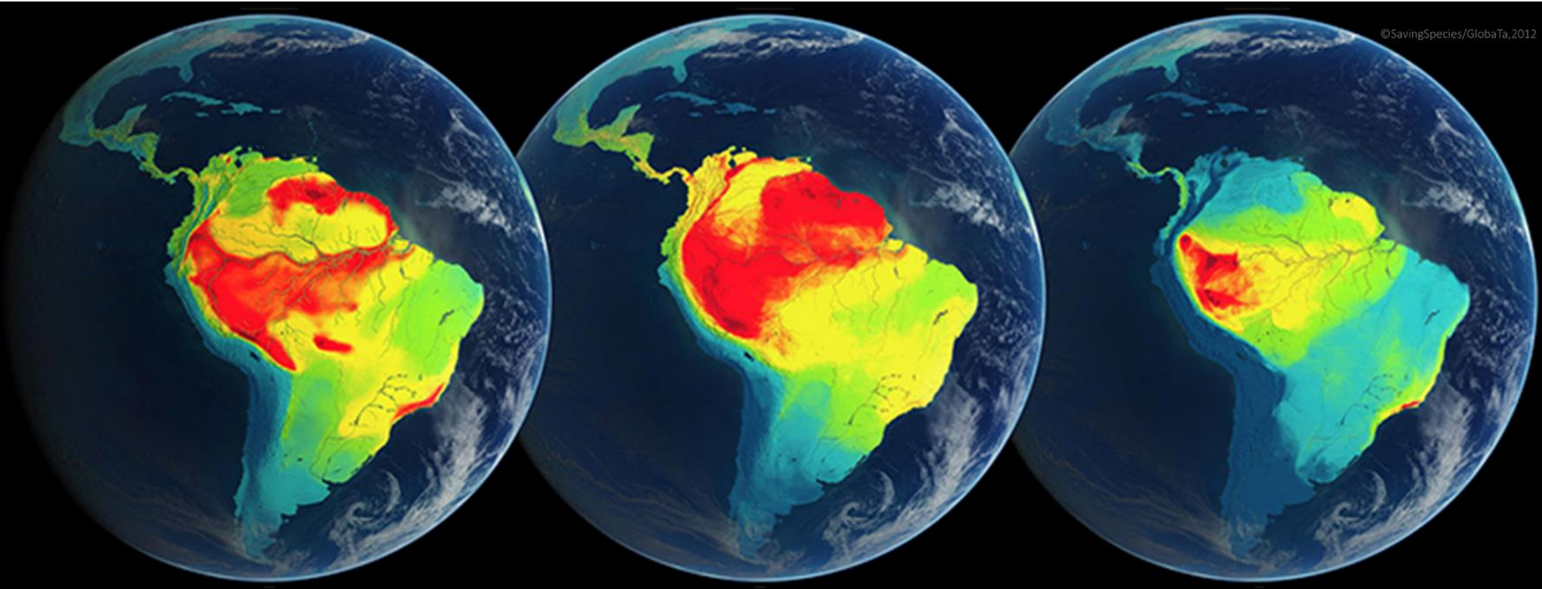


DOCTORAL THESIS

IMPROVING THE IDENTIFICATION OF PRIORITY AREAS FOR CONSERVING NEOTROPICAL BIODIVERSITY: ASSESSING UNCERTAINTIES IN SPATIAL CONSERVATION PRIORITIZATION

JAIME BURBANO GIRÓN

DOCTORADO EN ESTUDIOS AMBIENTALES Y RURALES

PONTIFICIA UNIVERSIDAD JAVERIANA - BOGOTA, COLOMBIA

IMPROVING THE IDENTIFICATION OF PRIORITY AREAS FOR CONSERVING NEOTROPICAL BIODIVERSITY: ASSESSING UNCERTAINTIES IN SPATIAL CONSERVATION PRIORITIZATION

Jaime Burbano-Girón

IMPROVING THE IDENTIFICATION OF PRIORITY AREAS FOR CONSERVING NEOTROPICAL BIODIVERSITY: ASSESSING UNCERTAINTIES IN SPATIAL CONSERVATION PRIORITIZATION

Jaime Burbano-Girón

Thesis submitted as a requirement for the degree of:
Ph.D., en Estudios Ambientales y Rurales

Thesis Director:
Dr., Andrés Etter Rothlisberger
Departamento de Ecología y Territorio
Pontificia Universidad Javeriana
Bogotá, Colombia

Thesis Advisors:
Dr., Kerstin Jantke
Research Unit Sustainability and Global Change
Hamburg University
Hamburg, Germany

Dr., Nicolás Urbina-Cardona
Departamento de Ecología y Territorio
Pontificia Universidad Javeriana
Bogotá, Colombia

Pontificia Universidad Javeriana
Facultad de Estudios Ambientales y Rurales
Doctorado en Estudios Ambientales y Rurales
Bogotá, D.C., Colombia
October, 2019

Acknowledgments

I am grateful to the Administrative Departamento Administrativo de Ciencia, Tecnología e Innovación (Colciencias) for funding my doctorate studies, and to the Facultad de Estudios Ambientales y Rurales of the Pontificia Universidad Javeriana for offering me the tools and the occasions to discuss and develop this research in the best way possible, I consider it my home. I am also grateful indeed to the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH) and all my colleagues from the Evaluation and Monitoring Program for all the support during the final steps of this process.

I want to especially thank Andrés Etter for the constant exchange of ideas, but particularly for being patient and understanding during the process of this thesis. Many thanks to Nicolás Urbina for being an excellent advisor, and for his support in the discussion and writing of this thesis. I also want to thank Tania Urquiza for supporting my internship at the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO) in México, and for her ideas in the first steps of this thesis. Finally, I want to give many thanks to Kerstin Jantke for all the support and significant contribution to this work through her expertise in conservation planning, and for hosting me at the Hamburg University in Germany.

I am very grateful to all the close people who helped me greatly during this time. To Andrea and my other Ph.D. colleagues. To Lina for critically reading the manuscript and providing suggestions that helped improve and clarify it. To Bibiana for her sharing and support during the writing process. To Maria Cecilia for being understanding with the completion of my thesis in this last year at Humboldt Institute. To Maria Isabel and Camilo for all your support and knowledge in data science. And thanks to Ana, for her friendship and all her sincere help.

I want to give special thanks to my friends and colleagues Natalia Buriticá and Maria Alejandra Molina for accept to be part of this thesis and for her permanent support during this research.

Finally, many thanks to my mother for her love and strength for so many years… And of course, thanks to Nicolás and Simona just for being their father.

Contents

Abstract

Critical thresholds in habitat reduction besides multiple threats such as climate change are leading to a biodiversity decline (Newbold *et al.* 2016; Betts *et al.* 2017; Melo *et al.* 2018; Roque *et al.* 2018), consistently predicted in multiple scenarios (Jenkins 2003; Thomas *et al.* 2004; Pereira *et al.* 2010; Bellard *et al.* 2012). Accordingly, extinction rates of species are now 8 to 100 times higher than those previously known (Ceballos *et al.* 2015). This biodiversity crisis imposes new challenges on conservation planning for prioritizing locations and efforts to guarantee the persistence of species and ecosystems over time (Meir *et al.* 2004; Wilson *et al.* 2016; Reside *et al.* 2018). The most common initiatives in conservation planning for safeguarding biodiversity and counteract biodiversity decline continue to be the expansion of the protected areas (PAs) systems (Jenkins & Joppa 2009; Watson *et al.* 2014). However, in a world increasingly dominated by human transformation processes (Ellis & Ramankutty 2008; Ellis 2011) and with limited economic resources for conservation (Wilson *et al.* 2009; Waldron *et al.* 2013), it is critical to expand this view and integrate conservation practices in human-modified landscapes (Ellis 2013).

The adequate allocation of the limited resources available for biodiversity conservation is crucial for achieving global, national, and sub-national conservation targets (Dobrovolski *et al.* 2014; Pouzols *et al.* 2014; Venter *et al.* 2014; Di Marco *et al.* 2016; Espirito-Santo *et al.* 2017). Consequently, a critical issue in spatial conservation prioritization should be to minimize the uncertainty about what and where to conserve, in order to maximize the success of conservation planning (Regan *et al.* 2009; Wilson *et al.* 2009). Thus, I tested in this thesis how robustness of the planning process may be increased by applying the three principles proposed in the systematic conservation planning framework, (1) representation, (2) persistence, and (3) cost-efficiency (Margules & Sarkar 2007), but also by highlighting the variability of the conservation prioritization process to diverse approaches using different information (Langford *et al.* 2011).

I evaluated the impact of several approaches and analyzed the sensitivity of the identification of priority areas for conservation in the Neotropics, one of the most biodiverse regions in the world, and also one with the most urgent needs of identifying conservation priorities. I present a comprehensive spatial conservation prioritization that addressed the composition (8563 spp.), structure (663 ecosystems), and function (5382 ecological groups) of biodiversity, showing the regional variability of conservation priorities according to the biodiversity attribute represented (Chapter 1). Also, I applied different approaches of costs and factors associated with the persistence of Neotropical biodiversity, and framed them in the land-sharing/sparing model to propose possible conservation actions in the region (Chapter 2). Finally, I evaluated multiple variables related to the systematic conservation planning principles, representation, persistence, and cost-efficiency, to analyze what factors better guide conservation priorities in the Neotropics across regional and national levels (Chapter 3).

My results showed that Aichi 11 target for conserving 17% of terrestrial biodiversity in the Neotropics cannot be fulfilled with the current PAs. The prioritized areas proposed, as well as PAs, meet on average 60% of conservation targets, but being 60% more efficient in the extent of area selected. I show that in the most threatened biodiversity hotspots, the effectiveness and representativeness of biodiversity depend strictly on the inclusion of new conservation areas. Comparing biodiversity attributes, I found a higher level of surrogacy using a compositional approach explained by the number of biodiversity features and their overlapping levels. However, conservation priorities vary regionally, suggesting that the use of a single biodiversity attribute, may lead to inaccurate selections of conservation priorities (Chapter 1).

I also found that costs are more influential in the selection of conservation areas than persistence measures. Using the variability in the priority areas found, we identified regions where land acquisition would be most suitable for conservation and restoration (land-sparing), and areas where conservation agreements would be more appropriate to implement restoration or wildlife-friendly farming conservation strategies (land-sharing) (Chapter 2). Through a sensitivity analysis, we found that representativeness of biodiversity, and particularly the proportion of natural habitats guides conservation priorities at the regional level, while the factors associated with costs and persistence are more critical at the Neotropical level. In the Neotropics, conservation priorities responded to the spatial conservation prioritization model, favoring complementarity and reducing conservation costs (Chapter 3). However, conservation planning at the regional level should consider several mechanisms to guarantee the success of biodiversity protection over time (Chapters 1, 2 and 3).

Finally, I concluded that there is no single approach or a combination of them, which cover the whole variability in spatial information on biodiversity, costs, and persistence to conservation. Regional differences in conservation areas selected influence conservation planning differently, consequently leading to identify distinct priorities and conservation actions related. The regional variability in conservation areas selection found indicates more different strategies that should be applied to conservation planning, since biodiversity attributes, and cost and persistence approaches guide the selection differently (Chapters 1 and 2). However, despite variability in conservation areas selection, we could identify priority areas where coincidences over multiple approaches occur (Chapters 1 and 2). In these areas, the uncertainty in defining priority areas is reduced, supporting the definition of more robust conservation priorities and actions by identifying those factors related to conservation areas selection (Chapter 3). These irreplaceable areas were located in critical and threatened global biodiversity hotspots, e.g., the Chaco, the Atlantic forest, the Pantanal, Cerrado, and Caatinga regions in Brazil, and the moist and dry forests of northern Andes (Chapters 1 and 2).

General Introduction

Background

Biodiversity decline (Newbold *et al.* 2016; Betts *et al.* 2017; Roque *et al.* 2018) imposes new challenges to conservation planning for prioritizing locations and efforts (Meir *et al.* 2004; Reside *et al.* 2018). The adequate allocation of limited resources available for biodiversity conservation is crucial for achieving global, national, and sub-national conservation targets (Dobrovolski *et al.* 2014; Pouzols *et al.* 2014; Venter *et al.* 2014; Di Marco *et al.* 2016). One common approach for conserving highly biodiverse regions is the establishment of protected areas (PAs); however, inconsistencies in their effectiveness and representativeness have been identified (Chape *et al.* 2005; Gaston *et al.* 2008; Fuller *et al.* 2010; Le Saout *et al.* 2013). For instance, in the Neotropics, one of the most biodiverse regions globally, the highest proportion of PAs (see Jenkins & Joppa 2009), but also the largest number of threatened species (see Hoffmann *et al.* 2010), and a gap in the species diversity representation (see Rodrigues *et al.* 2004; Wilson *et al.* 2011) are evident. Furthermore, studies involving spatial conservation prioritization over Neotropical countries are scarce (see Kukkala & Moilanen 2013; Wilson *et al.* 2016). These considerable gaps in research and protection of the Neotropics makes it a critical region to target conservation efforts.

Systematic Conservation Planning (SCP) is one of the leading frameworks for guiding decision making on where and what to conserve (Margules & Pressey 2000). SCP supports the identification of conservation areas employing a spatial conservation prioritization process based upon three principles: (1) represent the biodiversity of a particular region for ensuring its (2) persistence over time in a (3) cost-efficient way (Margules & Sarkar 2007). Interest in idetifiying conservation areas based on a spatial prioritization approach has considerably grown in the last decade (see Kukkala & Moilanen 2013). However, many prioritization exercises do not account for all three principles of SCP. Many studies only include representation, and some others use representation in combination with persistence or cost-efficiency (see Pressey *et al.* 2007; Kukkala & Moilanen 2013), but studies using all three criteria are scarce (but see, e.g., Wilson *et al.* 2006, 2011; Bode *et al.* 2008; Newbold & Siikamaki 2009; Visconti *et al.* 2010). Nevertheless, applying different principles or even different approaches to approximate the same principle in a spatial conservation prioritization exercise may lead to identifying substantially different networks of conservation areas (Brooks *et al.* 2006). These differences could result in allocating efforts, resources, and actions to regions in which successful protection of biodiversity is highly uncertain.

These dissimilarities imposed by each principle may impact conservation planning priorities differently (Bode *et al.* 2008). Therefore, to increase the robustness in the selection of conservation areas it is essential to quantify the magnitude of this impact, i.e., showing the sensitivity of the spatial conservation prioritization process to these differences (Langford *et al.* 2011). Sensitivity analyses lead to identifying critical parameters and factors for selecting conservation areas, which should be consired for aquiring more accurate information, but also for developing conservation actions based on them (Regan *et al.* 2009). This study evaluates the impact of including multiple approaches to the three principles of SCP (representation, persistence, and cost-efficiency), but also the sensitivity of multiple related-factors in the selection of conservation areas, and how coincidences and differences may guide more accurate designing and implementation of conservation priorities. This work is relevant and necessary since the study area, the Neotropics, is one of the most biodiverse regions in the world (Williams *et al.* 1997; Mittermeier *et al.* 1998, 2005; Reid 1998; Myers *et al.* 2000; Olson *et al.* 2001), but also one of the most threatened with an urgent need to set conservation priorities (Wilson *et al.* 2011, 2016).

The spatial conservation prioritization principles

The representation principle

For a comprehensive representation of biodiversity, its multiple levels, i.e., composition, structure, and function, have to be considered (Wilson *et al.* 2009), as these features characterize the biological diversity of a region (Franklin *et al.* 1981). Because no single surrogate is considered a comprehensive representation of biodiversity, a set of complementary surrogates is required (Noss 1990). Most traditional surrogates used in conservation planning can be separated into two groups: (1) cross-taxon or species-level surrogates, and (2) environmental or community-level surrogates. The firsts employ a particular set of species of better-studied groups for representing their corresponding taxon (e.g., carnivorous mammals for representing mammals, vascular plants for representing plants, or threatened birds for representing birds). These approaches commonly use the geographic distribution of individual species as indicators of the spatial pattern of the other species in the target taxon, or in complementary approaches as surrogates of the whole biodiversity allocation. This type of surrogates only represents the composition attribute of biodiversity. The latter use environmental data (e.g., abiotic spatial descriptors/predictors of emergent patterns in the distribution of biodiversity, abiotic environmental classifications, environmental diversity, habitat types, habitat complexity, or habitat structure), species ensembles at community or ecosystem level (e.g., vegetation types, ecoregions, floristic regions, biogeographic regions, or functional or phylogenetic diversity), or a combination of both. These approaches may represent the structural and functional attributes of biodiversity (Rodrigues & Brooks 2007; Ferrier *et al.* 2009).

However, complementary and comprehensive representations of biodiversity in spatial conservation exercises are scarce (but see, e.g., Strecker *et al.* 2011; Sobral *et al.* 2014). The most used approaches stick to the composition attribute, mainly employing birds, mammals, and vascular plant species (see Rodrigues & Brooks 2007). The environmental or community-level approaches for the structure attribute mostly use plant assemblages (e.g., Olson & Dinerstein 1998; WWF & IUCN 1998; Olson *et al.* 2001; Hoekstra *et al.* 2005; Kier *et al.* 2005), environmental classifications, (e.g., Ferrier & Graham 1997; Armstrong & van Hensbergen 1999; Araújo *et al.* 2001; Sanderson *et al.* 2002; Bonn & Gaston 2005; Trakhtenbrot & Kadmon 2005; Hortal *et al.* 2009), or land, habitat or ecosystems classifications (e.g., Wright *et al.* 1994; Bryant *et al.* 1997; Lombard *et al.* 1997; Pressey *et al.* 2000; Cowling & Heijnis 2001; Harborne *et al.* 2008). For functional attribute, representation approaches include environmental data proxies for representing process (Cowling & Pressey 2001; Pressey *et al.* 2003; Rouget *et al.* 2003; Klein *et al.* 2009), and species assemblages to represent functional or evolutionary traits (Moritz & Faith 1998; Forest *et al.* 2007; Loyola *et al.* 2008, 2009; Loyola & Diniz-Filho 2010; Safi *et al.* 2011; Stuart-Smith *et al.* 2013; Sobral *et al.* 2014; Zupan *et al.* 2014).

Although some priority areas show spatial mismatches when different surrogacy approaches are applied (Sobral *et al.* 2014), those where there is a congruence among the highest conservation priorities may ensure with a high probability of succes that conservation actions would achive a comprehensive protection of biodiversity (Strecker *et al.* 2011). Conversely, not congruent areas suggest that complementary surrogates for representing biodiversity are needed (Ferrier *et al.* 2009; Wilson *et al.* 2009), as they are representing different priorities and actions for conservation that should be considered over these regions.

The persistence principle

Dynamic threats call for special efforts in conservation planning (Pressey *et al.* 2007; Possingham *et al.* 2009; Hannah 2010; Visconti *et al.* 2010), since current conservation actions may be inefficient in protecting biodiversity against combined effects of biodiversity threats (Mantyka-Pringle *et al.* 2012).

Accordingly, including persistence criteria in conservation planning may improve the likelihood of successful conservation within conservation areas (Nicholson et al. 2006; Game et al. 2008; Tulloch et al. 2015). Until now, vulnerability to climate change (e.g., Carroll *et al.* 2010; Carvalho *et al.* 2011; Summers *et al.* 2012; Faleiro *et al.* 2013; Pacifici *et al.* 2015), and vulnerability to habitat loss/fragmentation (Cabeza 2003; Becker *et al.* 2010; Faleiro *et al.* 2013), in addition to landscape connectivity (e.g., Cabeza 2003; Rouget *et al.* 2006; Hodgson *et al.* 2009; Ryan *et al.* 2012), dispersal abilities (Carroll *et al.* 2003; Minor & Urban 2007), and population dynamics (meta-population models and population viability analyses) (e.g., Carroll *et al.* 2003; Nicholson *et al.* 2006), have been the most common approaches regarding persistence of biodiversity in conservation planning.

The inclusion of persistence may impose significant changes in the spatial distribution of conservation areas compared to those using only the representation principle (Carroll *et al.* 2003; Faleiro *et al.* 2013), increasing the variability of conservation areas selection by integrating the dynamics of threats into the spatial prioritization (Carvalho *et al.* 2011; Kujala *et al.* 2013). However, the inclusion of dynamic threats in the spatial conservation prioritization process is highly affected by current reserve selection algorithms. Most employed spatial conservation prioritization tools are not designed to deal with habitat dynamics (Costello & Polasky 2004; Pressey *et al.* 2004; Strange *et al.* 2006; Visconti *et al.* 2010), since computational capacity and complexity of these optimization problems (maximum gain or minimum loss) limits its application on large volumes of data (Possingham *et al.* 2009). Currently, these tools are limited to include vulnerability or uncertainty indexes as penalties for allocation, or structural connectivity measures (area-perimeter relationship, adjacency, compactness, boundary length, and patch size) for defining the spatial arrangement of the of conservation areas (Moilanen 2007; Ball *et al.* 2009; Ciarleglio *et al.* 2009; Pressey *et al.* 2009).

Other approaches have attempted to include species-specific responses to consider the persistence in the formulation of dymamic optimization problems. One common approach has been to consider the species-specific responses to habitat loss/fragmentation for defining conservation targets in habitat dynamic problems. Here, the spatial configuration, and the clustering pattern of priority areas depend on the species and targets employed (Cabeza 2003; Visconti *et al.* 2010). In this problem, simultaneously, both spatial configuration and clustering patterns are influenced by their surrounding lost or fragmented habitat, increasing the area selected for protection (Cabeza 2003; Faleiro *et al.* 2013). Howver, when dynamic optimization problems have been implemented in combination with land costs, conservation areas tend to become more isolated, smaller, and fewer through time, responding to the positive correlation between threats and costs (Visconti *et al.* 2010).

The fragmentation, size, and the number of conservation areas become more critical when other approaches are included in the planning process. For instance, when population models have been employed, linkage areas that are not chosen by reserve selection algorithms but whose protection strongly affected population viability have been identified (Carroll *et al.* 2003). Regarding these zones, connectivity approaches have been applied to select networks with high levels of structural connectivity between conservation areas based on minimum distances (e.g., Game *et al.* 2011), or by dispersal distance identifying possible new areas for species migration (e.g., Lemes & Loyola 2013).

The cost-efficiency principle

Investments in biodiversity conservation have to be efficiently allocated to better invest the limited resources for conservation (Wilson *et al.* 2011). Costs of conservation are highly variable over planning regions; thus, including spatially explicit costs is critical to guide the prioritization process to those areas where benefits of conservation may exceed their costs (Naidoo & Ricketts 2006; Naidoo *et al.* 2006). Conservation planning exercises including costs of conservation, show similar or better levels of biodiversity protection while investing fewer resources than those not considering them (Ando *et al.* 1998; Polasky *et al.* 2001; Stewart & Possingham 2005; Polasky 2008). However, the inclusion of costs in spatial conservation prioritization exercises has been delayed, and therefore its application is less common than the other two principles (Kukkala & Moilanen 2013).

Several approaches have been employed as conservation costs (Naidoo *et al.* 2006; Ban & Klein 2009). Possibly, the most used approximation are opportunity costs, the not perceived benefit by the best alternative use in a particular area (e.g., Norton-Griffiths & Southey 1995; Polasky *et al.* 2001; Balmford *et al.* 2003; Stewart *et al.* 2003; Stewart & Possingham 2005; Chomitz *et al.* 2005; Naidoo & Adamowicz 2006; Naidoo & Iwamura 2007; Cameron *et al.* 2008; Carwardine *et al.* 2008; Adams *et al.* 2010; Wintle *et al.* 2011; Jantke & Schneider 2011; Schröter *et al.* 2014). The concept of opportunity costs assumes that the cost of preserving a conservation area is equivalent to the unperceived income from the most profitable land use in a particular region. Since this is an indirect measure of conservation costs, it does not accurately reflect the economic costs of maintaining a conservation area; however, it is a more socially inclusive measure of the consequences of conservation planning (Naidoo *et al.* 2006; Ban & Klein 2009; Newbold & Siikamaki 2009). Moreover, this approach has greater availability of information than others, as in regions or countries, statistics of the income perceived by the different economic activities may be available (Balmford *et al.* 2003; Naidoo & Iwamura 2007).

Other approaches include direct economic costs of conservation, as well as non-monetary costs (Naidoo *et al.* 2006; Ban & Klein 2009). Direct economic approaches have been performed using costs of land acquisition (e.g., Wu 2000; Stoneham *et al.* 2003; Newburn *et al.* 2005), management costs (e.g., Moore *et al.* 2004; Wilson *et al.* 2011), transactions costs (including transactions for damage) (e.g., Barua *et al.* 2013), or restoration costs (e.g., Holl & Howarth 2000; Wilson *et al.* 2011). Non-monetary costs involve other indirect approximations for conservation costs, including uniform costs or area-based costs (e.g., Beck & Odaya 2001; Airamé *et al.* 2003; Stewart & Noyce 2003; Carvalho *et al.* 2010), multicriteria abiotic costs (e.g., Williams *et al.* 2003; Rouget *et al.* 2006), multicriteria environmental (biotic and socioeconomic) costs (e.g., Ferraro 2004), vulnerability to threats costs (e.g., Banks *et al.* 2005; Tallis *et al.* 2008; Ban *et al.* 2009), or multiple socioeconomic costs (Leathwick *et al.* 2008; Green *et al.* 2009).

Reducing uncertainty in the identification of spatial conservation priorities

Reducing the uncertainties on the identification of priority areas for conservation improves the success of decision-making on what and where to conserve. One way to support and strengthen this process is to explore the sensitivity of selected conservation areas to multiple models (Rae *et al.* 2007). The sensitivity analysis framework may clarify the importance of parameters involved in conservation areas selection, also providing certainty to conservation protocols, and supporting cost-efficient implementations of conservation actions (Roura-Pascual *et al.* 2010). Additionally, sensitivity analysis may be used to partially compensate gaps of information about some modeling parameters (Cabeza & Moilanen 2003), and to identify critical variables to be the focus of management and data refinement, which in turn may also be employed to simplify future models (McCarthy 2009).

Sensitivity analysis estimates how the variation (uncertainty) in the outputs of a model can be attributed to different changes in their inputs. If model outputs change disproportionately, then the sensitivity of the model to that perturbation will be significant (Crosetto *et al.* 2000). Modeling results in ecology and conservation often depend on a single case study with high variability in data, as well as low statistical generalization power, leading to high uncertainty in their results. Consequently, conservation planning methods using this information may produce decision-making based on a reduced certainty in the success of conservation actions. Thus, it is essential that methods applied in the SCP framework test their robustness to uncertainty and complexity (Langford *et al.* 2011).

The application of a formal sensitivity analysis in conservation planning is uncommon, but tipically involves population viability analysis (e.g., Naujokaitis-Lewis *et al.* 2009; Newbold & Siikamaki 2009), demographic analysis in aquatic species (e.g., Gerber & Heppell 2004; Micheli *et al.* 2004), and multicriteria prioritization using scoring methods that include biotic, abiotic, and socioeconomic parameters (e.g., Coppolillo *et al.* 2004; Pyke 2005; Rae *et al.* 2007; Wood & Dragicevic 2007; Xiaofeng *et al.* 2011). Most of the studies compare the differences among different parameters, variables, or approaches, but not strictly constitute a sensitivity analysis.

Particularly, in spatial conservation prioritization, comparisons or sensitivity analyses have been performed to evaluate several impacts. Some of these effects have been estimated as a result of the algorithms employed (e.g., Carvalho *et al.* 2010; Visconti *et al.* 2010), the conservation targets (e.g., Warman *et al.* 2004; Carvalho *et al.* 2010), the size and the shape of planning units (e.g., Warman *et al.* 2004), weight variability on biodiversity features (e.g., Warman *et al.* 2004; Moilanen *et al.* 2005; Leathwick *et al.* 2008), the use of different biodiversity features (e.g., Bode *et al.* 2008), the threat levels (e.g., Wilson *et al.* 2006; Bode *et al.* 2008), the costs data (e.g., Richardson *et al.* 2006; Bode *et al.* 2008; Carwardine *et al.* 2010), the scale of the information (e.g., Warman *et al.* 2004; Richardson *et al.* 2006), different spatial approaches to represent species (e.g., Araujo 2004; Wilson *et al.* 2005; Carvalho *et al.* 2010), and different taxa databases (e.g., Freitag & Jaarsveld 1998; Grantham *et al.* 2009).

Objectives

This thesis aims to evaluate the impact and uncertainty of using several approaches related to systematic conservation planning principles (representation, persistence, and cost-efficiency) on the identification of areas for conserving Neotropical biodiversity.

Specific objectives are:

1. Compare the differences in conservation areas selection under different representations for biodiversity attributes: composition structure, and function.

2. Evaluate the implications for conservation planning of appliying different persistence and costs approaches in the selection of conservation areas.

3. Analyze conservation areas selection based on multiple factors related to systematic conservation planning principles: representation, persistence, and cost-efficiency.

Overview of thesis structure

The thesis' chapters are based on three research papers corresponding to the development of the three specific objectives proposed. The papers are expected to be submitted to international peer-reviewed journals before the defense of this thesis.

Chapter 1: **An assessment of spatial conservation priorities for biodiversity attributes: composition, structure, and function of Neotropical biodiversity.** This chapter evaluates the representation principle of SCP. Here, we present a comprehensive evaluation of spatial conservation priorities for Neotropical biodiversity by including representation approaches for biodiversity attributes: composition (species), structure (ecosystems), and function (ecological groups). We evaluated the differences in conservation areas selected using several metrics: area, effectiveness, representativeness, aggregation level, and surrogacy level of biodiversity attributes, but also the differences in the type of conservation areas: current PAs, prioritized areas (those selected to complement the PAs), and total areas (PAs and prioritized areas). Metrics were compared for the entire Neotropics and over a regionalization approach using the Global 200 ecoregions (Olson & Dinerstein 1998) by country.

Chapter 2: **Understanding the effect of including costs and persistence in spatial conservation prioritization: an analysis of the land-sharing/sparing framework in the Neotropics**. This chapter addresses the cost-efficiency and persistence principles of systematic conservation planning. We show how the application of different cost and persistence approaches on spatial conservation prioritization may impose different conservation planning schemes at the landscape level based on the land-sharing/sparing framework. We evaluated coincidences and differences of conservation areas selected by each approach to propose possible conservation actions on the region based on the current land cover, landscape transformation, land rent, habitat fragmentation, and human influence.

Chapter 3: **Underlying and driving factors explaining the selection of priority areas in the Neotropical region**. In this chapter, we used the spatial prioritization approaches applied in Chapters 1 and 2 to explain the factors driving conservation areas selection. We applied a sensitivity analysis using the random forest algorithm and 70 explanatory variables related to systematic conservation planning principles: representation, persistence, and cost-efficiency. We evaluated 14 models to explain the conservation areas selection in prioritized areas (those selected to complement the PAs) at the Neotropical-level, and total areas (PAs and prioritized areas) for 13 different combinations between the Global 200 ecoregions and countries. Finally, we analyzed and compared the most significant variables at the Neotropical, ecoregion, and country-level, to show that factors explaining conservation areas selection differ across scales, and that these factors may guide more accurate designing and implementation of conservation priorities.

General conclusions: I present a general synthesis of results found in three previous chapters focused on how the application of different approaches to systematic conservation principles impacts the uncertainty in defining conservation priorities. I introduce some recommendations and limitations found in this work, also related to future research in spatial conservation prioritization and conservation planning.

Chapter 1. An assessment of spatial conservation priorities for biodiversity attributes: composition, structure, and function of Neotropical biodiversity

Jaime Burbano-Girón[1,2], Kerstin Jantke[3], Maria Alejandra Molina[1], Natalia Buriticá-Mejía[1], Nicolás Urbina-Cardona[1], Andrés Etter[1]

[1] Facultad de Estudios Ambientales y Rurales. Pontificia Universidad Javeriana. Bogotá, Colombia.
[2] Instituto de Recursos Biológicos Alexander von Humboldt. Bogotá, Colombia.
[3] Research Unit Sustainability and Global Change. Hamburg University. Hamburg, Germany.

Abstract

Given the increasing threats to biodiversity and limited resources for conservation, our knowledge about the uncertainty in surrogates for representing biodiversity needs to be improved in terms of their impact on conservation prioritization processes. We present a comprehensive evaluation of spatial conservation priorities for Neotropical biodiversity by including representation approaches for three biodiversity attributes: composition (species), structure (ecosystems), and function (ecological groups). We evaluated the differences in conservation areas selected for each attribute in the current PAs, prioritized areas (those selected to complement the PAs), and total areas (PAs and prioritized areas) for the entire Neotropics, and over a regionalization approach using the Global 200 Ecoregions by country. Finally, we identified critical regions where prioritized areas are crucial for achieving conservation targets. We found that the higher the number of biodiversity features considered and the lower their level of overlap is, the larger the area required to meet conservation targets is. Our results also support the premise that no single surrogate represents biodiversity comprehensively; the regional differences found explained the need for complementary surrogates and their effect in conservation areas representativeness. We also found that current PAs in the Neotropical region do not meet the Aichi 11 target for conserving 17% of biodiversity, but using our approach proposed this target can be fulfilled 60% more efficiently. Our combination of PAs and prioritized areas proposed could be considered an optimal spatial trade-off weighting both, effectiveness and representativeness in prioritized areas, and compactness in PAs.

Introduction

During the last five centuries, the drivers of global biodiversity change have led to species extinction rates between 8 to 100 times higher than those previously known, suggesting a near-threshold to enter to a sixth mass extinction (Ceballos *et al.* 2015, 2017). This rate is particularly alarming as it has experienced exponential growth during the last 200 years (see Ceballos *et al.* 2015), and because projections of future scenarios consistently predict a continued and further biodiversity decline (Jenkins 2003; Thomas *et al.* 2004; Pereira *et al.* 2010). Thus, increasing threats to biodiversity are imposing challenges that require prioritizing locations and actions for conservation planning (Meir *et al.* 2004; Reside *et al.* 2018).

Systematic Conservation Planning (SCP) is one of the leading frameworks for guiding decision making on where and what to conserve (Margules & Pressey 2000). The goal of its spatial prioritization process is to identify a network of conservation areas, which represents the biodiversity of a region and supports its persistence over time in a cost-efficient way (Margules & Sarkar 2007). The comprehensiveness of biodiversity is critical for achieving the representation principle in spatial conservation prioritization (Wilson *et al.* 2009; Linke *et al.* 2011). A comprehensive representation of biodiversity must account for three attributes: (1) composition, (2) structure, and (3) function (Franklin *et al.* 1981; Noss 1990). Thus, a set of complementary biodiversity representations is required because no single surrogate is considered comprehensive, and may be insufficient to represent and protect other components of biological diversity (Noss 1990; Bonn & Gaston 2005; Ferrier *et al.* 2009).

Traditional surrogates for species composition are birds, mammals, and vascular plants. Although available data on these groups is considered to be sufficient for representing unknown species (Rodrigues & Brooks 2007), spatial priorities for other groups like amphibians and reptiles may differ (Urbina-Cardona & Flores-Villela 2010). Thus, complementary cross-taxon surrogates, including groups of different taxa, may yet have a better performance for representing biodiversity in conservation planning (Bonn & Gaston 2005; Ferrier *et al.* 2009). Conventional approaches to represent structure include plant assemblages (e.g., Olson *et al.* 2001; Hoekstra *et al.* 2005; Kier *et al.* 2005), environmental classifications (e.g., Araújo *et al.* 2001; Trakhtenbrot & Kadmon 2005; Hortal *et al.* 2009), or land-cover, habitat or ecosystem classifications (Wright *et al.* 1994; Lombard *et al.* 1997; Harborne *et al.* 2008). Functional attribute approaches have involved environmental data proxies for representing process (Pressey *et al.* 2003; Rouget *et al.* 2003; Klein *et al.* 2009), and species assemblages to represent functional or evolutionary traits (e.g., Loyola *et al.* 2008; Loyola & Diniz-Filho 2010; Stuart-Smith *et al.* 2013).

Previous studies have evaluated the performance of different approaches for representing biodiversity, using only one of their attributes (mostly species composition or species diversity) (e.g., Rodrigues & Brooks 2007; Sebastião & Grelle 2009), or using more than one attribute (recently species diversity in combination with taxonomic, functional and/or phylogenetic diversity) (e.g., Sobral *et al.* 2014; González-Maya *et al.* 2016b). Results show that when species composition approaches cover groups within the same taxon, they are well represented up to the realm level (Rodrigues & Brooks 2007), but may vary with different categories for the species (e.g., endemics or threatened) (Urbina-Cardona & Flores-Villela 2010); while phylogenetic diversity approaches show spatial mismatches between diversity patterns among groups within the same realm (Zupan *et al.* 2014).

Furthermore, when different biodiversity representations are used, results show that one biodiversity attribute may not be an accurate approximation to represent other (e.g., taxonomic diversity priorities do not represent functional/phylogenetic diversity priorities) (Sobral *et al.* 2014; González-Maya *et al.* 2016a). Although there are areas where the analysis of a single taxon or functional and phylogenetic diversity spatially match (Bode *et al.* 2008; Strecker *et al.* 2011), they tend to occur over existing conservation areas (Rapacciuolo *et al.* 2019). These dissimilarities imposed by each approach may impact conservation planning in different ways (Brooks *et al.* 2006; Bode *et al.* 2008). Given the increasing threats to biodiversity and limited resources for conservation, our knowledge about the uncertainty in surrogates for representing biodiversity needs to be improved in terms of their impact on conservation prioritization processes.

We present a novel spatial conservation prioritization assessment using a comprehensive approach to represent biodiversity for the Neotropics, one the most biodiverse regions globally. We evaluated differences and surrogacy levels for spatial conservation priorities among the three biodiversity attributes: (1) composition (8563 terrestrial vertebrate species distributions), (2) structure (663 ecosystems), and (3) function (5382 ecological groups). We also assessed conservation areas selected evaluating both current protected areas (PAs) and those prioritized from our results using a regionalized approach involving ecoregions and countries. Finally, we identified critical regions where prioritized areas are crucial for achieving conservation targets in the Neotropics.

Method

Study area

Our study area comprises the Neotropics, including all terrestrial WWF Ecoregions (Dinerstein *et al.* 2017) intersected between the Tropic of Cancer and the Tropic of Capricorn (Figure 1). We excluded the Chilean matorral ecoregion due to its biogeographic and abiotic conditions, which are not typical of tropical environments. The study area covers around 17MM km^2, including the continental area of Belize, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana, Ecuador, Peru, Bolivia, Paraguay, most of the territory of Mexico and Brazil, and a small proportion of Chile and Argentina. It encompasses the whole basins of the Orinoco (1MM km^2) and Amazon rivers (6MM km^2), and the middle and northern Andes (3MM km^2 in total).

The Neotropics exhibit the highest levels of species richness and endemism, both globally and within the main taxa (amphibians, birds, mammals, and vascular and no-vascular plants). Most representative biomes are the tropical moist forest, the tropical dry forest, the savannas, and the Páramo. These biomes contain several hotspots of biodiversity, e.g., the Andes, the Brazilian Atlantic Forest and Cerrado regions, the Darien-Chocó-Pacific moist forest, and the Amazon rainforest (Olson & Dinerstein 1998; Myers *et al.* 2000; Mittermeier *et al.* 2005). However, the Neotropics also hosts the largest proportion of small range and threatened species (Hoffmann *et al.* 2010; Pimm *et al.* 2014), in addition to the highest deforestation rates (43,000 to 54,000km^2/yr) (Wright 2010; Aide *et al.* 2012), increasing the probability of biodiversity decline (Newbold *et al.* 2016; Betts *et al.* 2017; Roque *et al.* 2018).

Figure 1. Study area and proposed habitat classes.

Construction of biodiversity attributes

Composition

To evaluate biodiversity composition (Noss 1990), we employed a community composition approach using species potential distributions at 1km resolution. We employed all the range maps intersecting our study area available in the IUCN Red List of Threatened Species (https://www.iucnredlist.org/resources/spatial-data-download) and BirdLife (http://datazone.birdlife.org/species/requestdis), including 8563 species (amphibians: 2731, birds: 3649, mammals: 1331, and reptiles: 852). Potential distributions of species were delimited by their habitat to produce more accurate distributions that would represent a proxy to their area of occupancy (Phillips *et al.* 2006; Faleiro *et al.* 2013) (Figure S1). We spatialized the habitats for all species using the IUCN habitats categorization, and a standardization proposed with the ESA CCI Land Cover 2015 dataset v2.0.7 (https://maps.elie.ucl.

ac.be/CCI/viewer/) (Figure 1 and Table S1). For details on the construction of the composition attribute, selection of species, and habitat mapping, see Annex 1.

Structure

To evaluate the biodiversity structure attribute, we employed a habitat structure approach using ecosystems as a proxy (Noss 1990). We generated 663 ecosystems at 1km resolution as the intersection of the WWF Ecoregions, and the natural and degraded former forest classes of the habitats map (Figure 1 and Figure S2). We included a combination of secondary vegetation with corresponding natural habitats since these can provide complementary conservation services to biodiversity (Barlow *et al.* 2007; Dent & Joseph Wright 2009), and also contribute to improving biodiversity protection by achieving conservation targets (Mappin *et al.* 2019). All the ecosystems were reviewed visually to validate their occurrence. Ecosystems with a total area less than five pixels (an area of 25km^2) were excluded by aggregating them to their nearest neighborhood to prevent that irreplaceability could incorrectly guide conservation priorities towards these regions.

Function

For the function attribute, we used an ecological groups approach based upon species traits (Blaum *et al.* 2011) as a proxy for ecosystem processes (Noss 1990). We employed information summarized at the genus level (1754 genera) for three traits: (1) biomass (large, large-medium, medium, medium-small, and small sizes), (2) trophic guild (carnivorous, carnivorous-insectivorous, folivorous, frugivorous, frugivorous-granivorous, frugivorous-insectivorous, granivorous, hematophagous, herbivorous, insectivorous, nectarivorous, omnivorous), and (3) habit (freshwater, freshwater-marine, terrestrial, terrestrial-freshwater, terrestrial-marine, terrestrial-freshwater-marine). Data for traits was obtained from multiple sources and trait databases (Table S2). We constructed and validated the ecological groups in PRIMER-e software (Clarke & Gorley 2019) using the SIMPROF routine (Clarke *et al.* 2008), and a Dice/Jaccard presence/absence matrix. The resulting ecological groups were spatialized at 1km resolution by combining the distribution of the corresponding species for each genus and assigning their resulting ecological group. Finally, we intersected the 47 ecological groups generated with the WWF Ecoregions to differentiate the ecological processes at ecosystems level, producing a unique combination of 5382 ecological groups. For details on the construction of ecological groups, see Annex 2.

Comparison of biodiversity attributes approaches

Spatial conservation prioritization

The three required components for spatial conservation prioritization exercises were defined: the conservation features (what I want to conserve?), conservation targets (how much I want/need to conserve?), and planning units (over what potential sites I will select conservation areas?) (Game & Grantham 2008; Hanson *et al.* 2020a). Conservation areas were identified resolving the minimum set cover problem (Moilanen et al. 2009) for all the biodiversity attributes approaches separately (conservation features). The optimization process was performed using Prioritizr package in R (Hanson *et al.* 2020b), which uses integer linear programming to achieve conservation targets at the least cost (Beyer et al. 2016). We applied fixed targets (conservation targets) for each biodiversity feature (each species, ecosystem, or ecological group) and neither penalties nor constraints for them or the planning units (PUs) (10x10km grid) to evaluate the independent effect of composition, structure, and function approaches. We used the Convention on Biological Diversity's Aichi Target 11 to protect 17% of each biodiversity feature area (e.g., Venter et al. 2014; Mappin et al. 2019) as conservation target in our prioritization, and locked as PAs all PUs with at least 50% covered by the current PA system (e.g., Kark *et al.* 2009; Klein *et al.* 2009; Esselman & Allan 2011). We included all PAs with the IUCN categories I-IV (strict protection) (e.g., Jenkins & Joppa 2009; Kark *et al.* 2009) from the World Database on Protected Areas (IUCN & UNEP-WCMC 2018), as well as the documented indigenous lands from the Global Platform of Indigenous and Community Lands (LandMark) (http://www. landmarkmap.org/). We verified that this combination of PAs includes inside their boundaries 97% of natural land cover according to our habitat classes approach (Figure 1), supporting their inclusion. We included the proportion of transformed area (croplands, pasturelands, and urban areas in Figure 1) per planning unit as costs for minimizing the objective function.

Comparison of approaches

We ran 100 portfolios for each biodiversity attribute approach taking the best model run (least cost), and the selection frequency of each planning unit as a proxy for its irreplaceability (e.g., Stewart & Possingham 2005; Fuller *et al.* 2006; Dobrovolski *et al.* 2013). Additionally, a model including all the biodiversity attributes approaches (14,608 biodiversity features composed by 8563 species, 663 ecosystems, and 5382 ecological groups) was performed as reference for comparison (All BFs), assuming that this model represents the three biodiversity attributes for the Neotropical region. We evaluated the area (nPUs) (e.g., Nhancale & Smith 2011), effectiveness (MTA) (e.g., Müller *et al.* 2018), representativeness (PE) (e.g., McGowan *et al.* 2017), aggregation level (AGG) (e.g., Alagador & Cerdeira 2007), and surrogacy level (TMTA, TPE, KAPPA) for the best model run of all biodiversity attributes approaches and the reference model (Table 1). Also, we compared each approach in three types of areas: (1) current PAs, (2) prioritized areas (PRAs) (those selected to complement the PAs), and (3) total areas (TAs) (PAs and PRAs). Metrics were compared for the entire Neotropics and over a regionalization approach using the Global 200 (G200) ecoregions (Olson & Dinerstein 1998) by country (Figure S3).

Finally, differences on metrics for the selected conservation areas (Table 1) obtained from each biodiversity attribute approach (fixed factor with four levels: composition, structure, function, and the reference model with all the biodiversity features), and the type of area (fixed factor with three levels: total areas, PAs, and prioritized areas), were evaluated using a two-way permutational analysis of variance (PERMANOVA). PERMANOVA is a partitioning method based on distances that calculates p-values from a distribution-free permutation procedure (Anderson 2001, 2017). We used Euclidean distances between the values of metrics calculated in each ecoregion-country, and type III partial sums of squares running 9999 permutations in PRIMER-e software and the PERMANOVA *add on* (Clarke & Gorley 2019). Pair-wise comparisons among all levels per factor were evaluated through a pseudo-t-test (Anderson *et al.* 2008).

Table 1. Metrics employed to compare conservation areas selected among biodiversity attributes approaches.

Metric	Description	
Area Number of Planning Units (nPUs)	nPUs indicates the extension of the conservation areas selected. More efficient approaches should result in fewer nPUs selected for achieving conservation targets. nPUs are presented as a percentage relative to study area for total areas, and as a percentage relative to total areas for PAs and prioritized areas.	
Effectiveness Mean Target Achievement (MTA) (Jantke *et al.* 2019)	MTA indicates the mean proportion of target achievement of all biodiversity features represented in the conservation areas selected. It ranges between 0 and 100%. A value of 0 indicates that no biodiversity feature received any protection, and 100% indicates that the target was achieved for all biodiversity features. Our spatial conservation prioritization approach guarantees optimal solutions, i.e., it ensures that the MTA is 100% for total areas. MTA was calculated in R using the ConsTarget package (https://github.com/KerstinJantke/ConsTarget).	$\frac{\sum_{1=1}^{N} min\left(\left(\frac{(P_i/A_i)}{T}\right)\times 100,100\right)}{N}$ P is the area of conservation areas selected, and A is the total area for biodiversity feature i. T is the fixed proportional target protection level, and N is the total number of biodiversity features.
Representativeness Protection Equality (PE) (Chauvenet *et al.* 2017)	PE indicates the level of equity of the biodiversity features represented in the conservation areas selected. It is homologous to Gini index ranging between 0 and 1. A value of 1 indicates a perfectly homogenous biodiversity features representation, i.e., that all of them are equally protected in terms of their area. PE was	$\frac{\frac{1}{N}\times\left(\frac{1}{2}\sum_{i=1}^{N} p_i + \sum_{i=1}^{N-1} p_i \times (N-i)\right)}{\frac{1}{2}\times\sum_{i=1}^{N} p_i}\times 100$

Metric	Description	
	calculated in R using the ProtectEqual package (https://github.com/AChauvenet/ ProtectEqual). The metric was multiplied by 100 to be presented in the same range (0-100) of other metrics.	P is the area of conservation areas selected for biodiversity feature i, and N is the total number of biodiversity features.
Aggregation level Aggregation Index (AGG) (He *et al.* 2000)	AGG indicates the degree of compactness of the NCA. The index ranges between 0 and 100% and is estimated as the number of adjacencies divided by their maximum possible number. A value of 100% indicates maximum aggregation into a single compact patch reducing edge effects and fragmentation. AGG was calculated in R using the spatialEco package.	
Surrogacy Effectiveness Transposed Mean Target Achievement (TMTA)	We developed TMTA and TPE as new metrics for evaluating the surrogacy at the effectiveness (TMTA) and representativeness (TPE) levels. TMTA and PE area calculated for a set of biodiversity features, but employing a set of conservation areas obtained for a different set of biodiversity features. TMTA and TPE maintain the same logics for their estimation and ranging values of MTA and PE. We evaluated the effectiveness and representativeness of conservation areas selected for each biodiversity attribute to represent all biodiversity features.	
Surrogacy Representativeness Transposed Protection Equality (TPE)		
Surrogacy Spatial Agreement Kappa Index (KAPPA) (Cohen 1960)	The Kappa index was employed to estimate the spatial agreement of conservation areas selected for composition, structure, and function attributes with respect to the one generated for all biodiversity features. KAPPA ranges between 0 and 1. A value of 0 indicates that no single PUs was selected in both of the compared approaches, and 1 that the PUs selected were the same in both approaches. The index was multiplied by 100 to be presented in the same range (0-100) of other metrics.	

Results

Differences in biodiversity attributes and the type of area at the Neotropical level

We found differences in the spatial distribution of prioritized areas for the three biodiversity attributes approaches (Figure 2A-D). The spatial arrangement of selected conservation areas for the compositional attribute guided further conservation priorities concerning all biodiversity features (Table 2). There is a larger number of species (8563) than ecosystems (663) and ecological groups (5382); not surprisingly, our results show that more area is required to meet conservation targets in relation to the number of biodiversity features to represent (Table 3 and Table S4). However, the differences in area and aggregation level for each biodiversity attribute approach were not significant (Table 4), and the percentage of variance explained in the model by the biodiversity attribute factor for both metrics was the lowest (Figure 3). Therefore, biodiversity attributes approaches produced similar extensions and compactness in the conservation areas selected (Table 3 and Table 4), but not in their spatial distribution (Figure 2F and Table S4), differentially affecting the levels of representativeness and effectiveness

Differences between biodiversity attributes were the most significant factor of variability for the protection equality metric (Figure 3), supporting that type of surrogate employed is a critical factor for guaranteeing representativeness in conservation areas. Representativeness of biodiversity features was unequal (Table 3), leading to more inefficient conservation areas where some biodiversity features were barely represented, and others overrepresented. Particularly, the structural approach exhibits the lowest values (Table 3) and less significant differences (Table 4), consequently related to lower levels of surrogacy (Table 2). Conversely, the equality on biodiversity features of the functional attribute was the highest (Table 3), maintaining similar values of effectiveness, area, and aggregation than the other biodiversity attributes approaches (Table 3). These properties found in ecological groups supported their surrogacy level for compositional and structural attributes of biodiversity.

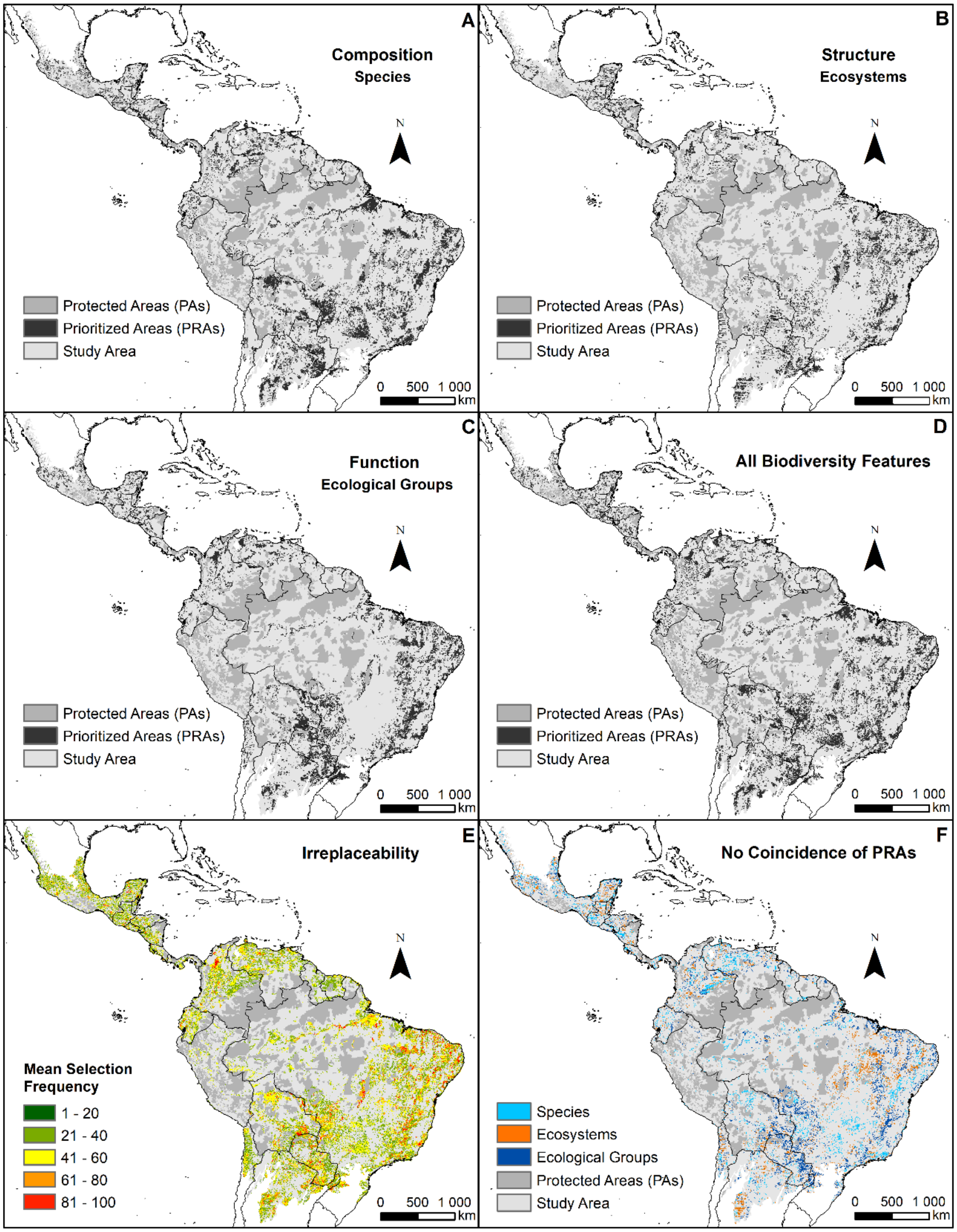


Figure 2. (A-D) Spatial distribution of conservation areas selected by biodiversity attribute approach. (E) Irreplaceability of prioritized areas (PRAs). Values correspond to the mean selection frequency in the three biodiversity attributes approaches and the reference approach including all biodiversity features. (F) No coincidence of prioritized areas (PRAs) between biodiversity features approaches, i.e., where planning units were selected in only one biodiversity attribute approach (see also Table S5).

Table 2. Surrogacy of conservation areas selected for biodiversity attributes with respect to all biodiversity features. Metrics were calculated separately in prioritized (PRAs) and total areas (TA).

Biodiversity attribute	Composition		Structure		Function	
Metric	Prioritized Areas (PRAs)	Total Areas (TA)	Prioritized Areas (PRAs)	Total Areas (TA)	Prioritized Areas (PRAs)	Total Areas (TA)
Effectiveness (TMTA)	57.35	95.44	36.67	88.53	46.72	91.75
Representativeness (TPE)	12.73	11.37	10.82	10.85	11.46	11.13
Spatial Agreement (KAPPA)	66.33	85.53	29.34	73.67	37.12	74.40

Table 3. Metrics for biodiversity attributes. nPUs are presented as a percentage relative to study area for total areas, and as a percentage relative to total areas for PAs and prioritized areas. The other metrics were calculated separately in each type of area (PAs, PRAs, and TAs).

Metric	Biodiversity Feature (BF)	Protected Areas (PAs)	Prioritized Areas (PRAs)	Total Areas (TAs)
Area (nPUs %)	Composition	66.89	33.11	29.82
	Structure	76.37	23.63	26.12
	Function	70.42	29.58	28.32
	All Biodiversity Features	66.15	33.85	30.15
Effectiveness (MTA %)	Composition	67.05	61.03	100.00
	Structure	41.99	61.63	100.00
	Function	57.19	58.75	100.00
	All Biodiversity Features	62.32	64.08	100.00
Representativeness (PE)	Composition	12.34	15.66	14.22
	Structure	7.70	12.15	12.25
	Function	18.22	17.85	23.95
	All Biodiversity Features	9.44	12.99	11.44
Aggregation level (AGG %)	Composition	83.99	48.96	73.91
	Structure	83.99	37.10	73.87
	Function	83.99	48.09	74.68
	All Biodiversity Features	83.99	45.85	72.49

The type of area was the most critical factor of variance in the models (Figure 3). The most relevant difference was the area/effectiveness relationship. Effectiveness values for PAs and prioritized areas were similar, but the number of planning units of prioritized areas was, on average, 60% smaller than PAs areas (Table 3). Also, representativeness was higher in prioritized areas (Table 3), supporting the achievement of conservation targets for biodiversity protection more equitably and efficiently. Conversely, aggregation was higher in PAs; thus, total areas proposed could be considered as a balanced proposal weighting both effectiveness and representativeness in prioritized areas, and aggregation in PAs.

Table 4. p-values resulting from PERMANOVAs for testing the differences of all the biodiversity attributes and the type of area. PERMANOVAs were applied to each metric and the corresponding pairwise combination of all levels. When permutations are under 100, PRIMER-e estimates the p-value using Monte-Carlo simulations (°); otherwise, the p-value from permutations is calculated (*) (Anderson & Robinson 2003; Anderson *et al.* 2008).

Factor / Levels	**Area (nPUs)**	**Effectiveness (MTA)**	**Representativeness (PE)**	Aggregation level (AGG)
Biodiversity attribute	0.96	0.00 ***	0.01 ***	0.04 **
Composition - Structure	0.22	0.10 *	0.04 °°	0.31
Composition - Function	0.22	0.27	0.07 °	0.24
Composition - All biodiversity features	0.22	0.28	0.38	0.25
Structure - Function	0.20	0.16	0.23	0.34
Structure - All biodiversity features	0.20	0.10 *	0.03 °°	0.35
Function - All biodiversity features	0.22	0.22	0.05 °	0.25
Type of area	0.00 ***	0.00 °°°	0.00 ***	0.00 ***
Total areas - Protected areas	0.03 **	0.03 °°	0.03 **	0.03 **
Total areas - Prioritized areas	0.03 **	0.03 °°	0.03 **	0.03 **
Protected areas - Prioritized areas	0.03 **	0.03 °°	0.03 **	0.03 **

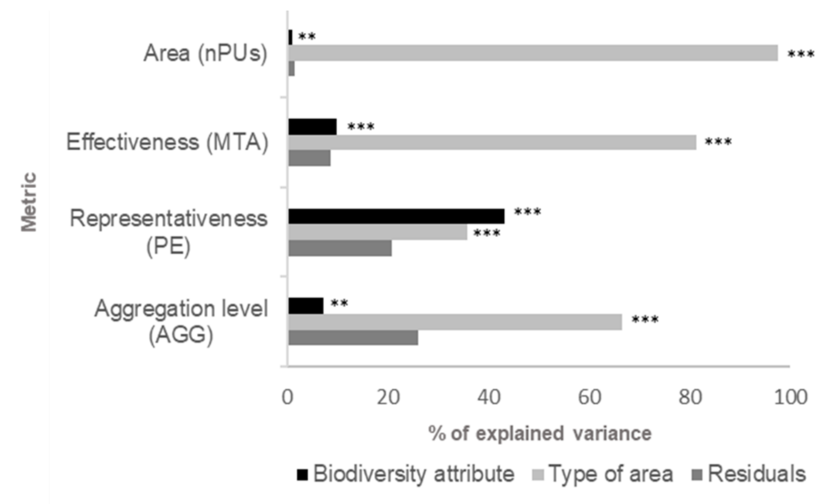


Figure 3. Percentage of explained variance of PERMANOVA models for the differences in biodiversity attributes, the type of area, and the residuals of the model. Both factors (biodiversity attributes and type of area) were significantly different for all variables to 99% (***) or 95% (**) of confidence. p-values correspond to those on each factor in Table 4.

Differences in biodiversity attributes and the type of area at the regional level

Differences in the type of areas were more important than differences in biodiversity attributes at the regional level, particularly for the area and effectiveness variables (Figure 3 and Figure 4A-B). We found critical regions where the area of prioritized areas is more than 80% of total areas, but also the highest effectiveness values occurred. In these regions, biodiversity conservation is more conditioned than in others since protection depends on the new PAs establishment, but besides, these areas would cover almost the total extension of the region. These regions include threatened biodiversity hotspots like the Atlantic forests, Cerrado and Pantanal regions, and dry forests of the Andean valleys of

Ecuador and Colombia (Figure 4A-B and Table S3). Conversely, the majority of the ecoregions of the Amazon basin, the middle Andes in Peru, and the Pacific moist forests already have most of their area protected and conservation targets achieved (Figure 4A-B and Table S3).

Higher representativeness values for prioritized areas than PAs also occur regionally. The highest values were found for the three types of areas in small and compact regions covering fewer biodiversity features. The Guyana, French Guyana, and Suriname, the Northern Andean Páramo of Venezuela, the moist forests of Napo (Ecuador) and Rio Negro-Juruá (Peru), the Pacific Mangroves of Colombia, the Paraguayan Pantanal, the Atlantic Forests of Argentina, and the Pine-Oak Forests of Honduras (Figure 4C and Table S3). However, biodiversity hotspots had the lowest values of representativeness since they support more biodiversity features into more complex spatial arrangements (Figure 4C and Table S3).

Aggregation patterns also followed the same levels found for the Neotropics. PAs have higher levels of aggregation and guide the patterns for total areas. The regions with the highest values in PAs occur over the Amazon basin and Guyana moist forests, the Llanos savannas of Venezuela, the Pacific moist forests, and the Pine-Oak forests in Guatemala (Figure 4D and Table S3). Conversely, regions with known fragmentation levels such as the northern Andes in Colombia and the dry forests of southern Mesoamerica had higher aggregation values in their prioritized areas, supporting that the establishment of prioritized areas proposed would improve connectivity in these critical areas.

Variability in the surrogacy level between biodiversity attributes is more evident for regions than for the Neotropics (Figure 5). The most significant differences in area, effectiveness, and spatial agreement were found for the structural approach, which also had the lowest values similar to the Neotropical level (Table 2). The similarities between the compositional and all biodiversity features remain constant at the regional level, showing higher overall levels of surrogacy (Figure 5 and Table 2). However, in the moist forests of Choco-Darién and the northern Andes in Colombia, the Venezuelan Llanos savannas, the moist forests of the Colombian Amazon, and the Atlantic forests of Paraguay, surrogacy levels are determined by the structural and functional approaches, supporting that conservation priorities may be guided by different biodiversity attributes regionally (Figure 5).

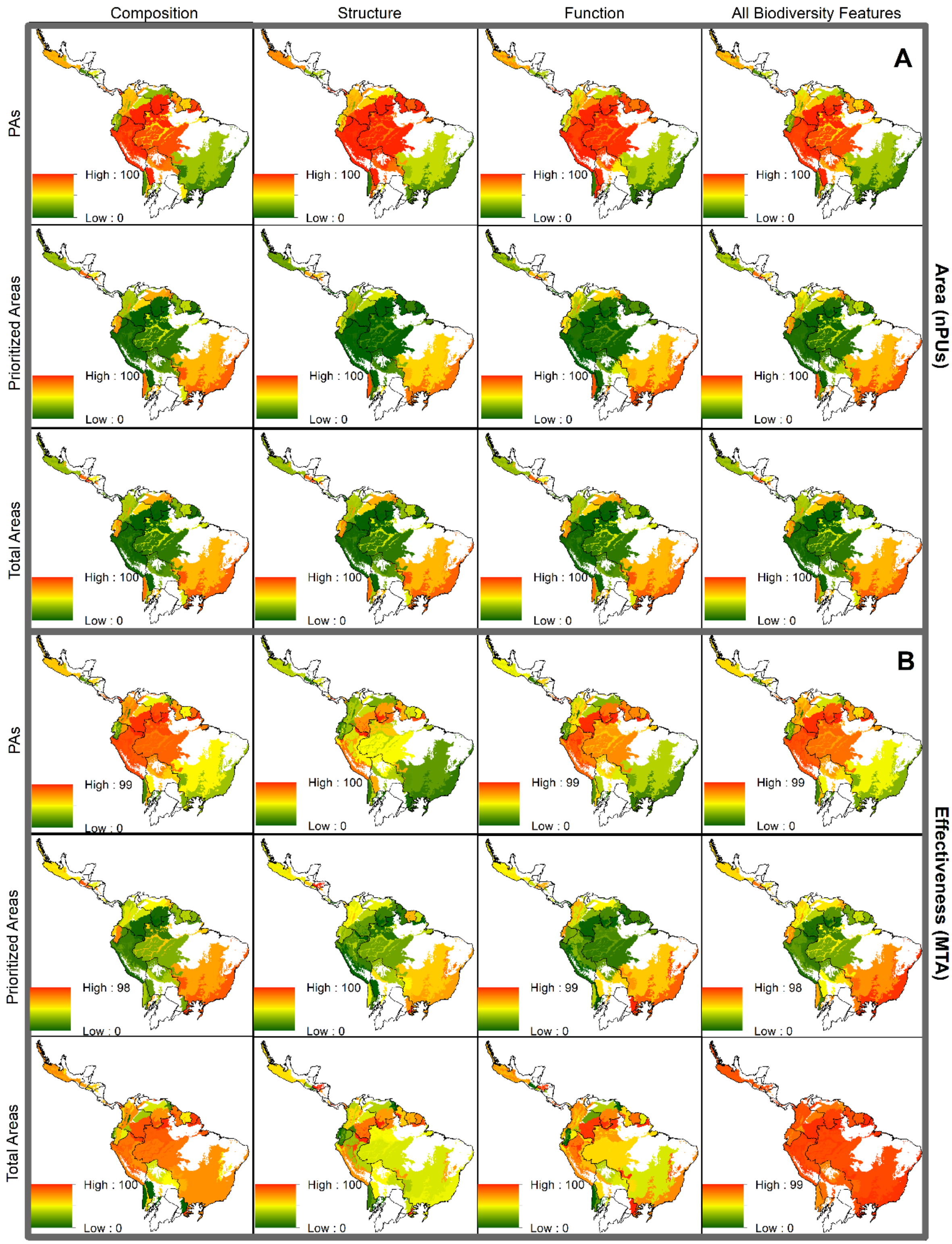


Figure 4. Area (A) and effectiveness (B) of biodiversity attributes approaches in the different types of areas regionally. The regions correspond to the Global 200 ecoregions and countries intersection.

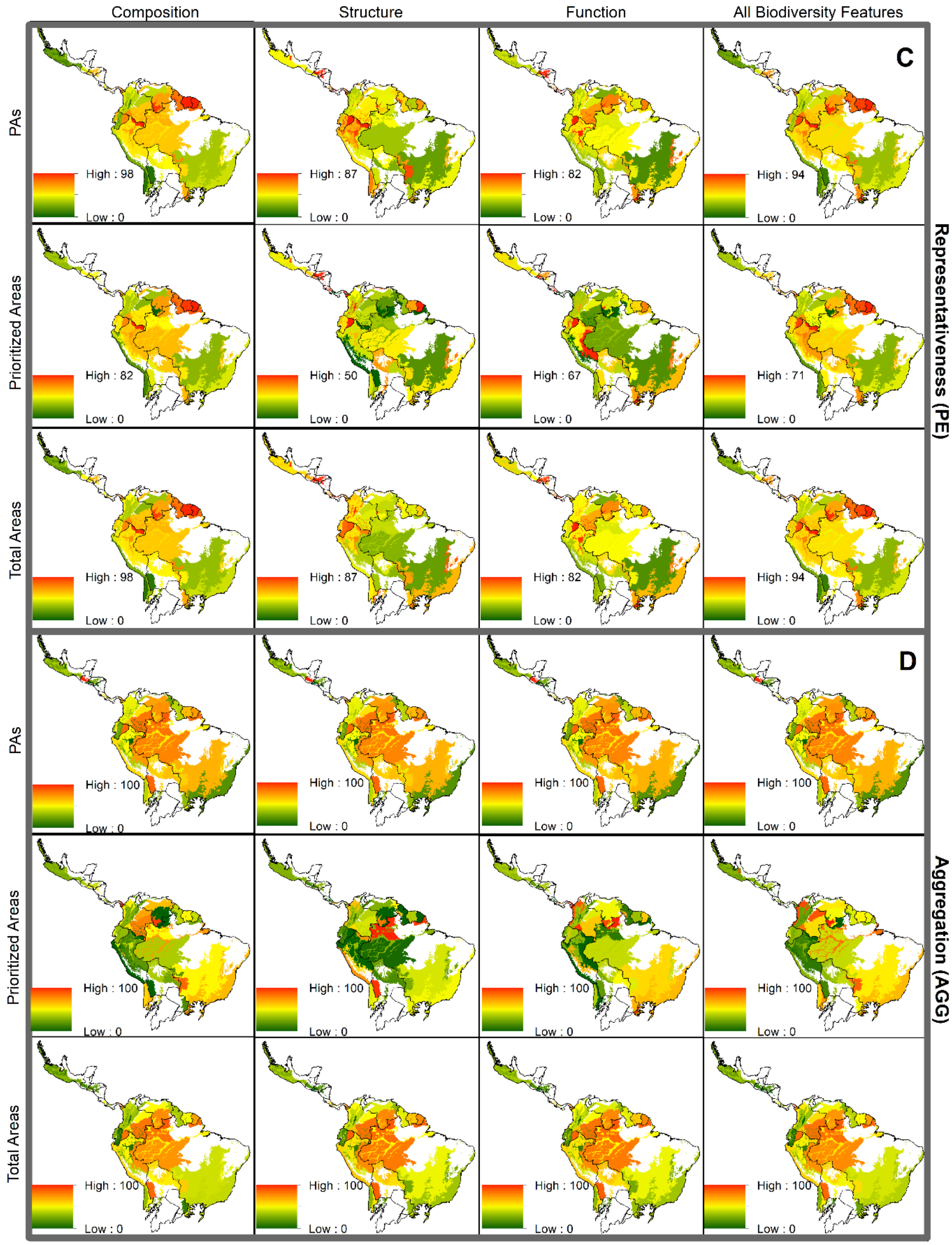


Figure 5 (cont.). Representativeness (C) and aggregation level (D) of biodiversity attributes approaches in the different types of areas regionally. The regions correspond to the Global 200 ecoregions and countries intersection.

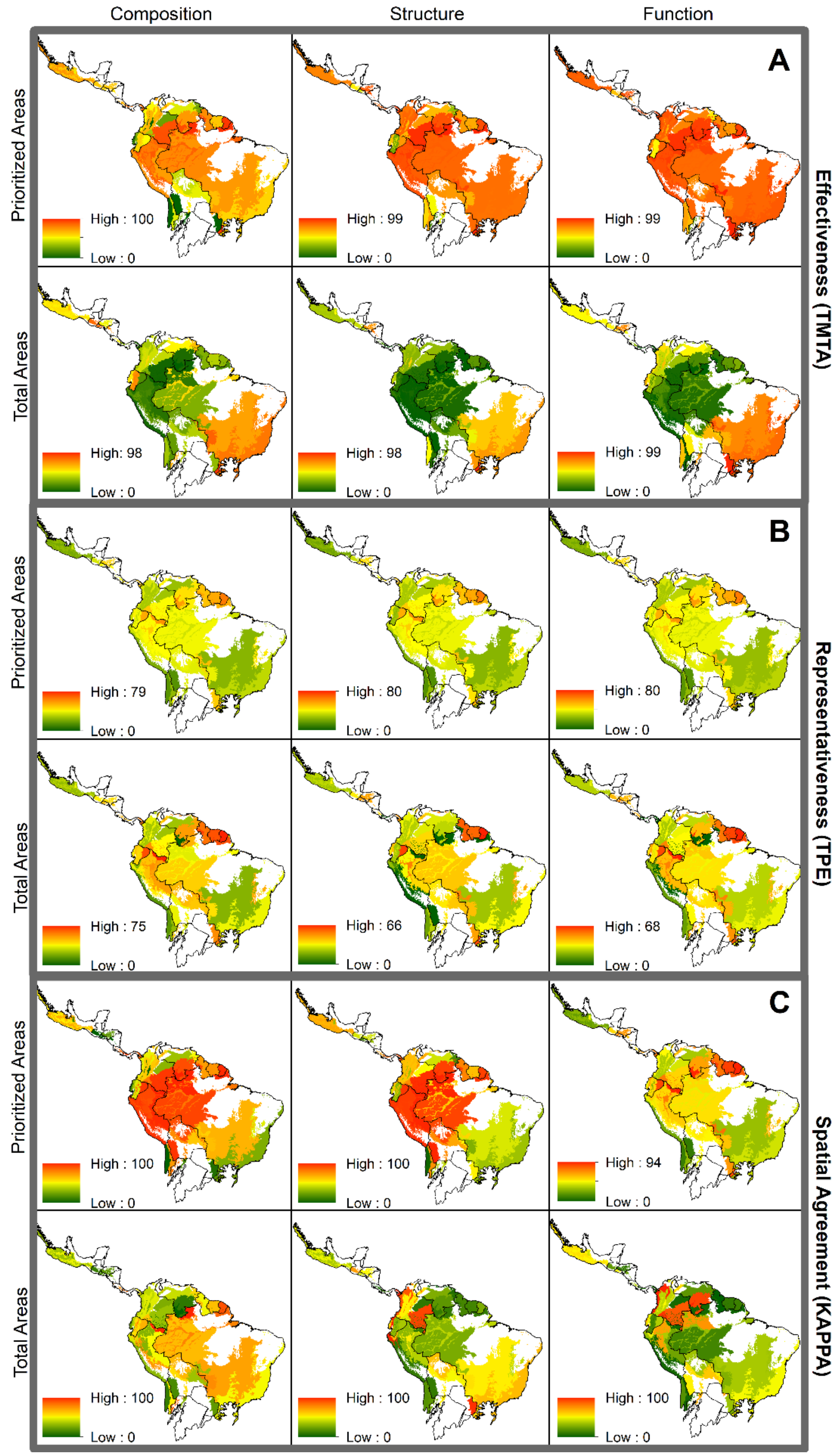


Figure 5. Surrogacy level in the effectiveness (A), representativeness (B), and spatial agreement (C) of biodiversity attributes approaches in the different types of areas regionally. Each attribute approach is compared to the reference model including all biodiversity features. Values of 100 indicate a perfect surrogacy. The Regions correspond to the Global 200 ecoregions and countries intersection. Surrogacy in PAs is equal for all biodiversity attributes since PAs are the same in all approaches.

Critical conservation areas for the conservation of Neotropical biodiversity

PAs did not fulfill Aichi target 11 for protecting 17% of biodiversity attributes in the Neotropical region. At the country level, the situation is critical for Paraguay, El Salvador, and Guatemala, where PAs guarantee less than 50% of protection target fulfilling, but where prioritized areas represent more than 70% of the areas necessary to achieve it (Table S5). Therefore, prioritized areas found are necessary for ensuring the representativeness of Neotropical biodiversity. These areas were mostly located in complementary regions distant from the large current PAs, concentrated in the Chaco region of Argentina and Paraguay; Atacama desert and dry Puna in Chile; Atlantic and Maranhão Babaçu forests, amazon floodplains (várzea), and Pantanal, Cerrado and Caatinga regions in Brazil; Benni floodplains in Bolivia; northern Andes of Ecuador and Colombia; savannas of Colombia and Venezuela; dry forests of Nicaragua, Honduras, El Salvador and México; and moist forest of central and eastern Mexico (Figure 2A-D). Moreover, the largest and most irreplaceable prioritized areas found (Figure 2E) coincide with critical and threatened (Table S6) hotspots of biodiversity: the Chaco, Atlantic forests, the Brazilian Pantanal, Cerrado, and Caatinga, the northern Andes, and Yucatán forests.

Discussion

Differences in biodiversity attributes approaches

According to our results, two critical issues should be considered regarding the differences found in the surrogacy level of BF approaches: (1) The number of BFs, and (2) the level of overlap of each approach. A large number of BFs with a low level of overlap require an extensive area to meet conservation targets. Unsurprisingly, the compositional attribute approach emerges as the best substitute guiding conservation priorities at the Neotropical level because of the number of species and their overlapping distributions, contrary to structural approach, since ecosystems are discrete non-overlapping features. These differences were more evident for the equality in representativeness metric, which is commonly higher in complementary cross-taxon surrogates than in environmental surrogates (Bonn & Gaston 2005; Rodrigues & Brooks 2007), coincidently with our findings for the species and ecological groups approaches.

However, regional differences found strengthen the need for complementary biodiversity attributes as surrogates for representing biodiversity (Bonn & Gaston 2005; Ferrier *et al.* 2009). Particularly, the largest spatial mismatches produced by our ecological groups approach support the importance of accounting the functional biodiversity attribute in conservation planning. More variability in conservation areas selection indicates more different strategies and actions that should be considered for biodiversity conservation (Brooks *et al.* 2006). Although the ecological groups is a novel approach in conservation planning exercises, it gives a functional outlook of main ecological processes such as herbivory, pollination, seed dispersal, and plague control (Sekercioglu 2012).

Results using other functional approaches such as phylogenetic or functional diversity, also showed spatial mismatches between priorities regarding taxonomic diversity (Sobral *et al.* 2014; González-Maya *et al.* 2016a, b), different land cover types (Morelli *et al.* 2018), and different taxonomic groups (Zupan *et al.* 2014). Nevertheless, coincident areas between compositional, structural and functional attributes regularly occur over high irreplaceable regions, as our proposed areas (Bode *et al.* 2008; Rapacciuolo *et al.* 2019). Therefore, the spatial congruences over areas of the highest conservation priority found, support that conservation actions may be simultaneously developed for multiple conservaton features towards a comprehensive, complementary, and efficient biodiversity conservation (Strecker *et al.* 2011).

Differences in the type of conservation areas

Most critical differences between PAs and prioritized areas concern efficiency. On average, prioritized areas were 60% more efficient in allocating less area to meet conservagtion targets than PAs. This result contrast with the increase in the number of PAs at a global level, which has been considered as an indicator of better representativeness and effectiveness without a clear measure of how current PAs contribute to meet conservation targets (Barr *et al.* 2011; Venter *et al.* 2014; Baldi *et al.* 2019). Nertheless, our results reveal that PAs of the Neotropics are not enough to meet the current target for protecting 17% of biodiversity as also found recently (Baldi *et al.* 2019), but improve this information showing where the current PAs do ensure the fulfilling of conservation targets regionally.

Aggregation patterns were higher in PAs since they are mostly located over large extensions of natural areas. Consequently, prioritized areas were mostly distributed in regions with known fragmentation levels, where the establishment of new conservation areas proposed would improve connectivity for supporting different ecological processes in these critical regions (Velez–Liendo *et al.* 2014; Clerici *et al.* 2019). Our results, also showed that representativeness is higher in prioritized areas than in PAs. Low values in the equality of representativeness for PAs have also been found using different surrogates and regionalization approaches (Kuempel *et al.* 2016). We found that the lowest values in representativeness occur in high biodiverse regions since there are more biodiversity features that need larger and more complex spatial arrangements of conservation areas to guarantee their protection. Lower values and more variability in protection equality have also been found in Neotropical ecoregions and countries (Barr *et al.* 2011; Baldi *et al.* 2019). Therefore, combination of current PAs and our prioritized areas proposed produce a balanced combination of conservation areas weighting both effectiveness and representativeness in prioritized areas, and aggregation in PAs.

Critical conservation areas for the conservation of Neotropical biodiversity

We identified critical hotspots of biodiversity where the achievement of conservation targets depends on the establishment of new conservation areas, but also where irreplaceability is consistent through all biodiversity attributes approaches, supporting decision making to take urgent conservation actions (Leal *et al.* 2005; Tabarelli *et al.* 2010; Roque *et al.* 2016). However, multiple drivers of change, mainly related to agricultural and livestock expansion threaten these regions (Table S6), in addition to more located landscape transformation drivers such as illegal mining (Deheza & Ribet 2012; Sánchez-Cuervo & Aide 2013b; Fagua & Ramsey 2019), large monocultures (Fearnside 2001; Richards 2011; Castiblanco *et al.* 2013), and infrastructure development (Nagendra *et al.* 2003; Pacheco *et al.* 2011; Romero-Ruiz *et al.* 2012). Moreover, these threats not only impose challenges for conserving biodiversity but also to communities, since these are the central figures supporting conservation actions over these regions (Miller & Hobbs 2002; Mace 2014). Therefore, efforts to conserve should be redoubled regarding the sustainable livelihoods of communities (Baptiste *et al.* 2017). Considering people in conservation increases its success by understanding the social and economic dynamics behind the threats, and the particular conservation needs of each area (O'Connor *et al.* 2003; Margules & Sarkar 2007; Castro-Nunez *et al.* 2017).

Conclusions

We presented a comprehensive spatial conservation prioritization employing representations for biodiversity composition, structure, and function in the Neotropics. From our results, we propose two critical issues that should be considered for surrogates in conservation planning: (1) the number of BFs, and (2) the level of overlap of each approach. The higher the number of biodiversity features and the lower their level of overlap is, the larger the area required to meet conservation targets is. Thus, our compositional attribute approach emerges as the best substitute for guiding conservation priorities at the Neotropical level, because of the number of species employed for different taxonomic groups and the high overlap among species distributions. Our results coincide with other studies suggesting that surrogacy in representativeness is higher in cross-taxon than in environmental substitutes of biodiversity (Bonn & Gaston 2005; Rodrigues & Brooks 2007).

The differences in biodiversity attributes approaches found were significant. Based on these results, we support the premise that complementary surrogates are needed in conservation planning since no single representation of biodiversity is comprehensive. Additionally, particular differences found in the equality of biodiversity attributes support that the type of surrogate employed is a critical factor for guaranteeing representativeness in conservation areas. We introduce a novel approach in conservation planning to represent the functional attribute of biodiversity, the ecological grouping approach. This approach has several advantages, it permits to combine compositional and structural biodiversity attributes, it is the most equally represented biodiversity attribute, it produces the most spatial mismatches concerning other biodiversity attributes accounting more variability for conservation strategies, and it represents a functional outlook for conservation planning of main ecological processes such as herbivory, pollination, seed dispersal, and plague control.

Current PAs in the Neotropical region do not meet the Aichi 11 target for conserving 17% of biodiversity; therefore, it is necessary to expand the current PAs, coinciding with regional and global results (Baldi *et al.* 2019). The most significant differences between PAs and prioritized areas were found regarding their efficiency. Prioritized areas meet conservation targets in the same proportion, but with higher levels of representativeness, and in 60% less area than PAs, supporting biodiversity protection more equitably and efficiently. Nevertheless, aggregation patterns were higher in PA; therefore our combination of PAs and prioritized areas proposed could be considered an optimal spatial trade-off weighting both, effectiveness and representativeness in prioritized areas, and aggregation in PAs.

We identified critical regions where the achievement of conservation targets depends on the establishment of new conservation areas. In these regions, the irreplaceability of prioritized areas is the highest, but also known critical and threatened global biodiversity hotspots ocurr. These areas are mostly located in the Chaco, the Atlantic forest, the Pantanal, Cerrado, and Caatinga regions in Brazil, and the moist and dry forests of northern Andes. We also identified critical countries where the establishment of new conservation areas is necessary, since current PAs guarantee less than 50% of Aichi target 11 fulfilling. These countries are Paraguay, El Salvador, and Guatemala.

Supplementary Data

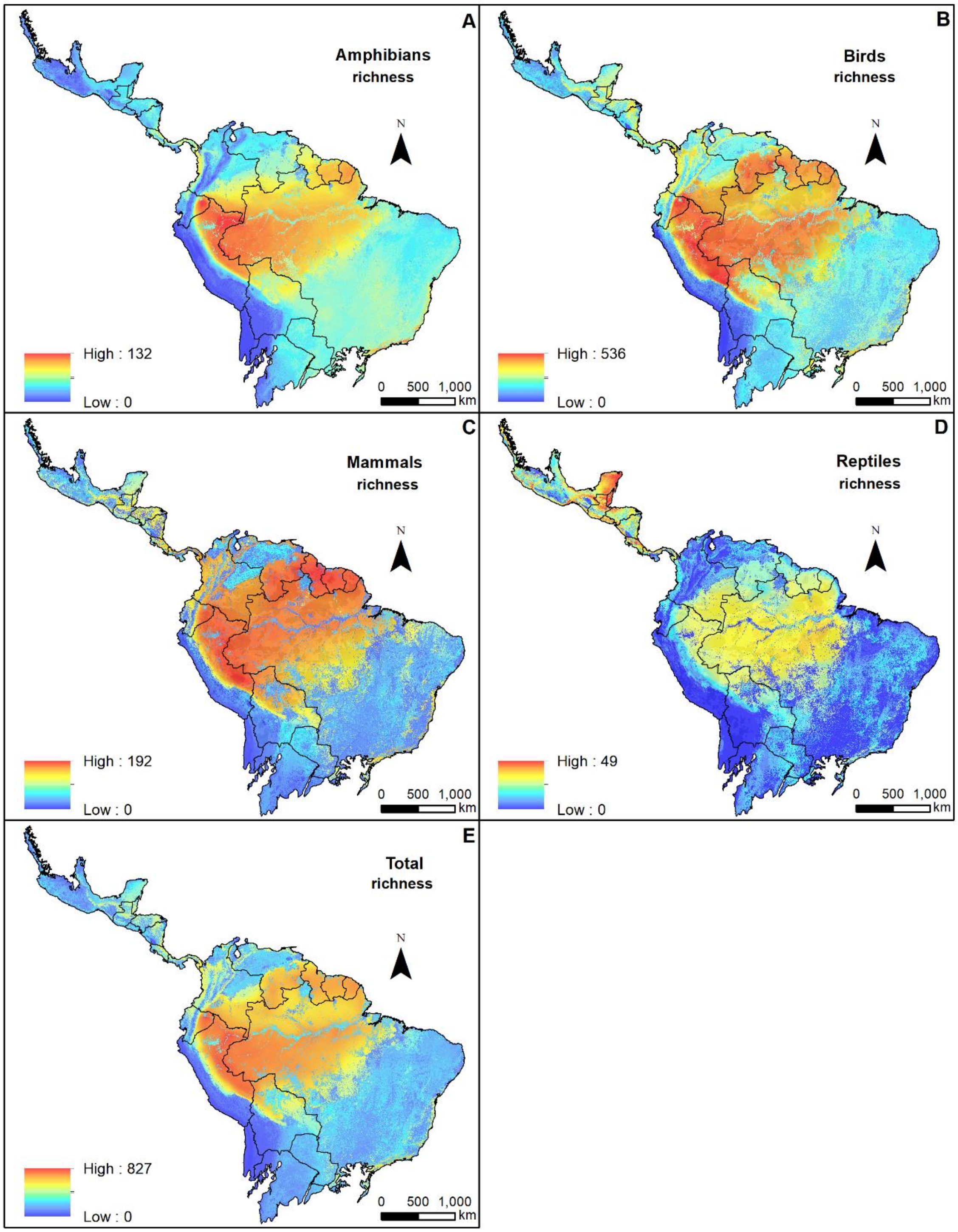


Figure S1. Richness of species distribution models delimited by habitats (Table S1). Species distribution models were employed as biodiversity features in the composition attribute approach.

Table S1. Habitats categories proposed, IUCN habitats categories (version 3.1 from 2012), and standardization of IUCN habitats with the land cover map. Most habitats not included from the IUCN categories do not represent tropical habitats or correspond to the marine biome. Other classes were not included as they do not find correspondence with the land cover classes.

Habitat Category Proposed	IUCN's Habitat Category	Land Cover Map Class
Subtropical/Tropical Moist Forests	Forest - SubtropicalTropical Moist Lowland Forest - SubtropicalTropical Moist Montane	Tree cover, broadleaved, evergreen, closed to open (>15%)
Subtropical/Tropical Dry Forests	Forest - SubtropicalTropical Dry	Tree cover, broadleaved, deciduous, closed to open (>15%) Tree cover, broadleaved, deciduous, closed (>40%) Tree cover, broadleaved, deciduous, open (15-40%)
Pine-Oak Forests	Forest - Temperate	Tree cover, needleleaved, evergreen, closed to open (>15%) Tree cover, needleleaved, deciduous, closed to open (>15%) Tree cover, needleleaved, deciduous, closed to open (>15%)
Subtropical/Tropical Mangrove Forests	Forest - SubtropicalTropical Mangrove Vegetation Above High Tide Level	Tree cover, flooded, saline water
Subtropical/Tropical Swamp Forests	Forest - SubtropicalTropical Swamp	Tree cover, flooded, fresh or brackish water
Savannas and Grasslands	Savanna - Dry Savanna - Moist Grassland - Temperate Grassland - SubtropicalTropical Dry Grassland - SubtropicalTropical High Altitude	Grassland
Shrublands	Shrubland - Temperate Shrubland - SubtropicalTropical Dry Shrubland - SubtropicalTropical Moist Shrubland - SubtropicalTropical High Altitude	Shrubland
Flooded Savannas and Grasslands	Grassland - SubtropicalTropical Seasonally WetFlooded Wetlands (inland) - Shrub Dominated Wetlands Wetlands (inland) - Bogs, Marshes, Swamps, Fens, Peatlands	Shrub or herbaceous cover, flooded, fresh/saline/brackish water
Water bodies	Wetlands (inland) - Permanent RiversStreamsCreeks (includes waterfalls) Wetlands (inland) - SeasonalIntermittentIrregular RiversStreamsCreeks Wetlands (inland) - Permanent Freshwater Lakes (over 8ha) Wetlands (inland) - SeasonalIntermittent Freshwater Lakes (over 8ha) Wetlands (inland) - Permanent Freshwater MarshesPools (under 8ha) Wetlands (inland) - SeasonalIntermittent Freshwater MarshesPools (under 8ha) Wetlands (inland) - Freshwater Springs and Oases Wetlands (inland) - Alpine Wetlands (includes temporary waters from snowmelt) Wetlands (inland) - Geothermal Wetlands Wetlands (inland) - Permanent Inland Deltas Wetlands (inland) - Permanent Saline, Brackish or	Water bodies

Habitat Category Proposed	IUCN's Habitat Category	Land Cover Map Class
	Alkaline Lakes Wetlands (inland) - SeasonalIntermittent Saline, Brackish or Alkaline Lakes and Flats Wetlands (inland) - Permanent Saline, Brackish or Alkaline MarshesPools Wetlands (inland) - SeasonalIntermittent Saline, Brackish or Alkaline MarshesPool ArtificialAquatic - Water Storage Areas (over 8ha) ArtificialAquatic - Ponds (below 8ha) ArtificialAquatic - Aquaculture Ponds ArtificialAquatic - Salt Exploitation Sites ArtificialAquatic - Excavations (open) ArtificialAquatic - Wastewater Treatment Areas ArtificialAquatic - Irrigated Land (includes irrigation channels) ArtificialAquatic - Seasonally Flooded Agricultural Land ArtificialAquatic - Canals and Drainage Channels, Ditches	
Rocky and Desert Areas	Rocky areas (e.g., inland cliffs, mountain peaks) Desert - Hot Desert - Temperate Desert - Cold	Sparse vegetation (tree, shrub, herbaceous cover) (<15%) Sparse herbaceous cover (<15%) Bare areas
Croplands	ArtificialTerrestrial - Arable Land ArtificialTerrestrial - Plantations ArtificialTerrestrial - Rural Gardens	Cropland, rainfed Cropland, tree or shrub cover Cropland, irrigated or post-flooding Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)
Pasturelands	ArtificialTerrestrial - Pastureland	Herbaceous cover
Urban Areas	ArtificialTerrestrial - Urban Areas	Urban areas
Subtropical/Tropical Heavily Degraded Former Forests	ArtificialTerrestrial - SubtropicalTropical Heavily Degraded Former Forest	Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (<50%) Mosaic tree and shrub (>50%) / herbaceous cover (<50%) Mosaic herbaceous cover (>50%) / tree and shrub (<50%)

Annex 1. Details on the construction of the composition attribute, selection of species, and habitat mapping.

We included in the analysis all the species of amphibians, birds, terrestrial mammals, and reptiles with a range map intersecting our study area available in the IUCN Red List of Threatened Species (https://www.iucnredlist.org/resources/spatial-data-download) and BirdLife (http://datazone.birdlife.org/species/requestdis). We identified 9008 species, 2859 amphibians, 3831 birds, 1410 mammals, and 908 reptiles. However, we attempt to include only Neotropical endemic species in the analysis; therefore, those species whose distribution ranges might not be present in the study area, but also those probably inhabiting non-Neotropical biomes were identified and excluded. For these species, conservation priorities are not in the Neotropics, and they can highly modify the selection of planning units. These species included small distributions inside our study area, which can directly affect irreplaceability. Then, we employed two criteria for species exclusion: (1) species in the borders (5km-buffer-region inside the study area) with more than 70% of their distribution within the study area, but also with less than 30% of their global distribution (species probably inhabiting only temperate regions); and (2) remaining all non-migratory species whose distribution in the study area was less than 5% of their global distribution (species probably inhabiting non-Neotropical biomes). Before excluding the species, their distributions were visually inspected to validate this decision. The species identified were mostly coastal species for birds, but also those inhabiting only the northern and southern boundaries of the study area for the other taxa. After this process, our final database employed 8563 species, 2731 amphibians, 3649 birds, 1331mammals, and 852 reptiles.

Range maps have been widely employed as a proxy for potential species distributions (e.g., Becker *et al.* 2010; Lawler *et al.* 2010; Trindade-Filho & Loyola 2011; Safi *et al.* 2011; Trindade-Filho *et al.* 2012b, a; Dobrovolski *et al.* 2013; Hidasi-Neto *et al.* 2013, 2015; Machado & Loyola 2013; Ficetola *et al.* 2014; Nori *et al.* 2015; Rodrigues *et al.* 2016), and have been considered as an accurate representation for the known distribution of most species at the global scale (e.g., for amphibians see Ficetola *et al.* 2014). However, range maps may produce omission and commission errors (Hurlbert & White 2005; Rondinini *et al.* 2006), particularly in tropical areas of South America and Asia (Velásquez-Tibatá *et al.* 2013; Ficetola *et al.* 2014), incorporating a high source of uncertainty to conservation planning (Pearson *et al.* 2006; Carvalho *et al.* 2011). Therefore, potential distributions of species were delimited by their habitat to produce more accurate distributions that would represent a proxy to their area of occupancy (Phillips *et al.* 2006; Faleiro *et al.* 2013). To assign each species to their corresponding habitat, we used the IUCN habitat categorization (Table S1), by including each category as search criteria in the IUCN Red List of Threatened Species database (https://www. iucnredlist.org/search). Thus, for each one of the habitats included (Table S1), all the species inhabiting the corresponding habitat were listed, and then for each one of the 8563 species, a list of habitats was produced. The habitats were spatialized by employing the land cover map from the ESA CCI Land Cover 2015 dataset v.2.0.7 (https://maps.elie.ucl.ac.be/CCI/viewer/), according to a standardization proposed between IUCN habitats categories and the land cover map (Table S1)

Figure S2. WWF Ecoregions (Dinerstein *et al.* 2017) and habitats proposed. The intersection of both produced the 663 ecosystems employed as biodiversity features representing the structure attribute approach.

Table S2. Sources and traits databases employed to generate the structure ecological grouping approach.

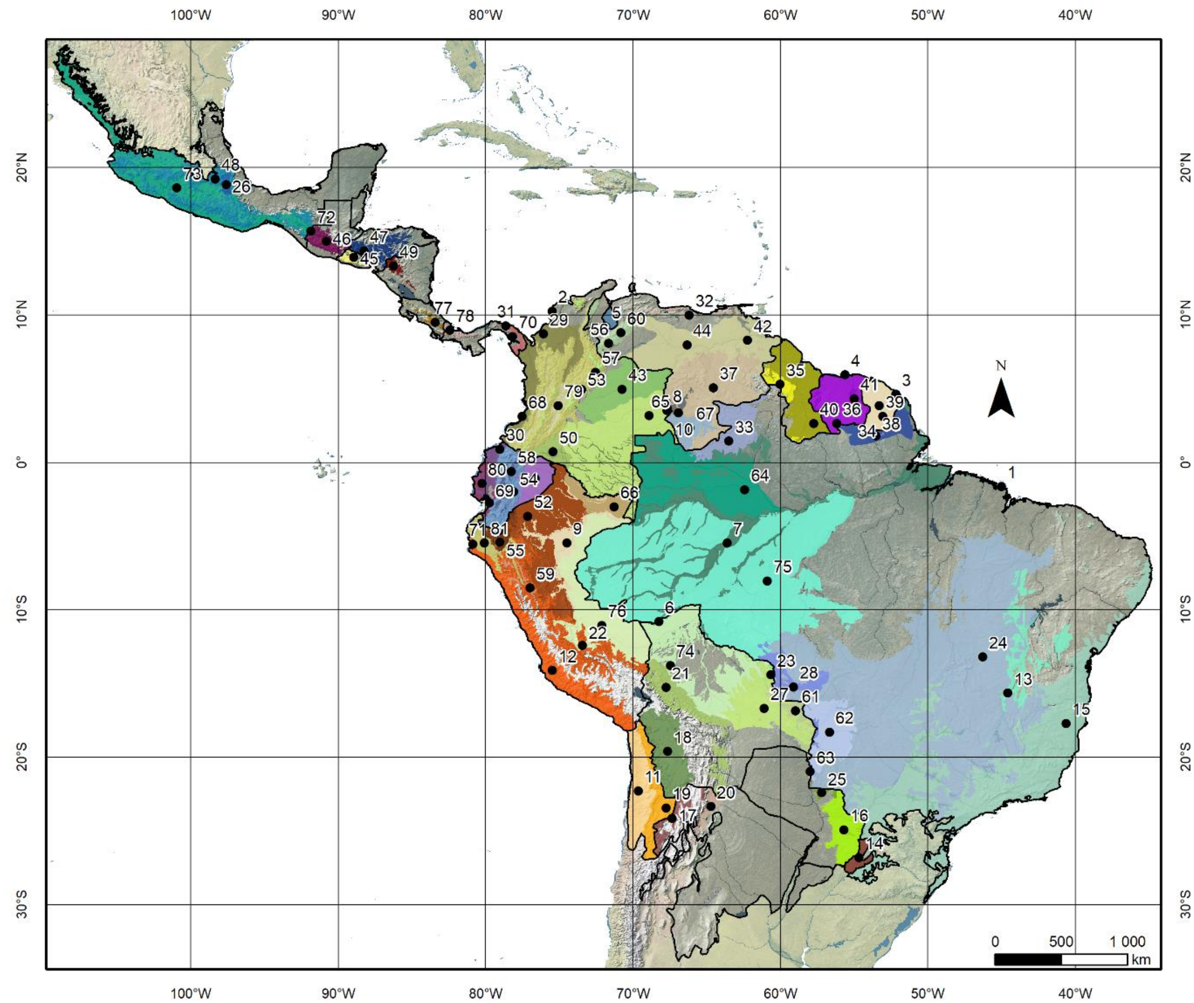
Group/Trait	Biomass	Trophic Guild	Habit
Amphibians	Amphibio (Oliveira *et al.* 2017), Allometry DB (Santini *et al.* 2018).	CS, Amphibian Web, Colombia diversidad biótica (http://www.colombiadiversidadbiotica.com/Sitio_web/LIBROS_DEL_I_AL_IV/LIBROS_DEL_I_AL_IV.html).	IUCN Red List
Birds	Amniote Life-History Database (Myhrvold *et al.* 2015), Avian Body DB (Lislevand *et al.* 2007), Eltontraits 1.0 (Wilman *et al.* 2014), Geographical Body-Size DB (Ramirez *et al.* 2008).	CS, BirdLife, The Cornell Lab of Ornithology, Handbook of the Birds of the World, Beauty of birds, The world bird database (https://avibase.bsc-eoc.org/avibase.jsp?lang=EN).	
Mammals	Eltontraits 1.0 (Wilman *et al.* 2014), Amniote Life-History Database (Myhrvold *et al.* 2015), Body Size And Insularity Status DB (Meiri *et al.* 2011), Minimum Area Requirements DB (Pe'er *et al.* 2014), PanTHERIA (Jones *et al.* 2009), Placement Non-Volant Mammals DB (Ernest 2003).	CS, Programa para la conservación de los murciélagos de Bolivia (http://murcielagosdebolivia.com/)	
Reptiles	Body Masses Extant DB (Slavenko *et al.* 2016), Body Temperature DB (Meiri *et al.* 2013), Insular Density DB (Novosolov *et al.* 2013), Lizard Species Weight And Svl Data (Meiri 2010), Lizard Trait Dataset (Meiri *et al.* 2012), Population Density DB (Novosolov *et al.* 2016), Snakes Length And Mass DB (Feldman & Meiri 2013), Squamate Masses DB (Meiri *et al.* 2015), Squamate Masses And Lengths DB (Feldman *et al.* 2016).	CS, Reptilia Web, Colombia Diversidad Biótica (http://www.colombiadiversidadbiotica.com/Sitio_web/LIBROS_DEL_I_AL_IV/LIBROS_DEL_I_AL_IV.html), Reptilia Web Ecuador (https://bioweb.bio/faunaweb/reptiliaweb/).	

The sources employed to obtain the data for trophic guild were also included to complete the information of biomass trait. CS - Common sources: IUCN Red List, Encyclopedia of Life (EOL), Animal Diversity Web (ADW), iNaturalist, American Museum of Natural History.

Annex 2. Details on the construction of ecological groups.

Ecological grouping using functional traits allows characterizing species' ecological roles across spatiotemporal gradients, supporting biodiversity conservation and management through a generalized community approach rather than based on single biodiversity features (Carvajal-Cogollo & Urbina-Cardona 2015). We selected traits accounting for species use of resources (Safi *et al.* 2011; Trindade-Filho *et al.* 2012b; Hidasi-Neto *et al.* 2015), influencing ecological characteristics like foraging behavior and home-range size (Luck *et al.* 2012), which in turn are closely related to critical ecosystem processes like pollination and seed dispersal (Sekercioglu 2012), but also to the impacts of different disturbance process such as habitat fragmentation and consequently edge effects (Pfeifer *et al.* 2017).

All traits were explored at the species level employing information from multiple sources and trait databases (Table S2). We ensured information of at least one species representing the genus for each trait. For trophic guild and habit traits we employed the most, or the two most frequent categories at the genus level. For body mass and body length, we summarized the information using the median value of the natural logarithm of body mass for birds, mammals and reptiles, and body length for amphibians. We categorized the biomass trait in small, medium, and large sizes employing the k-means algorithm by each combination of the categories of trophic guild and habitat traits. All categories of traits were converted to a dummy variable to calculate a presence/absence distance matrix using the Dice/Jaccard index. This similarity measure was employed to perform the ecological grouping and validate the resultant groups in PRIMER-e software (Clarke & Gorley 2019) using the SIMPROF routine after 9999 Monte Carlo simulations (Clarke *et al.* 2008). SIMPROF determines the number of significant clusters assuming no apriori groups by running multiple random organizations of the data observations.



id	G200 Ecoregion - Country	id	G200 Ecoregion - Country	id	G200 Ecoregion - Country
1	Amazon-Orinoco-Southern Caribbean Mangroves - Brazil	28	Chiquitano Dry Forests - Brazil	55	Northern Andean Montane Forests - Peru
2	Amazon-Orinoco-Southern Caribbean Mangroves - Colombia	29	Chocó-Darién Moist Forests - Colombia	56	Northern Andean Montane Forests - Venezuela
3	Amazon-Orinoco-Southern Caribbean Mangroves - French Guiana	30	Chocó-Darién Moist Forests - Ecuador	57	Northern Andean Páramo - Colombia
4	Amazon-Orinoco-Southern Caribbean Mangroves - Suriname	31	Chocó-Darién Moist Forests - Panama	58	Northern Andean Páramo - Ecuador
5	Amazon-Orinoco-Southern Caribbean Mangroves - Venezuela	32	Coastal Venezuela Montane Forests - Venezuela	59	Northern Andean Páramo - Peru
6	Amazon River and Flooded Forests - Bolivia	33	Guianan Highlands Moist Forests - Brazil	60	Northern Andean Páramo - Venezuela
7	Amazon River and Flooded Forests - Brazil	34	Guianan Highlands Moist Forests - French Guiana	61	Pantanal Flooded Savannas - Bolivia
8	Amazon River and Flooded Forests - Colombia	35	Guianan Highlands Moist Forests - Guyana	62	Pantanal Flooded Savannas - Brazil
9	Amazon River and Flooded Forests - Peru	36	Guianan Highlands Moist Forests - Suriname	63	Pantanal Flooded Savannas - Paraguay
10	Amazon River and Flooded Forests - Venezuela	37	Guianan Highlands Moist Forests - Venezuela	64	Rio Negro-Juruá Moist Forests - Brazil
11	Atacama-Sechura Deserts - Chile	38	Guianan Moist Forests - Brazil	65	Rio Negro-Juruá Moist Forests - Colombia
12	Atacama-Sechura Deserts - Peru	39	Guianan Moist Forests - French Guiana	66	Rio Negro-Juruá Moist Forests - Peru
13	Atlantic Dry Forests - Brazil	40	Guianan Moist Forests - Guyana	67	Rio Negro-Juruá Moist Forests - Venezuela
14	Atlantic Forests - Argentina	41	Guianan Moist Forests - Suriname	68	South American Pacific Mangroves - Colombia
15	Atlantic Forests - Brazil	42	Guianan Moist Forests - Venezuela	69	South American Pacific Mangroves - Ecuador
16	Atlantic Forests - Paraguay	43	Llanos Savannas - Colombia	70	South American Pacific Mangroves - Panama
17	Central Andean Dry Puna - Argentina	44	Llanos Savannas - Venezuela	71	South American Pacific Mangroves - Peru
18	Central Andean Dry Puna - Bolivia	45	Mesoamerican Pine-Oak Forests - El Salvador	72	Southern Mexican Dry Forests - Guatemala
19	Central Andean Dry Puna - Chile	46	Mesoamerican Pine-Oak Forests - Guatemala	73	Southern Mexican Dry Forests - Mexico
20	Central Andean Yungas - Argentina	47	Mesoamerican Pine-Oak Forests - Honduras	74	Southwestern Amazonian Moist Forests - Bolivia
21	Central Andean Yungas - Bolivia	48	Mesoamerican Pine-Oak Forests - Mexico	75	Southwestern Amazonian Moist Forests - Brazil
22	Central Andean Yungas - Peru	49	Mesoamerican Pine-Oak Forests - Nicaragua	76	Southwestern Amazonian Moist Forests - Peru
23	Cerrado Woodlands and Savannas - Bolivia	50	Napo Moist Forests - Colombia	77	Talamancan-Isthmian Pacific Forests - Costa rica
24	Cerrado Woodlands and Savannas - Brazil	51	Napo Moist Forests - Ecuador	78	Talamancan-Isthmian Pacific Forests - Panama
25	Cerrado Woodlands and Savannas - Paraguay	52	Napo Moist Forests - Peru	79	Tumbesian-Andean Valleys Dry Forests - Colombia
26	Chihuahuan-Tehuacán Deserts - Mexico	53	Northern Andean Montane Forests - Colombia	80	Tumbesian-Andean Valleys Dry Forests - Ecuador
27	Chiquitano Dry Forests - Bolivia	54	Northern Andean Montane Forests - Ecuador	81	Tumbesian-Andean Valleys Dry Forests - Peru

Figure S3. Regionalization approach. The G200 Ecoregions (Olson & Dinerstein 1998) by country.

Table S3 Highest values (80-100) of each metric by the Global 200 by country regionalization approach. Common and different regions (those not matching the common regions) are presented by biodiversity attribute and by type of area. Regions on PAs have the inverse patterns in prioritized areas, and vice-versa, i.e., a region with a high value in PAs for a metric have a low value for the same metric and in prioritized areas, and vice-versa. Consequently, regions where PAs or prioritized areas have higher values are guiding the conservation priorities regarding the corresponding metric.

		Species	Ecosystems	Ecological Groups	All Biodiversity Features	Common
Area (nPUs)	PAs	Chiquitano Dry Forests - Bolivia; Chiquitano Dry Forests - Brazil; South American Pacific Mangroves - Colombia	Amazon-Orinoco-Southern Caribbean Mangroves - French Guiana; Amazon-Orinoco-Southern Caribbean Mangroves - Suriname; Amazon-Orinoco-Southern Caribbean Mangroves - Venezuela; Amazon River and Flooded Forests - Brazil; Central Andean Dry Puna - Chile; Central Andean Yungas - Bolivia; Chiquitano Dry Forests - Bolivia; Coastal Venezuela Montane Forests - Venezuela; Guianan Moist Forests - Guyana; Guianan Moist Forests - Suriname; Napo Moist Forests - Colombia; Northern Andean Páramo - Ecuador; Northern Andean Páramo - Venezuela	Amazon-Orinoco-Southern Caribbean Mangroves - French Guiana; Amazon-Orinoco-Southern Caribbean Mangroves - Suriname; Amazon River and Flooded Forests - Brazil; Central Andean Dry Puna - Argentina; Central Andean Dry Puna - Chile; Guianan Moist Forests - Guyana; Guianan Moist Forests - Suriname; Northern Andean Páramo - Ecuador; Northern Andean Páramo - Venezuela		Amazon-Orinoco-Southern Caribbean Mangroves - Colombia; Amazon River and Flooded Forests - Colombia; Amazon River and Flooded Forests - Peru; Amazon River and Flooded Forests - Venezuela; Atacama-Sechura Deserts - Peru; Central Andean Dry Puna - Bolivia; Central Andean Yungas - Peru; Chocó-Darién Moist Forests - Panama; Guianan Highlands Moist Forests - Brazil; Guianan Highlands Moist Forests - French Guiana; Guianan Highlands Moist Forests - Guyana; Guianan Highlands Moist Forests - Suriname; Guianan Highlands Moist Forests - Venezuela; Guianan Moist Forests - Brazil; Guianan Moist Forests - French Guiana; Napo Moist Forests - Ecuador; Napo Moist Forests - Peru; Northern Andean Montane Forests - Peru; Northern Andean Páramo - Colombia; Northern Andean Páramo - Peru; Rio Negro-Juruá Moist Forests - Brazil; Rio Negro-Juruá Moist Forests - Colombia; Rio Negro-Juruá Moist Forests - Peru; Rio Negro-Juruá Moist Forests - Venezuela; South American Pacific Mangroves - Peru; Southwestern Amazonian Moist Forests - Bolivia; Southwestern Amazonian Moist Forests - Brazil; Southwestern Amazonian Moist Forests - Peru; Talamancan-Isthmian Pacific Forests - Costa rica; Talamancan-Isthmian Pacific Forests - Panama; Tumbesian-Andean Valleys Dry Forests - Peru
	PRAs	Amazon-Orinoco-Southern Caribbean Mangroves - Brazil; Amazon-Orinoco-Southern Caribbean Mangroves - Suriname; Atlantic Forests - Argentina; Mesoamerican Pine-Oak Forests - Guatemala; Mesoamerican Pine-Oak Forests - Nicaragua; Pantanal Flooded Savannas - Brazil	Atlantic Forests - Argentina; Atlantic Forests - Paraguay; Mesoamerican Pine-Oak Forests - Nicaragua	Amazon-Orinoco-Southern Caribbean Mangroves - Brazil; Atlantic Forests - Argentina; Atlantic Forests - Paraguay	Amazon-Orinoco-Southern Caribbean Mangroves - Brazil; Amazon-Orinoco-Southern Caribbean Mangroves - Suriname; Atlantic Forests - Paraguay; Mesoamerican Pine-Oak Forests - Guatemala; Pantanal Flooded Savannas - Brazil; Tumbesian-Andean Valleys Dry Forests - Colombia	Atacama-Sechura Deserts - Chile; Atlantic Forests - Brazil; Cerrado Woodlands and Savannas - Bolivia; Mesoamerican Pine-Oak Forests - El Salvador; South American Pacific Mangroves - Ecuador; South American Pacific Mangroves - Panama; Southern Mexican Dry Forests - Guatemala
	TAs					Amazon-Orinoco-Southern Caribbean Mangroves - Brazil; Amazon-Orinoco-Southern Caribbean Mangroves - Suriname; Atacama-Sechura Deserts - Chile; Atlantic Forests - Argentina; Atlantic Forests - Brazil; Cerrado Woodlands and Savannas - Bolivia; Mesoamerican Pine-Oak Forests - El Salvador; Mesoamerican Pine-Oak Forests - Guatemala; Mesoamerican Pine-Oak Forests - Nicaragua; Pantanal Flooded Savannas - Brazil; South American Pacific Mangroves - Ecuador; South American Pacific Mangroves - Panama; Southern Mexican Dry Forests - Guatemala

		Species	Ecosystems	Ecological Groups	All Biodiversity Features	Common
Effectiveness (MTA)	PAs	Amazon-Orinoco-Southern Caribbean Mangroves - French Guiana; Amazon-Orinoco-Southern Caribbean Mangroves - Suriname; Amazon River and Flooded Forests - Brazil; Amazon River and Flooded Forests - Peru; Chiquitano Dry Forests - Brazil; Chocó-Darién Moist Forests - Panama; Coastal Venezuela Montane Forests - Venezuela; Guianan Highlands Moist Forests - Venezuela; Guianan Moist Forests - French Guiana; Napo Moist Forests - Peru; Northern Andean Montane Forests - Venezuela; Northern Andean Páramo - Colombia; Northern Andean Páramo - Peru; Pantanal Flooded Savannas - Paraguay; Rio Negro-Juruá Moist Forests - Brazil; Rio Negro-Juruá Moist Forests - Colombia; Rio Negro-Juruá Moist Forests - Peru; Southwestern Amazonian Moist Forests - Brazil; Southwestern Amazonian Moist Forests - Peru; Talamancan-Isthmian Pacific Forests - Costa rica; Tumbesian-Andean Valleys Dry Forests - Peru	Northern Andean Páramo - Peru; Pantanal Flooded Savannas - Paraguay; Rio Negro-Juruá Moist Forests - Peru	Amazon-Orinoco-Southern Caribbean Mangroves - French Guiana; Amazon River and Flooded Forests - Peru; Chocó-Darién Moist Forests - Panama; Guianan Highlands Moist Forests - Venezuela; Napo Moist Forests - Peru; Northern Andean Páramo - Colombia; Northern Andean Páramo - Venezuela; Rio Negro-Juruá Moist Forests - Colombia; Talamancan-Isthmian Pacific Forests - Costa rica	Amazon-Orinoco-Southern Caribbean Mangroves - French Guiana; Amazon-Orinoco-Southern Caribbean Mangroves - Suriname; Amazon River and Flooded Forests - Peru; Chiquitano Dry Forests - Brazil; Chocó-Darién Moist Forests - Panama; Coastal Venezuela Montane Forests - Venezuela; Guianan Highlands Moist Forests - Venezuela; Guianan Moist Forests - French Guiana; Napo Moist Forests - Peru; Northern Andean Páramo - Colombia; Northern Andean Páramo - Peru; Pantanal Flooded Savannas - Paraguay; Rio Negro-Juruá Moist Forests - Brazil; Rio Negro-Juruá Moist Forests - Colombia; Rio Negro-Juruá Moist Forests - Peru; Southwestern Amazonian Moist Forests - Brazil; Southwestern Amazonian Moist Forests - Peru; Talamancan-Isthmian Pacific Forests - Costa rica; Tumbesian-Andean Valleys Dry Forests - Peru	Amazon River and Flooded Forests - Colombia; Amazon River and Flooded Forests - Venezuela; Atacama-Sechura Deserts - Peru; Central Andean Yungas - Peru; Guianan Highlands Moist Forests - Brazil; Guianan Highlands Moist Forests - French Guiana; Guianan Highlands Moist Forests - Guyana; Guianan Highlands Moist Forests - Suriname; Guianan Moist Forests - Brazil; Northern Andean Montane Forests - Peru; Rio Negro-Juruá Moist Forests - Venezuela; Talamancan-Isthmian Pacific Forests - Panama
	PRAs	Amazon-Orinoco-Southern Caribbean Mangroves - Brazil; Amazon-Orinoco-Southern Caribbean Mangroves - French Guiana; Amazon-Orinoco-Southern Caribbean Mangroves - Suriname; Atlantic Forests - Brazil; Cerrado Woodlands and Savannas - Bolivia; Cerrado Woodlands and Savannas - Paraguay; Mesoamerican Pine-Oak Forests - El Salvador; Mesoamerican Pine-Oak Forests - Guatemala; Northern Andean Páramo - Ecuador; Pantanal Flooded Savannas - Brazil; Pantanal Flooded Savannas - Paraguay	Mesoamerican Pine-Oak Forests - Honduras	Atlantic Dry Forests - Brazil; Atlantic Forests - Brazil; Atlantic Forests - Paraguay; Cerrado Woodlands and Savannas - Bolivia; Cerrado Woodlands and Savannas - Paraguay; Pantanal Flooded Savannas - Paraguay; South American Pacific Mangroves - Colombia; Southern Mexican Dry Forests - Guatemala	Amazon-Orinoco-Southern Caribbean Mangroves - Brazil; Amazon-Orinoco-Southern Caribbean Mangroves - French Guiana; Amazon-Orinoco-Southern Caribbean Mangroves - Suriname; Amazon-Orinoco-Southern Caribbean Mangroves - Venezuela; Atlantic Dry Forests - Brazil; Atlantic Forests - Brazil; Cerrado Woodlands and Savannas - Bolivia; Cerrado Woodlands and Savannas - Paraguay; Mesoamerican Pine-Oak Forests - El Salvador; Mesoamerican Pine-Oak Forests - Guatemala; Northern Andean Páramo - Venezuela; Pantanal Flooded Savannas - Brazil; Pantanal Flooded Savannas - Paraguay; Tumbesian-Andean Valleys Dry Forests - Ecuador	Atlantic Forests - Argentina

		Species	Ecosystems	Ecological Groups	All Biodiversity Features	Common
	TAs	Amazon-Orinoco-Southern Caribbean Mangroves - Brazil; Amazon-Orinoco-Southern Caribbean Mangroves - French Guiana; Amazon-Orinoco-Southern Caribbean Mangroves - Suriname; Amazon-Orinoco-Southern Caribbean Mangroves - Venezuela; Amazon River and Flooded Forests - Brazil; Atlantic Forests - Brazil; Central Andean Dry Puna - Chile; Central Andean Yungas - Bolivia; Cerrado Woodlands and Savannas - Bolivia; Cerrado Woodlands and Savannas - Brazil; Cerrado Woodlands and Savannas - Paraguay; Chihuahuan-Tehuac n Deserts - Mexico; Chiquitano Dry Forests - Bolivia; Choci-Dari n Moist Forests - Colombia; Coastal Venezuela Montane Forests - Venezuela; Guianan Moist Forests - French Guiana; Guianan Moist Forests - Guyana; Guianan Moist Forests - Suriname; Llanos Savannas - Venezuela; Mesoamerican Pine-Oak Forests - El Salvador; Mesoamerican Pine-Oak Forests - Guatemala; Mesoamerican Pine-Oak Forests - Mexico; Mesoamerican Pine-Oak Forests - Nicaragua; Napo Moist Forests - Ecuador; Napo Moist Forests - Peru; Northern Andean Montane Forests - Colombia; Northern Andean Montane Forests - Ecuador; Northern Andean Montane Forests - Venezuela; Northern Andean Páramo - Ecuador; Northern Andean Páramo - Venezuela; Pantanal Flooded Savannas - Bolivia; Pantanal Flooded Savannas - Brazil; Rio Negro-Juruá Moist Forests - Brazil; Rio Negro-Juruá Moist Forests - Peru; Southern Mexican Dry Forests - Mexico; Southwestern Amazonian Moist Forests - Bolivia; Southwestern Amazonian Moist Forests - Brazil; Southwestern Amazonian Moist Forests - Peru; Talamancan-Isthmian Pacific Forests - Costa rica; Tumbesian-Andean Valleys Dry Forests - Peru	Guianan Moist Forests - French Guiana; Mesoamerican Pine-Oak Forests - Nicaragua; Rio Negro-Juruá Moist Forests - Peru	Amazon-Orinoco-Southern Caribbean Mangroves - French Guiana; Amazon-Orinoco-Southern Caribbean Mangroves - Suriname; Amazon River and Flooded Forests - Brazil; Atlantic Forests - Brazil; Atlantic Forests - Paraguay; Central Andean Yungas - Bolivia; Cerrado Woodlands and Savannas - Bolivia; Cerrado Woodlands and Savannas - Paraguay; Chihuahuan-Tehuac n Deserts - Mexico; Choci-Dari n Moist Forests - Colombia; Chocm-Dari n Moist Forests - Ecuador; Guianan Moist Forests - Guyana; Guianan Moist Forests - Suriname; Mesoamerican Pine-Oak Forests - Mexico; Napo Moist Forests - Peru; Northern Andean Montane Forests - Colombia; Northern Andean Montane Forests - Venezuela; Northern Andean Páramo - Venezuela; Rio Negro-Juruá Moist Forests - Brazil; South American Pacific Mangroves - Colombia; Southern Mexican Dry Forests - Guatemala; Southern Mexican Dry Forests - Mexico; Southwestern Amazonian Moist Forests - Brazil; Southwestern Amazonian Moist Forests - Peru; Talamancan-Isthmian Pacific Forests - Costa rica	Amazon-Orinoco-Southern Caribbean Mangroves - Brazil; Amazon-Orinoco-Southern Caribbean Mangroves - French Guiana; Amazon-Orinoco-Southern Caribbean Mangroves - Suriname; Amazon-Orinoco-Southern Caribbean Mangroves - Venezuela; Amazon River and Flooded Forests - Brazil; Atlantic Forests - Brazil; Atlantic Forests - Paraguay; Central Andean Dry Puna - Bolivia; Central Andean Yungas - Argentina; Central Andean Yungas - Bolivia; Cerrado Woodlands and Savannas - Bolivia; Cerrado Woodlands and Savannas - Brazil; Cerrado Woodlands and Savannas - Paraguay; Chihuahuan-Tehuac n Deserts - Mexico; Chiquitano Dry Forests - Bolivia; Choci-Dari n Moist Forests - Colombia; Chocm-Dari n Moist Forests - Ecuador; Coastal Venezuela Montane Forests - Venezuela; Guianan Moist Forests - French Guiana; Guianan Moist Forests - Guyana; Guianan Moist Forests - Suriname; Llanos Savannas - Colombia; Llanos Savannas - Venezuela; Mesoamerican Pine-Oak Forests - El Salvador; Mesoamerican Pine-Oak Forests - Guatemala; Mesoamerican Pine-Oak Forests - Mexico; Mesoamerican Pine-Oak Forests - Nicaragua; Napo Moist Forests - Ecuador; Napo Moist Forests - Peru; Northern Andean Montane Forests - Colombia; Northern Andean Montane Forests - Ecuador; Northern Andean Montane Forests - Venezuela; Northern Andean Páramo - Venezuela; Pantanal Flooded Savannas - Bolivia; Pantanal Flooded Savannas - Brazil; Rio Negro-Juruá Moist Forests - Brazil; Rio Negro-Juruá Moist Forests - Peru; South American Pacific Mangroves - Colombia; Southern Mexican Dry Forests - Mexico; Southwestern Amazonian Moist Forests - Bolivia; Southwestern Amazonian Moist Forests - Brazil; Southwestern Amazonian Moist Forests - Peru; Talamancan-Isthmian Pacific Forests - Costa rica; Tumbesian-Andean Valleys Dry Forests - Ecuador; Tumbesian-Andean Valleys Dry Forests - Peru	Amazon River and Flooded Forests - Colombia; Amazon River and Flooded Forests - Peru; Amazon River and Flooded Forests - Venezuela; Atacama-Sechura Deserts - Peru; Atlantic Dry Forests - Brazil; Atlantic Forests - Argentina; Central Andean Yungas - Peru; Chiquitano Dry Forests - Brazil; Chocó-Darién Moist Forests - Panama; Guianan Highlands Moist Forests - Brazil; Guianan Highlands Moist Forests - French Guiana; Guianan Highlands Moist Forests - Guyana; Guianan Highlands Moist Forests - Suriname; Guianan Highlands Moist Forests - Venezuela; Guianan Moist Forests - Brazil; Mesoamerican Pine-Oak Forests - Honduras; Northern Andean Montane Forests - Peru; Northern Andean Páramo - Colombia; Northern Andean Páramo - Peru; Pantanal Flooded Savannas - Paraguay; Rio Negro-Juruá Moist Forests - Colombia; Rio Negro-Juruá Moist Forests - Venezuela; Talamancan-Isthmian Pacific Forests - Panama

		Species	Ecosystems	Ecological Groups	All Biodiversity Features	Common
Aggregation level (AGG)	PAs					Amazon-Orinoco-Southern Caribbean Mangroves - French Guiana; Central Andean Dry Puna - Bolivia; Cerrado Woodlands and Savannas - Bolivia; Chocó-Darién Moist Forests - Panama; Guianan Highlands Moist Forests - Brazil; Guianan Highlands Moist Forests - French Guiana; Guianan Highlands Moist Forests - Venezuela; Guianan Moist Forests - Brazil; Guianan Moist Forests - French Guiana; Llanos Savannas - Venezuela; Mesoamerican Pine-Oak Forests - Guatemala; Napo Moist Forests - Ecuador; Rio Negro-Juruá Moist Forests - Brazil; Rio Negro-Juruá Moist Forests - Colombia; South American Pacific Mangroves - Peru; Southwestern Amazonian Moist Forests - Brazil; Southwestern Amazonian Moist Forests - Peru
	PRAs	Chocó-Darién Moist Forests - Panama	Amazon-Orinoco-Southern Caribbean Mangroves - French Guiana; Central Andean Dry Puna - Bolivia; Guianan Highlands Moist Forests - Brazil; Guianan Moist Forests - Brazil; Northern Andean Páramo - Venezuela; Rio Negro-Juruá Moist Forests - Brazil; Southern Mexican Dry Forests - Guatemala	Amazon-Orinoco-Southern Caribbean Mangroves - French Guiana; Chocó-Darién Moist Forests - Panama; Guianan Highlands Moist Forests - Brazil; Pantanal Flooded Savannas - Paraguay; South American Pacific Mangroves - Panama; Southern Mexican Dry Forests - Guatemala	Southern Mexican Dry Forests - Guatemala	Guianan Highlands Moist Forests - French Guiana; South American Pacific Mangroves - Peru
	TAs		Amazon-Orinoco-Southern Caribbean Mangroves - French Guiana; Guianan Moist Forests - French Guiana; Southern Mexican Dry Forests - Guatemala	Amazon-Orinoco-Southern Caribbean Mangroves - French Guiana; Atlantic Forests - Argentina; Cerrado Woodlands and Savannas - Paraguay; Guianan Moist Forests - French Guiana; South American Pacific Mangroves - Panama; Southern Mexican Dry Forests - Guatemala	Southern Mexican Dry Forests - Guatemala	Central Andean Dry Puna - Bolivia; Chocó-Darién Moist Forests - Panama; Guianan Highlands Moist Forests - Brazil; Guianan Highlands Moist Forests - French Guiana; Guianan Highlands Moist Forests - Venezuela; Guianan Moist Forests - Brazil; Napo Moist Forests - Ecuador; Rio Negro-Juruá Moist Forests - Brazil; Rio Negro-Juruá Moist Forests - Colombia; South American Pacific Mangroves - Peru; Southwestern Amazonian Moist Forests - Brazil; Southwestern Amazonian Moist Forests - Peru

Table S4. Comparison of biodiversity approaches according to their no coincidence area. The no coincidence of prioritized areas corresponds to that planning unites selected where there was no coincidence among any BF approach in Figure 2F.

Biodiversity Feature	PRAs area	No coincidence area of PRAs	
	km²	km²	%
Species	1 705 605.79	366 305.21	21.48
Ecosystems	1 065 811.94	338 974.38	31.80
Ecological Groups	1 447 180.67	515 767.83	35.64

Table S5. Effectiveness and area calculated at country-level for the reference model including all biodiversity features and the three types of areas. The area is presented as a percentage relative to the country area for total areas, and as percentage relative to the total areas for the PAs and prioritized areas. Countries are sorted descending by their effectiveness in prioritized areas. The study area encompasses most of the territory of Mexico and Brazil, but only a small proportion of Chile and Argentina, therefore for these two last countries, results are not extrapolated to their entire area.

Country	Effectiveness (MTA)			Area (nPUs)		
	Total Areas	Protected Areas	Prioritized Areas	Total Areas	Protected Areas	Prioritized Areas
Paraguay	96.90	44.04	86.58	26.63%	29.08%	70.92%
Argentina*	92.98	21.36	86.55	19.02%	8.94%	91.06%
El Salvador	84.06	13.55	78.81	19.31%	2.00%	98.00%
Guatemala	89.53	28.48	70.51	18.43%	24.58%	75.42%
Mexico	97.41	54.26	69.90	23.26%	52.02%	47.98%
Ecuador	96.49	56.02	61.88	29.72%	65.20%	34.80%
Brazil	97.68	63.42	57.06	30.22%	64.48%	35.52%
Bolivia	91.95	69.13	57.01	34.13%	67.96%	32.04%
Costa rica	92.34	68.66	54.84	26.80%	64.05%	35.95%
Honduras	96.59	72.48	52.76	26.86%	60.81%	39.19%
Venezuela	97.00	75.52	50.36	28.57%	66.47%	33.53%
Nicaragua	94.26	74.64	49.53	37.12%	72.14%	27.86%
Suriname	94.74	59.27	45.43	17.38%	56.88%	43.12%
Belize	97.89	78.63	42.61	24.58%	72.88%	27.12%
Chile*	87.97	50.75	42.10	15.99%	34.02%	65.98%
Colombia	94.91	77.91	41.78	44.32%	83.46%	16.54%
Panama	92.62	79.45	36.43	40.55%	85.09%	14.91%
French Guiana	98.73	89.93	28.79	39.63%	93.42%	6.58%
Guyana	94.98	86.97	22.58	22.50%	80.43%	19.57%
Peru	97.67	93.02	15.69	40.93%	97.04%	2.96%

Table S6. Principal causes of habitat loss-fragmentation and degradation in the critical hotspots of biodiversity identified as priority for the establishment of new conservation areas.

Region	Main causes of habitat loss-fragmentation and degradation
Chaco region of Argentina and Paraguay	Pastures expansion for cattle (Caldas *et al.* 2015; Vallejos *et al.* 2015; Baumann *et al.* 2017).
Atlantic forests of Argentina, Paraguay, and Brazil	Soybean crop expansion (Dros 2004; Huang *et al.* 2007, 2009; Richards 2011; Da Ponte *et al.* 2017; Emmanuel *et al.* 2017).
Pantanal and Cerrado in Brazil	Expansion of pastures and commercial crops, dams construction, Paraguay river channeling, extensive and uncontrolled use of fire, and expansion of exotic pastures (Klink & Machado 2005; Françoso *et al.* 2015; Roque *et al.* 2016).
Caatinga in Brazil	Expansion of pastures and agricultural lands (mainly for fruits and soybean plantations), but also approx. 15% of the population of Brazil lives in this region in poverty conditions, leading to an intense desertification and biodiversity homogenization processes (Leal *et al.* 2005; Ribeiro-Neto *et al.* 2016).
Moist and dry forests of northern Andes of Ecuador and Colombia	Mainly driven by pastures expansion, but also by croplands in particular regions, with more intensity over fertile and accessible lowlands (Etter & van Wyngaarden 2000; Etter *et al.* 2008; Armenteras *et al.* 2011; Sánchez-Cuervo *et al.* 2012; Rodríguez Eraso *et al.* 2013a; Curatola Fernández *et al.* 2015). Particularly In Ecuador, the invasion of exotic species and tree plantations has contributed to high lands transformation (Farley 2007; Curatola Fernández *et al.* 2015), while in Colombia the relation illicit crops - armed conflict - land abandonment has mainly promoted natural forest regrowth and conservation (Dávalos 2001; Rincón-Ruiz *et al.* 2013; Sánchez-Cuervo & Aide 2013a), with minor focuses on deforestation frontiers (Chadid *et al.* 2015). However, the recent Colombian peace agreement has imposed new natural vegetation loss rates threatening critical remnant areas, even inside PAs (Armenteras *et al.* 2019; Clerici *et al.* 2019; Negret *et al.* 2019).
Llanos savannas of Colombia and Venezuela	Expansion of introduced pastures and agricultural lands, mainly rice and oil-palm plantations (Etter *et al.* 2010; Romero *et al.* 2010; Romero-Ruiz *et al.* 2012; Castiblanco *et al.* 2013). In a lower proportion, natural and induced fire dynamics (Romero *et al.* 2010), and petroleum and mining land conversion purposes (Romero-Ruiz *et al.* 2012).
Pine-Oak Forests of El Salvador, Guatemala, and Nicaragua	Croplands (mainly cotton, coffee, oil palm, maize, cassava, and fruits) and pastures (lesser extent) expansion (Redo *et al.* 2009; Pacheco *et al.* 2011; Schmitt-Harsh 2013). However, there is a recent increase in the pine-oak forest do to the Mesoamerican Biological Corridor, in combination to other factors like the reduction of governmental support for agricultural colonization and cattle ranching (Pacheco *et al.* 2011; Redo *et al.* 2012).
Dry forests of Guatemala	Agricultural and pasture expansion with further disturbances due to timber and firewood extraction, selective logging, and human settlement development (Chazdon *et al.* 2011).

Chapter 2. Understanding the effect of including costs and persistence in spatial conservation prioritization: an analysis of the land-sharing/sparing framework in the Neotropics

Jaime Burbano-Girón[1,2], Kerstin Jantke[3], Maria Alejandra Molina[1], Nicolás Urbina-Cardona[1], Bibiana Gómez-Valencia[2], Andrés Etter[1]

[1] Facultad de Estudios Ambientales y Rurales. Pontificia Universidad Javeriana. Bogotá, Colombia.
[2] Instituto de Recursos Biológicos Alexander von Humboldt. Bogotá, Colombia.
[3] Research Unit Sustainability and Global Change. Hamburg University. Hamburg, Germany.

Introduction

The designation and expansion of protected areas (PAs) continue to be the most common strategies to safeguard biodiversity and counteract biodiversity decline (Jenkins & Joppa 2009; Watson *et al.* 2014). However, in a world increasingly dominated by human transformation processes (Ellis & Ramankutty 2008; Ellis 2011), and with limited economic resources for conservation (Wilson *et al.* 2009; Waldron *et al.* 2013), it is becoming critical to expanding this view by integrating conservation and restoration practices also in human-modified landscapes (Ellis 2013). For instance, restoration of slightly human-modified under low threat pressures could increase the potential for meeting conservation targets, such as the Convention for Biological Diversity's Aichi target 11 which calls for 17% of the terrestrial area under protection by 2020 (Mappin *et al.* 2019). This model where the environmental quality of the agricultural matrix is enhanced with conservation practices and areas is associated with the land-sharing framework (Fischer *et al.* 2008; Perfecto & Vandermeer 2010). In this approach, biodiversity persistence is maximized over heterogeneous landscapes that promote species turnover and landscape connectivity, decreasing the impacts of biodiversity loss by habitat fragmentation and climate change (Fischer *et al.* 2008; Grau *et al.* 2013; Kremen 2015).

Conversely, highly degraded regions or those with high income from economic activities impose critical conservation costs (Polasky *et al.* 2005; Shackelford *et al.* 2015). In these regions, the land-sparing model prevails by intensifying economic activities, emphasizing biodiversity conservation in PAs outside the agricultural matrix. In this approach, the biodiversity threats are minimized over the areas designated for conservation, increasing the protection of rare species, since agriculture expansion may produce local extinctions of small range species (Green *et al.* 2005; Phalan *et al.* 2011).

However, both approaches, land-sharing and land-sparing are complementary, requiring careful design and implementation to be efficient (Phalan *et al.* 2011). Therefore, a strategic coordinated process to allocate regions for production, conservation, and restoration in transformed landscapes, is critical to meet conservation targets and achieve better benefits for all stakeholders (Schleupner & Schneider 2013).

Systematic Conservation Planning (SCP) is positioned as a leading framework for guiding decision making on where and what to conserve efficiently (Margules & Pressey 2000). Through a spatial prioritization process, SCP evaluates the performance of existing PAs and selects efficient locations for conservation actions (Ferrier & Wintle 2009; Wilson *et al.* 2009). The goal of this process is to identify a network of conservation areas under that meets three criteria: It should (1) represent the biodiversity of a particular region for supporting its (2) persistence over time in a (3) cost-efficient way (Margules & Sarkar 2007). Despite the growth of studies involving spatial conservation prioritization in the last two decades (see Kukkala & Moilanen 2013), inclusion of all three criteria for prioritizing is rare (but see, e.g., Wilson *et al.* 2006, 2011; Bode *et al.* 2008; Newbold & Siikamaki 2009; Visconti *et al.* 2010). Many studies only include representation, while others use representation in combination with persistence or cost-efficiency (see Pressey *et al.* 2007; Kukkala & Moilanen 2013).

Studies including persistence approaches have found significant dissimilarities in the spatial distribution, the clustering pattern, the isolation level, and the number of priority areas compared to studies accounting only for representation (Table S7) (Cabeza 2003; Carroll *et al.* 2003, 2010; Visconti *et al.* 2010; Faleiro *et al.* 2013). Incorporating cost-efficiency criteria improves the effectiveness of conservation areas, directing the spatial prioritization to those regions where benefits of conservation may exceed their costs (Naidoo *et al.* 2006). However, the spatial variance of cost-benefit relationship (Moore *et al.* 2004; Naidoo & Ricketts 2006; Naidoo *et al.* 2006; Jantke & Schneider 2011), as well as the different approaches employed for conservation costs (Table S7), imply that their inclusion into the planning process represents a considerable source of variability and uncertainty (Carwardine *et al.* 2010; Wintle *et al.* 2011).

Given the limited resources for conservation, it is crucial to better understand the effects of incorporating cost and persistence principles into spatial conservation prioritization (Pressey *et al.* 2004). For some regions, cost and persistence approaches are the most important factors of variability in conservation areas selection (Bode *et al.* 2008). In tropical regions, where complex and heterogeneous landscape mosaics of natural and transformed areas occurs (Bennett *et al.* 2006; Chazdon *et al.* 2009), conservation planning requires careful designs considering the variability in land costs and threats to biodiversity persistence (Pressey *et al.* 2007; Wilson *et al.* 2007). In this study, we explored cost and persistence approaches related to landscape transformation, land rent, habitat fragmentation, and human influence in the Neotropics, one of the most biodiverse and threatened regions globally. We evaluated coincidences and differences of conservation areas selected by each approach and their implications for conservation planning based on the land-sharing/sparing framework, including possible conservation mechanisms and actions on the region at the landscape level.

Method

Study area

We combined geographic and biogeographic criteria to take study area all the terrestrial and continental WWF Ecoregions (Dinerstein *et al.* 2017) intersected between the Tropic of Cancer and the Tropic of Capricorn (Figure 1). We manually exclude the Chilean matorral Ecoregion since it contains biogeographic and abiotic conditions that are not typical of tropical environments. Our study area (≈17MM km^2) includes the whole basins of the Orinoco (≈1MM km^2) and Amazon rivers (≈6MM km^2), and the middle and northern Andes (≈3MM km^2 in total). Also, it is delimited by 20 countries: Belize, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana, Ecuador, Peru, Bolivia, and Paraguay, most of the territory of Mexico and Brazil, and a small proportion of Chile and Argentina.

The Neotropics is probably the most biodiverse region in the world. In this area, the highest levels of species richness and endemism occur (Kier *et al.* 2005; Mittermeier *et al.* 2005) the most important hotspots of biodiversity like the northern Andes, Brazil's Atlantic Forest, Brazil's Cerrado, the Darien-Chocó-Pacific region, and the Amazon rainforest (Olson & Dinerstein 1998; Myers *et al.* 2000). Most of the biodiversity and natural ecosystems are over non-intervened regions (≈14MM km^2 - 81%) (Figure 1 and Table S8). Approximately 80% of Latin-American people live in urban zones (Grau & Aide 2008), representing only 0.3% (≈50M km^2) of the study area. Agricultural and livestock are the main socio-economic activities in Neotropical countries, although they do not contribute significantly to the gross domestic product. According to The World Bank, the average agriculture value added in the region, considering the last 15 years is only 5.5% (http://data.worldbank.org/indicator/

NV.AGR.TOTL.ZS). However, agriculture and pastures lands cover around 18% (≈3MM km^2) of the study area (Table S8). Most profitable agricultural and livestock products are also the most extensive and productive in the region, including cattle and pig meat, cattle milk, soybeans, sugar cane, maize, rice, bananas, and coffee (Table S9).

Figure 6. Study area and habitat classes proposed. Habit classes were taken from IUCN habitats categorization (Table S10). The habitats were spatialized by employing the land cover map from the ESA CCI Land Cover 2015 dataset v2.0.7 (http://maps.elie.ucl.ac.be/ CCI/viewer/index.php), according to the standardization proposed between both products (Table S10). The habitats map was produced in a 1km resolution.

Spatial conservation prioritization

We identified conservation areas resolving the minimum set cover problem (Moilanen *et al.* 2009). The optimization process was performed using the Prioritizr package in R (Hanson *et al.* 2020b), which employs integer linear programming to achieve conservation targets at the least cost (Beyer *et al.* 2016). We employed as biodiversity features the comprehensive approach proposed by Burbano-

Girón *et al.* (2019a), including a total of 14 609 biodiversity features composed of 8563 species, 663 ecosystems, and 5382 ecological groups. Cost and persistence approaches were included as costs in the objective function normalized in the range 1-101. We decided to normalize cost and persistence approaches to ensure that the magnitude of values did not affect the prioritization results. The linear normalization was applied in range 1-101 since planning units with costs equal to zero cancels the objective function of the prioritization process. We used fixed targets with no penalties and constraints for biodiversity features or the planning units (10x10km grid) to evaluate the separate effects of cost and persistence approaches in the absence of parameters affecting the variables of the model. We chose the goal of the Convention on Biological Diversity's Aichi Target 11 to protect 17% of each BF area (e.g., Venter *et al.* 2014; Mappin *et al.* 2019), locking as protected areas (PAs) all planning units with more than 50% of their area covered by existing PAs (e.g., Kark *et al.* 2009; Klein *et al.* 2009; Esselman & Allan 2011). PAs included IUCN categories I-IV (strict protection) taken from the World Database on Protected Areas (IUCN & UNEP-WCMC 2018) (Jenkins & Joppa 2009; Kark *et al.* 2009), and the documented indigenous lands from the Global Platform of Indigenous and Community Lands (LandMark) (http://www.landmarkmap. org/). We supported this combination of PAs in the proportion (97%) of natural land cover inside their boundaries according to our habitats approach (Figure 1).

Construction of costs approaches

Costs approaches were constructed based on the relationship of landscape transformation and land quality, as a proxy for land acquisition. This relationship considers that areas with higher vulnerability to landscape transformation and land quality are usually more expensive than low-vulnerability areas with poor land quality (Newburn *et al.* 2005). In this relationship, we assumed that land rent is a proxy for land quality. The higher the land rent is, the better the land quality is since more productive areas are located over more productive lands (Naidoo & Adamowicz 2006; Naidoo & Ricketts 2006). Thus, we used as proxies for conservation costs two approaches: (1) the proportion of transformed area, and (2) the land rent of crops and cattle, the more expansive activities in the Neotropics (Wassenaar *et al.* 2007; Grau & Aide 2008) (Table S8 and Table S9). These costs give approximate information on land acquisition costs (Newburn *et al.* 2005), a critical factor for defining land sharing or land sparing strategies in land planning and conservation (Fischer *et al.* 2008).

Landscape transformation

We included the percentage of the transformed area as a proxy for landscape transformation, as regions with larger transformed land proportion in the Neotropics are more likely to continue being transformed because of the wave generated by colonization fronts (Etter *et al.* 2006b, a). Moreover, the proportion of transformed area can also be considered as a proxy for degradation, being also applied in quantifying restoration costs (Gallo *et al.* 2009; Thompson *et al.* 2009; Lessmann *et al.* 2014) (Table S7). Thus, transformed area costs were estimated as the proportion of transformed habitats (croplands, pasturelands and urban areas) (Figure 1 and Table S8) (1km resolution) by planning unit (10x10km grid). We summed one unit to transformed area proportion to normalize it into the range 1-101.

Land rent

Land rent was employed as a proxy for land quality; areas with higher land rent commonly have higher yields, and are generally related to better soil suitability (Naidoo & Adamowicz 2006; Naidoo & Ricketts 2006). Land rent has also been widely used as a proxy for opportunity costs (e.g., Jantke & Schneider 2011; Venter *et al.* 2014; Mappin *et al.* 2019) (Table S7). We estimated the total land rent (1km resolution) as the summed land rent of crops and cattle per planning unit (10x10km grid), following the method proposed by Naidoo and Iwamura (2007), but employing different sources of information (Table S11). The land rent (USD/km^2) was calculated as the product of yield (in ton/km^2 for crops and $heads/km^2$ for cattle) and net production value (in USD/ton for crops and $USD/heads$ for cattle) (Table S11). Finally, the land rent was linearly normalized into the range 1-101.

Construction of persistence approaches

Persistence of biodiversity is inversely related to human influence (Sanderson *et al.* 2002; Etter *et al.* 2011; Venter *et al.* 2016b; Allan *et al.* 2019), which produces habitat loss and landscape fragmentation (de Thoisy *et al.* 2010; Hand *et al.* 2014; Betts *et al.* 2017). We constructed the persistence approaches based on the likelihood of biodiversity persistence in each planning unit (calculated as the inverted likelihood of persistence to include them as costs in the objective function). We employed two persistence approaches: (1) habitat fragmentation, which relates to the aggregation pattern and proportion of natural habitats, and (2) human influence, which relates to the threat level imposed on biodiversity from the human footprint.

Habitat fragmentation

Habitat fragmentation was estimated using the aggregation index (He *et al.* 2000) of natural and degraded habitats (1km resolution) per planning unit (10x10km grid) (Table S8). The aggregation index is a proxy for habitat fragmentation, considering the proportion between the number of adjacent cells of the same habitat and their maximum possible number in the planning unit. It took the value of 100 when the planning unit corresponded to a single habitat. We estimated the aggregation index using the spatialEco R package. The final aggregation index was calculated as the weighted average by the natural habitats area. The degraded habitats were included in the estimation previously multiplied by 0.5 to reduce its effect on the possible functional connectivity of the landscape matrix. Lower levels of fragmentation and higher habitats proportion in the landscape are closely related to reduced edge effects, critical ecosystem processes maintain, and species persistence (Fahrig 2003). Finally, the aggregation index was inverted to be included as costs in the objective function of the spatial prioritization, summing one to fit the 1-101 range.

Human influence

We employed the change (1993-2009) in the human footprint (1km resolution) proposed by Venter *et al.* (2016a, b), as a proxy for human influence on biodiversity persistence. Trade-offs between human influence and conservation are inverse related to biodiversity persistence; therefore, the higher the human footprint, the higher the likelihood of a planning unit to lose biodiversity (Shackelford *et al.* 2018; Weinzettel *et al.* 2018; Allan *et al.* 2019). The average footprint by planning unit (10x10km grid) was calculated and then linearly normalized in the range 1-101.

Comparison of cost and persistence approaches

We ran 100 portfolios for each cost and persistence approach taking the best model (the one with the least cost), and the selection frequency of each planning unit as a proxy for its irreplaceability (e.g., Stewart & Possingham 2005; Fuller *et al.* 2006; Loyola *et al.* 2013). We evaluated the differences in conservation areas for the best model run in terms of their spatial agreement (KAPPA), area (nPUs) (e.g., Nhancale & Smith 2011), effectiveness (MTA) (e.g., Müller *et al.* 2018), and aggregation level (AGG) (e.g., Alagador & Cerdeira 2007) (Table 5). We assessed these metrics in three types of areas: (1) the current PAs, (2) the prioritized areas (PRAs) (those selected to complement PAs), and (3) the total areas (TAs) (PAs and PRAs). We also considered the implications of the differences in cost and persistence approaches to conservation planning by calculating the proportion of natural, secondary, and transformed habitats in coincident and no coincident prioritized areas resulting in each approach, to finally analyze them under the land-sharing/sparing framework.

Table 5. Metrics employed to compare conservation areas selected among biodiversity attributes approaches.

Metric	Description	
Area Number of Planning Units (nPUs)	nPUs indicates the extension of the conservation areas selected. More efficient approaches should result in fewer nPUs selected for achieving conservation targets. nPUs are presented as a percentage relative to study area for total areas, and as a percentage relative to total areas for PAs and prioritized areas.	
Effectiveness Mean Target Achievement (MTA) (Jantke *et al.* 2019)	MTA indicates the mean proportion of target achievement of all biodiversity features represented in the conservation areas selected. It ranges between 0 and 100%. A value of 0 indicates that no biodiversity feature received any protection, and 100% indicates that the target was achieved for all biodiversity features. Our spatial conservation prioritization approach guarantees optimal solutions, i.e., it ensures that the MTA is 100% for total areas. MTA was calculated in R using the ConsTarget package (https://github.com/KerstinJantke /ConsTarget).	$\frac{\sum_{i=1}^{N} min\left(\left(\frac{(P_i/A_i)}{T}\right)\times 100,100\right)}{N}$ P is the area of conservation areas selected, and A is the total area for biodiversity feature i. T is the fixed proportional target protection level, and N is the total number of biodiversity features.
Aggregation level Aggregation Index (AGG) (He *et al.* 2000)	AGG indicates the degree of compactness of the NCA. The index ranges between 0 and 100% and is estimated as the number of adjacencies divided by their maximum possible number. A value of 100% indicates maximum aggregation into a single compact patch reducing edge effects and fragmentation. AGG was calculated in R using the spatialEco package.	
Spatial Agreement Kappa Index (KAPPA) (Cohen 1960)	The Kappa index was employed to estimate the spatial agreement of conservation areas selected between cost and persistence approaches. KAPPA ranges between 0 and 1. A value of 0 indicates that no single planning unit was selected in both of the compared approaches, and 1 that planning units selected were the same in both approaches. The index was multiplied by 100 to be presented in the same range (0-100) of other metrics.	

Construction of the land-sharing/sparing framework

We transformed the cost and persistence approaches applied into four components for determining land-sparing and land-sharing relationships, and to relate them to prioritized areas selected in spatial conservation prioritization exercises. The four components defined were: (1) areas with low landscape transformation, (2) areas with low land rent, (3) areas with low habitat fragmentation, and (4) areas with low human influence (Table 6). We assumed that priority areas selected under each component followed four related conditions accounting each approach in the land-sharing/sparing context (Table 6). We included the land cover type: natural, degraded, and transformed as a factor for defining the mechanisms and conservation actions according to general characteristics defining the land-sharing/sparing frameworks (Green *et al.* 2005; Fischer *et al.* 2008). We proposed two mechanisms: conservation agreements and land acquisition, and four actions: wildlife-friendly farming, active and passive restoration, and protection.

Table 6. Assumed conditions related to components of the land-sharing/sparing framework according to cost and persistence approaches applied.

	Approach	Component	Condition
Cost	Landscape Transformation	1. Areas with low landscape transformation	The higher the condition of naturalness, the lower the risk of landscape transformation, and the higher the success of conservation over time (Wassenaar *et al.* 2007; Schmitt-Harsh 2013).
	Land Rent	2. Areas with low land rent	Areas with lower rent may be less productive, and then, their acquisition costs should be less expensive (Newburn *et al.* 2005)
Persistence	Habitat Fragmentation	3. Areas with low habitat fragmentation	Non-fragmented areas with a high proportion of remaining natural habitat are critical for maintaining multiple ecological and evolutionary processes, and for guarantying species persistence (Fahrig 2003)
	Human Influence	4. Areas with low human influence	Areas with less human influence are generally isolated for reasons of accessibility; accordingly, their probability of transformation and acquisition costs should be low. Remaining natural areas under this condition also have a high probability of conservation success over time (Haines *et al.* 2008).

Results

Differences in cost and persistence approaches

We found differences in the spatial distribution of conservation areas for cost and persistence approaches (Figure 7 and Table 7). However, the variability for costs was lower than for the persistence approaches because of their higher coincidence and irreplaceability (Figure 8 and Table 8). Higher similarity in the location of prioritized areas occurred in the land rent approach associated with higher clustering patterns (Figure 7 and Table 9). Particularly, the habitat fragmentation approach had a lower level of clumpiness in total and prioritized areas (Table 9). Although inside the planning unit, the aggregation is high, prioritized areas were mostly located in heavily fragmented regions where planning units cannot be adjacent (Figure 7).

The landscape transformation approach involved more planning units, but its effectiveness in prioritized areas was also higher; conversely, the human influence approach involved less area but also lower effectiveness values (Table 9). The effectiveness of PAs was similar to prioritized areas, but with 60% less area, leading to more efficient biodiversity protection. Nevertheless, achieving the Aichi target 11's conservation target of 17% under protection requires the inclusion of both PAs and prioritized areas (Table 9). Therefore, the success of increasing the effectiveness and efficiency of conservation areas needs the expansion of the protected areas system.

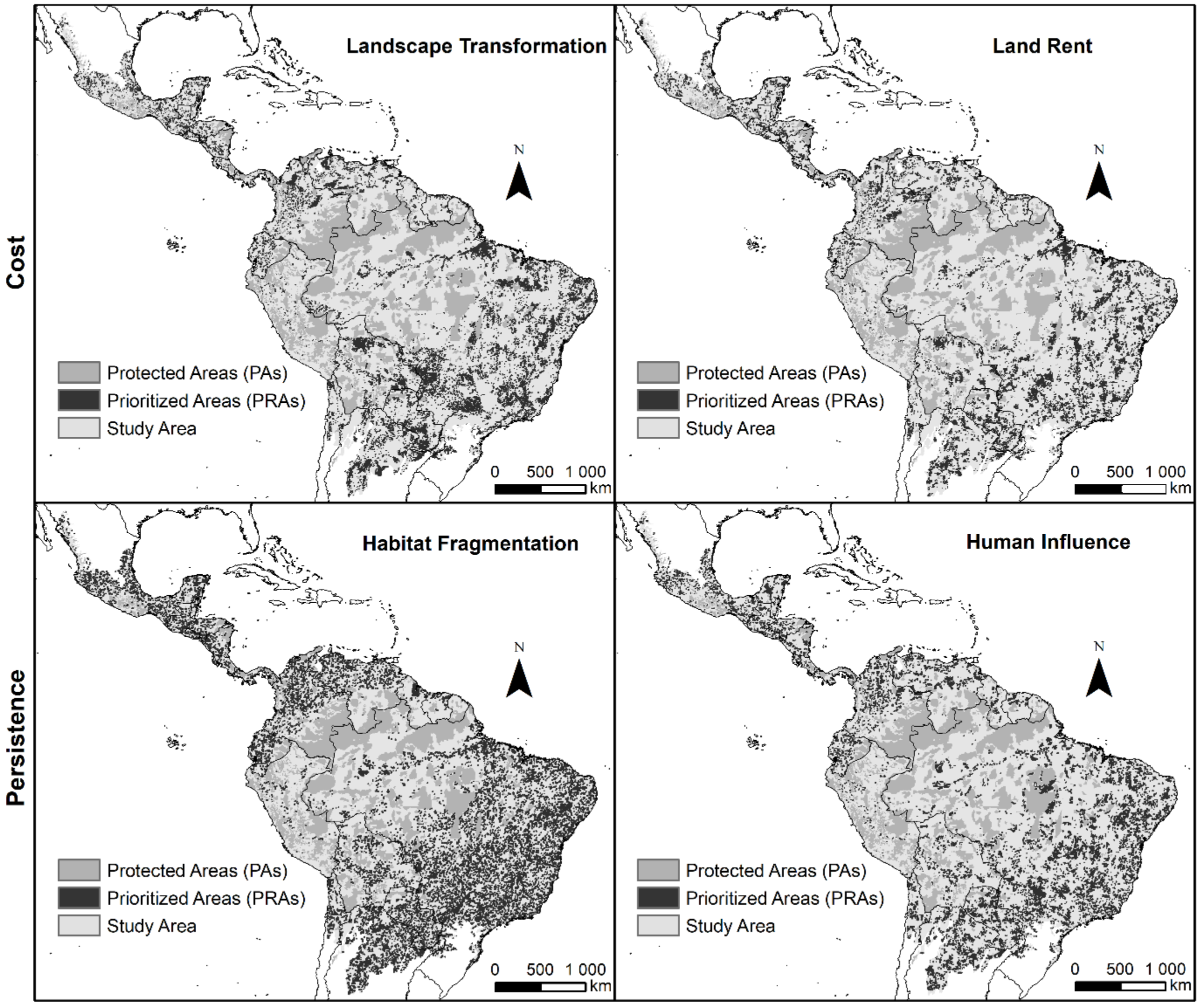


Figure 7. Spatial distribution of total areas (TAs) selected in each cost and persistence approach.

Table 7. Spatial agreement (Kappa Index) of cost and persistence approaches in total and prioritized areas. Kappa Index value in protected areas is one since they are the same for all approaches.

	Total Areas (TAs)				
Prioritized Areas (PRAs)	Costs / Persistence Approach	Landscape Transformation	Land Rent	Habitat Fragmentation	Human Influence
	Landscape Transformation	-	72	66	66
	Land Rent	32	-	68	70
	Habitat Fragmentation	16	16	-	67
	Human Influence	15	20	13	-

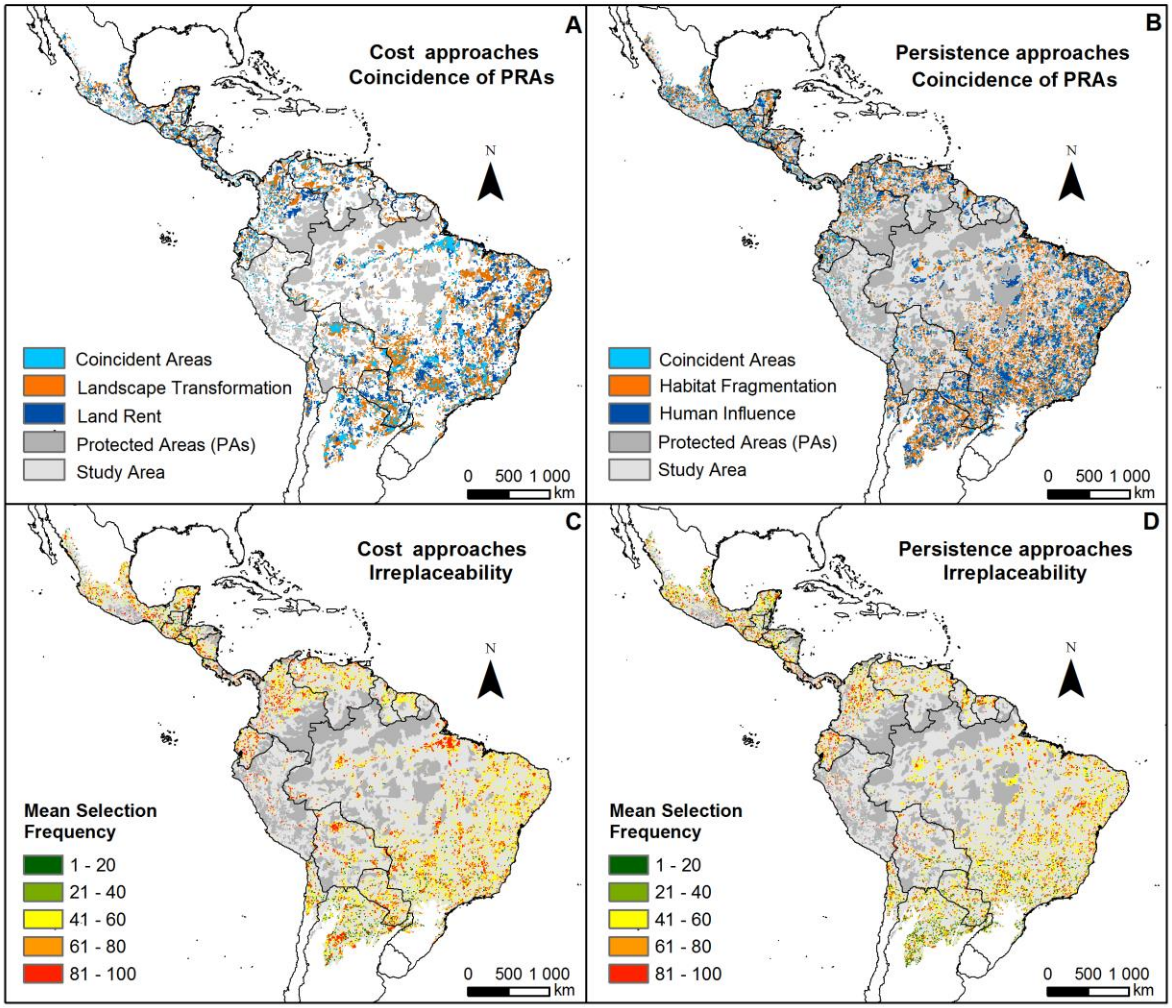


Figure 8. (A-B) Differences and coincidences of prioritized areas per cost and persistence approaches, i.e., planning units selected in both approaches (light blue) and just in one of the approaches (orange and dark blue). (C-D) Irreplaceability of prioritized areas. Values correspond to the mean selection frequency of planning units in both approaches of costs and persistence.

Table 8. Comparison of coincident and no coincident prioritized areas (PRAs) of cost and persistence approaches.

	Land Cover Type	Area (km^2)			
		Natural	Degraded	Transformed	Total PRAs
Costs	Coincident area	448 340	68 774	99 687	616 801
	Landscape Transformation	786 563	135 875	188 033	1 110 471
	Land Rent	486 134	82 128	274 033	842 295
	Total no coincident area	1 272 697	218 003	462 067	1 952 767
Persistence	Coincident Area	184 755	24 017	79 223	287 995
	Habitat Fragmentation	720 767	105 806	346 834	1 173 407
	Human Influence	632 284	107 291	341 444	1 081 019
	Total no coincident area	1 353 051	213 097	688 278	2 254 426

Table 9. Metrics for cost and persistence approaches. nPUs are presented as a percentage relative to study area for total areas, and as a percentage relative to total areas for PAs and prioritized areas. The other metrics were calculated separately in each type of area (PAs, PRAs, and TAs).

Metric	Costs / Persistence Approach	Protected Areas (PAs)	Prioritized Areas (PRAs)	Total Areas (Tas)
Effectiveness (MTA)	Landscape Transformation	62.32	64.08	100.00
	Land Rent	62.32	60.42	100.00
	Habitat Fragmentation	62.32	60.97	100.00
	Human Influence	62.32	57.31	100.00
Area (nPUs)	Landscape Transformation	66.18	33.82	30.14
	Land Rent	70.04	29.96	28.48
	Habitat Fragmentation	69.87	30.13	28.55
	Human Influence	71.41	28.59	27.93
Aggregation (AGG)	Landscape Transformation	83.99	45.85	72.49
	Land Rent	83.99	46.79	73.96
	Habitat Fragmentation	83.99	22.59	66.49
	Human Influence	83.99	39.01	72.04

Implications for conservation planning

Coincident and variable areas related to each cost and persistence approach could impact differently on conservation planning. A small number of no coincident priority areas were found in the land rent approach (Table 8), reflecting the importance of agricultural and cattle economies for concentrate activities in highly productive regions such as the Cerrado savannas in Brazil, the Andes, Caribbean and Oriniquia regions in Colombia, and the high and low lands of Mesoamerica (Figure 2A). More variable areas were found in the aggregation approach (Table 8), as a consequence of the high fragmentation levels of regions like the southwestern savannas and forests of South-America, and the low and high lands in the Andes, and Mesoamerica (Figure 2B). Nevertheless, similar differences in area were found in the other approaches (Table 8) since human-dominated landscapes prevail in these regions.

More coincident areas between approaches occurred for costs, they were 50% higher than for persistence approaches (616,801 vs. 287,995km^2), and correspond to 30% of no coincident areas (616,801 vs. 1,952,767 km^2) (Table 8), reducing, for instance, the uncertainty in resource allocation for land acquisition. Conversely, no coincident areas were 10% higher in persistence approaches (1,952,767 vs. 2,254,426km^2), and the proportion between coincident and no coincident areas was only 12% (287,995 vs. 2,254,426 km^2) (Table 8). All the approaches in their coincident and variable areas prioritize more natural than degraded and transformed areas (Table 8); therefore, more conservation planning strategies related to biodiversity protection than restoration should be considered.

The land-sharing/sparing framework in conservation planning

All-natural habitats, and coincident degraded and transformed areas were framed in the land-sparing model (Table 10). Conversely, areas where the four components did not coincide, and over degraded or transformed habitats were framed in the land-sparing model (Table 10). Land acquisition for protection was employed only for prioritized areas in natural habitats involving the land rent or the human influence approaches; while conservation agreements for protection were applied to prioritized areas selected in the other approaches over natural habitats (Table 10). Restoration was applied to degraded or transformed areas for coincident approaches by acquiring lands, and over areas where improving connectivity is necessary by conservation agreements (Table 10). Wildlife-friendly farming was included for degraded or transformed areas selected only in one of the approaches (Table 10).

Table 10. The analytical framework proposed for applying the land sharing and land sparing models using prioritized conservation areas (PRAs). The land management framework operates with two mechanisms: conservation agreements and land acquisition, and four actions, wildlife-friendly farming, active and passive restoration, and protection. Mechanisms and actions can be applied to the sharing or the sparing model according to the natural, degraded or transformed land cover.

	Approach	Component	Land management framework by land cover type		
			Natural	Degraded	Transformed
Costs	Coincident PRAs of cost approaches	Areas with low landscape transformation and land rent	Sparing: acquire land for protection	Sparing: acquire land for active or passive restoration	Sparing: acquire land for active restoration
	PRAs only in the transformed area approach	1. Areas with low landscape transformation	Sparing: conservation agreements for protection	Sharing: conservation agreements for active restoration where improving connectivity is required, and agriculture wildlife-friendly farming in the remaining area	Sharing: conservation agreements for agriculture wildlife-friendly farming
	PRAs only in the land rent approach	2. Areas with low land rent	Sparing: acquire land for protection		
Persistence	Coincident PRAs of persistence approaches	Areas with low habitat fragmentation and human influence	Sparing: acquire land for protection	Sparing: acquire land for active or passive restoration	Sparing: acquire land for active restoration
	PRAs only in the habitat fragmentation approach	3. Areas with low habitat fragmentation	Sparing: conservation agreements for protection	Sharing: conservation agreements for active restoration where improving connectivity is required, and agriculture wildlife-friendly farming in the remaining area	Sharing: conservation agreements for agriculture wildlife-friendly farming
	PRAs only in the human influence approach	4. Areas with low human influence	Sparing: acquire land for protection		

We found that land-sparing was the optimal landscape management option in regions with high proportions of natural remaining habitat like the Amazon or Chocó-Darién regions (Figure 9).

Conversely, the land-sharing model prevailed in some biodiversity hotspots, such as the Cerrado, Pantanal, and Caatinga Brazilian ecoregions, the dry Andean forest, and the Mesoamerican moist forests, where heterogeneous and human-dominated landscape mosaics occurred (Figure 9). Most characterizing mechanisms and actions in these regions were conservation agreements for wildlife-friendly farming in the land-sharing model, and land acquisition for protection in the sparing model (Figure 9).

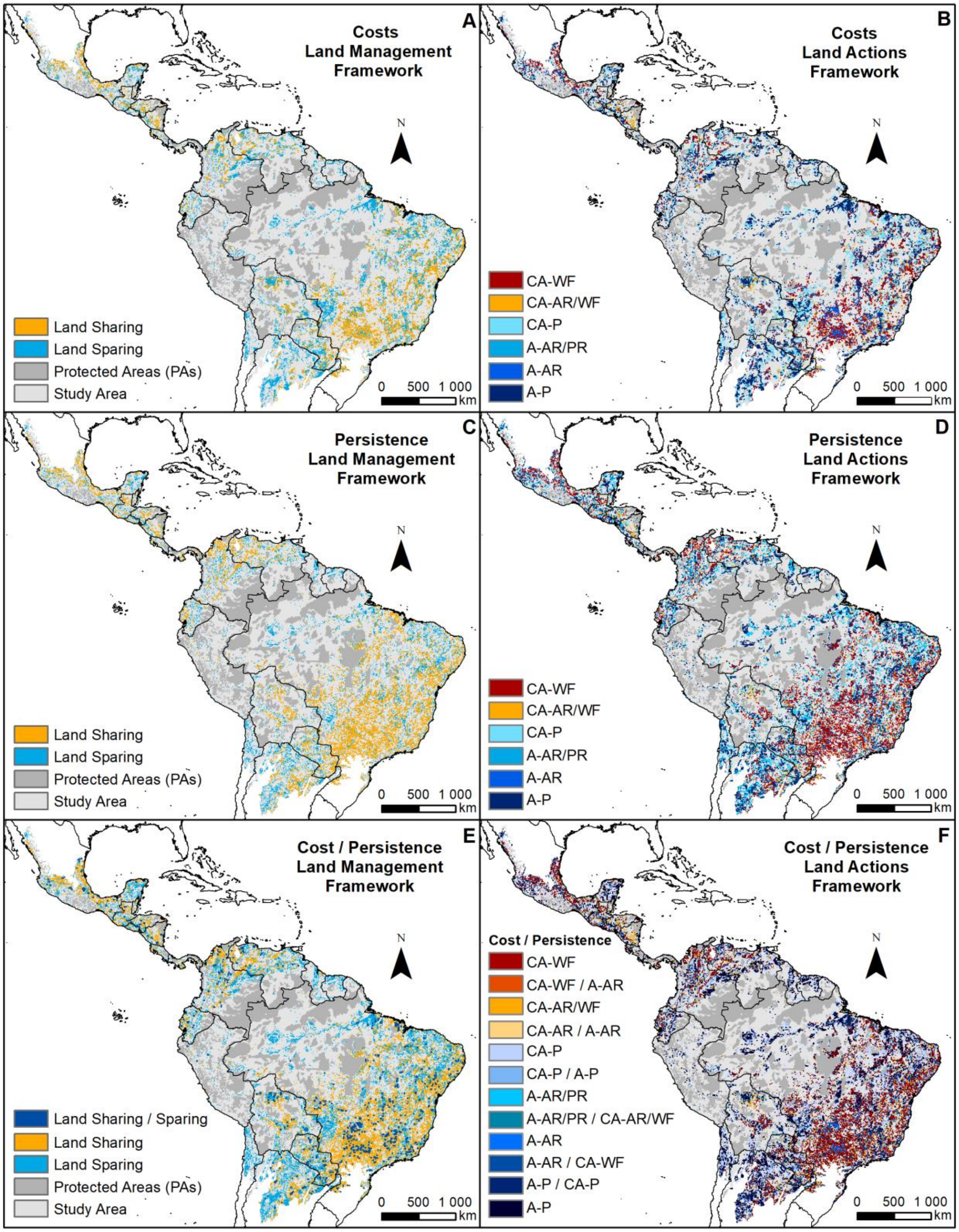


Figure 9. Applied analysis of the land sharing (orange colors) / sparing (blue colors) framework proposed (Table 10). Land management (left) and actions (right) were evaluated for costs (top) and persistence (middle) approaches, and the combination of both (bottom). Abbreviations for land actions correspond to those in our analytical framework proposed (Table 10). Mechanisms: conservation agreements (CA), and land acquisition (A); and actions: wildlife-friendly farming (WF), active (AR) or passive restoration (PR), and protection (P).

Discussion

Differences in cost and persistence approaches

Cost approaches guide in higher proportion the spatial prioritization, even when other factors accounting persistence are included, as founded by Bode *et al.* (2008). In our results, the most significant coincidences between priority areas were found for cost approaches; however, differences in non-coincident areas were more extensive in both cost and persistence approaches. These mismatches captured the complex landscape heterogeneity in the Neotropics regarding the approaches applied. Consequently, prioritized areas accounted critical aspects for conservation planning, such as the land-use/cover change (landscape transformation approach), the productivity of economic activities (land rent approach), the landscape fragmentation (habitat fragmentation approach), and the threats to biodiversity by the human expansion (human influence approach) (Grau *et al.* 2013).

Variability in conservation areas selection was critical in all approaches because it exceeds the coincident area. The distribution of priority areas was influenced by the current location of PAs since they are mostly placed over regions with large proportions of natural habitats and high aggregation levels, shifting prioritized areas over regions occupied by a complex mosaic of human intervention. In these regions, spatial heterogeneity explains the differences found (Naoe *et al.* 2015; Troupin & Carmel 2016). Notably, the low level of compactness and the not-overlapping area of the aggregation approach also supported the highly fragmented landscapes where prioritized areas were selected. In this approach, the impossibility of finding adjacent and not fragmented planning units leads to requiring more disconnected areas.

However, at the resolution employed, fragmentation patterns found could be misleading, i.e., we could have found aggregation patterns over regions with a higher degree of fragmentation than the evidenced in this analysis. Thus, this analysis should be applied at a higher resolution in smaller regions to compare some emerging effects. For instance, at more detailed scales, the effects of the aggregation level of agricultural matrices may influence species differently; in many cases may constitute the only habitat for native species (habitat supplementation), or in interaction with remnant natural habitats may be a mosaic of habitats for other species (habitat complementation) (Ries *et al.* 2004; Tscharntke *et al.* 2012), giving multiple conservation options to human-modified landscape management accounting more specific biodiversity responses, particularly in the land-sharing model (Gonthier *et al.* 2014).

PAs do not fulfill the conservation targets in the Neotropical region, as also was found in recent studies (Baldi *et al.* 2019). Therefore, the protection of prioritized areas is critical since they are necessary to achieve conservation targets, but also, they are 60% percent more efficient in conserving biodiversity. The low variability in effectiveness values of cost and persistence approaches compared to the differences found in the spatial arrangements of prioritized areas accounted for flexibility in spatial conservation prioritization (Moilanen 2008; Kukkala & Moilanen 2013). Similar levels in the efficiency of meeting conservation targets can be achieved using different portfolios of areas. However, this variability also poses challenges in the mechanisms and priority actions for the possible implementation of prioritized areas at a local level (Knight *et al.* 2006).

Implications for conservation planning in the land-sharing/sparing framework

Strategies to landscape management range from the political level to local implementation of conservation actions and involve multiple trade-offs (Grau *et al.* 2013; Mertz & Mertens 2017). Particularly, spatial optimization allows identifying areas of high importance for biodiversity (land-sparing) (Polasky *et al.* 2005; Fischer *et al.* 2008), expecting to increase the extent of protected areas. However, in regions where the landscape matrix is highly productive, other strategies should be considered (Driscoll *et al.* 2013; Dobrovolski *et al.* 2014). For instance, our prioritized areas, and especially those where the most significant variability occurs, are highly important for developing strategies framed in agricultural spatial arrangements for conservation (land-sharing) (Fischer *et al.* 2008). Our prioritized areas proposed, show that even in some places immersed in productive matrices, conservation is necessary to meet conservation targets. Furthermore, these areas are more efficient and maintaining similar representativeness values than the current protected areas (Burbano-Girón *et al.* 2019a).

The complementary and non-exclusive nature of land sharing/sparing models, particularly for tropical areas, has been conceptually proposed not only to guarantee biodiversity conservation but also for food supply (Fischer *et al.* 2008; Kremen 2015; Mertz & Mertens 2017). By employing our proposed framework at the Neotropical level, spatial patterns of land-sharing and land- sparing models may guide conservation priorities and meeting of conservation targets. Although it should be recognized that other factors may operate at the local level (Fischer *et al.* 2008), our results support regional landscape management at the Neotropical level. For instance, land-sparing has been proposed as an optimal landscape management option in places of low species turnover and with high proportions of remaining habitat (Green *et al.* 2005; Grau *et al.* 2013; Kremen 2015), like the Amazon or Chocó-Darién ecoregions, where our framework mostly recommend its implementation. Particularly, in the Brazilian Amazon, a land-sparing strategy for livestock production is currently being carried out (Mertz & Mertens 2017).

Conversely, in landscapes where beta diversity is significant, biodiversity conservation could be favored by the landscape heterogeneity of the land-sharing model, also promoting the improvement of other desired conditions like connectivity (Fischer *et al.* 2008; Grau *et al.* 2013; Kremen 2015). These regions are critical to conservation planning, as they are commonly found in areas of biodiversity hotspots and endemism in the Neotropics, such as the Cerrado, Pantanal, and Caatinga Brazilian ecoregions, the dry Andean forest, and the Mesoamerican moist forests. In our framework, these regions are shown as locations for mostly implement land-sharing model, but also they are one of the most threatened ecosystems (Leal *et al.* 2005; Portillo-Quintero & Sánchez-Azofeifa 2010; Roque *et al.* 2016). Therefore, we must make a special call concerning the situation of these regions, where the implementation of wildlife-friendly farming actions is mostly recommended according to our findings, but where specific areas to acquire lands for protection and restoration are also located (Figure 5). These zones proposed should be explored at lower resolutions, since the creation of protected areas has been urgently evidenced (Portillo-Quintero & Sánchez-Azofeifa 2010; Tabarelli *et al.* 2010; Françoso *et al.* 2015); therefore there is a real need to ensure persistence and exclude frequent and intense disturbances.

Finally, we should consider that applicating any of the models could produce adverse effects; for instance, the intensification of agriculture may increase the income of these activities in the future, leading to its subsequent expansion (Phelps *et al.* 2013). Consequently, proposed actions of one or the other model do not guarantee its success; instead, both approaches require careful design and implementation at the local level to be effective (Phalan *et al.* 2011; Grau *et al.* 2013). Different groups of organisms respond to different scales of landscape management; therefore, conservation of biodiversity requires multiple scales of conservation (Gonthier *et al.* 2014).

Conclusions

Cost approaches guide in higher proportion the spatial prioritization, even when other factors accounting persistence are included. The most significant coincidences between priority areas were found for cost approaches, but the differences in non-coincident areas were more extensive. Over coincident areas, more natural than degraded and transformed habitats were found; therefore, their protection is critical because here biodiversity should be better represented, and also they are immersed in a transformed and human-dominated landscape mosaic. Meanwhile, more significant regional variability indicates more different strategies that should be applied to landscape management, creating a complex mosaic of decisions that should be considered for conservation planning.

More variable regions coincided with critical hotspots of biodiversity, the Chaco, the Atlantic forest, the Pantanal, Cerrado, and Caatinga regions in Brazil, the moist and dry forests of northern Andes, and the Mesoamerican moist forests. In these regions, the variability of prioritized areas indicates that conservation targets could be met in flexible arrangements of conservation areas. Consequently, the fulfillment of conservation targets on these hotspots depends not only on the establishment of new protected areas but also in different conservation strategies to guarantee the success of conservation.

We proposed an analytical framework applying the land-sharing/sparing model based on the coincidence and variability of prioritized areas found. Coincident prioritized areas between approaches that are over natural habitats were proposed to be under strict protection, while degraded and transformed areas should be a focus of restoration processes. On these areas, the mechanism proposed was land acquisition based on four components: (1) low probability of landscape transformation, (2) low land rent, (3) low habitat fragmentation, and (4) low human influence. These areas were framed in the land-sparing model. Conversely, areas where the four components not coincided were framed in the land-sharing model. The mechanism proposed for these areas was conservation agreements to implement restoration or wildlife-friendly farming.

Supplementary Data

Table S7. Common approaches employed for including costs and persistence criteria in conservation planning.

Criteria	Common approaches where the criteria have been employed
Costs	Conservation costs have been included using four approaches. (1) Opportunity costs, the not perceived benefit by the best alternative use in an area (e.g., Norton-Griffiths & Southey 1995; Polasky *et al.* 2001; Balmford *et al.* 2003; Stewart *et al.* 2003; Stewart & Possingham 2005; Chomitz *et al.* 2005; Naidoo & Adamowicz 2006; Naidoo & Iwamura 2007; Cameron *et al.* 2008; Carwardine *et al.* 2008; Adams *et al.* 2010; Wintle *et al.* 2011; Jantke & Schneider 2011; Schröter *et al.* 2014; Venter *et al.* 2014; Mappin *et al.* 2019). (2) Direct economic cost approaches, employing costs of land acquisition (e.g., Wu 2000; Stoneham *et al.* 2003; Newburn *et al.* 2005), management costs (e.g., Moore *et al.* 2004; Wilson *et al.* 2011), transactions costs (including transactions for damage) (e.g., Barua *et al.* 2013), or restoration costs (e.g., Holl & Howarth 2000; Wilson *et al.* 2011). (3) Non-monetary costs, including uniform costs or area-based costs (e.g., Beck & Odaya 2001; Airamé *et al.* 2003; Stewart & Noyce 2003; Carvalho *et al.* 2010), multicriteria abiotic costs (e.g., Williams *et al.* 2003; Rouget *et al.* 2006), multicriteria environmental (biotic and socioeconomic) costs (e.g., Ferraro 2004), vulnerability to threats costs (e.g., Banks *et al.* 2005; Tallis *et al.* 2008; Ban *et al.* 2009), or multiple socioeconomic costs (Leathwick *et al.* 2008; Green *et al.* 2009). (4) Dynamic costs, employing stochastic dynamic programming to implement short-term gain maximization (e.g., Wilson *et al.* 2006), and short-term loss minimization heuristics for land acquisition (e.g., Wilson *et al.* 2006) and management costs (e.g., Bode *et al.* 2008); or employing deterministic integer programming problems to estimate the marginal land rent of agricultural production (e.g., Jantke & Schneider 2011).
Persistence	Persistence criteria have been mainly addressed by employing six approaches. (1) Modifying the targets of representation according to ecological requirements (Carwardine *et al.* 2009), e.g., the patch size (e.g., Lindenmayer & Possingham 1995), or population size (e.g., Carroll *et al.* 2003); or according to the threat level of the biodiversity features (e.g., Pressey *et al.* 2003; Carvalho *et al.* 2010; McGowan *et al.* 2017). (2) Including habitat dynamics (Possingham *et al.* 2009), e.g., using vegetation and disturbance dynamics (e.g., Leroux *et al.* 2007), or habitat loss (e.g., Costello & Polasky 2004; Strange *et al.* 2006; Visconti *et al.* 2010). (3) Forcing multiple and separate occurrences in the network of conservation areas (e.g., Rodrigues *et al.* 2000). (4) Employing the Vulnerability/Irreplaceability framework, by including a probability of persistence for planning units, or targeting sites where species are most likely to persist (e.g., Williams 1998; Araújo *et al.* 2002; Pressey *et al.* 2004, 2007; Brooks *et al.* 2006). (5) Employing vulnerability to threats as the likelihood of planning units to be converted to other uses (e.g., Banks *et al.* 2005; Tallis *et al.* 2008; Ban *et al.* 2009). (6) Including connectivity for maximizing the biophysical connections among conservation areas (e.g., Cabeza 2003; Rouget *et al.* 2006; Hodgson *et al.* 2009; Ryan *et al.* 2012).

Table S8. Habitat classes proportion in the study area according to the standardization proposed between IUCN habitats and the land cover map from the ESA CCI Land Cover 2015 dataset v2.0.7 (http://maps.elie.ucl.ac.be/CCI/viewer/index.php) (Table S10).

Habitat	Area (km^2)	Area (%)	Natural / Transformed
Croplands	1 279 117.75	7.58	Transformed
Pasturelands	1 797 122.56	10.66	Transformed
Urban Areas	50 686.50	0.30	Transformed
Permanent snow and ice	5 364.24	0.03	Natural
Rocky and Desert Areas	668 602.16	3.96	Natural
Water bodies	247 380.94	1.47	Natural
Flooded Savannas and Grasslands	328 944.06	1.95	Natural
Savannas and Grasslands	529 717.38	3.14	Natural
Shrublands	2 180 402.65	12.93	Natural
Pine-Oak Forests	108 594.47	0.64	Natural
Subtropical/Tropical Dry Forests	995 961.39	5.91	Natural
Subtropical/Tropical Mangrove Forests	28 835.37	0.17	Natural
Subtropical/Tropical Moist Forests	7 312 350.30	43.36	Natural
Subtropical/Tropical Swamp Forests	193 034.09	1.14	Natural
Subtropical/Tropical Heavily Degraded Former Forests	1 139 672.82	6.76	Degraded
Total	16 865 786.69	100	

Table S9. The 30 most profitable agricultural and livestock activities in 2013 for Central and South America according to FAO statistics (http://www.fao.org/faostat/en/#data). The yield for livestock has no take into account the animal unit factor.

Crop - Livestock	Net Production Value ($1000 constant 2004-2006 International USD)	Area (ha) / Heads	Production (ton)	Yield (ton/ha / ton/head)
Meat, cattle	49 115 644	79 034 579	17 941 676	0.227
Soybeans	39 049 109	55 911 493	156 746 250	2.803
Meat, chicken	32 760 241	11 149 473 000	23 235 494	0.002
Sugar cane	31 940 829	13 193 920	952 687 705	72.207
Milk, whole fresh cow	26 151 445	43 561 980	79 468 686	1.824
Maize	10 537 569	32 786 472	153 325 820	4.676
Meat, pig	10 501 979	82 685 903	6 752 549	0.082
Rice, paddy	7 000 228	5 043 743	26 591 581	5.272
Bananas	6 891 136	1 032 499	25 721 069	24.911
Eggs, hen, in shell	6 318 531	727 960 000	7 869 775	0.011
Coffee, green	5 318 109	4 972 699	4 794 289	0.964
Oranges	5 052 048	1 277 827	25 304 631	19.803
Grapes	4 955 652	572 313	7 579 221	13.243
Tomatoes	3 919 148	248 903	11 301 831	45.407
Wheat	3 405 404	8 630 446	23 134 025	2.681
Beans, dry	3 140 186	6 398 533	6 084 310	0.951
Mangoes, mangosteens, guavas	2 719 351	388 818	4 161 947	10.704
Potatoes	2 696 085	1 003 668	17 421 116	17.357
Pineapples	2 391 950	223 404	8 809 549	39.433
Seed cotton	2 301 837	2 048 887	6 448 648	3.147
Apples	2 252 598	191 934	5 161 266	26.891
Lemons and limes	2 162 841	314 309	5 593 277	17.795
Avocados	1 862 477	295 161	2 787 188	9.443
Cassava	1 755 981	2 202 901	31 165 906	14.148
Tobacco, unmanufactured	1 731 361	537 913	1 105 353	2.055
Cashewapple	1 703 320	612 431	1 743 025	2.846
Plantains	1 371 964	818 593	7 981 030	9.750
Chillies and peppers, green	1 354 695	179 789	3 213 950	17.876
Oil, palm fruit	1 305 665	1 138 633	16 953 904	14.890

Table S10. Habitats proposed, IUCN habitats categories (version 3.1 from 2012), and standardization with the land cover map from the ESA CCI Land Cover 2015 dataset v2.0.7 (http://maps.elie.ucl.ac.be/CCI/viewer/ index.php). Most habitats not included from the IUCN categories do not represent tropical habitats or correspond to the marine biome. Other classes may not be included as they do not find correspondence with the land cover classes.

Habitat Category Proposed	IUCN's Habitat Category	Land Cover Map Class
Subtropical/Tropical Moist Forests	Forest - SubtropicalTropical Moist Lowland Forest - SubtropicalTropical Moist Montane	Tree cover, broadleaved, evergreen, closed to open (>15%)
Subtropical/Tropical Dry Forests	Forest - SubtropicalTropical Dry	Tree cover, broadleaved, deciduous, closed to open (>15%) Tree cover, broadleaved, deciduous, closed (>40%) Tree cover, broadleaved, deciduous, open (15-40%)
Pine-Oak Forests	Forest - Temperate	Tree cover, needleleaved, evergreen, closed to open (>15%) Tree cover, needleleaved, deciduous, closed to open (>15%) Tree cover, needleleaved, deciduous, closed to open (>15%)
Subtropical/Tropical Mangrove Forests	Forest - SubtropicalTropical Mangrove Vegetation Above High Tide Level	Tree cover, flooded, saline water
Subtropical/Tropical Swamp Forests	Forest - SubtropicalTropical Swamp	Tree cover, flooded, fresh or brackish water
Savannas and Grasslands	Savanna - Dry Savanna - Moist Grassland - Temperate Grassland - SubtropicalTropical Dry Grassland - SubtropicalTropical High Altitude	Grassland
Shrublands	Shrubland - Temperate Shrubland - SubtropicalTropical Dry Shrubland - SubtropicalTropical Moist Shrubland - SubtropicalTropical High Altitude	Shrubland
Flooded Savannas and Grasslands	Grassland - SubtropicalTropical Seasonally WetFlooded Wetlands (inland) - Shrub Dominated Wetlands Wetlands (inland) - Bogs, Marshes, Swamps, Fens, Peatlands	Shrub or herbaceous cover, flooded, fresh/saline/brackish water
Water bodies	Wetlands (inland) - Permanent RiversStreamsCreeks (includes waterfalls) Wetlands (inland) - SeasonalIntermittentIrregular RiversStreamsCreeks Wetlands (inland) - Permanent Freshwater Lakes (over 8ha) Wetlands (inland) - SeasonalIntermittent Freshwater Lakes (over 8ha) Wetlands (inland) - Permanent Freshwater MarshesPools (under 8ha) Wetlands (inland) - SeasonalIntermittent Freshwater MarshesPools (under 8ha) Wetlands (inland) - Freshwater Springs and Oases Wetlands (inland) - Alpine Wetlands (includes temporary waters from snowmelt) Wetlands (inland) - Geothermal Wetlands Wetlands (inland) - Permanent Inland Deltas Wetlands (inland) - Permanent Saline, Brackish or Alkaline Lakes	Water bodies

Habitat Category Proposed	IUCN's Habitat Category	Land Cover Map Class
	Wetlands (inland) - SeasonalIntermittent Saline, Brackish or Alkaline Lakes and Flats Wetlands (inland) - Permanent Saline, Brackish or Alkaline MarshesPools Wetlands (inland) - SeasonalIntermittent Saline, Brackish or Alkaline MarshesPool ArtificialAquatic - Water Storage Areas (over 8ha) ArtificialAquatic - Ponds (below 8ha) ArtificialAquatic - Aquaculture Ponds ArtificialAquatic - Salt Exploitation Sites ArtificialAquatic - Excavations (open) ArtificialAquatic - Wastewater Treatment Areas ArtificialAquatic - Irrigated Land (includes irrigation channels) ArtificialAquatic - Seasonally Flooded Agricultural Land ArtificialAquatic - Canals and Drainage Channels, Ditches	
Rocky and Desert Areas	Rocky areas (e.g., inland cliffs, mountain peaks) Desert - Hot Desert - Temperate Desert - Cold	Sparse vegetation (tree, shrub, herbaceous cover) (<15%) Sparse herbaceous cover (<15%) Bare areas
Croplands	ArtificialTerrestrial - Arable Land ArtificialTerrestrial - Plantations ArtificialTerrestrial - Rural Gardens	Cropland, rainfed Cropland, tree or shrub cover Cropland, irrigated or post-flooding Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)
Pasturelands	ArtificialTerrestrial - Pastureland	Herbaceous cover
Urban Areas	ArtificialTerrestrial - Urban Areas	Urban areas
Subtropical/Tropical Heavily Degraded Former Forests	ArtificialTerrestrial - SubtropicalTropical Heavily Degraded Former Forest	Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (<50%) Mosaic tree and shrub (>50%) / herbaceous cover (<50%) Mosaic herbaceous cover (>50%) / tree and shrub (<50%)

Table S11. Details on the estimation of crops and cattle land rent.

<table>
<tr>
<td>Crops land rent</td>
<td>

To estimate the crops land rent ($LRcr$) (USD/km^2), we multiplied the crops yield (Ycr) (ton/km^2) and net production value ($NPVcr$) (USD/ton). Crops yield was calculated dividing crops area (km^2) by production (ton) using the information from national statistics at the municipality or state level (Table S12), or FAO statistics (http://www.fao.org/faostat/en/#data/QC/metadata) at country level (Table S12) ($NPVca_j$). Net production value ($NPVcr$) was obtained from FAO statistics at national level (http://www.fao.org/faostat/en/#data/QV/metadata) (Table S12), and was standardized to USD by ton by dividing it ($constant\ 2004-2006\ \ International\ USD$) in the total production reported by FAO (ton) (http://www.fao.org/faostat/en/#data/QC/metadata). For all data, we used the matching average of the last five years of information. The crops land rent ($LRcr_j$) in each administrative unit (municipality, state, or country) ($j = 1 \dots, m$) was estimated as the mean land rent of all its crops harvested ($i = 1 \dots, n$) (Table S12). Crops reported for each country were standardized to crops categories of the FAO commodity groups (http://www.fao.org/waicent/faoinfo/economic/faodef/faodefe.htm), using their genera or the scientific name in the cases where it was possible, or when a coincidence was found.

$$LRcr_j = \frac{\sum_{i=1}^{n} Ycr_{ij}NPVcr_{ij}}{n}$$

Eq. 1. Estimation of crops land rent in each administrative unit.

We excluded some crops from the analysis because of five reasons: (1) because no standardization was found in crops categories of the FAO commodity groups, (2) because the crop had a cultivated or harvested area less than 1km^2 or without information, (3) because the crop had zero tons produced or without information, (4) because the crop had no information on net production value, or (5) because the crop has never been harvested in the country according to FAO historic data. Additionally, after this process, some crops (e.g., tomatoes, chiles, strawberries, maize, pepper, and potatoes, among others) in some countries (Brazil, Chile, Colombia, Costa Rica, Mexico, and Peru) reached a disproportionally land rent ($> 3\,000\,000\ USD/km^2$) according to expert criteria. For these records (2 116 from 89 666) the mean land rent of the crop in the respective country was employed. After this depuration, we worked with 117 crops and 10 000 administrative units.

The administrative units were spatialized using the Global Administrative Areas dataset v3.6 (http://www.gadm. org) according to the level of information of crops statistics for each country (municipality, state, or country) (Table S12); we obtaining 8 158 administrative units. The correspondence between administrative units at the alphanumeric level (10 000), and spatial level (8 158) was 96% (7 797) after manually correct the names of both sources of information to match them as much as possible. For the inconsistent administrative units at the spatial level, land rent was estimated as the national average of all crops. Finally, land rent was calculated by planning unit (PU) ($LRcr_p$), as its weighted mean by the area of each administrative unit in each PU (A_{jp}). Then, the land rent value was updated by multiplying it by the area of croplands (A_{cr}) in each PU (km^2) (according to the habitats map, Figure 1), but dividing it by the total PU area (A_p) (10km^2) to maintain its units in USD/km^2 (Table S12).

$$LRcr_p = \frac{\left[\sum_{j=1}^{mp} LRcr_j \left(\frac{A_{jp}}{A_j}\right)\right] A_{cr}}{A_p}$$

Eq. 2. Estimation of crops land rent by planning unit.

</td>
</tr>
<tr>
<td>Cattle land rent</td>
<td>

Cattle land rent ($LRca$) (USD/km^2) was estimated as the product between cattle yield (Yca) ($heads/km^2$) and net production value ($NPVca$) ($USD/head$). The net production value was obtained from FAO statistics at the national level (http://www.fao.org/faostat/en/#data/QV/metadata) (Table S12) ($NPVca_j$), and was standardized to USD by head by dividing it ($constant\ 2004-2006\ \ International\ USD$) in the total production reported by FAO ($head$) (http://www.fao.org/faostat/en/#data/QC/metadata). We used average of Milk whole fresh cow and Meat indigenous cattle categories of FAO. Land rent was spatialized ($LRca_k$) (1km^2 resolution) per grid ($k = 1 \dots, q$) using the global gridded cattle product of Robinson *et al.* (2014) ($heads/km^2$). However, this layer was corrected using expert criteria, defining 500 cattle heads as maximum possible production. Finally, the land rent was calculated by PU ($LRca_p$), as the average of the grids of land rent inside each PU ($LRca_{kp}$). (Eq. 3).

$$LRca_p = \frac{\sum_{k=1}^{qp} Yca_k NPVca_j}{qp}$$

Eq. 3. Estimation of crops land rent by planning unit.

</td>
</tr>
</table>

Table S12. Source information summarized by country to calculate crops land rent. Data correspond to the area of the entire country and the average of the las five years of information, except for the area of the croplands from the habitats map, which correspond to 2015.

Country	Data level of national statistics	Country area (km^2)	Proportion of croplands from habitats map	Area (km^2)				Production (ton)		Yield (ton/km^2)		FAO Net Production Value (USD/ton)
				Croplands from habitats map	Cultivated area from national statistics	Harvested area from national statistics	Harvested area from FAO statistics	National statistics	FAO statistics	National statistics	FAO statistics	
Argentina	Municipality	4 223 459	42%	439 477	365 226	324 849	350 485	110 590 515	154 866 470	3 037	979	282
Belize	Country	23 104	5%	1 133	0	978	1 004	1 655 130	1 751 382	1 159	1 142	94
Bolivia	State	1 189 462	3%	40 403	38 023	38 041	36 993	15 926 556	16 926 114	544	527	226
Brazil	Municipality	8 980 050	11%	901 492	678 694	2 472 978	760 968	881 936 676	1 046 537 485	2 903	1 138	139
Chile	Municipality	1 035 178	15%	33 628	8 174	0	12 593	3 684 644	15 523 982	2 280	1 411	521
Colombia	Municipality	1 141 555	7%	78 911	34 380	29 315	45 209	38 938 521	68 462 413	918	1 233	209
Costa Rica	Municipality	54 382	8%	4 103	3 302	0	5 139	6 580 463	12 552 837	2 416	1 596	248
Ecuador	State	260 617	9%	21 341	1 311	1 191	23 420	454 038	24 404 244	478	623	247
El Salvador	Country	25 361	19%	4 498	0	7 866	7 807	8 587 724	8 685 271	1 285	1 252	119
French Guiana	Country	83 867	0%	78	0	140	142	104 797	105 681	1 303	1 261	249
Guatemala	Country	117 946	13%	15 860	0	22 775	24 382	40 542 904	44 717 690	1 328	1 333	120
Guyana	Country	205 745	0%	504	0	2 684	2 775	3 655 128	3 579 650	1 109	1 314	114
Honduras	Country	118 357	6%	6 983	0	10 557	12 606	8 842 548	10 947 219	1 320	1 305	191
Mexico	Municipality	2 349 621	10%	90 950	83 491	83 013	165 416	79 500 810	134 892 205	1 269	1 196	273
Nicaragua	Country	135 087	6%	8 359	0	10 652	10 513	8 910 416	9 099 571	1 564	1 512	174
Panama	Country	78 518	13%	9 108	0	2 793	2 855	3 590 390	3 677 231	1 285	1 280	261
Paraguay	Country	474 507	9%	42 473	0	56 742	57 866	24 490 620	27 113 271	921	925	198
Peru	State	1 341 847	2%	28 679	66 540	33 994	32 997	47 118 828	32 721 924	803	1 056	288
Suriname	Country	144 518	0%	519	0	696	726	549 559	561 930	1 506	1 492	241
Venezuela	Municipality	935 609	9%	85 242	12 593	11 951	15 148	12 487 829	13 926 254	1 283	1 309	459

Chapter 3. Underlying and explaining factors guiding the selection of priority areas for conservation in the Neotropical region

Jaime Burbano-Girón[1,2], Kerstin Jantke[3], Maria Alejandra Molina[1], Nicolás Urbina-Cardona[1], Maria Isabel Arce Plata[2], Camilo Alberto Herrera Rozo[4], Andrés Etter[1]

[1] Facultad de Estudios Ambientales y Rurales. Pontificia Universidad Javeriana. Bogotá, Colombia.
[2] Instituto de Recursos Biológicos Alexander von Humboldt. Bogotá, Colombia.
[3] Research Unit Sustainability and Global Change. Hamburg University. Hamburg, Germany.
[4] 42Data. Cali, Colombia.

Introduction

The adequate and well-informed allocation of the limited resources available for biodiversity conservation is crucial for achieving global, national, and sub-national conservation targets (Pouzols *et al.* 2014; Venter *et al.* 2014; Di Marco *et al.* 2016). Therefore, a critical issue in spatial conservation prioritization is to minimize the uncertainty about what and where to conserve, in order to enhance the likelihood of success in conservation planning (Regan *et al.* 2009; Wilson *et al.* 2009). Accordingly, while the robustness of spatial conservation prioritization is increased, certainty to conservation protocols can be strengthened by clarifying and understanding the importance of the factors involved in conservation areas selection (Langford *et al.* 2011). The increasing of robustness in spatial conservation prioritization is a critical and urgent need to improve the modeling process and guide the acquisition of more accurate information to support a successful and cost-efficient implementation and management of conservation actions (McCarthy 2009; Regan *et al.* 2009; Roura-Pascual *et al.* 2010).

Systematic Conservation Planning (SCP) is one of the foremost conceptual and methodological guides to explore where and what to conserve for decision making (Margules & Pressey 2000). SCP supports the identification of conservation areas employing a spatial conservation prioritization process based upon three principles: (1) represent the biodiversity of a particular region for ensuring its (2) persistence over time in a (3) cost-efficient way (Margules & Sarkar 2007). However, many prioritization exercises do not account for all three principles of SCP, i.e., representation, cost-efficiency, and persistence (see Pressey *et al.* 2007; Kukkala & Moilanen 2013), and only few studies have evaluated the impact of the three principles on the definition of priority areas (see e.g., Wilson *et al.* 2006; Bode *et al.* 2008).

Studies assessing representation in combination with cost-efficiency or persistences principles have shown that spatial prioritization is mainly sensitive to the type of cost data, and particularly to the resolution of cost information (Richardson *et al.* 2006). For instance, Bode *et al.* (2008) showed lower variability in priority areas selected when different representations were applied as biodiversity features, but higher variations with the inclusion of costs, followed by persistence approaches, indicating that costs and persistence principles guide in a higher proportion the selection of priority areas. Conversely, Carwardine *et al.* (2010) found that most representative and effective areas maintain high priorities regardless of the change in costs data, mostly depending on its importance for meeting conservation targets. These differences in the critical principles for priority areas selection may vary according to regional characteristics guiding conservation planning and decision making differently (Cabeza *et al.* 2010; Huber *et al.* 2010).

In this paper, we evaluate the sensitivity of priority areas selection using several approaches for biodiversity representation, persistence, and cost-efficiency applied to the Neotropical region, one of the most biodiverse regions globally, but also one of the most threatened with an urgent need to set conservation priorities (Wilson *et al.* 2011, 2016). We included multiple explanatory variables accounting for each approach to identify critical factors guiding the selection of priority areas. Finally, we analyzed and compared the most significant factors at the Neotropical, ecoregion, and country-level, to test if these explanatory factors vary regionally, and how they may guide more accurate design and implementation of conservation priorities. This analysis could be applied to conservation plans in different stages (Knight *et al.* 2006), and as a critical source to identify monitoring surrogates for conservation planning in priority areas, as well as the performance of these areas to ensure its persistence over time.

Method

Study area

Our study area comprises the Neotropics, delimited as the continental WWF Ecoregions (Dinerstein *et al.* 2017) intersected between the Tropic of Cancer and the Tropic of Capricorn (Figure 1). We manually exclude the Chilean matorral Ecoregion since it contains biogeographic and abiotic conditions that are not typical of tropical environments. The study area covers around 17MM km^2, including the continental area of Belize, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana, Ecuador, Peru, Bolivia, Paraguay, most of the territory of Mexico and Brazil, and a small proportion of Chile and Argentina. Our study area also includes the whole basins of the Orinoco (1MM km^2) and Amazon rivers (6MM km^2), and the middle and northern Andes (3MM km^2 in total).

The Neotropics exhibits the highest levels of species richness and endemism, both globally and within the main taxa (amphibians, birds, mammals, and vascular and no-vascular plants). Most representative biomes are the tropical moist forest, the tropical dry forest, the savannas, and the Páramo. These biomes contain several hotspots of biodiversity, e.g., the Andes, the Brazilian Atlantic Forest and Cerrado regions, the Darien-Chocó-Pacific moist forest, and the Amazon rainforest (Olson & Dinerstein 1998; Myers *et al.* 2000; Mittermeier *et al.* 2005). However, the Neotropics also hosts the largest proportion of small range and threatened species (Hoffmann *et al.* 2010; Pimm *et al.* 2014), in addition to the highest deforestation rates (43,000 to 54,000km^2/yr) (Wright 2010; Aide *et al.* 2012), increasing the probability of biodiversity decline (Newbold *et al.* 2016; Betts *et al.* 2017; Roque *et al.* 2018).

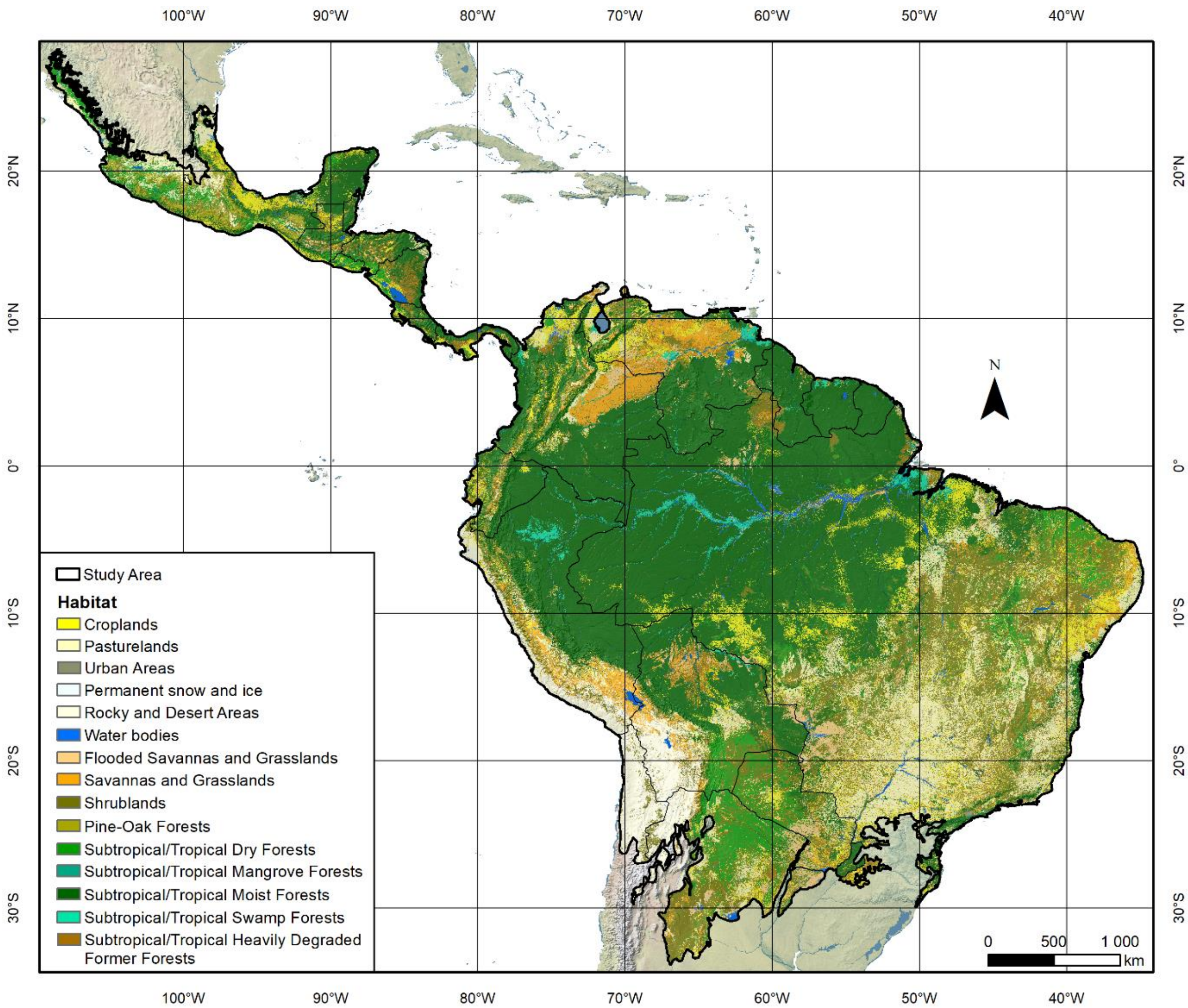


Figure 10. Study area and habitat classes. Habitats were defined as a standardization between the IUCN habitats categories and the Land Cover 2015 dataset v2.0.7 from ESA (https://maps.elie.ucl.ac.be/CCI/viewer/) (Table S1).

Most of the biodiversity and natural ecosystems are over non-intervened regions (14MM km^2 - 81%) (Figure 1 and Table S14). Approximately 80% live in urban zones, representing only 0.3% (50M km^2) of the study area (Grau & Aide 2008). Agricultural and livestock are the main socio-economic activities in Neotropical countries, although they do not contribute significantly to the gross domestic product. According to The World Bank, the average agriculture value added in the region, considering the last 15 years is only 5.5% (http://data.worldbank.org/indicator/ NV.AGR.TOTL.ZS). However, agriculture and pastures lands cover around 18% (3MM km^2) of the study area (Table S14). Most profitable agricultural and livestock products are also the most extensive and productive in the region, including cattle and pig meat, cattle milk, soybeans, sugar cane, maize, rice, bananas, and coffee (Table S15).

Selection of conservation areas

Conservation areas were selected by resolving the minimum set cover problem (Moilanen *et al.* 2009) using the Prioritizr package in R (Hanson *et al.* 2020b), which employs integer linear programming to achieve conservation targets at the least cost (Beyer *et al.* 2016). We employed fixed targets and no penalties or constraints for biodiversity features or planning units (PUs) (10x10km grid). The goal of the Convention on Biological Diversity's Aichi Target 11 to protect 17% of the area of each biodiversity feature (e.g., Venter *et al.* 2014; Mappin *et al.* 2019) was chosen, locking as protected areas (PAs) the planning units with at least 50% of their area covered by PAs (e.g., Kark *et al.* 2009; Klein *et al.* 2009; Esselman & Allan 2011). We included as PAs IUCN categories I-IV (strict protection) taken from the World Database on Protected Areas (IUCN & UNEP-WCMC 2018) (Jenkins & Joppa 2009; Kark *et al.* 2009), besides the documented indigenous lands taken from the Global Platform of Indigenous and Community Lands (LandMark) (http://www.landmarkmap.org/). This combination of PAs includes inside their boundaries, 97% of natural land cover (Figure 1 and Table S14).

We produced 16 conservation portfolios resolving different prioritization problems by combining the four approaches for biodiversity attributes used by Burbano-Girón *et al.* (2019a) (composition-species, structure-ecosystems, function-ecological groups, and the combination of all biodiversity features), and the two approaches for costs (landscape transformation and land rent) and persistence (habitat fragmentation and human influence) employed by Burbano-Girón *et al.* (2019b). Costs and persistence approaches were included as costs in the objective function normalized in the range 1-101. We decided to normalize cost and persistence approaches to ensure that the magnitude of values did not affect the prioritization results. The linear normalization was applied in range 1-101 since planning units with costs equal to zero cancels the objective function of the prioritization process. The conservation area selection variable corresponded to the planning units selected in the best solution (the one with the least cost), at least for one of the 16 portfolios of conservation areas produced. We ran the 16 approaches 100 times and proposed to employ the selection frequency of each planning unit as a proxy of its irreplaceability (e.g., Stewart & Possingham 2005; Fuller *et al.* 2006; Dobrovolski *et al.* 2013).

Analysis of conservation area selection

To evaluate the importance of different factors to conservation areas selection we employed a random forest analysis (Breiman 2001). The model was constructed with classification trees for predicting the selection of conservation areas (binary variable 1-0) using 70 explanatory variables related to the principles involving systematic conservation planning (representation, cost-efficiency, and persistence) (Margules & Sarkar 2007) (Table S16). The parametrization of the model employed a five-fold cross-validation method with two repetitions using the caret package in R. The model reached an accuracy of 94% (kappa = 0.9) employing 14 variables and 20% samples for validation (53,553 of 66,941 samples). The final model employed 504 trees and was constructed with eight trees to grow, and 14 variables randomly sampled at each split using the randomForest package in R.

The modeling followed a regionalization approach using ecoregions and countries as grouping-factor variables to evaluate the differences in the influence of explanatory variables. We evaluated the prioritized areas (PRAs) selected to complement the protected areas (PAs) at the Neotropical level, and the total areas (PRAs + PAs) at the ecoregion and country levels. We included total areas at the finer scales to balance the number of ones and zeros in the modeling process. The regionalization used the intersection between the Global 200 ecoregions (Olson & Dinerstein 1998) and countries previously employed by Burbano-Girón *et al.* (2019a). From the 81 resultant ecoregions-countries, we selected only five ecoregions based on three criteria; (1) to be a biodiversity hotspot, (2) to include the complete extension of the countries encompassing its distribution in our study area, and (3) to do not contain a high proportion of PAs inside their boundaries. Lower proportions of PAs guarantee that models at the ecoregion and country-level accounted for conservation areas selection instead of PAs occurrence. Thus, we evaluated the factors explaining the selection of conservation over 14 models: (1) prioritized areas at the Neotropical-level, and total areas for 13 different combinations among the ecoregions-countries selected: Llanos Savannas of (2) Colombia and (3) Venezuela; Northern Andean Montane Forests of (4) Colombia, (5) Ecuador, (6) Peru, and (7) Venezuela; (8) Northern Andean Páramo of Colombia, (9) Ecuador, (10) Peru, and (11) Venezuela; and Tumbesian-Andean Valleys Dry Forests of (12) Colombia, (13) Ecuador, and (14) Peru.

Variable Importance

Random forest evaluates through a sensitivity analysis the importance of all variables in the construction of each forest, determining those that contribute to the prediction through the split rule optimization. Variables that separate more observations share a higher contribution to explain the response variable (Breiman 2001). Then, we employed the conditional minimal depth metric to evaluate variable importance, but also the interactions of the variables to subset only the most important variables associated with each of the 14 models evaluated. The 14 variables selected in the model parameterization were chosen by calculating all pairwise minimal depth interactions between the response and the 70 explanatory variables (Ishwaran *et al.* 2010, 2011; Ehrlinger 2015).

Minimal depth assumes that variables with high impact on the prediction are those that most frequently split nodes nearest the trees' roots. This was calculated by averaging the depth of the split (value at the root is 0) for each variable over all the 504 trees within the forest (Ishwaran 2007; Ehrlinger 2015). The smaller the minimal depth, the more impact the variable had grouping the conservation areas selected; and hence, on the forest model prediction. The nearest the split node of a variable appears to another variable, more related they are. Variables interactions and their minimal depth were extracted from the model using the randomForestExplainer package in R. The (positive or negative) relationship between each response variable and explanatory variables was evaluated using the sign of the coefficient of a logistic regression. Finally, the correlation between the most important variables and the remaining explanatory variables was performed to show how other factors may be guiding the conservation area selection.

Results

Factors driving the selection of conservation areas

The spatial configuration of selected conservation areas was different both at the level of biodiversity representation (differences between rows in Figure 11), and at the level of cost and persistence approaches (differences between the columns in Figure 11). Best solution models combined (Figure 12A) did not present a pattern related to any of the selected portfolios (Figure 11), also evidenced in the high variability of the planning units selected (Figure 12B). However, some irreplaceable prioritized areas occurred over biodiversity hotspots such as the Chaco, Atlantic Forest, Cerrado, Pantanal and Caatinga regions in Brazil, dry forest of the Colombian and Ecuadorian valleys, northern Andes in Colombia, and dry and moist forests of Central America (Figure 12C).

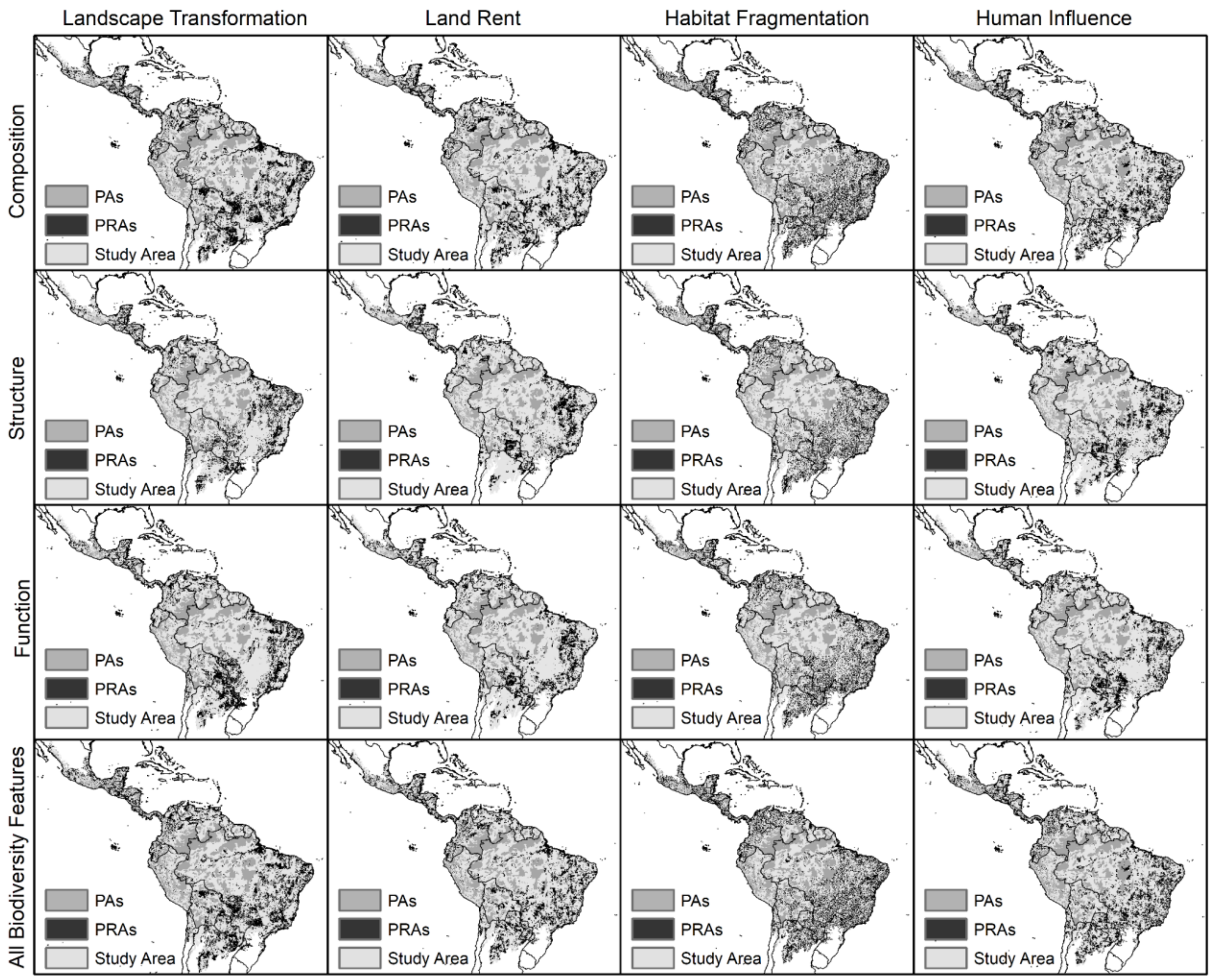


Figure 11. Spatial distribution of the 16 portfolios of conservation areas using biodiversity attributes approaches employed by Burbano-Girón *et al.* (2019a) (composition-species, structure-ecosystems, function-ecological groups, and the combination of all biodiversity features), and the two approaches for costs (landscape transformation and land rent) and persistence (habitat fragmentation and human influence) employed by Burbano-Girón *et al.* (2019b).

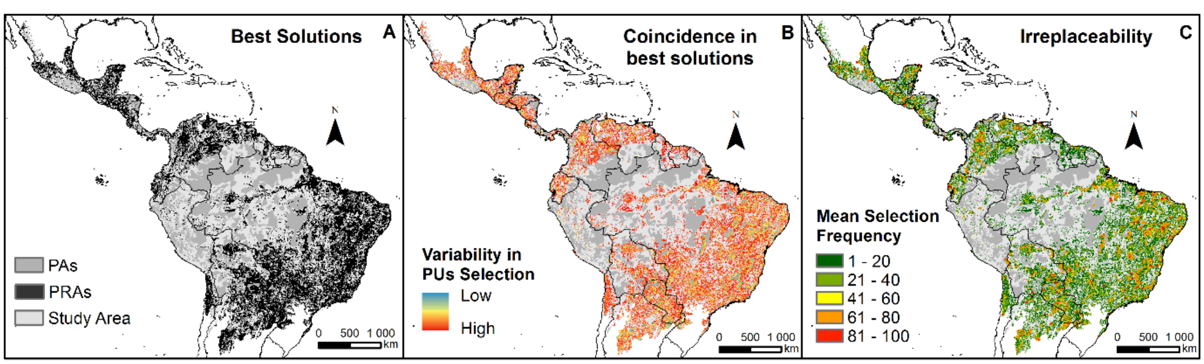


Figure 12. (A) Combination of conservation areas selected in the best solution for at least one of the 16 portfolios of conservation areas produced. (B) Coincidence of planning units (PUs) for the best solutions of the 16 portfolios produced. Where less coincidence occurs, more variability in the selection of conservation areas exists. (C)

Irreplaceability of prioritized areas. Values correspond to the mean selection frequency of the 100 runs for each of the 16 models of conservation areas produced.

The selection of conservation areas involved explanatory factors of the three principles of systematic conservation planning (Figure 13). Regarding representation, factors associated with the three dimensions of biodiversity were critical in the selection of prioritized areas (Figure 13 and Table S16). The composition of all the groups (amphibians, birds, mammals, and reptiles) synthesized in the richness of all species mostly supported biodiversity conservation prioritization for the entire Neotropical region. Land rent approach, and particularly the low rent of cattle lands was also a significant driver of conservation area selection (Figure 13). In persistence, both the low level of fragmentation, particularly in the moist forests, as well as the low levels of human influence mainly related to human footprint, population density, and density of roads and waterways also drove priority areas selection (Figure 13 and Table S16). In general, we found that current Neotropical conservation needs responded to the spatial conservation prioritization model, supporting biodiversity complementarity and reducing conservation costs and threats.

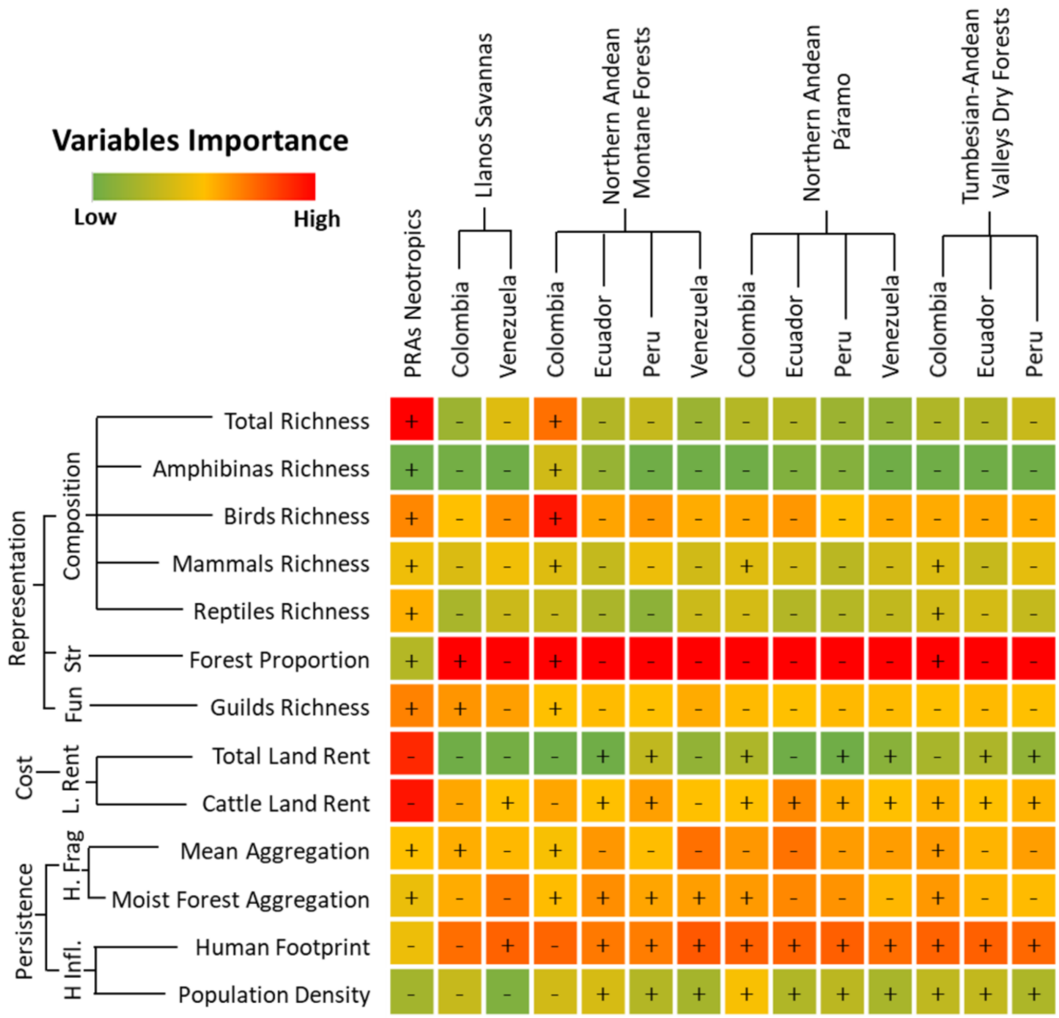


Figure 13. Variables importance (rows) for the 14 models (columns) to evaluate the factors related explaining conservation area selection. Most important variables (red) correspond to the lowest values of the pairwise minimal depth interactions between the response and the explanatory variables. Minimal depth assumes that variables with high impact on the prediction are those that most frequently split nodes nearest to the trees' roots (value at the root is 0). The positive or negative relationship between each response variable and explanatory variables was evaluated using the sign of the coefficient of a logistic regression. Abbreviations: Str-Structure Fun-Function, L Rent-Land Rent, H. Frag-Habitat Fragmentation, H Infl-Human Influence.

Regional factors driving the selection of conservation areas

Factors explaining the selection of regional conservation areas differed from the explanatory factors at the Neotropical level, although they did not differ significantly between regions and countries (Figure 13). The most important variable in the selection of conservation areas at the regional level was the proportion of moist forests. Areas with a high proportion of forest are inversely related to those with other natural habitats, particularly shrubs and savannas (Table S16). Therefore, prioritization is mostly guided by the proportion of remnant forests (positive relationship) or other natural habitats (negative relationship) at the ecoregion or country level. Other important variables were the human footprint, the level of aggregation of moist forests, the land rent of cattle, and the richness of birds and trophic guilds. Thus, at the regional level, the factors related to the three principles of systematic conservation planning also drove the selection of conservation areas.

In the Llanos Savannas, conservation areas were mostly located over riparian forests with lower levels of human intervention for Colombia, and over savannas for Venezuela. In the montane forest of Andean region, differences between countries are mainly driven by the proportion of remnant forests and human intervention. However, in Colombia, birds' richness of Andean montane forests was the most significant factor. Conversely, in the Páramo ecosystems, less significant differences were found, guided by mammals' richness and livestock activities in Colombia, which had a positive relationship with respect to the other three countries. On dry forests, also the differences were found in Colombia, with the most proportion of non-fragmented remnant forests, and mammals and reptiles' species.

Discussion

All the three principles of systematic conservation planning were found to be significant in the spatial prioritization of conservation areas in the Neotropical and its regional levels. This supports the importance of including different representations of biodiversity, and cost and persistence approaches in the selection of areas to build conservation networks (Margules & Sarkar 2007). We confirmed that comprehensiveness, adequacy, representativeness, and efficiency (CARE principles), are all necessary for an adequate spatial conservation prioritization (Linke *et al.* 2011).

Conservation area selection at the Neotropical level responds to the spatial conservation prioritization model following the minimum set cover problem (Moilanen *et al.* 2009), where biodiversity complementarity is prioritized while conservation costs and threats are reduced (Ferrier & Wintle 2009; Moilanen *et al.* 2009; Wilson *et al.* 2009). Our sensitivity results showed similar patterns to those found by Bode *et al.* (2008), low sensitivity to different representations of biodiversity since biodiversity priorities are mostly guided by composition attribute (species richness), but higher variations with the inclusion of costs, followed by persistence approaches. Furthermore, we show how spatial prioritization is mainly sensitive to the type of cost data (Richardson *et al.* 2006). Although different approaches for costs and persistence were included, the most critical variable driving conservation area selection was land rent, and particularly cattle land rent. This is in line with several studies that have shown that cattle is the most significant factor of landscape transformation in the Neotropics (e.g., Pacheco *et al.* 2011; Graesser *et al.* 2015). Particularly, the correlation between total land rent and the proportion of transformed area in the conservation areas selected also supported this relationship (Table S16).

Regional conservation priorities are driven by different biodiversity representations; however, for the Neotropical region as a whole, species composition is the best surrogate for representing biodiversity (Burbano-Girón *et al.* 2019a). Furthermore, species richness is highly related to other biodiversity attributes such as the proportion of forest ecosystems, richness of trophic guilds, and large and terrestrial-freshwater species richness (Table S16). Therefore, total species richness (representing species composition) is the second critical factor guiding the spatial selection of conservation areas in our models. Species richness is also a proxy for complementarity; where more species occur, more probability of achieving multiple targets in the same area exists (Wilson *et al.* 2009). Consequently, spatial conservation prioritization drives conservation area selection to those locations where representative and effective areas maintain high priorities regardless of changes in costs data, mostly depending on its importance for meeting conservation targets (Carwardine *et al.* 2010).

However, irreplaceable areas that are explained by endemism instead of species richness were also identified on critical biodiversity hotspots like the Andes, Atlantic Forest, Cerrado, Pantanal and Caatinga regions (Olson & Dinerstein 1998; Myers *et al.* 2000; Mittermeier *et al.* 2005). Although they are not related with any of the most important explanatory variables due to their small area, they are critical for conservation planning, These areas have the highest conservation priority because of their irreplaceability and vulnerability to threats (Brooks *et al.* 2006; Burbano-Girón *et al.* 2019a, b).

The largest areas of intact forest landscapes in the Neotropics occur in the Amazon and Choco-Darién regions (Potapov *et al.* 2008), where there is already a high proportion of conservation areas in diverse protection categories (Jenkins & Joppa 2009). Conversely, in the northern Andes, where the selection of conservation areas was analyzed over ecoregions, fragmentation levels are critically high as shown by several studies (Armenteras *et al.* 2011; Rodríguez Eraso *et al.* 2013a, b; Curatola Fernández *et al.* 2015; Clerici *et al.* 2019). This means, that the existence of fragmented natural land covers must guide conservation priorities over these regions since biodiversity declines and threats are most likely to occur when habitat availability is reduced to critical thresholds (Newbold *et al.* 2016; Betts *et al.* 2017; Roque *et al.* 2018). Moreover, biodiversity is better protected by minimizing human presence over intact and unfragmented landscapes (Ferreira *et al.* 2016; Betts *et al.* 2017);

therefore, the relationship between the proportion of natural habitats and the human footprint is critical for achieving successful conservation (Baldi *et al.* 2017, 2019), as is also supported by our results.

The meeting of conservation targets on mega-diverse countries must be a priority for effective global biodiversity conservation, (Bacon *et al.* 2019); however, most mega-diverse countries use different guidelines to select conservation areas. We suggest that in these countries it is possible to identify the most critical factors to define conservation priorities at the local level through the analysis of variables guiding the selection of conservation areas. For instance, our results show that conservation priorities for the Colombian Andes highlands should be defined based on their birds' species richness. Colombia is the country with the highest number of bird species and the Colombian Andes is an important center of endemism for this group (Cracraft & Prum 1988; Ocampo-Peñuela & Pimm 2014). Another example is the dry forest, one of the most threatened ecosystems globally. In this biome, besides the conservation of remnant forests, the priorities given by our models are the reduction of human footprint and livestock activities, which constitute the major threats for these ecosystems (Portillo-Quintero & Sánchez-Azofeifa 2010; Etter *et al.* 2018).

Conclusions

Regarding the Neotropical level, species richness and land rent were the most important factors guiding conservation priorities in our models. These results support that current Neotropical conservation needs respond to spatial conservation prioritization models that take into account biodiversity complementarity and the reduction of conservation costs and threats. Conversely, factors explaining the selection of regional conservation areas differed from those at the Neotropical level. Variables guiding the selection of conservation areas on Andean regions were the proportion of natural habitats and the human footprint. In these regions, fragmentation and human pressures are critical since biodiversity decline is most probable to occur when remnant habitat is reduced to critical thresholds, and biodiversity protection is more efficient by minimizing human presence over intact and unfragmented landscapes. Therefore, the relationship between conserve the proportion of natural cover and manage the human expansion at this regions should be critical for achieving conservation targets.

Differences at the country-level were driven by most biodiverse countries; consequently, more effective actions on biodiversity conservation should be focused on meeting conservation targets in mega-diverse countries. In these countries, it is possible to identify the most critical factors to define conservation priorities at finer scales through the analysis of variables guiding the selection of conservation areas. For instance, our results support that conservation priorities for moist montane forests of the Colombian Andes should be defined based on bird richness and the management of human expansion, while in dry forests should the focused on conserving remnant forests and reducing human pressures and livestock activities.

Variables accounting for representation, cost-efficiency, and persistence were found to be significant, both at the Neotropical and at the regional level, i.e., that the selection of conservation areas; and hence, conservation planning, is highly conditioned by the inclusion of different representations of biodiversity, cost and persistence approaches. Therefore, our results supported that a proper spatial conservation prioritization, and conservation planning strategies, should define priorities and actions accounting the three principles of systematic conservation planning, i.e., consider not only biodiversity objects, but also the management of economic activities and threats.

Supplementary Data

Table S13. Habitats categories proposed, IUCN habitats categories (version 3.1 from 2012), and standardization of IUCN habitats with the land cover map. Most habitats not included from the IUCN categories do not represent tropical habitats or correspond to the marine biome. Other classes were not included as they do not find correspondence with the land cover classes.

Habitat Category Proposed	IUCN's Habitat Category	Land Cover Map Class
Subtropical/Tropical Moist Forests	Forest - SubtropicalTropical Moist Lowland Forest - SubtropicalTropical Moist Montane	Tree cover, broadleaved, evergreen, closed to open (>15%)
Subtropical/Tropical Dry Forests	Forest - SubtropicalTropical Dry	Tree cover, broadleaved, deciduous, closed to open (>15%) Tree cover, broadleaved, deciduous, closed (>40%) Tree cover, broadleaved, deciduous, open (15-40%)
Pine-Oak Forests	Forest - Temperate	Tree cover, needleleaved, evergreen, closed to open (>15%) Tree cover, needleleaved, deciduous, closed to open (>15%) Tree cover, needleleaved, deciduous, closed to open (>15%)
Subtropical/Tropical Mangrove Forests	Forest - SubtropicalTropical Mangrove Vegetation Above High Tide Level	Tree cover, flooded, saline water
Subtropical/Tropical Swamp Forests	Forest - SubtropicalTropical Swamp	Tree cover, flooded, fresh or brackish water
Savannas and Grasslands	Savanna - Dry Savanna - Moist Grassland - Temperate Grassland - SubtropicalTropical Dry Grassland - SubtropicalTropical High Altitude	Grassland
Shrublands	Shrubland - Temperate Shrubland - SubtropicalTropical Dry Shrubland - SubtropicalTropical Moist Shrubland - SubtropicalTropical High Altitude	Shrubland
Flooded Savannas and Grasslands	Grassland - SubtropicalTropical Seasonally WetFlooded Wetlands (inland) - Shrub Dominated Wetlands Wetlands (inland) - Bogs, Marshes, Swamps, Fens, Peatlands	Shrub or herbaceous cover, flooded, fresh/saline/brackish water
Water bodies	Wetlands (inland) - Permanent RiversStreamsCreeks (includes waterfalls) Wetlands (inland) - SeasonalIntermittentIrregular RiversStreamsCreeks Wetlands (inland) - Permanent Freshwater Lakes (over 8ha) Wetlands (inland) - SeasonalIntermittent Freshwater Lakes (over 8ha) Wetlands (inland) - Permanent Freshwater MarshesPools (under 8ha) Wetlands (inland) - SeasonalIntermittent Freshwater MarshesPools (under 8ha) Wetlands (inland) - Freshwater Springs and Oases Wetlands (inland) - Alpine Wetlands (includes temporary waters from snowmelt)	Water bodies

Habitat Category Proposed	IUCN's Habitat Category	Land Cover Map Class
	Wetlands (inland) - Geothermal Wetlands Wetlands (inland) - Permanent Inland Deltas Wetlands (inland) - Permanent Saline, Brackish or Alkaline Lakes Wetlands (inland) - SeasonalIntermittent Saline, Brackish or Alkaline Lakes and Flats Wetlands (inland) - Permanent Saline, Brackish or Alkaline MarshesPools Wetlands (inland) - SeasonalIntermittent Saline, Brackish or Alkaline MarshesPool ArtificialAquatic - Water Storage Areas (over 8ha) ArtificialAquatic - Ponds (below 8ha) ArtificialAquatic - Aquaculture Ponds ArtificialAquatic - Salt Exploitation Sites ArtificialAquatic - Excavations (open) ArtificialAquatic - Wastewater Treatment Areas ArtificialAquatic - Irrigated Land (includes irrigation channels) ArtificialAquatic - Seasonally Flooded Agricultural Land ArtificialAquatic - Canals and Drainage Channels, Ditches	
Rocky and Desert Areas	Rocky areas (e.g., inland cliffs, mountain peaks) Desert - Hot Desert - Temperate Desert - Cold	Sparse vegetation (tree, shrub, herbaceous cover) (<15%) Sparse herbaceous cover (<15%) Bare areas
Croplands	ArtificialTerrestrial - Arable Land ArtificialTerrestrial - Plantations ArtificialTerrestrial - Rural Gardens	Cropland, rainfed Cropland, tree or shrub cover Cropland, irrigated or post-flooding Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)
Pasturelands	ArtificialTerrestrial - Pastureland	Herbaceous cover
Urban Areas	ArtificialTerrestrial - Urban Areas	Urban areas
Subtropical/Tropical Heavily Degraded Former Forests	ArtificialTerrestrial - SubtropicalTropical Heavily Degraded Former Forest	Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (<50%) Mosaic tree and shrub (>50%) / herbaceous cover (<50%) Mosaic herbaceous cover (>50%) / tree and shrub (<50%)

Table S14. Habitat classes proportion in the study area according to the standardization proposed between IUCN habitats and the land cover map from the ESA CCI Land Cover 2015 dataset v2.0.7 (http://maps.elie.ucl.ac.be/CCI/viewer/index.php) (Table S1).

Habitat	Area (km^2)	Area (%)	Natural / Transformed
Croplands	1 279 117.75	7.58	Transformed
Pasturelands	1 797 122.56	10.66	Transformed
Urban Areas	50 686.50	0.30	Transformed
Permanent snow and ice	5 364.24	0.03	Natural
Rocky and Desert Areas	668 602.16	3.96	Natural
Water bodies	247 380.94	1.47	Natural
Flooded Savannas and Grasslands	328 944.06	1.95	Natural
Savannas and Grasslands	529 717.38	3.14	Natural
Shrublands	2 180 402.65	12.93	Natural
Pine-Oak Forests	108 594.47	0.64	Natural
Subtropical/Tropical Dry Forests	995 961.39	5.91	Natural
Subtropical/Tropical Mangrove Forests	28 835.37	0.17	Natural
Subtropical/Tropical Moist Forests	7 312 350.30	43.36	Natural
Subtropical/Tropical Swamp Forests	193 034.09	1.14	Natural
Subtropical/Tropical Heavily Degraded Former Forests	1 139 672.82	6.76	Degraded
Total	16 865 786.69	100	

Table S15. The 30 most profitable agricultural and livestock activities in 2013 for Central and South America according to FAO statistics (http://www.fao.org/faostat/en/#data). The yield for livestock has no take into account the animal unit factor.

Crop – Livestock	Net Production Value ($1000 constant 2004-2006 International USD)	Area (ha) / Heads	Production (ton)	Yield (ton/ha / ton/head)
Meat, cattle	49 115 644	79 034 579	17 941 676	0.227
Soybeans	39 049 109	55 911 493	156 746 250	2.803
Meat, chicken	32 760 241	11 149 473 000	23 235 494	0.002
Sugar cane	31 940 829	13 193 920	952 687 705	72.207
Milk, whole fresh cow	26 151 445	43 561 980	79 468 686	1.824
Maize	10 537 569	32 786 472	153 325 820	4.676
Meat, pig	10 501 979	82 685 903	6 752 549	0.082
Rice, paddy	7 000 228	5 043 743	26 591 581	5.272
Bananas	6 891 136	1 032 499	25 721 069	24.911
Eggs, hen, in shell	6 318 531	727 960 000	7 869 775	0.011
Coffee, green	5 318 109	4 972 699	4 794 289	0.964
Oranges	5 052 048	1 277 827	25 304 631	19.803
Grapes	4 955 652	572 313	7 579 221	13.243
Tomatoes	3 919 148	248 903	11 301 831	45.407
Wheat	3 405 404	8 630 446	23 134 025	2.681
Beans, dry	3 140 186	6 398 533	6 084 310	0.951
Mangoes, mangosteens, guavas	2 719 351	388 818	4 161 947	10.704
Potatoes	2 696 085	1 003 668	17 421 116	17.357
Pineapples	2 391 950	223 404	8 809 549	39.433
Seed cotton	2 301 837	2 048 887	6 448 648	3.147
Apples	2 252 598	191 934	5 161 266	26.891
Lemons and limes	2 162 841	314 309	5 593 277	17.795
Avocados	1 862 477	295 161	2 787 188	9.443
Cassava	1 755 981	2 202 901	31 165 906	14.148
Tobacco, unmanufactured	1 731 361	537 913	1 105 353	2.055
Cashewapple	1 703 320	612 431	1 743 025	2.846
Plantains	1 371 964	818 593	7 981 030	9.750
Chillies and peppers, green	1 354 695	179 789	3 213 950	17.876
Oil, palm fruit	1 305 665	1 138 633	16 953 904	14.890

Table S16. Variables constructed to explain the selection of conservation areas related to each of the biodiversity attributes, and the costs and persistence approaches (at rows). All the variables were produced originally at 1km² resolution but were resampled to 10km² to match each planning unit. Also, correlation between explanatory variables (at rows) employed in the random forest analysis, and resultant most important variables (at columns). Most correlated variables are presented in bold. Abbreviations: Sruct. Ecosyst.-Structure Ecosystems, Fun. Ecolog. G-Fucntion Ecological Groups, Total Rich-Total Richness, Amp Rich-Amphibinas Richness, Birds Rich-Birds Richness, Mam Rich-Mammals Richness, Rep Rich-Reptiles Richness, Forest Prop-Forest Proportion, Guilds Rich-Guilds Richness, Total Lr-Total Land Rent, Cattle Lr-Cattle Land Rent, Agg-Mean Aggregation, Moist For Agg-Moist Forest Aggregation, Hfpf-Human Footprint, Pop Hfp-Population Density, Land. trans.-Landscape transformation, L. Rent-Land Rent

		Systematic conservation planning principle	Representation							Costs		Persistence			
		Approach	Composition Species					Struct. Ecosyst.	Fun. Ecolog. G	Land Rent		Habitat Fragmentation		Human Influence	
		Variable	Total Rich	Amp Rich	Birds Rich	Mam Rich	Rep Rich	Forest Prop	Guilds Rich	Total	Cattle	Agg	Moist For. Agg	HFP	Pop HFP
REPRESENTATION	Composition-species		-0.03	-0.08	-0.03	0.00	-0.04	0.01	-0.05	0.01	0.03	0.00	0.02	0.09	0.12
		Richness of range restricted birds	-0.03	-0.04	-0.02	-0.02	-0.04	-0.01	-0.03	0.02	0.03	-0.01	0.00	0.05	0.06
		Richness of range restricted mammals	-0.02	-0.04	-0.02	-0.01	-0.03	-0.01	-0.03	0.01	0.02	-0.01	0.00	0.05	0.06
		Richness of range restricted reptiles	-0.03	-0.05	-0.02	-0.01	-0.04	-0.01	-0.04	0.01	0.02	-0.01	0.00	0.06	0.08
		Richness of range restricted species	-0.03	-0.07	-0.03	-0.01	-0.05	0.00	-0.05	0.01	0.03	0.00	0.01	0.08	0.11
		Richness of amphibians	**0.86**	**1.00**	**0.83**	**0.73**	**0.69**	**0.59**	**0.73**	**-0.33**	**-0.47**	**0.47**	**0.63**	**-0.59**	**-0.61**
		Richness of birds	**0.99**	**0.83**	**1.00**	**0.93**	**0.66**	**0.73**	**0.80**	**-0.37**	**-0.50**	**0.58**	**0.78**	**-0.62**	**-0.61**
		Richness of mammals	**0.95**	**0.73**	**0.93**	**1.00**	**0.68**	**0.78**	**0.73**	**-0.37**	**-0.46**	**0.60**	**0.79**	**-0.55**	**-0.52**
		Richness of reptiles	**0.71**	**0.69**	**0.66**	**0.68**	**1.00**	**0.59**	**0.52**	**-0.29**	**-0.28**	**0.46**	**0.49**	**-0.44**	**-0.42**
		Total richness of species	**1.00**	**0.86**	**0.99**	**0.95**	**0.71**	**0.75**	**0.80**	**-0.38**	**-0.50**	**0.59**	**0.79**	**-0.62**	**-0.61**
	Structure-Ecosystems	Proportion of degraded forests	-0.38	-0.34	-0.36	-0.39	-0.31	-0.49	-0.34	0.30	0.27	-0.51	-0.30	0.36	0.34
		Proportion of forests	**0.75**	**0.59**	**0.73**	**0.78**	**0.59**	**1.00**	**0.66**	**-0.45**	**-0.47**	**0.66**	**0.81**	**-0.56**	**-0.46**
		Proportion of rocky areas	-0.13	-0.10	-0.14	-0.12	-0.09	-0.15	-0.20	0.01	-0.01	0.00	-0.14	0.05	0.07
		Proportion of savannas	-0.31	-0.23	-0.29	-0.33	-0.26	-0.52	-0.14	0.04	0.07	-0.13	-0.38	0.08	0.01
		Proportion of shrubs	-0.42	-0.35	-0.40	-0.43	-0.35	-0.54	-0.43	0.08	0.16	-0.21	-0.49	0.22	0.19
		Proportion of water bodies	-0.13	0.00	-0.13	-0.19	-0.10	-0.17	-0.07	-0.01	-0.02	-0.09	-0.12	0.01	0.01
		Ecosystems richness	-0.34	-0.31	-0.33	-0.33	-0.27	-0.36	-0.32	0.23	0.22	-0.37	-0.24	0.30	0.30
	Function-Ecological Groups	Richness of Carnivorous Spp.	0.07	0.16	0.08	-0.03	-0.03	-0.16	0.22	0.05	0.01	-0.06	0.01	0.00	-0.03
		Richness of carnivorous-insectivorous spp.	**0.63**	**0.62**	**0.62**	**0.58**	**0.56**	**0.67**	**0.69**	**-0.41**	**-0.45**	**0.48**	**0.58**	**-0.56**	**-0.51**
		Richness of folivorous spp.	**0.70**	**0.59**	**0.69**	**0.68**	**0.42**	**0.66**	**0.81**	**-0.27**	**-0.35**	**0.47**	**0.68**	**-0.45**	**-0.42**
		Richness of frugivorous spp.	**0.77**	**0.67**	**0.78**	**0.71**	**0.47**	**0.72**	**0.88**	**-0.35**	**-0.50**	**0.53**	**0.73**	**-0.61**	**-0.61**
		Richness of frugivorous-granivorous spp.	**0.71**	**0.62**	**0.71**	**0.68**	**0.47**	**0.65**	**0.83**	**-0.37**	**-0.47**	**0.52**	**0.69**	**-0.58**	**-0.59**
		Richness of frugivorous-insectivorous spp.	0.55	0.43	0.56	0.53	0.30	0.49	0.69	-0.25	-0.37	0.43	0.52	-0.46	-0.47
		Richness of granivorous spp.	**0.71**	**0.65**	**0.71**	**0.65**	**0.45**	**0.51**	**0.88**	**-0.29**	**-0.43**	**0.46**	**0.64**	**-0.57**	**-0.61**
		Richness of freshwater spp.	0.51	0.61	0.49	0.42	0.48	0.42	0.56	-0.25	-0.34	0.32	0.42	-0.45	-0.46
		Richness of freshwater-marine spp.	-0.08	-0.03	-0.08	-0.10	-0.07	-0.10	-0.07	0.02	0.03	-0.06	-0.08	0.05	0.05
		Richness of hematophagous spp.	0.53	0.43	0.52	0.55	0.33	0.45	0.64	-0.15	-0.27	0.33	0.53	-0.29	-0.31
		Richness of herbivorous spp.	0.57	0.49	0.57	0.53	0.40	0.46	0.79	-0.26	-0.37	0.40	0.51	-0.49	-0.52
		Richness of insectivorous spp.	0.53	0.57	0.54	0.45	0.29	0.27	0.75	-0.15	-0.35	0.28	0.45	-0.45	-0.52
		Richness of nectarivorous spp.	0.20	0.15	0.21	0.20	0.11	0.21	0.28	-0.06	-0.14	0.18	0.22	-0.18	-0.16
		Richness of omnivorous spp.	0.52	0.52	0.50	0.47	0.51	0.52	0.71	-0.36	-0.35	0.42	0.41	-0.48	-0.46

		Systematic conservation planning principle	Representation							Costs		Persistence			
		Approach	Composition Species					Struct. Ecosyst.	Fun. Ecolog. G	Land Rent		Habitat Fragmentation		Human Influence	
		Variable	Total Rich	Amp Rich	Birds Rich	Mam Rich	Rep Rich	Forest Prop	Guilds Rich	Total	Cattle	Agg	Moist For. Agg	HFP	Pop HFP
		Total richness of trophic guilds	**0.80**	**0.73**	**0.80**	**0.73**	**0.52**	**0.66**	**1.00**	**-0.35**	**-0.49**	**0.54**	**0.73**	**-0.63**	**-0.65**
		Richness of large spp.	**0.79**	**0.74**	**0.79**	**0.73**	**0.55**	**0.71**	**0.95**	**-0.41**	**-0.55**	**0.57**	**0.73**	**-0.68**	**-0.68**
		Richness of medium spp.	0.57	0.50	0.56	0.54	0.42	0.61	0.63	-0.17	-0.26	0.34	0.57	-0.37	-0.33
		Richness of medium-large spp.	0.58	0.54	0.59	0.50	0.33	0.40	0.77	-0.19	-0.31	0.33	0.54	-0.41	-0.41
		Richness of small spp.	0.55	0.48	0.54	0.53	0.41	0.42	0.75	-0.20	-0.28	0.35	0.51	-0.35	-0.39
		Richness of small-medium spp.	0.66	0.59	0.67	0.61	0.36	0.47	0.88	-0.24	-0.38	0.43	0.57	-0.51	-0.54
		Richness of spp. sizes	**0.80**	**0.73**	**0.80**	**0.73**	**0.52**	**0.66**	**1.00**	**-0.35**	**-0.49**	**0.54**	**0.73**	**-0.63**	**-0.65**
		Richness of terrestrial spp.	0.72	0.58	0.72	0.70	0.45	0.66	0.90	-0.31	-0.42	0.51	0.70	-0.53	-0.52
		Richness of terrestrial-freshwater spp.	**0.77**	**0.75**	**0.77**	**0.68**	**0.53**	**0.61**	**0.94**	**-0.34**	**-0.49**	**0.49**	**0.68**	**-0.63**	**-0.64**
		Richness of terrestrial-freshwater-marine spp.	0.53	0.54	0.53	0.46	0.32	0.36	0.72	-0.27	-0.38	0.39	0.46	-0.49	-0.52
		Richness of terrestrial-marine spp.	-0.42	-0.31	-0.41	-0.44	-0.33	-0.59	-0.35	0.23	0.26	-0.37	-0.48	0.30	0.23
		Total richness of habits	**0.80**	**0.73**	**0.80**	**0.73**	**0.52**	**0.66**	**1.00**	**-0.35**	**-0.49**	**0.54**	**0.73**	**-0.63**	**-0.65**
COSTS	L. Rent	Mean land rent of cattle	**-0.50**	**-0.47**	**-0.50**	**-0.46**	**-0.28**	**-0.47**	**-0.49**	**0.63**	**1.00**	**-0.51**	**-0.46**	**0.60**	**0.57**
		Mean land rent of crops	-0.25	-0.21	-0.24	-0.26	-0.23	-0.36	-0.22	0.95	0.36	-0.45	-0.23	0.36	0.29
		Total land rent	**-0.38**	**-0.33**	**-0.37**	**-0.37**	**-0.29**	**-0.45**	**-0.35**	**1.00**	**0.63**	**-0.54**	**-0.35**	**0.50**	**0.43**
	Land. trans.	Proportion of crops	-0.30	-0.25	-0.29	-0.31	-0.29	-0.42	-0.27	0.87	0.41	-0.53	-0.28	0.41	0.33
		Proportion of pastures	-0.24	-0.18	-0.25	-0.23	-0.14	-0.28	-0.23	0.12	0.32	-0.35	-0.26	0.31	0.27
		Proportion of urban areas	-0.04	-0.03	-0.04	-0.03	-0.03	-0.04	-0.05	0.01	0.01	-0.05	-0.03	0.17	0.09
		Proportion of transformed land cover	**-0.48**	**-0.38**	**-0.48**	**-0.47**	**-0.34**	**-0.58**	**-0.46**	**0.66**	**0.58**	**-0.68**	**-0.49**	**0.62**	**0.52**
PERSISTENCE	Habitat Fragmentation	Aggregation index of degraded forests	-0.32	-0.29	-0.30	-0.32	-0.27	-0.40	-0.28	0.24	0.21	-0.37	-0.25	0.29	0.27
		Aggregation index of dry forests	-0.34	-0.30	-0.36	-0.29	0.04	-0.13	-0.39	0.08	0.29	-0.12	-0.41	0.24	0.26
		Aggregation index of flooded savannas	-0.13	-0.06	-0.12	-0.16	-0.12	-0.20	-0.03	-0.02	-0.02	-0.07	-0.12	-0.04	-0.06
		Aggregation index of mangroves	-0.08	-0.07	-0.08	-0.08	-0.06	-0.04	-0.06	0.04	0.04	-0.03	-0.04	0.07	0.09
		Aggregation index of moist forests	**0.79**	**0.63**	**0.78**	**0.79**	**0.49**	**0.81**	**0.73**	**-0.35**	**-0.46**	**0.59**	**1.00**	**-0.53**	**-0.48**
		Aggregation index of pine-oak forests	-0.26	-0.23	-0.27	-0.23	-0.07	-0.05	-0.32	0.01	0.12	-0.05	-0.29	0.18	0.26
		Aggregation index of degraded forests	-0.15	-0.12	-0.16	-0.14	-0.10	-0.18	-0.20	0.02	0.00	0.00	-0.16	0.08	0.09
		Aggregation index of savannas	-0.31	-0.26	-0.30	-0.32	-0.27	-0.50	-0.19	0.08	0.10	-0.13	-0.37	0.14	0.08
		Aggregation index of shrublands	-0.46	-0.40	-0.44	-0.45	-0.37	-0.53	-0.48	0.12	0.20	-0.23	-0.49	0.29	0.27
		Aggregation index of glaciers	-0.03	-0.03	-0.03	-0.03	-0.03	-0.03	-0.04	0.00	0.00	0.00	-0.01	0.01	0.02
		Aggregation index of swamp forests	-0.03	0.03	-0.02	-0.08	-0.11	0.08	0.03	-0.09	-0.12	-0.02	-0.05	-0.11	-0.11
		Aggregation index of water bodies	-0.11	-0.01	-0.11	-0.16	-0.08	-0.14	-0.07	0.01	0.00	-0.06	-0.11	0.03	0.02
		Mean aggregation index of natural covers	**0.59**	**0.47**	**0.58**	**0.60**	**0.46**	**0.66**	**0.54**	**-0.54**	**-0.51**	**1.00**	**0.59**	**-0.57**	**-0.50**
	Human Influence	Builts	-0.16	-0.14	-0.17	-0.15	-0.11	-0.18	-0.17	0.17	0.17	-0.20	-0.15	0.57	0.32
		Night-time lights	-0.25	-0.22	-0.26	-0.23	-0.16	-0.27	-0.25	0.27	0.27	-0.30	-0.24	0.69	0.45
		Population density	-0.04	0.02	-0.03	-0.07	-0.09	-0.07	-0.03	0.04	-0.01	-0.11	-0.04	0.09	0.01
		Pressure of navigable waterways	**-0.61**	**-0.61**	**-0.61**	**-0.52**	**-0.42**	**-0.46**	**-0.65**	**0.43**	**0.57**	**-0.50**	**-0.48**	**0.88**	**1.00**
		Railways	-0.17	-0.14	-0.17	-0.15	-0.09	-0.17	-0.17	0.19	0.22	-0.20	-0.16	0.38	0.26
		Roads	**-0.52**	**-0.48**	**-0.52**	**-0.47**	**-0.32**	**-0.49**	**-0.52**	**0.39**	**0.49**	**-0.44**	**-0.48**	**0.75**	**0.59**
		The human footprint	**-0.62**	**-0.59**	**-0.62**	**-0.55**	**-0.44**	**-0.56**	**-0.63**	**0.50**	**0.60**	**-0.57**	**-0.53**	**1.00**	**0.88**

Overall Conclusions and Outlook

General Conclusions

The overall objective of this thesis was to investigate the uncertainty in conservation areas selection due to variability produced by applying different approaches framed in the three principles of systematic conservation planning: (1) representation, (2) persistence, and (3) cost-efficiency (Margules & Sarkar 2007). Addressing this goal, I highlight three main contributions from my work. First, it shows that there is no single approach or a combination of them, which cover the whole variability in spatial information on biodiversity, costs, and threats to conservation. Thus, my results throughout Chapters 1 and 2 support how regional differences in conservation areas selected influence conservation planning differently, consequently leading to identify distinct priorities and conservation actions related. More significant regional variability in conservation areas selection indicates more different strategies that should be applied to conservation planning. According to Chapter 3, the strategies proposed should include factors accounting the three principles of systematic conservation planning. Therefore, biodiversity conservation objects have to be regionally identified, and management actions for economic activities and biodiversity threats must be considered.

Second, despite variability in conservation areas selection, priority areas where coincidences over multiple approaches occur can be identified. In these areas, biodiversity conservation overcomes costs and threats, and consequently, the uncertainty in defining priority areas is reduced (Chapters 1 and 2). The identification of these areas in the Neotropics is a significant contribution to conservation planning for this region. I found that current PAs do not meet the Aichi 11 target for conserving 17% of biodiversity; therefore, it is necessary to expand the PAs system to new priority areas. Additionally, I found that these areas are, on average, 60% more efficient than current PAs, since they involve a smaller area (Chapters 1). Through my analysis, I identify the most suitable places where conservation priorities need to be defined, proposing conservation actions at the landscape-scale based on the land-sharing/sparing framework (Chapter 2). From these areas, I also identified locations of high irreplaceability, which are coincident with known critical and threatened global biodiversity hotspots. These areas are mostly located in the Chaco, the Atlantic forest, the Pantanal, Cerrado, and Caatinga regions in Brazil, and the moist and dry forests of northern Andes (Chapter 1).

Third, this work shows how uncertainty in the definition of conservation priorities and actions can be reduced by recognizing those factors related to conservation areas selection (Chapter 3). Applying a sensitivity analysis through multiple approaches using the principles of systematic conservation planning (Chapters 1 and 2), I found variables that significantly may drive conservation actions. In Chapter 3, for instance, I showed how in the northern Andes, a critical biodiversity hotspot, the factors explaining conservation areas selection found may be applied to support conservation strategies, e.g., use local conservation objects such as birds and remnant forest patches for conservation programs, and find management actions to reduce the impact of cattle ranching and the human expansion.

Main Specific Conclusions

Here I present the most relevant conclusions responding to my specific objectives proposed. To solve the first objective (Chapter 1), I performed a comprehensive work for spatial conservation prioritization including the three biodiversity attributes: composition, structure, and function. Based on the differences found in conservation areas selection, I proposed two critical issues that should be considered for defining biodiversity representations in conservation planning: (1) the number and type of biodiversity features employed, and (2) their spatial overlap. I found, that the higher the number of biodiversity features considered and the lower their level of overlap is, the larger the area required to meet conservation targets is. My results also supported the premise that no single surrogate represents biodiversity comprehensively; their regional differences explain the need for complementary surrogates and their effect in conservation areas representativeness. Particularly, I introduced a novel approach in conservation planning to represent the functional attribute of biodiversity through an ecological grouping approach. This approach has several advantages, it permits to combine compositional and structural biodiversity attributes since it employs species distributions over ecosystems, it is the most equally represented biodiversity attribute, it produces the most spatial mismatches concerning other biodiversity attributes accounting more variability for conservation strategies, and it represents a functional outlook for conservation planning of main ecological processes such as herbivory, pollination, seed dispersal, and plague control.

In objective 2 (Chapter 2), I defined the implications of employing different costs and persistence approaches in the selection of conservation areas, based on an analytical framework applying the land-sharing/sparing concept. Here, I compared coincidence and variability of conservation areas found using four criteria related to the costs and persistence approaches employed: (1) low probability to be affected by landscape transformation (prioritized areas under transformed areas costs approach), (2) low land rent (prioritized areas under land rent costs approach), (3) low habitat fragmentation (prioritized areas under aggregation level persistence approach), and (4) low human influence (prioritized areas under the human footprint approach). Coincident prioritized areas between approaches over natural habitats were proposed to be under strict protection, while degraded and transformed areas were proposed to be a focus of restoration processes. These areas were framed in the land-sparing model to prioritize land acquisition as a mechanism for conservation. Conversely, areas where the four components not coincided were framed in the land-sparing model, prioritizing conservation agreements to implement restoration or wildlife-friendly farming as conservation mechanisms.

In objective 3 (Chapter 3), I explained the selection of conservation areas through factors related to the three systematic conservation planning principles. Variables considering representation, cost-efficiency, and persistence were found significant, both for the entire Neotropics level, as well as for regional and country levels. Therefore, my results show that spatial conservation prioritization exercises and conservation planning strategies, should define priorities and actions accounting the three principles of systematic conservation planning, i.e., consider not only biodiversity objects, but also the management of economic activities and threats. The most significant factors found at the Neotropical level show how current conservation needs respond to the spatial conservation prioritization model, supporting biodiversity complementarity and reducing conservation costs and threats. However, factors explaining conservation areas selection in the Andes mainly follow the relationship between conserve the remnant natural habitats, and manage the livestock and the human expansion in the landscape. Also, I proposed that in general most biodiverse countries are critical for identifying the most important factors to define conservation priorities at finer scales, through the analysis of variables guiding the selection of conservation areas.

Limitations

While my work wishes to provide inputs for conservation planning, it should be clear that due to the scale of my analyses, it only permits the definition of conservation priorities and actions for the Neotropical region at a coarse level. However, this thesis gives clear some guidelines about how by using multiple approaches to spatial conservation prioritization, the uncertainty in conservation planning may be reduced. Furthermore, I show how priorities and actions related to local conservation needs can be defined at finer scales, by including multiple factors related to the three principles of systematic conservation planning.

Regarding the approaches employed to represent the principles of systematic conservation planning, I find the greatest limitations at the compositional approach in the representation principle, and the land rent approach in the cost-efficiency principle. Although potential distributions of species were delimited by species' habitats, which produced more accurate distributions (Phillips *et al.* 2006; Faleiro *et al.* 2013), range maps employed may produce omission and commission errors, incorporating a high source of uncertainty to conservation planning (Hurlbert & White 2005; Rondinini *et al.* 2006). Conversely, in the calculation of land rent for crops and livestock, the combination of different sources and scales of information, in addition to the impossibility of validating data, also imposes a high level of uncertainty.

The approaches applied to account persistence principle does not account for dynamic threats, since current prioritization tools are not designed to include it due to computational capacity and complexity of these optimization problems (Possingham *et al.* 2009). Currently, these tools are limited to include vulnerability or uncertainty indexes as penalties for allocation, or structural connectivity measures for defining the spatial arrangement of conservation areas (Moilanen 2007; Ball *et al.* 2009; Ciarleglio *et al.* 2009; Pressey *et al.* 2009). The lack of inclusion of dynamic threats to persistence may imply significant changes in the spatial distribution of conservation areas and conservation planning (Carroll *et al.* 2003; Faleiro *et al.* 2013), since conservation priorities and actions defined currently may be inefficient protecting biodiversity against combined effects of biodiversity threats (Mantyka-Pringle *et al.* 2012).

I did not consider any penalties in the configuration of spatial prioritization problems, and fixed biodiversity features targets were applied. Since these configurations remain constant in all the approaches employed, it allowed me to perform comparisons between the resultant conservation areas, evaluating the effect of the corresponding approach exclusively. However, I recognize that the use of some of the commonly employed penalties incorporated into the most common tools for resolving the minimum cover problem (e.g., Marxan and Prioritizr) (Ball *et al.* 2009; Moilanen *et al.* 2009), could have been relevant to address the persistence principle. For instance, to promote connectivity between conservation areas, the use of the boundary length modifier penalty (BLM) is recurrent (e.g., Carroll *et al.* 2003; Richardson *et al.* 2006; Beger *et al.* 2010), or also the modification of biodiversity features targets proportionally to their threat level (e.g., Pressey *et al.* 2003; Carvalho *et al.* 2010; McGowan *et al.* 2017).

The decision to include indigenous reserves as conservation figures within the PAs, was based on the high proportion of natural land cover within the limits of these areas (97%). Also, in the Neotropics, and particularly in the Amazon region, the presence and extensive proportion of indigenous communities from hundreds of years ago, in addition to its close relationship with the sustainable management of biodiversity supports my decision (Schwartzman & Zimmerman 2005). Moreover, on most of the indigenous reserves there is a positive relationship with biodiversity conservation (Nepstad *et al.* 2006; Armenteras *et al.* 2009). However, I recognize that it is not common to include this kind of areas in spatial conservation prioritization exercises since indigenous reserves are not considered a strict conservation category, and this may affect the comparability of my work.

Future Outlook

Spatial conservation prioritization is commonly applied in exercises at regional, national, or global levels, but its use at more detailed scales is not frequent. However, decision-making about, and implementation of conservation plans often occurs at the local scale. This calls for the importance to examine the differences found and the guiding factors in conservation areas selection at finer scales, in order to assess their actual influence on conservation priorities and actions. For instance, to replicate this analysis for decision-making at local scales, their integration on offsets designs could be evaluated, specifically on the location of actions intended at the protection, management or restoration of habitats (Pouzols *et al.* 2012). However, it should be recognized that the greatest limitation to this analysis at more detailed scales is the availability of spatial information on appropriate resolutions.

Along the three chapters, my analyses showed differences at the regional or country level, which were not evident in the entire Neotropics area. Accordingly, it is relevant to explore the differences in the effectiveness and representativeness of the selected conservation areas in different regionalization approaches. A significant replication of this analysis would be to evaluate differences in conservation areas selected to meet conservation targets by applying different regionalizations. Thus, the cost of conservation at different levels of coordination between countries could be assessed for achieving the Aichi 11 target (Bacon *et al.* 2019), and then analyze the efficiency of conservation areas concerning the fulfilling of conservation targets.

My results show that equality in the representativeness of biodiversity features was low. This means that some biodiversity features are overrepresented, while others are underrepresented in the conservation areas selected. In an ecological sense, the most threatened biodiversity features are expected to be those with greater representativeness for supporting their conservation (Pressey *et al.* 2003). However, if fixed targets are employed, a hypothesis that could be tested is that those biodiversity features most represented in conservation areas would be the most abundant and generalist (with less likelihood of threat). The principle of complementarity in the selection of conservation areas implicit in spatial prioritization algorithms support this premise (Moilanen *et al.* 2009), leading to compare and discuss the use of fixed vs. ecological relevant targets, in order to assess the level of representativeness according to the threat level of each biodiversity feature.

Throughout my work, I include seven metrics for evaluating conservation areas: the area (number of planning units), effectiveness (mean target achievement), representativeness (protection equality), aggregation level (aggregation index), and surrogacy level (kappa index, transposed mean target achievement, transposed protection equality). Two of these metrics were developed in this work, aimed at assessing the surrogacy. However, there are 13 or more core concepts proposed for spatial conservation prioritization (Kukkala & Moilanen 2013); from these, I identified some of them that do not have indicators to be evaluated, e.g., adequacy, comprehensiveness, complementarity, efficiency, and flexibility. An essential step towards reporting the level of protection of conservation areas would be the development of these and other indicators.

References

Adams, V.M., Pressey, R.L. & Naidoo, R. (2010). Opportunity costs: Who really pays for conservation? *Biol. Conserv.*, 143, 439–448.

Aide, T.M., Clark, M.L., Grau, H.R., Lopez-Carr, D., Levy, M. a, Redo, D., *et al.* (2012). Deforestation and Reforestation of Latin America and the Caribbean (2001 – 2010). *Biotropica*, 45, 262–271.

Airamé, S., Dugan, J.E., Lafferty, K.D., Leslie, H., McArdle, D.A. & Warner, R.R. (2003). Applying Ecological Criteria to Marine Reserve Design: A Case Study from the California Channel Islands. *Ecol. Appl.*, 13, S170–S184.

Alagador, D. & Cerdeira, J.O. (2007). Designing spatially-explicit reserve networks in the presence of mandatory sites. *Biol. Conserv.*, 137, 254–262.

Allan, J.R., Watson, J.E.M., Di Marco, M., O'Bryan, C.J., Possingham, H.P., Atkinson, S.C., *et al.* (2019). Hotspots of human impact on threatened terrestrial vertebrates. *PLoS Biol.*, 1–18.

Anderson, M.J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecol.*, 26, 32–46.

Anderson, M.J. (2017). Permutational Multivariate Analysis of Variance (PERMANOVA). *Wiley StatsRef Stat. Ref. Online*, Major Reference Works, 1–15.

Anderson, M.J., Gorley, R.N. & Clarke, K.. (2008). *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*. PRIMER-E, Plymouth, UK.

Anderson, M.J. & Robinson, J. (2003). Generalized discriminant analysis based on distances. *Aust. N. Z. J. Stat.*, 45, 301–318.

Ando, A.W., Camm, J., Polasky, S. & Solow, A. (1998). Species Distributions, Land Values, and Efficient Conservation. *Science (80-.).*, 279, 2126–2128.

Araujo, M.B. (2004). Matching species with reserves-uncertainries from using data at different resolutions. *Bilogical Conserv.*, 118, 533–538.

Araújo, M.B., Humphries, C.J., Densham, P.J., Lampinen, R., Hagemeijer, W.J.M., Mitchell-Jones, A.J., *et al.* (2001). Would environmental diversity be a good surrogate for species diversity? *Ecography (Cop.).*, 24, 103–110.

Araújo, M.B., Williams, P.H. & Turner, A. (2002). A sequential approach to minimise threats within selected conservation areas. *Biodivers. Conserv.*, 11, 1011–1024.

Armenteras, D., Rodríguez, N. & Retana, J. (2009). Are conservation strategies effective in avoiding the deforestation of the Colombian Guyana Shield? *Biol. Conserv.*, 142, 1411–1419.

Armenteras, D., Rodríguez, N., Retana, J. & Morales, M. (2011). Understanding deforestation in montane and lowland forests of the Colombian Andes. *Reg. Environ. Chang.*, 11, 693–705.

Armenteras, D., Schneider, L. & Dávalos, L.M. (2019). Fires in protected areas reveal unforeseen costs of Colombian peace. *Nat. Ecol. Evol.*, 3, 20–23.

Armstrong, A.J. & van Hensbergen, H.J. (1999). Identification of priority regions for animal conservation in afforestable montane grasslands of the northern Eastern Cape Province, South Africa. *Biol. Conserv.*, 87, 93–103.

Bacon, E., Gannon, P., Stephen, S., Seyoum-Edjigu, E., Schmidt, M., Lang, B., *et al.* (2019). Aichi Biodiversity Target 11 in the like-minded megadiverse countries. *J. Nat. Conserv.*, 51, 125723.

Baldi, G., Schauman, S., Texeira, M., Marinaro, S., Martin, O.A., Gandini, P., *et al.* (2019). Nature representation in South American protected areas: country contrasts and conservation priorities. *PeerJ*, 7, e7155.

Baldi, G., Texeira, M., Martin, O.A., Grau, H.R. & Jobbágy, E.G. (2017). Opportunities drive the global distribution of protected areas. *PeerJ*, 5, e2989.

Ball, I.R., Possingham, H.P. & Watts, M.E. (2009). Marxan and Relatives: Software for Spatial Conservation Prioritisation. In: *Spatial Conservation Prioritization – Quantitative Methods and Computational Tools* (eds. Moilanen, A., Wilson, K.A. & Possingham, H.P.). Oxford University Press, New York, pp. 185–195.

Balmford, A., Gaston, K.J., Blyth, S., James, A. & Kapos, V. (2003). Global variation in terrestrial conservation costs, conservation benefits, and unmet conservation needs. *Proc. Natl. Acad. Sci. U. S. A.*, 100, 1046–50.

Ban, N.C. & Klein, C.J. (2009). Spatial socioeconomic data as a cost in systematic marine conservation planning. *Conserv. Lett.*, 2, 206–215.

Ban, N.C., Picard, C.R. & Vincent, A.C.J. (2009). Comparing and Integrating Community-Based and Science-Based Approaches to Prioritizing Marine Areas for Protection. *Conserv. Biol.*, 23, 899–910.

Banks, S.A., Skilleter, G.A. & Possingham, H.P. (2005). Intertidal habitat conservation: identifying conservation targets in the absence of detailed biological information. *Aquat. Conserv. Mar. Freshw. Ecosyst.*, 15, 271–288.

Baptiste, B., Pinedo-Vasquez, M., Gutierrez-Velez, V.H., Andrade, G.I., Vieira, P., Estupiñán-Suárez, L.M., *et al.* (2017). Greening peace in Colombia. *Nat. Ecol. Evol.*, 1.

Barlow, J., Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Malcolm, J.R., *et al.* (2007). Quantifying the biodiversity value of tropical primary , secondary , and plantation forests. *Proc. Natl. Acad. Sci. U. S. A.*, 104, 18555–18560.

Barr, L.M., Pressey, R.L., Fuller, R.A., Segan, D.B., McDonald-Madden, E. & Possingham, H.P. (2011). A new way to measure the world's protected area coverage. *PLoS One*, 6.

Barua, M., Bhagwat, S.A. & Jadhav, S. (2013). The hidden dimensions of human-wildlife conflict: Health impacts, opportunity and transaction costs. *Biol. Conserv.*, 157, 309–316.

Baumann, M., Israel, C., Piquer-Rodríguez, M., Gavier-Pizarro, G., Volante, J.N. & Kuemmerle, T. (2017). Deforestation and cattle expansion in the Paraguayan Chaco 1987–2012. *Reg. Environ. Chang.*, 17, 1179–1191.

Beck, M.W. & Odaya, M. (2001). Ecoregional planning in marine environments: identifying priority sites for conservation in the northern Gulf of Mexico. *Aquat. Conserv. Mar. Freshw. Ecosyst.*, 11, 235–242.

Becker, C.G., Loyola, R.D., Haddad, C.F.B. & Zamudio, K.R. (2010). Integrating species life-history traits and patterns of deforestation in amphibian conservation planning. *Divers. Distrib.*, 16, 10–19.

Beger, M., Linke, S., Watts, M., Game, E., Treml, E., Ball, I., *et al.* (2010). Incorporating asymmetric connectivity into spatial decision making for conservation. *Conserv. Lett.*, 3, 359–368.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecol. Lett.*, 15, 365–377.

Bennett, A.F., Radford, J.Q. & Haslem, A. (2006). Properties of land mosaics: Implications for nature conservation in agricultural environments. *Biol. Conserv.*, 133, 250–264.

Betts, M.G., Wolf, C., Ripple, W.J., Phalan, B., Millers, K.A., Duarte, A., *et al.* (2017). Global forest loss disproportionately erodes biodiversity in intact landscapes. *Nature*, 547, 441–444.

Beyer, H.L., Dujardin, Y., Watts, M.E. & Possingham, H.P. (2016). Solving conservation planning problems with integer linear programming. *Ecol. Modell.*, 328, 14–22.

Blaum, N., Mosner, E., Schwager, M. & Jeltsch, F. (2011). How functional is functional? Ecological groupings in terrestrial animal ecology: Towards an animal functional type approach. *Biodivers. Conserv.*, 20, 2333–2345.

Bode, M., Wilson, K.A., Brooks, T.M., Turner, W.R., Mittermeier, R. a, McBride, M.F., *et al.* (2008). Cost-effective global conservation spending is robust to taxonomic group. *Proc. Natl. Acad. Sci. U. S. A.*, 105, 6498–6501.

Bonn, A. & Gaston, K.J. (2005). Capturing biodiversity: Selecting priority areas for conservation using different criteria. *Biodivers. Conserv.*, 14, 1083–1100.

Breiman, L. (2001). Random Forests. *Mach. Learn.*, 45, 5–32.

Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., *et al.* (2006). Global biodiversity conservation priorities. *Science (80-.).*, 313, 58–61.

Bryant, D., Nielsen, D. & Tangley, L. (1997). *THE LAST FRONTIER FORESTS. ECOSYSTEMS & ECONOMIES ON THE EDGE*. World Resources Institute, Washington, D.C.

Burbano-Girón, J., Jantke, K., Molina, M.A., Buriticá-Mejía, N., Urbina, N., Sánchez-Clavijo, L.M., *et al.* (2019a). An assessment of spatial conservation priorities for biodiversity attributes: composition, structure, and function of Neotropical biodiversity. In: *Doctoral Thesis. Improving the identification of priority areas for conserving Neotropical biodiversity: assessing uncertainties in spatial conservation prioritization*. Pontificia Universidad Javeriana, Bogota, Colombia.

Burbano-Girón, J., Jantke, K., Molina, M.A., Urbina-Cardona, N., Gómez-Valencia, B. & Etter, A. (2019b). Understanding the effect of including costs and persistence in spatial conservation prioritization: an analysis of the land-sharing/sparing framework in the Neotropics. In: *Doctoral Thesis. Improving the identification of priority areas for conserving Neotropical biodiversity: assessing uncertainties in spatial conservation prioritization*. Pontificia Universidad Javeriana, Bogota, Colombia.

Cabeza, M. (2003). Habitat loss and connectivity of reserve networks in probability approaches to reserve design. *Ecol. Lett.*, 6, 665–672.

Cabeza, M., Arponen, A., Jäättelä, L., Kujala, H., van Teeffelen, A. & Hanski, I. (2010). Conservation planning with insects at three different spatial scales. *Ecography (Cop.).*, 33, 54–63.

Cabeza, M. & Moilanen, A. (2003). Site-Selection Algorithms and Habitat Loss. *Conserv. Biol.*, 17, 1402–1413.

Caldas, M.M., Goodin, D., Sherwood, S., Campos Krauer, J.M. & Wisely, S.M. (2015). Land-cover change in the Paraguayan Chaco: 2000–2011. *J. Land Use Sci.*, 10, 1–18.

Cameron, S.E., Williams, K.J. & Mitchell, D.K. (2008). Efficiency and Concordance of Alternative Methods for Minimizing

Opportunity Costs in Conservation Planning. *Conserv. Biol.*, 22, 886–896.

Carroll, C., Dunk, J.R. & Moilanen, A. (2010). Optimizing resiliency of reserve networks to climate change: Multispecies conservation planning in the Pacific Northwest, USA. *Glob. Chang. Biol.*, 16, 891–904.

Carroll, C., Reed, F.N., Paquet, P.C. & Schumaker, N.H. (2003). Use of Population Viability Analysis and Reserve Selection Algorithms in Regional Conservation Plans. *Ecol. Appl.*, 13, 1773–1789.

Carvajal-Cogollo, J.E. & Urbina-Cardona, N. (2015). Ecological grouping and edge effects in tropical dry forest: reptile-microenvironment relationships. *Biodivers. Conserv.*, 24, 1109–1130.

Carvalho, S.B., Brito, J.C., Crespo, E.G., Watts, M.E. & Possingham, H.P. (2011). Conservation planning under climate change: Toward accounting for uncertainty in predicted species distributions to increase confidence in conservation investments in space and time. *Biol. Conserv.*, 144, 2020–2030.

Carvalho, S.B., Brito, J.C., Pressey, R.L., Crespo, E. & Possingham, H.P. (2010). Simulating the effects of using different types of species distribution data in reserve selection. *Biol. Conserv.*, 143, 426–438.

Carwardine, J., Klein, C.J., Wilson, K.A., Pressey, R.L. & Possingham, H.P. (2009). Hitting the target and missing the point: target-based conservation planning in context. *Conserv. Lett.*, 2, 4–11.

Carwardine, J., Wilson, K.A., Ceballos, G., Ehrlich, P.R., Naidoo, R., Iwamura, T., *et al.* (2008). Cost-effective priorities for global mammal conservation. *Proc. Natl. Acad. Sci. U. S. A.*, 105, 11446–11450.

Carwardine, J., Wilson, K.A., Hajkowicz, S. a., Smith, R.J., Klein, C.J., Watts, M., *et al.* (2010). Conservation planning when costs are uncertain. *Conserv. Biol.*, 24, 1529–1537.

Castiblanco, C., Etter, A. & Aide, T.M. (2013). Oil palm plantations in Colombia: a model of future expansion. *Environ. Sci. Policy*, 27, 172–183.

Castro-Nunez, A., Mertz, O., Buritica, A., Sosa, C.C. & Lee, S.T. (2017). Land related grievances shape tropical forest-cover in areas affected by armed-conflict. *Appl. Geogr.*, 85, 39–50.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M. & Palmer, T.M. (2015). Accelerated modern human – induced species losses : Entering the sixth mass extinction. *Sci. Adv.*, 1, 1–5.

Ceballos, G., Ehrlich, P.R. & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc. Natl. Acad. Sci.*, 114, E6089–E6096.

Chadid, M.A., Dávalos, L.M., Molina, J. & Armenteras, D. (2015). A Bayesian spatial model highlights distinct dynamics in deforestation from coca and pastures in an Andean biodiversity hotspot. *Forests*, 6, 3828–3846.

Chape, S., Harrison, J., Spalding, M. & Lysenko, I. (2005). Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. *Phil. Trans. R. Soc. B*, 360, 443–55.

Chauvenet, A.L.M., Kuempel, C.D., McGowan, J., Beger, M. & Possingham, H.P. (2017). Methods for calculating Protection Equality for conservation planning. *PLoS One*, 12, 1–17.

Chazdon, R.L., Harvey, C., Martínez-Ramos, M., Balvanera, P., Schondube, S., Ávila-Cabadilla, L.D., *et al.* (2011). Tropical dry forest biodiversity and conservation value in agricultural landscapes of Mesoameric. In: *Seasonally Dry Tropical Forests. Ecology and Conservation* (eds. Dirzo, R., Young, H.S., Mooney, H.A. & Ceballos, G.). Island Press, USA, pp. 195–219.

Chazdon, R.L., Harvey, C.A., Komar, O., Griffith, D.M., Ferguson, B.G., Martínez-Ramos, M., *et al.* (2009). Beyond Reserves: A Research Agenda for Conserving Biodiversity in Human-modified Tropical Landscapes. *Biotropica*, 41, 142–153.

Chomitz, K.M., Alger, K., Thomas, T.S., Orlando, H. & Nova, P. V. (2005). Opportunity costs of conservation in a biodiversity hotspot: the case of southern Bahia. *Environ. Dev. Econ.*, 10, 293–312.

Ciarleglio, M., Wesley Barnes, J. & Sarkar, S. (2009). ConsNet: New software for the selection of conservation area networks with spatial and multi-criteria analyses. *Ecography (Cop.).*, 32, 205–209.

Clarke, K.R., Somerfield, P.J. & Gorley, R.N. (2008). Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. *J. Exp. Mar. Bio. Ecol.*, 366, 56–69.

Clarke, R. & Gorley, R.N. (2019). PRIMER-e.

Clerici, N., Salazar, C., Pardo-Díaz, C., Jiggins, C.D., Richardson, J.E. & Linares, M. (2019). Peace in Colombia is a critical moment for Neotropical connectivity and conservation: Save the northern Andes–Amazon biodiversity bridge. *Conserv. Lett.*, 12, e12594.

Cohen, J. (1960). A Coefficient of Agreement for Nominal Scales. *Educ. Psychol. Meas.*, 20, 37–46.

Coppolillo, P., Gomez, H., Maisels, F. & Wallace, R. (2004). Selection criteria for suites of landscape species as a basis for site-based conservation. *Biol. Conserv.*, 115, 419–430.

Costello, C. & Polasky, S. (2004). Dynamic reserve site selection. *Resour. Energy Econ.*, 26, 157–174.

Cowling, R.M. & Heijnis, C.E. (2001). The identification of Broad Habitat Units as biodiversity entities for systematic conservation planning in the Cape Floristic Region. *South African J. Bot.*, 67, 15–38.

Cowling, R.M. & Pressey, R.L. (2001). Rapid plant diversification: planning for an evolutionary future. *Proc. Natl. Acad. Sci. U. S. A.*, 98, 5452–7.

Cracraft, J. & Prum, R.O. (1988). Patterns and processes of diversification: speciation and historical congruence in some Neotropical birds. *Evolution (N. Y).*, 42, 603–620.

Crosetto, M., Tarantola, S. & Saltelli, A. (2000). Sensitivity and uncertainty analysis in spatial modelling based on GIS. *Agric. Ecosyst. Environ.*, 81, 71–79.

Curatola Fernández, F.G., Obermeier, A.W., Gerique, A., López Sandoval, F.M., Lehnert, W.L., Thies, B., *et al.* (2015). Land Cover Change in the Andes of Southern Ecuador—Patterns and Drivers. *Remote Sens.*, 7, 2509–2542.

Dávalos, L. (2001). The San Lucas mountain range in Colombia: how much conservation is owed to the violence? *Biodivers. Conserv.*, 10, 69–78.

Deheza, E. & Ribet, U. (2012). Latin America's Mining Boom. *RUSI J.*, 157, 22–31.

Dent, D.H. & Joseph Wright, S. (2009). The future of tropical species in secondary forests: A quantitative review. *Biol. Conserv.*, 142, 2833–2843.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., *et al.* (2017). An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm. *Bioscience*, 67, 534–545.

Dobrovolski, R., Loyola, R., Da Fonseca, G.A.B., Diniz-Filho, J.A.F. & Araújo, M.B. (2014). Globalizing conservation efforts to save species and enhance food production. *Bioscience*, 64, 539–545.

Dobrovolski, R., Loyola, R.D., Guilhaumon, F., Gouveia, S.F. & Diniz-Filho, J.A.F. (2013). Global agricultural expansion and carnivore conservation biogeography. *Biol. Conserv.*, 165, 162–170.

Driscoll, D.A., Banks, S.C., Barton, P.S., Lindenmayer, D.B. & Smith, A.L. (2013). Conceptual domain of the matrix in fragmented landscapes. *Trends Ecol. Evol.*, 28, 605–613.

Dros, J.M. (2004). *Managing the soy boom: Two scenarios of soy production expansion in South America*. AIDEnvironment, Amsterdam.

Ehrlinger, J. (2015). ggRandomForests: Visually Exploring a Random Forest for Regression. *arXiv*, 1501.07196.

Ellis, E.C. (2011). Anthropogenic transformation of the terrestrial biosphere. *Philos. Trans. A. Math. Phys. Eng. Sci.*, 369, 1010–1035.

Ellis, E.C. (2013). Sustaining biodiversity and people in the world's anthropogenic biomes. *Curr. Opin. Environ. Sustain.*, 5, 368–372.

Ellis, E.C. & Ramankutty, N. (2008). Putting people in the map: anthropogenic biomes of the world. *Front. Ecol. Environ.*, 6, 439–447.

Emmanuel, D.P., Martina, F., Marthe, R. & Oscar, R. (2017). Forest cover loss in Paraguay and Ecosystem service approaches: an Upper Parana Forest study case. *Ecosyst. Serv.*, 24, 200–212.

Ernest, S.K.M. (2003). LIFE HISTORY CHARACTERISTICS OF PLACENTAL NONVOLANT MAMMALS. *Ecology*, 84, 3402–3402.

Espirito-Santo, M.M., Rankine, C., Sharp, I., Guzmán, J.A. & Sánchez-Azofeifa, G.A. (2017). Comparing MODIS and near-surface vegetation indexes for monitoring tropical dry forest phenology along a successional gradient using optical phenology towers. *Environ. Res. Lett.*, 12, 105007.

Esselman, P.C. & Allan, J.D. (2011). Application of species distribution models and conservation planning software to the design of a reserve network for the riverine fishes of northeastern Mesoamerica. *Freshw. Biol.*, 56, 71–88.

Etter, A., Andrade, A., Saavedra, K., Arevalo, P. & Amaya-Valderrama, P. (2018). *Risk assessment of Colombian continental ecosystems: An application of the Red List of Ecosystems methodology (v. 2.0).*

Etter, A., McAlpine, C.A., Phinn, S., Pullar, D. & Possingham, H.P. (2006a). Characterizing a tropical deforestation wave: a dynamic spatial analysis of a deforestation hotspot in the Colombian Amazon. *Glob. Chang. Biol.*, 12, 1409–1420.

Etter, A., McAlpine, C.A., Phinn, S., Pullar, D. & Possingham, H.P. (2006b). Unplanned land clearing of Colombian rainforests: Spreading like disease? *Landsc. Urban Plan.*, 77, 240–254.

Etter, A., McAlpine, C.A. & Possingham, H.P. (2008). Historical Patterns and Drivers of Landscape Change in Colombia Since 1500: A Regionalized Spatial Approach. *Ann. Assoc. Am. Geogr.*, 98, 2–23.

Etter, A., McAlpine, C.A., Seabrook, L. & Wilson, K.A. (2011). Incorporating temporality and biophysical vulnerability to quantify the human spatial footprint on ecosystems. *Biol. Conserv.*, 144, 1585–1594.

Etter, A., Sarmiento, A.H. & Romero, M.H. (2010). Land use changes (1970-2020) and the carbon emissions in the Colombian Llanos. In: *Ecosystem Function in Savannas Measurement and Modeling at Landscape to Global Scales* (eds. Hill, M.J. &

Hanan, N.P.). CRC Press, Boca Raton, Florida, USA, pp. 383–402.

Etter, A. & van Wyngaarden, W. (2000). Patterns of Landscape Transformation in Colombia, with Emphasis in the Andean Region. *AMBIO A J. Hum. Environ.*, 29, 432–439.

Fagua, J.C. & Ramsey, R.D. (2019). Geospatial modeling of land cover change in the Chocó-Darien global ecoregion of South America; One of most biodiverse and rainy areas in the world. *PLoS One*, 14, e0211324.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.*, 34, 487–515.

Faleiro, F. V., Machado, R.B. & Loyola, R.D. (2013). Defining spatial conservation priorities in the face of land-use and climate change. *Biol. Conserv.*, 158, 248–257.

Farley, K.A. (2007). Grasslands to tree plantations: Forest transition in the Andes of Ecuador. *Ann. Assoc. Am. Geogr.*, 97, 755–771.

Fearnside, P.M. (2001). Soybean cultivation as a threat to the environment in Brazil. *Environ. Conserv.*, 28, 23–38.

Feldman, A. & Meiri, S. (2013). Length – mass allometry in snakes (Appendix S1). *Biol. J. Linn. Soc.*, 108, 161–172.

Feldman, A., Sabath, N., Pyron, R.A., Mayrose, I. & Meiri, S. (2016). Body sizes and diversification rates of lizards, snakes, amphisbaenians and the tuatara. *Glob. Ecol. Biogeogr.*, 25, 187–197.

Ferraro, P.J. (2004). Targeting Conservation Investments in Heterogeneous Landscapes: A Distance-Function Approach and Application to Watershed Management. *Am. J. Agric. Econ.* , 86, 905–918.

Ferreira, J.N., Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., *et al.* (2016). Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature*, 535, 144.

Ferrier, S., Faith, D.P., Arponen, A. & Drielsma, M. (2009). Comunity-Level Approaches to Spatial Conservation Prioritization. In: *Spatial Conservation Prioritization – Quantitative Methods and Computational Tools* (eds. Moilanen, A., Wilson, K.A. & Possingham, H.P.). Oxford University Press, New York, pp. 110–121.

Ferrier, S. & Graham, W. (1997). *An evaluation of the effectiveness of environmental surrogates and modelling techniques in predicting the distribution of biological diversity.* Canberra, Australia.

Ferrier, S. & Wintle, B.A. (2009). Quantitative Approaches to Spatial Conservation Prioritization: Matching the Solution to the Need. In: *Spatial Conservation Prioritization – Quantitative Methods and Computational Tools* (eds. Moilanen, A., Wilson, K.A. & Possingham, H.P.). Oxford University Press, New York, pp. 1–15.

Ficetola, G.F., Rondinini, C., Bonardi, A., Katariya, V., Padoa-Schioppa, E. & Angulo, A. (2014). An evaluation of the robustness of global amphibian range maps. *J. Biogeogr.*, 41, 211–221.

Fischer, J., Brosi, B., Daily, G.C., Ehrlich, P.R., Goldman, R., Goldstein, J., *et al.* (2008). Should agricultural policies encourage land sparing or wildlife-friendly farming? *Front. Ecol. Environ.*, 6, 380–385.

Forest, F., Grenyer, R., Rouget, M., Davies, T.J., Cowling, R.M., Faith, D.P., *et al.* (2007). Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature*, 445, 757–760.

Françoso, R.D., Brandão, R., Nogueira, C.C., Salmona, Y.B., Machado, R.B. & Colli, G.R. (2015). Habitat loss and the effectiveness of protected areas in the Cerrado Biodiversity Hotspot. *Nat. e Conserv.*, 13, 35–40.

Franklin, J.F., Cromack, K.J., Denison, W., McKee, A., Maser, C., Sedell, J., *et al.* (1981). *Ecological characteristics of old-growth Douglas-fir forests*. USDA Forest Service General Technical Report PNW-118, Portland, OR.

Freitag, S. & Jaarsveld, a. S. Van. (1998). Sensitivity of selection procedures for priority conservation areas to survey extent, survey intensity and taxonomic knowledge. *Proc. R. Soc. B Biol. Sci.*, 265, 1475–1482.

Fuller, R. a, McDonald-Madden, E., Wilson, K.A., Carwardine, J., Grantham, H.S., Watson, J.E.M., *et al.* (2010). Replacing underperforming protected areas achieves better conservation outcomes. *Nature*, 466, 365–367.

Fuller, T., Munguía, M., Mayfield, M., Sánchez-Cordero, V. & Sarkar, S. (2006). Incorporating connectivity into conservation planning: A multi-criteria case study from central Mexico. *Biol. Conserv.*, 133, 131–142.

Gallo, J.A., Pasquini, L., Reyers, B. & Cowling, R.M. (2009). The role of private conservation areas in biodiversity representation and target achievement within the Little Karoo region, South Africa. *Biol. Conserv.*, 142, 446–454.

Game, E.T. & Grantham, H.S. (2008). *Marxan User Manual: For Marxan version 1.8.10*. University of Queensland and Pacific Marine Analysis and Research Association, St. Lucia, Queensland, Australia and Vancouver, British Columbia, Canada.

Game, E.T., Lipsett-Moore, G., Saxon, E., Peterson, N. & Sheppard, S. (2011). Incorporating climate change adaptation into national conservation assessments. *Glob. Chang. Biol.*, 17, 3150–3160.

Game, E.T., Watts, M.E., Wooldridge, S. & Possingham, H.P. (2008). Planning for Persistence in Marine Reserves: a Question of Catastrophic Importance. *Ecol. Appl.*, 18, 670–680.

Gaston, K.J., Jackson, S.F., Cantú-Salazar, L. & Cruz-Piñón, G. (2008). The Ecological Performance of Protected Areas. *Annu.*

Rev. Ecol. Evol. Syst., 39, 93–113.

Gerber, L.R. & Heppell, S.S. (2004). The use of demographic sensitivity analysis in marine species conservation planning. *Biol. Conserv.*, 120, 121–128.

Gonthier, D.J., Ennis, K.K., Farinas, S., Hsieh, H.Y., Iverson, A.L., Batáry, P., *et al.* (2014). Biodiversity conservation in agriculture requires a multi-scale approach. *Proc. R. Soc. B Biol. Sci.*, 281, 9–14.

González-Maya, J., Arias-Alzate, A., Granados-Peña, R., Mancera-Rodríguez, J. & Ceballos, G. (2016a). Environmental determinants and spatial mismatch of mammal diversity measures in Colombia. *Anim. Biodivers. Conserv.*, 39, 77–88.

González-Maya, J.F., Víquez-R, L.R., Arias-Alzate, A., Belant, J.L. & Ceballos, G. (2016b). Spatial patterns of species richness and functional diversity in Costa Rican terrestrial mammals: Implications for conservation. *Divers. Distrib.*, 22, 43–56.

Graesser, J., Aide, T.M., Grau, H.R. & Ramankutty, N. (2015). Cropland/pastureland dynamics and the slowdown of deforestation in Latin America. *Environ. Res. Lett.*, 10.

Grantham, H.S., Wilson, K.A., Moilanen, A., Rebelo, T. & Possingham, H.P. (2009). Delaying conservation actions for improved knowledge: How long should we wait? *Ecol. Lett.*, 12, 293–301.

Grau, H.R. & Aide, M. (2008). Globalization and land-use transitions in Latin America. *Ecol. Soc.*, 13, 16.

Grau, R., Kuemmerle, T. & Macchi, L. (2013). Beyond 'land sparing versus land sharing': environmental heterogeneity, globalization and the balance between agricultural production and nature conservation. *Curr. Opin. Environ. Sustain.*, 5, 477–483.

Green, A., Smith, S.E., Lipsett-Moore, G., Groves, C., Peterson, N., Sheppard, S., *et al.* (2009). Designing a resilient network of marine protected areas for Kimbe Bay, Papua New Guinea. *Oryx*, 43, 488–498.

Green, R.E., Cornell, S.J., Scharlemann, J.P.W. & Balmford, A. (2005). Farming and the fate of wild nature. *Science (80-.).*, 307, 550–555.

Haines, A.M., Leu, M., Svancara, L.K., Scott, J.M. & Reese, K.P. (2008). A theoretical approach to using human footprint data to assess landscape level conservation efforts. *Conserv. Lett.*, 1, 165–172.

Hand, B.K., Cushman, S.A., Landguth, E.L. & Lucotch, J. (2014). Assessing multi-taxa sensitivity to the human footprint, habitat fragmentation and loss by exploring alternative scenarios of dispersal ability and population size: A simulation approach. *Biodivers. Conserv.*, 23, 2761–2779.

Hannah, L. (2010). A global conservation system for climate-change adaptation: Special section. *Conserv. Biol.*, 24, 70–77.

Hanson, J., Schuster, R., Morrell, N., Strimas-Mackey, M., Watts, M., Arcese, P., *et al.* (2020a). *prioritizr: Systematic Conservation Prioritization in R. Syst. Conserv. Prioritization R*. Available at: https://prioritizr.net/articles/prioritizr.html. Last accessed 17 June 2020.

Hanson, J.O., Schuster, R., Morrell, N., Strimas-Mackey, M., Watts, M.E., Arcese, P., *et al.* (2020b). prioritizr: Systematic Conservation Prioritization in R.

Harborne, A.R., Mumby, P.J., Kappe, C. V., Dahlgren, C.P., Micheli, F., Holmes, K.E., *et al.* (2008). Tropical coastal habitats as surrogates of fish community structure, grazing, and fisheries value. *Ecol. Appl.*, 18, 1689–1701.

He, H.S., DeZonia, B.E. & Mladenoff, D.J. (2000). An aggregation index (AI) to quantify spatial patterns of landscapes. *Landsc. Ecol.*, 15, 591–601.

Hidasi-Neto, J., Loyola, R.D. & Cianciaruso, M. V. (2015). Global and local evolutionary and ecological distinctiveness of terrestrial mammals: identifying priorities across scales. *Divers. Distrib.*, 21, 548–559.

Hidasi-Neto, J., Loyola, R.D. & Cianciaruso, M.V. (2013). Conservation Actions Based on Red Lists Do Not Capture the Functional and Phylogenetic Diversity of Birds in Brazil. *PLoS One*, 8.

Hodgson, J.A., Thomas, C.D., Wintle, B.A. & Moilanen, A. (2009). Climate change, connectivity and conservation decision making: Back to basics. *J. Appl. Ecol.*, 46, 964–969.

Hoekstra, J.M., Boucher, T.M., Ricketts, T.H. & Roberts, C. (2005). Confronting a biome crisis: global disparities of habitat loss and protection. *Ecol. Lett.*, 8, 23–29.

Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T.M., Butchart, S.H.M., *et al.* (2010). The impact of conservation on the status of the world's vertebrates. *Science (80-.).*, 330, 1503–1509.

Holl, K.D. & Howarth, R.B. (2000). Paying for Restoration. *Restor. Ecol.*, 8, 260–267.

Hortal, J., Araújo, M.B. & Lobo, J.M. (2009). Testing the effectiveness of discrete and continuous environmental diversity as a surrogate for species diversity. *Ecol. Indic.*, 9, 138–149.

Huang, C., Kim, S., Altstatt, A., Townshend, J.R.G., Davis, P., Song, K., *et al.* (2007). Rapid loss of Paraguay's Atlantic forest and the status of protected areas - A Landsat assessment. *Remote Sens. Environ.*, 106, 460–466.

Huang, C., Kim, S., Song, K., Townshend, J.R.G., Davis, P., Altstatt, A., *et al.* (2009). Assessment of Paraguay's forest cover change using Landsat observations. *Glob. Planet. Change*, 67, 1–12.

Huber, P.R., Greco, S.E. & Thorne, J.H. (2010). Spatial scale effects on conservation network design: Trade-offs and omissions in regional versus local scale planning. *Landsc. Ecol.*, 25, 683–695.

Hurlbert, A.H. & White, E.P. (2005). Disparity between range map- and survey-based analyses of species richness: patterns, processes and implications. *Ecol. Lett.*, 8, 319–327.

Ishwaran, H. (2007). Variable importance in binary regression trees and forests. *Electron. J. Stat.*, 1, 519–537.

Ishwaran, H., Kogalur, U.B., Chen, X. & Minn, A.J. (2011). Random survival forests for high-dimensional data. *Stat. Anal. Data Min. ASA Data Sci. J.*, 4, 115–132.

Ishwaran, H., Kogalur, U.B., Gorodeski, E.Z., Minn, A.J. & Lauer, M.S. (2010). High-dimensional variable selection for survival data. *J. Am. Stat. Assoc.*, 105, 205–217.

IUCN & UNEP-WCMC. (2018). The World Database on Protected Areas (WDPA) [On-line], [December/2018].

Jantke, K., Kuempel, C.D., McGowan, J., Chauvenet, A. & Possingham, H.P. (2019). Metrics for evaluating representation target achievement in protected area networks. *Divers. Distrib.*, 25, 170–175.

Jantke, K. & Schneider, U. a. (2011). Integrating Land Market Feedbacks into Conservation Planning-A Mathematical Programming Approach. *Environ. Model. Assess.*, 16, 227–238.

Jenkins, C.N. & Joppa, L. (2009). Expansion of the global terrestrial protected area system. *Biol. Conserv.*, 142, 2166–2174.

Jenkins, M. (2003). Prospects for biodiversity. *Science (80-.).*, 302, 1175–1177.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., *et al.* (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, 90, 2648–2648.

Kark, S., Levin, N., Grantham, H.S. & Possingham, H.P. (2009). Between-country collaboration and consideration of costs increase conservation planning efficiency in the Mediterranean Basin. *Proc. Natl. Acad. Sci.*, 106, 15368–15373.

Kier, G., Mutke, J., Dinerstein, E., Ricketts, T.H., Küper, W., Kreft, H., *et al.* (2005). Global patterns of plant diversity and floristic knowledge. *J. Biogeogr.*, 32, 1107–1116.

Klein, C.J., Wilson, K.A., Watts, M.E.J., Stein, J., Berry, S., Carwardine, J., *et al.* (2009). Incorportating ecological and evolutionary processes into continental-scale conservation planning. *Ecol. Appl.*, 19, 207–217.

Klink, C.A. & Machado, R.B. (2005). Conservation of the Brazilian Cerrado Conservation of the Brazilian Cerrado. *Conserv. Biol.*, 19, 707–713.

Knight, A.T., Cowling, R.M. & Cambell, B.M. (2006). An Operational Model for Implementing Conservation Action. *Conserv. Biol.*, 20, 408–419.

Kremen, C. (2015). Reframing the land-sparing/land-sharing debate for biodiversity conservation. *Ann. N. Y. Acad. Sci.*, 1355, 52–76.

Kuempel, C.D., Chauvenet, A.L.M. & Possingham, H.P. (2016). Equitable Representation of Ecoregions is Slowly Improving Despite Strategic Planning Shortfalls. *Conserv. Lett.*, 9, 422–428.

Kujala, H., Moilanen, A., Ara??jo, M.B. & Cabeza, M. (2013). Conservation Planning with Uncertain Climate Change Projections. *PLoS One*, 8.

Kukkala, A.S. & Moilanen, A. (2013). Core concepts of spatial prioritisation in systematic conservation planning. *Biol. Rev.*, 88, 443–464.

Langford, W.T., Gordon, A., Bastin, L., Bekessy, S.A., White, M.D. & Newell, G. (2011). Raising the bar for systematic conservation planning. *Trends Ecol. Evol.*, 26, 634–640.

Lawler, J.J., Shafer, S.L. & Blaustein, A.R. (2010). Projected climate impacts for the amphibians of the western hemisphere. *Conserv. Biol.*, 24, 38–50.

Leal, I.R., Da Silva, J.M.C., Tabarelli, M. & Lacher, T.E. (2005). Changing the course of biodiversity conservation in the caatinga of northeastern Brazil. *Conserv. Biol.*, 19, 701–706.

Leathwick, J., Moilanen, A., Francis, M., Elith, J., Taylor, P., Julian, K., *et al.* (2008). Novel methods for the design and evaluation of marine protected areas in offshore waters. *Conserv. Lett.*, 1, 91–102.

Lemes, P. & Loyola, R.D. (2013). Accommodating Species Climate-Forced Dispersal and Uncertainties in Spatial Conservation Planning. *PLoS One*, 8.

Leroux, S.J., Schmiegelow, F.K.A., Lessard, R.B. & Cumming, S.G. (2007). Minimum dynamic reserves: A framework for determining reserve size in ecosystems structured by large disturbances. *Biol. Conserv.*, 138, 464–473.

Lessmann, J., Muñoz, J. & Bonaccorso, E. (2014). Maximizing species conservation in continental Ecuador: A case of systematic conservation planning for biodiverse regions. *Ecol. Evol.*, 4, 2410–2422.

Lindenmayer, D.B. & Possingham, H.P. (1995). Modelling the impacts of wildfire on the viability of metapopulations of the endangered Australian species of arboreal marsupial, Leadbeater's Possum. *For. Ecol. Manage.*, 74, 197–222.

Linke, S., Turak, E. & Nel, J. (2011). Freshwater conservation planning: The case for systematic approaches. *Freshw. Biol.*, 56, 6–20.

Lislevand, T., Figuerola, J. & Székely, T. (2007). Avian body sizes in relation to fecundity, mating system, display behavior, and resource sharing. *Ecology*.

Lombard, A.T., Cowling, R.M., Pressey, R.L. & Mustartf, P.J. (1997). Reserve selection in a species-rich and fragmented landscape on the Agulhas Plain, South Africa. *Conserv. Biol.*, 11, 1101–1116.

Loyola, R.D. & Diniz-Filho, J.A.F. (2010). Carnivore Protection : Including Biological Traits in Conservation Planning. *Curr. Conserv.*, 1, 6–7.

Loyola, R.D., Lemes, P., Nabout, J.C., Trindade-Filho, J., Sagnori, M.D., Dobrovolski, R., *et al.* (2013). A straightforward conceptual approach for evaluating spatial conservation priorities under climate change. *Biodivers. Conserv.*, 22, 483–495.

Loyola, R.D., Oliveira-Santos, L.G.R., Almeida-Neto, M., Nogueira, D.M., Kubota, U., Diniz-Filho, J.A.F., *et al.* (2009). Integrating economic costs and biological traits into global conservation priorities for carnivores. *PLoS One*, 4.

Loyola, R.D., De Oliveira, G., Diniz-Filho, J.A.F. & Lewinsohn, T.M. (2008). Conservation of Neotropical carnivores under different prioritization scenarios: Mapping species traits to minimize conservation conflicts. *Divers. Distrib.*, 14, 949–960.

Luck, G.W., Lavorel, S., Mcintyre, S. & Lumb, K. (2012). Improving the application of vertebrate trait-based frameworks to the study of ecosystem services. *J. Anim. Ecol.*, 81, 1065–1076.

Mace, G.M. (2014). Whose conservation? *Science (80-.).*, 345, 1558 LP – 1560.

Machado, N. & Loyola, R.D. (2013). A Comprehensive Quantitative Assessment of Bird Extinction Risk in Brazil. *PLoS One*, 8.

Mantyka-Pringle, C.S., Martin, T.G. & Rhodes, J.R. (2012). Interactions between climate and habitat loss effects on biodiversity: A systematic review and meta-analysis. *Glob. Chang. Biol.*, 18, 1239–1252.

Mappin, B., Chauvenet, A.L.M., Adams, V.M., Di Marco, M., Beyer, H.L., Venter, O., *et al.* (2019). Restoration priorities to achieve the global protected area target. *Conserv. Lett.*, 12, e12646.

Di Marco, M., Butchart, S.H.M., Visconti, P., Buchanan, G.M., Ficetola, G.F. & Rondinini, C. (2016). Synergies and trade-offs in achieving global biodiversity targets. *Conserv. Biol.*, 30, 189–195.

Margules, C.R. & Pressey, R.L. (2000). Systematic conservation planning. *Nature*, 405, 243–253.

Margules, C.R. & Sarkar, S. (2007). *Systematic conservation planning*. Cambridge University Press, Cambridge, UK.

McCarthy, M.A. (2009). Spatial Population Viability Analysis. In: *Spatial Conservation Prioritization – Quantitative Methods and Computational Tools* (eds. Moilanen, A., Wilson, K.A. & Possingham, H.P.). Oxford University Press, New York, pp. 122–134.

McGowan, J., Smith, R.J., Di Marco, M., Clarke, R. & Possingham, H.P. (2017). An Evaluation of Marine Important Bird and Biodiversity Areas in the Context of Spatial Conservation Prioritization. *Conserv. Lett.*, 00, 1–8.

Meir, E., Andelman, S. & Possingham, H.P. (2004). Does conservation planning matter in a dynamic and uncertain world? *Ecol. Lett.*, 7, 615–622.

Meiri, S. (2010). Length weight allometries in lizards. *J. Zool.*, 281, 218–226.

Meiri, S., Bauer, A.M., Chirio, L., Colli, G.R., Das, I., Doan, T.M., *et al.* (2013). Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. *Glob. Ecol. Biogeogr.*, 22, 834–845.

Meiri, S., Brown, J.H. & Sibly, R.M. (2012). The ecology of lizard reproductive output. *Glob. Ecol. Biogeogr.*, 21, 592–602.

Meiri, S., Feldman, A. & Kratochvíl, L. (2015). Squamate hatchling size and the evolutionary causes of negative offspring size allometry. *J. Evol. Biol.*, 28, 438–446.

Meiri, S., Raia, P. & Phillimore, A.B. (2011). Slaying dragons: Limited evidence for unusual body size evolution on islands. *J. Biogeogr.*, 38, 89–100.

Melo, I., Ochoa-Quintero, J.M., de Oliveira Roque, F. & Dalsgaard, B. (2018). A review of threshold responses of birds to landscape changes across the world. *J. F. Ornithol.*, 89, 303–314.

Mertz, O. & Mertens, C.F. (2017). Land Sparing and Land Sharing Policies in Developing Countries – Drivers and Linkages to Scientific Debates. *World Dev.*, 98, 523–535.

Micheli, F., Amarasekare, P., Bascompte, J. & Gerber, L.R. (2004). Including species interactions in the design and evaluation of marine reserves: some insights from a predator-prey model. *Bull. Mar. Sci.*, 74, 653–669.

Miller, J.R. & Hobbs, R.J. (2002). Conservation Where People Live and Work. *Conserv. Biol.*, 16, 330–337.

Minor, E.S. & Urban, D.L. (2007). Graph theory as a proxy for spatially explicit population models in conservation planning. *Ecol. Appl.*, 17, 1771–1782.

Mittermeier, R.A., Gil, P.R., Hoffman, M., Pilgrim, J., Brooks, T.M., Mittermeier, C.G., *et al.* (2005). *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions*. Conservation International.

Mittermeier, R.A., Myers, N., Thomsen, J.B., Fonseca, G.A.B. da & Olivieri, S. (1998). Biodiversity Hotspots and Major Tropical Wilderness Areas: Approaches to Setting Conservation Priorities. *Conserv. Biol.*, 12, 516–520.

Moilanen, A. (2007). Landscape Zonation, benefit functions and target-based planning: Unifying reserve selection strategies. *Biol. Conserv.*, 134, 571–579.

Moilanen, A. (2008). Generalized complementarity and mapping of the concepts of systematic conservation planning. *Conserv. Biol.*, 22, 1655–1658.

Moilanen, A., Franco, A.M.A., Early, R.I., Fox, R., Wintle, B. & Thomas, C.D. (2005). Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. *Proc. R. Soc. B-Biological Sci.*, 272, 1885–1891.

Moilanen, A., Possingham, H.P. & Polasky, S. (2009). A Mathematical Classification of Conservation Prioritization Problems. In: *Spatial Conservation Prioritization – Quantitative Methods and Computational Tools*. Oxford University Press, New York, pp. 28–42.

Moore, J., Balmford, A., Allnutt, T. & Burgess, N. (2004). Integrating costs into conservation planning across Africa. *Biol. Conserv.*, 117, 343–350.

Morelli, F., Benedetti, Y., Perna, P. & Santolini, R. (2018). Associations among taxonomic diversity, functional diversity and evolutionary distinctiveness vary among environments. *Ecol. Indic.*, 88, 8–16.

Moritz, C. & Faith, D.P. (1998). Comparative phylogeography and the identification of genetically divergent areas for conservation. *Mol. Ecol.*, 7, 419–429.

Müller, A., Schneider, U.A. & Jantke, K. (2018). Is large good enough? Evaluating and improving representation of ecoregions and habitat types in the European Union's protected area network Natura 2000. *Biol. Conserv.*, 227, 292–300.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.

Myhrvold, N.P., Baldridge, E., Chan, B., Sivam, D., Freeman, D.L. & Ernest, S.K.M. (2015). An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology*, 96, 3109–000.

Nagendra, H., Southworth, J. & Tucker, C. (2003). Accessibility as a determinant of landscape transformation in western Honduras: linking pattern and process. *Landsc. Ecol.*, 18, 141–158.

Naidoo, R. & Adamowicz, W.L. (2006). Modeling opportunity costs of conservation in transitional landscapes. *Conserv. Biol.*, 20, 490–500.

Naidoo, R., Balmford, A., Ferraro, P.J., Polasky, S., Ricketts, T.H. & Rouget, M. (2006). Integrating economic costs into conservation planning. *Trends Ecol. Evol.*, 21, 681–687.

Naidoo, R. & Iwamura, T. (2007). Global-scale mapping of economic benefits from agricultural lands: Implications for conservation priorities. *Biol. Conserv.*, 140, 40–49.

Naidoo, R. & Ricketts, T.H. (2006). Mapping the economic costs and benefits of conservation. *PLoS Biol.*, 4, e360.

Naoe, S., Katayama, N., Amano, T., Akasaka, M., Yamakita, T., Ueta, M., *et al.* (2015). Identifying priority areas for national-level conservation to achieve Aichi Target 11: A case study of using terrestrial birds breeding in Japan. *J. Nat. Conserv.*, 24, 101–108.

Naujokaitis-Lewis, I.R., Curtis, J.M.R., Arcese, P. & Rosenfeld, J. (2009). Sensitivity analyses of spatial population viability analysis models for species at risk and habitat conservation planning. *Conserv. Biol.*, 23, 225–229.

Negret, P.J., Sonter, L., Watson, J.E.M., Possingham, H., Jones, K.R., Cesar, S., *et al.* (2019). Emerging evidence that armed conflict and coca cultivation influence deforestation patterns. *Biol. Conserv.*, 108176.

Nepstad, D., Schwartzman, S., Bamberger, B., Santilli, M., Ray, D., Schlesinger, P., *et al.* (2006). Inhibition of Amazon Deforestation and Fire by Parks and Indigenous Lands. *Conserv. Biol.*, 20, 65–73.

Newbold, S.C. & Siikamaki, J. (2009). Prioritizing conservation activities using reserve site selection methods and population viability analysis. *Ecol. Appl.*, 19, 1774–1790.

Newbold, T., Hudson, L.N., Arnell, A.P., Contu, S., De Palma, A., Ferrier, S., *et al.* (2016). Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science (80-.).*, 353, 288 LP – 291.

Newburn, D., Reed, S., Berck, P. & Merenlender, A. (2005). Economics and land-use change in prioritizing private land conservation. *Conserv. Biol.*, 19, 1411–1420.

Nhancale, B.A. & Smith, R.J. (2011). The influence of planning unit characteristics on the efficiency and spatial pattern of systematic conservation planning assessments. *Biodivers. Conserv.*, 20, 1821–1835.

Nicholson, E., Michael, I., Frank, K., Rochester, A., Pressey, R.L. & Lindenmayer, D.B. (2006). A new method for conservation planning for the persistence of multiple species. *Ecol. Lett.*, 9, 1049–1060.

Nori, J., Lemes, P., Urbina-Cardona, N., Baldo, D., Lescano, J. & Loyola, R.D. (2015). Amphibian conservation, land-use changes and protected areas: A global overview. *Biol. Conserv.*, 191, 367–374.

Norton-Griffiths, M. & Southey, C. (1995). The opportunity costs of biodiversity conservation in Kenya. *Ecol. Econ.*, 12, 125–139.

Noss, R.F. (1990). Indicators for Monitoring Biodiversity: A Hierarchical Approach. *Conserv. Biol.*, 4, 355–364.

Novosolov, M., Raia, P. & Meiri, S. (2013). The island syndrome in lizards. *Glob. Ecol. Biogeogr.*, 22, 184–191.

Novosolov, M., Rodda, G.H., Feldman, A., Kadison, A.E., Dor, R. & Meiri, S. (2016). Power in numbers. Drivers of high population density in insular lizards. *Glob. Ecol. Biogeogr.*, 25, 87–95.

O'Connor, C., Marvier, M. & Kareiva, P. (2003). Biological vs. social, economic and political priority-setting in conservation. *Ecol. Lett.*, 6, 706–711.

Ocampo-Peñuela, N. & Pimm, S.L. (2014). Setting Practical Conservation Priorities for Birds in the Western Andes of Colombia. *Conserv. Biol.*, 28, 1260–1270.

Oliveira, B.F., São-Pedro, V.A., Santos-Barrera, G., Penone, C. & Costa, G.C. (2017). AmphiBIO, a global database for amphibian ecological traits. *Sci. Data*, 4, 1–7.

Olson, D.M. & Dinerstein, E. (1998). The Global 200: A Representation Approach to Conserving the Earth's Most Biologically Valuable Ecoregions. *Conserv. Biol.*, 12, 502–515.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., *et al.* (2001). Terrestrial Ecoregions of the World: A New Map of Life on Earth. *Bioscience*, 51, 933–938.

Pacheco, P., Aguilar-Støen, M., Börner, J., Etter, A., Putzel, L. & Diaz, M. del C.V. (2011). Landscape Transformation in Tropical Latin America: Assessing Trends and Policy Implications for REDD+. *Forests*, 2.

Pacifici, A.M., Foden, W.B., Visconti, P., Watson, J.E.M., Butchart, S.H.M., Kovacs, K.M., *et al.* (2015). Assessing species vulnerability to climate change. *Nat. Clim. Chang.*, 5, 215–225.

Pe'er, G., Tsianou, M.A., Franz, K.W., Matsinos, Y.G., Mazaris, A.D., Storch, D., *et al.* (2014). Toward better application of minimum area requirements in conservation planning. *Biol. Conserv.*

Pearson, R.G., Thuiller, W., Araújo, M.B., Martínez-Meyer, E., Brotons, L., McClean, C., *et al.* (2006). Model-based uncertainty in species range prediction. *J. Biogeogr.*, 33, 1704–1711.

Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., *et al.* (2010). Scenarios for Global Biodiversity in the 21st Century. *Science (80-.).*, 330, 1496–1501.

Perfecto, I. & Vandermeer, J. (2010). The agroecological matrix as alternative to the land-sparing/agriculture intensification model. *Proc. Natl. Acad. Sci. U. S. A.*, 107, 5786–5791.

Pfeifer, M., Lefebvre, V., Peres, C.A., Banks-Leite, C., Wearn, O.R., Marsh, C.J., *et al.* (2017). Creation of forest edges has a global impact on forest vertebrates. *Nature*, 551, 187–191.

Phalan, B., Onial, M., Balmford, A. & Green, R.E. (2011). Reconciling food production and biodiversity conservation: Land sharing and land sparing compared. *Science (80-.).*, 333, 1289–1291.

Phelps, J., Carrasco, L.R., Webb, E.L., Koh, L.P. & Pascual, U. (2013). Agricultural intensification escalates future conservation costs. *Proc. Natl. Acad. Sci. U. S. A.*, 110, 7601–7606.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006). Maximum entropy modeling of species geographic distributions. *Ecol. Modell.*, 190, 231–259.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., *et al.* (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science (80-.).*, 344, 1246752.

Polasky, S. (2008). Why conservation planning needs socioeconomic data. *Proc. Natl. Acad. Sci. U. S. A.*, 105, 6505–6506.

Polasky, S., Camm, J.D. & Garber-Yonts, B. (2001). Selecting biological reserves cost-effectively: An application to terrestrial vertebrate conservation in Oregon. *Land Econ.*, 77, 68–78.

Polasky, S., Nelson, E., Lonsdorf, E., Fackler, P. & Starfield, A. (2005). Conserving species in a working landscape: land use with biological and economic objectives. *Ecol. Appl.*, 15, 1387–1401.

Da Ponte, E., Roch, M., Leinenkugel, P., Dech, S. & Kuenzer, C. (2017). Paraguay's Atlantic Forest cover loss – Satellite-based change detection and fragmentation analysis between 2003 and 2013. *Appl. Geogr.*, 79, 37–49.

Portillo-Quintero, C.A. & Sánchez-Azofeifa, G.A. (2010). Extent and conservation of tropical dry forests in the Americas. *Biol. Conserv.*, 143, 144–155.

Possingham, H.P., Moilanen, A. & Wilson, K.W. (2009). Accounting for Habitat Dynamics in Conservation Planning. In: *Spatial Conservation Prioritization – Quantitative Methods and Computational Tools* (eds. Moilanen, A., Wilson, K.A. & Possingham, H.P.). Oxford University Press, New York, pp. 135–144.

Potapov, P., Yaroshenko, A., Turubanova, S., Dubinin, M., Laestadius, L., Thies, C., *et al.* (2008). Mapping the World ' s Intact Forest Landscapes by Remote Sensing. *Ecol. Soc.*, 13, 16.

Pouzols, F.M., Burgman, M.A. & Moilanen, A. (2012). Methods for allocation of habitat management, maintenance, restoration and offsetting, when conservation actions have uncertain consequences. *Biol. Conserv.*, 153, 41–50.

Pouzols, F.M., Toivonen, T., Di Minin, E., Kukkala, A.S., Kullberg, P., Kuusterä, J., *et al.* (2014). Global protected area expansion is compromised by projected land-use and parochialism. *Nature*, 516, 383–386.

Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M. & Wilson, K.A. (2007). Conservation planning in a changing world. *Trends Ecol. Evol.*, 22, 583–592.

Pressey, R.L., Cowling, R.M. & Rouget, M. (2003). Formulating conservation targets for biodiversity pattern and process in the Cape Floristic Region, South Africa. *Biol. Conserv.*, 112, 99–127.

Pressey, R.L., Hager, T.C., Ryan, K.M., Schwarz, J., Wall, S., Ferrier, S., *et al.* (2000). Using abiotic data for conservation assessments over extensive regions: Quantitative methods applied across New South Wales, Australia. *Biol. Conserv.*, 96, 55–82.

Pressey, R.L., Watts, M.E. & Barrett, T.W. (2004). Is maximizing protection the same as minimizing loss? Efficiency and retention as alternative measures of the effectiveness of proposed reserves. *Ecol. Lett.*, 7, 1035–1046.

Pressey, R.L., Watts, M.E., Barrett, T.W. & Ridges, M.J. (2009). The C-Plan Conservation Planning System : Origins , Applications , and Possible Futures. In: *Spatial Conservation Prioritization – Quantitative Methods and Computational Tools* (eds. Moilanen, A., Wilson, K.A. & Possingham, H.P.). Oxford University Press, New York, pp. 211–234.

Pyke, C.R. (2005). Assessing suitability for conservation action: Prioritizing interpond linkages for the California tiger salamander. *Conserv. Biol.*, 19, 492–503.

Rae, C., Rothley, K. & Dragicevic, S. (2007). Implications of error and uncertainty for an environmental planning scenario: A sensitivity analysis of GIS-based variables in a reserve design exercise. *Landsc. Urban Plan.*, 79, 210–217.

Ramirez, L., Diniz-Filho, J.A.F. & Hawkins, B.A. (2008). Partitioning phylogenetic and adaptive components of the geographical body-size pattern of New World birds. *Glob. Ecol. Biogeogr.*, 17, 100–110.

Rapacciuolo, G., Graham, C.H., Marin, J., Behm, J.E., Costa, G.C., Hedges, S.B., *et al.* (2019). Species diversity as a surrogate for conservation of phylogenetic and functional diversity in terrestrial vertebrates across the Americas. *Nat. Ecol. Evol.*, 3, 53–61.

Redo, D., Joby Bass, J.O. & Millington, A.C. (2009). Forest dynamics and the importance of place in western Honduras. *Appl. Geogr.*, 29, 91–110.

Redo, D.J., Grau, H.R., Aide, T.M. & Clark, M.L. (2012). Asymmetric forest transition driven by the interaction of socioeconomic development and environmental heterogeneity in Central America. *Proc. Natl. Acad. Sci.*, 109, 8839 LP – 8844.

Regan, H.M., Ensbey, M.J. & Burgman, M.A. (2009). Conservation Prioritization and Uncertainty in Planning Inputs. In: *Spatial Conservation Prioritization – Quantitative Methods and Computational Tools* (eds. Moilanen, A., Wilson, K.A. & Possingham, H.P.). Oxford University Press, New York, pp. 145–57.

Reid, W. V. (1998). Biodiversity hotspots. *Trends Ecol. Evol.*, 13, 275–280.

Reside, A.E., Butt, N. & Adams, V.M. (2018). Adapting systematic conservation planning for climate change. *Biodivers. Conserv.*, 27.

Ribeiro-Neto, J.D., Arnan, X., Tabarelli, M. & Leal, I.R. (2016). Chronic anthropogenic disturbance causes homogenization of plant and ant communities in the Brazilian Caatinga. *Biodivers. Conserv.*, 25, 943–956.

Richards, P.D. (2011). Soy, cotton, and the final Atlantic Forest frontier. *Prof. Geogr.*, 63, 343–363.

Richardson, E.A., Kaiser, M.J., Edwards-Jones, G. & Possingham, H.P. (2006). Sensitivity of marine-reserve design to the spatial resolution of socioeconomic data. *Conserv. Biol.*, 20, 1191–1202.

Ries, L., Fletcher, R.J., Battin, J. & Sisk, T.D. (2004). Ecological responses to habitat edges: Mechanisms, models, and variability explained. *Annu. Rev. Ecol. Evol. Syst.*, 35, 491–522.

Rincón-Ruiz, A., Pascual, U. & Flantua, S. (2013). Examining spatially varying relationships between coca crops and associated factors in Colombia, using geographically weight regression. *Appl. Geogr.*, 37, 23–33.

Robinson, T.P., Wint, G.R.W., Conchedda, G., Boeckel, T.P. Van, Ercoli, V., Palamara, E., *et al.* (2014). Mapping the Global

Distribution of Livestock. *PLoS One*, 9, e96084.

Rodrigues, A.S.L., Andelman, S., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling, R.M., *et al.* (2004). Effectiveness of the global protected area network in representing species diversity. *Nature*, 428, 640–643.

Rodrigues, A.S.L. & Brooks, T.M. (2007). Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. *Annu. Rev. Ecol. Evol. Syst.*, 38, 713–737.

Rodrigues, A.S.L., Gaston, K.J. & Gregory, R.D. (2000). Using presence-absence data to establish reserve selection procedures that are robust to temporal species turnover. *Proc. Biol. Sci.*, 267, 897–902.

Rodrigues, J.F.M., Olalla-Tárraga, M.Á., Iverson, J.B., Akre, T.S.B. & Diniz-Filho, J.A.F. (2016). Time and environment explain the current richness distribution of non-marine turtles worldwide. *Ecography (Cop.).*, n/a-n/a.

Rodríguez Eraso, N., Armenteras, D. & Retana Alumbreros, J. (2013a). Land use and land cover change in the Colombian Andes: dynamics and future scenarios. *J. Land Use Sci.*, 8, 1–21.

Rodríguez Eraso, N., Armenteras, D. & Retana, J. (2013b). Effectiveness of protected areas in the Colombian Andes: Deforestation, fire and land-use changes. *Reg. Environ. Chang.*, 13, 423–435.

Romero-Ruiz, M.H., Flantua, S.G.A., Tansey, K. & Berrio, J.C. (2012). Landscape transformations in savannas of northern South America: Land use/cover changes since 1987 in the Llanos Orientales of Colombia. *Appl. Geogr.*, 32, 766–776.

Romero, M.H., Etter, A., Sarmiento, A.H. & Tansey, K. (2010). Spatial and temporal variability of fires in relation to ecosystems, land tenure and rainfall in savannas of northern South America. *Glob. Chang. Biol.*, 16, 2013–2023.

Rondinini, C., Wilson, K.A., Boitani, L., Grantham, H. & Possingham, H.P. (2006). Tradeoffs of different types of species occurrence data for use in systematic conservation planning. *Ecol. Lett.*, 9, 1136–1145.

Roque, F.D.O., Menezes, J.F.S., Northfield, T., Ochoa-Quintero, J.M., Campbell, M.J. & Laurance, W.F. (2018). Warning signals of biodiversity collapse across gradients of tropical forest loss. *Sci. Rep.*, 8, 1–7.

Roque, F.O., Ochoa-Quintero, J., Ribeiro, D.B., Sugai, L.S.M., Costa-Pereira, R., Lourival, R., *et al.* (2016). Upland habitat loss as a threat to Pantanal wetlands. *Conserv. Biol.*, 30, 1131–1134.

Rouget, M., Cowling, R.M., Lombard, A.T., Knight, A.T. & Kerley, G.I.H. (2006). Designing large-scale conservation corridors for pattern and process. *Conserv. Biol.*, 20, 549–561.

Rouget, M., Cowling, R.M., Pressey, R.L. & Richardson, D. (2003). Identifying spatial components of ecological and evolutionary processes for regional conservation planning in the Cape Floristic Region, South Africa. *Divers. Distrib.*, 9, 191–210.

Roura-Pascual, N., Krug, R.M., Richardson, D.M. & Hui, C. (2010). Spatially-explicit sensitivity analysis for conservation management: exploring the influence of decisions in invasive alien plant management. *Divers. Distrib.*, 16, 426–438.

Ryan, M.G., Harmon, M.E., Birdsey, R. a, Giardina, C.P., Heath, L.S., Houghton, R. a, *et al.* (2012). The Role of Landscape Connectivity in Planning and Implementing Conservation and Restoration Priorities. *Issue Ecol.*, 13, 1–16.

Safi, K., Cianciaruso, M. V, Loyola, R.D., Brito, D., Armour-Marshall, K. & Diniz-Filho, J.A.F. (2011). Understanding global patterns of mammalian functional and phylogenetic diversity. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.*, 366, 2536–2544.

Sánchez-Cuervo, A.M. & Aide, T.M. (2013a). Consequences of the armed conflict, forced human displacement, and land abandonment on forest cover change in Colombia: A multi-scaled analysis. *Ecosystems*, 16, 1052–1070.

Sánchez-Cuervo, A.M. & Aide, T.M. (2013b). Identifying hotspots of deforestation and reforestation in Colombia (2001-2010): Implications for protected areas. *Ecosphere*, 4.

Sánchez-Cuervo, A.M., Aide, T.M., Clark, M.L. & Etter, A. (2012). Land Cover Change in Colombia: Surprising Forest Recovery Trends between 2001 and 2010. *PLoS One*, 7, e43943.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A. V. & Woolmer, G. (2002). The Human Footprint and the Last of the Wild. *Bioscience*, 52, 891.

Santini, L., BenÍtez-LÓpez, A., Ficetola, G.F. & Huijbregts, M.A.J. (2018). Length–mass allometries in amphibians. *Integr. Zool.*, 13, 36–45.

Le Saout, S., Hoffmann, M., Shi, Y., Hughes, A., Bernard, C., Brooks, T.M., *et al.* (2013). Protected areas and effective biodiversity conservation. *Science (80-.).*, 342, 803–5.

Schleupner, C. & Schneider, U.A. (2013). Allocation of European wetland restoration options for systematic conservation planning. *Land use policy*, 30, 604–614.

Schmitt-Harsh, M. (2013). Landscape change in Guatemala: Driving forces of forest and coffee agroforest expansion and contraction from 1990 to 2010. *Appl. Geogr.*, 40, 40–50.

Schröter, M., Rusch, G.M., Barton, D.N., Blumentrath, S. & Nordén, B. (2014). Ecosystem Services and Opportunity Costs Shift Spatial Priorities for Conserving Forest Biodiversity. *PLoS One*, 9, e112557.

Schwartzman, S. & Zimmerman, B. (2005). Conservation Alliances with Indigenous Peoples of the Amazon. *Conserv. Biol.*, 19, 721–727.

Sebastião, H. & Grelle, C.E.V. (2009). Taxon surrogates among Amazonian mammals: Can total species richness be predicted by single orders? *Ecol. Indic.*, 9, 160–166.

Sekercioglu, C.H. (2012). Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. *J. Ornithol.*, 153, 153–161.

Shackelford, G.E., Steward, P.R., German, R.N., Sait, S.M. & Benton, T.G. (2015). Conservation planning in agricultural landscapes: Hotspots of conflict between agriculture and nature. *Divers. Distrib.*, 21, 357–367.

Shackelford, N., Standish, R.J., Ripple, W. & Starzomski, B.M. (2018). Threats to biodiversity from cumulative human impacts in one of North America's last wildlife frontiers. *Conserv. Biol.*, 32, 672–684.

Slavenko, A., Tallowin, O.J.S., Itescu, Y., Raia, P. & Meiri, S. (2016). Late Quaternary reptile extinctions: size matters, insularity dominates. *Glob. Ecol. Biogeogr.*, 25, 1308–1320.

Sobral, F.L., Jardim, L., Lemes, P., Machado, N., Loyola, R.D. & Cianciaruso, M. V. (2014). Spatial conservation priorities for top predators reveal mismatches among taxonomic, phylogenetic and functional diversity. *Nat. Conserv.*, 12, 150–155.

Stewart, R.R. & Noyce, T. (2003). Opportunity cost of ad hoc marine reserve design decisions: an example from South Australia . *Mar. Ecol. Prog. Ser.*, 253, 25–38.

Stewart, R.R., Noyce, T. & Possingham, H.P. (2003). Opportunity cost of ad hoc marine reserve design decisions: an example from South Australia. *Mar. Ecol. Ser.*, 253, 25–38.

Stewart, R.R. & Possingham, H.P. (2005). Efficiency, costs and trade-offs in marine reserve system design. *Environ. Model. Assess.*, 10, 203–213.

Stoneham, G., Chaudhri, V., Ha, A. & Strappazzon, L. (2003). Auctions for conservation contracts: an empirical examination of Victoria's BushTender trial. *Aust. J. Agric. Resour. Econ.*, 47, 477–500.

Strange, N., Thorsen, B.J. & Bladt, J. (2006). Optimal reserve selection in a dynamic world. *Biol. Conserv.*, 131, 33–41.

Strecker, A.L., Olden, J.D., Whittier, J.B. & Paukert, C.P. (2011). Defining conservation priorities for freshwater fishes according to taxonomic, functional, and phylogenetic diversity. *Ecol. Appl.*, 21, 3002–3013.

Stuart-Smith, R.D., Bates, A.E., Lefcheck, J.S., Duffy, J.E., Baker, S.C., Thomson, R.J., *et al.* (2013). Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature*, 501, 539–42.

Summers, D.M., Bryan, B.A., Crossman, N.D. & Meyer, W.S. (2012). Species vulnerability to climate change: impacts on spatial conservation priorities and species representation. *Glob. Chang. Biol.*, 18, 2335–2348.

Tabarelli, M., Aguiar, A.V., Ribeiro, M.C., Metzger, J.P. & Peres, C.A. (2010). Prospects for biodiversity conservation in the Atlantic Forest: Lessons from aging human-modified landscapes. *Biol. Conserv.*, 143, 2328–2340.

Tallis, H., Ferdaña, Z. & Gray, E. (2008). Linking Terrestrial and Marine Conservation Planning and Threats Analysis. *Conserv. Biol.*, 22, 120–130.

de Thoisy, B., Richard-Hansen, C., Goguillon, B., Joubert, P., Obstancias, J., Winterton, P., *et al.* (2010). Rapid evaluation of threats to biodiversity: Human footprint score and large vertebrate species responses in French Guiana. *Biodivers. Conserv.*, 19, 1567–1584.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., *et al.* (2004). Extinction risk from climate change. *Nature*, 427, 145–148.

Thompson, M., Vlok, J., Rouget, M., Hoffman, M.T., Balmford, A. & Cowling, R.M. (2009). Mapping grazing-induced degradation in a semi-arid environment: A rapid and cost effective approach for assessment and monitoring. *Environ. Manage.*, 43, 585–596.

Trakhtenbrot, A. & Kadmon, R. (2005). ENVIRONMENTAL CLUSTER ANALYSIS AS A TOOL FOR SELECTING COMPLEMENTARY NETWORKS OF CONSERVATION SITES. *Ecol. Appl.*, 15, 335–345.

Trindade-Filho, J., de Carvalho, R.A., Brito, D. & Loyola, R.D. (2012a). How does the inclusion of Data Deficient species change conservation priorities for amphibians in the Atlantic Forest? *Biodivers. Conserv.*, 21, 2709–2718.

Trindade-Filho, J. & Loyola, R.D. (2011). Performance and consistency of indicator groups in two biodiversity hotspots. *PLoS One*, 6.

Trindade-Filho, J., Sobral, F.L., Cianciaruso, M.V. & Loyola, R.D. (2012b). Using indicator groups to represent bird phylogenetic and functional diversity. *Biol. Conserv.*, 146, 155–162.

Troupin, D. & Carmel, Y. (2016). Landscape patterns of development under two alternative scenarios: Implications for conservation. *Land use policy*, 54, 221–234.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., *et al.* (2012). Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol. Rev.*, 87, 661–685.

Tulloch, V.J.D., Tulloch, A.I.T., Visconti, P., Halpern, B.S., Watson, J.E.M., Evans, M.C., *et al.* (2015). Why do We map threats? Linking threat mapping with actions to make better conservation decisions. *Front. Ecol. Environ.*, 13, 91–99.

Urbina-Cardona, J.N. & Flores-Villela, O. (2010). Ecological-niche modeling and prioritization of conservation-area networks for Mexican herpetofauna. *Conserv. Biol.*, 24, 1031–1041.

Vallejos, M., Volante, J.N., Mosciaro, M.J., Vale, L.M., Bustamante, M.L. & Paruelo, J.M. (2015). Transformation dynamics of the natural cover in the Dry Chaco ecoregion: A plot level geo-database from 1976 to 2012. *J. Arid Environ.*, 123, 3–11.

Velásquez-Tibatá, J., Salaman, P. & Graham, C.H. (2013). Effects of climate change on species distribution, community structure, and conservation of birds in protected areas in Colombia. *Reg. Environ. Chang.*, 13, 235–248.

Velez–Liendo, X., Adriaensen, F. & Matthysen, E. (2014). Landscape assessment of habitat suitability and connectivity for Andean bears in the Bolivian Tropical Andes. *Ursus*, 25, 172–187.

Venter, O., Fuller, R.A., Segan, D.B., Carwardine, J., Brooks, T.M., Butchart, S.H.M., *et al.* (2014). Targeting Global Protected Area Expansion for Imperiled Biodiversity. *PLoS Biol.*, 12.

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., *et al.* (2016a). Global terrestrial Human Footprint maps for 1993 and 2009. *Sci. Data*, 3, 273–281.

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., *et al.* (2016b). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat. Commun.*, 7, 12558.

Visconti, P., Pressey, R.L., Segan, D.B. & Wintle, B. a. (2010). Conservation planning with dynamic threats: The role of spatial design and priority setting for species' persistence. *Biol. Conserv.*, 143, 756–767.

Waldron, A., Mooers, A.O., Miller, D.C., Nibbelink, N., Redding, D., Kuhn, T.S., *et al.* (2013). Targeting global conservation funding to limit immediate biodiversity declines. *Proc. Natl. Acad. Sci.*, 110, 12144 LP – 12148.

Warman, L.D., Sinclair, A.R.E., Scudder, G.G.E., Klinkenberg, B. & Pressey, R.L. (2004). Sensistivity of systematic reserve selectionn to decisions about scale, biological data, and targets: case study from southern british columbia. *Conserv. Biol.*, 18, 655–666.

Wassenaar, T., Gerber, P., Verburg, P.H., Rosales, M., Ibrahim, M. & Steinfeld, H. (2007). Projecting land use changes in the Neotropics: The geography of pasture expansion into forest. *Glob. Environ. Chang.*, 17, 86–104.

Watson, J.E.M., Dudley, N., Segan, D.B. & Hockings, M. (2014). The performance and potential of protected areas. *Nature*, 515, 67–73.

Weinzettel, J., Vačkář, D. & Medková, H. (2018). Human footprint in biodiversity hotspots. *Front. Ecol. Environ.*, 16, 447–452.

Williams, P.H. (1998). Key sites for conservation: area - selection methods for biodiversity. In: *Conservation in a changing world: integrating process into priorities for action* (eds. Mace, G.M., Balmford, A. & Ginsberg, J.R.). Cambridge University Press, Cambridge, pp. 211 – 249.

Williams, P.H., Gaston, K.J. & Humphries, C.J. (1997). Mapping biodiversity value worldwide: combining higher-taxon richness from different groups. *Proc. R. Soc. London. Ser. B Biol. Sci.*, 264, 141–148.

Williams, P.H., Moore, J.L., Toham, A.K., Brooks, T.M., Strand, H., D'Amico, J., *et al.* (2003). Integrating biodiversity priorities with conflicting socio-economic values in the Guinean–Congolian forest region. *Biodivers. Conserv.*, 12, 1297–1320.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027–2027.

Wilson, K.A., Auerbach, N.A., Sam, K., Magini, A.G., Moss, A.S.L., Langhans, S.D., *et al.* (2016). Conservation Research Is Not Happening Where It Is Most Needed. *PLOS Biol.*, 14, e1002413.

Wilson, K.A., Cabeza, M. & Klein, C.J. (2009). Fundamental Concepts of Spatial Conservation Prioritization. In: *Spatial Conservation Prioritization – Quantitative Methods and Computational Tools* (eds. Moilanen, A., Wilson, K.A. & Possingham, H.P.). Oxford University Press, New York, pp. 16–27.

Wilson, K.A., Evans, M.C., Di Marco, M., Green, D.C., Boitani, L., Possingham, H.P., *et al.* (2011). Prioritizing conservation investments for mammal species globally. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.*, 366, 2670–2680.

Wilson, K.A., McBride, M.F., Bode, M. & Possingham, H.P. (2006). Prioritizing global conservation efforts. *Nature*, 440, 337–340.

Wilson, K.A., Underwood, E.C., Morrison, S.A., Klausmeyer, K.R., Murdoch, W.W., Reyers, B., *et al.* (2007). Conserving biodiversity efficiently: What to do, where, and when. *PLoS Biol.*, 5, 1850–1861.

Wilson, K.A., Westphal, M.I., Possingham, H.P., Elith, J. & Wilson Westphal, M. I., Possingham, H. P., Elith, J, K.A. (2005). Sensitivity of conservation planning to different approaches to using predicted species distribution data. *Biol. Conserv.*, 122, 99–112.

Wintle, B. a., Bekessy, S. a., Keith, D. a., van Wilgen, B.W., Cabeza, M., Schröder, B., *et al.* (2011). Ecological–economic optimization of biodiversity conservation under climate change. *Nat. Clim. Chang.*, 1, 355–359.

Wood, L.J. & Dragicevic, S. (2007). GIS-based multicriteria evaluation and fuzzy sets to identify priority sites for marine protection. *Biodivers. Conserv.*, 16, 2539–2558.

Wright, R.G., MacCracken, J.G. & Hall, J. (1994). An ecological evaluation of proposed new conservation areas in Idaho: Evaluating proposed Idaho national parks. *Conserv. Biol.*, 8, 207–216.

Wright, S.J. (2010). The future of tropical forests. *Ann. N. Y. Acad. Sci.*

Wu, J. (2000). Slippage Effects of the Conservation Reserve Program. *Am. J. Agric. Econ.* , 82, 979–992.

WWF & IUCN. (1998). *Centers of Plant Diversity*. WWF & IUCN, Cambridge.

Xiaofeng, L., Yi, Q., Diqiang, L., Shirong, L., Xiulei, W., Bo, W., *et al.* (2011). Habitat evaluation of wild Amur tiger (Panthera tigris altaica) and conservation priority setting in north-eastern China. *J. Environ. Manage.*, 92, 31–42.

Zupan, L., Cabeza, M., Maiorano, L., Roquet, C., Devictor, V., Lavergne, S., *et al.* (2014). Spatial mismatch of phylogenetic diversity across three vertebrate groups and protected areas in Europe. *Divers. Distrib.*, 20, 674–685.