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**SPATIAL INSIGHTS FOR MANAGEMENT AND CONSERVATION
OF ECOSYSTEM SERVICES AND BIODIVERSITY FOR A
SUSTAINABLE FUTURE**

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SPATIAL INSIGHTS FOR MANAGEMENT AND CONSERVATION
OF ECOSYSTEM SERVICES AND BIODIVERSITY FOR A SUSTAINABLE FUTURE

Orientador: Prof. Dr. Milton Cezar Ribeiro

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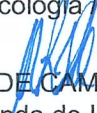
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To past, current and future generations.

*Ao meu pai e à minha mãe,
à minha irmã e ao meu irmão,
aos meus dois preciosos sobrinhos.*

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*“in order to change an existing imagined order,
we must first believe in an alternative imagined order.”*

Yuval Noah Harari

Sapiens: A Brief History of Humankind, p. 118

RESUMO

INFORMAÇÕES ESPACIAIS PARA GESTÃO E CONSERVAÇÃO DOS SERVIÇOS ECOSISTÊMICOS E DA BIODIVERSIDADE PARA UM FUTURO SUSTENTÁVEL

Compreender como os padrões e processos da paisagem afetam a biodiversidade e os serviços ecossistêmicos (ES) – benefícios que as pessoas recebem da natureza – é fundamental para prever suas respostas às mudanças no uso da terra. Para avançar na pesquisa, desenvolver e fornecer informações espaciais apropriadas para as tomadas de decisão, utilizei modelagem e proposições teóricas para expandir o conhecimento sobre serviços ecossistêmicos, biodiversidade e o papel desempenhado pelos seres humanos na conservação da paisagem e seu manejo sustentável. No capítulo 1, considerando a teoria atual e as lacunas de conhecimento acerca de ES, eu propus um *framework* para entender melhor os efeitos da estrutura da paisagem no fluxo de ES, um dos componentes da cadeia de provisão de ES. Com base na literatura, discuti os efeitos da composição e configuração da paisagem nos fluxos de ES, de acordo com seus mecanismos. Enfatizei a necessidade de caracterizar a oferta, o fluxo e a demanda de cada ES, a fim de quantificar e abordar completamente os aspectos espaciais da provisão de ES. No Capítulo 2, identifiquei *hotspots* de biodiversidade usando Modelos de Distribuição de Espécies (SDM) baseados em clima e paisagem para indicar áreas prioritárias para conservação e aquelas ameaçadas por mudanças rápidas no uso da terra, impulsionadas pelo desmatamento e expansão agrícola. Os *hotspots* de biodiversidade representam as áreas com potencial para hospedar várias espécies-chave e, portanto, estas são regiões-chave para serem protegidas. A seleção das espécies e a interpretação dos resultados dos modelos foram realizadas para o Maranhão (um estado brasileiro), enquanto a coleta e modelagem dos dados foram realizadas para um limite ecológico mais amplo. Indiquei as áreas com maior sobreposição de *hotspots* de espécies e não abrangidas pelas áreas protegidas existentes como prioritárias para ações de conservação. Reconheci a necessidade urgente de monitorar áreas com expansão agrícola. Por fim, concluí a tese com uma síntese das principais contribuições, recomendações para futuras pesquisas e uma reflexão sobre as lições aprendidas durante o desenvolvimento do meu doutorado.

PALAVRAS-CHAVE: estrutura da paisagem; fluxo de serviço ecossistêmico; área prioritária para conservação; modelo de distribuição de espécie; Maranhão; sustentabilidade

ABSTRACT

SPATIAL INSIGHTS FOR MANAGEMENT AND CONSERVATION OF ECOSYSTEM SERVICES AND BIODIVERSITY FOR A SUSTAINABLE FUTURE

Understanding how landscape patterns and processes affect biodiversity and ecosystem services (ES) – the benefits people receive from nature – is fundamental to predict their responses to land use change. To advance research, develop, and deliver appropriate spatial information for decision-making, I used models and theory to expand the knowledge about ecosystem services, biodiversity and the role played by humans in landscape conservation and sustainable management. In Chapter 1, taking into account the current theory and knowledge gaps related to ES, I proposed a framework to better understand the effects of landscape structure on the flow component of the ES supply chain. Based in the literature, I discussed the effects of landscape composition and configuration in the ES flows, according to their mechanisms. I emphasized the need to characterize the supply, flow and demand of each ES in order to quantify and thoroughly address the spatial aspects of ES provision. In Chapter 2, I identified biodiversity hotspots using climate- and landscape-based Species Distribution Models (SDM) to indicate priority areas for conservation and those areas threatened by fast land use change driven by deforestation and agriculture expansion. Biodiversity hotspots allowed the recognition of areas with the potential to host several key species and, therefore, those are key regions to be protected. The selection of species and the interpretation of model outputs were conducted for Maranhão, a state in Brazil, while data collection and modelling itself were carried out for a broader ecological boundary. I indicated the priority areas to be conserved as those with higher overlap of species hotspots and not encompassed by existing protected areas. I recognize urgent need to monitor areas with agriculture expansion. Lastly, I concluded the thesis with a synthesis of the main contributions, recommendations for further research and a reflection on the lessons learned during the development of my PhD.

KEYWORDS: landscape structure; ecosystem service flow; priority area for conservation; Species Distribution Model; Maranhão; sustainability

RESÚMEN

INFORMACIÓN ESPACIAL PARA GESTIÓN Y CONSERVACIÓN DE LOS SERVICIOS DE ECOSISTEMAS Y DE LA BIODIVERSIDAD PARA UN FUTURO SOSTENIBLE

Comprender cómo los patrones y procesos del paisaje afectan la biodiversidad y los servicios del ecosistema (ES) – los beneficios que las personas reciben de la naturaleza – es fundamental para predecir sus respuestas al cambio en el uso de la tierra. Para avanzar en la investigación, desarrollar y entregar información espacial apropiada para la toma de decisiones, utilicé modelos y teoría para expandir el conocimiento sobre los ES, la biodiversidad y el papel que juegan los humanos en la conservación del paisaje y su gestión sostenible. En el Capítulo 1, teniendo en cuenta la teoría actual y las brechas de conocimiento relacionadas con los ES, propuse un marco para comprender mejor los efectos de la estructura del paisaje en el componente de flujo de la cadena de provisión de ES. Con base en la literatura, discutí los efectos de la composición y configuración del paisaje en los flujos de ES, de acuerdo con sus mecanismos. Destaqué la necesidad de caracterizar la oferta, el flujo y la demanda de cada ES para cuantificar y abordar a fondo los aspectos espaciales de la provisión de ES. En el Capítulo 2, identifiqué los puntos críticos de biodiversidad utilizando los modelos de distribución de especies (SDM) basados en el clima y el paisaje para indicar áreas prioritarias para la conservación y aquellas áreas amenazadas por el cambio rápido del uso de la tierra impulsado por la deforestación y la expansión de la agricultura. Los puntos críticos de biodiversidad permitieron reconocer las áreas con el potencial de albergar varias especies clave y, por lo tanto, las regiones clave a proteger. La selección de especies y la interpretación de los resultados del modelo se realizaron para el estado brasileño de Maranhão, mientras que la recolección de datos y el modelado en sí se llevaron a cabo para un límite ecológico más amplio. Indiqué las áreas prioritarias a ser conservadas como aquellas con mayor superposición de puntos críticos de especies y no abarcadas por áreas protegidas existentes. Reconocí la necesidad urgente de monitorear áreas con expansión agrícola. Finalmente, concluí la tesis con una síntesis de las principales contribuciones, recomendaciones para futuras investigaciones y una reflexión sobre las lecciones aprendidas durante el desarrollo de mi doctorado.

PALABRAS CLAVE: estructura del paisaje; flujo de servicio ecosistémico; área prioritaria para la conservación; modelo de distribución de especie; Maranhão; sustentabilidad

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BACKGROUND

Humanity is a pervasive species that managed to reach every corner of the planet. Even if there were hidden, or unexplored venues, if any of us acknowledges its existence, one could argue it does not exist at all.

Nature and Conservation

Conservation is a human action – be it to protect nature from humans or to spare it for humans themselves. Mace (2014) provoked this debate by showing the changes over time of conservation goals and the science underpinning them. According to her, for some decades, conservation science was targeted at sparing pristine natural assets from human interference. The Anthropocene has come to shift that framing into a more integrative one, in which people are viewed as part of nature. Thus, science has had to dive into human-nature relationships and envision their sustainable co-existence (Johnson et al., 2017). The complexity of social-ecological systems, once we frame people and nature together (i.e. a biocentric worldview), demands further collaboration between social and natural sciences (Bennet et al. 2015). So far, sustainability has evolved as the most promising idea to guide us into the future.

Sustainability

Science has managed to evolve the concept of sustainability since the 1980's (Sartori et al., 2014), however, its conversion into practice is yet to be broadly incorporated by humanity (Purvis et al., 2019). Strong sustainability argues that our “finite planet cannot sustain human life with an economy that intends unlimited growth” (Morandín-Ahuerma et al., 2019). Also, sustainability relies on consumption behavior that do not deteriorate ecosystems and leads to social equity (Morandín-Ahuerma et al., 2019). Having economic values over culture is driving humanity past planetary boundaries. In great effort to reverse this trend and rethink human activities, the Sustainable Development Goals (SDG) were proposed to guide human actions towards a sustainable future (UN, 2016), addressing human population growth, the role of economy in serving us (and not otherwise), greenhouse gases emissions, pollution, biodiversity loss and the spread of invasive alien species, among several other goals (Griggs et al., 2013; Morandín-Ahuerma et al., 2019; Ripple et al., 2017). Changing and adjusting our societal, institutional and individual behaviour towards sustainable habits is the way forward to guarantee nature's limits are not surpassed (Griggs et al., 2013; Rockström et al., 2009).

Science Goals, Economic ‘Rules’ and Political Decisions

If we could evaluate the positions and responsibilities assumed by scientists, economists and politicians in human societies, we could find that scientists are usually engaged with facts and knowledge derived from sound scientific analysis (Bradford, 2017); while economists are mostly driven by people’s behaviour and choices in different contexts (Guerry et al., 2015); and politicians would search for ways to please those who have the power to keep them in power and prioritize decisions based on public opinion (i.e. populism; Dal Bó et al., 2017).

Who rules the world? I wish the answer was “Girls”, but we are not there yet. Instead, most nations have political leaders that respond to international markets and aim at economic growth. Rarely, governments main goals are to promote equity and pay off historical debts towards unprivileged groups. Even more unexpected is to have politicians that fight historical privileges. And even when parts of society disagree with politicians’ behaviour, very little can they do to demand changes. Recently, however, participatory approaches have emerged to give voice to different groups interested in a matter so that decisions and plans could address diverse interests (Arnstein, 2019). Yet, most decisions still rely on economic profit over environmental viability, and the two overrule social justice. Building a dam that harms indigenous communities, building a road that passes over a low-income neighborhood, undertaking new mineral exploitation and annulling a protected area for that: these are political decisions, pushed by economic pressure from private companies in detriment of less privileged communities. This is how the world works.

Should scientists become politicians, should economists remember they are social scientists, or should politicians become extinct? Integration among social, environmental and economic sciences are leading the way towards better decision-making (Guerry et al., 2015). From the science perspective, bridging the gap between science and society and the gap between theory and practice can put humanity on the sustainability path (Griggs et al., 2013). The role of scientists in overcoming the gap between science and policy has usually been performed as translating scientific discoveries to decision makers. Decades have passed to prove this is not enough. Communicating scientific advances to the general public and discussing the social implications of research outcomes has recently begun to be one of the scientist’s duties (Dickson, 2010). Scientists have the power to go further

and have stakeholders be part of the construction of knowledge since the beginning: from the conception of a research project to its closure (Elena M Bennett et al., 2015). Therefore, engaging with on the ground practitioners, NGOs, communities, and any other groups of interest has been explored through participatory approaches (Angelstam et al., 2019a) and the co-production of knowledge “to ensure that interventions and policies have appropriate impact and can operate across multiple temporal and spatial scales” (Elena M. Bennett et al., 2015).

The Ecosystem Service Framework

The concept of Ecosystem Services (ES) emerged in line with the concept of strong sustainability, which primarily claims the non-substitutability of natural capital (Ekins et al., 2003), and the creation of a shared vision of what a sustainable society would actually look like (Costanza et al., 1997). It derived from Westman’s (1977) idea of nature’s services and was later coined as ES by Ehrlich and Ehrlich (1981). Despite some variation in the concept, ES has drawn attention to the benefits that ecosystems generate for humans (Costanza et al., 1997; Daily et al., 1997; De Groot et al., 2002). Such benefits, that sustain and fulfill human life, result from the interactions among living and non-living elements of the ecosystems and human-engineered components of social-ecological systems (Daily et al., 1997; Guerry et al., 2015). More than that, the concept of ES “provides a valuable framework to define and analyse linkages and dependencies between natural and human systems” (Burkhard et al., 2010).

Biodiversity plays a pivotal role for ecosystem functions maintenance, and therefore, for ES provision (Harrison et al., 2014). Boosted by the relevance of biodiversity and ES for the human wellbeing, some notable initiatives spread out to society the outlook of the challenging paradigm of sustainability: the Millennium Ecosystem Assessment (MA, 2005), The Economics of Ecosystems and Biodiversity (TEEB, 2010) and the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES, 2012; see Box 1 for more information). All of them converged in the combination of economy, ecology and society for the sustainable stewardship of natural capital (Angelstam et al., 2019a). The integration of participatory methods to improve ES frameworks, in a variety of social contexts, has proven to enhance social learning, build capacity and trust as well as work as a tool to mediate power relations (Davies et al., 2015). In the local level, it can offer an alternative source of income via Payment for Ecosystem Services (PES; Wang et

al., 2017). Another advantage in the use of ES frameworks is that they can be used to evaluate progress towards sustainability (to monitor the SDGs and the Aichi Targets; CBD, 2010), by monitoring the state and trends of ES provision and biodiversity (Geijzendorffer et al., 2017).

Box 1: Main international initiatives that spread out to society the challenges in the pursuit of sustainability.

MA – Millennium Ecosystem Assessment (MA, 2005)

The first comprehensive global assessment of the implications of ecosystem change for human wellbeing. It can be also considered the scientific basis for action needed to enhance the conservation and sustainable use of those systems and their contribution to people. ES are grouped into a) provision (e.g., food and water supply), b) regulation (e.g., climate regulation), c) cultural (e.g., recreational, spiritual activities), and d) support (e.g., photosynthesis). All these services performed for free by ecosystems are widely assumed to contribute to poverty alleviation and the degradation of these services is also assumed to result in negative effects on human wellbeing (Tallis et al., 2008). In this sense, a fully developed economics should routinely incorporate the value of ES into its analyses (Chapin et al., 2010; Polasky, 2012).

TEEB – The Economics of Ecosystems and Biodiversity (TEEB, 2010)

Five years after the MA a new global initiative emerged, TEEB, which focused on “making nature’s values visible”. Its principal objective is to mainstream the values of biodiversity and ES into decision-making at all levels. It aims to achieve this goal by following a structured approach to valuation that helps decision-makers recognize the wide range of benefits provided by ecosystems and biodiversity, demonstrate their values in economic terms and, where appropriate, suggest how to capture those values in decision-making.

IPBES – Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES, 2012)

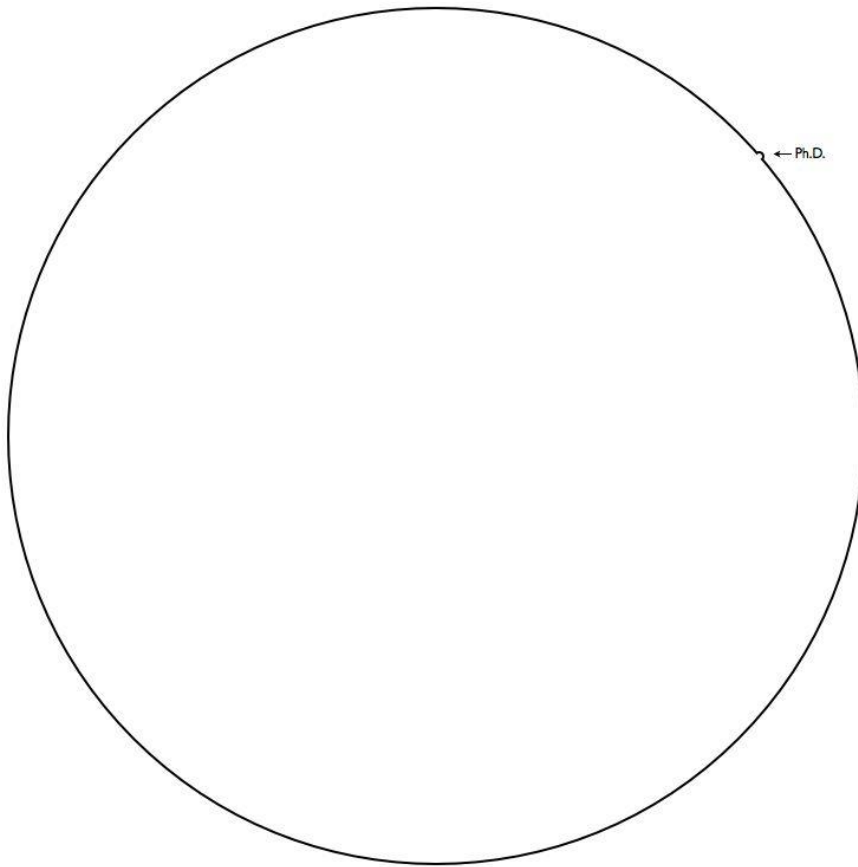
Despite the complexity of ES identification, quantification and valuation advances in data acquisition, methods and technology regarding ES approach have been consistent since the MA (Guerry et al., 2015). The next step requires the inclusion of such advances in the implementation of action plans, management and policies.

The IPBES was proposed as a mechanism to further strengthen the science-policy interface on biodiversity and ES. IPBES contributes to existing processes that ensure that decisions are made on the basis of the best available scientific information on conservation, sustainable use of biodiversity and ES. It was established in 2012 as an independent intergovernmental body open to all member countries of the United Nations. The members are committed to building IPBES as the leading intergovernmental body for assessing the state of the planet’s biodiversity, its ecosystems and the essential services they provide to society. More recently, they incorporated the concept of Nature’s Contributions to People (NCP) to broaden perspectives about the relationships between people and nature and include different worldviews (Díaz et al., 2018).

Spatial Planning Matters

Spatial planning provides the basis for the development and implementation of good governance by integrating legal, economic, social, and rights-based instruments (Albert et al., 2020). It provides the on-the-ground link for economic, social and environmental policies. Furthermore, the use of spatial instruments in decision making across scales emerges as a powerful tool to balance diverse interests (Angelstam et al., 2019a) and promote the engagement of stakeholders in planning decisions (Albert et al., 2020). One of the challenges highlighted by Albers et al. (2020) to target biodiversity and ES in spatial planning is having spatial information in appropriate resolution for multiple scales (i.e. different spatial resolution and extents of influence; Jackson and Fahrig, 2015). Besides, understanding how landscape patterns and processes affects biodiversity and ES is key to predict their responses to land use change and deliver appropriate spatial information (Jones et al., 2013). The inclusion of ES and biodiversity as targets in spatial planning requires not only tools capable of analysing trade-offs (Jones et al., 2013) and dealing with power asymmetries (Reed et al., 2017), but also a deeper understanding of how landscape patterns affects both of them (Jones et al., 2013).

Ruckelshaus et al. (2015) listed some lessons learned from 20 cases of application of biodiversity and ES information in decision-making. Among them, they recognized that creating a mutual understanding of ES and biodiversity-related information in an iterative science-policy process increases credibility and legitimacy of information to support decisions, despite being time consuming (Ruckelshaus et al., 2015). They also indicate that engaging with stakeholders to know what they need and empowering local experts enhance credibility and ownership of ES models and information resulting in effective contribution for the decision-making process (Ruckelshaus et al., 2015).



Keep pushing.

Matt Might¹
The Illustrated Guide to a Ph.D.²

¹ <http://matt.might.net/> Accessed in Jan/2020.

² <http://matt.might.net/articles/phd-school-in-pictures/> Accessed in Jan/2020.

MOVING THE GEAR AND PUSHING THE KNOWLEDGE FRONTIER

A conceptual framework to link landscape structure and ecosystem services

Contributions from Chapter 1

Economic demands and society's desires are drivers of land use modification with consequences to environmental conditions. Although there is a strong relation between land cover and ecosystems capacity to provide ES, some services may not present such a straightforward relationship, depending more on the condition and spatial pattern of land cover or even on social and economic configuration (Remme et al., 2014). In those cases, different data types – such as ecosystem condition and produced capital or human labor – can be combined to better represent ES in a given area (Hein, 2010).

The ES supply chain encompasses the components and processes of the provision of ES, which combines the supply (ecosystems assets) and the demand (people's needs) through flow (the 'delivery' of the service that is converted into benefit). Even though measuring and quantifying ES has been an intensively developing field (Willemen et al., 2015), further research is necessary to advance our understanding on how landscape structure affects the ES supply chain. Compelled by Michell et al. (2015) and their proposition on how landscape fragmentation *per se* (*sensu* Fahrig, 2003) can influence ES supply and flow, the purpose of Chapter 1 is to further explore how other landscape structure attributes (i.e. composition and configuration) may affect ES flow. Based on the literature and much discussion with my collaborators, I developed a theoretical framework hypothesising on the effects of landscape structure on ES flow. For this, we considered both the proportion of supply and demand within a landscape, and how ES flow mechanisms may work.

Among the potential contributions that may emerge from Chapter 1 are: 1) provoking the debate on how to address landscape influences on ES flow in future research; 2) building consensus regarding the components of the ES supply chain; and 3) advancing the understanding of landscape effects on them to assist spatial planning.

Contributions from Chapter 2

The expansion of agricultural land and other human activities (e.g., mining, transport infrastructure and urbanization) in developing countries has been positively reflected in economic growth. On the other hand, fast modification of landscapes causes ecosystem degradation that changes ecosystem functioning and their capability of generating services (Hein et al., 2016) that benefit human beings. Most tropical regions worldwide have gone through rapid land use change and biodiversity loss (Alroy, 2017). Within the current institutional decision-making framework, mainly based on economic profits, ecosystems and biodiversity are undervalued (UNEP-WCMC, 2015).

Pushing the economic paradigm to the edge, the United Nations, along with other organizations, have developed the System of Environmental Economic Accounting (SEEA). The SEEA has been tested worldwide under the Experimental Ecosystem Accounting to develop and test measures of environmental assets, ecosystem stocks and services. In the future, the SEEA will be coupled with the System of National Accounts (SNA), that measures the economic activity in an integrated set of macroeconomic accounts. Ultimately, the goal is to shift the current economic paradigm that does not consider the degradation of environmental resources towards a different perspective that combines economic indicators with environmental ones (for further information on the SEEA EEA see Appendix 1).

To accomplish this challenge, governments have been encouraged to develop the thematic accounts, which includes separately accounting for: air emissions; agriculture, forestry and fisheries; energy; water³; land use; ecosystem; biodiversity; and others. The proposition of Chapter 2 emerged to further develop the Biodiversity Account in tropical regions. The use of up to date modelling techniques to spatially quantify species diversity can be applied over time to set a baseline (using the climatic niche combined with 'original' land cover) and estimate changes over time (according to variation in land use).

³ The Brazilian Institute of Geography and Statistics (IBGE) has developed the SEEA for water, published in 2018, referring to the period between 2013 to 2015. Access in: Jan/2020. Available at: <

Even though the use of spatial information about biodiversity to prioritize areas for conservation is not new, it is still necessary in regions that do not have this type of information. The contributions of Chapter 2 are: 1) the use of a combined modelling approach to inform priority areas for conservation based on the potential spatial allocation of biodiversity hotspots; 2) the coupling of ecological and administrative boundaries to such approach; 3) the potential collaboration among experts to build up species databases for regions under intense land use change; and 4) the further development of the biodiversity accounts in the scope of the SEEA EEA.

THESIS OUTLINE

To develop my research, I used models and theory to expand the knowledge about ES, biodiversity and the role played by humans in landscape conservation and sustainable management. As I adventured myself through the ES field, I realized the complexity of human-nature related approaches and the two chapters presented here reflect my interdisciplinary nature. I was pushed by the constant desire of contributing to environmental decisions and management aimed at sustainable land use. In the ES framework, I recognized a fertile field for the integration of environmental, social and economic perspectives. I also realized the challenge presented by the complexity of this framework in bridging the gap between scientists and practitioners.

Chapter 1 initiated as a collective construction, for which I took the lead and based on much discussion, organized a theoretical proposition for understanding the effects of landscape structure on the flow component of the ES supply chain. Based in the literature, we discussed the effects of landscape composition and configuration in the ES flow. We emphasized the need to characterize the supply, flow and demand of each ES in order to quantify and thoroughly address how landscape structure can shape the ES flow.

Chapter 2 was developed to spatially address the status of biodiversity using Species Distribution Models (SDM) and the EcoLand approach, that combines climate- and landscape-based SDM. We adopted a broader modelling area based on ecological characteristics of species (to avoid model overfitting) and analysed the outputs for a more restrict spatial administrative boundary at the state level. We combined high values of the EcoLand as hotspots for several species and evaluated their utility in the identification of priority and threatened areas in face of deforestation and agriculture expansion.

After the two chapters, there is a closing section, in which I present a synthesis, recommendations and a personal reflection about the PhD challenges. Lastly, I present the additional activities I developed during my PhD, followed by my list of publications and a brief story about myself.

CHAPTER 1 – A CONCEPTUAL FRAMEWORK TO LINK LANDSCAPE STRUCTURE AND ECOSYSTEM SERVICES

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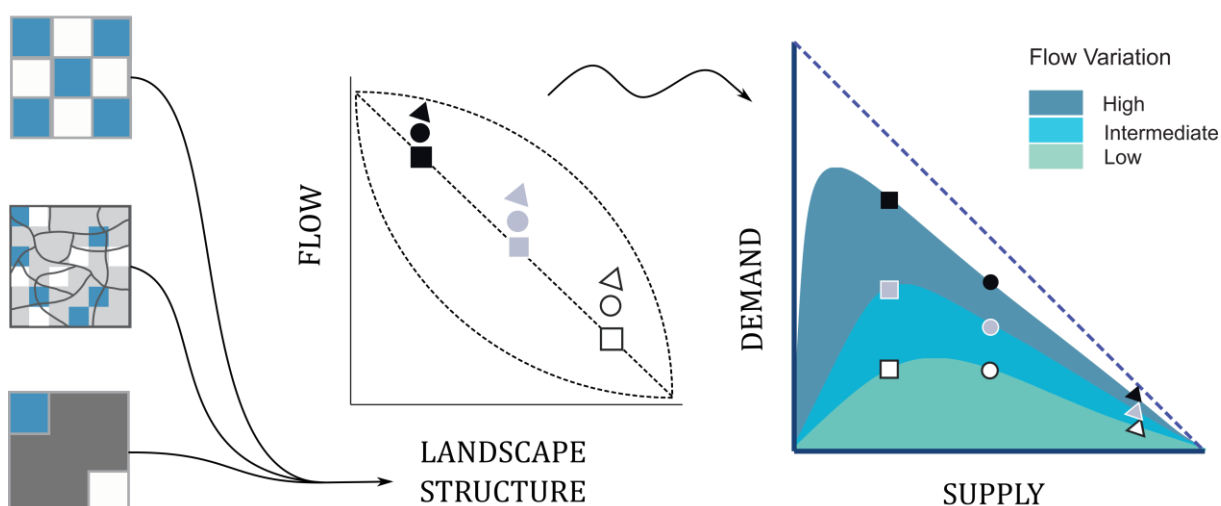
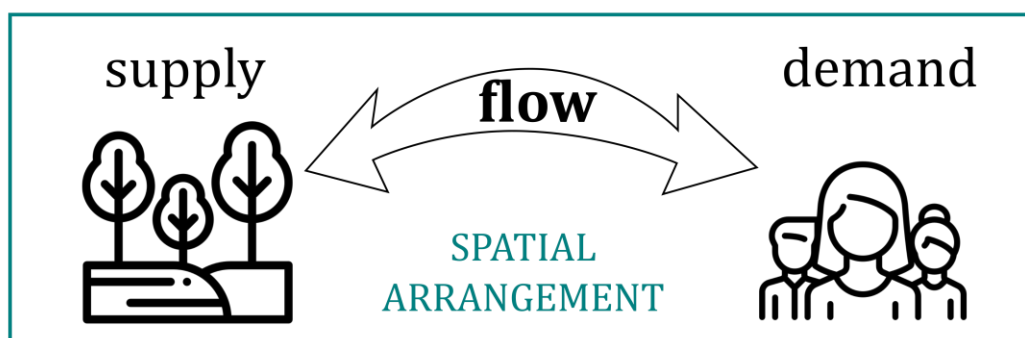
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ABSTRACT

The spatial arrangement of supply and demand along with landscape composition and configuration can determine the flow of ES. Therefore, understanding the effects of landscape structure in the components of the ES supply chain is fundamental to promote adequate landscape management that can, at the same time, guarantee sustainable provision of ES and the maintenance of ecosystem functions and biodiversity. In this research we investigate how ES flow can vary according to landscape structure, being facilitated or prevented to occur depending on the amount and spatial arrangement of ES supply and demand, as well as other landscape features. We addressed, besides habitat fragmentation *per se*, other landscape attributes – such as isolation, network complexity and matrix resistance – modulate the ES flow. Moreover, we postulated that the spatial arrangement of supply and demand areas determines the intensity of flow and whether maximum ES flow is attainable. We assume that certain landscape attributes will influence ES flow positively and others negatively, depending on the ES evaluated. Highly fragmented landscapes are expected to facilitate flow to a certain degree for pollinators, shaping pollination at local and landscape levels. Additionally, increasing isolation between supply and demand areas will decrease flow of pest control. Complementarily, network complexity may facilitate flow not depending on distance, but on existing connections, as is the case of outdoor recreation, whereas anthropogenic matrix resistance may be the limiting aspect in other cases. However, supply and demand can be overlapped in space and other elements may occur in the landscape, also interfering in ES flow. Thorough assessments of ES must account for the ES supply chain as a whole and further understand flow mechanisms in order to evaluate how landscape management can effectively optimize ES provision.

Keywords: Ecosystem Service Flow; Landscape Composition; Landscape Configuration

Potential Target Journals: Ecosystem Services; Trends in Ecology & Evolution; People and Nature

CONTEXT

Origin - the workshop

During five days in April 2018, I participated in the Workshop “Linking Landscape Structure to Ecosystem Services”, held at the Institute of Advanced Studies of the University of São Paulo. It was organized by Prof. Dr. Jean Paul Metzger and his team of the Landscape Ecology and Conservation Lab (LEPaC). The focus of the workshop was to promote a debate and collaboration among its participants to tackle the relationship between landscape structure and the components of the ES supply chain (supply-flow-demand). FAPESP (Project #217/50015-5) funded the event.

Conception of the idea

Extensive debate was carried out along those days and establishing a common language was the first main challenge in the pursuit of new ideas and ways to further develop our understanding on how landscape influences ES. Several possible paths emerged during the very fruitful discussion. In the end of the workshop, the most successful ideas were intended to become papers. Out of three, I ended up in charge of one of them which focused on a spatial approach to further explore how landscape composition and configuration influence ES components.

Embodiment – proposition and development

As the first author in a varied group of collaborators, I struggled to translate into a manuscript outline the goals discussed during the workshop. After virtual meetings, several visits to LEPaC in São Paulo and plenty of reading, little by little, the manuscript gained shape.

1. INTRODUCTION

Intense human-induced landscape modification – mostly led by urbanization and agriculture expansion – deteriorates ecosystems conditions and directly affects biodiversity and ecosystem functions (Johnson et al., 2017; Maxwell et al., 2016). Consequently, the provision of ecosystem services (ES) that sustain human wellbeing are declining globally (IPBES, 2019). Increasing human population is accompanied by higher demands for resources, such as food, water and energy (de Amorim et al., 2018; de Fraiture and Wichelns, 2010; Godfray et al., 2010). Effective landscape management is required to guarantee the sustainable use of environmental assets, to assure the maintenance of adequate amounts of ES supply and to safeguard equity in the access of ES (Berbés-Blázquez et al., 2016; de Groot et al., 2010). The ES supply chain is composed of three components: supply, demand, and flow. The spatial arrangement of supply and demand along with landscape composition and configuration can determine the flow of ES (Bagstad et al., 2014). Therefore, understanding the effects of landscape structure in the components of the ES supply chain is fundamental to promote adequate landscape management that can, at the same time, guarantee sustainable provision of ES and the maintenance of ecosystem functions and biodiversity.

The supply and the demand components of the ES chain have been more extensively addressed in spatial terms, but not the flow. In this research we investigate how ES flow can vary according to landscape structure (composition and configuration), being facilitated or prevented to occur depending on the amount and spatial arrangement of ES supply and demand as well as other elements throughout the landscape.

2. DECOMPOSING THE ECOSYSTEM SERVICE CONCEPT

The ES concept is a plural concept, able to navigate from a boundary object (i.e. adaptable to context and robust enough to enable communication) to a set of institutionalized infrastructures to operationalize the framework (Ainscough et al., 2019). Due to its complexity and interdisciplinarity, the characterization of ES as an applicable framework in distinct socio-environmental contexts has been widely discussed in the literature (Costanza et al., 2017). Decomposition of the ES supply chain has become more consensual as research digs deep in quantification and valuation methods and requires the distinction between the steps for ES provision. It becomes clear that the actual realization of an ES will only occur with the *flow* of ES from *supply* areas to *demand* areas

(Burkhard et al., 2014; Schröter et al., 2018; Villamagna et al., 2013). Hereafter, we assume the provision of ES depends on these three components: a) supply as the ecosystem capacity or potential to provide a given service; b) flow as the actual realization of a service or its translation into benefits for people; and c) demand as the service needed, desired or required by people (see Glossary for more details).

While natural sciences embrace the supply side of ES (Martínez-Harms and Balvanera, 2012), broader participation of social sciences has further developed the demand side of ES (Wolff et al., 2017, 2015). Still, an interdisciplinary approach between economics, natural, and social sciences has been fundamental to integrating ES components and to address ES flow (Baró et al., 2016; Felipe-Lucia et al., 2015; Geijzendorffer et al., 2015; Palomo et al., 2013; Schröter et al., 2018). Interdisciplinarity is essential in this field, mostly because ES flows oscillate from geophysical and ecological processes (e.g., air mass movement for air pollution filtering; and the movement of organisms for pollination and biological pest control; de la Barrera et al., 2016; Grote et al., 2016; Medeiros et al., 2019) up to cultural appropriation (e.g., symbolism related to nature bonding; Fish et al., 2016; Schirpke et al., 2018), human agency and economic transactions (e.g., crop transportation and markets; Yu et al., 2013).

Despite some variation in the definition of ES flow, there is a certain consonance in the way researchers address it. They may address the spatial matches and mismatches between supply and demand using the term ES flow itself (as in Baró et al., 2016; Felipe-Lucia et al., 2015; Ortiz et al., 2018; Palomo et al., 2013; Schirpke et al., 2019; Wolff et al., 2015) or, in other cases, using different terms (e.g., “actual use” in Schröter et al., 2012, “match” in Schulp et al., 2014). Some studies also deal with the spatial congruence of ES supply and demand, without directly addressing ES flows (see Geijzendorffer et al., 2015; Stürck et al., 2014; Willemen et al., 2012). Consolidation in the definition of ES flow is an ongoing process, and the understanding of its role in management and planning is of utmost importance to advance the discussion in the ES field.

Environmental planning to secure the sustainable use of multiple ES depends on our comprehension of landscape relationships with ES supply, flow and demand and the spatial links between these ES components. Landscape management to optimize ES flow can be further developed by understanding (i) the spatial scale of ES components (Lamy et al., 2016; Mitchell et al., 2015b; Schirpke et al., 2019a; see Glossary), (ii) the spatial

(mis)matches between supply and demand (Baró et al., 2017; Geijzendorffer et al., 2015; Syrbe and Walz, 2012) and (iii) how landscape structure modulates ES flows (Baró et al., 2016) and therefore ES provision. Here we propose a spatially explicit framework relating landscape structure to ES focusing on ES flow.

3. HOW TO LINK LANDSCAPE STRUCTURE TO ECOSYSTEM SERVICES?

Several studies evaluated the relationship between landscape and specific ES, limiting their analysis to how certain landscape attributes affect ES supply (for a few examples see Hodder et al., 2014; Inkoom et al., 2018; Liu et al., 2017; for reviews see Duarte et al., 2018; Lamy et al., 2016; Mitchell et al., 2013; Verhagen et al., 2016). There is a recurrent recognition of trade-offs between provisioning and regulating services as the landscape is managed to increase the supply of one type of ES over the other (Jopke et al., 2015; Raudsepp-Hearne et al., 2010). A simple explanation lies in the fact that most regulating services are provided by natural ecosystems whereas provisioning services – such as food, timber and fiber – come mostly from agroecosystems that are expanded at the expense of natural areas. In this example, increasing the provision of food would lead to decreases in pollination services (see meta-analysis on landscape structure effects on ES by Duarte et al., 2018). However, consideration of ES components separately (supply, flow and demand) can reveal more complex relationships between different ES, as well as how landscape structure shapes ES (Schirpke et al., 2019a).

On the demand component of ES, there is evidence that demand for multiple ES direct or indirectly drives landscape modifications (Willemen et al., 2012). These drivers usually manifest in the form of economic pressures on crop, animal, and industrial production, resulting in land-use change (von Haaren et al., 2019). Main drivers of forest loss worldwide include agricultural expansion for commodities and food production as well as forestry and wildfire (Curtis et al., 2018). As a consequence of increasing provisioning services several regulating services are threatened without being accounted for (e.g., flood control, water regulation and carbon storage). Consequently, a number of attempts to manage land use and reduces the chances of undesired changes emerge in the form of policies, governance or market instruments.

There are cases in which different spatial scales of supply and demand or a lack of a thorough description of the ES flow mechanism limit the assessment of ES instead of promoting an integrative spatial approach for landscape structure and ES components (cf.

(Serna-Chavez et al., 2014). Still, the application of the ES framework has led to a broader understanding of decoupled ES (i.e. when supply and demand occur at different spatial scales or landscapes, see Glossary) and, therefore, international or interregional flows have become more tangible (see Kastner et al., 2011; Koellner et al., 2019; Schröter et al., 2018). Despite relevant advances in integrative approaches for non-decoupled ES (i.e. when the ES supply and demand occur within a landscape, see Glossary), the understanding of how landscape structure affects flow is still superficial. We know that distance-dependent ES flows (e.g., pollination, in which the distance from crops to natural habitats matters; (Brosi et al., 2008; Ferreira et al., 2015) are usually most affected by landscape configuration (Baró et al., 2016; Mitchell et al., 2014), especially by the arrangement of supply and demand in space and which land uses lie between them (Serna-Chavez et al., 2014).

Landscape structure has been commonly addressed through habitat loss and fragmentation, landscape complexity, spatial heterogeneity and connectivity, however not always using similar metrics and hindering comparison between studies (Duarte et al., 2018; Fahrig et al., 2011; Larterra et al., 2012; Mitchell et al., 2015a, 2013). Serna-Chavez et al. (2014) suggest that landscape metrics can assist the assessment of ES flow, once anthropogenic or natural barriers can affect landscape permeability for ES flows. Mitchell et al. (2015b) made a theoretical proposition about the effects of landscape fragmentation *per se* (*sensu* Fahrig, 2003) on ES supply and flow, without explicitly addressing ES demand. However, the understanding of ES flow, especially for non-decoupled ES, depends on the recognition of demand areas that benefit from ES flow (Serna-Chavez et al., 2014).

For a better understanding on how landscape structure influences ES components (supply, flow and demand) and thus ES provision, going beyond only the effects of habitat fragmentation *per se* (Fahrig, 2003; Mitchell et al., 2015b), we need to fulfil several knowledge gaps: a) understanding the socio-economic drivers of landscape modification; b) how to predict trends and variation of ES responses to landscape structure over time; and c) critically assess synergies and trade-offs between emerging patterns of multiple ES. Thus, by further understanding the spatial distribution of supply and demand and the mechanisms of flow we can comprehensively understand how to manage landscapes to enhance supply and promote the sustainable flow of ES to meet existing demands.

Based on the ES theoretical framework (Figure 1), here we address how the ES supply and demand ratio (see Glossary), their spatial arrangement, and landscape structure modulate ES flow. For this we a) demonstrate how different landscape features can affect ES flow; b) integrate neutral areas in the landscape composition exploring the supply/demand spatial relationship including supply/demand overlap; and c) point out the challenges and propose a research agenda to enable landscape management to optimize ES flow.

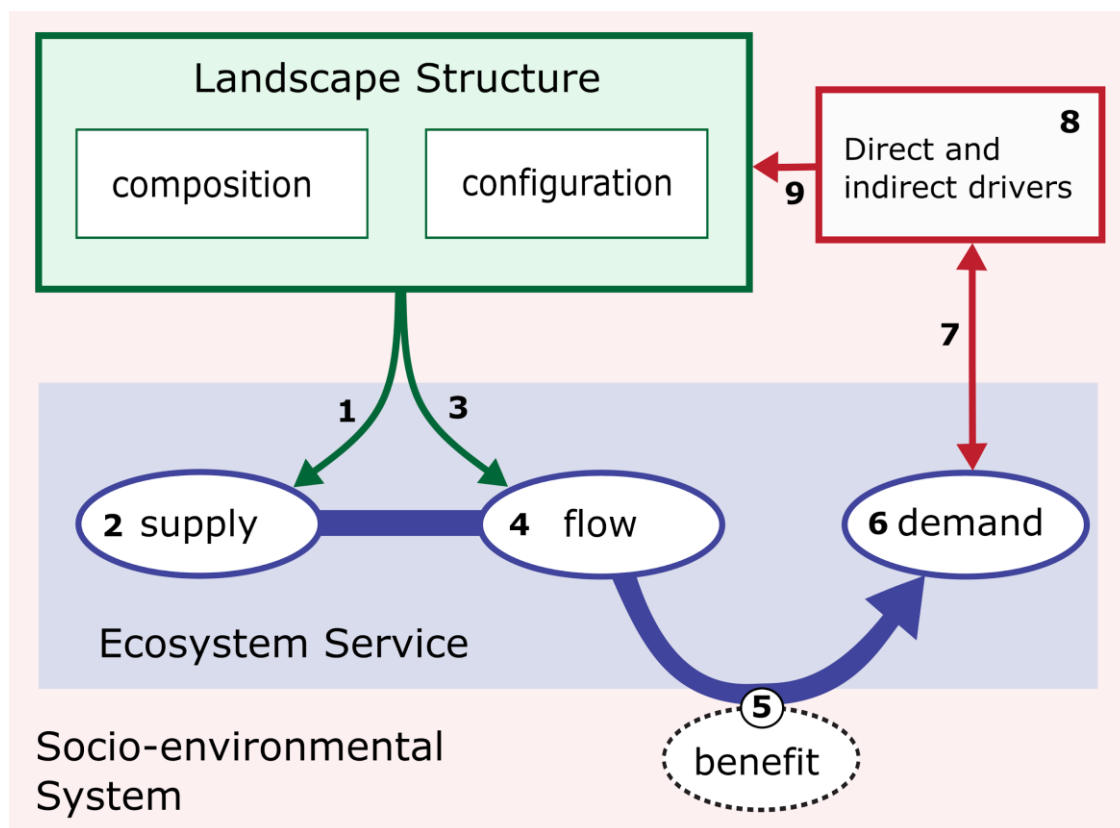


Figure 1: Conceptual model linking landscape structure and components of the ES supply chain. Landscape structure (both composition and configuration) can directly influence the condition of ecosystems (1) (e.g., their amount in the landscape or the quality of ecological processes within them) and, therefore, their capacity to supply ES (2). Landscape structure can also modulate the actual flow of ES (3), shaping their direction, permeability and amount (4). The demand fulfilment depends on the flow of ES and the conversion of ES supply into a benefit for humans (5). We argue that demand is mostly influenced by social aspects (6) and can be one of the drivers (7, 8) of changes in landscape configuration and composition. Other drivers (8) such as climate change, infrastructure development and urban expansion, can also lead to landscape modification (9). Similarly, political and economic instruments (8), like Payment for Ecosystem Services (PES), can be used to manage landscapes (9) with the purpose of increasing benefits to people via supply enhancement (1) or flow facilitation (3). (Adapted from Mitchell et al., 2015b).

4. ES FLOW MODULATED BY LANDSCAPE STRUCTURE

ES flow can be modulated by the spatial arrangement of ES supply and demand areas. Therefore, identifying and mapping such elements is a first step to clarify how ES flow occurs within landscapes. The way each ES is delivered to people (whether it depends on a specific medium to be transferred or not) is crucial to identify which landscape attributes to account for. Several researches explicitly describe ES flow mechanisms (Table S1), many of which are modulated by landscape structure. For instance, the flow of regulating services, like pollination and biological pest control within agroecosystems, depends on the effects of the landscape on pollinator communities and their ability to move. Whereas the flow of cultural services such as outdoor recreation depends mostly on transportation infrastructure connecting people to green spaces (Balmford et al., 2015).

To further explore the variation of ES flow we must investigate how it is modulated by the landscape and understand which landscape attributes may boost or hinder ES flow depending on the ES and the spatial distribution of supply and demand areas. For example, the erosion control service relies on a slope to be delivered, as well as on the location of vegetated areas (supply) and human settlements (demand) (Baró et al., 2017). In this case, the ES flow consists of risk reduction, meaning that the prevention of erosive processes (flow) benefits downslope human settlements. Modifying land use by removing natural vegetation uphill to create pastures, for example, would reduce the supply and flow for this regulating service, regardless to sparing adjacent downhill vegetation. Fragmentation or the aggregation of supply in this case could entirely modify the flow of the erosion control. Not only the amount of supply but how it is arranged may interfere in how much service is provided. In a steep slope landscape, the more aggregated the uphill vegetation is, the more it prevents erosion. However, in a hilly but not so steep region, a certain degree of fragmentation may optimize the amount of service provided.

In another case, pollination is modulated by the capacity of pollinators that inhabit surrounding forest patches (supply) to move to a pollination-dependent crop (demand) to perform the pollination service by visiting multiple flowers. In this example, a more fragmented landscape may result in more contact (edge) between supply and demand facilitating the access of pollinators to crops to perform pollination (Figure 2a). In less fragmented landscapes with a continuous habitat patch adjacent to a large homogeneous

pollination-dependent crop, core crop areas would be more difficult to be reached by pollinators due to distance and possibly to movement resistance imposed on pollinators by crop matrix.

Recreation services usually depend on people's mobility via any means of transportation, be it terrestrial, aerial or waterway. As an illustration, consider a park with natural attractions such as an impressive waterfall (supply). Visitation of the waterfall will depend on peoples' will to visit this location (demand) and their ability to get there (i.e. the existence of roads, bus lines, bike paths or the proximity to a train station). In this example, ES flow occurs when people commute from their homes to the park. Distance from residence to the park may act as a limiting factor (Figure 2b), that can be overcome by the existence of transportation infrastructure (Figure 2c). However, the spatial arrangement of transportation infrastructure can be heterogeneous and focused on a particular demand, for instance, connecting the park to the main nearby urban centre. In this case, it could be easier for people that live in the city to access the park instead of inhabitants of a closer nearby rural neighbourhood, due to accessibility (Figure 2c).

Moreover, timber, as a provision ES, depends on forest condition and tree stocks (supply), on logging activity, and transport capacity (ES flow) to be properly delivered (Figure 2c). In this example, demand for timber could be any factory or industry that uses timber as a raw material (Kastner et al., 2011). Besides, the matrix could pose a resistance to the access to timber (Figure 2d). If a certain tree species was to be reached within a dense forest, relief, streams and understory vegetation can be an obstacle to reach and transport timber to nearby roads. Or else, the presence of a navigable river can facilitate access to certain remote areas.

In these examples we illustrated how landscape configuration and the presence of certain elements within the landscape can facilitate or hinder the ES flow depending on its mechanism and the arrangement of supply and demand in space. In summary, we expect that combined landscape characteristics will present different effects on the flow, and the complexity of such combinations must be explored in further research.

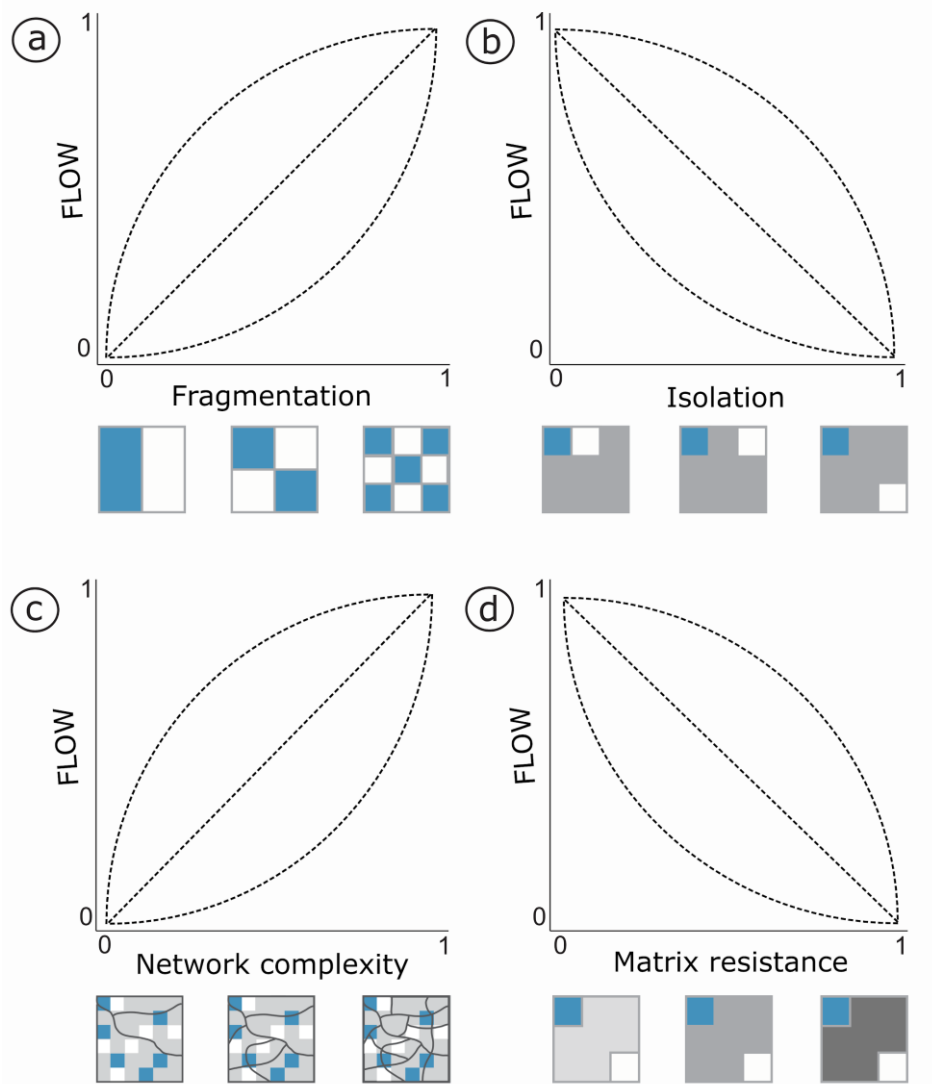


Figure 2: Landscape management to optimize flow must rely on the effects of landscape configuration and composition on ES flow. We assume that certain landscape attributes will influence ES flow positively and others negatively, depending on the ES evaluated. Higher levels of fragmentation *per se* are expected to increase interspersed between supply and demand, facilitating flow to a certain degree for pollination (a). Increasing isolation between supply and demand areas will decrease flow of pest control (b). Complementarily, network complexity may facilitate flow not depending on distance, but on existing connections, as is the case of outdoor recreation (c). Likewise, matrix resistance may be the limiting aspect in other cases (d).

5. THE SPATIAL RELATIONSHIP BETWEEN ECOSYSTEM SERVICE COMPONENTS

5.1. Supply-demand ratio and flow variation for rival and nonrival ESs

Given a hypothetical landscape in which all the space is occupied by ES supply or demand areas, varying from being totally occupied by demand to totally occupied by

supply, the maximum flow of a non-rival ES (see ES rivalry in Glossary) is not limited by the amount of supply once the flow can continuously occur without decreasing the supply. In such cases, the spatial arrangement of supply and demand in the landscape may prevent the maximum flow to occur (Figure 3a), leaving unattended demand. Using microclimate regulation as an example of non-rival ES, consider an urban green space capable of reducing heat islands within 100-m buffer area in a neighborhood (ES supply), no matter how many people stand in this buffered area (ES demand), the maximum flow will not be limited by demand. Therefore, if the maximum amount of demand possible is placed within the 100m buffer, the flow will be enough to satisfy it. Notice that in this case (and in others for which distance matters), the spatial distribution of supply can restrict the flow of the service depending on distance between supply and demand areas (Figure 3a and c). On the other hand, the maximum flow of a rival ES is limited by supply (Figure 3b). Using organic fruit produced in a community urban garden as an example of rival ES, the amount of supply will determine the demand that can be fulfilled. As demand for those organic fruit increases along with the number of people in the local community, the flow will be limited by the amount of fruit produced (Figure 3b).

In a landscape perspective, the arrangement of supply and demand areas determines the intensity of flow and whether maximum ES flow is attainable. In the case of microclimate regulation, the flow will vary depending on the interspersion and size of green areas. The more interspersed (i.e. fragmented) among households and sidewalks the higher the flow of the service (black filled symbols in Figure 3a and c). If all green space is concentrated in only one area or portion of the urban landscape, the temperature will be lower in this area and its 100-m surroundings but all the rest of the neighborhood further than that will not receive the flow (unfilled symbols in Figure 3a and c). For the provision of organic fruit, people living further from the garden could have more limited access to the fruits, while people living adjacent to it could have more ready-to-go access. In this example, ES flow can be modulated by distance between supply and demand and maybe the more centralized the garden is the higher the flow (grey and black filled circles in Figure 3b and c).

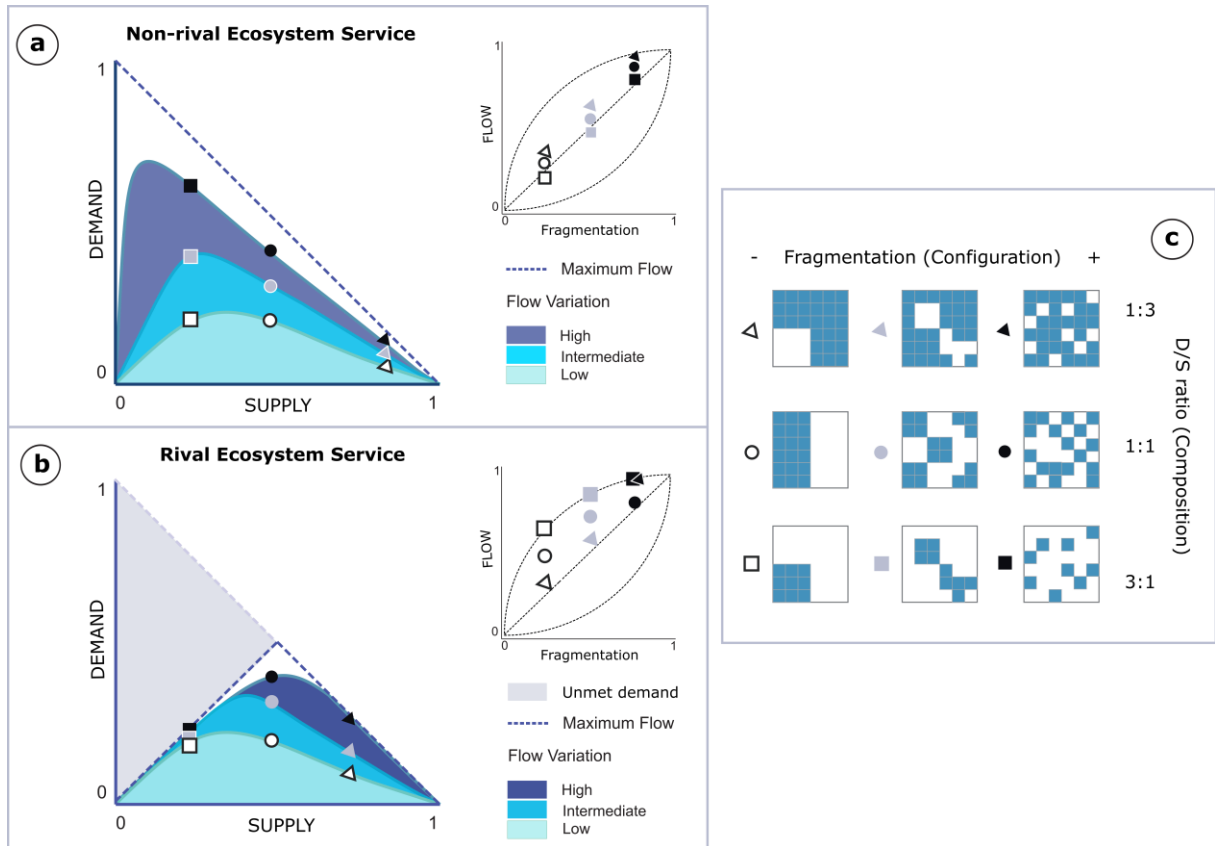


Figure 3: Variation of flow along a demand/supply ratio for (a) non-rival and (b) rival ecosystem services. Here we use a (c) variation in the degree of fragmentation between demand and supply units to illustrate how it may affect flow (a and b). Maximum flow (dashed line) is limited by supply for rival ecosystem services (b). Blue shades illustrate flow variation under different landscape structure (a and b). White areas below dashed line (maximum flow) represent unmet demand when supply is available (a and b); grey area above dashed line represents unmet demand due to supply unavailability (b). Black, grey and unfilled symbols represent possible landscapes with a varying degree of fragmentation and D/S ratio. Examples of flow representation illustrate the difference between non-rival and rival ES: for the first, flow from the same supply unit may attend multiple demand units while for the second, flow from one supply unit to a demand unit prevents the flow to another demand unit.

5.2. Neutral areas interference in ES

In a real landscape, the existence of supply and demand areas is usually accompanied by pervasive neutral areas (i.e. any land cover or land use that is not a supply or demand area for a given ES), different from what is shown in Figure 4a. In such cases, the supply-demand ratio is affected by a decrease in demand areas (Figure 4b), a decrease in supply areas (Figure 4c) or in both (Figure 4d). Using pollination as an example of a regulation service, in a landscape with forest remnants inhabited by pollinators (supply areas) and agricultural lands with a pollination-dependent crop (demand), the existence

of pastures dominated by an exotic grass species could be considered a neutral area for the pollination service, once it is not supply or demand area (Greenleaf et al., 2007; Ricketts, 2001). In this example, the amount (composition) and spatial arrangement (configuration) of landscape elements determine whether pollinators that inhabit the forest remnants can reach the crops and perform the service of pollination (i.e. ES flow).

If pastures were not present, the configuration of habitat and crop would modify ES flow, possibly more interspersed landscapes would have higher ES flow (darker blue in Figure 4a) and less fragmented landscapes would have lower ES flow (lighter blue in Figure 4a). In a landscape with neutral areas substituting demand areas (Figure 4b), more habitat with some pasture and less crops, because the amount of crop (demand) is lower, maximum flow decreases accordingly (dashed line in Figure 4b). If pastures remain spatially between habitat and crops – and depending on crop depth in m – they may pose resistance to pollinators movement and prevent them from reaching core crop areas, consequently lowering ES flow (lighter blue flow in Figure 4b). On the other hand, when neutral areas substitute supply areas (Figure 4c), less habitat can still be enough to enable maximum ES flow depending on the landscape configuration. Lower amounts of habitat can still allow high ES flow when there is a high amount of edge between habitat and crops (darker blue areas in Figure 4c). However, if there is pasture in between them, again, ES flow will be reduced. Most certainly, landscapes with higher amounts of pastures would hinder pollinator movement from habitat to crops because the chance of pastures being present between them is higher (Figure 4d). However, ES flow would depend on the configuration of such elements.

Using the microclimate regulation example, if there were empty lots (neutral areas) among the households in the neighborhood, that same amount of green space would be capable of supplying that same amount of service, however because demand is reduced, so is the maximum flow (dashed line in Figure 4b). In this same example, if neutral areas replace supply (Figure 4c) and demand remains the same, maximum flow can still be enough to fulfill demand. We understand that the arrangement (i.e. landscape configuration) of households, green spaces and empty lots (demand, supply and neutral areas respectively) will determine ES flow (Figure 4).

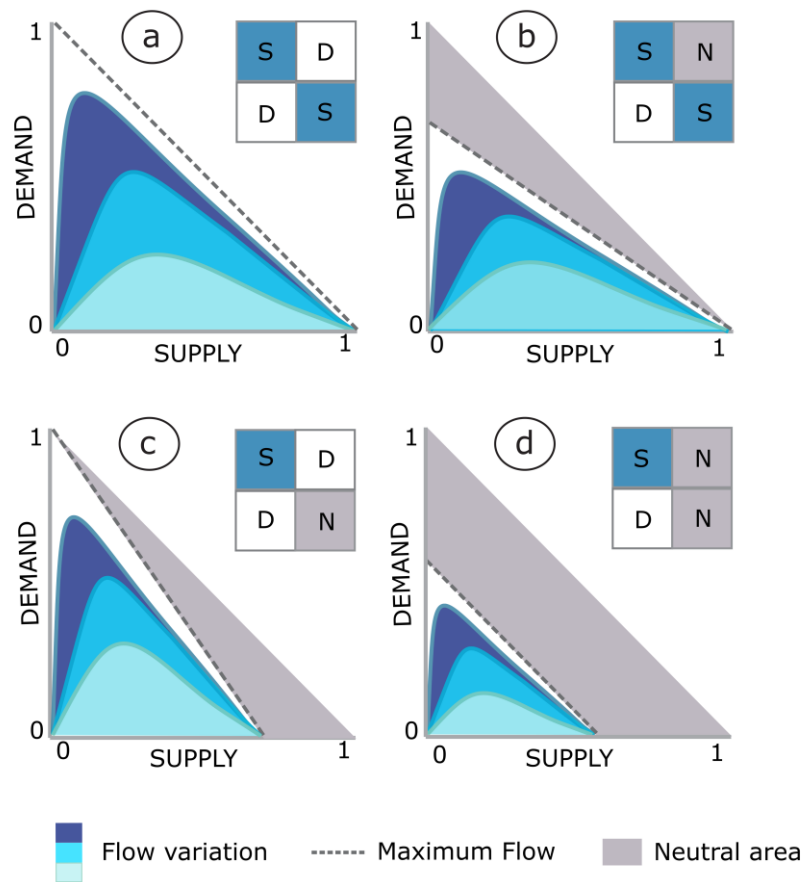


Figure 4: Variation in the amount of neutral areas (N) will modify the maximum flow of ecosystem service (dashed lines) within a landscape. We exemplify a landscape with ecosystem service demand (D) and supply (S) areas in the absence of neutral areas (a); a landscape with neutral areas replacing and thus reducing demand areas (b); a landscape with neutral areas replacing and thus reducing supply areas (c); and finally a landscape with neutral areas replacing and reducing both demand and supply areas (d).

5.3. Spatial overlap can expand supply-demand ratios and ES flow

In other cases, supply and demand areas may be totally or partially overlapped in the landscape (Figure 5). Nonetheless, ES flow may still be affected by supply and demand spatial arrangement. As an example, the service of pest control depends on the existence of natural enemies that inhabit forest remnants (supply) and perform this regulation service in nearby crops (demand) (Boesing et al., 2017). In this case, ES flow would vary according to contact and distance between forest and crop (as the variation in the blue areas in Figure 5a). Spatial overlap can be exemplified for the same service in agroforestry systems which can host pest controllers (supply) and at the same time can be the demand area for pest control (Figure 5c) (Perfecto et al., 2004). A combination of both cases, with forest remnants, crop areas and agroforestry, represents a partial overlap (Figure 5b). For

biological pest control (Medeiros et al., 2019), the arrangement of supply and demand in space, as well as the overlap will determine flow. The closer supply and demand are the higher the flow (Blanche et al., 2006). When overlapped, we expect maximum flow to be the highest (compare blue flow variation areas in Figure 5a with 5b and 5c). On the other hand, the less overlap between supply and demand are, the lower the flow between them (as in the light blue area in Figure 5a).

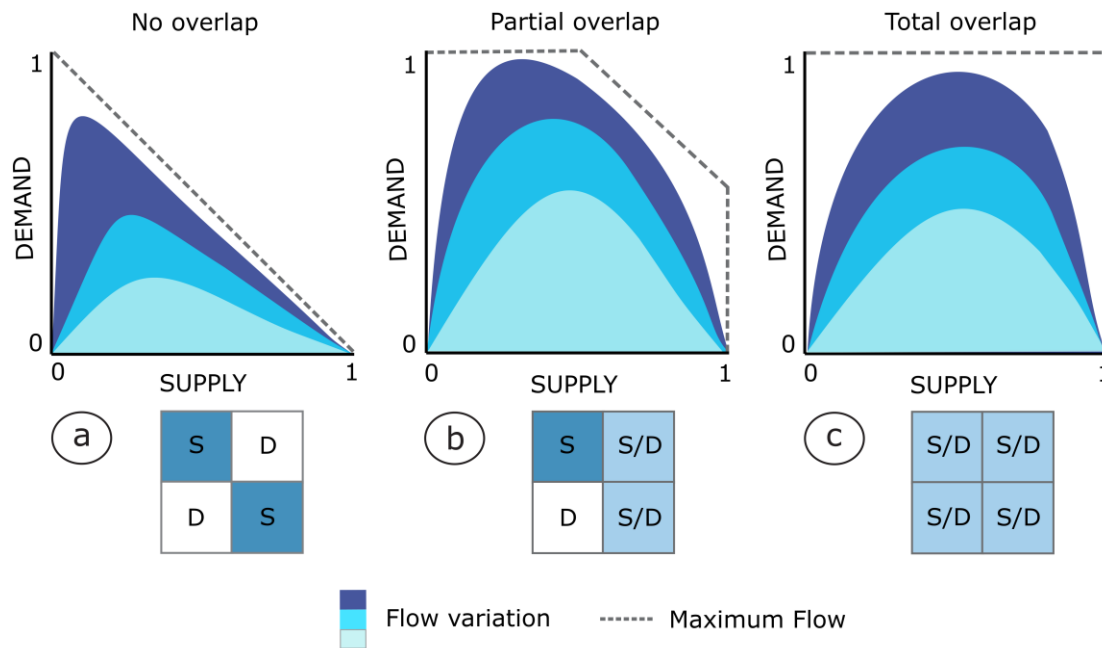


Figure 5: Landscapes may contain spatial overlap between ecosystem service demand (D) and supply (S) areas. For landscapes in which there is no overlap, maximum flow of ecosystem services (dashed line) may occur between supply and demand areas (a). Flow can vary below maximum according to other landscape attributes (blue gradient). In some cases, there might be a partial overlap between supply and demand areas (b) or a more extreme total overlap may take place (c).

6. CHALLENGES AND RESEARCH AGENDA

Using landscape planning to optimize flow between supply and demand might be a feasible way to achieve more sustainable practices and long-term ES provision. If research efforts integrate all three components of the ES supply chain (supply, flow and demand) in the assessments and improve the understanding on how landscape patterns influence each one of them, landscape can be managed more efficiently to optimize flow, enhance supply and regulate demand for ES. In order to advance our framework, some challenges must be overcome:

6.1. Quantifying supply and demand variation using comparable units

In our framework we assume a non-variation of supply and demand per area unit. However, ecosystems conditions are heterogeneous and highly influenced by landscape composition and configuration, which have important consequences for ES provision. Thus, when accounting for ES supply one must take the variation of ecosystem condition into consideration. Likewise, ES demand per area unit depends on the development of methods and tools to estimate how much service people need by household or other spatial demand unit. Demand will vary depending on population density, consumption habits and culture. Such quantification and mapping should be further developed in collaboration between natural and social sciences. Besides, one may argue that landscape structure may also affect demand. Thus, another challenge remains: how do environmental aspects influence demand allocation? Once we have supply and demand quantified and mapped, understanding flow mechanisms and the spatial match between supply and demand will allow the management and sustainable plan of ES provision within a landscape or even outside of it through interregional flows for decoupled ESs.

Another aspect to be considered is how high demands and flow for certain ES may end up degrading the supply (decreasing its quantity and quality). This is more straightforward for rival ES, but it may also occur for non-rival ES. For example, high visitation rates (flow) in protected areas can degrade hiking paths as well as the attractiveness of the place, thus degrading supply of the recreational service. Controlling the access of visitors (flow) may be enough to prevent degradation of supply and ensuring the long-term flow of this service.

6.2. Managing demand to enable optimal flow

Demand can be managed by the development of people's awareness about ES provision and therefore enabling their engagement in the development of policies to guarantee ES provision in the future. Demand management may become feasible with the recognition of societies needs and priorities regarding ES provision. However, for this purpose government, institutions and other interests must be aligned in the pursuit of collective wellbeing and sustainable practices. A few aspects to be considered, other than natural and social sciences joining efforts, are: a) how feasible it is to manage demand; b) how to develop and improve methods to assess people's desires and needs; and, c) how

to value ES and benefits, not exclusively in monetary terms, so that governments can excel in serving citizens' needs, while institutions can seek more sustainable practices. Therefore, linking this to a landscape perspective is also necessary to elucidate how the fulfillment of a local demand depends on local supply or on the supply of other landscapes (further regions).

6.3. Exploring how neutral areas in the landscape affect ES flow

What we call neutral areas here are in fact the landscape matrix, or land-uses other than those that characterize supply or demand areas. Neutral areas may be different for each ES, so we must consider this variation when dealing with multiple ES. Moreover, although not captured in our framework, neutral areas vary on how much resistance and/or reduction they can cause on flow. For example, different agricultural areas can impose different movement resistance to birds (Barros et al., 2019; Boesing et al., 2017), thus the presence of a particular agricultural area between supply and demand areas can increase or decrease biological pest control services provided for demand areas by these natural enemies (Medeiros et al., 2019). Therefore, elucidating the different roles of such neutral areas in the connection between supply and demand and the modulation of flow for different ES is the next step to be taken. For this, describing and clarifying flow mechanisms (i.e. those mediated by animal movement, people's movement, mass movement, transport infrastructure, trading and market prices) and how they vary across neutral areas will guide the further comprehension of the role of anthropogenic matrix attributes (e.g., diversity, resistance, similarity, contact, distance).

6.4. Understanding the scale of effect on flow management

Managing landscapes to improve ES flow requires not only the comprehension of flow mechanisms but also the adoption of multi-scale approaches. ES flows within a landscape or region is not limited by administrative boundaries. The multi-scale ES flow management depend on people, governments and institutions to be on the same page, specially when ES supply and demand are decoupled. Knowing and recognizing who will be affected by management decisions is a promising way to go and improve spatial planning by including landscape effects on ES flows, as pointed out in this study.

6.5. Incorporating synergisms and trade-offs in the spatial explicit framework

Identifying synergies and trade-offs when evaluating ES bundles has implications for landscape management with ES maintenance goals, including enhancing supply, optimizing flow and coupling it with demand. The proposed spatial framework emphasises that ES synergies and trade-offs can be fully captured with consideration of all three ES components and their relationship with landscape structure. Therefore understanding how landscape composition and configuration affect ES supply (e.g., Duarte et al., 2018) is essential, but not enough. Researchers must also address how landscape structure relates to ES demand and flow to predict the consequences of landscape management to ES provision. Likewise, existing research focusing on multiple services (e.g., Lamy et al., 2016; Mitchell et al., 2014), ES bundles (e.g., Baró et al., 2017), and synergies and trade-offs (e.g., Power, 2010; Schirpke et al., 2019a) also evidenced the urge to integrally address the spatial aspect of ES supply, flow and demand to inform environmental planning and sustainable use of ES.

6.6. Integrating temporal variation on ES assessments

Temporal variation in ecosystem conditions and consequently in ES supply brings consequences to flow and demand fulfilment. Nonetheless, demand also varies over time due to social aspects affecting people's desires and needs from nature. This perspective has gained attention in planning initiatives for sustainable futures due to the fact that in order to guarantee long-term ES provision, we need to account for variations of both supply and demand through time and thus its effect on ES provision. This means that not only the spatial variation influences ES provision but also the way each component changes over time. Despite the very long way to go in the development of spatio-temporal approaches, scientists' awareness of such temporal variations may be the necessary heads up for management and policy development for the present time.

Another promising strategy to account for temporal variation in ES provision is incorporating the ES framework into both, the conservation and restoration agendas. This could assist the development of a sustainable management of ES over time. Because supply can be both protected or 'created' (i.e. restored, regenerated or recovered; Chazdon, 2008) or enhanced to assist unfulfilled demand, the restoration agenda could incorporate ES. More specifically on the restoration of ecosystems, once restored areas

have the potential to provide several ES, choosing where to restore can optimize ES flow. Similarly, research efforts could address whether there is a minimum amount of supply to guarantee long-term ES flow without affecting ES supply maintenance (Hein et al., 2016).

GLOSSARY

Ecosystem Service Supply Chain: parts of ecosystem service realization that generates benefits to people from ecosystems (Tallis et al., 2012). These components consist of the ecosystem service supply, ecosystem service flow and ecosystem service demand.

Ecosystem Service Supply: the potential of an ecosystem to provide an ecosystem service irrespective of it being used, recognized or valued by humans (Mitchell et al., 2015b; Tallis et al., 2012).

Even though ES supply per spatial unit may vary according to the ecosystem type and its condition, here we refer to supply as the area of the ecosystem that has the potential to supply a certain ES, without accounting for such variation.

Ecosystem Service Flow: the delivery of an ecosystem service to people; the actual production of a service experienced by people (Villamagna et al., 2013); the transfer of service from supply to demand through space and time (Bagstad et al., 2013; Serna-Chavez et al., 2014). ES flow characteristics are specific to each service (Serna-Chavez et al., 2014).

Ecosystem Service Demand: the amount of service required or desired by people (Villamagna et al., 2013; Wolff et al., 2017, 2015), even in cases in which they are not aware of such needs. ES demand can be expressed in terms of risk reduction, preferences and values, direct use or consumption of goods and services (Brander and Crossman, 2017; Wolff et al., 2017, 2015).

Here we assume the demand area as the location of people who require or desire the ES in question despite variations between these areas, such as population, or cultural differences

Ecosystem Service Provision: the delivery of a service to be used or enjoyed by people (Mitchell et al., 2015b; Villamagna et al., 2013).

Benefit: positive change in people's wellbeing (Tallis et al., 2012) as a result of ES flow from ES supply meeting an existing ES demand.

Neutral Area: an area in the landscape that is neither supply or demand for the ES in question, but that can contribute to ES flow (i.e. facilitate, hinder or be neutral to it). Here we assume that neutral areas do not interfere in supply and demand even though in landscape contexts such interactions are prone to generate variability.

Ecosystem Service Rivalry and Excludability: to be rival means that the use of an ecosystem service by one person precludes the use of it by another person (Fisher et al., 2009). To be excludable means that one person can keep another from using or accessing an ecosystem service (Fisher et al., 2009). Marketed goods are usually rival and excludable; however, it is possible to fit ecosystem services along a continuum from rival to non-rival and from excludable to non-excludable.

Decoupled Ecosystem Service: when the supply of and demand for an ES occur at different spatial scales or in different landscapes (Burkhard et al., 2014; Fisher et al., 2009). Inversely, **non-decoupled ES** is when an ES has its supply and demand occurring within the same landscape. The spatial relationship between supply and demand has been previously classified as in situ, omnidirectional, and directional (Burkhard et al., 2014).

Ecosystem Condition: refers to the integrity and state or functioning of an ecosystem, ultimately determining its capacity to supply ES (Burkhard and Maes, 2017; UN, 2014).

Landscape Structure: spatial composition (the number of existing elements) and configuration (how they are arranged in space) of the landscape (Wu, 2013).

Spatial Scale: the extent and grain of the physical structure of the system and the distance and range in which its processes occur (Dungan et al., 2002).

Supply and Demand Ratio: the proportion between the amount of ecosystem service supply area and the amount of ecosystem service demand area, here considered for non-decoupled ES. Even though we acknowledge the existence of variation in supply and demand per area unit, here we do not take this variation into account.

Table S1: Summarized characterization of ecosystem service components (supply, flow and demand), measurements and proxies used in previous research.

ECOSYSTEM SERVICE	SUPPLY	FLOW	DEMAND
Provisioning Services			
Water provision for irrigation ^a	location of groundwater basins and their annual recharge	infrastructure for extraction, distribution and irrigation; Basin recharge rate (soil infiltration capacity and topography)	agricultural areas dependent on groundwater irrigation
Urban agriculture ^b	organoponics and urban agriculture	crop yield of vegetables and fruits	minimum recommended intake of fruits and vegetables for all inhabitants in residential areas
Drinking water provision ^c	water availability	water usage	water requirement
Grassland biomass ^c	forage production	the actual used fraction of forage	energy demand of forage feeding livestock species
Fuel wood ^c	increment of above-ground biomass in forests	timber removals (forest accessibility and in-site conditions)	fuel wood requirements based on statistics of consumption, building areas and heating degree days
Regulating Services			
Filtration of surface water ^c	potential nitrogen filtration capability	amount of nitrogen filtered by ecosystems	amount of nitrogen introduced in ecosystems
Protection of areas against avalanches, mudslides and rockfalls ^c	forest area with a protective effect	forest area with a protective effect for human infrastructure	area of human infrastructure located in avalanche and rock-fall hazard zones
Climate regulation ^a	primarily, tropical (including peat forests) and boreal forest (hotspots)	tropical, sub-tropical and mid-latitude agricultural areas vulnerable to changes in precipitation and temperature	vegetation and soil interactions with the atmosphere (photosynthesis, soil and plant evapotranspiration, soil heterotrophic respiration, albedo, etc.)
Carbon sequestration ^c	the annual rate of CO ₂ sequestration by above- and below-ground biomass in forests	equal to supply	the annual rate of CO ₂ emissions

Air purification ^d	urban vegetation (trees and shrubs)	air quality improvement by removing pollutants	the magnitude of pressures on air quality and population exposed to these pressures
Pollination ^a	natural and semi-natural habitats	foraging ranges of pollinator species, pollen transportation and deposition, abundance and effectiveness of pollinating organisms	agricultural areas dependent on or profiting from biotic pollination
Erosion regulation	soil classification, soil organic matter, standing vegetation	control of landslides and amount of sediment retained by ecosystems in stakeholder areas	risk of soil erosion
Cultural Services			
Outdoor recreation ^d	availability of recreational sites	proximity from people's homes to recreational sites	population density (assuming all inhabitants have similar desires)
Outdoor recreation ^c	recreation opportunities provided by ecosystems	visitation rates	density of potential beneficiaries derived from the number of residents and overnight stays of tourist
Outdoor Recreation ^b	urban green spaces considering threshold values of crowding	inhabitants of urban areas from which dwellers can reach urban green spaces considering access and a maximum travel distance	the minimum availability of recreational green spaces within maximum distances from home including all urban residential zones
Symbolic species ^c	spatial distribution of habitats of selected symbolic plants and animals	mapping of the occurrence of selected symbolic plants and animals in hotel names	not mentioned

^a Serna-Chavez et al., 2014; ^b Ortiz et al., 2018; ^c Schirpke et al., 2019a; ^d Baró et al., 2016

CHAPTER 2 – IDENTIFYING HOTSPOTS FOR BIODIVERSITY CONSERVATION: FROM ECOLOGICAL TO ADMINISTRATIVE BOUNDARIES

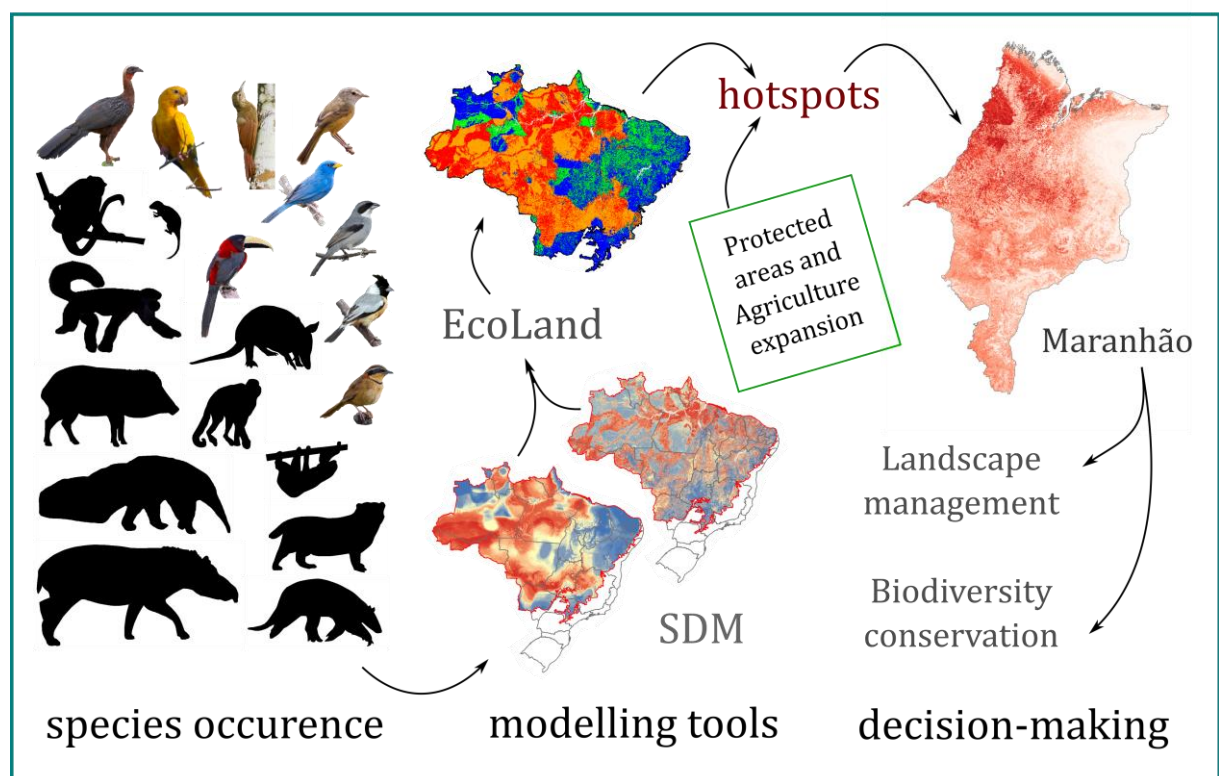
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ABSTRACT

Biodiversity conservation is vital to maintain ecological functions that provide ecosystem services that sustain human life. Most tropical regions with vast biodiversity have incomplete species databases. Even in these cases, Species Distribution Models (SDM) have been widely applied in the design of conservation and land management actions. In this study, we proposed the use of a climate- and landscape-based SDM approach to identify biodiversity hotspots to aid management decisions in face of fast land use change. Maranhão State, one of the frontiers of deforestation and agriculture expansion in Brazil, was used as a study case. We selected nine bird and twelve mammal species of ecological relevance in the Amazon and Cerrado areas of the state and adopted a broader modelling background, according to species distributions range. We used the ensemble of five replicates of four different algorithms to come up with a frequency probability of each species occurrence for climatic and landscape variables. We considered areas with high climate and high landscape suitability as species hotspots. Then, we quantified the spatial overlap of these hotspots and analysed their spatial distribution regarding recent land use conversion and existing protected areas network. Our results showed that 90% of the Maranhão State is a hotspot for at least one species, whereas ~30% of its area is a hotspot for more than five species. Agricultural areas in 2018 had ~31% of overlap with hotspots for more than five species, which may be critical for biodiversity conservation in these regions. Out of the total area with some degree of legal protection, 48.2% hosts hotspots for more than five species. We indicated the priority areas to be conserved as those with higher overlap of species hotspots and not encompassed by existing protected areas. We recognize urgent need to monitor areas with agriculture expansion. Biodiversity hotspots allowed the recognition areas with the potential to host several species and therefore the identification of key regions to be protected.

Keywords: Species Distribution Modelling; Maranhão; Neotropical biodiversity; Conservation Biogeography

Potential target journals: Conservation Biology; Biodiversity Conservation; Perspectives in Ecology and Conservation

1. INTRODUCTION

1.1. Biodiversity to inform decision-making

Biodiversity knowledge should not be used exclusively to guide conservation actions. More than its conservation relevance, it has been proven to maintain ecological functions that provide ecosystem services that sustain human life (Balmford et al., 2002). It is agreed internationally that nations development should be based on environmental sustainability, social equity and economic prosperity (Griggs et al., 2013). Therefore, environmental concerns along with biodiversity knowledge must also take part in economic and political decisions if we want to move towards a sustainable future (Anand and Sen, 2000). Specially in countries with emerging economies such as Brazil, China and India – which present extensive territories and a wide variety of ecosystems – economic goals and political decisions must take environmental issues into account (Liu et al., 2015). For a country to develop, not only power generation, transport infrastructure, tax incentives and multilateral agreements with international companies should occupy the national agenda (Costanza, 2014), but also biodiversity, water, carbon emissions and land use dynamics.

Historically, landscape management and conservation actions in Brazil have always been a controversial matter in the political arena. Despite the fact that the country harbors an immense neotropical biodiversity and has an advanced environmental legislation, economic policies have recurrently and indirectly driven to deforestation and biodiversity loss (Pereira et al., 2019; Magnusson et al., 2018). In Brazil, conservation planning has evolved in the national agenda with several efforts for the identification of spatial gaps in the protected areas network (Fonseca and Venticinque, 2018; Oliveira et al., 2017). Additionally, prioritization strategies have also been drawn by the national environment ministry to all Brazilian biomes (Brasil, 2018), with parallel efforts from the scientific community (see Castro and Albernaz, 2016; Laurance, 2005; Ribeiro et al., 2018 for the Amazon; Ribeiro et al., 2011; Scarano et al., 2015 for the Atlantic Forest; Brum et al., 2019; Carranza et al., 2014; Sano et al., 2019 for the Cerrado; Oliveira and Bernard, 2017 for the Caatinga and, Overbeck et al., 2015 for Pantanal and Pampas).

1.2. Accounting for biodiversity

In the last decades, international efforts to measure various dimensions of biodiversity and their change over time are reflected in the development of a wide range

of biodiversity indicators and biodiversity monitoring systems. Biodiversity – as the variety of ecosystems, species and genes (CBD, 1992) – is a key aspect for the maintenance of ecosystems' functions and resilience (Fischer et al., 2006). The Living Planet Index (LPI) and the Group of Earth Observations Biodiversity Observation Network (GEO BON) initiatives are examples of efforts to comply with biodiversity measurements in the global scale. The LPI is based on population trends of vertebrate species (WWF, 2014), for which data is mostly available in Europe and North America. The GEO BON Essential Biodiversity Variables (EBV) drive data integration and monitoring efforts to cover critical gaps (Proença et al., 2017) and is also applicable to national levels (Turak et al., 2017).

Two other well-established measures of biodiversity are the Nature Index (NI; Certain et al., 2011) and the IUCN Red List of Threatened Species (IUCN, 2018). The NI is based on expert judgement, monitoring estimates and model-based estimates (Certain et al., 2011; Skarpaas et al., 2012). However, it depends on a wide network effort for data and expert assessment, adequate to be pursued in an institutional (e.g., governmental) initiative. The IUCN Red List evaluates the conservation status, trends and threats of species according to their change in rareness (Butchart et al., 2004). It operates mainly in the global level, but it also provides guidelines for national and regional assessments performed in many countries. In Brazil, many species do not present enough data to have their status verified. Another IUCN initiative, the Red List of Ecosystems (IUCN, 2016), is beginning to be developed worldwide as a common effort to set an internationally accepted ecosystem classification (Keith et al., 2013).

1.3. Dealing with data scarcity

Biodiversity data in tropical regions have spatial and temporal gaps that constrain their quality for broader applications (Oliveira et al., 2017; Tessarolo et al., 2017). In countries as large as Brazil and with highly diverse tropical environments, compilation of national wide comprehensive biodiversity datasets is challenging. Recent initiatives such as the Neotropical, Atlantic, Brazil, and Amazonia series organize biodiversity data and make them publicly available in the form of data-papers (for examples, see Galetti and Ribeiro, 2018, and P. M. Santos et al., 2019). Despite them, there are scattered data among grey literature, university libraries and unpublished compilations retained by experts. Therefore, compiling, organizing and publishing existing data allows for great advances in science.

1.4. Using Species Distribution Models (SDM) and the EcoLand analysis

Ecological models, such as Species Distribution Models (SDM), are tools with strong predictive capabilities and great potential for extrapolation based on incomplete data (Villero et al., 2017). SDM have a wide range of applications for biodiversity conservation and management actions (Guisan et al., 2013; Villero et al., 2017). SDM are favoured by the increasing availability of species data, enhanced processing capacity of computers and GIS software and, the ongoing improvement of spatial analyses (Brown et al., 2017; Jetz et al., 2012; Naimi and Araújo, 2016). However, many of the applications of this method are based on how climate variables condition the suitability of habitats for probable species occurrence (e.g., de Carvalho et al., 2017; Guisan et al., 2013; Zimmermann et al., 2010), without considering habitat availability and landscape attributes.

In human-dominated landscapes, anthropogenic and landscape influences are recognized as interfering factors in species distributions at local and regional scales. Therefore, it is necessary to include those influences in SDM for conservation purposes (Sobral-Souza et al., in prep). The EcoLand analysis was proposed to combine climate- and landscape-based models to generate results that reflect the climatic niche of species and the landscape constraints for their distribution (Ferro e Silva et al., 2018; J. P. Santos et al., 2019; Sobral-Souza et al., in prep). Ferro e Silva et al. (2018) concluded that the use of the EcoLand analysis to predict risk areas of Chagas disease in the state of Paraná in Brazil, based on the vector species potential distribution, generated good predictive models (Ferro e Silva et al., 2018). Furthermore, Santos et al. (2019), in their assessment of fruit-feeding butterfly richness throughout the Brazilian Atlantic Forest using the EcoLand Analysis, recognized landscape structure as a primary factor for species maintenance (J. P. Santos et al., 2019).

Another relevant aspect is the difference between the scale of ecological processes and Institutional organizations. Combining ecological and institutional scales properly is key to guarantee that conservation policies reflect in ecological processes and that environmental integrity guides political decisions (Figure 1). Here, we explore the use of modelling tools in generating comprehensive information to aid policy and management decisions in face of fast land use change. In this study, our goal is to use existing data and modelling strategies to identify biodiversity hotspots and indicate priority areas for

conservation coupling ecological and institutional scales in a tropical country. We evaluate whether current land use (year 2018) has taken place over biodiversity hotspots (modelled for 2008) and how protected areas overlap with them. This modelling approach can be widely applied worldwide, particularly in tropical regions where systematized species data are rather scattered and monitoring biodiversity is recent. We also addressed the challenges of compiling data; selecting species, modelling background, climatic and landscape variables.

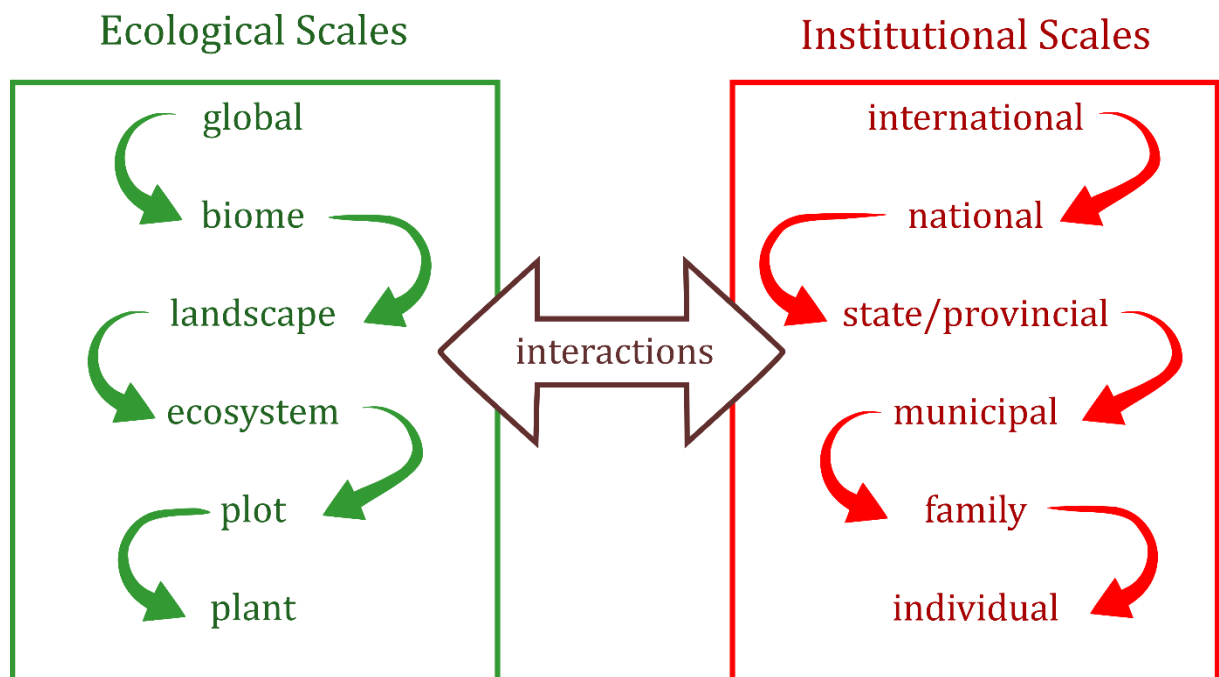


Figure 1: Coupling ecological and institutional scales demands for adequate interactions between both systems. Here we combined species distribution modelling at the biome scale to inform decision-making at the state level. Adapted from Hein et al., 2006.

2. MATERIAL AND METHOD

2.1. Study area: from ecological to institutional boundaries

Policy and decision-making usually follow institutional scales, whereas ecological processes are limited by environmental boundaries (Figure 1). We used a Brazilian state to illustrate how the ecological information can be clipped to inform management decisions. Located in the north coast of Brazil, the state of Maranhão has an area of 329,642 km² and a population of ca. 7 million inhabitants distributed in 217

municipalities (IBGE, 2018). With a population density of less than 20 inhabitants per km², 38.4% of its population lived in rural areas in 2010 (IBGE, 2010).

The state presents a transition zone between Amazon and Cerrado biomes, and originally Amazon covered 34.6% and the Cerrado 65.4% of the state area (IBGE 2019). In the east limit of the state, border with Piauí, Maranhão presents an ecotone between Cerrado and the Caatinga biomes (IBGE 2019). Economic growth in the state has been based on agribusiness expansion (see Sup. Mat. Box 1, for more information on economics), particularly cattle ranching and soybean crops. Nonetheless, this expansion comes at the cost of natural areas conversion, with a large amount of forests and other natural vegetation being replaced by exotic grass for pastures and other crops for grain production (Figure 2).

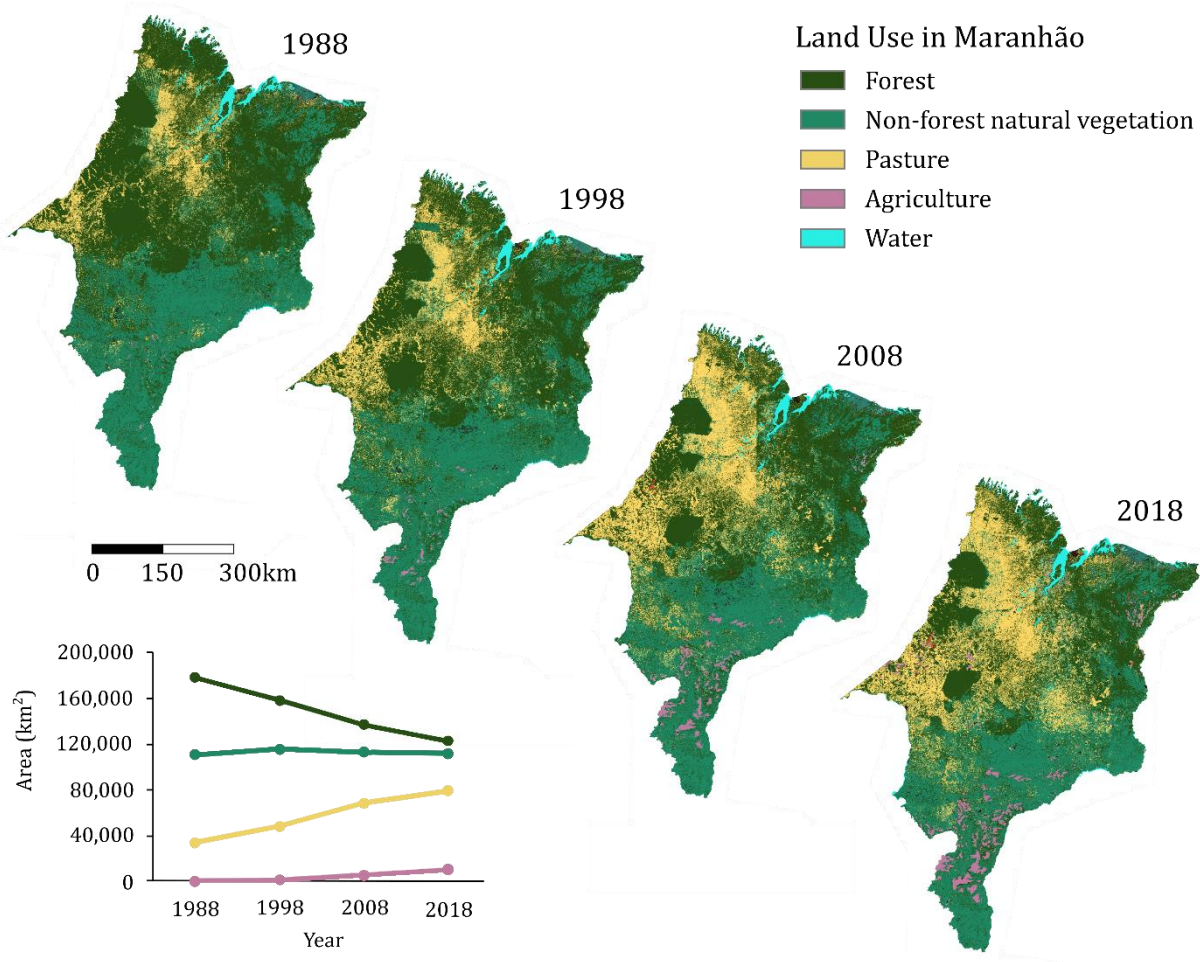


Figure 2: Land use change in Maranhão State, north coast of Brazil, in the years 1988, 1998, 2008 and 2018. Maps derived from land use classes of MapBiomas Collection 4 (MapBiomas, 2019).

To couple the administrative and ecological boundaries, we funnelled species selection to those relevant to assist state level decisions. However, species distribution is determined by climate and landscape characteristics that exceed the state limit. Therefore, to thoroughly assess species distribution we used a modelling background area larger than the state limit to prevent model overfitting and to generate more accurate modelling output maps. The background area for the modelling procedure encompassed four Brazilian biomes (Figure 3). We included the biomes that comprised most of the known distribution areas of the selected species, 1) the Amazon and 2) the Cerrado. We also included 3) the Pantanal because several species that occur in the Amazon extend their distribution to that region and there is a considerable amount of data for that region, and 4) the Caatinga, because it is contiguous to the Cerrado limit in the state of Maranhão and most species that occur in the Cerrado may also be present in that transition zone (see Sup. Mat. Box 2 for brief description of each biome). We also used the same environmental variables to model species distribution to allow the comparison of modelling outputs.

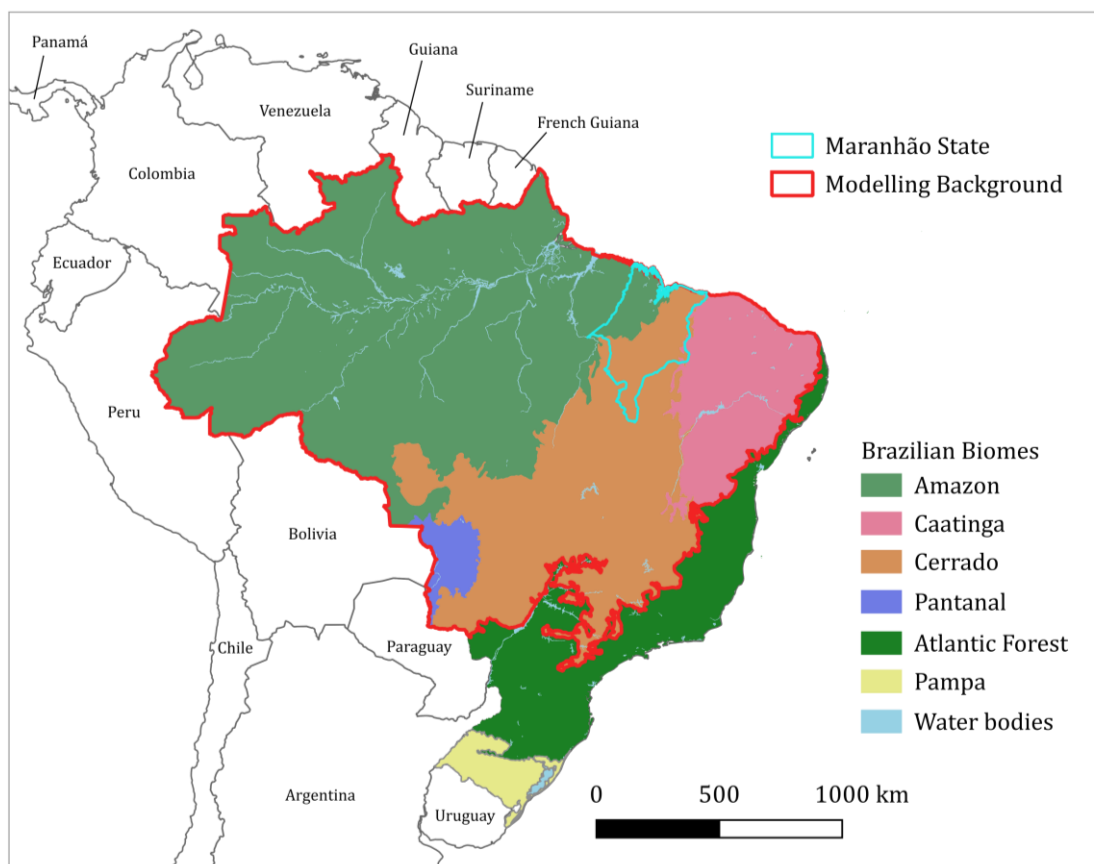


Figure 3: Brazilian biomes, the modelling background area (in red) and the boundary of the focal state of Maranhão (in cyan blue), based on IBGE, 2004.

2.2. Datasets

Ad-hoc consultation for species selection

Taxonomic groups of birds and mammals were chosen according to data availability and accessibility to experts. Within the selected groups, we performed ad-hoc consultations to select species with relevant ecological functions that occur in the Cerrado and the Amazon of Maranhão. We also considered the following criteria: species endemism, conservation concern and known distribution. In addition, we only kept species with more than five occurrence records.

Species data

Birds: We compiled occurrence records of bird species from 1) a Brazilian citizen-science peer-reviewed database WikiAves (www.wikiaves.com) and 2) the Brazilian public database *Portal da Biodiversidade* (portaldabiodiversidade.icmbio.gov.br). We collected the species locations using the online WikiAves platform that contains either a photographic or an audio record to confirm species identification. The authors of the records were consulted for georeferenced location of occurrences when they were not available in the database (tool recently implemented), in some cases they provided additional unpublished data. For each record we compiled the geographic coordinates and verified the location through Google Earth. In order to ensure model quality, we discarded data that showed potentially wrong locality (i.e. when the environment did not correspond with the requirements of the species).

Mammals: For mammal species we compiled occurrence data from different sources including 1) the Brazilian public database *Portal da Biodiversidade*, 2) Global Biodiversity Information Facility (GBIF; www.gbif.org; only considered from 1998 to 2016 and with coordinates that were not a reference to the municipality or museums), 3) a dataset from the Threatened Biodiversity Project funded by Maranhão State Government and 4) other datasets shared from direct contact with experts (published and unpublished).

We gathered species occurrence data and evaluated the final amount of records and their spatial coverage compared to IUCNs range for each species to deliberate on data sufficiency. Although IUCN maps may have some inconsistencies with species distribution in some cases, they are useful in providing an overview of the extent of occurrence of the

studied taxa. We filtered the temporal variation of the records and kept those ranging from 1998 to 2017. We also performed an environmental rarefaction of all the occurrence data to avoid redundancy (Fourcade et al., 2014). Using SDMtoolbox (Brown, 2014) in ArcGIS 10.2, we removed species records with environmental redundancy within a 50 km radius and a minimum distance of 2 km. The environmental filter consisted of five classes divided by natural breaks, generated using the percentage of eigenvalues from the principal component analysis (PCA) of the nineteen CHELSA variables.

Selection of climatic and landscape variables

We used the CHELSA climatological data, which are the downscaled model outputs of temperature and precipitation global estimates to a high resolution of 30 arc sec (ca. 1 km), comprising the period from 1979 to 2013 (Karger et al., 2017). We performed a factorial analysis to select the variables with larger variability within the modelling background (Ferreira e Silva et al., 2018; Sobral-Souza et al., 2015). We selected six variables, according to the multivariate scree plot (Figure S1). The ones with higher absolute values in the factorial analysis indicated the highest contribution to the variation in the extent of the modelling background. Whenever values were close, we selected them based on their biological significance considering the selected species (Table S1). After these steps the following environmental layers were kept: 1) mean diurnal range; 2) isothermality; 3) temperature seasonality; 4) mean temperature of warmest quarter; 5) precipitation of wettest quarter; and 6) precipitation of driest quarter (Figure S2).

The landscape layers were initially selected to represent the attributes for which we assumed variability would play an important role in the distribution of the selected species. We selected the following landscape layers: 1) vegetation homogeneity (Tuanmu and Jetz, 2015); 2) terrain slope (de Morisson Valeriano and de Fátima Rossetti, 2012); 3) percentage of natural forest cover (MapBiomas, 2015); 4) percentage of natural non-forest cover (MapBiomas, 2015); and 5) anthropogenic influence (i. e. Human Footprint; Venter et al., 2018; Figure S3). We evaluated the Pearson correlation between them to avoid redundancy (see Sup. Mat. Box 3 for details). The five landscape variables showed lower ($r < 0.5$) and no significant correlation (Figure S4). Vegetation homogeneity was derived from data from 2001 to 2005; percentage of natural forest cover natural non-forest cover were calculated for 2008; the human footprint stands for 2009.

2.3. EcoLand analysis

We used the EcoLand analysis (Ferro e Silva et al., 2018; J. P. Santos et al., 2019) that combines climate- and landscape-based Species Distribution Models (SDM) to generate an indicator of relative species richness for birds and mammals (Figure 4). Despite temporal variation in species, climate and landscape data, we consider our models to be representative of 2008, due to information on natural land cover being from that year.

SDM - algorithms and ensemble

We fitted SDM using four different algorithms (BIOCLIM, SVM, Maxent, and Gower), that were then combined in a consensus map of potential species distribution according to the climatic niche (climate-based SDM) and the landscape suitability (landscape-based SDM). We applied the same steps of frequency ensemble forecasting described by Ferro e Silva et al. (2018) and J. P. Santos et al. (2019), but using 5 replicates. This resulted in 20 climate-based and 20 landscape-based SDM maps for each species with $\sim 1 \text{ km}^2$ cell-size resolution. Then we transformed each replica model outputs in binary maps using the threshold values of “maximum sum of specificity and sensitivity”, the most effective threshold to presence only methods (Liu et al., 2016), for each species. We assigned 0 when the species was not expected to occur (unsuitable), and 1 when it was expected to occur (suitable). After that, we summed the replicates of each algorithm, which resulted in a frequency of suitability varying from 0 to 5. Finally, we summed the resulting sum of each algorithm. Which resulted in a frequency of suitability of replicates and algorithms combined, varying from 0 to 20 (Figure 4). This final output represented the sum of predictions of species occurrence in each cell. This final layer was converted to present values varying from 0 to 1, dividing by the total numbers of models (20), resulting in a frequency model.

EcoLand and thresholds

For the EcoLand analysis we generated a scatterplot of climate-based and landscape-based suitability for each species. For both, we classified values higher than 0.5 as of high suitability and equal or lower than 0.5 of low suitability. This resulted in four combinations: high suitability for climate-based and landscape-based SDM (HcHl); high suitability for climate-based SDM and low suitability for landscape-based SDM (HcLl); low suitability for climate-based SDM and high suitability for landscape-based SDM (LcHl);

low suitability for climate- and landscape-based SDM (LcLl; Figure 4). This classification was plotted in a final map to find this spatial classification.

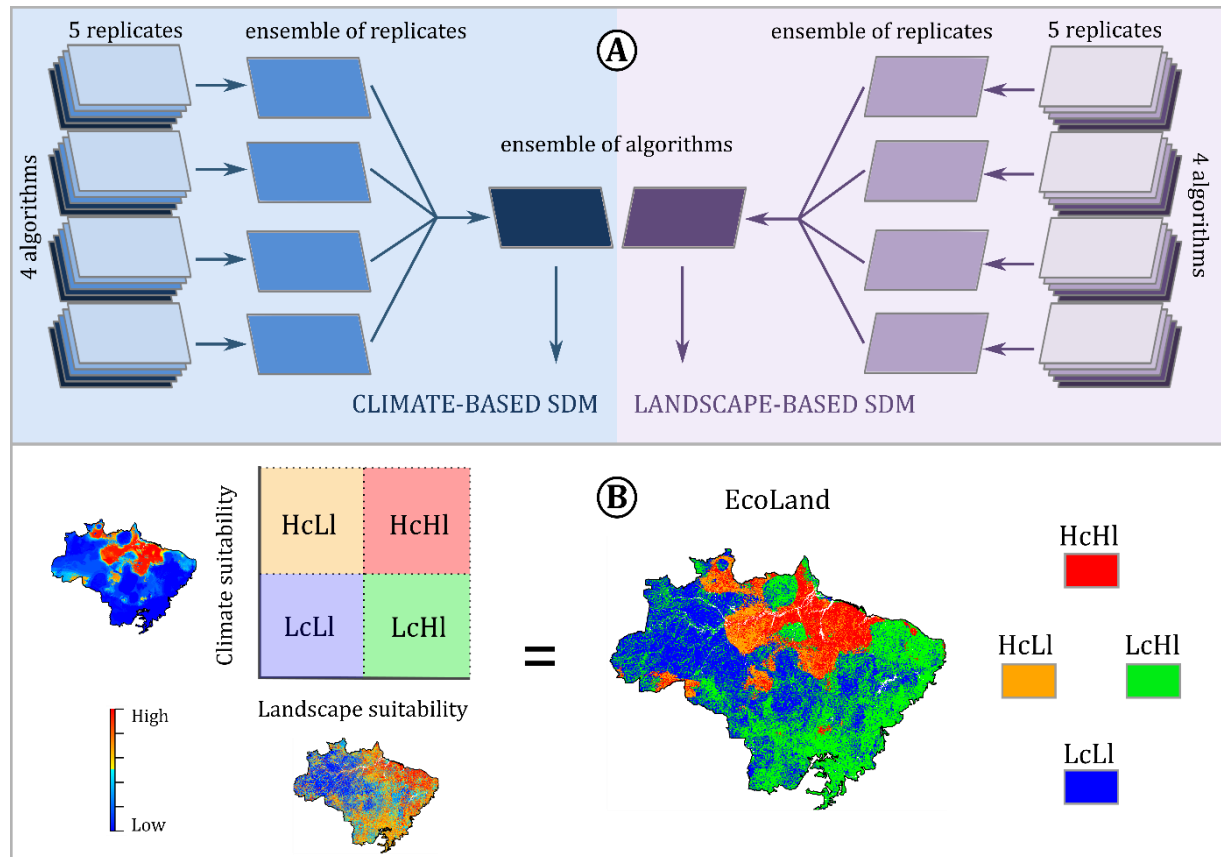


Figure 4: Ensemble of Species Distribution Models and resulting combination of climate- and landscape-based models (A); EcoLand analysis combining climate- and landscape-based suitability models (HcHl - high climate and high landscape suitability; HcLl - high climate and low landscape suitability; LcHl - low climate and high landscape suitability; LcLl - low climate and low landscape suitability).

Identifying biodiversity hotspots

We considered cells with high suitability for climate- and landscape-based SDM (HcHl) as hotspots for each species. These areas reflect the combination of climate and landscape suitability and consequently, the most adequate areas for species occurrence. Since the hotspots were identified per species and we were combining them to reflect biodiversity, we considered an overlap of more than 5 species highly significant. Therefore, we presented our results with either the real sum of species hotspots or we classified them in: no species hotspots (0); 1 to 5; and more than 5 species (>5).

We summed the hotspots for the selected species of Amazon birds, Cerrado birds, all birds, all mammals, and birds and mammals together. Then, we clipped these final hotspots sums (representative of 2008) for Maranhão State to evaluate where hotspots were more concentrated and recognize those areas as priority areas for conservation purposes. We also verified how hotspots overlap with land use in 2018 (MapBiomas, 2019), inferring that non-habitat areas in 2018 were no longer adequate for species occurrence. For this, we clipped the hotspots layers using each of the three main land uses in 2018 as a mask (natural forest, non-forest natural areas and agriculture). Finally, we verified whether hotspots were encompassed by existing protected areas. We clipped the hotspots using the georeferenced location of Brazilian indigenous lands, national and state protected areas, obtained at the Environmental Ministry (available at: <https://www.mma.gov.br/areas-protegidas/cadastro-nacional-de-ucs/dados-georreferenciados.html>).

3. RESULTS

3.1. Species datasets

Initially, we selected five Amazon bird species, five Cerrado bird species and 20 mammal species from small- to large- sized (Table S2). We compiled a total of 1,367 records of the 10 bird species and we gathered a total of 14,508 records of the mammal species (Table S3). After we performed the environmental filter to avoid redundancy, the final dataset contained 1,062 records of birds and 3,322 records of mammals (Table S3). Out of the final dataset used for modelling purposes, about 43% of the bird records were from WikiAves and 57% from the Portal da Biodiversidade, while about 51% of the mammal records were from Neotropical Xenarthans Dataset (P. M. Santos et al., 2019 previous to its publication), 7.2% from *Portal da Biodiversidade*, 0.8% from GBIF, all of which public databases. The remaining 41% were gathered from specialist researchers, out of which 4.3% were published or about to be and 36.7% were unpublished data.

From the final dataset, we maintained the five bird species from Cerrado: *Charitospiza eucosma*, *Euscarthmus rufomarginatus*, *Melanopareia torquata*, *Neothraupis fasciata*, *Porphyrospiza caerulescens*, and four bird species from the Amazon: *Dendrocolaptes medius*, *Guaruba guarouba*, *Penelope pileata*, *Pteroglossus bitorquatus*

(Table 1). Despite its conservation relevance, *Piculus paraensis* was excluded due to its limited number of records (only 4).

Table 1: Selected bird species, number of records in the final dataset (# rec), their common names in English and Portuguese and their status in the IUCN Red List (IUCN, 2018). LC – least concern; NT – near threatened; VU – vulnerable; EN – endangered; CR – critically endangered.

Family	Icon ⁴	Species	# rec	Common name in English	Common name in Portuguese	IUCN Red List
Thraupidae		<i>Charitospiza eucosma</i>	163	coal-crested finch	mineirinho	NT
Tyrannidae		<i>Euscarthmus rufomarginatus</i>	68	rufous-sided pygmy-tyrant	maria-corruiira	NT
Melanopareiidae		<i>Melanopareia torquata</i>	157	collared crescentchest	tapaculo-de-colarinho	LC
Thraupidae		<i>Neothraupis fasciata</i>	164	white-banded tanager	cigarra-do-campo	NT
Thraupidae		<i>Porphyrospiza caerulescens</i>	135	blue finch	campainha-azul	NT
Dendrocolaptidae		<i>Dendrocolaptes medius</i>	8	todd's woodcreeper	arapaçu-barrado-do-leste	-
Psittacidae		<i>Guaruba guarouba</i>	104	golden parakeet	ararajuba	VU
Cracidae		<i>Penelope pileata</i>	86	white-crested guan	jacupiranga	VU
Ramphastidae		<i>Pteroglossus bitorquatus</i>	113	red-necked aracari	araçari-de-pescoço-vermelho	EN

Out of the 20 mammal species we maintained 12, being three Primates: *Alouatta belzebul*, *Cebus kaapori*, and *Chiropotes satanas*; two Rodents: *Dactylomys dactylinus*, and *Echimys chrysurus*; four Xenarthans: *Choloepus didactylus*, *Dasypus kappleri*, *Myrmecophaga tridactyla*, and *Priodontes maximus*; one Perissodactyla: *Tapirus terrestris*; one Artiodactyla: *Tayassu pecari*; and one Carnivora: *Speothos venaticus* (Table 2). The

⁴ Bird icons developed using photos from WikiAves platform with authors' consent. Credits per species go to Zé Maria (*Charitospiza eucosma*), Frederico Tavares (*Euscarthmus rufomarginatus*); Saulo Gomes (*Melanopareia torquata*), Kacau Oliveira (*Neothraupis fasciata*), Roseanne Almeida (*Porphyrospiza caerulescens*), Pablo Cerqueira (*Dendrocolaptes medius*), André Grassi (*Guaruba guarouba*), Luiz Fernando Matos (*Penelope pileata*), Lindolfo Souto (*Pteroglossus bitorquatus*).

other six species were excluded from the analysis after expert consultation (see Table S4 for further explanation).

Table 2: Selected mammal species, number of records in the final dataset (# rec), their common names in English and Portuguese and their status in the IUCN Red List (IUCN, 2018). LC – least concern; NT – near threatened; VU – vulnerable; CR – critically endangered.

Group	Icon	Species	# rec	Common name in English	Common name in Portuguese	IUCN Red List
Primate		<i>Alouatta belzebul</i>	20	Red-handed howler monkey	Guariba-de-mãos-ruivas	VU
Primate		<i>Cebus kaapori</i>	40	Ka'apor capuchin	cairara Ka'apor	CR
Primate		<i>Chiropotes satanas</i>	37	Black bearded saki	cuxiú-preto	CR
Rodent		<i>Dactylomys dactylinus</i>	12	-	rato do bambu; toró	LC
Rodent		<i>Echimys chrysurus</i>	8	-	rato estrela	LC
Xenarthra		<i>Choloepus didactylus</i>	92	Linné's two-toed sloth	Preguiça-real	LC
Xenarthra		<i>Dasypus kappleri</i>	167	Greater long-nosed armadillo	Tatu-de-15-quilos	LC
Xenarthra		<i>Myrmecophaga tridactyla</i>	1159	Giant anteater	Tamanduá-bandeira	VU
Xenarthra		<i>Priodontes maximus</i>	471	Giant armadillo	Tatu-canastra	VU
Artiodactyla		<i>Tayassu pecari</i>	436	White-lipped peccary	Queixada	VU
Perissodactyla		<i>Tapirus terrestris</i>	422	Lowland tapir	Anta	VU
Carnivora		<i>Speothos venaticus</i>	28	Bush dog	Cachorro-vinagre	NT

3.2. SDM maps per species

We evaluated the final climate- and landscape-based SDM ensemble outputs of each species individually. We consulted experts about their perception of the outputs. Out of the nine bird species, the climate and landscape SDM presented reliable outputs even though few unusual records could be spotted out of species range (Figure S5). For the 20 mammal species, six of them were excluded from the hotspot analysis (see Table S4 for

further explanation). For the remaining 12, experts confirmed the adequacy of outputs (Figure S6) even though some of the records were identified as outliers (e.g., a record of *Alouatta belzebul* in the state of Mato Grosso, central west of Brazil).

3.3. EcoLand analysis and species hotspots

From the EcoLand analysis performed for each selected species of birds (Figure S7) and mammals (Figure S8) we considered the cells with HcHI as hotspots for species occurrence. The resulting sum of hotspots for Amazon birds and Cerrado birds varied from 0 to 5 and from 0 to 4, respectively. The resulting sum of all nine bird species had a maximum sum of 6 due to little habitat overlap between Amazon and Cerrado species (Figure 5). The resulting sum of mammal species had a maximum value of 10, while biodiversity, the combination of birds and mammals, reached 14 (Figure 5). The darker shades of red in the biodiversity hotspots map represent the areas with suitability for more species, therefore, more relevant for conservation purposes (Figure 5).

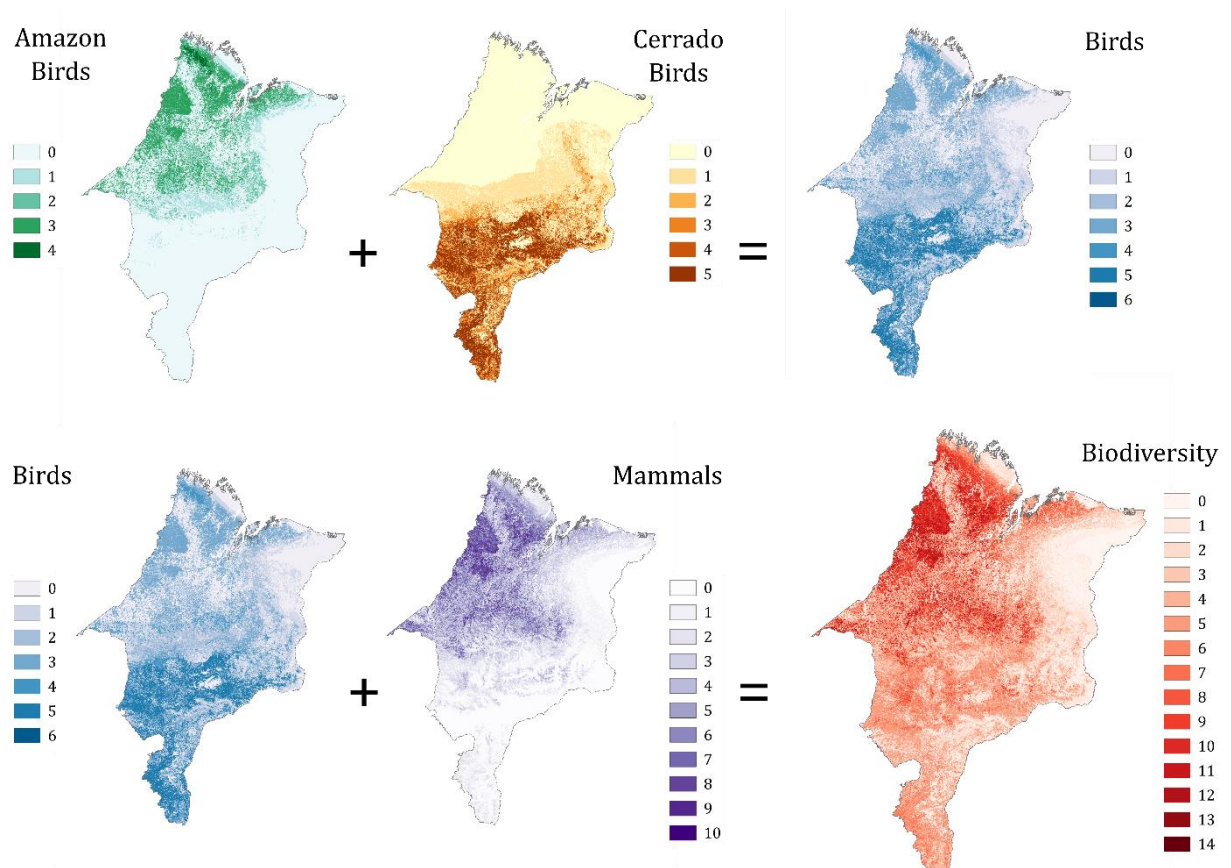


Figure 5: Sum of overlapped high values of climate- and landscape-based models (EcoLand – HcHI) for Amazon bird species, Cerrado bird species, both combined, mammal species and Biodiversity (as the sum of birds and mammals).

Great part of Maranhão State (~90%) is highly suitable for at least one species, whereas more than 30% of its area is a hotspot for more than five species (red shades in Figure 6). Bird species hotspots are less overlapped throughout the state. Most area with bird hotspots host from 1 to 3 species (Bird blue shades in Figure 6).

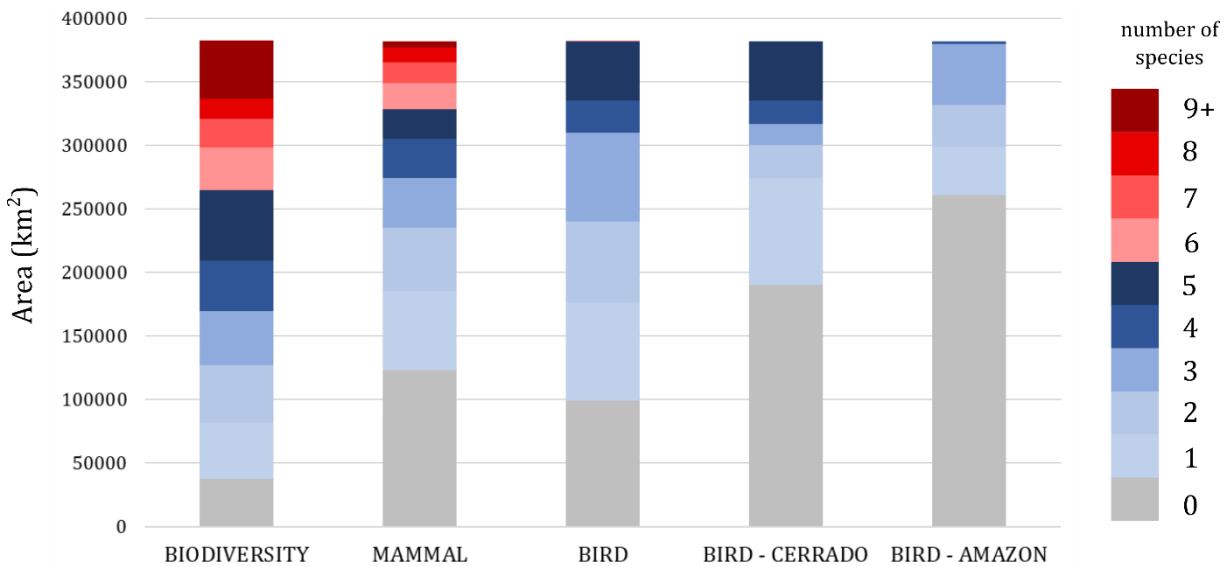


Figure 6: Amount of area suitable for species occurrence in Maranhão State. Biodiversity represents mammals and birds combined; Bird includes Amazon and Cerrado species combined.

3.4. Species hotspots and land use change

Combining species hotspots to land use in Maranhão in the year 2018, we verified that natural land cover (including forest and non-forest environments) still holds great part of the biodiversity hotspots (Figure 7). Natural land cover accounts for 273,048 km² of which 30% overlaps with biodiversity hotspots with more than five species (Figure 7; Table S5). Increasing agricultural areas (Figure 1) accounted for 104,118 km², out of which 31.8% overlaps with suitable areas for more than five species (33,107 km²; Table S5) and 63.6% overlaps with hotspots for 1 to 5 species (66,247 km²).

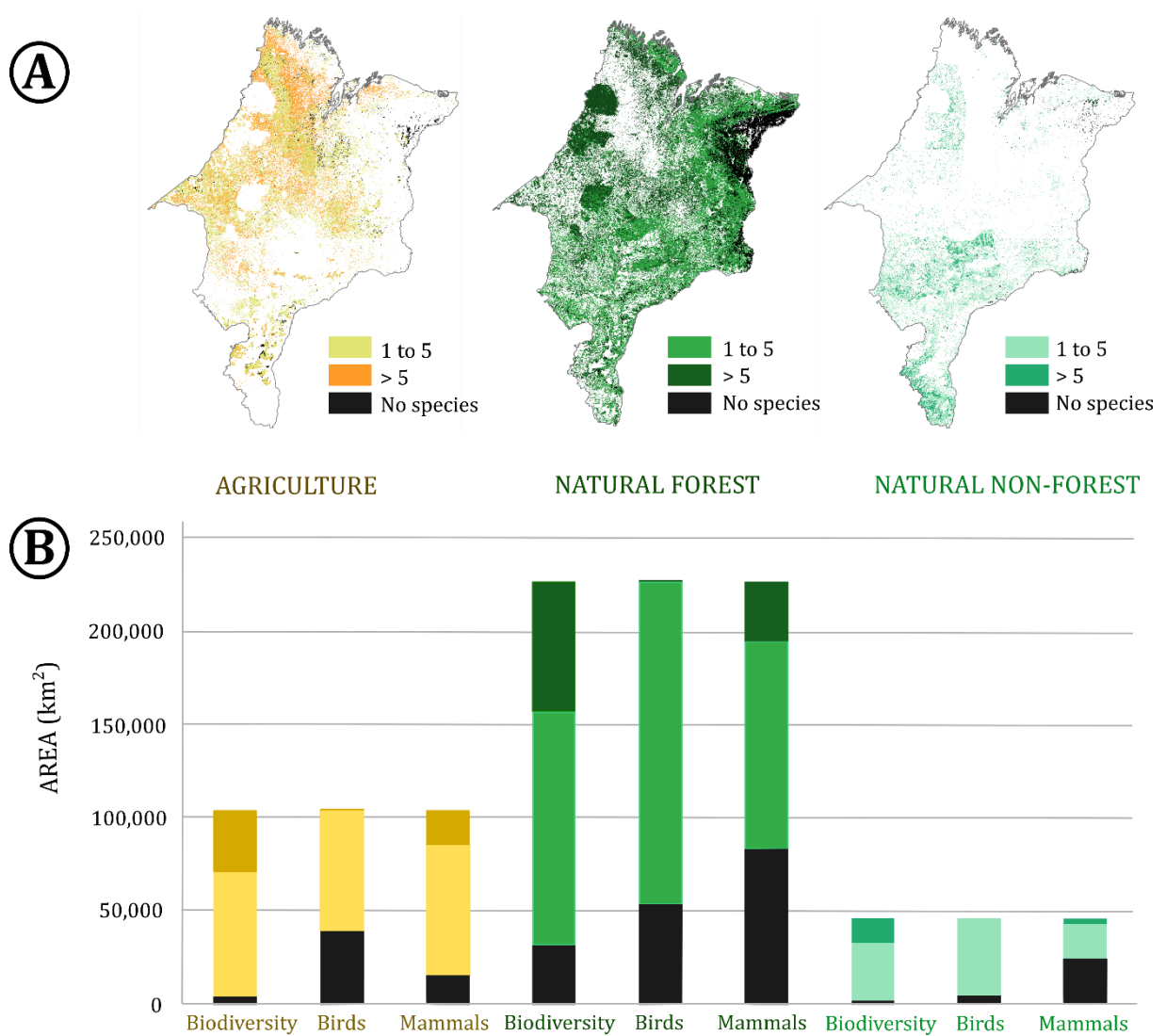


Figure 7: Overlap between species hotspots and three main classes of land use in 2018, in Maranhão State. (A) Spatial distribution of biodiversity hotspots overlapping agriculture (including pastures and crops), natural forest and natural non-forest areas; (B) Total area of overlap between each land use and species hotspots.

3.5. Species hotspots and protected areas

As for how much protected areas overlap with species hotspots, we verified that out of the ~70,817 km² with some degree of legal protection, 48.2% hosts hotspots for more than five species and 44.4% for 1 to 5 species. However, there are three main types of protected areas: Indigenous Lands, Conservation Units with Integral Protection and Conservation Units with Sustainable Use. The two first are far more restrictive than the third. It is remarkable though, that more than 40% of hotspots for at least one species within protected areas are covered by the less restrictive type (Figure 8).

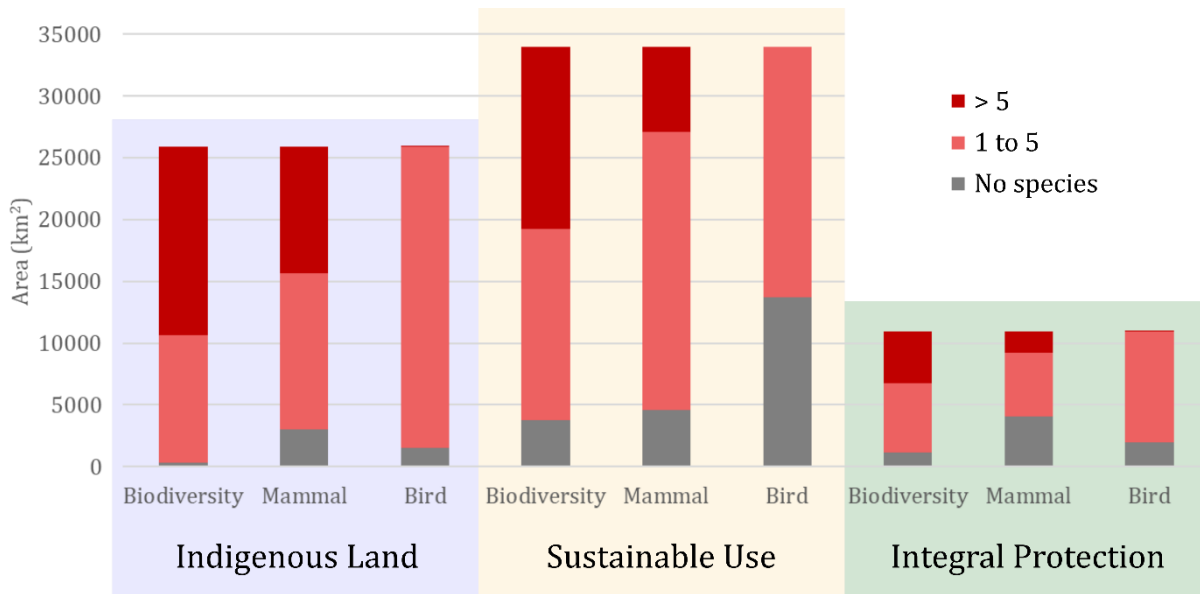


Figure 8: Total area of species hotspots within three different types of protected areas in Maranhão State.

4. DISCUSSION

Despite intense land use change over the last decades, with pronounced expansion of agriculture, the natural areas of Amazon rainforest and Cerrado in the state of Maranhão host several sensitive and vulnerable bird and mammal species. Modelling the broader distribution of several species generated an interesting representation of hotspots for their occurrence. Biodiversity hotspots (the sum of all selected species hotspots) allowed the recognition areas with the potential to host several species and therefore the identification of key regions to be protected. Here we address the advantages of using new modelling approaches and our proposed hotspots to identify priority areas for conservation and management. We discuss how our results contribute to the diagnosis of land use modification over biodiversity hotspots and the coverage of existing protected areas. We also discuss the importance of open data and accuracy of species occurrence databases to achieve reliable model outputs.

4.1. Hotspots and conservation priorities

Despite the differences in species used and modelling procedures, the bird hotspots partially coincide with those presented by de Carvalho et al. (2017), especially when analysing them separately by biome (Figure 5). We also verified some considerable

overlap to priority areas indicated by de Carvalho (2017) in the biodiversity hotspots with birds and mammals combined. We verified that for Cerrado birds two areas show high suitability for all the five species used in the analysis (Figure 9). The first one is in the extreme south of the state (Figure 9A) and the second is in the southeast of the state (Figure 9B). Both areas overlap with national high priority areas for conservation, respectively: *Chapada Sudoeste do Piauí, Maranhão e Tocantins* (CP-471), and *Área do Mirador-Uruçuí* (CP-480; MMA, 2003a).

Evaluating the biodiversity hotspots, we recognized some relevant areas in the Amazon region of the state, particularly in the northwest. First, the area adjacent to Indigenous Land Alto Turiaçu and the area partially comprised by APA Baixada Maranhense (Figure 9C). Other areas of concern in the Amazon side of Maranhão stand in the surroundings of Gurupi Reserve, mostly to the west and north of the Reserve (Figure 9D). In the Cerrado part of the state, the biodiversity hotspots map shed light to the area halfway between the National Park Chapada das Mesas and the Indigenous Land Krikati (Figure 9E). Even though scattered, this area may be relevant for connectivity in the Cerrado landscape. We claim that to make justice to the northeast region of the state, Caatinga species must be included in the hotspot analysis once the region comprises the transition zone between the two biomes (Figure 9F).

4.2. SDM, EcoLand and hotspots

Increasing data availability enables the use of SDM to elucidate how species occur under different climate and landscape conditions (e.g., Bertassoni et al., 2019; De Marco et al., 2018; Velazco et al., 2019). However, the combination of multiple SDM and the use of the EcoLand analysis have the potential to be applied to propose solutions for environmental management addressing a variety of species. In this sense, climate and landscape suitability allow decisions to rely in both long term environmental species requirements and short-term landscape change trends (Ferreira e Silva et al., 2018; J. P. Santos et al., 2019). Species selection or more inclusive species lists (as data become more reliable and accessible) can provide different combinations for the hotspot analysis presented here. This procedure can further promote the interaction and debate between species specialists, modelling experts and decision-makers to evaluate adequacy and interpretation of model outputs (Villero et al., 2017).

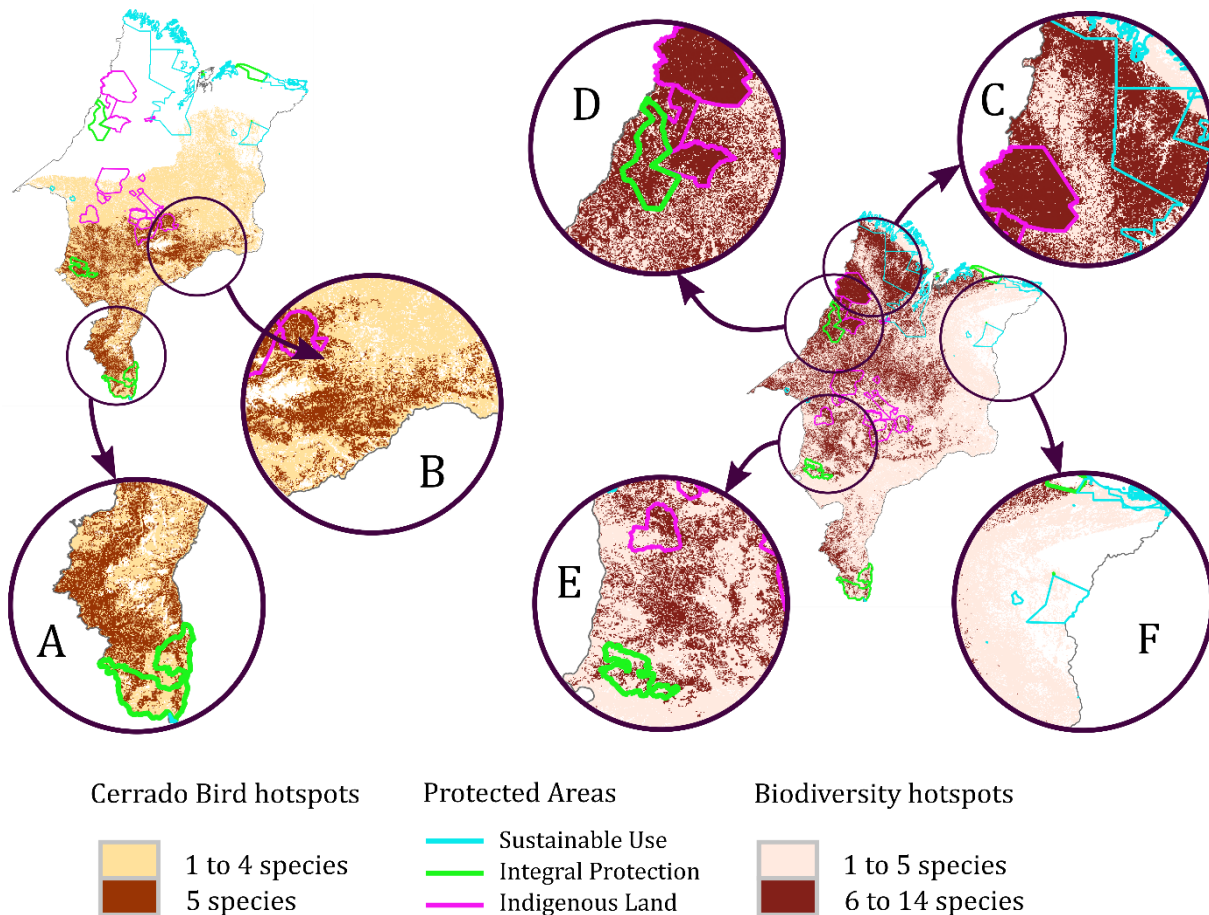


Figure 9: Hotspots for Cerrado bird species outside protected areas. A – Southwestern Plateau (in the border with the states of Piauí and Tocantins); B – Mirador-Uruçuí area. Biodiversity hotspots as an indicative of priority areas for conservation and further research in Maranhão State. C) Surroundings of Indigenous Land Alto Turiaçu and adjacencies of APA Baixada Maranhense; D) Gurupi Reserve and its surroundings; E) hotspot between National Park Chapada das Mesas and the Indigenous Land Krikati; F) transition zone between Cerrado and Caatinga lacking hotspots.

4.3. Land use change over hotspots

Inevitably, pastures and crops have expanded over natural areas with high climate and landscape suitability for species occurrence. In this study, species were selected for their ecological relevance and vulnerability in Maranhão State. And even though agricultural expansion brings economic profits, it comes at the cost of biodiversity loss. The prevalence of pastures, as the expanding agricultural activity in the Amazon part of the state, since the 1980s' (Figure 2), means that such overlap between predicted hotspots and this land use prevents species to inhabit those areas (Figure 7B). The same applies for the expansion of crops in the Cerrado part of the state (Figure 2). In other words, most

hotspots overlapping current agricultural activities are no longer suitable for species occurrence (Figure 7). Whereas for the natural environments, the overlap with hotspots is highly desirable for conservation purposes (Figure 7), providing legal enforcement takes place. Land use change over time is led by political and economic drivers and present relevant environmental consequences. Supporting political decisions with current knowledge on biodiversity and up to date modelling tools enables the negotiation of best strategies for the state development, not only accounting for economic profit but also for environmental benefits.

4.4. Data availability

Monitoring land use change is the primary source of information for landscape planning once it reveals trends and drivers. Mapping tools have increasingly improved and become a priority for research institutions and political agencies. The MapBiomass initiative provides an open platform with a time series of land use maps for the entire area of Brazil (from 1985 to 2018). A simple evaluation of land use change in Maranhão State reveals that agriculture, including pastures and crops, has been pervasively increasing over the decades since the 1980's (Figure 1).

Understanding biodiversity distribution in space, has a complementary role to land use change in assisting planning decisions. Species databases are also evolving fast. Despite global datasets, such as GBIF⁵, VertNET⁶ and eBIRD⁷; regional, peer-reviewed and open databases are gaining importance not only in Brazil, but also worldwide. In Brazil, we recognize the governmental effort to increase the quality of data in *Portal da Biodiversidade*⁸, but we also highlight the role of research institutions and universities in leading the compilation of unpublished species datasets and making them available in open access renowned journals (e.g., Galetti and Ribeiro, 2018; P. M. Santos et al., 2019). Citizen Science has also become a powerful source of data. As a successful example, the WikiAves⁹ can be recognized as a useful and reliable platform based on birdwatching data engaged in a peer review process.

⁵ <https://www.gbif.org/>

⁶ <http://vertnet.org/>

⁷ <https://ebird.org/home>

⁸ <https://portaldabiodiversidade.icmbio.gov.br/portal/>

⁹ <https://www.wikiaves.com.br/>

5. CONCLUSION

The EcoLand analysis and the hotspots approach can be applied to other states or even to the national level to inform species conservation actions and priority areas for the implementation of new protected areas. Nonetheless, including other species and groups to the hotspot analysis could translate in more representative results. Substantial modification of biodiversity distribution due to environmental changes (Dornellas et al. 2014) can compromise the functioning of ecosystem and the services they provide that support human wellbeing (Mace et al. 2012). Using modelling as a tool to spatially analyse such changes and consequences can be very useful to inform decision makers, managers and practitioners. However, not only synthetic and straightforward results must be presented, but also their demand and needs should guide modelling choices (Villero et al., 2017). Seeking to bridge the science-police gap, modelling experts can provide guidelines to assist the selection of species and the development of biodiversity monitoring strategies at different institutional levels. For a comprehensive spatial approach on biodiversity variation over time, different ecosystems require different indicator species.

SUPPLEMENTARY MATERIAL

Box 1: The Economics of Maranhão

The wealth produced in Maranhão in 2017 reached a total of R\$ 89.5 billion (IMESC, 2019). Economic development in Maranhão State is increasingly based on the exports of agricultural and mineral commodities with little added value and low engagement in productive chains (Holanda, 2013). Mineral commodities accomplished for a substantial parcel of exportation in 2013: 40% based on aluminum, 20.8% on iron complex and 4.2% in gold. Followed by agriculture that stood for 32.2% of exportation of soybean, corn and cotton in 2013 (IMESC, 2015). This model, highly dependent on international cycles, could be replaced by activities that aggregate occupational and fiscal innovation (Holanda, 2013). Silviculture and forest extraction had increased in the state (21.6% per year between 2000 and 2013) due to demand for charcoal for pig iron production and eucalyptus plantation intensification in the central and east portions of the state (Holanda, 2013; IMESC, 2015). The other two main agriculture activities are cattle farming and mechanized soybean farming, mostly in the south and east of the state (IMESC 2015). Currently, estimates point to more than 7.5 million livestock units produced in the state, an evidence of cattle farming expansion (Lago, 2012; Tannús, 2012). Despite coast extension and favorable climatic conditions, permanent crops and fish production was not substantial in 2015. Whereas temporary crops presented considerable increase in planted area (43.2%) including the main produced items in the state: soybean, corn, bean, rice, cotton, cassava and sugar cane (Holanda, 2013). Net added value in Maranhão State by sector, in 2014, was distributed in agriculture with 10.8%, industry 17.9% and services with 71.3% (IMESC, 2016).

Box 2: The biomes behind our modelling background

The Amazon originally occupied more than 4 million km² in Brazil (~49.5% of the Brazilian territory; IBGE, 2019). It is still the largest continuous tropical forest in the planet, and it has an extremely high biodiversity. It has high levels of precipitation and it is composed of various vegetation types such as *terra firme* (dry lands with 50m tall trees and open forest floor), *igapó* and *várzea* (both seasonally inundated forests). In the Amazon, the most common pattern of land use conversion is from forest to pasture and then to agriculture (Lapola et al., 2014). Economic development in the Amazon unfolds over extraction activities followed by land use and land cover modification. Despite the forest magnitude and great extension, deforestation to expand pastures has been the main cause of biodiversity loss. Other recurrent threats to Amazonia are expansion of primary and secondary road networks, growing demands for agricultural land, over exploitation of many natural resources and construction of hydroelectric dams.

The Cerrado is the second largest Brazilian biome, which originally occupied almost 2 million km² (~23.3% of the Brazilian territory; IBGE, 2019). Comparable to a tropical savannah, the Cerrado is composed of several phytophysiognomies with high biodiversity. Land use has changed more than half of the Cerrado, with natural habitat giving place mainly to pastures and crops (Klink and Machado, 2005). Nonetheless, Strassburg et al. (2017) claim that it is possible to reconcile agriculture expansion and conservation efforts.

The Pantanal is one of the largest freshwater wetlands in the planet, encompassing ~193 thousand km² in the center of South America, center-west of Brazil (~1.8% of the Brazilian territory; IBGE, 2019). It is a lowland with a very dynamic regime with river channels shifts and flood-pulse responses to intensive rainfall in the wet season (Pupim et al., 2017). Seasonal flooding influences vegetation distribution (mostly dry savanna and natural grass; Pott and Pott, 2004). Relevant economic activities in the region include cattle ranching and tourism (Pott and Pott, 2004). Habitat conversion and increase in unsustainable agricultural practices go against the RAMSAR Convention in Wetlands (Roque et al., 2016).

The Caatinga is the Brazilian biome of drylands that covers ~862 thousand km² in northeast Brazil (~10% of the Brazilian territory; IBGE, 2019). Despite its high biodiversity and endemism (Hauff, 2010; Portillo-Quintero and Sánchez-Azofeifa, 2010), the Caatinga is one of the poorest regions in Brazil. The region is vulnerable to climate changes and already has areas under desertification (Seddon et al., 2016). Due to several threats (e.g., deforestation for livestock farming, logging for firewood, agriculture, hunting, fragmentation by roads, misuse of fire) (Castelletti et al., 2003; Leal et al., 2005), about 46% of its area has been deforested (MMA, 2015) and only 1.2% under full protection in precarious conditions and decreasing funds (Oliveira and Bernard, 2017).

Box 3: Landscape Variables

We used the EartEnv homogeneity layer, a second-order texture measure calculated as the similarity of EVI between adjacent pixels, as a representation of spatial habitat heterogeneity (Tuanmu and Jetz, 2015). Homogeneity varies from 0 to 1 and indicates a negative relationship to heterogeneity.

We used terrain slope information from the Topodata databank refined from Shuttle Radar Topography Mission (SRTM) to the Brazilian territory (de Morisson Valeriano and de Fátima Rossetti, 2012) available at Ambdata website (<<http://www.dpi.inpe.br/Ambdata>>) of the Brazilian Institute of Space Research (INPE).

We used the MapBiomas (2015) to derive two binary maps, one with natural forest cover and another with natural non-forest cover. We calculated each class percentage using a 1km window and resampled original 30x30 m pixel to ~1x1 km to match other layers resolution.

The 2009 Human Footprint (Venter et al., 2018) is a global map that combines several information layers representative of human pressure on the environment in 2009. The eight variables combined in the human footprint are 1) built-up environments, 2) population density, 3) electric power infrastructure, 4) crop lands, 5) pasture lands, 6) roads, 7) railways, and 8) navigable waterways. It has a spatial resolution of ~1 km² (Venter et al., 2018).

Table S1: Loadings of factorial analysis performed to select climatic variables. In red are the selected variables, and in yellow, variables not selected, despite their high values after expert deliberation.

CHELSA Variables	MR2	MR4	MR3	MR5	MR6	MR1
1=Annual Mean Temp. [°C*10]	0.969644	-0.072940	0.050341	-0.111648	0.100418	-0.016889
2=Mean Diurnal Range [°C]	-0.147147	-0.522338	-0.503845	0.458874	-0.105620	0.474993
3=Isothermality	0.211288	0.373405	-0.005959	-0.232317	0.856235	-0.049790
4=Temp. Seasonality [std dev]	-0.132603	-0.257690	-0.424157	0.808206	-0.261676	0.058243
5=Max Temp. of Warmest Month [°C*10]	0.744185	-0.487948	-0.169144	0.172123	-0.245460	0.272170
6=Min Temp. of Coldest Month [°C*10]	0.757701	0.208380	0.329419	-0.389561	0.206223	-0.255454
7=Temp. Annual Range [°C*10]	-0.201837	-0.515110	-0.414687	0.471882	-0.352220	0.415144
8=Mean Temp. of Wettest Quarter [°C*10]	0.773525	0.028372	-0.207646	0.144570	0.141941	-0.020467
9=Mean Temp. of Driest Quarter [°C*10]	0.881663	0.017258	0.244087	-0.254122	0.131568	-0.125051
10=Mean Temp. of Warmest Quarter [°C*10]	0.953352	-0.223744	-0.065434	0.140175	-0.092008	0.039130
11=Mean Temp. of Coldest Quarter [°C*10]	0.860080	0.008663	0.241037	-0.423639	0.124107	-0.042034
12=Annual Precipitation [mm/year]	-0.062431	0.554916	0.759681	-0.248702	-0.019411	-0.045342
13=Precipitation of Wettest Month [mm/month]	-0.039747	0.121071	0.980836	-0.112805	0.020053	-0.000372
14=Precipitation of Driest Month [mm/month]	0.023690	0.949453	0.195589	-0.099749	0.210991	0.024629
15=Precipitation Seasonality [coef. of variation]	0.108908	-0.871425	-0.116922	0.156239	0.026044	0.249859
16=Precipitation of Wettest Quarter [mm/quarter]	-0.048922	0.127556	0.979536	-0.128674	-0.006170	0.004001
17=Precipitation of Driest Quarter [mm/quarter]	0.018537	0.949254	0.205536	-0.104273	0.204920	0.012816
18=Precipitation Warmest Quarter [mm/quarter]	-0.441294	0.658844	0.040157	0.039837	0.094782	0.041699
19=Precipitation of Coldest Quarter [mm/quarter]	0.353847	0.092206	0.626668	-0.108640	0.075809	-0.230149

Table S2: Selected species and the criteria used.

Bird Species - CERRADO / ECOTONE		
Species	Distribution and Endemism	Conservation status
1. <i>Charitospiza eucosma</i>	South and northeast of Maranhão	Near Threatened globally (IUCN Red List 2017); Dependent on habitat conservation (Lopes, 2009)
2. <i>Euscarthmus rufomarginatus</i>		Near Threatened globally (IUCN Red List 2017); Dependent on habitat conservation (Lopes, 2009)
3. <i>Melanopareia torquata</i>		Dependent on habitat conservation (Lopes, 2009)
4. <i>Neothraupis fasciata</i>		Near Threatened globally (IUCN Red List 2017); Dependent on habitat conservation (Lopes, 2009)
5. <i>Porphyrospiza caerulescens</i>	South and northeast of Maranhão	Near Threatened globally (IUCN Red List 2017); Dependent on habitat conservation (Lopes, 2009)
Bird Species –AMAZON		
Species	Distribution and Endemism	Conservation status
1. <i>Dendrocolaptes medius</i>	Endemic to Centro Belém	Not considered yet by BirdLife International (recently recognized as a species); Endangered (MMA, 2003b); Considered threatened (Batista et al., 2013)
2. <i>Guarouba guarouba</i>	Endemic to Amazon	Vulnerable (IUCN Red List 2017)
3. <i>Piculus paraensis*</i>	Endemic to Centro Belém	Not considered yet by BirdLife International (recently recognized as a species); Considered threatened (Del-Rio et al., 2013)
4. <i>Penelope pileata</i>	Endemic to Centro Belém	Not considered yet by BirdLife International (recently recognized as a species); Vulnerable (IUCN, 2014 <i>apud</i> Lima et al., 2014); Considered threatened (Somenzari and Silveira, 2015)
5. <i>Pteroglossus bitorquatus</i>	Endemic to Centro Belém	Not considered threatened by BirdLife International because it is a subspecies; Vulnerable (MMA, 2003b)

Mammal Species – MARANHÃO STATE AND SURROUNDINGS (AMAZON AND CERRADO)		
Species	Distribution and Endemism	Conservation status
1. <i>Alouatta belzebul</i>	Endemic distribution in Eastern Amazon; Occurrence in relevant areas in MA	Vulnerable (IUCN, 2018)
2. <i>Cebus kaapori</i>	Endemic distribution in Eastern Amazon; Occurrence in relevant areas in MA	Critically Endangered (IUCN, 2018; MMA, 2014)
3. <i>Chiropotes satanas</i>	Endemic distribution in Eastern Amazon; Occurrence in relevant areas in MA	Critically Endangered (IUCN, 2018; MMA, 2014)
4. <i>Choloepus didactylus</i>	Limit of its distribution is in MA Amazon	
5. <i>Chrysocyon brachyurus</i> *	Expanded north boundary distribution in south MA	Vulnerable (MMA, 2014); Near Threatened (IUCN, 2018)
6. <i>Coendou nycthemera</i> (<i>Coendou koopmani</i>)*	Unexpected occurrence in MA; Expanding distribution	Data Deficient (IUCN, 2018)
7. <i>Cyclopes didactylus</i> *	Expected occurrence in MA; Taxonomic issues	
8. <i>Dactylomys dactylinus</i>	Unexpected occurrence in MA; Expanding distribution	Least Concern (IUCN, 2018)
9. <i>Dasyopus beniensis</i> *	Taxonomic issues	
10. <i>Dasyopus kappleri</i>	Unexpected occurrence in MA; Expanding distribution	Least Concern (IUCN, 2018)
11. <i>Echimys chrysurus</i>	Unexpected occurrence in MA; Expanding distribution	Least Concern (IUCN, 2018)
12. <i>Leopardus colocolo</i> *	Unexpected occurrence in MA; Expanding distribution	Vulnerable (MMA, 2014); Near Threatened (IUCN, 2018)
13. <i>Lycalopex vetulus</i> *	Unexpected occurrence in MA; Expanding distribution	Vulnerable (MMA, 2014); Least Concern (IUCN, 2018)
14. <i>Myrmecophaga tridactyla</i>	Expected occurrence	Vulnerable (MMA, 2014; IUCN, 2018)
15. <i>Ozotoceros bezoarticus</i> *	Scattered distribution throughout South America	Near threatened (IUCN, 2018)
16. <i>Panthera onca</i> *	Keystone species; Flagship species	Locally Threatened (MMA, 2014); Near Threatened globally (IUCN, 2018)
17. <i>Priodontes maximus</i>	Ecosystem engineer	Vulnerable (MMA, 2014; IUCN, 2018)
18. <i>Speothos venaticus</i>	Expected occurrence	Locally Vulnerable (MMA, 2014); Near Threatened (IUCN, 2018)
19. <i>Tapirus terrestres</i>	Ecosystem engineer	Vulnerable (MMA, 2014; IUCN, 2018)
20. <i>Tayassu pecari</i>	Ecosystem engineer	Vulnerable (MMA, 2014; IUCN, 2018)

Table S3: Number of occurrence records of selected bird and mammal species initially compiled (TOTAL COUNT), the total amount of records after environmental filter was performed (FILTER COUNT).

Bird Species	TOTAL COUNT	FILTER COUNT
CERRADO total	966	687
<i>Charitospiza eucosma</i>	199	163
<i>Euscarthmus rufomarginatus</i>	83	68
<i>Melanopareia torquata</i>	225	157
<i>Neothraupis fasciata</i>	249	164
<i>Porphyrospiza caerulescens</i>	210	135
AMAZON total	401	315
<i>Dendrocolaptes medius</i>	8	8
<i>Guaruba guarouba</i>	132	104
<i>Penelope pileata</i>	106	86
<i>Piculus paraensis</i> *	4	4
<i>Pteroglossus bitorquatus</i> <i>bitorquatus</i>	151	113
Total for Bird Species	1367	1062
Mammal Species	TOTAL COUNT	FILTER COUNT
<i>Alouatta belzebul</i>	248	40
<i>Cebus kaapori</i>	47	37
<i>Chiropotes satanas</i>	30	20
<i>Choloepus didactylus</i>	270	92
<i>Chrysocyon brachyurus</i>	459	103
<i>Coendou nycthemera</i>	7	7
<i>Cyclopes didactylus</i>	174	69
<i>Dactylomys dactylinus</i>	15	12
<i>Dasypus beniensis</i>	20	12
<i>Dasypus kappleri</i>	457	167
<i>Echimys chrysurus</i>	9	8
<i>Leopardus colocolo</i>	58	26
<i>Lycalopex vetulus</i>	25	16
<i>Myrmecophaga tridactyla</i>	5996	1159
<i>Ozotoceros bezoarticus</i>	52	29
<i>Panthera onca</i>	791	168
<i>Prionomys maximus</i>	1578	471
<i>Speothos venaticus</i>	59	28
<i>Tapirus terrestris</i>	2768	422
<i>Tayassu pecari</i>	1445	436
Total for Mammal Species	14508	3322

*this species was not included in the modelling procedures.

Table S4: Mammal species excluded from the hotspot analysis and the main reason for their exclusion. DD – Data Deficient; LC – Least Concern; NT – Near Threatened.

Group	Icon	Species	# rec	Common name in English	Common name in Portuguese	IUCN Red List	Reason for exclusion
Rodent		<i>Coendou nycthemera</i>	7	Black dwarf porcupine	Porco-espinho; cuandu-preto	DD	High degree of uncertainty in SDM outputs (ad-hoc consultation)
Xenarthra		<i>Cyclopes didactylus</i>	174	Silky anteater	Tamanduaí	LC	Taxonomic issues (Miranda et al., 2018)
Xenarthra		<i>Dasyus beniensis</i>	12	---	Tatu-de-15-quilos	---	Taxonomic issues (Feijó and Cordeiro-Estrela, 2016)
Artiodactyla		<i>Ozotoceros bezoarticus</i>	29	Pampas deer	Veado-campeiro	NT	No relevant suitability detected by SDM in Maranhão State*
Carnivora		<i>Chrysocyon brachyurus</i>	103	Maned wolf	Lobo-guará	NT	No relevant suitability detected by SDM in Maranhão State*
Carnivora		<i>Leopardus colocolo</i>	26	Pampas cat	Colocolo	NT	No relevant suitability detected by SDM in Maranhão State*
Carnivora		<i>Lycalopex vetulus</i>	16	Hoary fox	Raposa-do-campo	LC	No relevant suitability detected by SDM in Maranhão State*
Carnivora		<i>Panthera onca</i>	168	Jaguar	Onça-pintada	NT	High degree of uncertainty in SDM outputs (ad-hoc consultation)

* Species are known to occur in Maranhão State; however, species register predominantly occur in other regions preventing their prediction with less records.

This could be the consequence of sampling bias.

Table S5: Area considered hotspots in Maranhão State and its overlapping with main land uses in 2018. Agriculture includes crops and pastures, and forest and non-forest were derived from MapBiomas classification of natural areas in Collection 4.

	Agriculture			Forest			Non-forest			Maranhão State		
Species_freq	Biodiversity	Birds	Mammals	Biodiversity	Birds	Mammals	Biodiversity	Birds	Mammals	Biodiversity	Birds	Mammals
1 to 5	66,247	64,622	70,703	125,250	172,984	111,787	31,484	40,752	18,866	227,629	282,105	205,350
> 5	33,107	6	18,248	69,759	24	31,808	12,404	0	2,413	116,551	30	52,988
No species	4,764	39,490	15,167	32,019	54,020	83,433	2,132	5,268	24,741	37,429	99,474	123,271
Total area (km ²)	104,118			227,028			46,020			381,609		

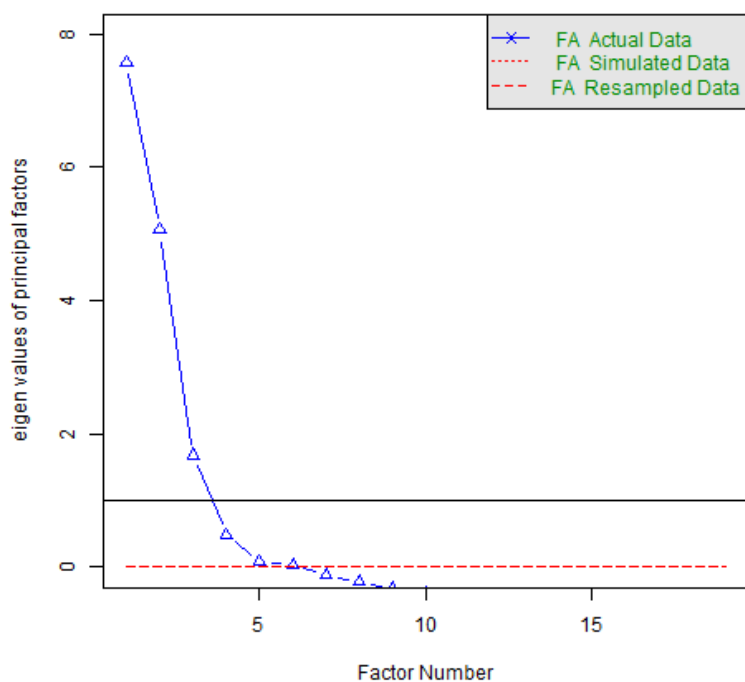


Figure S1: Multivariate scree plot from the Factorial Analysis (FA) for the selection of climatic variables, indicating the number of variables responsible for most variation.

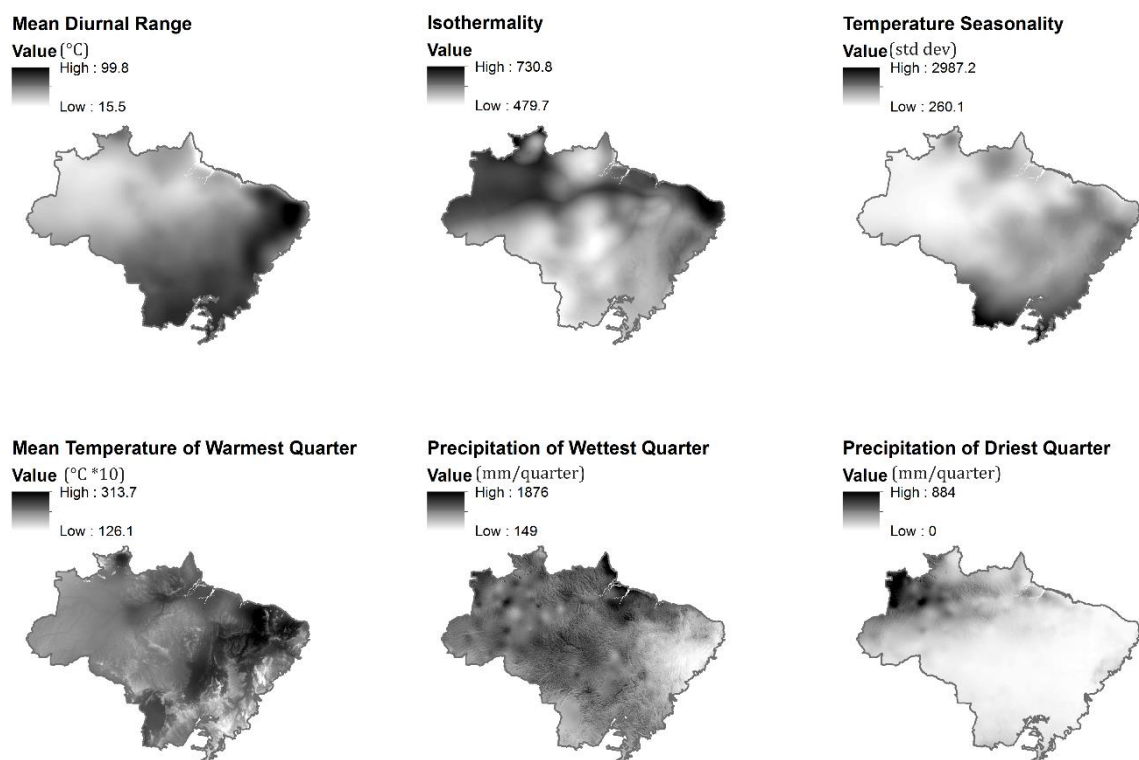


Figure S2: Maps depicting the variation of each of the selected climatic variables throughout the modelling background.

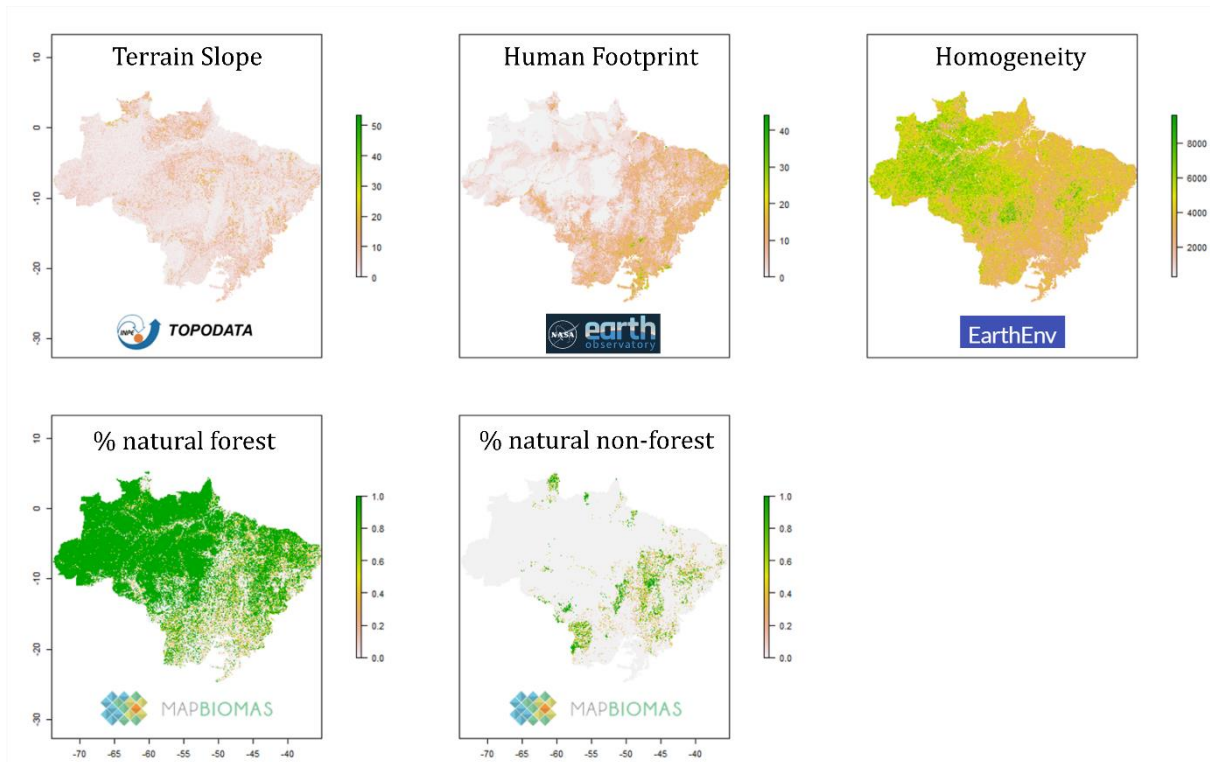


Figure S3: Maps depicting the variation of each of the selected landscape variables throughout the modelling background.

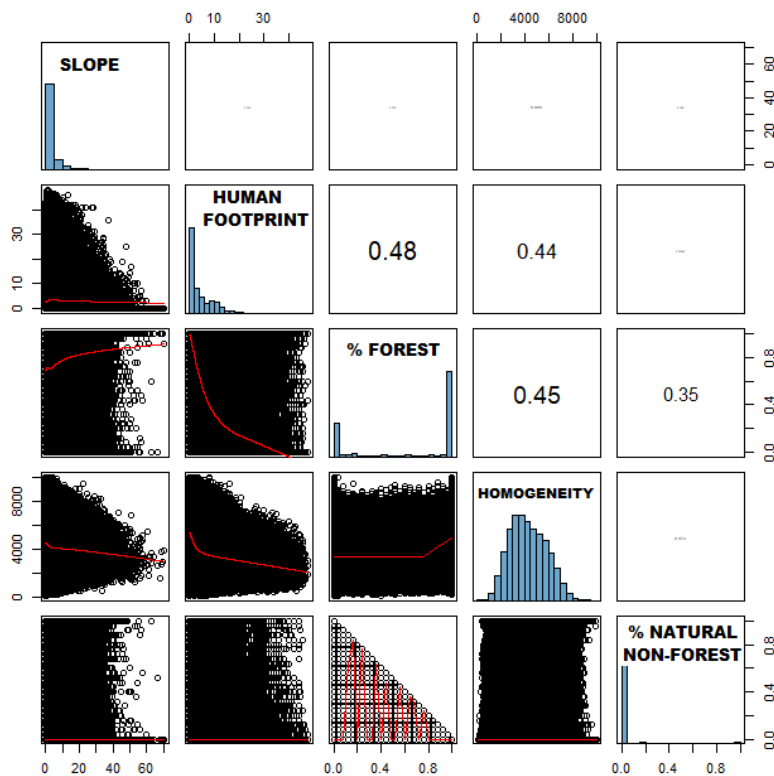


Figure S4: Value frequency and correlation plot of selected landscape variables.

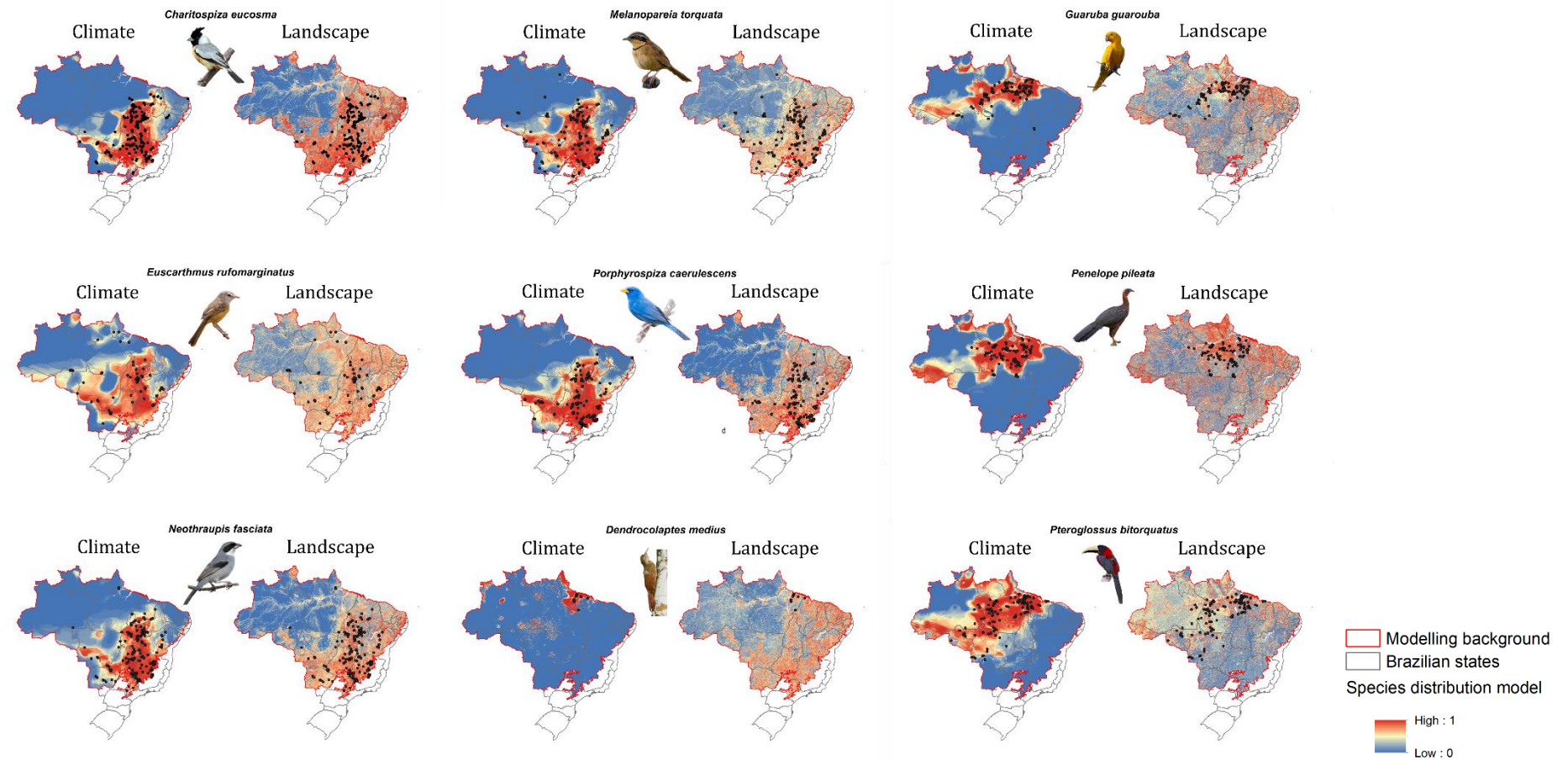


Figure S5: Final ensemble of climate- and landscape-based Species Distribution Models of selected bird species.

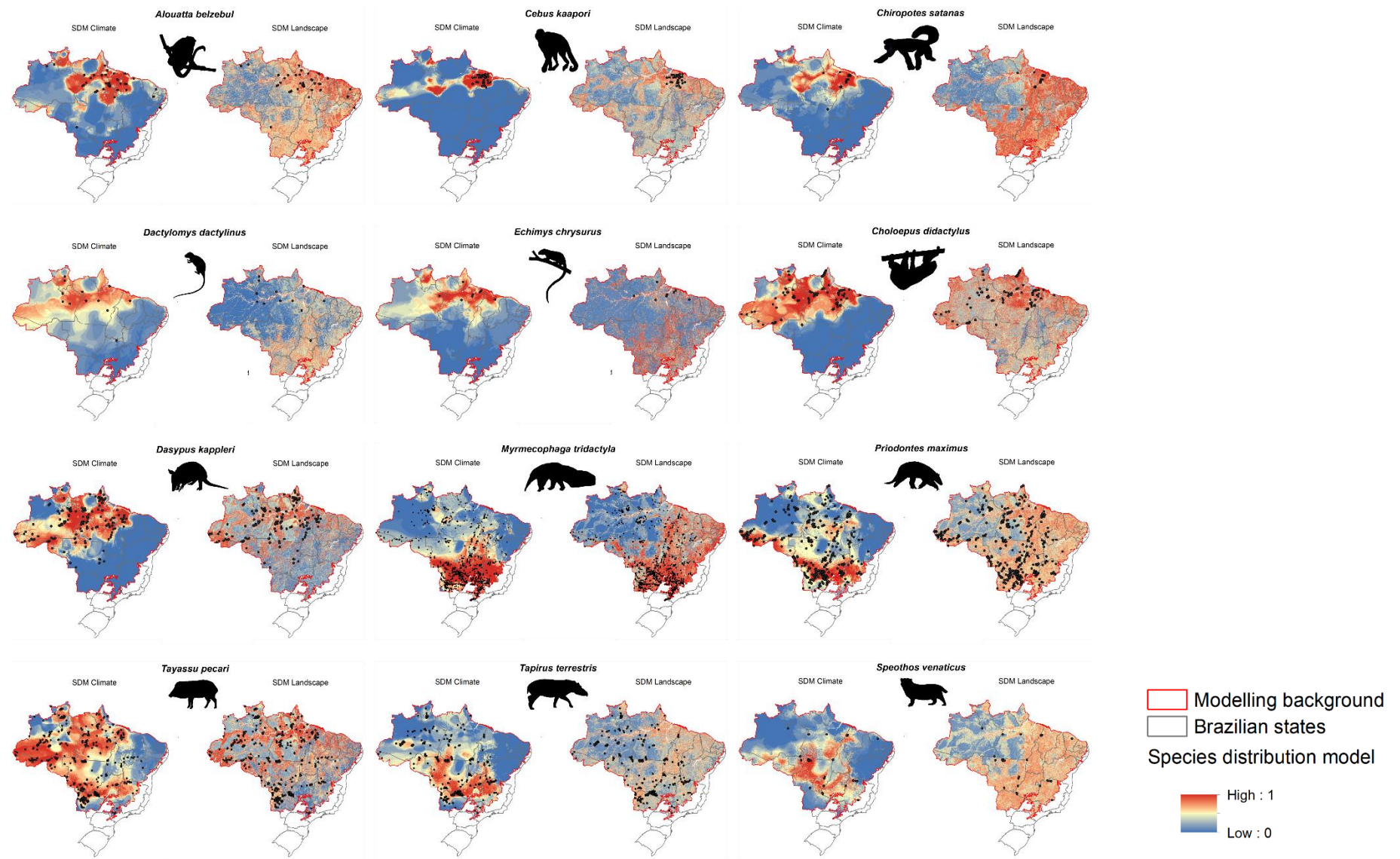


Figure S6: Final ensemble of climate- and landscape-based Species Distribution Models of selected mammal species

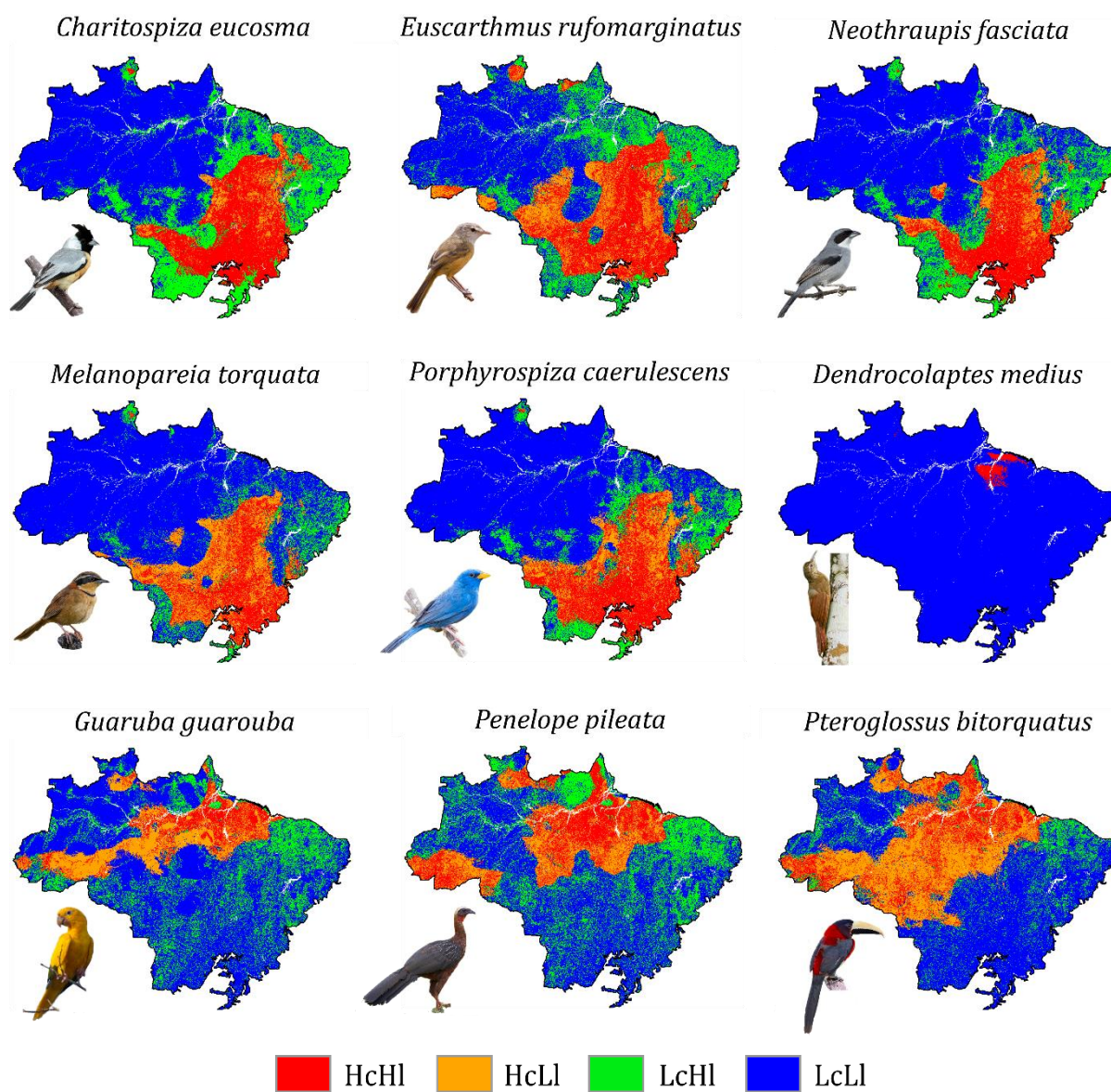


Figure S7: EcoLand of each bird species. H – High, L – Low, c – climate, l – landscape.

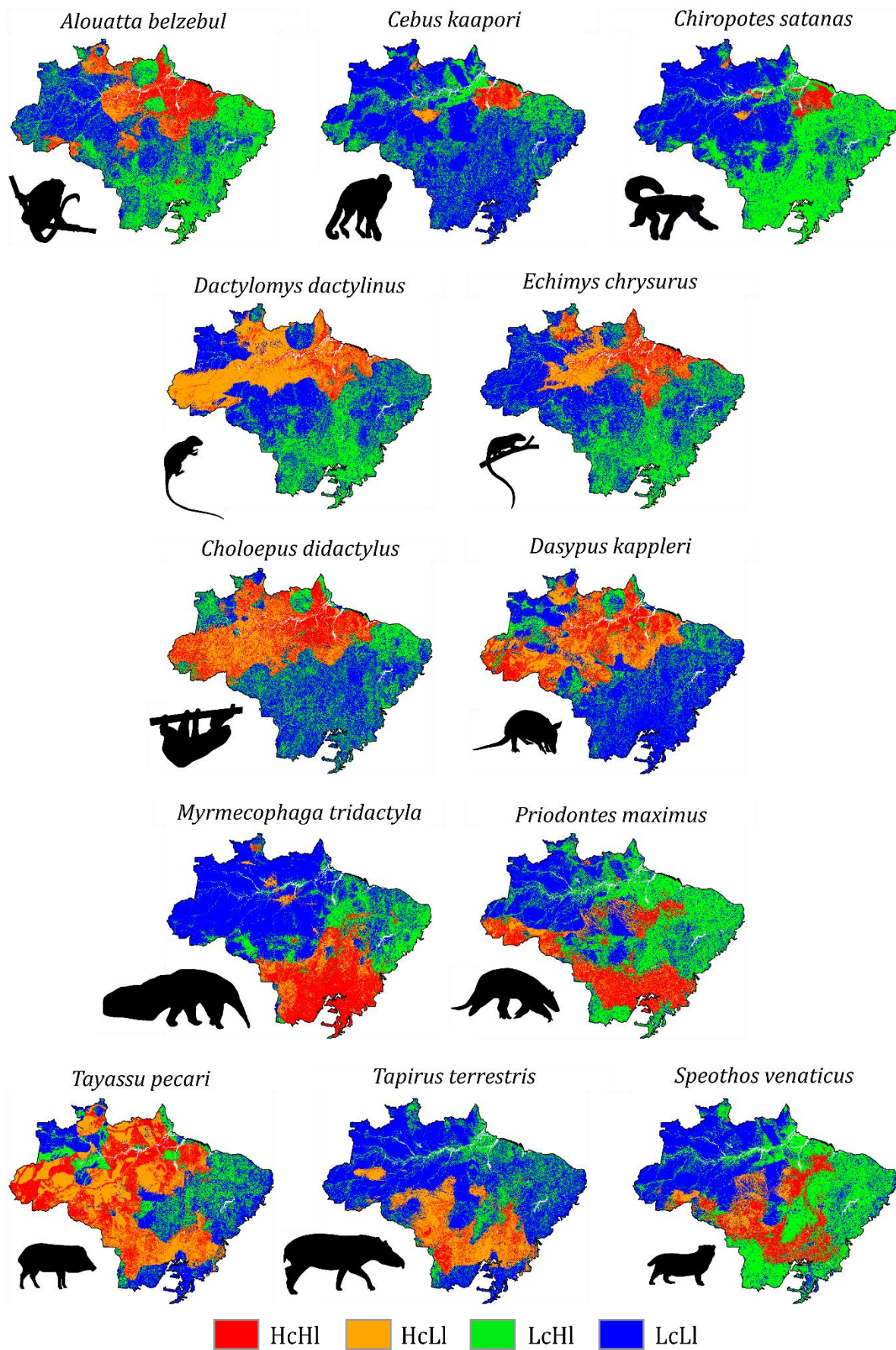


Figure S8: EcoLand of each mammal species. H – High, L – Low, c – climate, l – landscape.

CONTRIBUTIONS AND RECOMMENDATIONS

*"Everything always changes and nothing remains still...
...you cannot step twice into the same stream"
Heraclitus of Ephesus (535 BC–475 BC)*

Step Out of the Science Sphere and Bridge the Theory-Practice Gap

Shifting the current economic paradigm towards the sustainability ideals has emerged as a promising venue to ensure wellbeing for the increasing human population, without surpassing the planetary boundaries. Since their proposition in 2015, the Sustainable Development Goals (SDGs) have been debated and advances have been made to address their interdependencies and overlaps (Nilsson et al., 2016). Efforts to operationalize the 2030 Agenda on Sustainable Development (UN, 2016) and avoid perverse trade-offs indicate that coordination across sectors, societal actors and among different income countries is key (Stafford-Smith et al., 2017). The implementation of such transformative agenda takes place in diverse local contexts under the lead of national governments.

Science may have a significant contribution for action to take place, by designing innovative strategies to transform and monitor the outcomes of current and new practices (Sachs et al., 2019). Successful accomplishment of these tasks depends on scientists' engagement with real world events and on-the-ground practices. For the natural scientists concerned with biodiversity conservation, in the words of van der Leeuw (2018), "we must now go a step further and finally acknowledge that the real sustainability challenge is societal, not environmental." This can be interpreted by natural scientists as an invitation to join forces with social scientists to anticipate and prepare societies for the changes to come. Positive transformation can result from acknowledging and understanding these changes; informing societies and stakeholders; communicating to the general public; developing innovative solutions; securing adaptive capacities for governance; and strengthening societies' resilience.

Contributions to the Field

The sustainability paradigm requires a general understanding of current and future human impacts on the planet, so that we have the chance to adapt and avoid undesirable outcomes. Hence, planning the use of the space, in the form of environmental or landscape planning, it is possible to reach better outcomes if it is based in the

understanding of spatial processes and patterns. Spatial science has evolved along with processing capacities of computers and high-quality data availability. It has improved the way several scientific disciplines address the complex issues faced by socio-environmental systems in local, regional and global scales. Taking all into account, advances in this field has increasingly provided reliable spatial information for decision-makers and stakeholders.

Nonetheless, science is not the solution to all problems. Much on the contrary. Despite all the elucidation on the consequences of biodiversity loss and ecosystems degradation to the provision of ES and human wellbeing, many other *forces* influence decisions towards the unsustainable use of land and overexploitation of resources worldwide. Therefore, sound science is not enough to ensure humanity will choose the promising paths for a sustainable future. Many of the humanity's possible future trajectories will take their course in spite of scientific warnings and discoveries. Yet, in the brief history of humans inhabiting the planet, drastic turning points can always be triggered by scientific innovation (e.g., navigation capacity; medical advances; technological development). Therefore, it is important to recognize that science and knowledge have a role to play in the course of history, "but we are no different from other citizens in society, except that we have been trained in a particular way of thinking that is as relevant to the dynamics of society as any other" (van der Leeuw, 2018).

In a general view, my PhD research and all the challenges faced along with it, contributed to my formation as a scientist and widened my perspective and understanding of the current endeavours towards a sustainable future. I developed both chapters presented here motivated by the potential of ES frameworks in raising awareness about the benefits humans get from biodiversity and nature. I defined the two main chapters of this thesis and my participation in other academic activities with the main goal of using the ES concept potential to connect environmental, social and economical spheres in a common language. It was very challenging but very gratifying at the end. This connection can be explored in the ES framework by quantifying, mapping, valuing and communicating. On pursuing this venue, I realized how challenging it was. First, because it is a consolidating field, in which concepts and tools are being tested. Second, because even though divergent and confronting ideas enrich the scientific debate, they can also undermine the consolidation of practices.

Chapter 1*A conceptual framework to link landscape structure and ecosystem services***Achievements**

The effervescent field of ES presents new propositions and discoveries each day. Many of them closely related to 1) the spatial quantification of the ES supply chain components (Baró et al., 2016; Egarter Vigl et al., 2017; Schirpke et al., 2019a; Schulp et al., 2014); 2) the links between biodiversity and ES (Elena M. Bennett et al., 2015; Harrison et al., 2014; Landis, 2017; Ricketts et al., 2016; Sandifer et al., 2015); 3) the usefulness of ES framework to sustainability (Geijzendorffer et al., 2017; Schröter et al., 2017); 4) landscape approaches to ES (Angelstam et al., 2019b; Boesing et al., 2017; Duarte et al., 2018; Grafius et al., 2018; Grass et al., 2019; Lamy et al., 2016; Mitchell et al., 2015b; Schröter and Remme, 2016); 5) specific studies addressing ES flows (Bagstad et al., 2013; Schröter et al., 2014); 6) interregional ES flows (Koellner et al., 2019; Schirpke et al., 2019b; Schröter et al., 2018); and 7) the contributions from ES to land management (Guerry et al., 2015; Jones et al., 2013; Ruckelshaus et al., 2015; Sitas et al., 2014). This wide variety of research lines show the versatility of the ES framework and its plurality of applications.

In Chapter 1, I developed a theoretical approach to link landscape structure and ES flows. I showed how addressing landscape structure influences on the ES flow can contribute to comprehensively acknowledge the ES supply chain in spatial terms. I discussed the role landscape composition and configuration play in the ES flow, given that each ES has their mechanisms of conversion into benefits. For instance, I discussed how landscape can modulate the flow of pollination and pest control services, depending on how it affects organisms' capacity to move. The spatial arrangement of supply and demand, their interspersions and the presence of different anthropogenic matrix in a landscape can facilitate or hinder organisms' movement and ES delivery. Differently, recreational and many other cultural services rely on the movement of people (demand) to enable ES flow. In these cases, accessibility, transportation infrastructure, and the maintenance of trails are examples of landscape attributes that can be managed to facilitate flow. Some regulation services – such as microclimate, erosion and flood control – will have their flow modulated by the shape, size and allocation of supply and demand

within the landscape. On the other hand, provision services like food provision may be decoupled from demand (i.e. are located in distant areas) and present more complex flow mechanisms. This is the case of agricultural items that are transported to meet demands elsewhere (not explored in Chapter 1).

Pitfalls

Our theoretical proposition requires further debate, application and testing. While the scientific community working with ES is advancing in the consolidation of concepts and tools, the vast literature and the fast development of the field worldwide prevents individual researchers from keeping up with all the literature. Therefore, the challenge to substantially develop a theoretical proposition with loads of new research coming out each day is never-ending. To accomplish chapter 1, I had to learn how to select and concentrate my reading efforts. Besides, not being in a research group focused on ES, prevented further debate among peers. Fortunately, with the support of my supervisor, I successfully managed this disadvantage, and fruitfully engaged with researchers and research groups from other Brazilian universities and from abroad (reflected in my several co-authors).

Further Development

Further empirical testing to quantify and evaluate the effects of landscape structure on ES flow must be done through observation and experimentation. However, landscape studies are costly and time-consuming. Nevertheless, long-term and collaborative monitoring can be coupled with ongoing research initiatives to optimise design and financial investments. Additionally, reviews and meta-analysis can accelerate advances in the ES field (e.g., Duarte et al., 2018). For this purpose, academics should foresee such application of their individual results and make their raw data publicly available along with their publications. Another challenge in this field lies in the temporal assessment of landscapes and ES. Evaluating how the provision of ES varies over time along with land use can indicate whether ES flow is depleting or degrading ES supply.

Chapter 2

*Identifying hotspots for biodiversity conservation:
from ecological to administrative boundaries*

Achievements

In Chapter 2, I provided spatial information to prioritize conservation efforts using species hotspots as an indicator. I applied up to date modelling tools to identify and prioritize key areas for biodiversity conservation in the state of Maranhão, Brazil. The state is in a region in Brazil with relatively cheap prices for land and reduced environmental law enforcement, despite its significant biodiversity. However, fast land use change in both the Amazon and the Cerrado areas in Maranhão calls for a more comprehensive land use management that combines the effectiveness of protected areas and increasing agricultural activities. Besides the modelling approach itself and the application of its results, I experienced the argumentative power derived from the use of reliable datasets in collaboration with species experts and feedbacks on model outcomes.

Since the 1980's, Maranhão State presented substantial expansion of crops and pastures over natural areas of Amazon rainforest and Cerrado, which host several sensitive and vulnerable bird and mammal species. The approach to map biodiversity hotspots allowed the identification of areas with high potential to host several key species and propose their legal protection. The same method can be applied to other states and to the national level to inform species conservation actions.

Pitfalls

Because I was a beginner in the ES field when I initially developed my research project, most of its preliminary goals shifted along the course of my PhD. To make the best out of the opportunities I had, I immersed myself on the SEEA EEA framework (Appendix 1). After spending several months getting acquainted with it to develop my sandwich proposal, I learned that the complexities of the framework and the lack of sufficient data prevented me from fully developing the initial idea. Instead, I shifted to an alternative project and spent the rest of my internship building up collaborations with species experts and compiling data to run the Species Distribution Models (SDM). Eventually, the main contribution of Chapter 2, shifted from being the further development of the Experimental Ecosystem Accounts to a punctual contribution to the Maranhão State.

I acknowledge that modelling a higher number of species and including a variety of other taxa to evaluate hotspots is fundamental to guarantee a comprehensive assessment of biodiversity. Nevertheless, the consultation of experts for the selection of ecologically relevant species adds reliability to our results. Additionally, the temporal variation of the compiled species datasets (ranging from 1998 to 2017) reflects a limitation for this type of method, that represents a trade-off between quantity and temporal accuracy. Temporal filters should be further tested to verify the relevance of the time range for the landscape-based models. Another limitation of our modeling approach is the non-feasibility of field validation, due to the number of species and extent of the modelling background. Finally, I consider that the lack of stakeholder participation along the process is a drawback in the further utilization of the results in spatial planning. Reliability and trust in the outputs would have come easily if the engagement with decision-makers and local experts was held since the beginning of the process.

Further Development

Although I did not model species distribution over time, the development of species distribution models based on climate and landscape variables separately, generates outputs that vary in distinct time frames and could serve different purposes. The climate-based models can be used to understand species distribution in the long-term, assuming climate has not changed in the past century. It can also be projected (i.e. extrapolated) to the future, by assuming that climate change scenarios will shift species distribution. The landscape-based models can be used to reflect short-term landscape modification, assuming the caveat of datasets temporal variation. In this case, the SDM combined in the EcoLand analysis can be a starting point to evaluate changes in biodiversity over time (due to land use change) considering a comprehensive list of species of various taxa is used. The SEEA EEA framework, requires a benchmark for present and future evaluation of biodiversity. I argue that the EcoLand approach could be easily tested by governmental institutions that wish to develop the biodiversity account.

Self-criticism and Reflection

*"If you push through that feeling of being scared, that feeling of taking risk, really amazing things can happen."
Maria Mayer (1906 – 1972)*

Personally, the PhD journey brought me the strange realization that science is not the solution to all the problems of modern society. As pointed by van der Leeuw (2018):

"Part of the disconnect between scientists and the wider civil society is the fact that scientists are perceived as arrogant, while they are not aware that they are so perceived. They have been trained to strongly believe in the superiority, values and results of a particular way of thinking that does not resonate with non-scientists, and they are often not capable of (or inclined to) relativizing the contribution of that approach. Their great strength is in rationally reducing the dimensionality of complex phenomena to the point that clarity is gained, but in the process they often discard so many dimensions that their scientific thinking to an extent loses the relation to the reality it attempts to 'explain' (van der Leeuw, 2018, p.1594)".

This statement seems reasonable to me possibly because I deeply felt this disconnection between science and society in my PhD daily life. Therefore, I reckon it is time, for me as a scientist, to use my skills and capacities to engage in participatory approaches, supported by the fertile fields of knowledge co-production and social learning. Scientists have the power to alert society to prepare to deal and adapt to the changes ahead (van der Leeuw, 2018). To successfully accomplish this, the scientific agenda must include the identification of local practitioners' and decision-makers' demands, as well as the communication of scientific outputs to decision-makers and the general public. Scientists have the chance to innovate and dive into interdisciplinary research, joining efforts with other agents of change to contribute and lead the way towards a sustainable future.

Science is a hard game to play. Mostly, because players find in their self-criticism the most relentless judge. Research activities never follow a regular rhythm. They include collecting, treating and analysing data; searching and reading the classic and latest literature on the topic; learning how to operate new tools and software; taking courses, attending conferences, networking. The diversity and dynamism of these activities require a steady spirit. At the same time, scientists must balance their work with the other activities in their life. Under pressure, many of us collapse. Pressure for publications and citations, together with a competitive work environment are the recipe to 'burn out'. Throughout my PhD journey, I preached about having a healthy lifestyle, balancing work,

social life, relationships, and spirituality. Having accomplished my journey joyfully and in good health, I believe I must have done something right. Not that there is a “one-fits-all” recipe, but the search for balance should be among the goals of a successful PhD.

Along my joyful journey, there were downsides: the impostor syndrome and the loss of sense. The first was triggered by the competitive environment among Brazilian postgraduates, in which the more papers you have, the better researcher you are. I always faced publications as the natural consequence of research, as the mean by which we share discoveries and results with our peers. Having it as a target never felt right (and still does not). So, I stick to my beliefs and the consequence was the sensation I was an impostor. My salvation to this was, first, believing in my friends and colleagues, who told me I was a competent researcher; and, second, being aware the impostor syndrome exists and haunts many PhD candidates. The second downside came along with the irrefutable political scene set in Brazil in 2019. Once again, trusting my friends and hearing from more experienced people that the country was not *doomed* forever eased my spirit and allowed my positive self to frame reality once more. I am sure I would never be able to overcome difficulties without a little (and fundamental) help from my friends.

Girl Power

"It came in on me loud and clear that I was the only one who could imprison (or release) me, that I was the only one I could do anything about changing. So I let go of my anger and negativism and made a decision to simply be totally loving, open and vulnerable all the time."
(Arleen Lorrance, 1974, p. 85)

Another hard challenge I take the freedom to address here relates to the role played by women doing science. I have spent most of my PhD working days in two great workspaces, both with a majority of women. But make no mistake, in both places, men prevailed in the leadership positions. Actually, all the leading spots were occupied by men. This is evidence of customary challenges faced by women in the academic work environment in male-dominated cultures (Howe-Walsh and Turnbull, 2016). Among the difficulties pointed out by these authors are: 1) the absence of recognition; 2) the lack of female role models; 3) not being heard or taken seriously, whereas having to deal with mansplaining; 4) harassment; 5) gender discrimination in peer-review scoring processes; 6) existence of 'male networks' acting against women's career progression; 7) higher propensity to the impostor syndrome and consequent enhancement of fear of failure. In many situations, some of these difficulties preclude women from applying to new positions (for fear of failing or because they think they are not good enough) and prevent them from advancing in their careers (Howe-Walsh and Turnbull, 2016).

Previous generations of daunting women have led the way towards overcoming gender discrimination. To succeed, they had to play hard. Many of them stiffened up and avoided being emotional (as if this was a sign of weakness, it is not!); others gave up personal choices, such as parenthood, and endured being treated differently by doing so. I would like to thank all these courageous and powerful women that made my life much easier. I acknowledge their efforts and accomplishments and I also dare pick up from where they left off and continue pursuing changes in the academic environment and in our society.

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APPENDIX 1

The System of Environmental Economic Accounting Framework

In recent years, the System of Environmental-Economic Accounting (SEEA; UN, 2014) – developed by the United Nations to be coupled with the System of National Accounts (SNA; UN, 2009) – has gained traction as a consistent measurement framework to integrate ecosystem assets and services with economic activities at the national level (UN, 2016). Timely, the SEEA Experimental Ecosystem Accounting (SEEA EEA) and its technical recommendations (UN, 2016, 2014b) were proposed to promote extensive experimentation and application worldwide. Indeed, ecosystem diversity and data availability across nations challenge the operationalization of the environmental accounts proposed in the SEEA EEA. Strong collaborations between academic and governmental institutions, professionals and specialists from several areas are fundamental for the learn-by-doing development of environmental accounts, see Australian experience as an example (Vardon et al., 2018).

The utmost goal of the SEEA is to insert ecosystems conditions and services provision to national wide agendas, coupled with economic and political matters. However, the operationalization of the Environmental Accounts demands experimentation and adaptive strategies in which ES are quantified in biophysical and monetary terms, as well as their use by human populations and their change over time.

The SEEA is composed of four main accounts, briefly described here. Initially, ecosystems diversity is addressed in the SEEA EEA via the Ecosystem Extent Account, in which ecosystems are mapped based on land use, land cover and habitat types using remote sensing data. Complementarily, the Ecosystem Condition Account aims to evaluate the integrity and state of an ecosystem, as well as describe its functioning. This condition account poses several challenges such as the development of adequate indicators and the implementation of feasible monitoring. Then, the Ecosystem Services Supply and Use Accounts are composed by the quantification in spatial and monetary terms. However, many decisions from the selection of ES to the most appropriate mapping and valuation technique, are conditioned to data availability and further scientific development and testing in this field.

Parallel to the development of the main accounts, other specific aspects of the environmental-economic relationship that are policy relevant in sub-national levels are being assessed separately in thematic accounts (UN, 2016). Among them, the land, water and carbon accounts have showed advances in their elaboration, while still being developed for energy, material flow, agriculture, forestry, fisheries, air emissions and biodiversity.

Accounting for Biodiversity in the Environmental Accounts

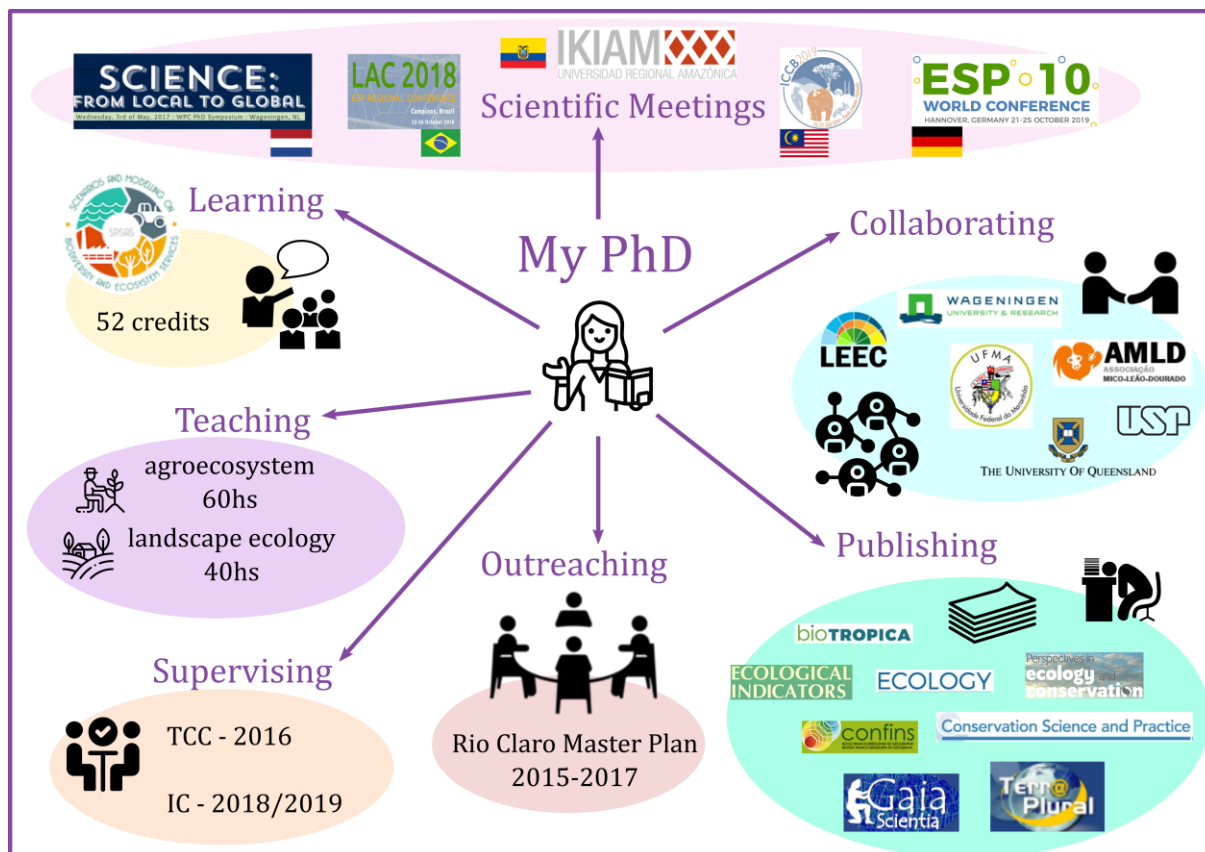
The Biodiversity Account can particularly not only assist the further development of the Ecosystem Extent and Condition Accounts, but it can also be related to several Ecosystem Services and their supply and use accounts. Despite the complexity of the link between biodiversity and ES, their multi-layered relationship has been recognized and addressed by scientists (e.g., Balvanera et al., 2014; Harrison et al., 2014; Mace et al., 2012; Sandifer et al., 2015).

In most cases, the Biodiversity Account has been developed for species-level biodiversity using simple counts of the number of species (Edens and Hein, 2013; Obst and Vardon, 2014; UNEP, 2017). However, future development should target the inclusion of population size and genetic diversity to assess biodiversity (CBD, 1992; UNEP, 2017). In addition, many countries worldwide are still developing their biodiversity databases and monitoring systems, while many others are far from having sufficient knowledge on this field. For this purpose, having a wide range of tools and technical guidance that fits diverse contexts around the globe is key to allow the inclusive insertion of the environmental accounts.

There have been some advances in testing different approaches to biodiversity accounting (Bond et al., 2013; McDonald, 2011; Remme et al., 2016; UNEP-WCMC, 2016). However, expressing biodiversity in a limited set of broadly applicable and easy to understand indicators is not straightforward (Remme et al., 2016). More experimental approaches should be proposed and tested in the coming years for a variety of ecosystems in different contexts (UNEP, 2017), including data scarce regions. Apart from supporting other accounts, biodiversity information has a great potential to aid conservation and management decisions (Blicharska et al., 2019).

ADDITIONAL ACTIVITIES

Throughout my PhD years, I actively engaged in diversified activities. Some of them mandatory in the pursuit of my degree; others mandatory in the pursuit of my professional and personal realization. Here I briefly list them.



Outreach

Jul 2015 – 2017 Coordination of the University Workgroup in support of the development of the municipality master plan in Rio Claro, São Paulo, Brazil.

Concluded Supervisions

Dec/2016 Fernanda Nogueira Lopes – Bachelor Thesis: “Public use concession in strictly protected areas: processing Bill 249/2013 and potential implications of Law 16.260/2016 in São Paulo State”

Ongoing Supervisions

Mar/2018	Isabella Cassimiro – Scientific Initiation in Biological Sciences (PIBIC/CNPq Grant): “Forest species movement across the matrix: an approach using roadkill data”
Aug/2018	Luigi Francesco Galbiate – Scientific Initiation in Ecology: “Roadkill monitoring strategies efficiency near Protected Areas: by car, by bike or on foot?”
Aug/2019	Francielli Carvalho – Scientific Initiation in Environmental Sciences: “Urban Ecosystem Services in a medium-sized city in Brazil”

Teaching

1st term 2019	Universidade Estadual Paulista (UNESP) Rio Claro/ Brazil Agroecosystems Course - undergraduate Ecology students. Teaching. 60hrs
Jul/2015	Universidade Federal Rural de Pernambuco (UFRP) Recife/Brazil Landscape Ecology Course – Master and PhD students in the Post-graduation Program in Forest Sciences. Teaching. 40hrs

Scientific Meetings

Oct/2019	ESP 10 – World Conference – Hannover, Germany (Oral Presentation: Landscapes as the spatial agent connecting ecosystem services components)
Jul/2019	29th International Congress for Conservation Biology – Malaysia (Oral Presentation: Linking landscape structure to ecosystem services)
Oct/2018	ESP regional conference Latin America – Brazil (Oral presentation: Insights on biodiversity accounting in tropical regions)
May/2017	4th Wageningen PhD Symposium "Science: from local to global". Wageningen University and Research – the Netherlands (Oral presentation: Presentation: Finding order in chaos: Getting through

your PhD; Poster: Academia's role in participatory decision making; Convener)

- Mar/2017 Student Conference on Conservation Science, University of Cambridge – United Kingdom (Attendee)
- Aug/2016 II International Ecology Symposium, Universidade Federal de São Carlos – Brazil (Attendee)

Courses and Training

- Oct/2019 JCR team – D3. Natural Capital training: From the biophysical mapping to the accounting of Ecosystem Services in physical and monetary terms. (8h) ESP10 World Conference Hannover, Germany.
- Jul/2019 São Paulo School of Advanced Science on Scenarios and Modelling. (120h). Grant from Fundação de Amparo à Pesquisa do Estado de São Paulo, FAPESP, São Pedro – SP, Brazil.
- Oct/2018 TEEB Regional-Local training: Understand Ecosystem Services and use them for influencing political decision-making processes (8h). Latin America and Caribbean ESP Regional Conference Campinas – SP, Brazil.

LIST OF PUBLICATIONS

Research Papers

ASSIS, J. C.; GIACOMINI, H.; RIBEIRO, M. C. 2019. Road Permeability Index: Evaluating the heterogeneous permeability of roads for wildlife crossing. *Ecological Indicators* 99: 365-374.

ASCENSÃO, F.; NIEBUHR, B. B.; MORAES, A. M.; ALEXANDRE, B. R.; ASSIS, J. C.; et al. 2019. End of the line for the golden lion tamarin? A single road threatens 30 years of conservation efforts. *Conservation Science and Practice* e89.

CIOCHETI, G.; ASSIS, J. C.; RIBEIRO, J. W.; RIBEIRO, M. C. 2017. Highway Duplication and Underpass Influences on Vertebrate Road Mortality. *Biotropica* 49 (6): 765-769.

PENA, J. C.; ASSIS, J. C.; SILVA, R. A.; CAMPANHA, L.; PAGANI, M. I.; RIBEIRO, M. C. 2017. Beyond the mining pit: the academic role in social deliberation for participatory environmental planning. *Perspectives in Ecology and Conservation* 15: 194-198.

LOPES, F. N.; PAGANI, M. I.; ASSIS, J. C. 2019. Concessão de uso em unidades de conservação de proteção integral: a tramitação do Projeto de Lei 249/2013 e potenciais implicações da Lei 16.260/2016 no Estado de São Paulo. *Gaia Scientia* 13: 73-91.

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ABOUT THE AUTHOR

I always compared myself to my brother. We are opposites. He is a practical and I am a theoretical. Back in our teens, whenever he decided he wanted to learn or do something, he would take the challenge to its last consequences: daily practices and persistence leading him to succeed. On the contrary, I was the unskilful girl with great ideas that would never materialize. I never knew if he ever envied my capacity to theorize the way I longed for his ability to learn from trial and error. As a 'young adult', however, I feel comfortable to say I've learned to accept myself for who I am and embrace my own aptitudes. I also can accept and admire other people's skills. I choose to join capacities with them so that we can go further in any project or dream we may have collectively.



As a scientist I have the irrefutable chance to put all my skills as a theoretical into practice (this may sound contradictory though, after the previous paragraph). My point is that science has room for creativity and imagination. This being the case, I get to spend all my theorizing and thinking capacity trying to expand a little bit the current 'frontier of knowledge'. It can sound pretentious, but let's be honest: science is, in its core, the search for the unknown, and despite all the 'drama', we (scientists) are all trying to push that frontier further and in most cases, also contribute to the greater good.

I am still in search of my ikigai. Balance between passion, vocation and duty seems impossible to translate in one occupation or profession. However, we (scientists again) have the ability to engage in several activities at once (and in most cases be carried away or overwhelmed by them). Nonetheless, I am quite convinced this is how I can manage to have an enjoyable and meaningful life these days. In the age in which human beings are more individualistic and connected than ever, the power to reach out others like yourself (be it next door or next continent) is in our hands. Having approached the end of my PhD journey, I can assure myself that I am a collective being. I need people like my brother and so many other diverse and unique beings around me, engaging and committing to common goals to live a happy life and contribute to our species sustainable prevalence in the planet.