach will allow a better understanding of the combined effects of location, design, management and threats on the overall effectiveness of protected areas. This will improve recommendations as to the targeting of conservation efforts in existing protected areas and in the establishment of successful future areas.

TABLES

Box 1. Interactions between the main factors driving protected area effectiveness.

The effectiveness of protected areas is made up of two components, representation (i.e. sampling biodiversity features and ecological processes) and persistence (i.e. promoting the long-term survival of those conservation features sampled). The effectiveness of protected areas is driven by multiple factors, such as location, spatial design, management and threats, which in turn are influenced by the socio-economic context in which a protected area is immersed . Knowledge of the interactive effects of these factors on representation and persistence is crucial to succeed in the long term protection of conservation features.

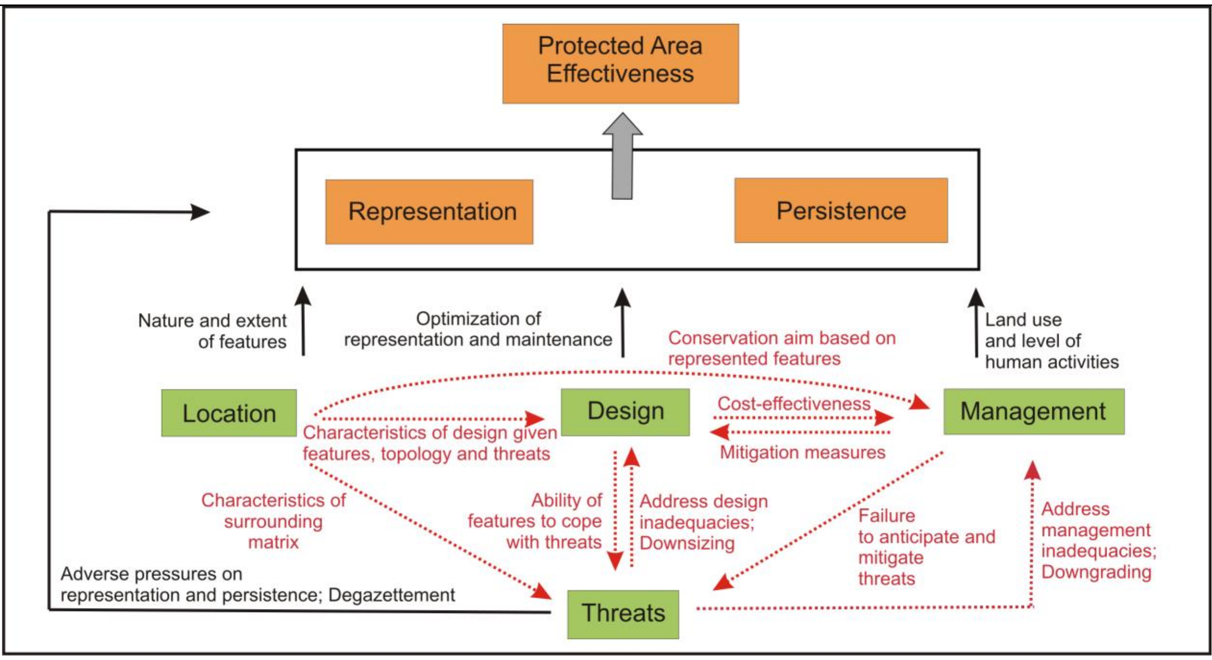


Figure I. Scheme showing potential combined effects between location, design, management and threats to a protected area. All these influence the main components of protected area effectiveness, representation and persistence. Black-continuous arrows represent direct effects, whereas red-broken lines represent indirect interactive effects by which a factor changes the direct effect of another factor. The text close to each arrow denotes the type of influence between factors.

Table 1. Summary of studies that have independently assessed the effects of location, spatial design, management strategies and threats on representation and persistence.

Factor	Effect on representation	Effect on persistence
Location	(Watson *et al.* 2011; Durán *et al.* 2013a)	(Bruner *et al.* 2001; DeFries *et al.* 2010; Laurance *et al.* 2012a)
Spatial design		
Area	(Marianov *et al.* 2008; Lasky & Keitt 2013)	(Marianov *et al.* 2008; Lindsey *et al.* 2011; Lasky & Keitt 2013)
Shape	(Heegaard *et al.* 2007; Yamaura *et al.* 2008)	(Woodroffe & Ginsberg 1998; Balme *et al.* 2010; Gill *et al.* 2014)
Connectivity	(Brudvig *et al.* 2009; Seiferling *et al.* 2012)	(Cerdeira *et al.* 2010; Reddy *et al.* 2012)
Proximity	(Williams 2008)	(Haight & Travis 2008; Kitzes & Merenlender 2013)
Buffer zone	(Palomo *et al.* 2013)	(Harper *et al.* 2008; DeFries *et al.* 2010)
Management strategy	(Laurance *et al.* 2012a; Durán *et al.* 2013a)	(Kerbiriou *et al.* 2009; Leroux *et al.* 2010; Sachedina & Nelson 2010; Pettorelli *et al.* 2012)
Threat		
Habitat transformation	(Laurance *et al.* 2012a; Gross *et al.* 2013)	(Joppa *et al.* 2008; Funi & Paese 2012; Gross *et al.* 2013)
Over-exploitation	(Laurance *et al.* 2012a)	(Hilborn *et al.* 2006; Linder & Oates 2011; Effiom *et al.* 2013)
Biotic exchange	(Laurance *et al.* 2012a; Vardien *et al.* 2013)	(Rao *et al.* 2010)
Pollution/Nutrient loading	(Laurance *et al.* 2012a)	(McDonald *et al.* 2009)

Table 2. Summary of studies that have evaluated pair-wise interactions between the main factors of protected area effectiveness: location, design, management and threats.

	Location	Design	Management	Threat
Location	**************			
Design	(Hurley *et al.* 2012; Palomo *et al.* 2013)	***************		
Management	(Bryan & Crossman 2008; Joppa & Pfaff 2009; Hansen *et al.* 2011)	(Peres 2005; Goetz *et al.* 2009; Lockwood 2010)	***************	
Threats	(Foxcroft *et al.* 2007; Gimmi *et al.* 2011; Hamilton *et al.* 2013)	(Glen *et al.* 2013; Watson *et al.* 2013; Gill *et al.* 2014)	(Paruelo *et al.* 2005; Vardien *et al.* 2013)	************

APPENDICES

APPENDIX 2: *Representation of ecosystem services by terrestrial protected areas: Chile as a case study* ***(CHAPTER 2)***

Table A2.1 Protected area categories used in this study, and their associated management strategies defined under the International Union for Conservation of Nature (IUCN) regulatory framework.

Protected area category	Institution administrator	Management aims	IUCN category
National Park (SNASPE)	CONAF	Protection and conservation of natural scenic beauty, flora and fauna. Only scientific and educational activities are allowed.	II
National Reserve (SNASPE)	CONAF	Conservation through managed intervention of natural resources	IV
Natural Monument (SNASPE)	CONAF	Protection of a specific natural feature with aesthetic, historical or scientific value.	III
Nature sanctuary	National Monument Board	Conservation for scientific or government purpose.	V
Lands of national heritage	Ministry of National Heritage	Conservation of natural ecosystem and national patrimony. Sustainable management of natural resources are allowed.	IV
Priority Sites for Biodiversity Conservation	CONAMA	NA	No category
Private Protected Areas	Private	NA	No category

Table A2.2 Summary of values used in calculating agricultural production (FAO 2000)

Crop	USD/tonne
Alfalfa	80
Apples	196.4
Appricot	262.8
Artichok	374.9
Asparragus	658.4
Avocado	1132.7
Barley	165.3
Carrot	145.5
Cherry	810.6
Chickpea	639.4
Grape	230.2
Green bean	342.8
Kiwi	162.7
Lemon	238.6
Lentils	443.5
Lettuce	329.8
Maize	127.6
Oats	120.5
Onion	276.6
Orange	164.4
Pea	346.1
Peach	293.6
Pear	224.4
Plum	163.2
Potato	155.7
Pumpkin	165.8
Sugar beet	55.4
Sunflower	237.2
Tobacco	1679.3
Tomato	302.9
Watermelon	181.8
Wheat	95.2

Table A2.3 Average of NDVI values and coverage characteristics of different vegetation types in Chile.

Vegetation type	NDVI average	Area coverage (km^2)	Proportion of area	Weighted average (NDVI average x proportion of area)
Forest	0.627	191,704	0.253	0.158
Crops	0.564	8,803	0.012	0.006
Peatland	0.487	19,708	0.026	0.012
Steppe	0.346	43,945	0.058	0.02
Shrubland	0.341	152,203	0.201	0.068
Wetland	0.177	1,129	0.001	0.0002
Bare areas[(1)]	0.174	338,799	0.447	0.078
			Total NDVI average	**0.34**

[(1)] Bare areas category includes iceland, rock and sand.

Table A2.4 Biodiversity representation by species group in the five management categories and the suggested sites for the new integrated protection system (PSBC and Private protected areas). A ratio of > 1 indicates that a particular group is over-represented relative to what would be expected for its area; values < 1 indicate under-representation. 'All management strategies' refers to the area covered by all the seven categories. PA: Protected Area; PSBC: Priority sites for biodiversity conservation.

PA Category	Amphibians	Mammals	Birds	Plants
Ministry of Heritage lands	**2.36**	0.90	1.00	0.50
National Parks	**1.06**	0.72	0.92	0.39
National Reserve	0.76	0.56	0.83	0.51
Natural Monument	0.72	**1.36**	0.98	0.84
Nature Sanctuary	**2.92**	**1.22**	1.09	0.75
PSBC	**5.46**	**4.05**	**4.16**	**4.69**
Private PA	0.43	0.25	0.25	0.18
All management strategies	**1.06**	0.75	0.92	0.59

Table A2.5 Land use cover within the current Chilean protected areas system (Scenario 1).

Vegetation type	Percentage of total area
Forest	34.15
Crops	0.0007
Peatland	9.48
Steppe	3.1
Shrubland	2.72
Wetland	0.38
Bare areas(1)	50.14

(1) Bare areas category includes iceland, rock and sand.

Table A2.6 Land cover within each of the five management categories and the suggested sites for the new integrated protection system (PSBC and Private protected areas). PA: Protected Area; PSBC: Priority sites for biodiversity conservation.

	Percentage of area							
PA Category	Forest	Crops	Peatland	Steppe	Shrubland	Wetland	Bare areas(1)	**Coverage area (km^2)**
Ministry of Heritage lands	43.58	0	11.37	2.13	9.48	0	33.31	1,796
National Parks	30.17	0	7.62	2.91	2.15	0.33	56.8	93,104
National Reserve	39.39	0	13.76	3.58	2.67	0.48	40.09	52,824
Natural Monument	7.4	0	0	9.21	10.93	7	65.44	381
Nature Sanctuary	53.75	0.002	0	2.17	11.49	0	32.60	4,594
PSBC	30.33	0.28	1.88	3.22	35.21	0.06	29.02	42,591
Private PA	48.18	0.45	0.23	2.1	29.63	0.06	19.33	9,867

(1) Bare areas category includes iceland, rock and sand.

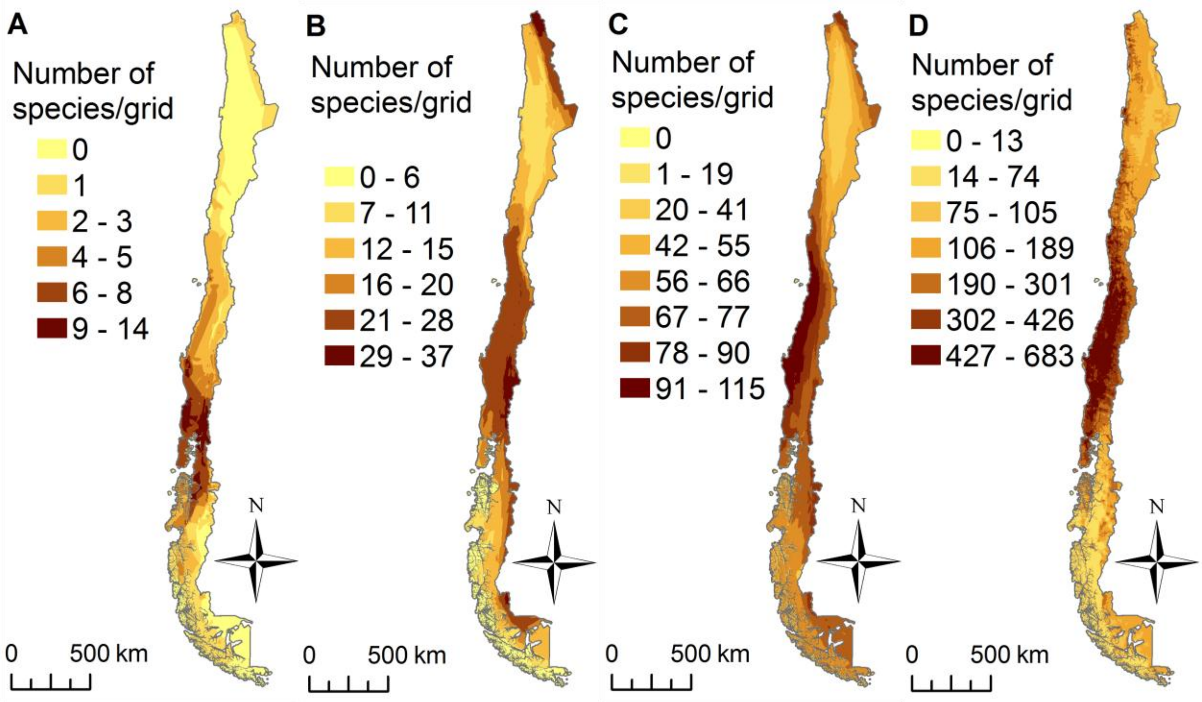


Figure A2.1 Distribution maps of species richness for four taxonomic groups at 1 km^2 grid resolution. a) Amphibians, b) Mammals, c) Birds and d) Plants.

APPENDIX 3: *Existing protected areas, historical design guidelines and the implications for conservation* **(CHAPTER 3)**

Table A3.1 Examples of studies evaluating level of fragmentation within protected areas. For each study the coefficient of variation of NDVI is indicated.

Country	Protected Area	Description	Source	Coefficient of variation of NDVI
Mexico	Monarch Butterfly Biosphere Reserve	'Statistical analyses found no significant differences of loss rates of conserved canopy cover forest between LTU with and without FMP, nor with other change processes such as recovery and re-vegetation'.	(Navarrete *et al.* 2011)	0.0013
Guatemala	Tinkal National Park	[a]No land cover change observed within the protected area (Table 2)	(Nagendra 2008)	0.018
Indonesia	Gunung Palung National Park	'Our satellite, Geographic Information System, and field-based analyses show that from 1985 to 2001, Kalimantan's protected lowland forests declined by more than 56%'.	(Curran *et al.* 2004)	0.037
Peru	Tambopata National Reserve	'Illegal gold mining was identified as a further direct driver of deforestation in Tambopata National Reserve causing small-scale forest clearing, particularly along riverbanks'.	(Vuohelainen *et al.* 2012)	0.047
Jamaica	Blue Mountains National Park	'Fragmentation continued post-establishment, and manifested itself in an increasing number of smaller more vulnerable fragments; the number of fragments increased by 60%, and the mean fragment size decreased by 40%. Core areas decreased with ensuing increases in edge lengths, and fragments became more isolated from one another'.	(Chai *et al.* 2009)	0.058
Trinidad y Tobago	Caroni Swamp Reserve Forest Reserve	'Results show that the classification of Caroni immediately identifies a shift towards anthropogenic land cover types, suggesting an increase in human activity within the park. This finding is further supported by the continuous measures used, such as decreases in mean NDVI and greenness values suggesting a decrease in the amount or health of the vegetation'.	(Gibbes *et al.* 2009)	0.185
Mexico	Xochimilco World Heritage Site	'The results show an alarming rate of urbanisation in 17 years. LULC change runs in one direction from all other land use categories towards urban land use'.	(Merlín-Uribe *et al.* 2013)	0.257

[a] This is a description of the results presented in Table 2 on Negendra 2008. It is not a literal text extraction from the paper

Table A3.2 Examples of ecological densities for mammal species. Herbivorous and carnivorous species were selected for three different size categories: small, medium and large (Data source: PanTHERIA; Jones et al. 2009). Area required to protect a minimum viable population (MVP) was calculated by dividing a rule-of-thumb estimate of the number of adult individuals required to maintain a MVP (Reed *et al.* 2003) by the ecological density of each species. Area= 7,000/density.

Consumer type	Size category	Adult body mass (g)	Species	Ecological density (individuals/ km^2)	Area required to maintain MVP (km^2)	Percentage of PAs would maintain a MVP (%)
Herbivore	Small	10	*Reithrodontomys megalotis*	1,152.4	6.1	25.1
	Medium	6,528	*Phascolarctos cinereus*	163.01	42.9	11.6
	Large	3,269,794	*Elephas maximus*	0.53	13,207.5	0.2
Carnivore	Small	9	*Sorex araneus*	1,859.01	3.7	29.8
	Medium	4,820	*Vulpes vulpes*	1.1	6,636.6	0.5
	Large	158,623.9	*Panthera leo*	0.11	63,636.4	0.03

Table A3.3 Examples of dispersal ability for mammal species. Herbivorous and carnivorous species were selected for three different size categories: small, medium and large (Data source: (Whitmee & Orme 2013).

Consumer type	Size category	Adult body mass (g)	Species	**Dispersal ability (km)**	Percentage of PA equally or closer (%)
Herbivore	Small	36	*Myodes rufocanus*	0.3	55.3
	Medium	2,685	*Trichosurus vulpecula*	5.5	80.4
	Large	16,850	*Macropus rufogriseus*	46.5	97.5
Carnivore	Small	52	*Antechinus minimus*	0.04	49.3
	Medium	31,756	*Canis lupus*	96.3	99.1
	Large	158,623	*Panthera leo*	12.3	89.3

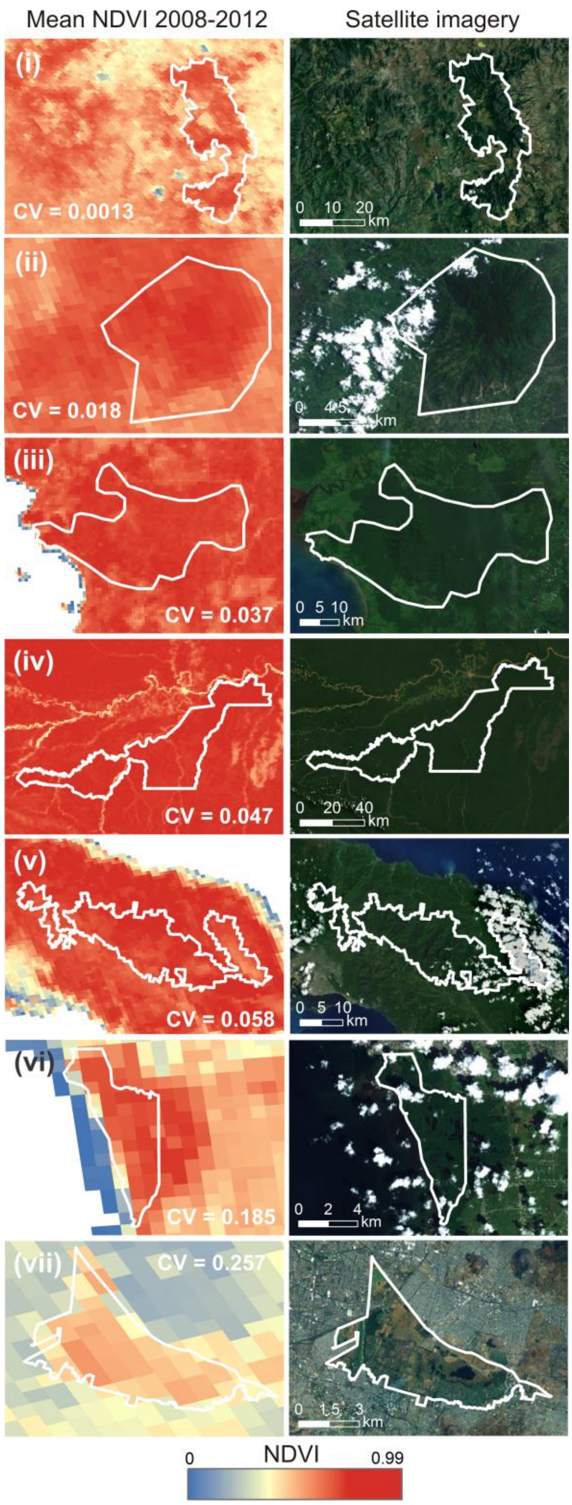


Figure A3.1 Comparison between NDVI composites showing the coefficient of variation (CV) calculated from NDVI pixels extracted from within PA boundaries and satellite imagery for seven Brazilian PAs. (i) Monarch Butterfly Biosphere Reserve, (ii) Tinkal National Park, (iii) Gunung Palung National Park, (iv) Tambopata National Reserve, (v) Blue Mountains National Park, (vi) Caroni Swamp Reserve Forest Reserve, (vii) Xochimilco World Heritage Site.

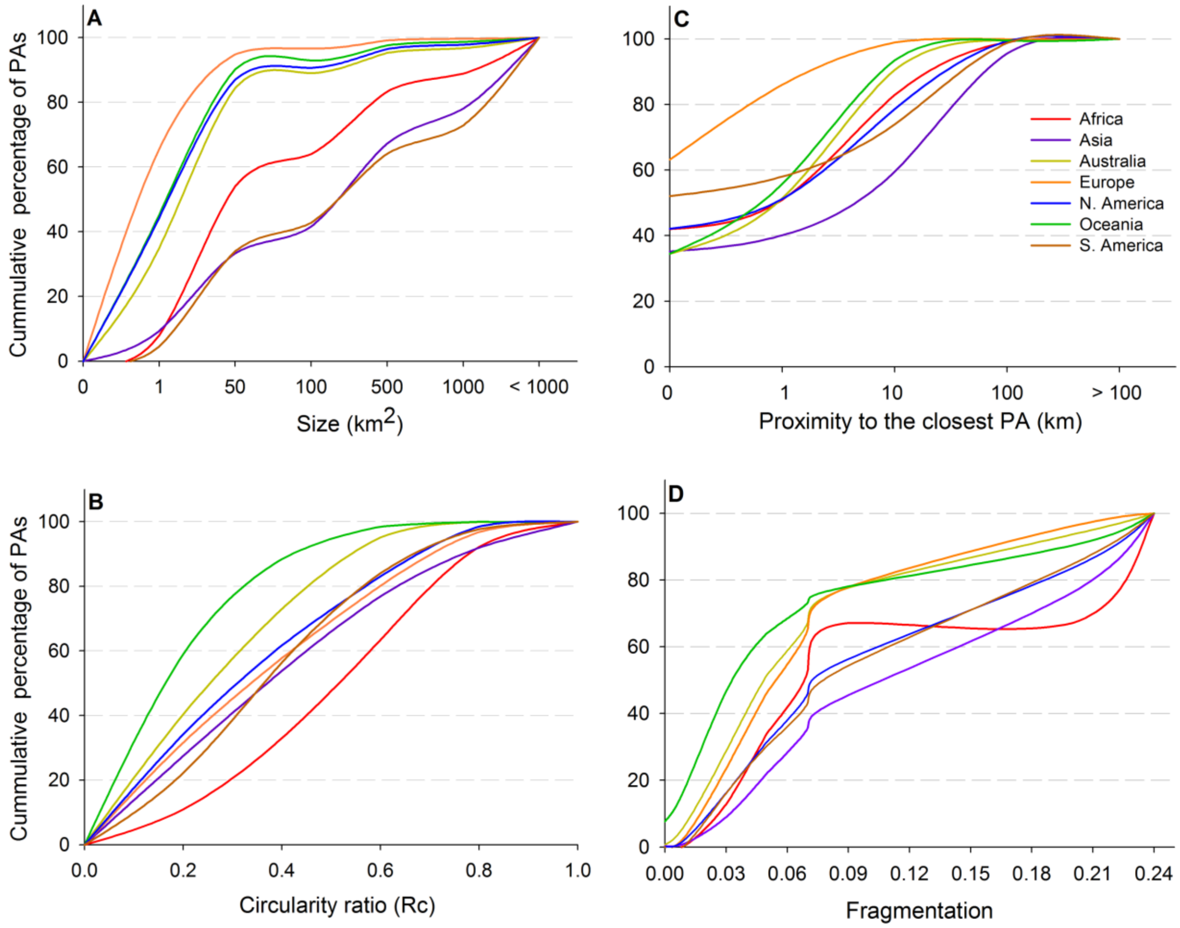


Figure A3.2 Cumulative percentage distribution of PAs for four spatial attributes - size, shape, proximity and fragmentation - in seven different regions (Africa, Asia, Australia, Europe, North America, Oceania and South America). **A)** Size of PAs, **B)** Shape of PAs expressed by circularity ratio (Rc), **C)** Proximity among PAs, **D)** Fragmentation level within PAs estimated from coefficient of variation (CV) calculated from NDVI pixel values extracted from within PAs.

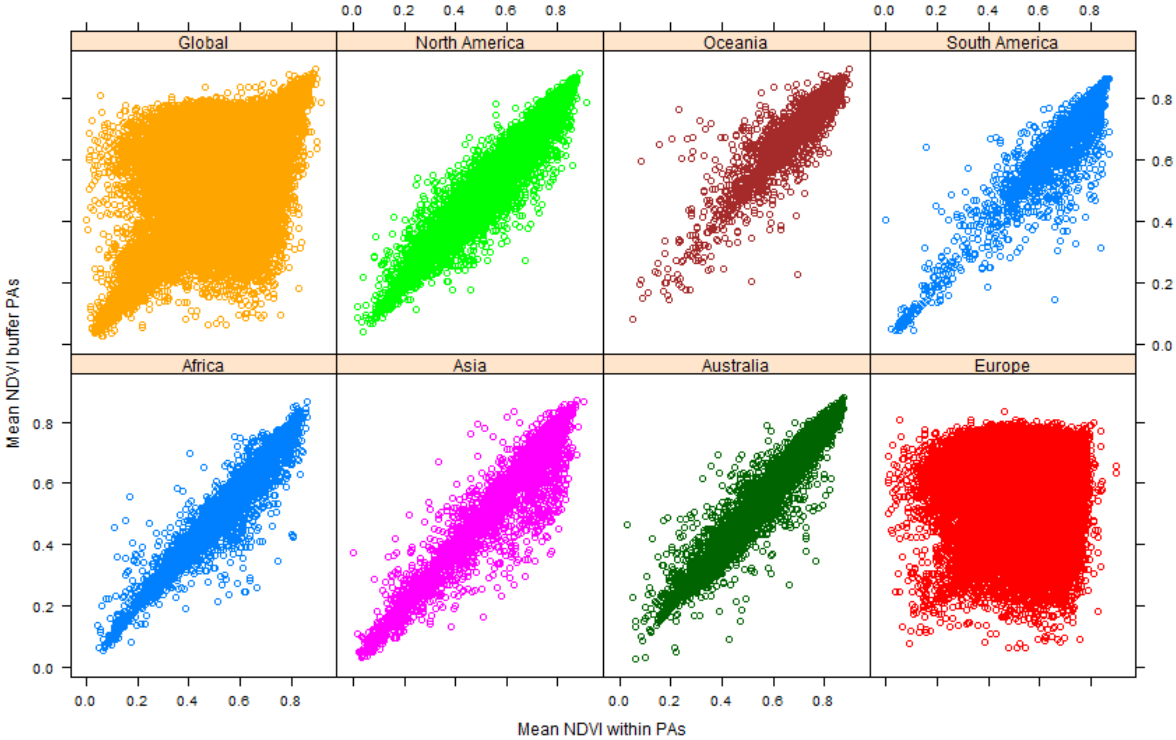


Figure A3.3 Relations between mean NDVI within PAs (pp-PA) and their associated buffers (pp-Buffer). These relations were extracted from Major Axis Regressions calculated for the global and seven regional sets of PAs.

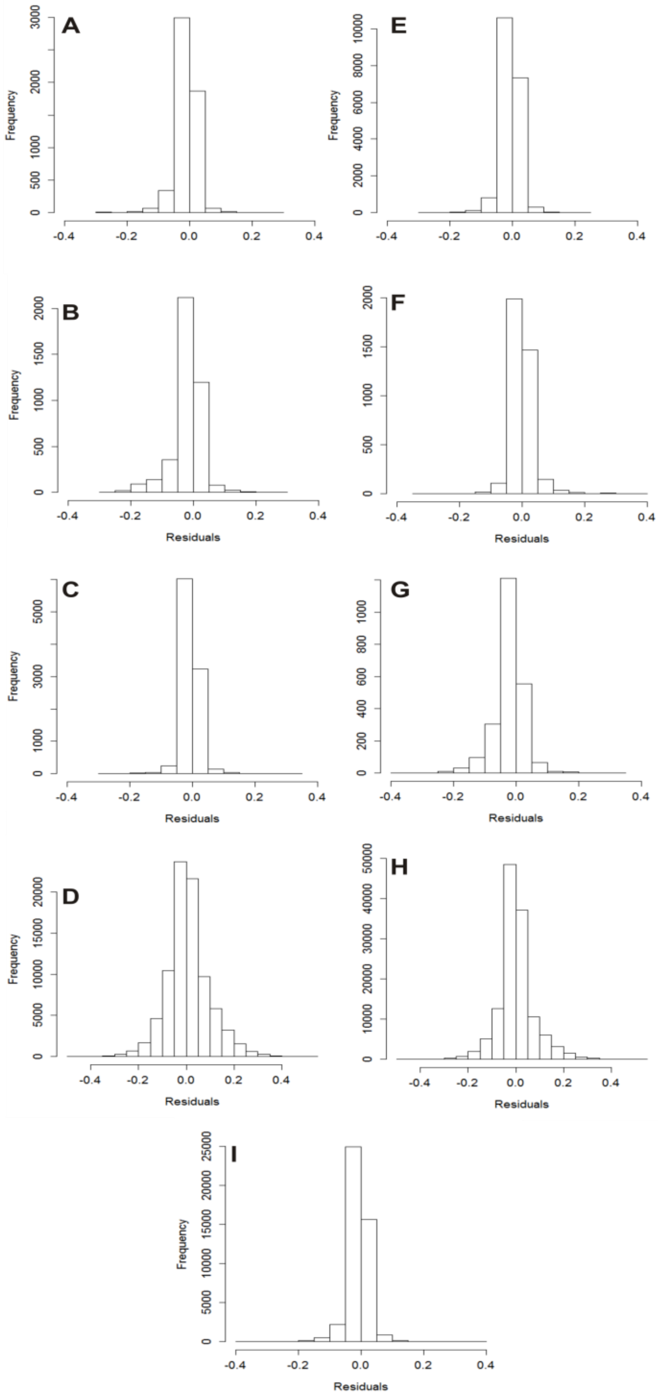


Figure A3.4 Histogram of residuals extracted from major axis regressions between mean NDVI within PAs (pp-PA) and their associated buffers (pp-Buffer). Residuals were calculated against a slope equal to 1 and intercept of 0. These relations were calculated for the global and seven regional sets of PAs. A) Africa, B) Asia, C) Australia, D) Europe, E) North America, F) Oceania, G) South America, H) Global, and I) Global omitting Europe.

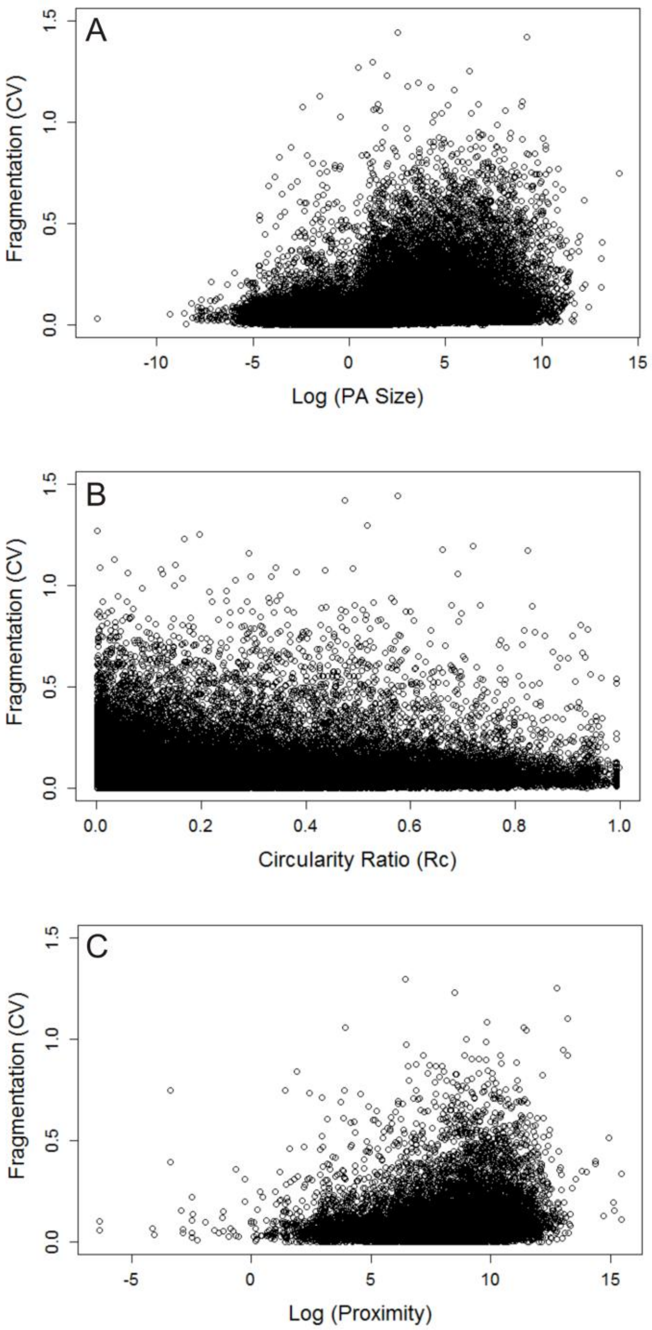


Figure A3.5 Relationships between PA spatial attributes. **A)** Fragmentation vs. Log (Size); **B)** Fragmentation vs. Circularity Ratio, and **C)** Fragmentation vs. Log (Proximity).

APPENDIX 4: *Biodiversity representation within protected areas is associated with multiple interacting spatial design features* **(CHAPTER 4)**

Appendix 4.1

In order to account for the effect of habitat type in species richness representation we incorporated ecoregion categories as a random effect in the models. An ecoregion or ecological region is a biogeographic regionalization of the Earth's terrestrial biodiversity and is a good representation of the distribution of distinct assemblages of species and communities. In 2008 The Nature Conservancy (TNC) made a global vector digital map of 867 ecoregion categories freely available (http://maps.tnc.org/gis_data.html). In order to assign each protected area to its corresponding ecoregion category, the distributions of protected areas and terrestrial ecoregions were overlapped and intersected with the default function in ArcGIS 10. Thus, a subset of 130 ecoregion categories were assigned to individual protected areas. Full description of dataset available on: http://maps.tnc.org/files/metadata/TerrEcos.xml.

Table A4.1 Generalized linear mixed model (glmm) testing the fixed effect of the spatial attributes of a protected area on its species richness representation. Fixed effects are area, shape index, proximity to the nearest protected area, and fragmentation level. Latitude of each protected area was characterised by its centroid and used as a covariate. Glmm was carried out for four different protected area datasets, which had species richness of amphibians, birds, mammals and all three taxa together. Country of each protected area, nested in the respective continent, was included as a random effect.

	Estimate	SE	z-value	Relative importance	95% confidence interval
Amphibian (n=335 PAs)					
Intercept	17.79	4.27	4.16***		(9.42, 26.17)
Area	7.01	1.86	3.37***	1.00	(3.36, 10.65)
Shape	-3.29	1.42	2.33*	0.92	(-6.07, -0.52)
Proximity	2.12	1.62	1.25ns	0.42	(-1.19, 5.41)
Fragmentation	-9.49	1.52	6.23***	1.00	(-12.48, -6.51)
Latitude	-10.36	3.89	2.66**	1.00	(-18.00, -2.73)
Area*Fragmentation	-10.61	2.75	3.86***	1.00	(-16.00, -5.21)
Area*Shape	0.28	5.48	0.053ns	0.23	(-10.45, 11.03)
Fragmentation*Shape	2.15	3.05	0.71ns	0.28	(-3.83, 8.14)
Fragmentation*Latitude	16.15	3.12	5.17***	1.00	(10.03, 22.28)
Birds (n= 454 PAs)					
Intercept	193.21	16.66	11.59***		(160.56, 225.86)
Area	64.47	14.43	4.47***	1.00	(36.18, 92.76)
Shape	-62.65	10.46	5.99***	0.52	(-83.13, -42.14)
Proximity	-12.38	10.48	1.18ns	0.41	(-32.92, 8.17)
Fragmentation	-48.24	10.97	4.39***	1.00	(-69.73, -26.74)
Latitude	-95.57	20.21	4.72***	1.00	(-135.18, -55.95)
Area*Fragmentation	-84.48	21.32	3.96***	1.00	(-126.26, -42.69)
Area*Shape	7.96	46.01	0.17ns	1.00	(-82.23, 98.13)
Fragmentation*Shape	33.20	21.83	1.52ns	0.52	(-9.59, 75.99)
Fragmentation*Latitude	87.73	21.11	4.15***	1.00	(46.36, 129.09)
Mammals (n= 377 PAs)					
Intercept	48.67	1.75	27.79***		(45.14, 51.22)
Area	24.79	4.53	5.46***	1.00	(14.34, 32.55)
Shape	-1.85	3.27	0.56ns	1.00	(-8.57, 4.60)
Proximity	5.18	2.95	1.76ns	0.58	(-0.84, 10.82)
Latitude	-25.27	3.44	7.32***	1.00	(-29.81, -17.55)
Fragmentation	-13.56	3.13	4.33***	1.00	(-20.08, -7.97)
Area*Fragmentation	-27.71	6.63	4.18***	1.00	(-40.38, -13.94)
Area*Shape	31.69	12.78	2.48*	0.95	(6.14, 56.59)
Fragmentation*Shape	8.11	6.59	1.23ns	0.92	(-2.32, 23.88)
Fragmentation*Latitude	32.90	5.64	5.84***	1.00	(22.68, 44.86)
All taxa (n= 405 PAs)					
Intercept	283.79	19.69	14.41***		(245.21, 322.37)
Area	75.61	17.21	4.39***	1.00	(41.88, 109.33)
Shape	-73.03	14.59	5.01***	1.00	(-112.01, -53.43)
Proximity	-47.19	15.07	3.13**	1.00	(-77.13, -18.90)
Fragmentation	-80.86	17.76	4.55***	1.00	(-115.66, -46.05)
Latitude	-178.09	30.39	5.86***	1.00	(-237.66, -118.53)
Area*Fragmentation	-92.23	28.30	3.26**	1.00	(-147.69, -36.76)
Area*Shape	-26.60	47.68	0.56ns	0.29	(-120.05, 66.84)
Fragmentation*Shape	48.80	29.77	1.63	0.57	(-9.56, 107.15)
Fragmentation*Latitude	145.46	33.38	4.35***	1.00	(80.03, 210.89)

APPENDIX 5: *Global spatial coincidence between protected areas and metal mining activities* **(CHAPTER 5)**

Table A5.1 Percentage of mines occurring in each of four distance bands from protected areas, compared with respective null models. Protected Areas: PAs.

		Percentage of observed mines					**Percentage of mines within PAs and buffers by null model (mean ± SD)**				**Percentage of randomization larger than observed (%)**
Geographic Region	Metal	Within	1km	1-5km	5-10km	Total	Within	1km	1-5km	5-10km	
Global	Al	0.14	0.00	0.21	0.28	**0.63**	0.22±0.1	0.04±0.06	0.12±0.10	0.13±0.9	17
	Cu	2.05	1.06	4.87	6.84	**14.81**	5.18±0.72	0.81±0.20	2.93±0.38	3.37±0.48	0
	Fe	1.48	0.85	2.61	2.68	**7.62**	3.15±0.45	0.47±0.18	1.69±0.33	1.99±0.29	28
	Zn	3.03	0.99	2.82	3.95	**10.79**	3.52±0.56	0.47±0.20	1.92±0.41	2.28±0.34	0
Africa	Al	1.53	0	0	1.5	**3.05**	0.63±0.6	0.02±0.13	0.13±0.29	0.16±0.38	0
	Cu	0.76	0.76	19.08	13.74	**34.35**	7.77±2.21	0.61±0.66	2.64±1.45	3.06±1.6	0
	Fe	0.76	0	2.29	0.76	**3.81**	1.7±1.02	0.09±0.28	0.50±0.59	0.62±0.67	16
	Zn	0.76	0	1.52	0	**2.29**	1.54±0.96	0.14±0.35	0.59±0.68	0.62±0.63	54
Asia	Al	0	0	0.25	0	**0.25**	0.21±0.18	0.01±0.04	0.06±0.13	0.09±0.15	50
	Cu	2.48	0.74	0.49	3.73	**7.46**	3.18±0.76	0.27±0.27	1.21±0.49	1.63±0.59	9
	Fe	2.48	0.99	3.48	3.73	**10.69**	5.3±1.05	0.48±0.35	2.06±0.8	2.66±0.8	44
	Zn	2.73	0	0.49	2.98	**6.21**	2.6±0.78	0.24±0.28	1.02±0.49	1.43±0.61	21

Europe	Al	0	0	0.46	0.46	**0.93**	0.15±0.23	0.02±0.09	0.2±0.26	0.17±0.32	4
	Cu	4.21	2.8	6.54	5.14	**18.69**	4.57±1.52	1.11±0.67	4.49±1.34	4.32±1.38	0
	Fe	1.87	2.8	4.67	2.8	**12.15**	2.49±0.97	0.61±0.51	2.42±0.95	2.42±1.05	0
	Zn	10.28	4.67	6.07	9.81	**30.84**	4.91±1.62	1.29±0.73	4.93±1.42	5.08±1.56	0
N. America	Al	0	0	0	0.38	**0.38**	0.04±0.12	0.01±0.05	0.03±0.1	0.05±0.13	0
	Cu	1.52	0.38	6.84	8.36	**17.11**	3.68±1.05	1.26±0.55	4.75±1.26	5.54±1.26	15
	Fe	0.38	0	0.76	0	**1.14**	0.06±0.48	0.18±0.26	0.81±0.59	0.82±0.49	91
	Zn	1.14	0.76	5.32	7.22	**14.44**	3.42±1	1.15±0.64	4.15±1.22	4.87±1.06	25
Oceania	Al	0	0	0	0	**0**	0.15±0.28	0.04±0.15	0.08±0.21	0.08±0.21	44
	Cu	0	0.63	5.66	8.8	**15.09**	5.24±1.84	1.15±0.83	3.78±1.45	3.83±1.52	23
	Fe	0	1.26	0.62	3.14	**50.3**	2.84±1.25	0.53±0.55	2±1.15	1.66±0.98	84
	Zn	0	0.62	3.14	1.26	**50.3**	2.35±1.15	0.53±0.57	1.68±0.97	1.51±1.01	61
S. America	Al	0	0	0	0	**0**	0.42±0.41	0.016±0.08	0.13±0.19	0.14±0.22	90
	Cu	2.01	1.2	0.8	4.41	**8.43**	10.28±1.85	0.71±0.48	2.58±0.92	3.02±0.98	100
	Fe	2.01	0	2.81	4.41	**9.23**	4.89±1.5	0.3±0.33	1.11±0.64	1.39±0.79	16
	Zn	2.41	0.4	1.6	3.21	**7.63**	5.65±1.32	0.35±0.4	1.22±0.73	1.66±0.69	65

Table A5.2 Percentages of the global protected area land surface with mines within different buffer zones.

Geographic region	Within	1 km	1-5 km	5-10 km	Total
Africa	0.01	0.001	0.41	0.53	**0.95**
Asia	5.03	0.03	0.14	0.11	**5.31**
Europe	0.43	0.04	0.10	0.24	**0.81**
North America	0.47	0.04	0.08	0.66	**1.24**
Oceania	0.00	0.02	0.13	0.09	**0.24**
South America	0.17	0.004	5.00	0.25	**5.43**
Total	**6.11**	**0.13**	**5.86**	**1.88**	**13.97**

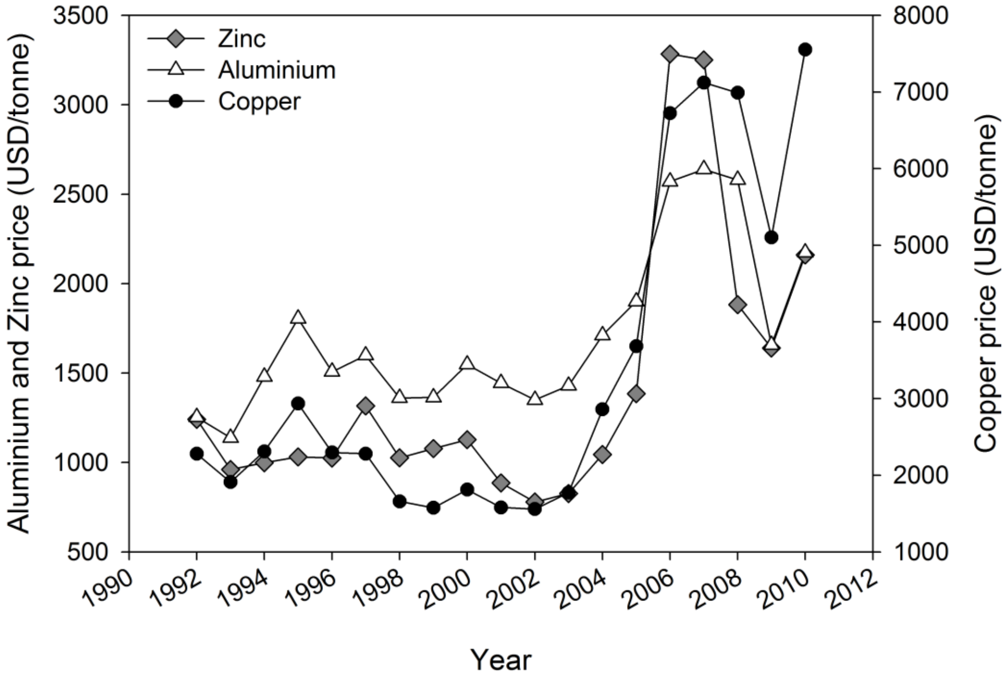


Figure A5.1 Annual price fluctuation of three metals, aluminum. copper and zinc. (Information source: Raw Material Group)

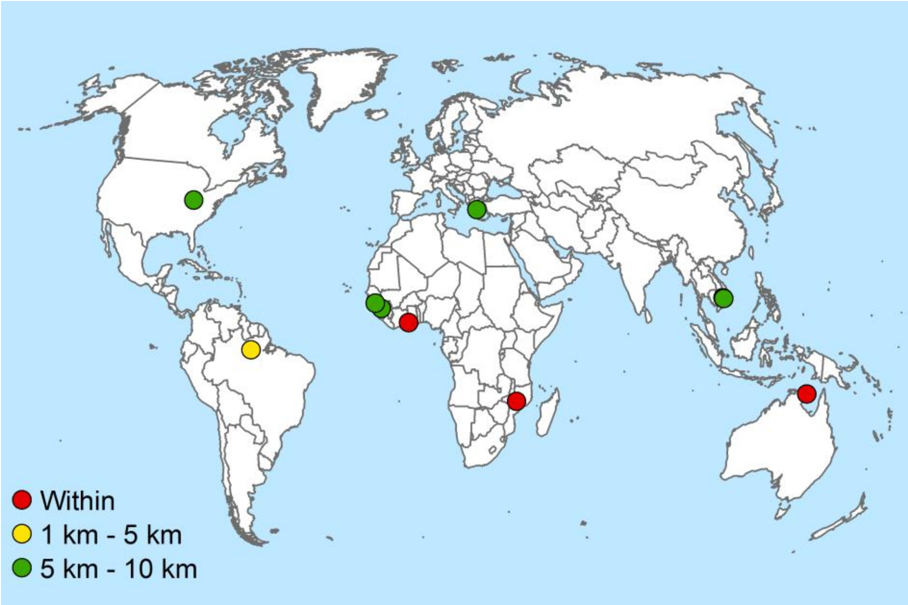


Figure A5.2 Global distribution of **bauxite** mines at different levels of proximity from protected areas.

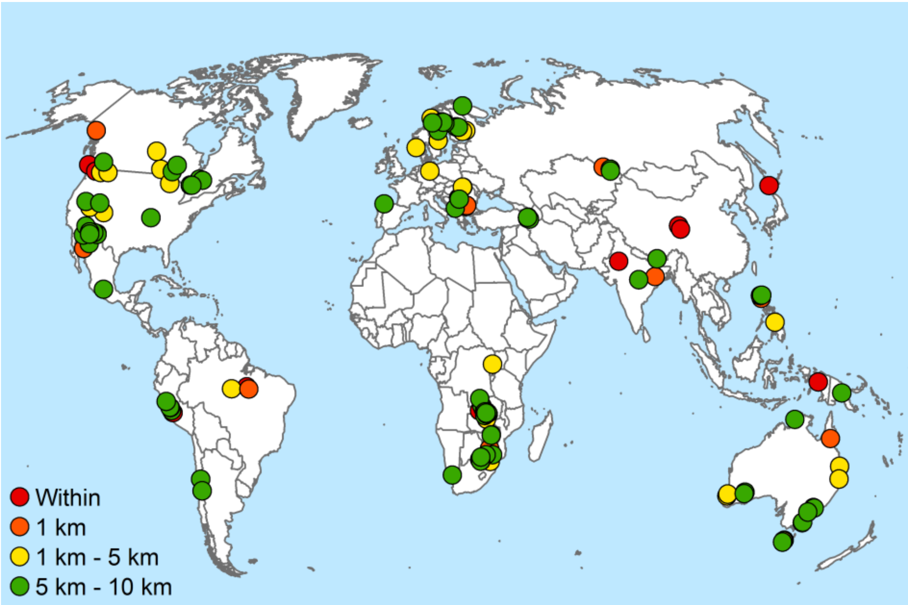


Figure A5.3 Global distribution of **copper** mines at different levels of proximity from protected areas.

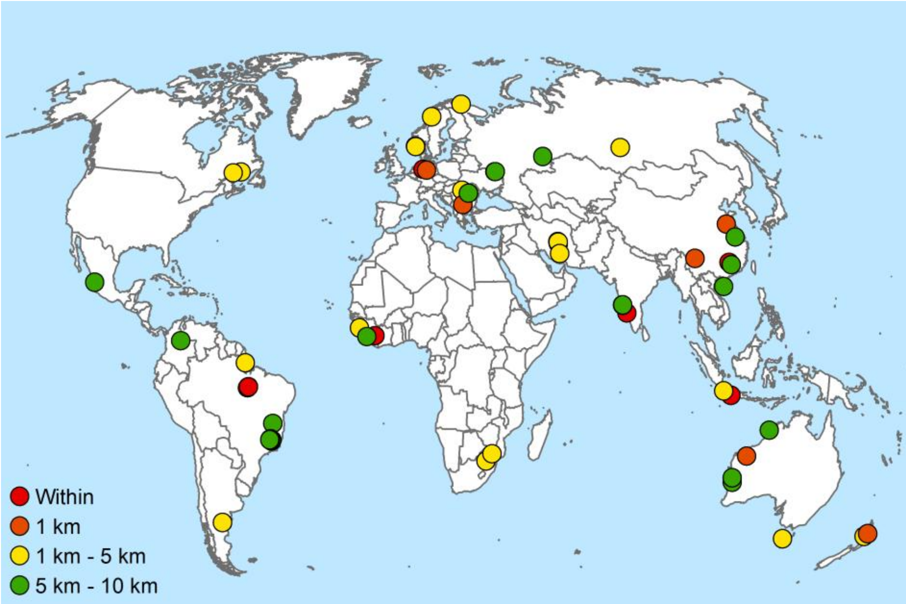


Figure A5.4 Global distribution of **iron** mines at different levels of proximity from protected areas.

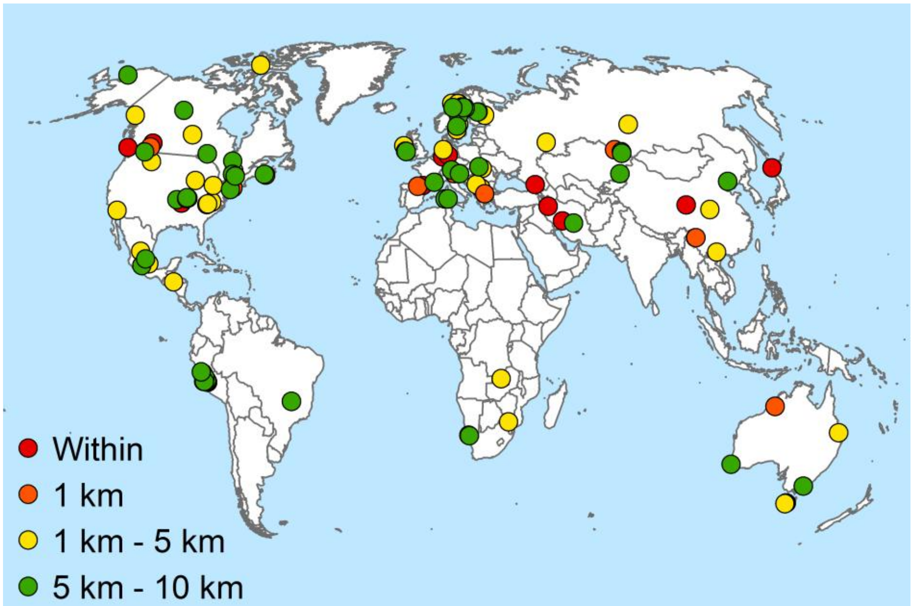


Figure A5.5 Global distribution of **zinc** mines at different levels of proximity from protected areas.

APPENDIX 6: *Exclusion of agricultural lands in spatial conservation prioritization strategies: consequences for biodiversity and ecosystem service representation* **(CHAPTER 6)**

Table A6.1 Spatial overlap between multiple prioritized features for three different resolutions in the 'top 17%' of the landscape using all species (below-right) and threatened species (above-bold). 'Feature-only': prioritization with each variable alone; 'All, agri. x': all species weighted equally, carbon 1.0 and agriculture 0, -1.0 and +1.0 respectively.

	Bio. only			Carb. only			Agr. only			All, agri x 0			All, agri x -1			All, agri x 1		
Biodiversity only	**************			**13.4**	**8.3**	**16.7**	**23.8**	**27.6**	**37.7**	**26.5**	**17.1**	**16.7**	**11.0**	**6.4**	**1.4**	**30.4**	**20.3**	**30.6**
Carbon only	16.7	13.5	25.0	**************			**7.3**	**2.8**	**11.1**	**84.6**	**90.4**	**100**	**71.2**	**44.3**	**27.8**	**54.0**	**61.9**	**66.7**
Agriculture only	25.9	25.9	44.4	7.3	5.8	11.1	**************			**11.9**	**9.5**	**11.1**	**0.2**	**0.0**	**0.0**	**44.7**	**42.5**	**44.4**
All, agri. x 0	23.5	13.5	25.0	91.9	100	100	9.7	5.8	11.1	**************			**62.9**	**39.9**	**27.8**	**65.3**	**65.3**	**66.7**
All, agri. x -1	11.4	6.3	0.0	71.6	44.3	27.8	0.2	0.0	0.0	67.1	44.3	27.8	**************			**39.4**	**27.7**	**20.8**
All, agri. x 1	28.7	23.0	47.2	58.4	61.9	66.7	44.6	42.5	44.4	63.5	61.9	66.7	41.9	27.8	20.8	**************		
Resolution	*10k*	*0.5°*	*2°*	*10k*	*0.5°*	*2°*	*10k*	*0.5°*	*2°*	*10k*	*0.5°*	*2°*	*10k*	*0.5°*	*2°*	*10k*	*0.5°*	*2°*

Table A6.2 Relative weightings assigned to agriculture-carbon combined strategies.

Agriculture Positive Weighted		Agriculture Negative Weighted	
Carbon	**Agriculture**	**Carbon**	**Agriculture**
64*n*	0.0155*n*	64*n*	-0.0155*n*
32*n*	0.0312*n*	32*n*	-0.0312*n*
16*n*	0.0625*n*	16*n*	-0.0625*n*
8*n*	0.125*n*	8*n*	-0.125*n*
4*n*	0.25*n*	4*n*	-0.25*n*
2*n*	0.5*n*	2*n*	-0.5*n*
n	*n*	*n*	-*n*
0.5*n*	2*n*	0.5*n*	-2*n*
0.25*n*	4*n*	0.25*n*	-4*n*
0.125*n*	8*n*	0.125*n*	-8*n*
0.0625*n*	16*n*	0.0625*n*	-16*n*
0.0312*n*	32*n*	0.0312*n*	-32*n*
0.0155*n*	64*n*	0.0155*n*	-64*n*

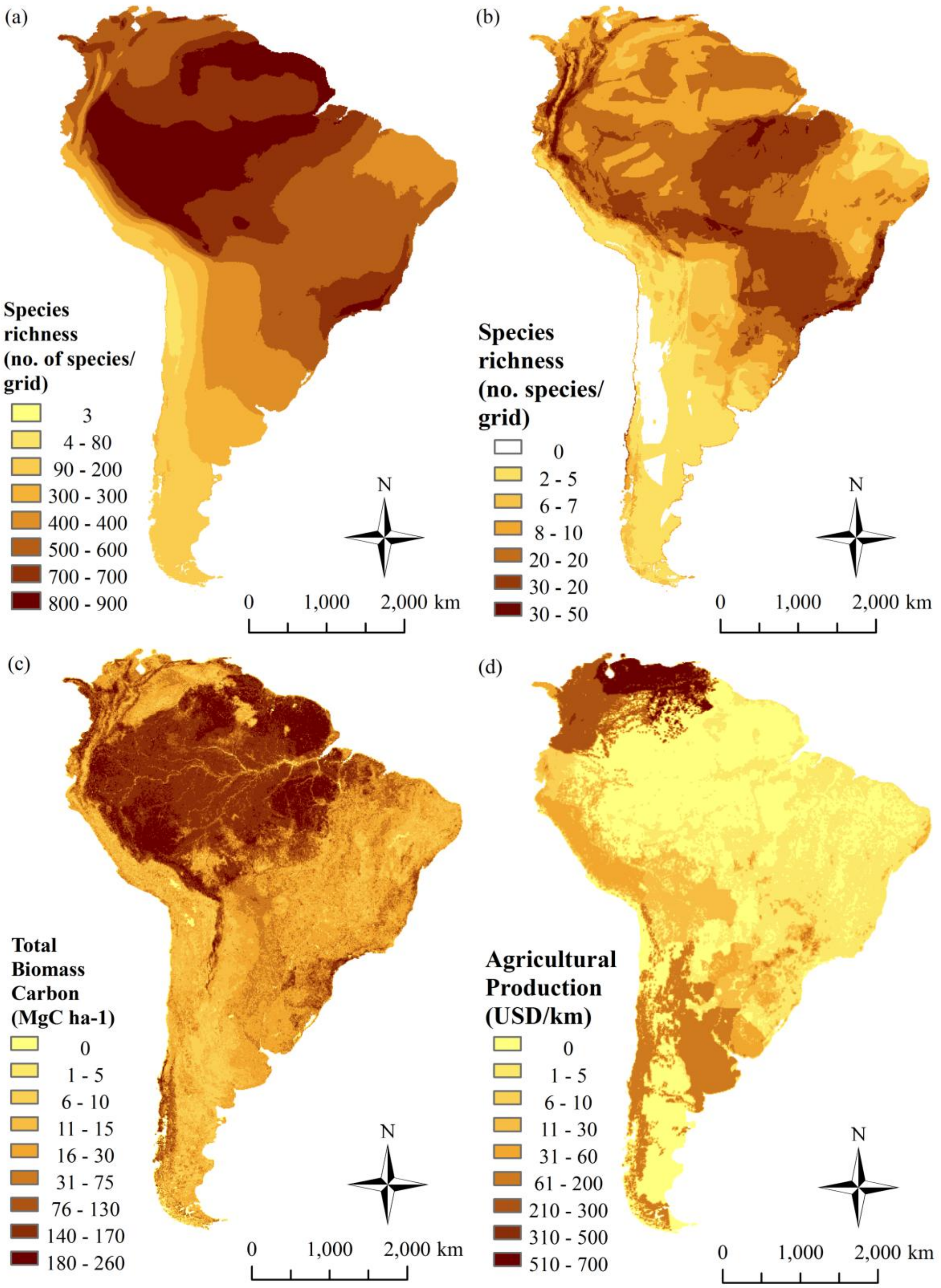


Figure A6.1 Distribution maps of (a) All species, (b) Threatened species, (c) Carbon and (d) Agricultural production in South America.

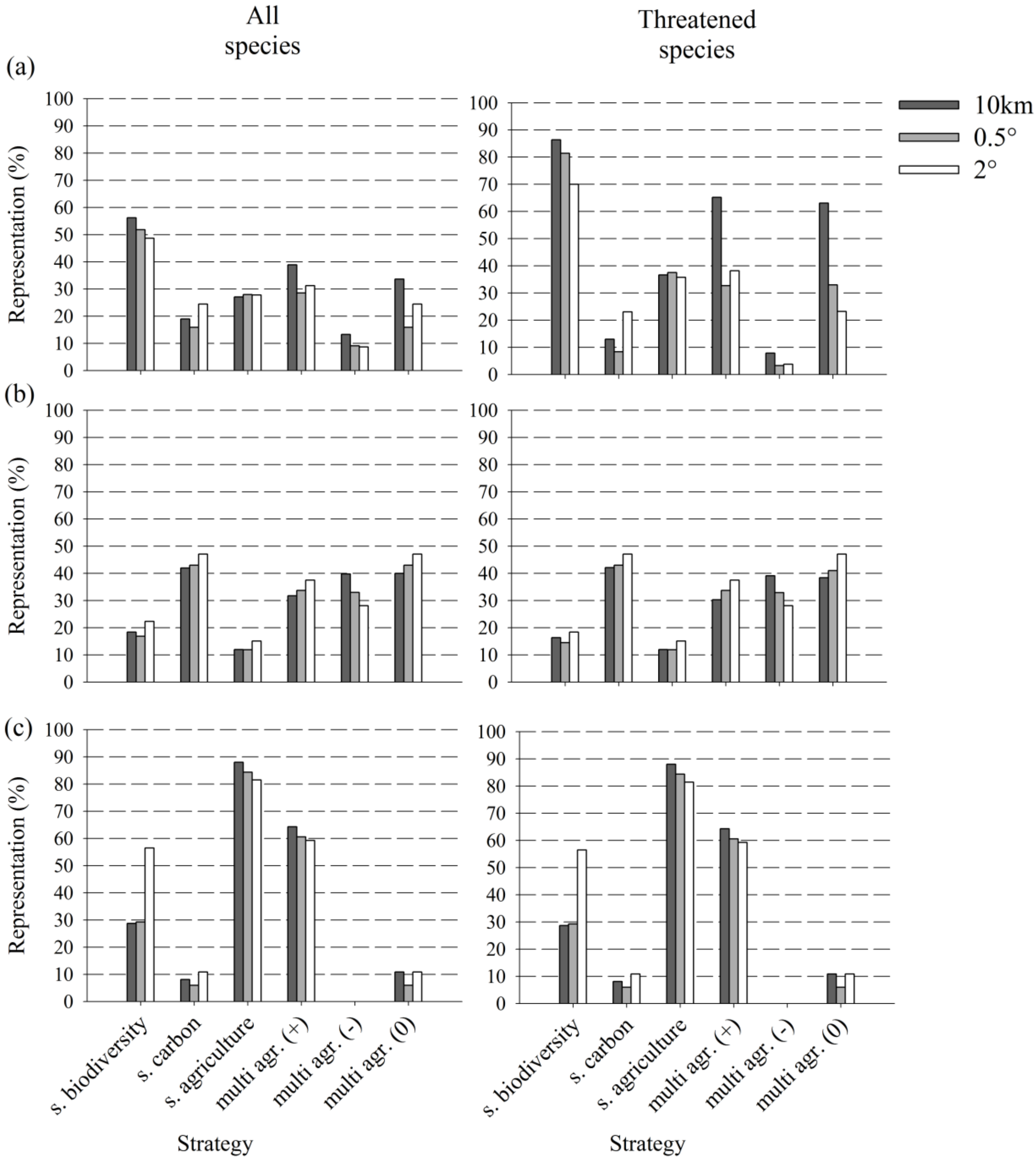
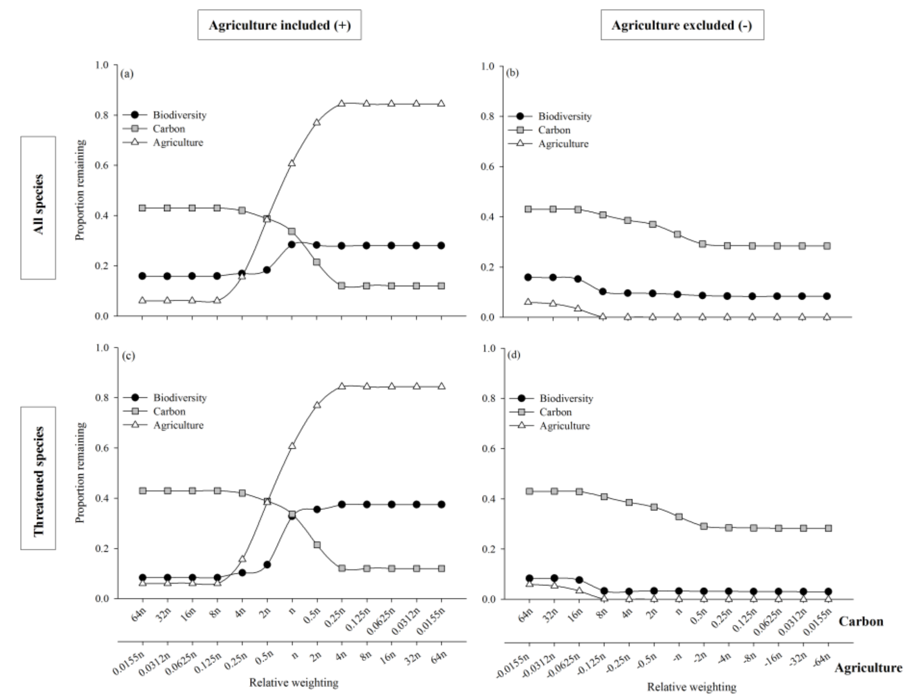


Figure A6.2 Representation of (a) Biodiversity, (b) Carbon and (c) Agriculture in single and multi-criterion prioritization strategies at different resolutions 10 km, 0.5° and 2.0°. 'S. feature': prioritization with each variable alone; 'Multi agr. (x)': all species weighted equally, carbon 1.0 and agriculture 0, -1.0 and +1.0, respectively.

i) 0.5° x 0.5° resolution



ii) 2° x 2° resolution

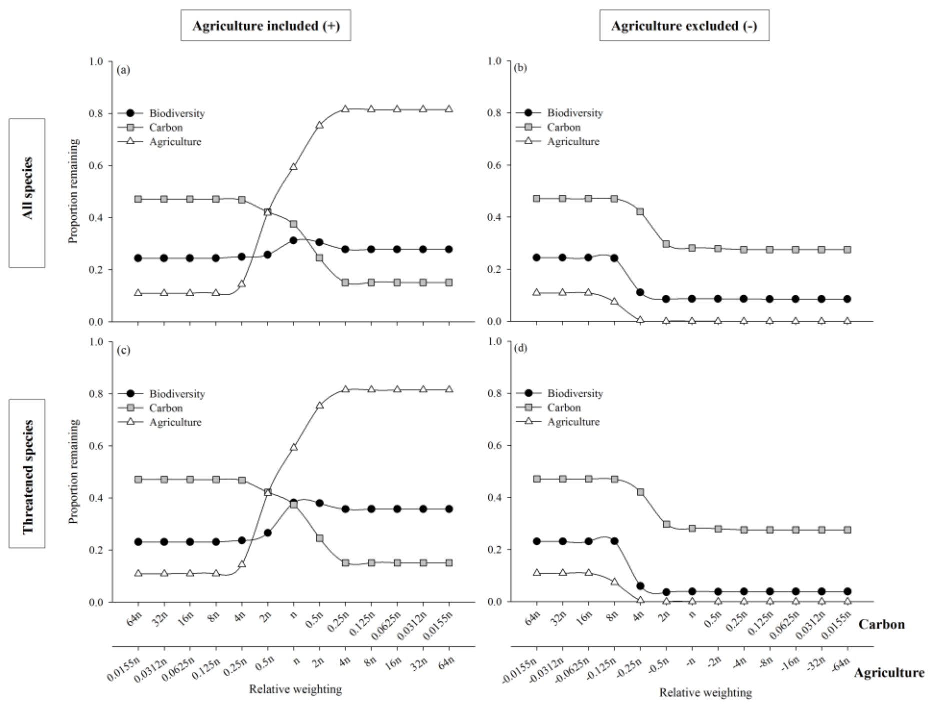


Figure A6.3 Relative weightings given to carbon *vs.* agriculture whilst biodiversity weight was kept constant at 1.0, for the two coarsest resolutions, (i) 0.5° x 0.5° and (ii) 2° x 2°. Within each figure, (a-b) Using all species, agriculture is weighted positively and negatively, respectively; (c-d) Using threatened species, agriculture is weighted positively and negatively, respectively.

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