Linking people and nature in the multifunctional landscapes of Eastern Amazonia

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Declaration

I, Sérgio André Guerreiro Milheiras, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis. All contributions by others to my thesis are stated below.

The research reported in Chapter 2 has been published in a peer-reviewed journal, as referenced the following paragraph. I conceptualised this research, carried out the analysis, and wrote the chapter. Georgina Mace contributed to writing and editing it. The comments by two anonymous reviewers were also incorporated.

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In Chapter 3, Ana Euler and Adalberto Ribeiro contributed to sampling design. In Chapter 4, Marcelino Guedes contributed to sampling design, while Fernando Silva, André Freitas, Jessie Pereira, Thamara Zacca, Junia Yasmin, and three local tree parataxonomists contributed to species identification.

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Abstract

Preserving the benefits that ecosystems provide to society is increasingly recognised as an essential goal in policymaking. Biodiversity has a role in the provision of many of those benefits. Yet, the ways through which biodiversity and ecosystem services interact are still poorly understood, especially in the tropics. This is particularly relevant in a context of increasing anthropogenic disturbance and biodiversity loss in tropical forests that can have unexpected impacts on ecosystem service provision.

In this thesis I explore the links between biodiversity, ecosystem services, and forest management in the forest-rich multifunctional landscapes of Eastern Amazonia in Brazil.

I develop a simple method to quantify ecosystem services at large scales, identify spatial associations between them, and explore the impact of land use change on the capacity of forests to provide those services. Agricultural land and forests had higher provision levels. Results also show that in forests this provision varies nonlinearly with distance to forest edge.

Next, I explore the degree to which local communities perceive the links between biodiversity and ecosystem services and, in turn, if that perception influences their attitudes towards conservation. I find that respondents aware of more relationships between biodiversity and ecosystem services were also more likely to have a positive attitude towards nature conservation. Overall perception of those links was relatively high in the study area.

I also provide evidence of how different taxa respond to forest management regimes of widespread occurrence in the region. I find that increased forest use intensity can have negative effects on the communities of trees, dung beetles, and fruit-feeding butterflies.

Finally, I measure the simultaneous provision of five ecosystem services along a gradient of forest use intensity. Multifunctionality levels were higher under moderate or low intensity levels associated with higher tree richness. The indirect effect mediated by biodiversity loss was on average at least as severe as the direct effect of forest use intensification on multifunctionality.

Overall, this thesis adds new empirical evidence to our understanding of the relationship between people and nature in the Amazonian forest.

Impact Statement

This thesis supports that biodiversity conservation and ecosystem service provision in forest-rich human modified landscapes can potentially be reconciled when sustainable landscape configurations are preserved. It also suggests that forest conservation strategies that move beyond classic dichotomies, such as between intrinsic and instrumental values of nature, or sparing versus sharing land for biodiversity, are better fitted for real-world contexts, where complex landscape configurations integrating undisturbed areas with moderate and intensive uses are more likely to meet the demands and preferences of multiple stakeholders.

Chapter 2 provides a methodology for the assessment of spatial patterns of ecosystem service provision in regions with high forest cover and low data availability, which can offer useful evidence to support land use management decisions.

Furthermore, results in Chapter 3 suggest that improving awareness of the role biodiversity plays in the provision of ecosystem services should be seen, for example by conservationist organisations aiming to increase support for conservation measures, as a viable communication approach, part of a multifaceted strategy that can be tailored to specific audiences.

Results in Chapter 4 also have implications for policy by highlighting the contrasting impact that different forest management regimes can have on biodiversity, including moderate uses that have received less attention in the literature.

In the face of increasing anthropogenic pressures, including climate change, sustainable forest management requires solutions that break deforestation cycles. Results in Chapter 5 suggest that if we are to achieve sustainable solutions that preserve tropical forests on the long term, multifunctionality needs to be more effectively incorporated into land use policies and planning. By considering the interdependencies between multiple ecological functions and being adaptable to specific socioecological contexts, multifunctionality approaches provide a suitable foundation for the search of land use management solutions that minimise trade-offs and maximise synergies between the priorities of multiple stakeholders.

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Chapter 1: Introduction

1.1. Overview

It falls on society the choice to whether safeguard the resources, including land, needed for the long-term preservation of biodiversity and for sustaining the provision of ecosystem services in all biomes impacted by man. Approaches to define a safe operating space for human societies at planetary scale suggest that high-risk thresholds might be approaching or have already been surpassed for different processes fundamental to the functioning of the Earth-system (Steffen et al. 2015), which in turn are related with the continuing biodiversity loss that already stands amongst the major current drivers of global ecosystem change (Hooper et al. 2012).

Science can contribute towards more informed decision making on this topic, as demonstrated in the Millennium Ecosystem Assessment (MEA, 2003). More recently, the Aichi Biodiversity Targets set by the UN Convention of Biological Diversity highlight the relevance of restoring and safeguarding the “essential services” provided by ecosystems (Target 14). On the other hand, neglecting to use the increasing body of knowledge on ecosystems and their services in policy development might eventually result in undesired consequences through feedbacks that we still do not fully comprehend (Carpenter et al. 2009). Despite being increasingly recognised that loss of biodiversity exacerbates change in ecosystem processes and services, many of these interrelationships are not yet completely understood (e.g., Cardinale et al. 2012; Díaz et al. 2006).

Further work is therefore required to quantify ecosystem services and identify relations with biodiversity and land use patterns in a way that acknowledges the complexity of socio-ecological systems (Bennett et al. 2009; Díaz et al. 2006). This has greater chances of success if based on easily repeatable methods (Carpenter et al. 2009). Thus, this literature review aims to provide an overview of the work and methodologies developed, particularly in the last decade, to characterise the patterns of ecosystem service provision under different land uses.

1.2. Biodiversity and Ecosystem Services

1.2.1. Current understanding of ecosystem services

The concept of ecosystem services (ES) can be traced back to the 1980s and even before (e.g., Daily et al., 1997; de Groot et al., 2010). After a couple of seminal works in the late 1990s (Costanza et al., 1997; Daily et al., 1997) the concept started gaining traction and being increasingly incorporated by scientists, while appealing also to the sphere of policy making. In 2005 the conclusion of UN's Millennium Ecosystem Assessment (MEA) was a milestone that further consolidated that path. Subsequent studies, most prominently The Economics of Ecosystems and Biodiversity (TEEB, 2010) and UK's National Ecosystem Assessment (UK NEA, 2011), continued its further integration as a policy-relevant concept, while the associated body of research also continued to increase exponentially (Fisher et al., 2009).

One of the strengths at the core of the ES framework is that it aims to incorporate concepts from different areas of knowledge in order to improve our understanding of the relations between society and nature, analysed in the context of social-ecological systems (Carpenter et al., 2009), which facilitates a larger social acknowledgement of indirect use values of ecosystems, while also expanding support for biodiversity protection (Goldman et al., 2008). This is arguably an ambitious task bound to attract some criticism (Lele et al., 2013). The common omission of disservices and of trade-offs between different beneficiary groups, supplemented with the concern that it will promote the commodification of nature and its capitulation to market rules, are some of the issues raised. Schröter et al. (2014) usefully analyse seven of the most frequent critiques to the ES framework and propose corresponding counter-arguments and ways forward to make the framework more inclusive. For example, to those that argue the ES are too vaguely defined, the authors respond that the concept provides space for debate, transdisciplinary methodological progress and bridges between science and policy.

Fisher et al. (2008) define ecosystem services as “the aspects of ecosystems utilised (actively or passively) to produce human well-being” which include “ecosystem organisation (structure), operation (process), and outflows, if they are consumed or utilised by humanity either directly or indirectly”. That definition is based on the more stringent version proposed by Boyd and Banzhaf (2007) that “final ecosystem services are components of nature, directly enjoyed, consumed, or used to yield human well-being”. Both aim to improve the most widespread definition, proposed in the Millennium Ecosystem Assessment (2003), which states that “ecosystem services are the benefits people obtain from ecosystems”. This nuanced improvement aims to reduce possible ambiguities associated with MEA (2003) definition, which is particularly relevant for ES valuation efforts.

It is important to make a clear distinction between ecosystem processes and services, with the former being defined as “changes in the stocks and/or flows of materials in an ecosystem, resulting from interactions among organisms and with their physical-chemical environment” (Mace et al., 2012). The distinction between ecosystem services and goods (or benefits) is also relevant, where the latter are defined as “the objects from ecosystems that people value through experience, use or consumption, whether that value is expressed in economic, social or personal terms” (UK NEA, 2011). To avoid double counting the same service, intermediate ecosystem services should also be distinguished from final ecosystem services (Boyd and Banzhaf, 2007), where only the latter are directly linked to goods (UK NEA, 2011). In addition, the place of biodiversity within the ES concept might also be a source of ambiguity (Mace et al., 2012).

When mapping ecosystem services, it might add clarity if areas where ES are generated are distinguished from those where ES (or the corresponding benefits) are consumed. Luck et al. (2003) initially proposed the concept of service-providing unit to mean the individuals from a given species that are necessary to provide an ES. This was later expanded in Luck et al. (2009a) adding populations, communities, functional groups, interaction networks, or habitats as potential service providers. There are different possible interactions between service providing areas and service benefiting areas, as described in Fisher et al. (2009). The authors argue that making this distinction helps explain the spatial-temporal dynamics of ecosystems, the influence of the demand side on services and the public/private condition of resulting benefits. It implies a flow of ES from one area to the other, where flow is defined as “the spatially explicit routing of an ecosystem service from sources to users” (Bagstad et al., 2013). It also allows distinguishing the total ecosystem capacity to provide an ES and the share that actually reaches beneficiaries (Bagstad et al., 2013; van Oudenhoven et al., 2012).

1.2.2. Proposed frameworks for ecosystem services

Different studies have attempted to classify the various ES into categories that can be generalised, although no typology has become entirely dominant. The reaction to a classification proposed by Wallace (2007) exemplifies this state of affairs (Fisher and Turner, 2008; Costanza, 2008). In fact, it can be argued that such consensus would not even be desirable because a classification should remain adaptable to each particular situation and the objectives of the study (Costanza, 2008). Nevertheless, an effective typology should in principle share some common characteristics, such as clear definition of the concepts used (Wallace, 2007). Consequently, ecosystem services can be categorised and organised in different ways, depending on the social and ecological context where they will be applied. There is not a one-size-fits-all solution (Costanza, 2008).

Fisher et al. (2009) synthesise characteristics of ES that should be taken into account when attempting to define and classify them, namely their public–private good aspect (i.e., rival or non-rival; excludable or non-excludable), their spatial and temporal dynamism, the possible joint production of benefits by various ES, the complexity and uncertainty associated with ES provision and interactions, and ES dependence on beneficiaries (e.g., the same ecosystem might provide different benefits to different social groups).

MEA (2003), inspired by previous works such as Costanza et al. (1997) or de Groot et al. (2002), classified ES into four major categories: provisioning, regulating, cultural, and supporting services. Most studies generally continue to be based on this ES classification system, albeit with adjustments and improvements. For example, the UK NEA (2009) distinguishes intermediate and final ES in its framework in order to avoid double counting of the same ES in its valuation of goods generated from ES supply. A related example is the omission of supporting services in TEEB (2010), which were considered a subset of ecological processes, with habitat services being highlighted instead, a category that had already been used in de Groot et al. (2002). Recent publications have continued to propose further developments to ES frameworks, which have included efforts to provide guidelines that improve the robustness and reliability of ES assessments (Crossman et al., 2013; Seppelt et al., 2012), to integrate ES spatial dynamics (Bagstad et al., 2013; Serna-Chavez et al., 2014), or to promote the establishment of a common international classification (Haines-Young and Potschin, 2018).

From a policy making perspective, the effectiveness of an ES framework is likely to be dependent on different factors, such as the inclusion of economic arguments, delivering results in a common language that indicates tangible short term benefits to livelihoods, and frequent dialogue across sectors (Fisher et al., 2008).

1.2.3. Linking biodiversity and ecosystem services

The understanding of how biological diversity change affects the functioning of ecosystems and society has greatly increased in the last two decades (Cardinale et al., 2012). Functional traits, species richness, genetic diversity, are some of the components of biodiversity that can offer different perspectives on how biodiversity influences ES supply, as they might affect differently each ES (Díaz et al., 2006; Mace et al., 2012). Yet, most studies have focused on species richness at local to regional spatial scales, while functional and structural components have remained less studied (Feld et al., 2009; Harrison et al., 2014). It is also known that biodiversity influences ecosystem services at different stages, namely: as a regulator of ecosystem processes (e.g., decomposition is influenced by what species are present in the soil); as a final ecosystem service (e.g., genetic diversity of species related with crops); and as a good itself that can be valued (e.g., more biodiverse landscapes are more valued for ecotourism purposes) (Mace et al., 2012).

Although in many cases data are insufficient to establish relationships and in a few other no significant connections were identified, the literature supports the existence of links, either positive or negative, between biodiversity and various ecosystem services and functions (Cardinale et al., 2012). And new evidence is continually being added on the influence of biodiversity on ecosystem functioning, which might in fact become stronger as more ecosystem functions are considered (Lefcheck et al., 2015). However, besides the simultaneous effects of different components of biodiversity, other sources of uncertainty on the extent of these links remain, such as the limited comprehensiveness of many ES assessments (Balvanera et al., 2014). For example, few studies consider any flows of ES, through external effects or trading, beyond the initially defined study area (Seppelt et al., 2011). In general, an improved integration of the fields of Biodiversity and Ecosystem Services (BES) and Biodiversity and Ecosystem Functioning (BEF) can yield interesting results towards a better understanding of these interrelationships (Cardinale et al., 2012).

Harrison et al. (2014) provides an additional perspective to the analysis of links between biodiversity components and ecosystem services, demonstrating their interdependence and complexity. Based on 530 studies, they found that most relationships identified in the literature were positive. Regarding what biodiversity components are more commonly used, the review highlighted five: species abundance, species richness, species size/weight, community/habitat area, and community/habitat structure. Species abundance was found to be particularly used for assessing relationships with pest regulation, pollination and recreation; while for species richness that was the case for timber production and freshwater fishing.

In terms of spatial analysis, different studies have suggested the congruence between biodiversity and ES might sometimes be low, particularly due to the effect of provisioning services (Chan et al., 2006; Cimon-Morin et al., 2013), although results vary depending on the area and scale considered (Anderson et al., 2009), which suggests joint ES and biodiversity protection might not always be possible. That is in line with the spectrum of human activities associated with increasing the provision of specific ES, normally provisioning, which frequently leads to negative effects on biodiversity (e.g., Phalan et al., 2013).

1.2.4. Focus on forests and the tropics

Tropical forests concentrate higher levels of species richness than any other biome in the planet (MEA, 2003). That ecological complexity can provide valuable insights of how sustained loss of biodiversity can affect ecosystem functioning, services and corresponding well-being to humans (Edwards et al., 2014c). However, it is also more challenging to study and results from studies located in other regions might not always paint an accurate picture when extrapolated to the tropics (Christie et al., 2012). Recent large-scale research initiatives, such as the SAFE (Stability of Altered Forest Ecosystems) project, are helping to overcome the lack of data specific for tropical forests (Fayle et al., 2015).

Forested areas are known to have an affinity with particular ecosystem services, such as carbon storage, prevention of erosion, air quality control, recreation, timber provision, or the regulation of soils and water (Gamfeldt et al., 2013; Maes et al., 2012a). Historically, these areas have been increasingly converted by humans to maximise the share of provisioning services supplied. For example, in Brazil less than 12% of the original extent of the Atlantic Forest remains (Ribeiro et al., 2009). These changes in the bundle of ES provided involve trade-offs, which in turn might lead to winners and losers amongst the beneficiaries (Howe et al., 2014). For example, by planting a monoculture of eucalyptus for timber production, the provision of water downstream might be particularly affected, where those that benefit from the first will probably not be the same that are affected by the second (Chisholm, 2010).

Focusing on the case of production forests, they can be considered the ground level in terms of tree species richness in forests, against which is possible to analyse the effects of tree diversity on the provision of ES (Cardinale et al., 2012; Gamfeldt et al., 2013). Analysing the effects on other taxonomic groups might also yield interesting results (e.g., Barlow et al., 2007a). In fact, it has been shown that even in this intensely managed land use tree species richness shows positive relationships to different services, including soil carbon storage, berry collection or game production (Gamfeldt et al., 2013).

1.3. Multiple approaches to ecosystem service mapping and quantification

In the last decade numerous studies have attempted to map and quantify ES at different scales, in different biomes and using different methods. These studies can be associated with a variety of research questions, including on the congruence of ES with biodiversity, synergies/trade-offs between ES, ES cost-benefit and valuation, ES supply and demand, or identification of priority areas for policy purposes (Maes et al., 2012b). In turn, this has resulted in a large variety of possible approaches to answer those questions.

Naidoo et al. (2008) references six potentially relevant elements to consider when analysing ES in a spatial context, namely, the rate of service production, service flow from production area, beneficiaries involved, economic value per unit service (for valuation), probability of system conversion to another state, and change in service provision (or value) if converted. However, reliable data for all the elements is frequently not available, especially when considering multiple services (Maes et al., 2012b). To circumvent this insufficiency, many studies have either estimated ecosystem services from proxies or used coarse-resolution datasets (Eigenbrod et al., 2009), which might not accurately reflect primary data (Eigenbrod et al., 2010) or not be available at the desired scale (Naidoo et al., 2008).

In overall, it is possible to roughly divide studies by considering the type of approach. They can analyse data primarily biophysical (e.g., Dearing et al., 2012) or socioeconomic (including economic valuation or expert consultation; e.g., Martín-López et al., 2012). However, most studies blur even this broad distinction, through interdisciplinary approaches that combine methods from different fields in order to better account for different ES (e.g., Raudsepp-Hearne et al., 2010). Adding to this, ES mapping efforts will usually focus on a specific spatial scale, either local (e.g., Greenleaf and Kremen 2006), regional (e.g., Fisher et al., 2011), or global (e.g., Naidoo et al., 2008). Alternatively, major approaches to ES mapping can also be divided as those that do and do not require primary data from the area studied (Eigenbrod et al., 2010). The use of primary data through representative sampling or modelling of relationships between ES and environmental variables allows reaching more trustworthy results. On the other hand, secondary data requires the use of proxies, based either on land cover or expected causal links (Eigenbrod et al., 2010).

Several case studies have worked on specific methodological aspects relevant in ES assessments. From considering multiple time periods (Lautenbach et al., 2011) or spatial scales (Felipe-Lucia et al., 2014), to the measurement of ES from calculated indexes (Luck et al., 2009b) or using modelling tools (Nelson et al., 2009). Others have prioritised analysis of links with policymaking (Fisher et al., 2011), land-use scenarios (Ditt et al., 2010), trade-offs (Jopke et al., 2015), ES demand (García-Nieto et al., 2013), economic valuation (Morri et al., 2014), ES flows (Bagstad et al., 2014), or proxy-based indicators (Egoh et al., 2008; Willemen et al., 2013).

Literature reviews have attempted to provide a better overview of existing methodological approaches to ES mapping and quantification. Martínez-Harms and Balvanera (2012) categorised 70 identified studies along five criteria: ES category, data availability, data source type, scale and methods used. According to their results, regulating services are more commonly studied, with secondary data being more used than primary data. Furthermore, biophysical data is more frequently employed, principally derived from land cover variables, and analyses tend to focus on either the regional or national scale. Regarding the methodologies used in ES assessment, the authors separated five groups: regression models, which quantify the relation between response and explanatory variables; extrapolation of primary data to the studied area; expert knowledge, where experts rank ES provision in a certain area; look-up tables, i.e., estimating a single ES value per land cover class; and, the most frequently applied in the literature, causal relationships, i.e., proxy-based approaches.

Seppelt et al. (2011) considered 153 publications, published until 2010 and focussing only on the regional scale. It reiterates that secondary data is more commonly used, while adding that most of which is also non-validated. This review has interesting findings, such as that only 21% of the studies sampled gave specific recommendations to policy makers or other stakeholders, a low share considering the ‘policy affinity’ of the ecosystem service concept. In addition, uncertainty concerns are not discussed in half of the studies and, while most of them include more than one ES, interactions between them are mostly not taken into consideration. Another interesting result is that slightly more publications prefer to define the border of the study area based on administrative borders than biophysical ones. Amongst other recommendations, the authors argue in favour of “biophysical realism”, if reliable results are to be achieved when measuring ES.

1.3.1. Biophysical approaches

Measuring ES directly through the collection of biophysical data is considered one of the most reliable approaches available (Seppelt et al., 2011). However, it is not applicable to all services and study purposes. Furthermore, it is often too expensive or time demanding to reach an appropriate sampling intensity (Eigenbrod et al., 2010). Making extrapolations from land use and land cover data is a simpler approach to derive information on ES, since it uses remote sensing data that is usually readily available. That might be useful at larger scales, when there is a clear link between land use and service provision (e.g., crop production), or when no other data is available (Maes et al., 2012b). However, it might lead to potentially misleading results (Eigenbrod et al., 2010). Secondary data from a trusted source is also often used to circumvent limitations to primary data collection. This applies particularly for provisioning services (e.g. food or timber), which governmental statistics departments usually include in their own data collection. Some institutions are now starting to include broader ecosystem services assessments in their data collection (e.g., Action 5 of the European Commission Biodiversity Strategy to 2020).

1.3.2. Socioeconomic approaches

In the last decades, the valuation of ecosystem service benefits has received increasing attention (Turner et al., 2003). ES assessments are strengthened when they establish clear relationships between economic activities and ecosystem functioning (Haines-Young, Potschi and Kienast, 2012). The field has come a long way since the influential, but contested, paper by Costanza et al. (1997), which used values calculated in other studies to infer the global value of ES (benefit transfer). An example of a recent significant contribution was UK’s National Ecosystem Assessment, which used spatially explicit models together with valuation methods to estimate economic values for ES (Bateman et al., 2011).

At the base of economic approaches applied to biodiversity is the concept of Total Economic Value (TEV), which develops an anthropocentric perspective, through use and non-use values, of how biodiversity influences human well-being. Christie et al. (2012) provide a comprehensive review of the methods available to value contribution of biodiversity to human well-being. They divide the valuation approaches into those that use monetary or non-monetary techniques. For the first, the methodologies described are: market prices; replacement costs; damage cost avoided; production function; travel cost; hedonic pricing; contingent valuation; choice modelling; deliberative valuation; and value transfer. As for non-monetary techniques, the paper indicates: questionnaires; interviews; focus groups; citizen juries; health-based approaches; Q-methodology; Delphi surveys; participatory rural appraisals (PRA); participatory action research (PAR); and systematic reviews. The challenges associated with their application include literacy and language barriers, difficulty gaining access to marginal groups, or lack of local scientific capacity to contribute to the implementation of the research. Further detail on these methodologies can be found on Christie et al. (2012) or on additional references such as TEEB (2010).

If high uncertainty in the application of other tools for ES mapping cannot be avoided, an alternative is to take advantage of experts' judgement, presuming they will be able to give qualified opinions that, while with a degree of subjectivity, might nevertheless provide results close to reality (Jacobs et al., 2015). With that input it is possible to develop "matrix models" providing estimates of ES per land use/cover class. The flexibility of the tool is one of its main advantages, which should include a transparent description of the methodology to increase confidence in the results (Jacobs et al., 2015). Matrix models have been implemented in a variety of studies and settings, such as Palomo et al. (2013), which mapped the capacity of protected areas to provide ES using the input of experts. It should also be noted that methodological tools originating from social sciences, such as questionnaires or semi-structured interviews, allow assessing the perceptions and preferences towards ecosystem services of different interest groups or the beneficiaries of ES (e.g., Martín-López et al., 2012).

1.3.3. Interdisciplinary approaches

Due to the different categories of ES and possible objectives of a particular study, each will have higher affinity with a particular set of methods. For example, focusing on biophysical data might be less useful when assessing cultural ES, while if the objective is the monetary valuation of an ES, economic tools are required. Therefore, when assessing multiple ES, the best option is often to use a mixed approach, which is in fact encouraged and in tune with the interdisciplinary nature of the ES field (e.g. Larigauderie et al., 2012). Several studies develop their own mixed methodological approaches, but some tools have also been developed to provide guidelines for the implementation of interdisciplinary approaches, such as the Toolkit for Ecosystem Service Site-based Assessment (TESSA), which focuses on the measurement and monitoring of ES at site scale. This helps non-specialists select accessible methods for the assessment of different ES at a scale relevant for local decision making (Peh et al., 2013).

Furthermore, there are currently a variety of modelling approaches to generate spatially explicit estimations of the supply of ecosystem services, calculated using ecological production functions and economic valuation methods. They are usually flexible in the amount of data required to feed the model and require varying levels of technical capacity to use (Peh et al., 2013). Current available approaches include InVEST, MIMES, and ARIES.

InVEST (Integrated Valuation of Ecosystem Services and Tradeoffs) is a spatially explicit modelling toolkit that predicts how land use changes affect ecosystem services and biodiversity conservation (Nelson et al., 2009). It also integrates data on the demand of ecosystem services to generate results on their value to people. Therefore, by aggregating 17 models, it allows to quantify, map, and value different ES at landscape scale, with the possibility to present the results either on biophysical or monetary terms. Water quality, recreation, or agricultural production are amongst the ES that can be assessed.

MIMES (Multiscale Integrated Model of Ecosystem Services) is a multi-scale integrated set of models that assess the value of ecosystem services (Boumans et al., 2015). It integrates site-specific and spatial data in order to evaluate trade-offs in space and/or time, in a way that aims to account for the dynamic feature of socio-ecological systems.

ARIES (ARtificial Intelligence for Ecosystem Services) employs a Bayesian statistical approach to quantify the flow of services and their uncertainty from its source to the beneficiaries, which enables the quantification of actual, instead of potential, service provision (Villa et al., 2014). Sources, sinks, and use are measured with biophysical or categorical units, but not monetary ones, through an automated data integration process using an extensive database featuring multiscale GIS data and ecosystem service models. It aims to produce results that translate the dynamic complexity of ES in an accessible way that does not require extensive data gathering or expert knowledge (Villa et al., 2014).

1.3.4. Indicators for ecosystem service assessment

Reflecting the variety of possible methodological approaches, the actual indicators and units used in ES assessment are also varied, which in fact restricts the potential for comparisons between different studies (Feld et al., 2009). Van Oudenhoven et al. (2012) developed a set of criteria on which the usefulness of ES indicators can be evaluated, namely: flexible selection process; consistency; comprehensive; sensitive to changes in land management; temporarily explicit; spatially explicit; scalable; and credibility. For its Dutch case-study at landscape scale, the authors selected different sets of indicators for ecosystem properties, functions (defined as the ecosystem's capacity to provide the ecosystem service), and for service provision.

Even for ES that are relatively easy to measure, with reliable data sources available, is possible to find multiple indicators in the literature. Water supply, for example, can be measured through the average annual precipitation minus average annual evapotranspiration (Chan et al., 2006), the percentage of wetlands and lakes (Maes et al., 2012a), water price (Morri et al., 2014), among several other used indicators (e.g., Egoh et al., 2008; Kroll et al., 2012; Serna-Chavez et al., 2014). This reflects how ecosystems might influence the water cycle in different ways, such as canopy rain interception, litter absorption, or storage in soils and underground (Guo et al., 2000). Studies might also focus on measuring only certain uses (e.g. irrigation) or total water supply, for example (Baral et al., 2013).

1.4. Thesis overview and structure

This thesis aims to contribute to the Biodiversity and Ecosystem Services research theme by furthering our understanding of the relationships between biodiversity, ecosystem services, and forest use management in tropical forest-rich human modified landscapes. It engages with the challenge of reconciling increased demand for provisioning ecosystem services with the conservation of biodiversity and multifunctionality in tropical forests.

In Chapter 2 I explore the spatial relationships between nine ecosystem services at regional scale. I quantify their provision, identify spatial associations, and explore how the land use change influences the capacity of forests to provide those services. The methodology developed provides a balanced analysis of different ecosystem service categories, using a relatively high number of services that can be quantified at low cost, over large spatial extents, in areas with limited data availability.

In Chapter 3 I analyse whether people living in areas of high relevance to conservation perceive the links between biodiversity and ecosystem services. I also consider which factors influence that perception and if that perception has an influence on attitudes towards conservation. I survey 401 people in households located in the north-eastern region of the Amazon forest. There is a lack of empirical evidence exploring how awareness of the relationships between biodiversity and ecosystem services influences support for conservation measures. This chapter aims to address that gap.

Chapter 4 quantifies the impact of four regionally expressive forest uses on biodiversity. For this analysis, I collect data on butterflies, dung beetles, and trees from

24 sampling sites. The chapter addresses the following objectives: (1) compare the levels of species richness, abundance, and community structure of the three taxa between old-growth forests, Brazil nut extraction areas, selective logging areas, and eucalyptus plantations; (2) assess if fruit-feeding butterflies, dung beetles, and trees exhibit congruent responses to forest use change; (3) explore how the results can contribute to nature conservation and sustainable forest management.

Chapter 5 considers the impact of forest use intensification and tree species loss on the multifunctionality of tropical forests. Multifunctionality is calculated based on the capacity of the four forest uses sampled, at 24 sampling sites, to provide timber, Brazil nuts and soils that can be used for agriculture, store carbon, and harbour species with cultural value. The objectives are to: i) analyse the effect of tree species richness on the supply of individual ecosystem services; ii) analyse the effect of tree species richness on forest multifunctionality; iii) compare the direct effect of forest use intensification on forest multifunctionality with the indirect effect mediated by biodiversity.

Finally, in Chapter 6 I discuss the findings of the analytical chapters and their implications for forest management and biodiversity conservation in the forest-rich human-modified landscapes of Eastern Amazonia.

Chapter 2: Spatial overlap and the impact of land use change on ecosystem service provision in a tropical region with high forest cover

2.1. Abstract

Ecosystem service (ES) assessments have flourished globally in recent years and are now frequently used by policymakers and environmental managers. However, data scarce regions continue to be less well studied, limiting the comprehensiveness of the approach and its potential benefits. Here, I aim to assess multiple ES and their spatial relationships in a region with high tropical forest cover, the state of Amapá, in the Brazilian Amazon. I develop a simple method to measure nine ES, identify spatial associations between them, and explore the impact of land use change on the capacity of forests to provide those services. The ES analysed include biodiversity, regional climate regulation, indigenous heritage, agricultural production, and NTFP extraction. Both negative (n=20) and positive (n=12) spatial associations are found, with agricultural land and forests having the highest total ES provision. I also show that provision in forests varies nonlinearly with distance to forest edges. In the face of currently unavoidable data scarcities in high biodiversity tropical areas, I show that this approach can provide useful evidence for land use management decisions.

2.2. Introduction

Only sustainable development pathways can halt the systematic loss of tropical forests that is leading to widespread ecosystem simplification (Lewis et al., 2015). Ecosystem service assessments contribute to the creation of those pathways by integrating people-nature interactions and promoting resilience in social-ecological systems (Carpenter et al., 2009). Yet, the interrelationships between multiple ecosystem processes and services, and biodiversity remain poorly understood (Cardinale et al., 2012), with lack of reliable data frequently preventing simultaneous analysis of the relations between multiple services (Maes et al., 2012b).

Across the world, most remaining forest areas are now within 1 km of their edges, which compromises their ecological processes and conservation value (Haddad et al., 2015) and leads to significant impacts that are often not considered in conservation plans (Barlow et al., 2016). That anthropogenic disturbance is likely to also have an effect, not necessarily negative, on ES provision, both on the capacity of an ecosystem to provide an ES and/or on the actual delivery (flow) of that service to people (Mitchell et al., 2015). In the face of continuing land use change, analysing how the multifunctionality of high forest cover landscapes are impacted requires further research (Mori et al., 2017), including on the complex and context-dependent links between biodiversity and ES (Mace et al., 2012).

Amapá state in northern Brazil is an ideal site to study people-nature interactions in social-ecological systems with high forest cover. More than two thirds of the territory is covered by trees with a deforestation rate currently lower than most Brazilian Amazon states. Three local-level Payments for ES (PES) projects have been developed in the state and there were political attempts to approve state-level legislation to frame ES projects and establish specialised institutions to manage them, which have not yet passed to law (Pavan and Cenamo, 2012). For many communities in the state the forest provides vital resources and a source of income (Viana et al., 2014), benefits which are in turn dependent on functioning ecosystems with high levels of diversity (Allan et al., 2015). If protected, these biodiversity-rich forests, including multiple species with untapped potential use, can be the foundation for innovative development solutions for the region (Nobre et al., 2016). Therefore, knowing how, when, and where ecosystem services are or could be co-produced by social–ecological systems can help local policy makers achieve sustainable resource management solutions (Bennett et al., 2015).

ES assessments in the literature are currently skewed towards temperate and high-income countries (Clarke et al., 2017; Martinez-Harms et al., 2015). Conducting additional research focused in tropical regions, including in Latin America (Balvanera et al., 2012), will contribute valuable insights on biodiversity, ecosystem functioning, services and corresponding human well-being in an area of high ecological complexity. This includes identifying the mechanisms behind the simultaneous response of multiple services and the effect of land use patterns through integrated social-ecological approaches (Bennett et al., 2009). Furthermore, the majority of ES assessments undertaken to date deal with less than six ES (Nahuelhual et al., 2015; Seppelt et al., 2012). Recent advances in the availability of remote sensing data open new options for the quantification and mapping of multiple ES at low cost (Ayanu et al., 2012, Cord et al., 2017), which are explored here.

My goal is to quantify ES provision in a region of high forest cover in the Amazon and assess how ES interact with land use change, particularly at forest edges. Using a flexible ES mapping and quantification approach, I analyse the relationships among 9 ES, including spatial associations among them (Rodríguez et al., 2006), and consider how edge effects linked to anthropogenic disturbance may reduce the capacity of forests to provide those services. While most studies assessing the relationships among ES focus mainly on the provisioning category (Howe et al., 2014), the ES selected here aimed to achieve a balanced analysis by integrating three provisioning, three regulating, and three cultural services. These services fit under the same conceptual framework used in the Millennium Ecosystem Assessment (MEA, 2003). They are connected to beneficiaries via flows, although the flows are measured at a coarse resolution that makes it difficult to measure the scale of the flow or to differentiate among beneficiaries. Further assessments of demand, along with an analysis of interactions between services, would underpin relevant policy responses.

The objectives of this chapter are to (i) analyse the spatial interrelationships between 9 ES at regional scale; (ii) explore the influence of edge effects on ES provision at tropical forest landscapes; and (iii) consider the policy implications of the results for Amapá state, Brazil.

2.3. Methodology

2.3.1. Study Area

This study focuses on Amapá, north Brazil, one of the states of the Brazilian Amazon. The climate is tropical, the mean annual rainfall is around 2300 mm, with a wetter season from January to June, and a mean temperature fluctuating around 27 ºC throughout the year (INMET, 2018). Amongst the Brazilian states, Amapá has the highest proportion of its territory under some kind of protection, in total around 70% of the state (Pereira et al., 2010). These protected areas are managed either by federal-level or state-level institutions, and include areas under strict protection, where permanent human presence is not permitted, and sustainable use areas, where local communities are allowed to pursue natural resource-based activities with low impact.

2.3.2. ES mapping and quantification

I gathered information on 9 ES as summarised in Table 1, which were all mapped into GIS data layers (Figure A1 in Appendix A). The year 2014 was used as reference for most indicators. All indicators measure ES flow to beneficiaries at varying scales (local, regional, or global). Beneficiaries at varying scales, including global, can exert their influence in local/regional policy processes in the Amazonian region. For example, in Amapá Conservation International, a US non-governmental organisation, had an active participation in the development of the Amapá Biodiversity Corridor, a large network of protected areas, whose main goal is the protection of local biodiversity (CI, 2018).

Table 1. Characteristics of the data used to quantify the 9 ES included in this study.

ES category	ES	Data sources	Indicator	Unit
P	NTFP extraction	IBGE (2015), INCRA (2016)	Presence of sustainable use reserves and extractive settlements	km^2
P	Timber production	IBGE (2015), Almeida et al. (2016)	Presence of timber plantations	km^2
P	Agricultural production	Almeida et al. (2016)	Presence of agricultural activities	km^2
R	Aboveground carbon storage	Avitabile et al. (2016)	Aboveground biomass	Mg/ha
R	Local climate regulation	MODIS (2016a)	Land surface temperature	ºC
R	Regional climate regulation	MODIS (2016b)	Terrestrial evapotranspiration	mm/yr
C	Indigenous heritage	IBGE (2015)	Presence of indigenous reserves	km^2
C	Biodiversity	SEMA-AP (2012), ICMBIO (2016), GBIF (2016)	Plant species richness	# species
C	Recreation	Sharp et al. (2016)	Geotagged photographs	photo user days /yr

Notes: P= Provisioning; R= Regulating; C= Cultural. NTFP refers to non-timber forest products. Institutional acronyms are detailed in the references.

Aboveground carbon storage

Data from Avitabile et al. (2016) were used to map aboveground carbon storage quantities, using aboveground biomass as an indicator. The 1-km spatial resolution of the source data was converted to 0.01 degrees (~1.1 km) by averaging the values of neighbouring cells.

Agricultural production

The INPE TERRACLASS land use map for 2014 was used to identify where agricultural areas occur in the state, indicating the presence of agricultural production. INPE’s map includes different typologies associated with agricultural activities (Almeida et al., 2016), which were all joined into one overall agriculture class for this analysis. The spatial resolution of the source data is 30 m, which when converted to 0.01 degrees (~1.1 km), resulted in the disappearance of some of the smaller agricultural patches.

Biodiversity

This layer measures plant species richness. I frame biodiversity as a cultural ES (Mace et al., 2012) and assume that areas with higher levels of species are more highly valued by people for cultural reasons (Morse-Jones et al., 2012). Plant richness data with corresponding spatial coordinates were extracted in January 2016 from GBIF (2016) and ICMBIO (2016) databases and linked with a state government vegetation cover map (SEMA-AP, 2012). Classes in that map were aggregated to: floodplains, forest, savannah, forest alluvial, and secondary vegetation. It was then possible to calculate on ArcGIS the total number of plant species present within each of these classes (Table A4 in Appendix A).

Indigenous heritage

The presence of indigenous reserves is used as an indicator of a cultural ES (see Chan et al. 2012). These reserves represent the heritage of indigenous populations present in the state and are vital for maintaining their way of life. Input data is from the Brazilian government and updated as of 2015 (IBGE, 2015), although no changes in number or size of the reserves occurred since the 1990s.

Local climate regulation

MODIS MOD11A2 data for 2014 were used to measure mean annual temperature in Amapá (MODIS, 2016a). The first complete 8-day period for each month of the year was used. This indicator reflects the ecosystem service of local climate regulation, significant in a region where maximum daily temperatures remain above 30 ºC for most of the year. Forests are recognised to contribute to this local temperature regulation (Bright et al., 2017; Li et al., 2015). Higher provision corresponds to lower temperature in the source data. The spatial resolution of the source data was 1 km.

NTFP extraction

Sustainable use protected areas in Brazil allow for the legal extraction of non-timber forest products (NTFP) and many were established with the intention of protecting certain local communities engaged in extractive practices, such as Brazil nut collection. Since these areas are more likely to have NTFPs as a vital economic activity, this layer included all sustainable use protected areas (IBGE, 2015) and extractive settlements (INCRA, 2016) in Amapá.

Recreation

The InVEST (v. 3.3.2) recreation model was used to estimate patterns of recreational use in the state. The model uses an as indicator the total number of annual person-days of photographs uploaded to the photo-sharing website flickr, from 2005 to 2014 (Sharp et al., 2016).

Regional climate regulation

MODIS MOD16A3 data set for 2014 was used to quantify annual evapotranspiration in Amapá (MODIS, 2016b). While itself an ecosystem process, evapotranspiration is used here as an indicator for the ecosystem service of regional climate regulation. Evapotranspiration from the Amazon forest contributes significantly to the water flow reaching the farm-rich areas of southern Brazil (Spracklen et al., 2012). The spatial resolution of the source data was 1 km.

Timber production

This layer identifies areas where legal timber production is occurring. This currently consists of two large monoculture (eucalyptus) plantations managed by private companies. As of 2014 (the reference year) selective logging was not occurring in the state at a commercial scale and was therefore not considered. Spatial data was extracted from IBGE (2015) and Almeida et al. (2016).

ES provision index

All ES map layers (Table 1) were produced in raster format with the same spatial alignment, extent and grid cell resolution (0.01 decimal degrees, equivalent to ~1.1 km). Layers with continuous data (i.e., aboveground carbon storage, local and regional climate regulation, biodiversity, and recreation) were classified into five classes with equal intervals and normalised into a 0 to 1 scale, where 1 corresponds to the category with the highest ES supply. For binary variables, 1 corresponds to the service occurring in that grid cell. For all layers with vector source data, polygons had to cross the centre of the grid cell to be detected. All layers were overlapped and added to create the ES index map. All ES analysed are weighted equally in the index, which assumes these ES are equally valued by beneficiaries. Timber, NTFP (non-timber forest products), and indigenous heritage could not overlap, due to regulations of the Brazilian protected area system, which required minor adjustments to adjacent borders (i.e., removing one of them in the few raster cells where they overlapped). The following datasets had values considered implausible and therefore outliers which were removed from the analysis: for temperature data points higher than 35 ºC (assumed to be measurement errors); for evapotranspiration values more than -/+ 3 standard deviations from the mean (also assumed to be measurement errors); for recreation, values clearly within urban areas, namely the state capital, because that area concentrates more than half of the state population, so photos taken there are less likely to have any correlation with recreation involving natural elements. The classes in the ES index map, shown in Figure A2 (Appendix A), were defined using the Jenks optimisation method, which minimises within-class and maximises between-class variance (Mitchell, 1999), but produces a unique solution for each data distribution. For individual ES layers, categorisation with equal intervals was preferred, which is more comparable across maps.

Land use categories

Land use categories were extracted from the INPE TERRACLASS map from 2014 (Almeida et al., 2016; map shown in Figure A3, Appendix A). For analysis the input categories were aggregated into the following categories, “Forest”, “Non-forest”, “Agriculture”, “Secondary vegetation”, and “Others”.

2.3.3. Data analysis

Spatial analysis was undertaken using ArcGIS 10.3. Resulting ES spatial data covering all of Amapá, at a resolution of 0.01 degrees (~1.1km), were then exported to R v3.3.2 (R Core Team, 2017) for statistical analysis. Only data points simultaneously within the extent of all layers fully covering the map (i.e., aboveground carbon storage, biodiversity, local and regional climate regulation) were used for statistical analysis, which excluded a few points, mainly at the map borders and the eastern tip of the state, which was not covered by the aboveground carbon storage source data. That resulted in a data set with a total of 110,983 data points.

When analysing the interactions among the 9 individual ES, my focus is on the direction of the association rather than its strength. Previous studies on the spatial associations of multiple ES frequently use the Pearson correlation test (e.g., Chan et al., 2006). However, the present study integrates a total of four binary variables (agriculture, NTFP, heritage, timber) and five ordinal variables (each with five categories), making a parametric method such as Pearson correlation less appropriate. Instead, I use Kendall’s tau coefficient as measure of association, calculated with the ‘stats’ package in R, which measures the proportion of concordant pairs in the sample minus the proportion of discordant pairs (Gibbons and Chakraborti, 2003). Statistical significance is assessed with two-tailed tests and $\alpha = 0.05$. No strength threshold was used for the correlations. The correlations reported here provide information on the level of spatial congruence between ES rather than on the specific functional links between them.

This is an exploratory study using descriptive analytical tools and its main purpose is identifying large-scale associations among ES rather than developing models to test causal linkages between them. Hence, I have not taken specific approaches to address autocorrelation. Spatial correlations between ES are the patterns I aim to analyse (Hawkins, 2012). The method used should be robust to bias, including spatial autocorrelation, and the pairwise correlations would have withstood a more conservative significance level (Fortin and Dale, 2005), as all statistically significant tau coefficients calculated had p-values lower than 0.01.

To complement and validate the pairwise correlations, additional approaches were carried out, namely: polychoric correlation, where all variables were analysed as ordinal; and Kendall tau correlation on larger scales, by joining 2x2 and 3x3 spatial units, where the resulting value is the average of the input units. Polychoric correlation is used due to its suitability for categorical data (Holgado-Tello et al., 2010), while changes in scale aim to reduce the effective sample size to assess if that produces changes in the results (Fortin and Dale, 2005).

All plots were produced with ‘ggplot2’ package. In graphs with 95% confidence interval error bars, confidence intervals were calculated by doubling the standard error of the mean. A robust post-hoc test (Herberich et al., 2010) was performed to assess whether differences in the means of different samples are significant.

2.4. Results

2.4.1. Pairwise associations between ecosystem services

Out of a total of 36 possible pairwise spatial interactions between the 9 ES under analysis, 32 were statistically significant, 12 of them were positive correlations and 20 were negative. For biodiversity (*Biodiv* in Table 2), positive correlations among services were found with aboveground carbon storage (*Agb*), regional (*Reg.cli*) and local climate (*Loc.cli*) regulation, indigenous heritage (*Herit*), and NTFP extraction (*NTFP*). Negative correlations among services were identified affecting agricultural production (*Agri*), recreation (*Recr*), and timber extraction (*Timber*). All pairwise associations involving timber production were negative. Agricultural production and NTFP extraction also showed a large number of negative associations. In contrast, local climate regulation and biodiversity had the highest number of positive associations.

Table 2. Pairwise Kendall tau correlation coefficients between the 9 ES analysed.

	Agb	*Agri*	*Biodiv*	*Reg.cli*	*Herit*	*NTFP*	*Recr*	*Loc.cli*
Agri	-	1						
Biodiv	+	-	1					
Reg.cli	+	*n.s.*	+	1				
Herit	*n.s.*	-	+	+	1			
NTFP	-	-	+	-	-	1		
Recr	-	+	-	-	*n.s.*	-	1	
Loc.cli	+	-	+	+	+	+	-	1
Timber	-	-	-	-	-	-	*n.s.*	-

Notes*: n.s.* – non-significant. More details on the coefficients and p-values can be found in Table A1. *Biodiv*: biodiversity; *Agb*: aboveground carbon storage; *Reg.cli*: regional climate regulation; *Loc.cli*: local climate regulation; *Herit*: indigenous heritage; *NTFP*: NTFP extraction; *Agri*: agricultural production; *Recr*: recreation; *Timber*: timber extraction.

In complement to Table 2 I used three validation approaches (polychoric correlation, Kendall tau correlation on joined 2x2 spatial units and on joined 3x3 spatial units), which largely confirmed the results in Table 2 (see Table A2 in Appendix A). The sign of those pairwise correlations was always the same as shown in Table 2. There were minor differences in the significance of the results, although there was no case where the three validation approaches were in agreement between themselves but in disagreement with Table 2. Therefore, I opted to maintain the results of the Kendall pairwise correlations on the original data set without changes, while showing in Table S2 the complete results of the validation approaches.

Associations between provisioning and regulating services, or provisioning and cultural, were mostly negative (87.5% and 75% of associations, respectively), while in regulating-cultural positive associations were more common (62.5%) (Table A3 in Appendix A).

2.4.2. Ecosystem service output and land cover

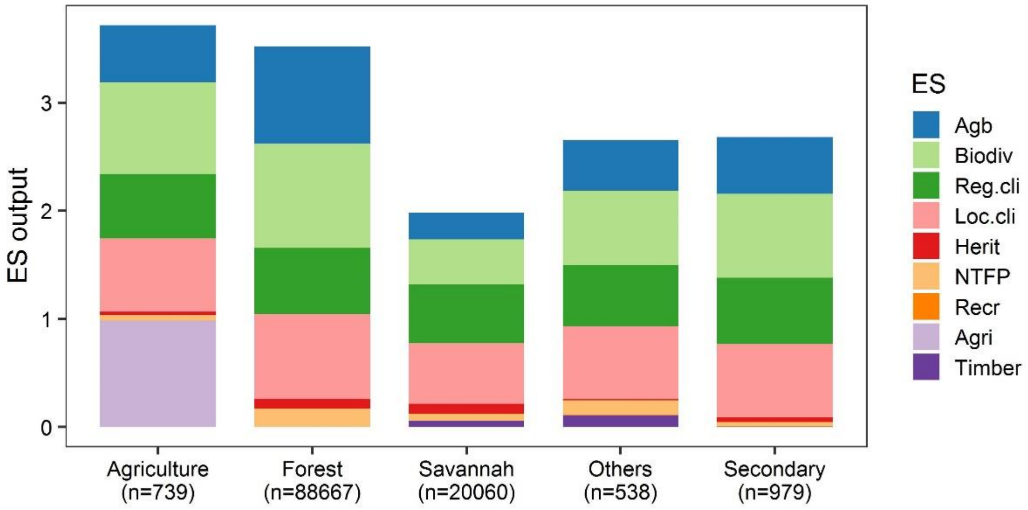

Figure 1. Bar plots showing the variation in ES provision across land-use types in Amapá, namely the mean total ES output for each land use category and the contribution of each individual ES for that total output. In parenthesis I indicate the number of spatial units in each category. “Secondary” refers to secondary vegetation. *Biodiv*: biodiversity; *Agb*: aboveground carbon storage; *Reg.cli*: regional climate regulation; *Loc.cli*: local climate regulation; *Herit*: indigenous heritage; *NTFP*: NTFP extraction; *Agri*: agricultural production; *Recr*: recreation; *Timber*: timber extraction.

Considering the relationship between ES provision and land cover across the 5 categories of land cover (Figure 1), I find that agricultural areas have the highest mean ES output, followed closely by forests, which also occupies a much larger part of Amapá than agriculture. Savannah has the lowest total ES output of all the categories. According to the post-hoc test, the only categories with means not significantly different from each other were ‘others’ and ‘secondary vegetation’. Analysing the proportions of each ES across land cover types shows that, as expected, the ES present across the entire area (i.e., that cover Amapá map completely), namely biodiversity, local and regional climate regulation, and aboveground carbon storage, are responsible for most of the ES output (Figure 1). Fig.1 also shows that the total mean ES output from agricultural areas surpassed forests due to agricultural production, which only occurs in that land cover category. In general, forests have significantly higher mean outputs than other land covers for the following individual ES: biodiversity, local climate regulation, and aboveground carbon storage.

2.4.3. Edge effect on forest ecosystem service output

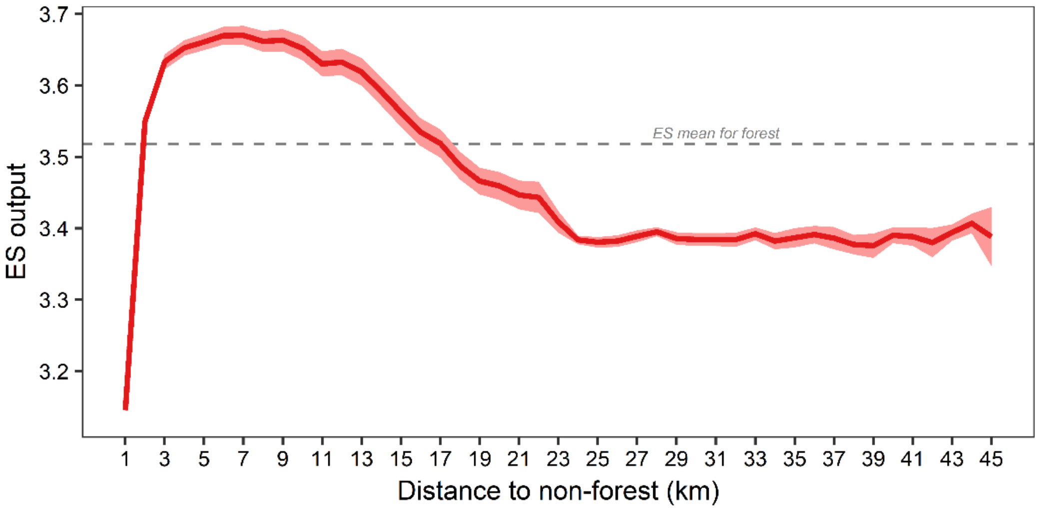

Figure 2. ES provision in forest in relation to distance to its edge. Y-axis represents the mean output for spatial units in the distance interval [x-1,x[. The overall mean ES provision for forest is indicated by the dashed grey line. Error bars in light red correspond to 95% confidence intervals.

I also analyse the effect of distance on mean ES provision in all forest cover (maximum distance to edge found was 45 km) (Figure 2). It is possible to see a nonlinear response of ES provision with distance, where provision is clearly reduced very near the forest edge (up to 1 km), but it then becomes higher than average in a range from 1 to 15 km from the edge. I find that both forest edges resulting from natural transition (mostly forest-savannah) and from deforestation show a similar pattern, although mean forest ES output was consistently lower in natural transition edges (Figure A4 in Appendix A). Figure A5 (Appendix A) decomposes the edge effect reported in Figure 2 by the provision of each ES analysed.

2.5. Discussion

2.5.1. Negative spatial associations are predominant

Both positive and negative associations were identified in the interactions of 9 different ES co-occurring in this tropical region with high forest cover and low deforestation. Negative spatial interrelationships (n=20) between services exceeded the positive (n=12). When considering associations involving at least one provisioning service, most of them (84.2%) are negative, while for associations involving at least one cultural or regulation ES the negative ones are considerably less common (55.6% and 52.6%, respectively) (Table A3 in Appendix A). This is in line with previous findings that trade-offs among ES are more likely to involve provisioning services (Howe et al., 2014).

Timber production is the only ES with all ES associations categorised as negative. This is probably explained by its indicator being under the most intensive land use of the three provisioning ES analysed. NTFP extraction and agricultural production also showed a large number of negative associations, which were expected in the case of agriculture (e.g. Newbold et al., 2014). Interestingly, despite occurring in the forest, NTFP extraction had negative interrelationships with certain ES normally associated with high tree cover, such as aboveground C storage, but not others, such as local temperature regulation. Local and regional climate regulation shared with biodiversity the highest number of positive associations. The important role played by trees is a common feature for both these regulating services, so it is not surprising that they share most of the same links with other ES.

Most associations between biodiversity and other ES are positive. Negative correlations occurred with agricultural and timber production and recreation. These spatial links seem to be generally in line with those found in previous studies (e.g., Cardinale et al., 2012; Cimon-Morin et al., 2013). Previous studies suggested the congruence between biodiversity and other ES might sometimes be low, particularly due to trade-offs with provisioning services (Chan et al., 2006; Cimon-Morin et al., 2013), and this study seems to point in the same direction, as two thirds of the negative spatial correlations involving biodiversity are with provisioning services. Of the three provisioning services considered, only NTFP extraction had a positive association with biodiversity. This extraction occurs in large forest protected areas with small local communities, which seems to translate in minimal impacts to biodiversity, as supported by the literature (Putz et al., 2001), although, as for all other associations found, the result reflects the spatial dynamics of their provision in Amapá but says little about functional biodiversity links. These would need to be determined using more refined methodologies, most likely using manipulations or experimental studies (Cardinale et al., 2012).

2.5.2. Agriculture increases output of provisioning services at the expense of cultural and regulating services

Most deforestation in Brazil results from conversion to agricultural uses (De Sy et al., 2015), which in this analysis was found to be a land use of high ES output. However, the results also show that direct trade-offs will be a consequence of that conversion, mostly to the benefit of one provisioning service (agricultural production). In relation to forests, the output in agricultural areas is higher for provisioning services and lower for regulating and cultural services, suggesting trade-offs that might be amplified as agricultural development increases, particularly if at the expense of forests. At the moment farming in Amapá still consists mostly of small-scale and recently deforested areas, occurring next to forests, with a relatively low prevalence of intensive farming. Therefore, many of the spatial units categorised in this study as ‘Agriculture’ might in fact retain high forest cover. Under more intensified production systems, it is likely that the concentration on provisioning services in agricultural areas will become more prominent. In fact, the only ES analysed here under intensive production (timber) was also the only one that registered negative spatial correlations with all other ES analysed. Furthermore, it is relevant to observe that since forest occupies an area more than 100 times larger than farming areas in the state, its ES supply to local, regional and global beneficiaries continues to be substantially higher in absolute terms.

2.5.3. Non-linear response of ecosystem service provision to tropical forest edges

The analysis of edge effects on forest ES provision indicates a non-linear relationship with distance to the edge. Previous studies have shown that edge effects have an impact on biodiversity, which might be due to different biotic and abiotic factors, such as increased wind disturbance, elevated tree mortality, altered community structure, or facilitation of invasion by disturbance-adapted species (Harper et al., 2005; Laurance et al., 2002a), or direct within-forest anthropogenic disturbances (Barlow et al., 2016). Those factors might also be causing the negative effect on ES provision in areas close to the edge, up to a distance of 1km, but do not explain the above average rise of ES provision at medium distances (1-15 km). That rise is more likely to be related to increased accessibility to people, reflecting an increased ES flow rather than a change in capacity (Mitchell et al., 2015). This therefore seems to indicate that accessible and healthy forest areas are providing more services to local beneficiaries than remote forests, while maintaining high levels of provision for services with beneficiaries at regional and global scales. Figure A5 (Appendix A) indicates that the below mean output at 0 to 1km from forest edge is driven mostly by aboveground carbon storage, biodiversity, and local climate regulation, although it is also present in NTFP extraction and indigenous heritage. The latter two ES also explain the above average rise at medium distances (1-15 km).

This non-linear edge pattern with distance occurs not only close to deforestation but also in areas of natural transition, indicating it might be a consequence of a natural gradient between land uses rather than anthropogenic disturbance. However, it still shows that deforestation, by increasing habitat fragmentation and the edge:area ratio, has indirect impacts on forest ES provision. Furthermore, the boost to ES provision observed in the 1 to 15 km range will very likely only be maintained in forests with low levels of degradation and high biodiversity (Allan et al., 2015), and is not likely to be maintained in fragmented and small forest patches (Mitchell et al., 2015). With 70% of remaining global forests now within 1 km of their edges (Haddad et al., 2015), taking this impact into account becomes more important, although it rarely is (Barlow et al., 2016). The results also shown a difference between mean forest ES provision in edges caused by deforestation or natural transition (Figure A4 in Appendix A). While this difference can be attributed to the likely higher number of local ES beneficiaries in more deforested areas (leading to increased flow), it cannot be excluded the possibility that this indicates a temporal response lag, implying that the full impact on ES provision of newer forest edges is not expressed immediately.

2.5.4. Caveats and limitations

In this study all indicators measure actual provision, albeit at a coarse resolution. Four of the indicators used were binary, simply reflecting presence/absence of ES flow to beneficiaries in that spatial unit, rather than also giving information on its volume or intensity. NTFP extraction is overestimated, because while that activity is much more likely to occur in sustainable use reserves than elsewhere in the state, particularly for Brazil nuts, it will not cover the complete extension of the reserve. Indicators that had continuous source data were also converted to a coarser categorical (ordinal) scale. The value of the output in areas of occurrence for binary indicators, e.g. agricultural production, was equal to the maximum possible output value for categorical indicators (i.e., equal to 1 on a 0-1 scale), which might inflate their weight for total ES provision. Although this limits more refined analyses, I argue that the insights it provides on the direction of spatial interactions between ES at a large scale are robust, and relevant for lesser studied regions.

The coarse representation of the indicators used may help in addressing another limitation, namely the absence of data validation and quality control (Hamel and Bryant, 2017). For binary variables this absence should have minimal consequences because data comes mostly from the same source, the Brazilian government (IBGE, INCRA, ICMBIO, and Embrapa are public bodies) and consists of spatial delineation of protected areas and land use, which is likely to have only minor inconsistencies near the borders. Continuous source data based on remote sensing (i.e., aboveground C storage, local and regional climate regulation) was processed in a way that might dilute the potential impact of outliers and bias, by averaging neighbouring source data cells to create 0.01 degree cells (around 1.1 km) and converting the range to five ordered categories. Temporal mismatch between the variables is also sometimes an issue in ES assessments (de Groot et al., 2010), which was mostly avoided in this study by using 2014 as reference year. Nevertheless, temporal mismatch might be inflating the biodiversity values found in agricultural land, for example, as sampling might have occurred before conversion to agriculture. This can also be a result of the small-scale agriculture that is prevalent in Amapá, due to the retention of at least some original forest cover in spatial units that were categorised as agriculture.

This research provides a snapshot of ES supply in Amapá and does not consider whether current provision will be sustainable in the long term. Protected areas in the state, more than 40% of them allowing sustainable use (Viana et al., 2014), currently cover substantial forest areas, including near human populations, indicating that provision could be sustained by the current level of protection, as long as they continue to have public support (Bernard et al., 2014) and use intensity remains low (Allan et al., 2015).

2.5.5. Policy implications

This work highlights the high multifunctionality of tropical forests in Amapá, providing a broad range of services to beneficiaries at scales from local to global. This is particularly the case for the forests most at risk of deforestation and degradation due to their higher accessibility. The preservation of these forests functions as a buffer between intact forest landscapes (including one of the largest tropical forest protected areas in the world, the “Parque Nacional Montanhas do Tumucumaque”) and human activities, while still providing relevant benefits to local communities. Finding solutions that guarantee long term sustainability of these buffer areas should therefore be a priority for policy makers and conservationists alike. Progressing on a combination of different policies, including economic incentives and deterrents, seems the most promising option to achieve that outcome (Nepstad et al., 2014). Moderate intensity uses such as NTFP extraction and selective logging should also play a role (Rockwell et al., 2015). Further focus by researchers, particularly from interdisciplinary perspectives, on how low deforestation activities can sustain rural development in the tropics is also needed.

I also present additional evidence in support of not neglecting the impact of forest disturbance on the supply of a variety of ES. Decreases in supply can be mitigated by reducing forest fragmentation and deforestation.

Another relevant policy implication of this study is that, in Amapá, protecting forests seems to be positively correlated with the protection of its aboveground carbon stocks and biodiversity. Therefore, recent developments in the state, by both local authorities and international institutions, towards a functioning PES scheme based on the REDD+ (Reducing Emissions from Deforestation and Forest Degradation) framework, seems to be a viable way for reaching conservation outcomes while addressing climate change, if known constrains with the approach are surpassed (Wunder, 2007).

2.6. Conclusions

I present a flexible ES assessment approach, adapted to the context of a region with high tropical forest cover and relatively limited data and information. It reveals significant spatial variation in ES supply, including both positive and negative associations between different ES. It also reveals that ES provision vary substantially near forest edges. This rapid, straightforward methodology can be applied in other regions with limited data availability to provide, at a low cost, a broad perspective of ES provision over large spatial extents that can be useful to support policy making processes. This flexibility also enables the integration of a higher number of ES leading to a more comprehensive perspective on the multiple spatial interactions occurring in the study area. Results apply to Amapá state, north Brazil, but are relevant for other areas with similar conditions, particularly the countries that, like Amapá, are part of the Guiana Shield. This region is characterised by high forest cover and low deforestation rates, sharing many of the same land use management challenges as Amapá. Results also add to the available evidence on the supply of ES derived from ecosystems in Latin America, with emphasis on the Amazon forest. Despite limitations associated with the approach, I believe it provides valuable inputs for land use management in a data scarce region.

Data availability

The dataset used in this chapter is available at http://discovery.ucl.ac.uk/1553305/

Chapter 3: Does perception of the link between biodiversity and ecosystem services influence attitudes towards nature conservation?

3.1. Abstract

The way relationships between people and nature are perceived has changed through time. One recent development is that society is now more aware of the services ecosystems provide to people. Conservationists expect that a better perception of these services will contribute to strengthening support for the conservation of those same ecosystems. However, the empirical evidence confirming this claim is scarce. Here I assess the degree to which people perceive the links between biodiversity and ecosystem services (BES) that are supported in the scientific literature. I also analyse the factors that influence people's perceptions, and whether people's perceptions in turn have an influence on their attitudes towards conservation. Using questionnaires, I surveyed 401 people in urban and rural communities in the eastern Amazon region of Brazil. I find that respondents who are aware of more BES links are more likely to have a positive attitude towards nature conservation. BES perceptions in this study are positively influenced by experience of Brazil nut extraction and income level. In general respondents recognised that biodiversity plays a role in ecosystem service provision, especially in the provisioning and cultural categories. My findings corroborate the use of the ecosystem services framework in conservation outreach and suggest that measures improving awareness of the role biodiversity plays in the provision of several vital services to people might be an effective way to gain support for nature conservation among the public, including in areas of high conservation interest.

3.2. Introduction

At the core of the Ecosystem Services (ES) framework is the underlying assumption that people become more supportive of conservation measures when they are aware of the services nature provides to society. For example, in the seminal book "Nature's Services" (Daily, 1997), the authors state as a main motivation for its publication the "near total lack of public awareness of social dependence upon natural ecosystems", which "represents a major hindrance to the formulation and implementation of policy designed to safeguard earth's life-support systems". Since then the ES concept has progressed and pushed forward science-based policies at different levels (Costanza et al., 2017). However, empirical evidence confirming that original assumption remains scarce.

The way nature-people interactions are perceived changes through time (Mace, 2014). A better understanding of that perception provides a valuable perspective to conservation science, through the lenses of social sciences (Bennett et al., 2017). Perception studies can provide insights on different aspects of conservation, such as its social impacts, ecological outcomes, social acceptability, or the legitimacy of its governance, which in overall makes it better equipped to evaluate the effectiveness of conservation measures (Bennett, 2016).

Both perceptions and attitudes are frequently explored in conservation science. Since both these concepts transferred from psychology are used in this study, it is important to clarify what I mean by them. Attitudes are defined as “an individual's consistent thoughts or feelings towards a thing, person, object or issue, (…) likely to determine how the individual would react towards it” (Winstanley, 2006), while perceptions are “the act or process by which individuals are able to translate information from the external world into an experience of objects, sounds [and other stimuli]” (Winstanley, 2006). In this study I use the term ‘perception’ due to its frequent adoption in conservation literature (Bennett, 2016). I use it as a synonym for behavioural belief, which has an influence on attitudes, as framed in the Theory of Planned Behaviour (Ajzel, 1991). Therefore, when discussing perceptions, I am actually referring to the salient beliefs about the attitude object, which is the behaviour (Ajzel, 1991). As for attitudes, they are one of the direct determinants of behaviour, or at least intended behaviour, according to the same theory (Ajzel, 1991). For this study the behaviours I am ultimately interested in are those that might be linked to decisions that could have a direct impact on conservation, such as voting for a politician with an agenda favourable (or not) to conservation or choosing to support conservation projects in some way.

Different studies have proven that people are aware of a variety of ES being provided by nature (e.g. Pfund et al., 2011; Zhang et al., 2016). These perceptions might indeed help shape how communities make decisions on natural resource management (Fernandez-Llamazares et al., 2016), although different social actors might have different priorities (García-Llorente et al., 2016). A variety of factors have been found to influence how people perceive and value those ES, such as gender (Villamor and van Noordwijk, 2016), education (Sodhi et al., 2010b), location (Muhamad et al., 2014), involvement in certain activities such as agriculture (Cáceres et al., 2015) or participatory landscape management (Paudyal et al., 2015), frequency of visits to the forest (Carignano Torres et al., 2016), or interaction with protected areas (Allendorf and Yang, 2013), among others. People also are able to distinguish ES provision associated with different ecosystems (Caceres et al., 2015). In forest-rich environments, it has been found that locals are well aware of ES, especially of services in the provisioning category (Zhang et al., 2016), but are also aware of less obvious services such as benefits to health or local climate regulation (Meijaard et al., 2013).

There has been considerable scientific progress on the study of ES as mechanistic functions of biodiversity (Ricketts et al., 2016) and this linkage is frequently acknowledged in policy discourses (Posner et al., 2016). But there is little evidence that the general public actually recognises the role that biodiversity plays in ES provision. Despite the variety of studies on how ES are perceived, few of them make the explicit link with biodiversity, which is the element that conservation science is ultimately interested in. Interestingly, there is evidence that perceived species richness might have a stronger effect on human well-being than actual species richness (Dallimer et al., 2012; Pett et al., 2016), which reflects the limited ability of individuals to accurately perceive the biodiversity surrounding them (Pett et al., 2016). Another study found that perceived species richness did increase with true species richness but was overestimated when there were relatively few species and increasingly underestimated with more species (Lindemann-Matthies et al., 2010). This detachment demonstrates how people might be unable to fully relate to biodiversity and helps explain why strategies promoting flagship species are instead often preferred in conservation (Veríssimo et al., 2011). For local communities in forest rich areas land use change might exacerbate this detachment, as those living in deforested areas may start gradually losing cultural values associated with forests (Abram et al., 2014).

Using data from questionnaires applied in households located in the eastern region of the Amazon forest, I explore the relationship between people’s perception of the role of biodiversity on ecosystem service provision and their attitudes towards conservation. Within the ES framework, I expect that a greater awareness of biodiversity and ecosystem service (BES) links should lead to an increased support for conservation measures. Furthermore, I explore which factors have an influence on that BES awareness. In sum, this study focuses on the following three questions: (1) do people in the study area perceive forest BES links? (2) which factors influence the perception of forest BES in the study area?, and (3) does forest BES perception influence attitudes towards conservation measures?

3.3. Methodology

3.3.1. Study area

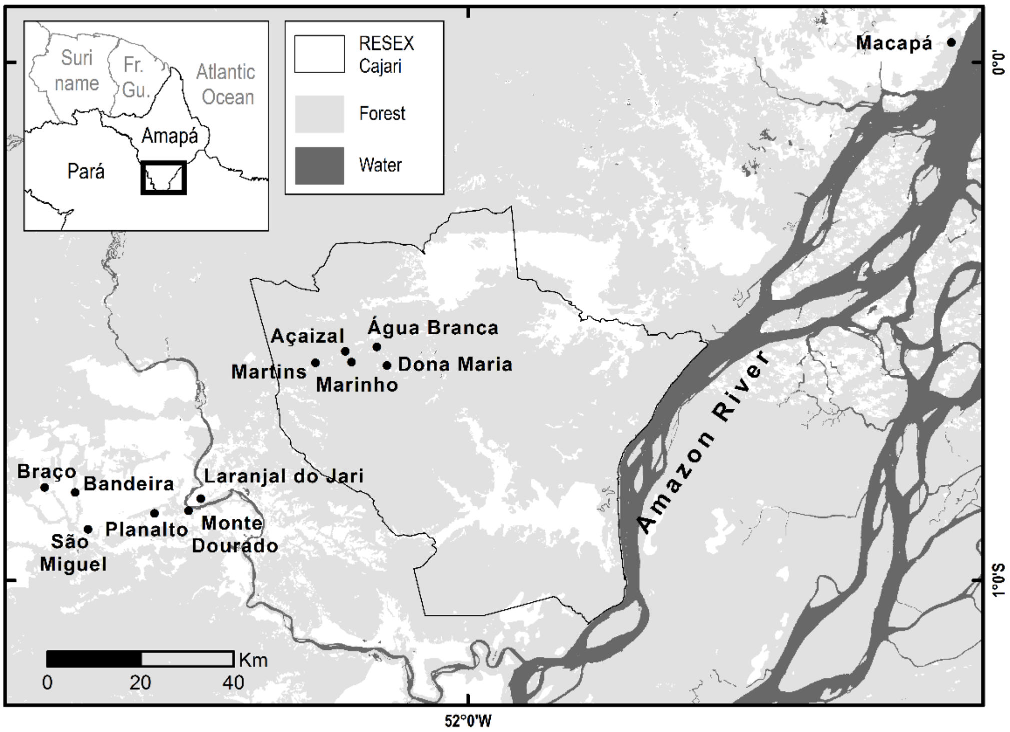

Figure 3. Map of the localities where surveys were undertaken. The extent of the study area in north Brazil is highlighted in the inset. Land use data shown is from INPE (Almeida et al., 2016) and the location of the sampled localities was obtained from Open Street Map. Areas in white are classified as non-forest. 'RESEX' is a sustainable use protected area category in Brazil. Coordinates are indicated at the margins of the map.

This research was conducted in the eastern region of the Brazilian Amazon, specifically near the east-west Amapá-Pará border and in the capital of the state of Amapá (Macapá). Twelve localities were sampled (Figure 3), three of which (Laranjal do Jari, Macapá, and Monte Dourado) include most of the local population and were categorised as urban (see Table B1 in Appendix B). All the other localities sampled are villages with no more than a few hundred households. According to the last census (IBGE, 2010), the study area has a low demographic density (0.46-1.29 people per km^2), with the exception of the municipality of Macapá (62.14 people per km^2). Forest cover is high (Almeida et al., 2016) (Figure 3). Of the sampled localities, five (Água Branca, Açaizal, Martins, Dona Maria, Marinho) are part of a 5324 km^2 sustainable use protected area (IUCN category VI), created in 1990 to protect and manage the extractive activities of the local population. North of the study area there is a large network of protected areas comprising 12.4 million ha (Ministerial order 04/2013, Brazilian Ministry of the Environment). The services sector has the largest impact in the local economy (IBGE, 2017), however other activities such as timber production from Eucalyptus plantations or Brazil nut extraction are also relevant, especially at the east-west Amapá-Pará border region.

3.3.2. Data collection

Six interviewers surveyed 12 localities (Figure 3) using standard questionnaires. All interviewers were recruited locally. Five were in university or vocational studies and one was a Brazil nut producer with previous experience in questionnaire application. All received the same prior training on the purpose of the survey and on its application. The questionnaires were applied at household level. In the urban localities (comprising 73.6% of all respondents), three neighbourhoods were randomly selected and within them the first street to be visited in each day was also randomly selected. In rural localities streets could not be randomly selected due to their small size. Interviewers were instructed to visit every other house in each street, while alternating between male and female respondents, whenever possible. This resulted in good gender balance (see Table 4). Different interviewers contributed reasonably equally to the overall data (12.0% to 22.7%) (see Table B1). The content of the questionnaire applied can be found in Appendix B (Text B1).

I consider biodiversity ecosystem service relationships (BES) both jointly, and disaggregated into three categories representing different service types, namely provisioning (BpES), regulating (BrES), and cultural (BcES). The questionnaire was structured in 7 sections: (i) forest use; (ii) perceptions on BpES; (iii) perceptions on BrES; (iv) perceptions on BcES; (v) attitudes towards conservation; (vi) biodiversity knowledge; (vii) socioeconomic factors. The sections measuring perceptions and attitudes consisted of ten items each, scored using a 5-point Likert scale with responses ranging from “Completely agree” to “Completely disagree”. The order of the items within each section was randomised and a balance was maintained between positively or negatively framing the items (i.e., if BES link has a positive or negative impact), to avoid acquiescence and social desirability biases. The sentences framed BES links in comparative terms for biodiversity, aiming to assess if ES provision is perceived to vary between forests with lower and higher levels of disturbance (i.e., indication of lower [higher] forest disturbance is used as proxy of higher [lower] ecological diversity, respectively). I only included BES links that are supported in the literature, although some links can be complex and context dependent(see references in Text B2, Appendix B). The vocabulary was kept as simple as possible. Terms such as biodiversity or species are therefore absent. The sentences used to measure attitudes towards conservation were based on the environmental attitudes inventory developed by Milfont and Duckitt (2010), plus a few other references (Piédallu et al., 2016; Walpole and Goodwin, 2001). I assessed biodiversity knowledge (section VI of the questionnaire) by showing, in random order, 10x10 cm colour images of six animals and six plants and asking if respondents believed those species occurred locally, when only half of them did. I selected species (Text B1, Appendix B) with distinctive visible features and, in case of animals, of at least partial diurnal habits and not particularly small or rare. Pilot work was carried out that allowed to refine the sentences used and to guarantee that the terminology used was clear to the target population. The questionnaires were anonymous. All respondents gave prior voluntary and informed consent to participate in this research.

3.3.3. Data analysis

I conducted a total of 524 face-to-face questionnaires. However, during data processing, 97 questionnaires with missing data in any of the variables of interest were excluded. Additionally, I excluded 16 respondents that were under 18 years old; eight respondents that were visiting and did not live in the sampled localities; and two questionnaires that were considered of poor quality due to their very high share of neutral answers. That led to a final dataset of 401 respondents. Answers to negatively framed items were inverted. After an initial inspection of the distribution of the response variables in the 5-point Likert scale (Figure B1 in Appendix B), I decided to convert answers to a binary scale, with ‘1’,’2’, ‘3’ converted to 0 and ‘4’, ‘5’ to 1, where 1 corresponds to an identified BES link or a positive attitude towards a conservation measure. This was required due to uncertainty on whether respondents were sensitive to all the degrees of agreement/disagreement.

Numerical variables were standardised (i.e., subtraction of the mean and division by the standard deviation). I used a post-hoc Dunn test to assess if BES perception was significantly different between the three ES categories. To answer research questions (2) and (3) I used generalised linear mixed models (GLMM) with a logistic link function and a random factor for interviewers. The four binary response variables are: perception of BpES links, perception of BrES links, perception of BcES links, and attitudes towards conservation (described in Table 4). The 10 explanatory variables used to assess research question (2) fall into 3 categories: knowledge of the local natural environment, socioeconomic factors, and composition-based metrics of landscape structure (Table 4). Spatial information about the sampled localities was obtained from Open Street Map (2018) and, for the ‘forest nearby’ variable, forest cover was obtained from INPE TERRACLASS data for 2014 (Almeida et al., 2016). Interviewers were included as random factors to account for any unknown differences in their application of the questionnaires. The localities were also tested as random factors. Since I am interested in all explanatory variables, none were dropped from the models. Instead I acknowledge model selection uncertainty and carry out model averaging, which allows exploring the relative importance of the variables from an information theory perspective, based on Akaike’s Information Corrected Criterion (AICc) (Burnham and Anderson, 2002). Relative importance is estimated by summing the Akaike weights across all the possible models (Burnham and Anderson, 2002). Since I am interested in the variables absolute effect size, natural (i.e., conditional) model averaging was used (Galipaud et al., 2017), using all possible models to guarantee that there is balance in the number of models containing each variable (Burnham and Anderson, 2002). For research question (3), the perception variables were used as predictors to assess how perceptions of BES links influence attitudes towards conservation. Confidence intervals were computed using the bootstrap percentile method, repeated 1,000 times. Spatial analysis was carried out in ArcGIS 10.3. Data analysis was conducted in R (R Core Team, 2017), with package ‘lme4’ used for the GLMMs and package ‘MuMIn’ used for multi-model inference, while ‘ggplot2’ was used for graphical outputs, with the exception of Figure B1 (Appendix B) that was produced using ‘likert’ package. Package ‘car’ was used to calculate the variance inflation factors shown in Table B5 (Appendix B).

Table 3. Description of the ten explanatory and five response variables used in the analysis.

Variables	Description
Age	Age of the respondent, in years.
Biodiversity	Measures knowledge of local fauna and flora. Relative frequency of correct identifications of local occurrence of 6 animals and 6 plants.
Brazil nut	Categorical variable indicating if the respondent extracts Brazil nut from the forest.
Education	Educational level.
Forest nearby	Forest area (in ha) in a 3-km radius around the locality. Land use spatial data: INPE TERRACLASS for 2014. Localities spatial data: Open Street Map.
Forest use	Frequency of visits to the forest.
Gender	Categorical variable indicating the gender of the respondent.
Income	Income level.
Landowner	Categorical variable indicating whether respondents own land.
Rural	Laranjal do Jari, Macapá, and Monte Dourado were categorised as urban (categorised as towns in Open Street Map), the remaining localities were categorised as rural.
Perceived BpES links	Total number of perceived links between biodiversity and provisioning services.
Perceived BrES links	Total number of perceived links between biodiversity and regulating services.
Perceived BcES links	Total number of perceived links between biodiversity and cultural services.
Overall BES perception	Sum of perceived links between biodiversity and ecosystem services from all three categories considered.
Attitudes towards conservation	Total number of positive attitudes towards conservation.

Table 4. Descriptive summary of the sample (N=401) using absolute frequencies, except for 'Age' where the mean and standard deviation are shown.

Age	**x̄:** 39.6	**s.d.:** 15.9		
Gender	**F**: 218	**M**: 183		
Monthly income	**< R$937:** 231	**R$937-1874:** 103	**> R$1874:** 67	
Education level	**No school:** 22	**Primary:** 148	**Secondary:** 180	**Superior:** 51
Motives for forest entry	**Provisioning:** 124	**Cultural:** 173	**Others:** 59	
Land owner	**No:** 325	**Yes:** 76		
Raises livestock	**No:** 395	**Yes:** 6		
Farming	**No:** 255	**Yes:** 146		
Brazil nut production	**No:** 322	**Yes:** 79		
Used any forest product last month	**No:** 147	**Yes:** 242		
Income from forest products last month	**No:** 272	**Yes:** 114		

Notes: Not all factors add up to N=401, due to NAs. For the complete version of this table, including NAs and complete notes, see Table B1 in Appendix B.

3.4. Results

3.4.1. Overall BES perception

The sample consists of 401 collected questionnaires. Table 4 provides its descriptive summary. Respondents mostly identified the existence of a linkage between biodiversity and the provision of ecosystem services. Overall, three quarters of all BES links considered by respondents were identified although the strength of perceptions varied amongst service categories. The link between cultural ES and biodiversity was more frequently perceived (87.6% of responses), while for provisioning BES (72%) and regulating BES (65.3%) the values were relatively lower (Figure 4). A post-hoc Dunn test confirmed the significant differences in the mean number of identified BES links between all ES categories (p-value<0.001). In Table B2 (Appendix B) I show the share of identified links, per sentence used in the questionnaire, which ranged from a minimum of 29.7% to a maximum of 97.0%.

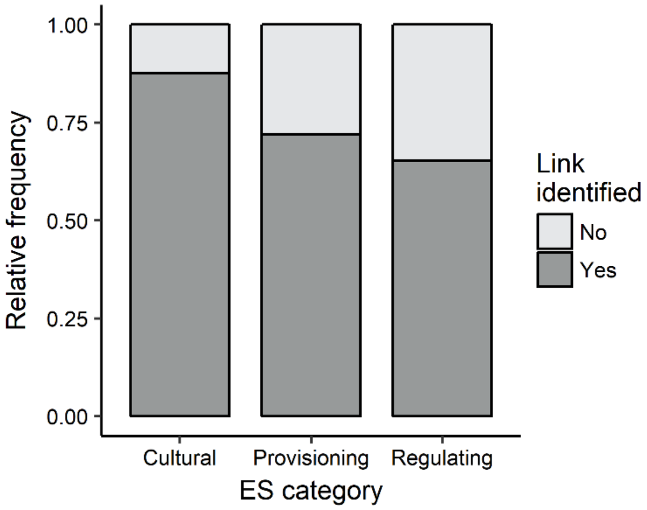

Figure 4. Overview of BES perception by ES category. This plot indicates the relative frequency of BES links, per ES category, that were identified by respondents (N=401). For each category respondents were asked about 10 BES links.

3.4.2. Factors influencing BES perception

Table 5. Coefficients (β), standard error (SE), and the 95% confidence interval of the averaged model with overall BES perception as response variable. The confidence intervals that do not include zero are shown in bold.

	β	**SE**	**95% C.I.**
Intercept	1.097	0.143	**0.816, 1.377**
Age	-0.013	0.024	-0.059, 0.034
Biodiversity knowledge	0.009	0.024	-0.037, 0.056
Brazil nut production	0.311	0.092	**0.129, 0.492**
Education	0.001	0.026	-0.051, 0.053
Forest nearby	0.053	0.071	-0.087, 0.193
Forest use	0.021	0.028	-0.033, 0.076
Gender:M	-0.083	0.047	-0.176, 0.009
Income	0.061	0.025	**0.011, 0.110**
Land owner	0.047	0.061	-0.073, 0.167
Rural	-0.111	0.099	-0.305, 0.083

Of the 10 independent variables analysed, being involved in Brazil nut extraction and level of income are the most influential affecting variance in overall BES perception (Table 5). People that are involved in Brazil nut extraction and those with higher levels of income are more likely to perceive BES links. The calculation of variance inflation factors (VIFs) did not detect strong levels of multicollinearity in this model (Table B5 in Appendix B). When performing the analysis per ES category (Figure 5) it is possible to detect a few variations in relation to the overall model. For BrES links, none of the variables stand out as significant. For BcES links, Brazil nut extraction is positively related with their perception, while respondents living in a rural area are less likely to perceive them. And for BpES links, there is also a positive effect for Brazil nut extraction.

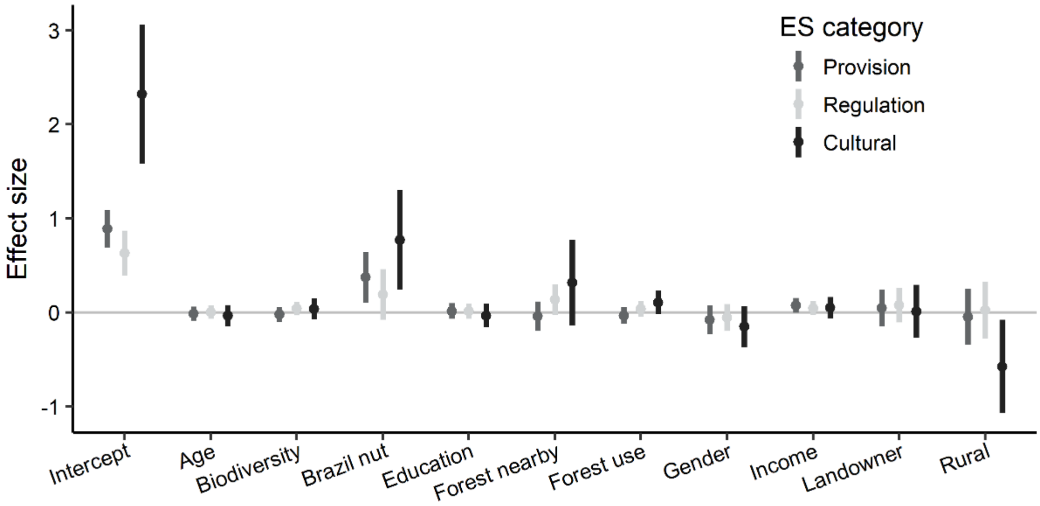

Figure 5. Effect sizes (log odds) and corresponding 95% confidence intervals of the 10 independent variables under analysis, plus the model intercept, in relation to the perceived BES links, per ES category. The coefficients shown result from the conditional averaged models using BES perception for each ES category as the respective response variables.

Table 6 provides the relative importance of each variable in relation to the others using information theory (Burnham and Anderson, 2002). When all BES perceptions are analysed jointly, Brazil nut extraction is the most supported variable (99%), followed by income level (88%) and gender (64%), in line with the results in Table 5. It is interesting to note that the amount of forested area in a 3km radius was the most supported variable (54%) for regulating BES. The correlation coefficients between explanatory variables can be found in Table B4 (Appendix B). The eight models for overall BES perceptions with substantial level of empirical support (Δ AICc <2) are presented in Table B3 (Appendix B).

Table 6. Relative importance of the explanatory variables used in the models with BES perceptions as response, both jointly and disaggregated by ES category.

	Provision	**Regulation**	**Cultural**	**Overall**
Age	0.28	0.27	0.30	0.29
Biodiversity knowledge	0.30	0.39	0.30	0.28
Brazil nut production	0.94	0.49	0.96	0.99
Education	0.28	0.27	0.29	0.27
Forest nearby	0.29	0.54	0.45	0.32
Forest use	0.32	0.35	0.58	0.33
Gender	0.38	0.32	0.48	0.64
Income	0.68	0.43	0.35	0.88
Land owner	0.29	0.34	0.27	0.33
Rural	0.28	0.28	0.84	0.41

3.4.3. BES perception and attitudes towards conservation

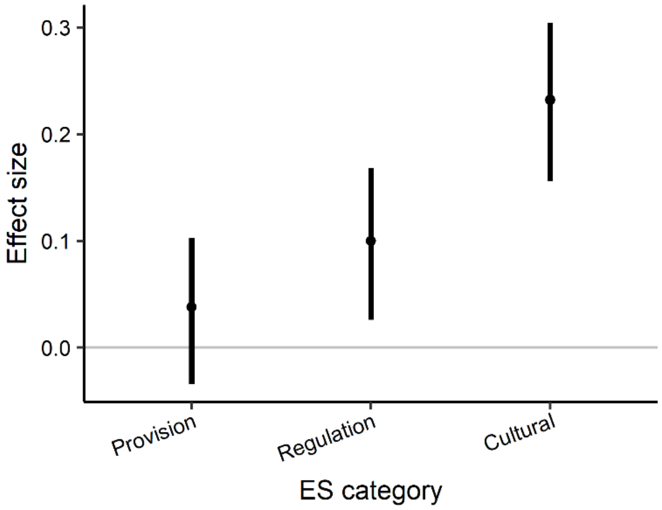

Figure 6. Effect sizes (log odds) and corresponding 95% confidence intervals in the model assessing if BES perceptions, per ES category, influence attitudes towards conservation, where a positive effect translates into higher likelihood of conservation support.

Results show that attitudes towards conservation are positively related with perception of regulating and cultural BES links (Figure 6). And when all ES categories are analysed as a single explanatory variable, its coefficient is β= 0.116 (%95 CI= ±0.028), confirming that respondents with higher BES perception are more likely to have a positive attitude towards nature conservation. 84.2% of sentences measuring attitudes towards conservation (Section V of the questionnaire in Text B1) were answered positively (Table B2), which indicates high support for conservation measures in the study region.

3.5. Discussion

There was a gap in the level of awareness of the role of biodiversity in provisioning and especially regulating ES, in relation to cultural, which should be considered by institutions trying to engage people in conservation using an ES discourse. Respondents were insufficiently aware of the influence of biodiversity on rates of infectious diseases (Keesing et al., 2010), for example. In fact, regulating ES are more prone to be overlooked due to their complexity and not being directly used by people (Sutherland et al., 2018). ES perceptions that differ from formal scientific knowledge have been reported in previous works, amongst farmers (Lamarque et al., 2011) or forestry specialists (Carnol et al., 2014), for example. ES research is an emergent and inherently context-dependent subject, integrating methods from different disciplines, which therefore leads to some difficulty producing clear messages that can be easily assimilated by other fields (Polasky et al., 2015). Nevertheless, results show reasonably high awareness of BES links in the local communities sampled, confirming previous studies reporting fairly detailed understanding of ecosystem processes by local communities (e.g., Ronnback et al., 2007).

Individuals participating in Brazil nut extraction were more likely to perceive overall BES links, particularly cultural and provisioning BES links. These results seem to be solely linked to Brazil nut extraction since, despite most producers living in a rural setting, those effects are not repeated when considering all rural inhabitants sampled. In contrast, rural inhabitants were actually less likely to recognise BcES links. Therefore, results suggest that being a rural dweller, by itself, is not enough to increase BES perceptions. While being directly involved in an extractive activity closely connected with the forest significantly increases awareness of the importance of biodiversity for local livelihoods and culture.

Income also stands out as a relevant explanatory factor for the variation in overall BES perception. ES flow is socially conditioned by dynamic mechanisms of access (Daw et al., 2011). This might lead to people with higher income being able to afford experiencing a greater variety of ES and therefore being more aware of how biodiversity influences their supply. On the other hand, education has no effect on the measured perceptions. Education and income are poorly correlated in the sampled respondents, with more than two thirds (73.1%) of respondents at the higher income level not actually having reached university or a post-secondary school technical course. The lack of effect from education also suggests local schools might not be focusing enough on environmental education, at least regarding the role of biodiversity in ES.

Additionally, while previous studies have presented contrasting results on the influence of gender on perspectives towards ES (e.g., Martín-López et al., 2012; Villamor and van Noordwijk, 2016), in this study results point towards females being more likely to perceive BES links. As for perceptions on BrES, no meaningful relations were identified. However, the area of forest cover within a 3km radius had the highest relative importance, which suggests individuals living in closer contact with biodiversity tend to be more likely to perceive its role on regulating ES, such as local climate regulation or soil erosion control. Previous studies have identified awareness of regulating services to be generally low (Zhang et al., 2016).

Higher awareness of both cultural and regulating BES had a positive relationship with favourable attitudes towards conservation. This might be a consequence of the intangible dimensions of values that underline our perspectives on ES and corresponding benefits (Chan et al., 2012). Individuals with a more biocentric perceptive of the world might have a more comprehensive appreciation of the role of biodiversity in the services nature provides us, which in turn makes them more likely to be supportive of conservation efforts. On the other hand, the recognition of provisioning BES links did not have the same effect on attitudes towards conservation. This might be a reflection of individuals with higher provisioning BES perception also being more inclined to prioritise an instrumental use of nature over its long-term conservation. Nevertheless, while these results seem to be at least partially explained by individuals leaning more towards instrumental or intrinsic values of nature, focusing solely on this dichotomy might provide an incomplete picture of how people relate with nature (Chan et al., 2016).

Support for conservation by communities in the study area might come from the recognition of the relevance of local ES provision to their well-being. While there is limited evidence of which ES management strategies help overcome poverty (Suich et al., 2015), at the very least ES provide a valuable safety net for vulnerable groups (Barrett et al., 2011), when granted access to them (Daw et al., 2011). That is the case in the study area, which includes a sustainable use protected area, whose purpose is, among others, protecting local beneficiaries of ES. Additionally, the high levels of conservation support and awareness of BES links found in the study area might also be a consequence og its socio-political context. In the 1990s there was a strong push of the sustainable development agenda by the state government of Amapá, with the implementation of the PDSA programme (Programa de Desenvolvimento Sustentável do Amapá), which later influenced other state level sustainable development programmes in the Amazon region (Viana et al., 2014). Presently, conservation measures seem to be highly supported in the region, although there will likely be variations between different social groups (García-Llorente et al., 2016).

Further research into novel approaches, such as conservation marketing (Wright et al., 2015), should provide clearer answers on the best ways to frame biodiversity to convey effective messages that advance conservation goals. This study presents site-specific results that should be interpreted within the context of a forest-rich biodiverse tropical landscape. People living near forests might be more aware of the multiple ES provided locally (Muhamad et al., 2014). Furthermore, it is known that spatial variations in perceptions towards forest use and management can occur within the same region (Meijaard et al., 2013).

One of the limitations of this study is that it makes no distinction between different stakeholder groups, which might have different priorities in ecosystem service management (García-Llorente et al., 2016). It would be interesting, and a possible venue for follow-up studies, to contrast these results with perceptions of policymakers in the study area or of communities in other geographies, measured using the same methodology. Another potential limitation is that I aimed to measure a relationship, between biodiversity and ES, which might be difficult for respondents to grasp, even if I kept the language as simple as possible, used proxies to convey different biodiversity levels, and tried to frame the sentences in comparative terms. Also, BES relationships might be non-linear or respond to thresholds (Cardinale et al., 2012), which makes them more difficult to understand. Finally, while causal inferences based on surveys can be established provided they are supported by a solid theoretical framework (De Vaus, 2002), researchers are advised to be careful when attributing causal links based on survey data. Nevertheless, I am confident, based on the Theory of Planned Behaviour (Ajzel, 1991), that BES perceptions, used here as synonymous of behavioural beliefs, are expected to influence attitudes towards conservation and not the opposite.

Previous studies had shown that awareness of the ES concept and its relationship to human well-being is positively related with attributing higher value to conservation (Castro et al., 2011). To my knowledge the present study is the first to suggest the same holds true for awareness of the role biodiversity plays in ES provision.

3.6. Conclusions

This chapter examines the intuitive, yet largely unverified, assumption that by casting light on the benefits biodiverse ecosystems provide to society, people are more likely to support conservation measures. The results indicate that higher awareness of the role biodiversity has on ecosystem services might indeed increase support for measures that protect those ecosystems, with implications for conservation engagement and outreach. Anthropogenic pressure on forests continues to increase and as a response pro-conservation groups need to explore multifaceted approaches to engage with those less inclined to protect it. Furthermore, people with more positive attitudes towards conservation should also be more likely to integrate pro-conservation behaviours in their daily lives, which can have broader implications in their communities by influencing how local forests are managed or which routes of development are locally favoured, for example. Results also indicate how the role of biodiversity in regulating ecosystem services is being overlooked, despite their crucial importance of these services to people. Therefore, this study suggests there are currently untapped potentialities on how awareness of ES, linked with biodiversity, can push forward the conservation agenda among the general public, including in local communities living at the frontline of conservation, in biodiverse regions under increasing anthropogenic pressure. Pristine forests provide irreplaceable globally relevant services that will only persist if the socio-ecological systems at its fringes are sustainable in the long term, instead of continuously expanding. To achieve such an ambitious goal, conservationists should explore all viable strategies, including making sure that society is aware of what it gains from preserving nature and acknowledges the species, ecological processes, and ecosystems involved.

Ethical approval

This research was approved by the Ethics Committee of Universidade Federal do Amapá (UNIFAP) and the Brazilian Committee of Ethics in Research (CONEP) under the registry number 84189518.0.1001.0003.

Data availability

The dataset used in this chapter is available at http://discovery.ucl.ac.uk/10070645

Chapter 4: Patterns of biodiversity response along a gradient of forest use in Eastern Amazonia, Brazil

4.1. Abstract

Tropical forest landscapes fulfil many functions, with long-term management being essential to their development while safeguarding these functions, including their natural values. However, our knowledge of how different configurations of those landscapes affect biodiversity is limited. Here, I analyse the responses of different taxa to varying forest management regimes. The four forest management categories are old-growth forest, Brazil nut extraction areas, reduced impact logging areas, and eucalyptus plantations. Within six independent replicates of each category three taxa, fruit-feeding butterflies, dung beetles, and trees (diameter at breast height ≥10cm), were sampled. Forests under moderate use contained similar, albeit slightly lower, diversity levels relative to old-growth forests, while communities in plantations had relatively lower species richness. Increased forest use intensity is likely to cause negative effects on the richness of tree, dung beetle, and fruit-feeding butterfly communities in eastern Amazon. Nevertheless, a landscape matrix with forest under varying use intensities can potentially help reconcile the production of goods that support local livelihoods and biodiversity conservation.

4.2. Introduction

The Amazonian forest is a rich and unique ecosystem of global conservation relevance (Watson et al., 2018). However, projections suggest that up to 40% of it might be cleared by 2050, greatly increasing the threat to its biodiversity (Ter Steege et al., 2015). This is particularly problematic due to the possible existence of ecological thresholds in regional temperature or deforestation levels that, if crossed, might result in large-scale conversion to savanna (Nobre et al., 2016). Human-modified landscapes can provide suitable habitat for many species, function as corridors between protected areas, or buffer the effects of more intensely managed systems (Bhagwat et al., 2008, Santos-Heredia et al., 2018). Their potential value for biodiversity conservation is maximised in mostly forested landscapes with low human density and is dependent on factors such as species distributions, landscape spatial configuration, climate, or patterns of human disturbance (Melo et al., 2013). Our understanding of how human-modified landscapes should be managed to guarantee long-term persistence of biodiversity and ecosystem service provision is limited (Melo et al., 2013). Still, the harvesting of natural products seems crucial to push development paths in tropical regions towards sustainability (McNeely and Schroth, 2006; Nobre et al., 2016). More research is therefore needed on how landscape-level dynamics, including extractive activities, interact with biodiversity, ecosystem services and rural livelihoods (Chadzon et al., 2009). This might require monitoring multiple taxa due to idiosyncratic responses to disturbance and natural community variation (e.g., Kessler et al., 2009; Beiroz et al., 2017).

Invertebrates are important indicators of forest disturbance that tend to respond rapidly to disturbance due to their short generation times and high growth rates (Sodhi et al., 2010a). They are also vital for the maintenance of several ecosystem processes (Wilson 1987), which can be compromised by land use change (Santos-Heredia et al., 2018). Species with restricted geographic ranges or forest specialists tend to be particularly vulnerable to disturbance (Lewis, 2001; Sodhi et al., 2010a), while other species will be more tolerant to the light and humidity conditions that occur in edges and areas of higher human disturbance (Cajaiba et al., 2017; Davis et al., 2000). This study samples two relatively well studied groups, fruit-feeding butterflies and dung beetles. Both have some characteristics that increase their suitability as ecological models, such as relatively large body sizes, ease of sampling and a relatively well-known taxonomy (Ribeiro and Freitas, 2012). Their responses to disturbance are not necessarily congruent due to different life histories (Davis et al., 2000; Schulze et al., 2004). The feeding specialisations seen in some butterfly species do not seem to occur in dung beetles, for example. The involvement of dung beetles (Coleoptera: Scarabaeinae) in ecosystem processes is well studied, including their impact on nutrient cycling, bioturbation, and secondary seed dispersal (Nichols et al., 2008). Fruit-feeding butterflies (Lepidoptera: Nymphalidae) in the neotropical region are included in the Satyrinae, Biblidinae, Charaxinae and Nymphalinae subfamilies of Nymphalidae (Lucci Freitas et al., 2014).

Several studies have considered the impact of forest disturbance on butterflies and dung beetles. Most studies seem to agree that moderate disturbance factors, such as selective logging or agroforestry, will have significantly fewer effects on diversity compared to more intensive land uses (Gibson et al., 2011). Diversity might actually increase in disturbed sites, although that might simply reflect an increase in generalists with lower conservation value (Bobo et al., 2006; Fermon et al., 2005). Selectively logged forests can retain most of the species found in intact forest (Edwards et al., 2014b), although effects will depend on logging intensity or the time passed since the last logging event (Burivalova et al., 2014; Edwards et al., 2014b). Many studies have reported small changes between intact forests and selective logging in most biodiversity metrics analysed (Ghazoul, 2002; Hamer et al., 2003; Lewis, 2001; Ribeiro and Freitas, 2012; Slade et al., 2011), although important ecological processes may nevertheless be affected even under low intensity logging (França et al., 2017).

The impact of other moderate forest uses has also been considered in the literature, especially in agroforestry landscapes. Despite the varied agroforestry systems considered in different studies, results seem to generally indicate that these landscapes have intermediate conservation value, lower than intact forests and higher than monocultures (Bobo et al., 2006; Harvey et al., 2006). When compared with selective logging, agroforestry systems also seem to have slightly lower biodiversity (Korasaki et al., 2013; Nichols et al., 2007).

Under more intensive land uses, even when only considering tree monocultures, the negative impacts on biodiversity can be considerably higher, indicating that only low diversity communities are able to persist in severely modified landscapes (Davis et al., 2000; Edwards et al., 2014b; Gardner et al., 2008; Nichols et al., 2007; Wilcove et al., 2013). Nevertheless, these areas might be able to harbour a large number of primary forest species when situated within a landscape matrix containing a high proportion of intact forest (Barlow et al., 2007a).

Trees are the main structural components of forests and tree community change can help predict changes in other taxa (Barlow et al., 2007a; Bobo et al., 2006). They are severely affected by land use intensification (Philpott et al., 2008; Schulze et al., 2004) and tree communities might not resemble those of intact forests even several decades after disturbance (Richardson and Peres, 2016; Sodhi et al., 2010a). However, they are also more challenging to use as biodiversity indicators than insects, as the impacts on species composition of biotic or abiotic factors might take years to manifest, even on seedling regeneration (Darrigo et al., 2016). Amazonian tree flora, despite being one of the most diverse globally, is poorly known, with a recent study estimating that at least 36% of all Amazonian tree species would likely qualify as threatened under IUCN Red List criteria, if more data was available (Ter Steege et al., 2015). Tree species with certain traits, such as reliance on mammal pollinators, might be more vulnerable to extinction (Sodhi et al., 2010a). Agroforestry and especially plantations might have a clearer negative impact on plant richness than logging (Gerstner et al., 2014; Quazi and Ticktin, 2016), although the high diversity levels in logged forests might not reflect conservation value if diversity is maintained high due to fast-growing early successional species (Sodhi et al., 2010a). Reduced impact logging by itself does not guarantee sustainable forest management, including the long-term persistence of the targeted species, with factors such as the duration of the rotation cycles or the amount of timber harvested being determinant (Richardson and Peres, 2016; Sodhi et al., 2010a).

This study focuses on different biodiversity indicators in forest uses of varying intensity in north-east Amazon. Complementary metrics are preferable as species richness by itself might provide an incomplete perspective of community changes (Brose et al., 2003). For example, Barlow et al. (2007b) found that butterfly community composition was a better indicator of habitat change than either richness or abundance. Also, asymptotic richness estimators seem better suited than observed species richness to provide lower-bound estimates for diverse groups such as tropical arthropods (Gotelli and Colwell, 2001). Variation in biodiversity indicators may also be sensitive to scale (e.g., França et al., 2017), geographic region (e.g., Burivalova et al., 2014), disturbance type (e.g., Gibson et al., 2011), or vertical stratification (e.g., Fermon et al., 2005). For insects the effects of both inter and intra-annual temporal dynamics might be particularly relevant (Barlow et al., 2007b; Beiroz et al., 2017; Hamer et al., 2005). Furthermore, the choice of taxa under analysis can also be important. Studies focusing on multiple taxa have shown that responses to disturbance can be similar but will not always be congruent, hindering the possibility of finding a universal indicator taxon (Barlow et al., 2007a; Edwards et al., 2014b; Lawton et al., 1998; Schulze et al., 2004). Even within lower taxonomic ranks (e.g., subfamily) the responses to disturbance might vary (Barlow et al., 2007b; Ghazoul, 2002).

Here, I aim to explore whether fruit-feeding butterfly, dung beetle, and tree communities are randomly distributed in space in a landscape with varying forest management regimes. My main objective is to compare the conservation value, i.e., the capacity to support biodiversity, of four relevant forest uses for northeast Amazon forest, namely old-growth forest, Brazil nut extraction areas, selective logging areas, and eucalyptus plantations. While old-growth forests are sampled here as baselines, the focus of this research is on forest uses directly used by people within forested socio-ecological systems, therefore excluding secondary forests, which mostly benefit people indirectly, as a vital component of the shifting agriculture cycle (Brown and Lugo, 1990). More specifically, the objectives of this study can be formulated in the following way: (1) compare the levels of species richness, abundance, and community structure of the three taxa between old-growth forests, Brazil nut extraction areas, selective logging areas, and eucalyptus plantations; (2) assess if fruit-feeding butterflies, dung beetles, and trees exhibit congruent responses to forest use change; (3) explore how the results can contribute to nature conservation and sustainable forest management.

4.3. Methodology

4.3.1. Study site

The study was developed at the east-west border between Amapá and Pará, two states in the Brazilian Amazon forest (Figure 7). Forest cover is relatively high. Human density is low and concentrated on the margins of Jari River. The landscape is characterised by a large eucalyptus plantation and natural forest under different management regimes, with an incipient presence of intensive agricultural production. The climate is tropical, the mean annual rainfall is around 2300 mm, with a wetter season from January to June, and a mean temperature fluctuating around 27 ºC throughout the year (INMET, 2018). The terrain is dominated by moderate slopes and low elevations. The sampling points ranged from 45 to 217 metres above sea level and slopes ranged from 0.1 to 9.2 degrees. According to IBGE (2003), the soil is classified as "*latossolo"* (ferralsol) in all sampling points, except for PRI2, which is *"argissolo"* (acrisol).

The sampling focuses on four forest uses: intensive eucalyptus plantations, reduced impact logging, Brazil nut extraction, and old-growth forest. The eucalyptus (*Eucalyptus urograndis*) plantations, managed by Jari Celulose, lie mostly on the Pará side of the study area. The company operates on 129,224 ha of land, which are integrated in around 1.2 million ha owned by its parent company (Grupo Jari). The areas sampled were planted between 2011 and 2013.

Those 1.2 million ha also include the land managed by Jari Florestal, a different company within the same group, created in 2002 to conduct selective logging on 545,025 ha. The selective logging areas sampled were cut for the first time in 2013 and 2014 and the timber extracted ranged from 9.2 to 16.2 m^3 ha^{-1}.

Any Brazil nut (BN) tree (*Bertholletia excelsa*) easily accessible within the study area is likely to have its fruits collected or sold to local intermediaries, but one of the few areas where the activity is managed by local communities and legally protected is the extractive protected area RESEX Cajari (IUCN category VI), located in the Amapá side of the study area. BN trees tend to have an uneven distribution throughout their range, occurring in clusters (Mori and Prance, 1990), locally called as "castanhais", although this clustered distribution can become near random in forests with higher canopy openness (Wadt et al., 2005). At the RESEX, the BN trees used locally by the community were mapped as part of a project in collaboration with the state government (Costa, 2018). Local fruit fall and collection occur mostly between January and April. Commercial logging is illegal within the RESEX.

Old-growth forest sampling sites were located in terra firme (non-flooded) dense forest, half in the western part of the study area, closer to the eucalyptus plantations and selective logging sampling points, the other half inside the RESEX in the eastern part of the study area. Their selection was also constrained by accessibility factors. These sites reflect the conditions of local old-growth forest, which are not necessarily completely undisturbed. Distance to the closest secondary road in old-growth forest sampling points ranged from 1.2 to 4.2 km. According to TERRACLASS land use map (Almeida et al., 2016), sites PRI1 and PRI2 are less than 100m from the forest edge (22.2m and 17.5m, respectively) due to mapping inaccuracy, since field measurements had put both distances to edge slightly above the 100m threshold. Mean distance to forest edge for all old-growth sites is 1057.1m. Sites PRI2 and PRI6 had trace indications of past disturbance events (fire and selective logging, respectively) that could not be confirmed in INPE deforestation data or MODIS fire data. Since the sites sampled are relatively accessible, they might also experience low to moderate levels of hunting pressure.

Soil samples were analysed at Embrapa laboratories in Macapá, Amapá. For each site the combined sample, collected with a soil auger for the 0-10cm layer, consisted of a soil mixture from five subplots separated 50m along a linear transect. Slope and elevation were measured at each site through the use of a Haglöf EC-II electronic clinometer and a Garmin GPSMAP 64s, respectively. Slope was determined by measuring the angle, at 10 metres distance, of a reference point at eye height. Plot level slope and elevation are an average of seven measurements taken at the centre and borders of the tree plots.

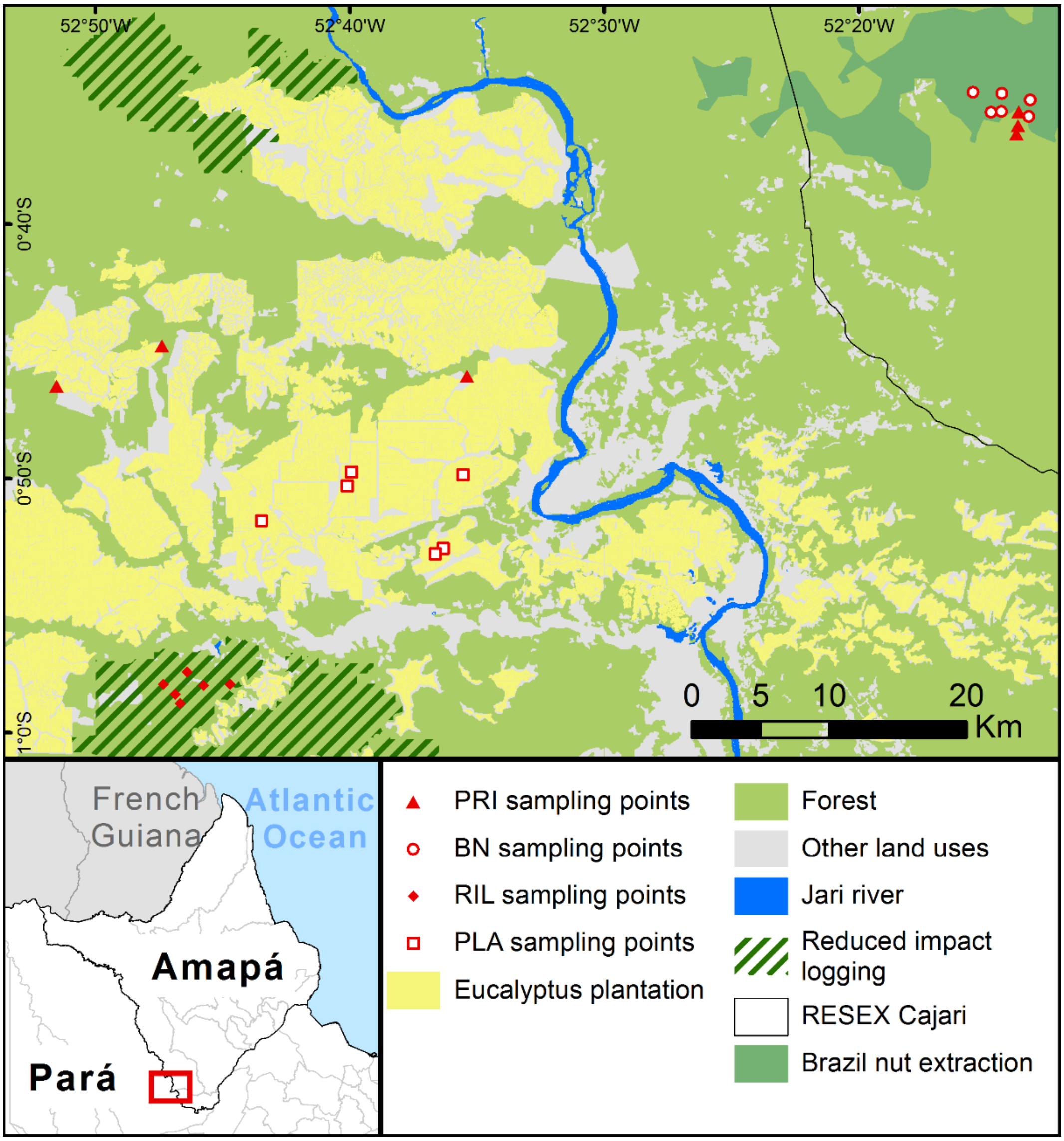

Figure 7. Map of the study area. Abbreviations refer to old-growth forest (PRI), Brazil nut extraction (BN), reduced impact logging (RIL), eucalyptus plantation (PLA). RESEX is a protected area category in Brazil. The Brazil nut extraction area delineates the area, within the RESEX, where Brazil nut trees have been mapped (Costa, 2018). Latitudinal and longitudinal coordinates are indicated at the margins of the map.

Sampling was conducted at the same locations for dung beetles, butterflies, and trees (Figure 7). The first butterfly trap was installed 30 metres from the tree plots. Dung beetle traps were also installed 30 metres from the tree plots, in the opposite direction (i.e., 100 metres from the first butterfly trap). All sampling sites were separated by more than 500m (range: 0.61-76.08 km; mean: 37.34 km; standard deviation: 26.99 km). All points, except for PRI1 and PRI2 (see previous paragraph), were more than 100m from the edge of the correspondent forest category (range: 0.018-3.21 km, mean: 1.24 km, standard deviation: 0.92 metres). Site location was georeferenced with a Garmin GPSMAP 64s.

4.3.2. Dung beetle sampling

Dung beetles (Scarabaeidae) were sampled, using baited pitfall traps, in May-July 2017 with replication in October-December 2017, covering the peaks of the wet and dry seasons in order to account for seasonality (Korasaki et al., 2013). I sampled a total of 24 sites, six sites in each of the four forest uses under analysis. Each sampling unit consisted of three traps placed three meters apart in a triangular arrangement. Traps were collected after 24h. Previous studies have shown that 24h sampling periods for dung beetles produce reliable biodiversity metrics (e.g., França et al., 2016). Trap configuration consisted of a rain cover (plastic plate with 25.5 centimetres diameter, placed 16 centimetres from the ground), from which a meshed nylon bag containing the bait was suspended, directly above a buried plastic container (13 centimetres height x 11.5 centimetres diameter). A third of the container was filled with salted water. The bait used was human dung (~30g), which has proven to be effective bait for dung beetles (Marsh et al., 2013). Specimens were stored in alcohol at 70%. After triage by morphospecies using an available taxonomic key (Vaz-de-Mello et al., 2011), the material was sent to the Federal University of Pará, where taxonomist Prof. Fernando Barbosa corrected and validated the species identification list.

4.3.3. Butterfly sampling

Frugivorous butterflies (Nymphalidae) were sampled using fruit-baited cylindrical traps (van Someren-Rydon traps), following established guidelines (Lucci-Freitas et al., 2014; Van Swaay et al., 2015). Fieldwork took place between May-July 2017 and was replicated between October-December 2017, to account for seasonal fluctuations (Hamer et al., 2005). Each sampling unit consisted of a linear transect with four traps separated by 30 metres. The base of the traps hung between 1 m and 1.5 m above the ground. The bait was banana fermented for 48h. Six sampling units were installed in each of the four forest uses under analysis. After installation, traps remained set for six days and were visited every 48h to replace the bait and record the individuals captured. In total sampling effort was equivalent to 1152 trap-days (288 per forest use). Each captured individual was identified, photographed with a macro lens, marked with a black or silver sharpie, and released. At least one voucher specimen per species was retained as reference. The collected individuals were sent to State University of Campinas in São Paulo, where their identification was verified by the team of Prof. André Lucci Freitas. Recaptures were not used in the analyses to avoid overestimating butterfly abundance (Ribeiro et al., 2008). The main identification references used were Warren et al. (2013); Nield (1996, 2008), and D’Abrera (1987, 1988).

4.3.4. Tree sampling

Trees with diameter at breast height (DBH) equal or above to 10 centimetres were sampled in 0.4ha plots (100x40m). Sampling was conducted between July and October 2017. Plot establishment followed the guidelines from Phillips et al. (2016). Six plots were set in each forest use under analysis, totalling 24 plots. The plots were first stringed, and then coordinates, elevation and slope were registered at each plot corner and its centre. Each plot took around 2 days to sample, except for eucalyptus plantations, where it was faster. Plot orientation was equally divided between N-S and E-W. All trees with DBH≥10cm within the plot were measured and tagged. Voucher photos were taken of each species with a small cut in the trunk and leaf close-up when available. The height of 10 trees per DBH class (10-20 cm; 20-30 cm; 30-50 cm; >50 cm) was measured with a clinometer. When buttresses prevented the measurement of DBH, tree diameter was calculated using digital camera photos, as described in Phillips et al. (2016). Lianas with DBH≥10cm were excluded due to uncertainty in their taxonomy and would have added 65 individuals with 12 different common names to the dataset. Species identification was carried out by three experienced local parataxonomists, two of them trained by Jari Florestal. Common names were converted to scientific names using Jari Florestal’s species list developed for the local tree community.

4.3.5. Data analysis

Species richness was compared between the four forest uses sampled using individual-based species accumulation curves with 95% confidence intervals (Gotelli and Colwell, 2001). Since observed species richness is likely to be underestimated (Brose et al., 2003), I used the species richness estimator JACK2 to estimate the actual species pool in each forest type sampled. Community structure was measured using Bray-Curtis dissimilarity index. Coefficients of association between different biodiversity indicators or taxa were calculated with Spearman's rho, a rank-based measure of association, except for community structure, which used the Mantel statistic to calculate the Spearman correlation between two dissimilarity matrices. Species diversity was measured using Simpson’s index of diversity. Species-rank abundance distributions are plotted in Figure C1 (Appendix C).

Non-metric multidimensional scaling (NMDS) was conducted to represent the patterns of assemblage composition in the insect taxa sampled. A tree NMDS was not carried out due to the artificial tree composition in plantations. Kruskal-Wallis rank sum chi-squared tests were conducted for each taxon to test whether their richness and abundance exhibit the same distribution in each forest use. This was followed by Dunn's z test for pairwise comparisons between forest uses with a Holm p-value adjustment to correct for multiple comparisons. Kruskal-Wallis test was also used to test for homogeneity of observed species abundance distributions between forest uses (Table C2 in Appendix C). Analysis of similarities (ANOSIM) was used to test for differences in community structure between forest uses.

To further assess if variation in species richness and abundance between forest uses can be explained by natural variation rather than forest use, I developed generalised linear models (GLM) on the relationship between richness/abundance and forest use plus three environmental variables: slope, elevation, and sand percentage in the soil. Soil texture can influence dung beetle communities and soil sand percentage has been used as its indicator, due to the high correlation with silt and clay concentrations (Gries et al., 2012). That correlation was observed in the soils sampled for this study (rho coefficients of -0.846 and -0.928 for sand/clay and sand/silt, respectively). I also maintained sand percentage in the soil as an explanatory variable in the models for trees and butterflies due to the known influence of soil on forest structure and dynamics (Quesada et al., 2012) (Table C3 in Appendix C). Furthermore, I performed an analysis of variance (ANOVA) to assess if the models with forest use plus the three environmental variables as predictors significantly explained more variance than the same models with forest use as the only explanatory variable (see Table C4 in Appendix C).

Species preferences for specific forest uses were assessed, using package 'indicspecies', through indicator species analysis, which measures the association of individual species to one or a combination of forest uses (De Cáceres et al., 2010). These associations were tested using a permutation test with a stricter threshold for significance of 0.01, so that only the stronger associations are considered (Table C1 in Appendix C).

I include in Appendix C plots to help characterise the different forest uses sampled (Figure C5 in Appendix C). The plots show variance between forest uses in four factors: canopy openness, distance to road, deforestation within 5km, and fire occurrences within 5km. Canopy openness was measured with CAN_EYE (Weiss and Baret, 2017) and the angle of view of the lens used to obtain the images was 83°. The share of canopy cover was obtained by averaging the values from seven images for each sampling each, six of them equally separated along the limits of the tree plots and the additional one at the centre of the plot. The other three factors were calculated in ArcGis 10.3. Data on fire occurrences was obtained from MOD14A1 (NASA MODIS).

All fire occurrences within a 5km radius since the start of the dataset in 2000 were counted for each sampling site. Deforestation within a 5km radius of each sampling point was obtained from the INPE PRODES dataset up to 2017. The data to calculate distance to the nearest road in each sampling point was obtained from the forestry company, Jari, which manages the plantation and RIL areas. This road data is more detailed than the equivalent from the Brazilian government, because it includes logging roads, some of them rarely used and not regularly maintained.

To consider spatial autocorrelation between sampling sites, three different approaches were used. Mantel correlograms (Legendre and Legendre, 2012) were used to visualise the correlation structure between community dissimilarity and distance between samplings points, within each forest use (Figure C3 in Appendix C). The values for the distance matrix indicating the shortest geodesic distance between each sampling point were calculated in ArcGis 10.3. I also calculated the overall correlation coefficient, using the Mantel test, between the dissimilarity and distance matrices. Finally, Moran's I autocorrelation coefficient was calculated using package ‘ape’.

In order to assess if the results are robust and resistant to any inaccuracy in species level identification, the analysis was repeated at genus level, with similar results to those shown. The number of genus across sites is highly correlated with species richness for all taxa analysed (Butterflies: rho= 0.96; Dung beetles: rho= 0.86; Trees: rho=0.95). Figure C1 (Appendix C) shows rank abundance curves both at species and genus level.

Unless stated otherwise, all analysis was conducted in R3.4.3. (R Core Development Team, 2017) in packages ‘vegan’ and ‘stats’. All plots were created using ‘ggplot2’. In the results and discussion sections, I use the following abbreviations for each forest use: PRI- old-growth forest; BN- Brazil nut extraction areas; RIL- reduced impact logging areas; and PLA- eucalyptus plantations.

4.4. Results

4.4.1. Richness and abundance analysis

Table 7. Observed species richness (S_obs), estimated species richness (S_est), abundance (N), and Simpson's index of diversity (1-D), per taxon and forest use. PRI: old-growth forest; BN: Brazil nut extraction areas; RIL: reduced impact logging areas; and PLA: eucalyptus plantations.

	Butterflies				**Dung beetles**				**Trees**			
	S_obs	S_est	N	1-D	S_obs	S_est	N	1-D	S_obs	S_est	N	1-D
PRI	42	62	334	0.950	38	51	262	0.937	216	324	1076	0.986
BN	50	62	415	0.948	24	37	236	0.845	156	231	1076	0.974
RIL	44	61	317	0.913	29	43	215	0.909	163	246	938	0.974
PLA	37	61	806	0.824	19	32	110	0.851	2	4	2584	0
Total	78	100	1872	0.946	59	86	823	0.949	287	409	5674	0.789

I sampled a total of 1872 butterflies of 78 different species (Table 7), from the subfamilies Charaxinae (tribes Preponini and Anaeini), Biblidinae (tribes Catonephelini, Ageroniini, Epiphelini), Nymphalinae (tribes Nymphalini, Coeini, Junoniini), Satyrinae (tribes Satyrini, Brassolini, Morphini). Butterfly species richness was 42 in old-growth forest (PRI). It increased to 50 in Brazil nut extraction areas (BN) and to 44 in the reduced impact logging (RIL) areas but decreased to 37 in the eucalyptus plantations (PLA). Differences in richness were significant between BN and PLA (z= 3.37, p-value< 0.001). Butterfly abundance was significantly different between plantations and all other forest uses, BN (z= -2.29, p-value= 0.044), RIL (z= -3.41, p-value= 0.002), and PRI (z= 3.12, p-value= 0.004).

For dung beetles, I sampled 823 individuals of 59 different species (Table 7), from tribes Ateuchini, Delthochilini, Coprini, Oniticellini, Onthophagini, and Phanaeini. Dung beetle species richness was 38 in the old-growth forest. It decreased to 24 species in BN and 29 in RIL and was the lowest in PLA with 19 species. PLA-RIL (z= 2.84, p-value=0.011) and PLA-PRI (z= -2.92, p-value= 0.01) were the only forest use pairs with significant differences for dung beetle richness. Pairwise post-hoc testing indicates a difference in mean abundance between PLA and PRI (z= -2.47, p-value= 0.04).

I sampled 5674 trees belonging to 287 different species and 48 different families (Table 7). As expected, intensive eucalyptus plantation sites had negligible levels of tree species richness. Old-growth forest sites had the highest number of species (216), which decreased to 156 in BN sites and 163 in RIL sites. Post-hoc pairwise tests identified significant differences for tree richness between PLA-PRI (z= -4.02, p-value<0.001) and PLA-BN (z= 2.67, p-value= 0.019). Mean tree abundance was the highest in eucalyptus plantations with considerable variation between plantation sites (mean= 430.7, standard deviation= 66.2), due to the higher occurrence of trunks with DBH<10cm in some sites (see Figure C2-a, Appendix C). Differences in tree abundance were significant for PLA-RIL (z= -4.21, p-value<0.001) and PLA-PRI (z= 2.47, p-value= 0.034).

Prior to the post-hoc pairwise testing between forest uses indicated above, a non-parametric Kruskal-Wallis rank sum test confirmed that abundance levels showed significant variation among forest uses for butterflies (χ^2= 14.33, p-value= 0.002) and trees (χ^2= 17.79, p-value< 0.001), but not for dung beetles (χ^2= 6.50, p-value= 0.0897). The test also confirmed forest use affects species richness in butterflies (χ^2= 11.60, p-value= 0.009), trees (χ^2= 16.73, p-value< 0.001), and dung beetles (χ^2= 11.34, p-value=0.010). Considering abundances at species level (Table C2, Appendix C), 20.3% of dung beetle species had significant differences between forest uses, as well as 33.3% of the butterfly species, and 22.6% of tree species, including the Brazil nut tree *Bertholletia excelsa* (χ^2= 9.45, p-value= 0.024).

When the influence of forest use on abundance and richness was modelled in combination with additional environmental variables as predictors, namely slope, elevation, and sand percentage in the soil, none of the environmental variables was significantly related to the respective response variables (Table C3, Appendix C). The non-significant effects of the selected environmental variables on the species richness and abundance of the three taxa sampled are also supported by the absence of a significantly better fit when comparing the full models with the simpler models without environmental variables (Table C4, Appendix C). The full models also allow to compare abundance and richness levels between the forest uses, using PRI as reference category, while adjusting for the three environmental variables used. This has allowed to confirm all significant differences involving PRI that were identified in the previous paragraphs using Dunn's z test. The adjusting of the model with the three environmental variables additionally identified a significant difference in butterfly richness between PRI and BN, as well as in tree richness for the PRI-BN and PRI-RIL forest use comparisons.

The trends captured by the different biodiversity metrics and taxa considered were not necessarily always congruent. For example, the relationship between abundance and species richness depended on the taxa considered (butterflies: rho=0.0, p-value=0.998; dung beetles: rho= 0.79, p-value<0.001; trees: rho=-0.43, p-value=0.037). Analysis between abundance and diversity showed that more trees, were correlated with lower diversity (rho= -0.59, p-value=0.002), while that was not the case for dung beetles (rho= 0.61, p-value= 0.002) or butterflies (rho= -0.40, p-value=0.056).

4.4.2. Comparison among forest uses

Species accumulation curves (Figure 8) started to stabilise but did not plateau, indicating actual species richness was higher than sampled, as confirmed by the differences between observed and estimated species richness in Table 7. Different taxa showed different responses in terms of species richness. Old-growth forest registered, as expected, the highest estimated richness when considering trees and dung beetles, but for butterflies there were no distinguishable differences with other forest uses.

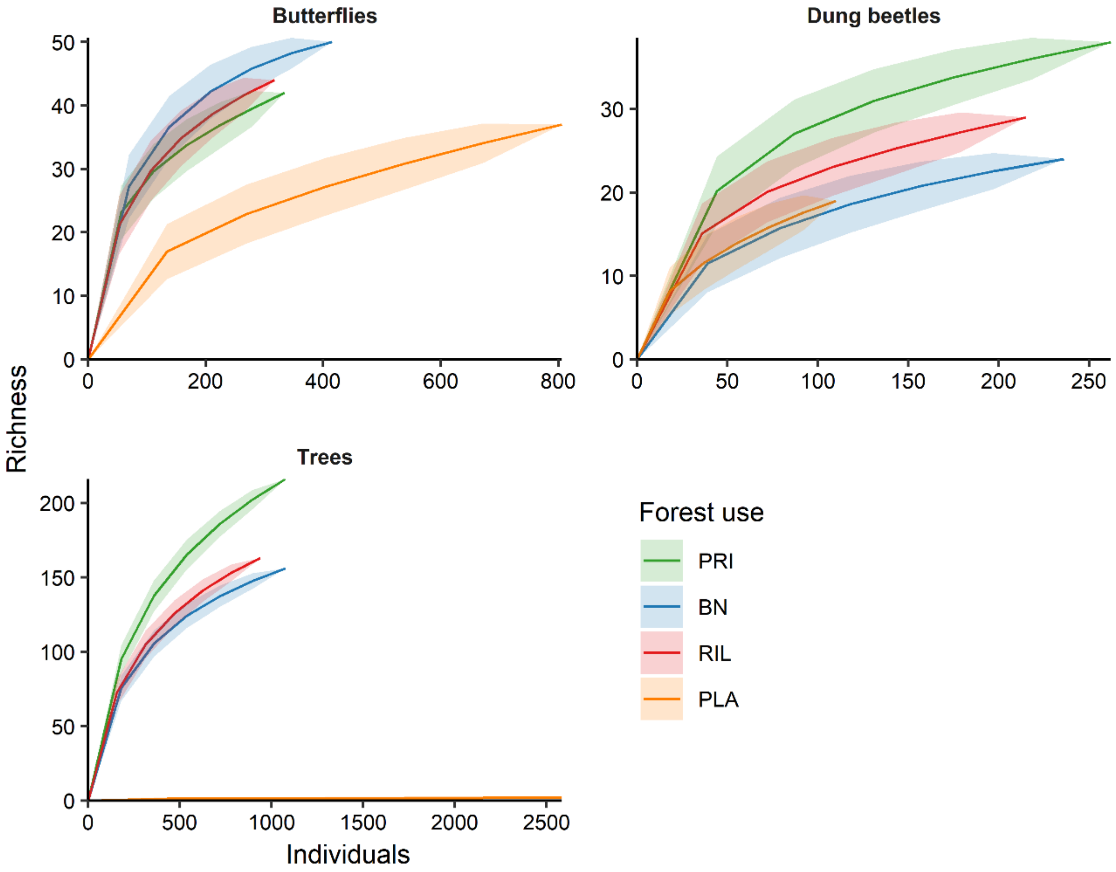

Figure 8. Individual-based species accumulation curves, per forest use, for sampled butterflies, dung beetles, and trees. PRI: old-growth forest; BN: Brazil nut extraction areas; RIL: reduced impact logging areas; and PLA: eucalyptus plantations.

Ordination diagrams, obtained through a distance-based method (NMDS), for dung beetles and butterflies (Figure 9) provide visual representation of the similarity of communities in BN, old-growth, and RIL forests, while eucalyptus plantations form an independent cluster. Nevertheless, an analysis of similarities (ANOSIM) to test, within each taxon analysed, differences in community structure between forest uses, returned significant differences for all pairwise combinations considered, except between BN and PRI in trees (R= 0.14, p-value= 0.11).

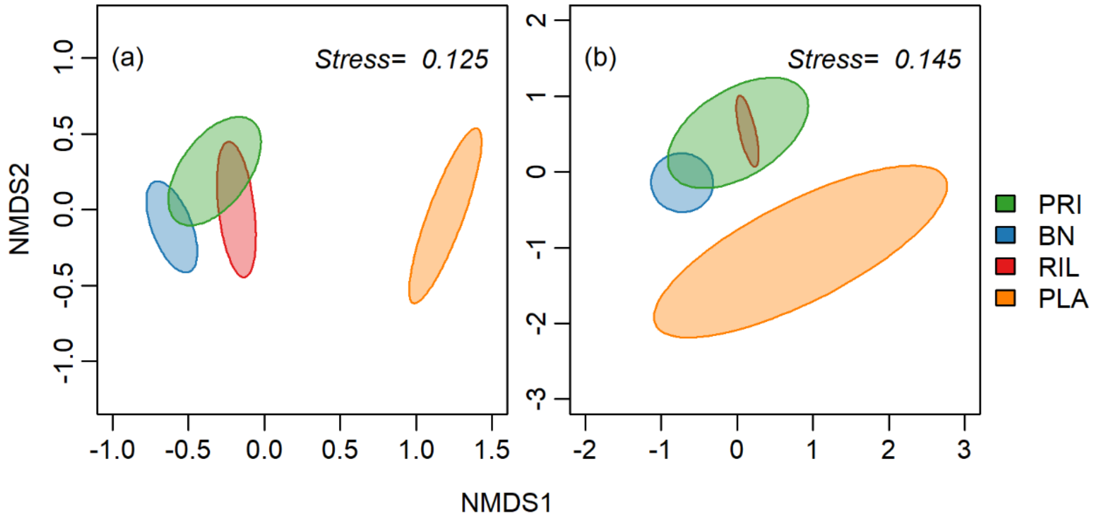

Figure 9. NMDS site ordination diagrams for (a) butterflies and (b) dung beetles. The ellipses are convex hulls that enclose all points within the same forest use. Trees were not included due to the tree species composition in eucalyptus plantations. PRI: old-growth forest; BN: Brazil nut extraction areas; RIL: reduced impact logging areas; and PLA: eucalyptus plantations.

4.4.3. Congruence among taxa

Cross-taxon congruence between beetle and butterfly richness or abundance is low (Table 8). There is however a positive correlation between both the insect taxa and tree richness. The higher abundance of both butterflies and trees in eucalyptus plantations contributes to the positive correlation of their abundance, while the relationship is reversed between tree and dung beetle abundance. The impact of plantations in these results was confirmed by removing plantation data from the analyses, which resulted in no significant cross-taxon relation for both richness and abundance. Variation of community structure across sites was highly positively correlated between all taxa (Table 8).

In order to further explore the relation between the insect taxa and trees, I also considered the correlation of insect abundance and richness with other tree metrics (tree density and tree basal area), which confirms that butterflies were more abundant in areas with lower tree basal area (rho= -0.72, p-value<0.001) and higher tree density (rho= 0.61, p-value= 0.002), while dung beetle communities were richer in forests with the opposite characteristics (tree basal area: rho= 0.61, p-value= 0.002; tree density (rho= -0.49, p-value=0.015).

Table 8. Pairwise correlation across sites, for species richness, abundance, and community composition, between the different taxa analysed. Correlation coefficients for richness and abundance were calculated using Spearman rho. Composition was determined with the Mantel statistic, also using a Spearman correlation.

	Dung beetles	**Butterflies**
	Richness	
Butterflies	0.064	
Trees	0.503*	0.414*
	Abundance	
Butterflies	-0.320	
Trees	-0.412*	0.609**
	Community structure	
Butterflies	0.748***	
Trees	0.731***	0.870***

Notes: *** p-value ≤ 0.001; ** p-value ≤ 0.01; * p-value ≤ 0.05

4.4.4. Species unique to each forest use

The analysis of old-growth forest species shared with other forest uses shows similar patterns across taxa, with plantations having the lowest amount of species also occurring in old-growth forest (Figure 10-a). Butterflies in BN areas show the highest ratio, with more than 80% of species in old-growth forest also occurring there. Old-growth forest had the highest share (more than 20%) of unique dung beetle species sampled, in contrast with the response observed for butterflies, where old-growth forest had the lowest share of unique species. Plantations registered the second largest share of unique species for both insect taxa (Figure 10-b).

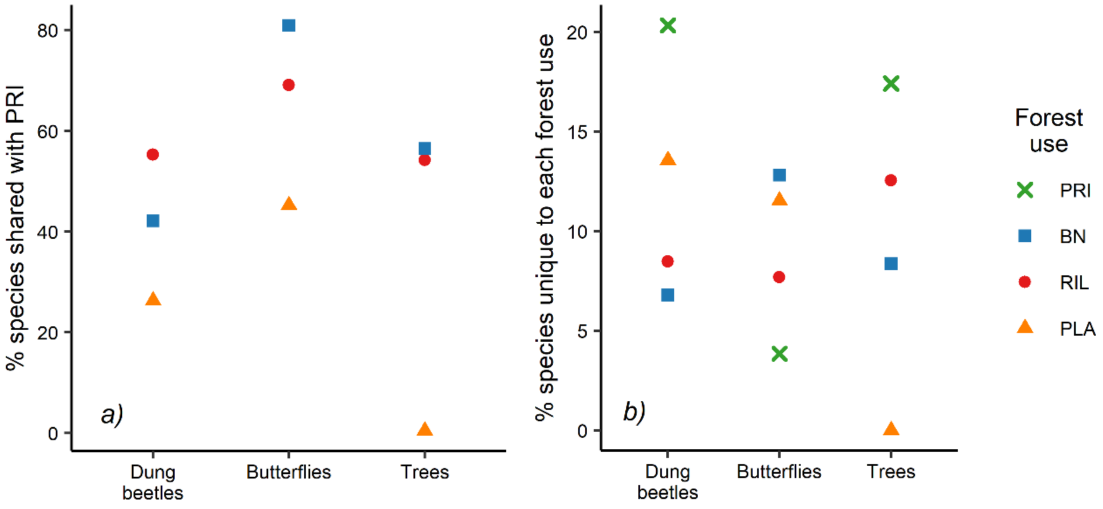

Figure 10. Species uniqueness between forest uses. a) Percentage of species shared between pristine forest and the other forest uses, per taxon; b) Percentage of species unique to each forest use in relation to observed taxa richness. PRI: old-growth forest; BN: Brazil nut extraction areas; RIL: reduced impact logging areas; and PLA: eucalyptus plantations.

4.4.5. Seasonal effects

A comparison of the dung beetles and butterflies sampled, across all sites, in the wetter and drier seasons showed distinct seasonal trends (Figure 11), with butterflies showing significantly higher levels of abundance (χ^2= 14.494, p-value< 0.001) and richness (χ^2= 5.82, p-value = 0.016) in the wetter season, while for dung beetles the differences between seasons were not significant. Sites with higher butterfly richness (rho= 0.590, p-value= 0.002) and abundance (rho= 0.454, p-value= 0.026) were roughly the same in both seasons, while for dung beetles that correlation was not significant for richness (rho= 0.399, p-value= 0.054) nor abundance (rho= -0.099, p-value= 0.644). Plantations accounted for most of the increase in butterfly abundance in the wetter season (Figure C4 in Appendix C).

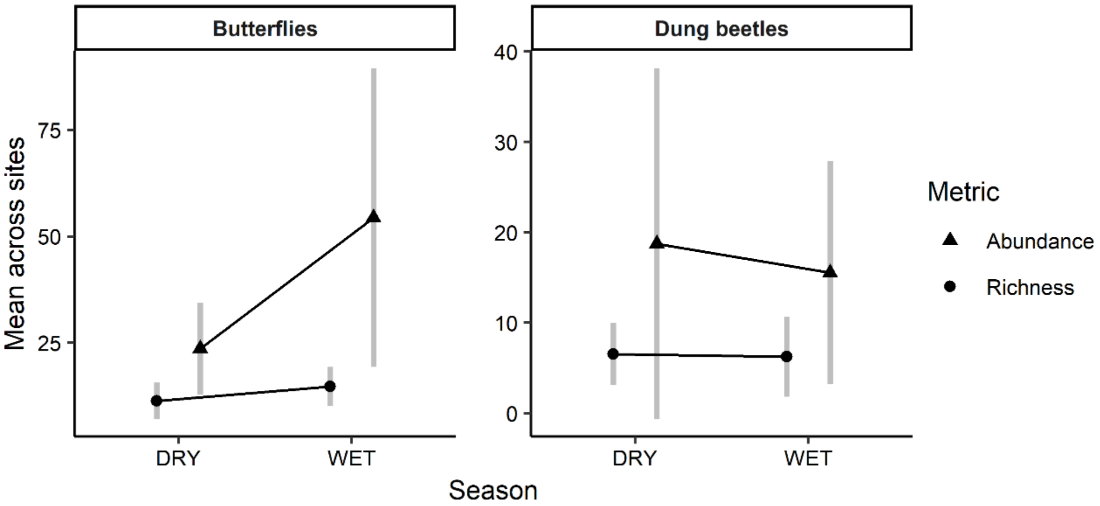

Figure 11. Seasonality in species richness and abundance for butterflies and dung beetles across sampling sites. Vertical grey lines represent standard deviation.

4.4.6. Spatial autocorrelation

Spatial autocorrelation among sampling sites was considered from different perspectives. Mantel correlograms representing variation of the dissimilarity indices with distance between sampling sites within the same forest treatment offered little evidence of within forest use autocorrelation, with most relations fluctuating around zero with non-significant coefficients (Figure C3 in Appendix C). However, when just computing correlations between community dissimilarity matrices for each taxon and a plot distance matrix, it showed significant positive correlations for butterflies (r= 0.32, p-value= 0.001), dung beetles (r= 0.25, p-value= 0.001), and trees (r= 0.33, p-values= 0.002). Finally, I also calculated the Moran's I autocorrelation coefficient for abundance and richness of the three taxa sampled. The null hypothesis of zero spatial autocorrelation was rejected for butterfly richness (I= -0.25, p-value< 0.001) and for tree richness (I= -0.18, p-value< 0.001) and abundance (I= -0.14, p-value= 0.02). The negative sign suggests dispersion is relatively higher than what would be expected in a random spatial configuration.

4.5. Discussion

4.5.1. Response to forest use change

This study provides further evidence of how communities of dung beetles, fruit-feeding butterflies, and trees respond to forest management regimes with widespread occurrence in the Amazon. Results also show generally similar trends between taxa, with Brazil nut extraction areas and selective logging areas sustaining richness levels slightly lower than old-growth forests, except for butterflies, while communities in eucalyptus plantations were less diverse, although still retaining considerable conservation value. Species accumulation curves, pairwise testing of the mean differences in abundance and richness between forest uses and ordination analysis all confirm the substantial gap between plantations and the other uses analysed.

This study supports conclusions reached by previous works, namely that (i) forest disturbance reduces biodiversity in tropical forest landscapes (Barlow et al., 2016; Gibson et al., 2011), (ii) selectively logged forests retain considerable conservation value (Berry el al., 2010; Edwards et al., 2014b), and (iii) eucalyptus plantations are not necessarily devoid of biodiversity (Barlow et al., 2007a; Gardner et al., 2008). Additionally, results also indicate that Brazil nut extraction areas retain levels of diversity similar to selective logging areas, in contrast to what is suggested by Gibson et al. (2011), where impacts of the ambiguously defined category “other extracted forests” are closer to agroforestry or plantations.

The impact of selective logging and plantations on dung beetles is relatively strong when compared with other studies (Berry et al., 2010; Gardner et al., 2008; Nichols et al., 2007). The reduction of observed richness in BN areas is also relatively strong, falling in the lower end of the range for agroforestry in Nichols et al. (2007). BN and RIL had similar levels of species richness. Trees showed a similar pattern to dung beetles, but with the obvious loss of diversity in eucalyptus plantations. Butterflies were the exception to the general trend, with richness numbers in moderate and intensive uses very close to those of intact forests, a response to disturbance that has been found in other butterfly studies (Fermon et al., 2005; Sant’anna et al., 2014), although it differs from what Barlow et al. (2007b) found for secondary forests in the same region.

More relevant for conservation than total variation in richness is to understand how many species present in intact areas are retained in other forest uses, as these species tend to be more specialised and vulnerable to change (Fermon et al., 2005; Sodhi et al., 2010a). When considering the percentage of species that are unique to each forest use, values were generally low. Barlow et al. (2007a) found ca. 22%, 32%, and 57%, of butterfly, dung beetle, and tree species, respectively, occurring only on old-growth forests, while here those values were 4%, 20%, and 17%. These lower values reflect the closer similarity between communities in old-growth forests and the moderate use forests studied here and absent in Barlow et al. (2007a). Analysing species uniqueness from a different perspective, Barlow et al. (2007a) found that ca. 60% and 42% of butterfly and dung beetle species occurring in old-growth forests were shared with plantations, while results here indicated 45% and 26%, respectively. Other studies have also reported relatively higher levels of shared species than those found here (Berry et al., 2010; Edwards et al., 2014b; Nichols et al., 2007). The high mean distance between sampling points in this study might be a contributing factor to that difference. It is also interesting to note that the share of old-growth forest species occurring in other forest uses is always higher for butterflies than dung beetles likely reflecting their higher mobility. The considerable share of unique insect species in plantations should mostly include species better adapted to the conditions found in open habitats (Gardner et al., 2008; Hamer et al., 2003). An indicator species analysis (Table C1, Appendix C) confirmed that some species sampled are associated with particular forest uses. No dung beetle species was characteristic of plantations, but that was the case for seven out of the 19 indicator species identified in butterflies.

In overall, the levels of species richness sampled here, especially when estimated richness is considered, were reasonably similar to those found in previous studies, with higher sampling efforts, done in the same region. Barlow et al. (2007b) sampled 128 butterfly species, while total estimated richness here was 100. Gardner et al. (2008) sampled 85 dung beetle species, while in this study the estimated richness was 86. Barlow et al. (2007a) sampled trees and lianas in the region at genus level, finding 219 genera, while this study only sampled 162 genera, excluding lianas. However, the tree sample in this study, which points to 171 species ha^{-1} if plantations are excluded, does not seem underestimated when compared with the mean 152 tree species per hectare in South American forests estimated by Sullivan et al. (2017).

Abundance of the two insect taxa analysed showed contrasting trends. Dung beetle abundance decreased gradually from old-growth forests to moderate use areas and dropped considerably in plantations. This is in line with results for the same region (Gardner et al., 2008), but differs from other studies (Berry et al., 2010; Nichols et al., 2007). Gardner et al. (2008) points to differences in biogeographical context and landscape-level effects between different studies as possible explanations for the discrepancy. Butterfly abundance more than doubled in plantations in relation to old-growth forests, while in a previous study for the same region it had more than quadrupled (Barlow et al., 2007b). This was mostly driven by a few species of subfamilies Nymphalinae and Satyrinae that became hyper-abundant in plantations (Figure C4, Appendix C), due to their high tolerance to disturbance (Barlow et al., 2007b; Fermon et al. 2005).

4.5.2. Congruence between taxa

Several multitaxon studies considered potential cross-taxon congruence (e.g., Barlow et al., 2007a; Edwards et al., 2014b). In fact, the search for a taxon that can accurately predict the responses of multiple other taxa is not new (e.g., Kremer, 1992). However, while those relations have been found for some groups, results have generally found idiosyncratic responses to disturbance that prevent focusing on a unique indicator (Gardner et al., 2009). Even lower taxonomic levels, such as butterfly subfamilies, might exhibit distinct responses (Barlow et al., 2007b; Hamer et al., 2003). Nevertheless, results here point towards trees being the best indicator of all the taxa analysed, as it is the only taxon whose variations in richness, abundance, and composition, are significantly correlated with all the other taxa analysed (Table 8). This is expected since both dung beetles and butterflies respond to changes in vegetation structure (Hamer et al., 2003; Gardner et al., 2008). Trees have been identified as good indicators of community change in other studies (Bobo et al., 2006; Philpott et al., 2008; Schulze et al., 2004), although they are not necessarily better suited as indicators than other taxa (Barlow et al., 2007a; Kessler et al., 2009). The positive correlation between dung beetle and tree richness was identified in a previous study in the same region, as well as the high correlations in community structure between dung beetles, trees, and butterflies (Barlow et al., 2007a). Additionally, here I also report significant associations for abundance between trees and the insect taxa (with contrasting directions) and a positive association between tree and butterfly richness (Table 8).

Seasonality effects might lead to low annual intra-taxa congruence in biodiversity sampling (Hamer et al., 2005). Here I found no evidence of richness or abundance seasonality in dung beetles across all forest uses, but both butterfly richness (χ^2= 5.82, p-value= 0.016) and abundance (χ^2= 14.94, p-value< 0.001) were significantly higher in the wet season. These increases were steeper for plantations (Figure C4, Appendix C). This variation might reflect natural inter-annual variation in community dynamics (Beiroz et al., 2017), but also be related to differences in community structure in each forest use (Barlow et al., 2007a). Indeed, the increased abundance in plantations registered here was mostly driven by a few species of Satyrinae (e.g., *Paryphthimoides* *sp.*) and Nymphalinae (e.g., *Hamadryas feronia*) that were rare or absent in the other forest uses.

4.5.3. Caveats and limitations

It is relevant to highlight that the results presented here apply to a forest human-modified landscape not only containing considerable pools of intact forest but also largely surrounded by it. Therefore, extrapolating these results to landscapes under larger scale intensification processes should be avoided, due to potentially differentiated impacts of fragmentation and spill-over effects (Gardner et al., 2008; Korasaki et al., 2013; Nichols et al., 2007).

While I consider the data collected is representative of forest use conditions in the study area, the results should be interpreted with caution. Further sampling could particularly clarify the similarities and differences between communities in reduced impact logging and Brazil nut extraction areas. Still, the levels of species richness found here compare reasonably well to those found in previous studies in the same region with higher sampling efforts (Barlow et al., 2007a; Gardner et al., 2008; Sullivan et al., 2017). Environmental factors, such as climate, slope, and elevation, were relatively similar between all sampling points, leading me to suggest that the reported differences in species richness and abundance are a consequence of forest use intensity. Nevertheless, this study cannot exclude the possibility that those changes are being driven by unknown natural biotic or abiotic factors. Different forest use intensities can lead to variation in the occurrence of logging, hunting, or fire events, which indeed greatly affect natural communities in tropical forests (Barlow et al., 2016; Brodie et al., 2015). These disturbances have an impact on environmental factors such as canopy cover, canopy height, or resource availability, which also have an effect on the communities of the taxa sampled (Barlow et al., 2007a; Cajaiba et al., 2017; Darrigo et al., 2016; Hamer et al., 2003). However, this study focuses on analysing the response to the forest use categories considered and does not intend to identify the specific factors that are driving that variation.

It should also be noted that the analysis was not corrected for the negative spatial autocorrelation detected for butterfly and tree richness and tree abundance, which I interpreted as a consequence of the spatial configuration of the sampling points (see Figure 7).

4.5.4. Implications for forest management

This study demonstrates that both RIL and BN areas have high conservation value when inserted within a landscape matrix integrating substantial levels of intact forest. In fact, both these moderate forest uses seem to retain communities closer to those found in intact forests than the secondary forests that also occur within the same landscape (Barlow et al., 2007a; Gardner et al., 2008). This implies that the allocation of a larger share of resources to the promotion and development of moderate forest use regimes that are able to prevent deforestation on the long term could benefit conservation at landscape scale. Biodiversity-friendly forest uses increase the probability of reaching sustainable landscapes where people and forests are able to coexist on the long-term (Melo et al., 2013) and also facilitate the effective implementation of Brazilian law (Law 12.651/2012), which requires that at least half, and up to 4/5, of every rural estate in the Amazon region should preserve its forest cover.

Intact forests are irreplaceable (Gibson et al., 2011) and their protection is highly dependent on the establishment of effective integral protected areas (Gray et al., 2016). Nevertheless, sustainable use forests can be relevant as part of an extended network of protected areas, providing viable corridors for movement between undisturbed areas or functioning as buffers that prevent forest encroachment (Bhagwat et al., 2008; McNeely and Schroth, 2006). Having clusters of intact forest within human-modified landscapes increases system resilience and is fundamental to keep the species pools that can recolonise regenerating forests (Melo et al., 2013; Oliver et al., 2015). In contrast, disturbed forests might provide unstable, and poorly known, ecological conditions due to nonlinear dynamics, threshold effects, and higher frequency of disturbance events, which might have unexpected impacts even on species that currently seem to be tolerant to some disturbance (Barlow et al., 2016; Gardner et al., 2009).

4.6. Conclusions

This study demonstrates that increased forest use intensity is likely to cause negative effects on the communities of trees, dung beetles, and fruit-feeding butterflies of eastern Amazon. It therefore highlights the importance of preserving old-growth forests. Nevertheless, it also shows that biodiversity loss under extractive forest uses that introduce moderate disturbance can be relatively low, when part of a landscape matrix with a substantial share of undisturbed forest. The two moderate uses analysed here, Brazil nut extraction and reduced impact logging, both seem to hold similar conservation value for the taxa studied and retain communities that are relatively close to those in old-growth forests, while intensive eucalyptus plantations have higher impact on biodiversity. Results also indicate that studies considering multiple taxa and biodiversity metrics are more likely to provide an appropriate perspective of how communities respond to disturbance in tropical forests. Therefore, this study suggests that sustainable forest use management entails safeguarding a healthy matrix of undisturbed forest and should take advantage of the potential of moderate forest uses to conciliate economic considerations and biodiversity conservation.

Data availability

The datasets used in this chapter are available at http://discovery.ucl.ac.uk/10070652

Chapter 5: Linking biodiversity and multifunctionality in a tropical forest landscape

5.1. Abstract

Land use intensification is increasing the vulnerability of human-modified forest landscapes to anthropogenic disturbance and forest degradation. This results in biodiversity loss with poorly understood consequences for the capacity of tropical forests to provide multiple ecosystem services with benefits to humans. A relationship between biodiversity and multifunctionality (i.e., simultaneous provision of multiple ecosystem services) has previously been identified, but mostly limited to controlled experiments or less biodiverse temperate ecosystems. Here, I measured biodiversity using species richness and the simultaneous provision of five ecosystem services in 24 sampling sites along a gradient of forest use intensity in Eastern Amazonia. The four forest uses sampled were old-growth areas, Brazil nut extraction, reduced-impact logging, and eucalyptus plantations. Using GLMs and path analysis, I modelled the impact of tree richness loss on the provision of individual ecosystem services and on overall forest multifunctionality. Multifunctionality levels were higher under moderate or low intensity forest uses that preserve higher tree richness. I also found that indirect effects mediated by biodiversity loss were on average at least as severe as direct effects of forest use intensification on multifunctionality.

5.2. Introduction

Land use intensification continues to drive the disappearance of natural forests in Latin America (De Sy et al., 2015). Landscapes managed to prioritise provisioning ecosystem services (ES), often do so at the expense of other services (Howe et al., 2014). The recognition of these trade-offs is important for conservation strategies (Adams et al., 2004). However, productive goals and natural forests are not necessary incompatible, particularly at landscape scale (Tscharntke et al., 2005). Under the right set of regulations and management, tropical human-modified landscapes with high forest cover can reconcile provisioning services with biodiversity conservation and the supply of other ecosystem services (Melo et al., 2013). It is also at this scale that the preservation of a matrix of well-connected reservoirs of healthy habitat is most relevant for biodiversity conservation (Gardner et al., 2009; Loreau et al., 2003; Melo et al., 2013). Furthermore, when multiple services provided by forest landscapes are valued, the simplification of forests for intensified uses becomes less likely (Law et al., 2017).

However, until recently there was little evidence of how biodiversity relates to the simultaneous provision of multiple ecosystem services (Balvanera et al., 2014; Tscharntke et al., 2005). Several studies over the last few decades have made it increasingly clear that biodiversity loss can affect individual ecosystem processes and services, leading to the conclusion that healthy ecosystems help maintain the flow of several services that people value (Cardinale et al., 2012; Hooper et al., 2005). This is also the case when focusing specifically on forests (Thompson et al., 2011). There are also several lines of evidence that the impact of biodiversity change can be stronger when multiple functions are considered simultaneously (Lefcheck et al. 2015).

Multifunctionality can be defined as the capacity of ecosystems to simultaneously provide multiple ecosystem functions and services (Manning et al., 2018; Mastrangelo et al., 2014). The concept is often linked to the larger spatial scales that are relevant for managers, often at the landscape level (Manning et al., 2018). A landscape can be defined as a spatially explicit socio-ecological system, delineated for specific objectives and uses, where different social and ecological actors interact, constrained by biophysical and social processes (Eigenbrod, 2016; Sayer et al., 2013). These processes can be shaped at different scales through trade-offs, synergies, flows, interactions, time lags, and external drivers (Sayer et al., 2013). The multiple uses of forests, including the goods and services they provide, are also valued differently by different stakeholders, leading to trade-offs that reflect different needs and preferences (Sayer et al., 2013).

It is possible to distinguish between multifunctionality linked to ecosystem function, which looks into the simultaneous supply of multiple ecological functions or processes, and multifunctionality linked to ecosystem services, which focuses on the services jointly provided by ecosystems that bring benefits to people (Manning et al., 2018), although some studies have included both services and processes in their measures of multifunctionality (Allan et al., 2015). Either way, any multifunctionality measure will always use a subset of all functions and services co-occurring within ‘real-world’ ecosystems (Manning et al., 2018). The number of functions used and how they are standardised can influence results (Gamfeldt and Roger, 2017; Meyer et al., 2018).

Multifunctionality research suggests that the impact of biodiversity might be underestimated when focusing on its relationship to individual functions and that more species help maintain multiple functions at higher levels (Lefcheck et al., 2015; Soliveres et al., 2016). Higher plant richness, for example, can have a positive impact on multifunctionality and that effect can be stronger as more functions are analysed (Lefcheck et al., 2015). While other studies also reported a stronger effect of biodiversity with more functions added (e.g., Meyer et al., 2018), this result has been contested and might actually just reflect the average effect on each added function (Gamfeldt and Roger, 2017). The particular combination of functions under consideration also can determine the degree to which links with biodiversity exist (Meyer et al., 2018). Nevertheless, multiple species do seem to be required to maintain multifunctionality, even those that seem functionally redundant (Isbell et al., 2011). That conclusion also seems to apply across multiple trophic groups, where their effect on ecosystem functioning can be as strong as the effect of abiotic factors or land-use intensity (Soliveres et al., 2016). Another study also found that land use effects mediated by biodiversity loss can be as strong as the direct impact of land use on multifunctionality (Allan et al., 2015). Most studies focus on the effects of species richness, but other biodiversity metrics, such as functional-trait diversity and community composition, have also been found to influence multifunctionality (Schuldt et al., 2018). Multifunctionality scores implicitly incorporate trade-offs or synergies between services (Byrnes et al. 2014). The occurrence of trade-offs precludes simultaneous maximisation of all functions or services assessed, which might require setting apart areas for biodiversity protection, for example (Meyer et al., 2018).

In this chapter, I analyse the relationship between forest use intensification, biodiversity, and forest multifunctionality. Multifunctionality is calculated based on the capacity of the sampled sites to provide five ecosystem services: timber production, Brazil nut production, carbon storage, soil quality for agriculture, and the cultural value of biodiversity. These links are poorly understood and need to be further integrated into analyses of forest ecosystems (Mori et al., 2017). The specific objectives are to: i) analyse the effect of tree species richness on the supply of individual ecosystem services; ii) analyse the effect of tree species richness on forest multifunctionality; iii) compare the direct effect of forest use intensification on forest multifunctionality with the indirect effect mediated by biodiversity.

5.3. Methodology

This study focuses on the potential supply of five ecosystem services: timber production, Brazil nut production, carbon storage, soil quality, and biodiversity. The measurements for each service are then used to calculate forest multifunctionality. The first two are straightforward provisioning services, likewise for the categorisation of carbon storage as regulating service. In contrast, soil fertility has had different designations in the main ES conceptual frameworks, although always within the regulating category, with the exception of the now obsolete categorisation as a supporting service in the MEA (2003). In TEEB (2010) this service is designated as ‘Maintenance of soil fertility’, ‘Detoxification and purification of soil’ in UK NEA (2011), and in the latest version of the Common International Classification of Ecosystem Services (Haines-Young and Potschin, 2018) this service fits within the group ‘Regulation of soil quality’ and the class ‘Decomposition and fixing processes and their effect on soil quality’. Biodiversity has a complex relationship with the ES framework, not least because of its multiple definitions and metrics, but chiefly due to its impact on multiple ecosystem functions, including services, at different scales (Cardinale et al., 2012; Mace et al., 2012). Here it is treated both as an ecosystem service in itself due to its cultural value, using butterfly and dung beetle richness as indicators, and as a factor that has a direct influence on the ecological processes that contribute to ecosystem services, using tree species richness as an indicator.

5.3.1. Study area

Data collection was conducted in the eastern region of the Brazilian Amazon, around the east-west Amapá-Pará border along Jari River. The region has high forest cover (Almeida et al., 2016) and low human densities (0.46-1.29 people per km^2) (IBGE, 2010). Mean annual rainfall is around 2300 mm, with a wetter season from January to June, and mean temperature fluctuates around 27 ºC throughout the year (INMET, 2018). Soils are predominantly ferralsols and acrisols (IBGE, 2003). Timber production and non-timber forest products are important outputs of the local economy (IBGE, 2017).

5.3.2. Data collection

Sampling occurred in four different local typologies of tree-covered land reflecting a gradient of forest use, from undisturbed areas to moderate and intensive uses. These uses, all with a wide expression in the region, were eucalyptus plantations, reduced impact logging areas, Brazil nut extraction areas, and undisturbed forest. Eucalyptus plantations have a considerable coverage in the region – a total 129,224 ha of land. Organised extraction of Brazil nuts (*Bertholletia excelsa*) occurs mostly in protected areas in the region. Sampling sites for this use were located in RESEX Cajari, a federal-level protected area (IUCN category VI). Reduced impact logging sites sampled a 545,025 ha concession within 10 ha blocks cut for the first time in 2013 or 2014. Old-growth forest sampling sites were located in terra firme (non-flooded) dense forest, half of them in the western part of the study area and closer to eucalyptus plantations and reduced impact logging areas, the other half in the eastern part and closer to Brazil nut extraction areas.

In 24 sampling sites, six per each type of forest use, I sampled communities of frugivorous butterflies, dung beetles, and trees, as well as the soil. Butterfly sampling points consisted of four cylindrical traps placed 30 apart along a linear transect. Each dung beetle sampling point consisted of three baited pitfall traps placed three meters apart from each other. In both cases sampling was conducted twice at the same sites to account for seasonality effects in those communities (Hamer et al., 2005). Trees with diameter at breast height equal or above to 10 centimetres were sampled in 0.4ha plots (100x40m). More details on butterfly, dung beetle, and tree sampling can be found in Chapter 4.

Soil samples were analysed at Embrapa laboratories in Macapá, Amapá. For each site the combined sample, collected with a soil auger for the 0-10cm layer, consisted of a soil mixture from five subplots separated 50m along a linear transect. Slope and elevation were also measured at each site through the use of a Haglöf EC-II electronic clinometer and a Garmin GPSMAP 64s, respectively. For both variables the plot level values average seven measurements taken at the centre and borders of the tree plots. All sampling sites were separated by more than 500m (range: 0.61-76.08 km; mean: 37.34 km; standard deviation: 26.99 km).

5.3.3. Ecosystem service indicators

Biodiversity

This indicator aims to measure the cultural value of biodiversity. It makes the assumption that people, particularly global beneficiaries, value species richness as a cultural service, i.e., sites with higher number of species are more valued (Morse-Jones et al., 2012). I use the sum of dung beetle and butterfly species richness as the indicator after standardising the richness data for each taxon by the respective maximum value.

Brazil nuts

To compare the potential supply of Brazil nuts in the forest uses sampled I used abundance data for *Bertholletia excelsa* across sites. Fruit production can vary considerably per tree and per year (Zuidema and Boot, 2002). Therefore, since I did not collect fruit production data, I assumed the average annual fruits produced per tree to be 102 (95%CI: 21.5 - 474.4), based on the average found over three years in Zuidema and Boot (2002). I also used averaged measurements of fruit weight (0,73kg) and seeds (24.5% of fruit weight), available in the literature (Paiva, 2009), to calculate potential nut production (in kg).

Carbon storage

Tree carbon storage, based on tree trunk diameter at breast height and tree species data, was estimated for the different forest uses, using aboveground biomass as indicator, following the protocol associated with ‘BIOMASS’ R package (Réjou-Méchain et al., 2017). Tree species names were first checked for errors. Next, wood density values were obtained for each taxon through the global wood density database (Zanne et al., 2009). The database did not include the Eucalyptus hybrid planted in the sampling sites (*Eucalyptus urograndis*), so that value was obtained in the literature (Gonçalez et al., 2014). Wood density data were available for several species (55.1% of total tree richness), but some values had to be inferred from genus (41.1%) or family (3.8%) levels. Tree heights were calculated from a height-diameter model (Chave et al., 2014). Aboveground biomass (in tonnes per hectare) was then calculated through Equation 4 in Chave et al. (2014).

Soil quality for agriculture

Soil quality is measured based on the adequacy of its chemical proprieties for potential agricultural use. Seven soil proprieties of importance for agriculture were aggregated, with equal weights, to create an index of soil quality for agricultural use. The seven properties measured were the concentrations in the soil of phosphorus, potassium, calcium+magnesium, aluminium, cation-exchange capacity, base saturation percentage, and sum of the bases. The thresholds for quality were obtained from a study detailing the properties that Brazilian soils should have to be considered suitable for agriculture (Ramalho Filho and Beek, 1995). Each parameter was coded as 1 if it passed the threshold, 0 if not. Higher index values indicate soils that require less intervention (i.e., chemical stabilisation) before agricultural use.

Timber

This service measures the capacity of different forest uses to supply timber . Since denser woods tend to be more valued, the indicator used here is volume multiplied by wood density. Tree basal areas were calculated using the diameter at breast height data. Volume measurements were obtained by multiplying tree basal areas with corresponding tree heights estimated by a height-diameter model (equation 6a in Chave et al., 2014). Wood density values were obtained as described in the carbon storage section. In order to identify tree species with commercial value, three main sources were used, namely, a global list of commercial timber tree species (Mark et al., 2014), a list of the species considered of “high” or “recognised” value for the timber industry by Amapá forestry department (IEF-AP, 2014), and a working list of all local species with commercial value used by the forestry company managing the logging concession. These three lists were crossed and species appearing in at least two of them were categorised in this study as having commercial value. Species appearing in only one of the lists were included if they were also present in the timber sales registry maintained by Pará state government (SEMA-PA, 2016). The final list of commercial species used can be found in Table D3 (Appendix D). This indicator measures timber capacity rather than actual provision, therefore commercial species occurring in RESEX Cajari or in areas of old-growth forest were also accounted for.

Multifunctionality score

Multifunctionality is analysed using a threshold approach. Both the threshold and averaging approaches are frequently used in the multifunctionality literature and both have limitations (Byrnes et al., 2014). However, the threshold approach enables more nuanced inferences (Lefcheck et al., 2015; Manning et al., 2018). The multifunctionality score, as calculated through the threshold approach, counts the number of ES that are being provided above a certain threshold. It allows an assessment of whether multiple services are being provided at high values, while the averaging approach simply indicates the averaged provision of all services considered, so does not measure how many services are being provided and can be strongly influenced by just one successful service. In this study there was no objective way to determine the thresholds and so multiple thresholds were tested (Byrnes et al., 2014). I used thresholds of 30%, 60%, and 90% of the maximum, after which provision is considered to be occurring, to assess the effects of tree richness and forest use on multifunctionality (Schuldt et al., 2018). All ES considered in this analysis were standardised by the maximum value ($f(x) = x / \max(x)$). This is more easily interpretable than the commonly used alternative of the 0 to 1 range standardisation, which forces the minimum observed value to be zero, even if this value is actually high in absolute terms (Byrnes et al., 2014; Gamfeldt and Roger, 2017). None of the measured ES provision values are categorised as potential outliers, therefore the maximum value used in the standardisation consists of one value, instead of an average of a certain number of the highest values. As an exception, in soil agricultural potential, the maximum value used was seven (i.e., the total number of functions that calculated the index used as indicator), rather than the maximum observed value.

When assessing the direct and indirect effects of forest use intensification on multifunctionality, three different hypothetical stakeholder groups were considered, giving different weights to each ES and therefore leading to different multifunctionality scores. Stakeholder group 1 gives equal weight to carbon storage and biodiversity and excludes the remaining services; stakeholder group 2 gives equal weight to timber production, Brazil nut extraction, and soil quality, excluding the remaining services; and stakeholder group 3 considers all five services with equal weight between them. These three groups aim to reflect contrasting valuations of forest ES provision. Some forest users might prioritise provisioning services over other services (group 2), while other beneficiaries might give highest value to services more associated with nature conservation (group 1). Group 3 provides a basis for comparison by allocating equal value to all five services.

5.3.4. Data analysis

The effects of tree richness on the provision of individual ES and on multifunctionality was assessed by fitting generalised linear models with gaussian error distributions. Plant richness is frequently used as indicator of biodiversity in multifunctionality studies (e.g., Isbell et al., 2011). Here I considered tree richness as a factor regulating ecosystem processes, while insect richness is used as an indicator of the provision of a cultural service. Table D2 (Appendix D) shows the regression coefficients of all models with the multifunctionality scores as response variables, for the different hypothetical stakeholder groups and at the three thresholds, and with tree richness as a predictor, while also adjusting for the effect of slope and elevation. Both slope (range: 0.1 to 9.2 degrees) and elevation (range: 45-217 metres) varied only slightly between sampling sites. Non-parametric Kruskal-Wallis rank sum chi-squared tests were used to determine if there were differences between forest uses in the levels of individual ES provision and site-level multifunctionality. Post-hoc Dunn tests corrected for multiple comparisons (Holm p-value adjustment) were conducted for pairwise comparisons between forest uses.

In order to determine the effect of forest use intensity, both direct and mediated by tree richness, I used a path analysis model (Figure 12), a variation on structural equation modelling where all variables are observed, i.e., without latent variables (Hayes, 2013). Forest use intensity is a variable that combines, with equal weighting, four elements associated with forest disturbance, each measured at site level: canopy openness, distance to nearest road, deforestation within a radius of 5km, and number of fires within a radius of 5km. More details on how each component was measured can be found in Chapter 4. This variable was also normalised by its maximum value. All analysis was conducted on R (version 3.4.3). Plots were designed using ‘ggplot2’ and path analysis was carried out on ‘lavaan’. The ES indicators used here measure potential ES provision rather than the flow of services to actual beneficiaries.

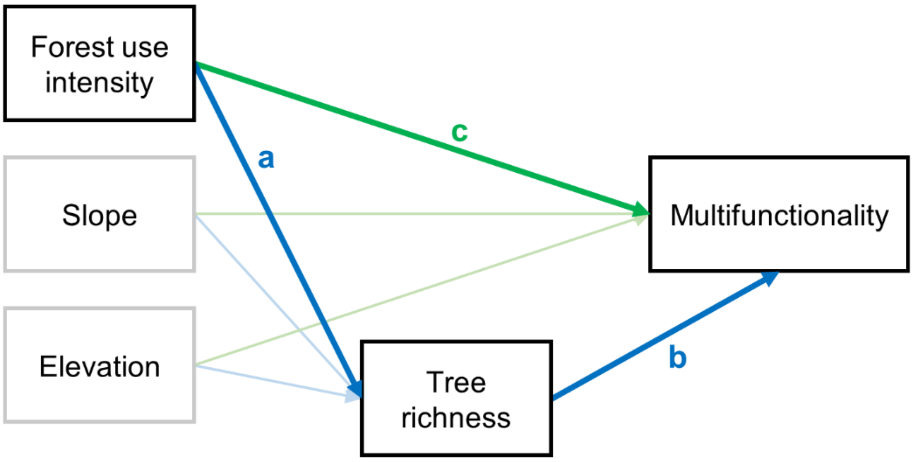

Figure 12. Path analysis model used for analysing the effect of forest use intensity on forest multifunctionality. The total effect adds the direct effect (path c) on multifunctionality and the indirect effect (multiplication of paths a and b).

5.4. Results

5.4.1. Ecosystem service provision

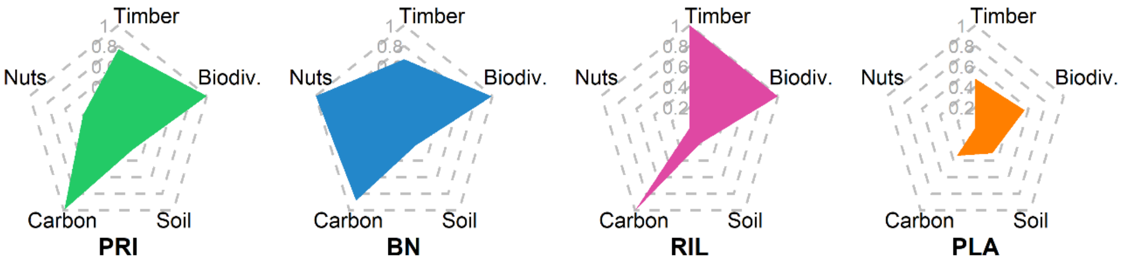

Figure 13. Radar charts of potential ecosystem service provision per forest use. PRI: old-growth forest; BN: Brazil nut extraction area; RIL: reduced impact logging; PLA: eucalyptus plantation. Provision values were normalised to the maximum across all sites.

ES provision varied between the different forest uses considered (Figure 13). Differences were significant for carbon storage (χ^2= 13.4, p-value= 0.004), Brazil nut production (χ^2= 9.4, p-value= 0.02), timber production (χ^2=8.2, p-value= 0.04), and biodiversity (χ^2=10.8, p-value= 0.01), but not soil quality (χ^2=5.9, p-value =0.12).

Brazil nut trees only occurred in Brazil nut extraction and old-growth forests, but at a higher density in the former, resulting in higher potential provision of Brazil nuts. Carbon storage was relatively high in all forest uses with the exception of eucalyptus plantations. Across sites, the mean value, in Mg, of aboveground tree biomass was 119.9±42.6 for PRI, 106.2±15.4 for BN, 121.0±20.4 for RIL, and 41.6±13.9 for PLA. As for biodiversity as a cultural service, the eucalyptus plantations also had a lower provision value, in relation to the similarly high levels in the other forest uses. The soil index indicates that soil quality for agriculture is low in all forest uses. Of the seven functions used to build the index, only PLA had an average of more than two functions above the thresholds used (2.2+0.8). Timber production values were generally high, but values were significantly higher in RIL than in PLA (z= 2.78, p-value= 0.017). While plantations had the highest density of commercial trees, they also had on average lower tree height, tree basal area, and wood density, leading to slightly lower values of timber output.

Tree species richness had significant positive linear relationships with carbon storage, insect richness, and timber production (Figure 14). This indicates that the provision of those services is the highest in sites with higher tree richness. The models fitted the data poorly when Brazil nut extraction and soil quality were the dependent variables. The correlation coefficients between tree richness and the five ES measured, as well as between each ES, vary from low to moderate and can be found in Table D1 (Appendix D). Figure D1 (Appendix D) compares individual ES provision between PLA and the uses in native forest grouped (BN, RIL, PRI). Furthermore, Figure D2 (Appendix D) shows the same analysis as Figure 14 on a subset of data where eucalyptus plantation sites are removed.

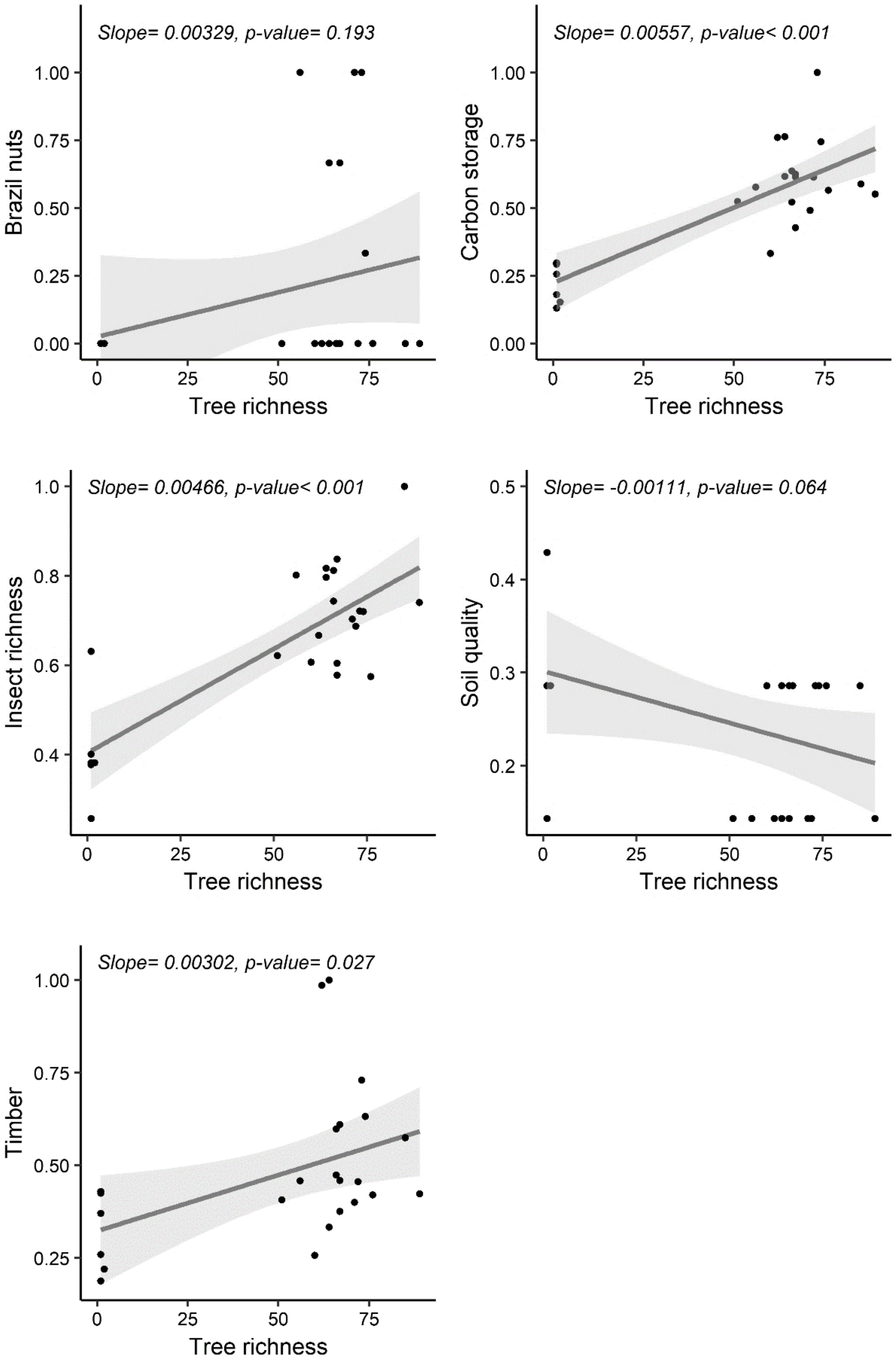

Figure 14. Relationship between the provision of five ecosystem services and tree species richness. The regression lines were fitted using generalised linear models with a Gaussian error distribution. Light grey areas indicate the 95% confidence intervals of model errors.

5.4.2. Forest multifunctionality

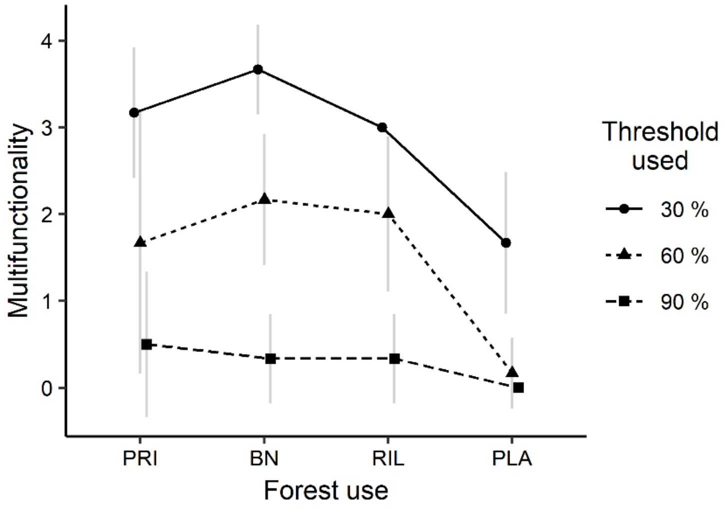

Figure 15. Mean multifunctionality levels across sites per forest use. Vertical grey lines indicate standard deviation. The thresholds indicate the fraction of the highest observed output value, per ecosystem service, above which the service output was counted in the multifunctionality score. PRI: old-growth forest; BN: Brazil nut extraction area; RIL: reduced-impact logging; PLA: eucalyptus plantation.

Multifunctionality levels varied between forest uses (Figure 15). Kruskal-Wallis tests confirm there are differences between forest uses when multifunctionality is measured with 30% (χ^2= 13.9, p-value= 0.003) or 60% (χ^2= 11.5, p-value= 0.009) thresholds. And post-hoc pairwise tests confirm that the significant differences are between eucalyptus plantations and all the other three forest uses. The maximum possible value for multifunctionality is five, however the maximum observed was four. Similar multifunctionality levels were measured for PRI, BN, and RIL. While RIL had no Brazil nut extraction, that was compensated by high levels of supply of other measured ES. As expected, mean multifunctionality values were higher when lower thresholds were used.

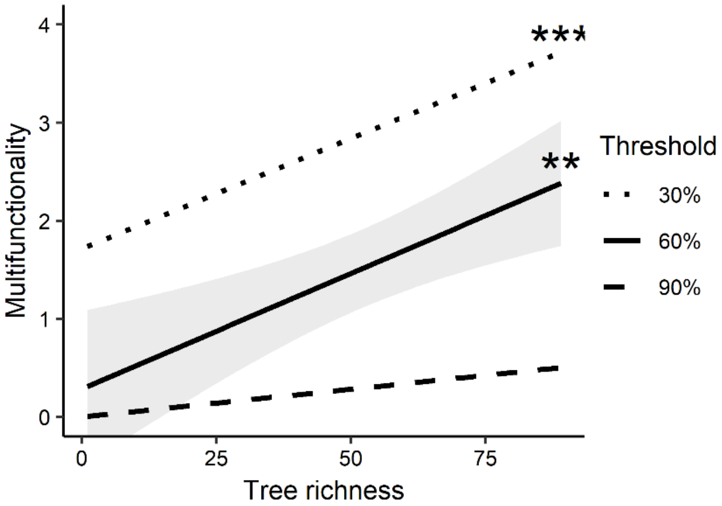

Figure 16. Regression lines, fitted with Gaussian generalised linear models, for the effect of tree richness on site multifunctionality measured at different thresholds. Light grey area shows the 95% confidence interval for the 60% threshold multifunctionality model. Asterisks indicate p-values for the slopes: ** equals p-value≤0.01; *** p-value≤0.001.

Tree richness levels influence site multifunctionality when multifunctionality is calculated with the less restrictive thresholds of 30% or 60%, but the effect disappears with the 90% threshold (Figure 16). For the 60% threshold, this indicates that the multifunctionality score, which can range between 0-5, increases by 0.02± 0.01 for each additional tree species added, i.e., adding 50 species to the ecosystem leads to one additional service being provisioned at a level 60% above its maximum observed value.

I also analysed the direct and indirect (i.e. mediated by tree richness) impacts of forest use intensity on multifunctionality, when ES are valued differently by hypothetical stakeholder groups (Figure 17). The direct effect can be interpreted as the effect of forest use intensification on multifunctionality when tree richness remains constant. On the other hand, the indirect effect shows how use intensification is affecting multifunctionality through its impact on tree richness. For the nature-focused stakeholder 1, the effect of intensification on multifunctionality is much higher when mediated by tree richness at threshold 30%. Stronger negative indirect effects, in relation to direct effects, were also observed at threshold 30% for the multifunctionality score with all ES equally balanced. As for the production-focused multifunctionality score (stakeholder 2), none of the effects were significant.

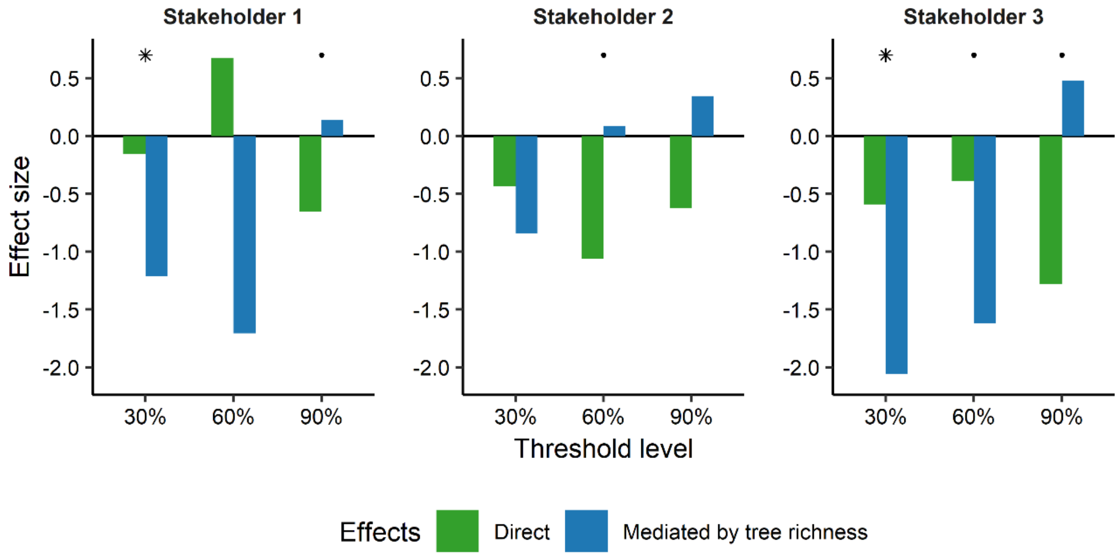

Figure 17. Direct and indirect effects of forest use intensification on forest multifunctionality. Indirect effects are mediated by changing tree richness and are calculated by multiplying the effect of forest use intensity on tree richness with the effect of tree richness on multifunctionality (see Figure 12). Asterisks indicate significant (p-value≤ 0.05) total effects (i.e., indirect plus direct effects) and points indicate p-values lower than 0.10. The stakeholder groups reflect contrasting perspectives on forest ES provision, where stakeholder group 1 only value services associated with nature conservation (carbon storage and biodiversity), group 2 only value forests for their productive potential (timber, Brazil nuts, and soil quality), and group 3 allocates equal value to all five services.

5.5. Discussion

5.5.1. Linking biodiversity and forest multifunctionality

Multifunctionality levels were generally higher under moderate or low intensity uses than under a more intensified regime. This supports the role of moderate forest uses in the sustainable management of human-modified forest landscapes (Bicknell et al., 2015; Edwards et al., 2014c; Putz et al., 2001). In fact, the multifunctionality levels found in moderate use sites are not significantly lower than in sites located in less undisturbed areas. Eucalyptus plantations fall short on the supply of most services analysed, showing that its specialisation on one function leads to trade-offs with other services, including locally valued ones such as Brazil nut extraction.

Intensification at site level is frequently associated with local loss of biodiversity (Newbold et al., 2015). Here, I find that tree richness has a positive impact on forest multifunctionality. When use intensification and tree richness are modelled together, the negative effects of intensification on multifunctionality are exacerbated by its negative impact on tree richness, revealing an indirect path through which forest use intensification influences forest multifunctionality. The averaged coefficients for the three threshold levels, when all functions are considered (i.e., stakeholder 3), indicate that indirect effects are on average at least as strong as direct effects (-1.07±1.4 and -0.75±0.47, respectively). This is in line with what was found for a study analysing the direct effect of land use intensity on grassland multifunctionality and the effect mediated by plant richness (Allan et al., 2015). Calculating multifunctionality by either allocating more weight to services linked to the production of goods (timber, Brazil nuts, soil quality) or in contrast by focusing on services whose provision has the lowest impact on forests (carbon storage and biodiversity), leads to divergent results. For the nature focused multifunctionality score (stakeholder 1), at the 30% threshold, the indirect effect is considerably stronger than the direct one, indicating that mediation through tree richness explains most of the total effect of intensification. As for the production focused multifunctionality score, no significant effect was found, although results suggest that at threshold 60% tree species loss caused by intensification might be linked to an increase in services leading to the supply of marketable goods.

5.5.2. Effect of biodiversity on the supply of individual ecosystem services

Some of the ES analysed were impacted by tree richness change (Gamfeldt et al., 2013). Results corroborate previous findings that less biodiverse tropical forests have reduced capacity to store carbon (Poorter et al., 2015). However, this positive link between tree diversity and carbon storage at site scale, might disappear at larger scales (Sullivan et al., 2017). Mean aboveground biomass per 0.4 ha ranged between 41.6±13.9 Mg in plantations and 121.0±20.4 Mg in RIL areas. The value for old-growth areas was 119.9±42.6 Mg, which when converted to carbon using the mean carbon fraction for tropical angiosperms (0.471), is in line with mean carbon stocks per unit area reported for South America in Sullivan et al. (2017). Most carbon in tropical forests is stored in tree biomass (Pan et al., 2011).

Congruence between changes in tree communities and co-occurring taxa can be relatively high (Barlow et al., 2007a). This was demonstrated in Chapter 4 for tree richness and species richness of both insect taxa sampled. Therefore, it is unsurprising that results show a link between higher tree richness and higher levels of the indicator used to measure biodiversity as a cultural service. It has been previously found that both butterfly and dung beetle richness can be correlated with changes in tree richness (Barlow et al., 2007b; Schulze et al., 2004). The congruence in the responses of both indicators to environmental change is also reinforced by the positive correlation (rho= 0.526, p-value= 0.008) shown in Table D1 (Appendix D).

Results do not show a link between tree richness and the soil's capacity to support agricultural uses. The slightly higher output of this ES in plantations (Figure D1, Appendix D) is likely to reflect a biased selection of areas for eucalyptus plantations based on soil conditions or soil improvement measures carried out by the land manager. Nevertheless, positive causal links between plant diversity and both soil organic matter and nutrient remineralisation have been reported in the literature (Cardinale et al., 2012). It has also been reported that the eastern area of Amazonia has intensely weathered soils that are nutrient poor (Quesada et al., 2010), which explains why the index developed to measure soil's affinity with agricultural requirements had generally low values. Previous research in the region has also found a link between several ecological processes in forests and soil conditions (Quesada et al., 2012).

The provision of Brazil nuts was not related with tree richness levels. While Brazil nut trees only occurred in Brazil nut extraction areas (4 sites) and, to a smaller degree, in old-growth forests (2 sites), the small sample size did not permit reaching conclusive results. Brazil nut trees are forest specialists dependent on large bees and agoutis for pollination and seed dispersal (Mori and Prance, 1990), but they also require light from canopy gaps for sprouting and seem to be tolerant to some disturbance (Paiva et al., 2011).

As for timber production, the link found with tree richness reflect the choice of indicator, volume of the commercial species present, including both planted eucalyptus and native species, weighted by wood density. Furthermore, it deals with ecosystem capacity rather than actual provision. Within plantations higher tree richness is linked to higher timber production (Piotto, 2008). There is also evidence that selective logging in more pristine forests generates higher timber revenues per unit area because managers target high-value species that become scarce or absent in more accessible areas (Richardson et al., 2016). While the higher tree density in plantations is not enough to compensate relatively lower tree volumes and wood densities, leading to the lower timber output reported here, this indicator does not take into account the much shorter cutting cycles of plantations. Overall, results indicate that intensive plantations are able to reach comparable total volumes of marketable timber, albeit of lower value, but with the vital difference that this capacity can all be converted to actual timber production, in a considerably shorter time frame and without additional loss of natural forests.

It is also relevant to mention that when ES provision at all the uses of native forest are grouped together and compared with provision from eucalyptus plantations (Figure D1, Appendix D), it identifies significant differences between those two groups in the provision of carbon storage, insect richness, and timber provision, in line with the results presented in section 5.4.1. Only Brazil nut provision, which had significantly different provision when the forest uses are compared separately, lost that effect, due to the various plots in native forests where no Brazil nut tree occured. These results suggest that the significant relationships between tree richness and ES provision shown in Figure 14 are being driven by the difference between native forests and plantations. This is confirmed in Figure D2 (Appendix D), which replicates the same analysis without plantation sampling sites and demonstrates that when plantation data is removed none of the relationships between tree richness and ES provision are significant.

5.5.3. Caveats and limitations

This study focuses on the capacity of the ecosystem to provide the five services measured rather than its actual flow to beneficiaries, which has implications for how results can be interpreted. And it presumes linear supply–benefit relationships for the services considered (Manning et al., 2018). Both capacity and flow are components of ES provision and both can be directly affected by ecological pressures (Villamagna et al., 2013). Here, this distinction is particularly relevant for soil quality for agriculture and timber production. While both services are included in multifunctionality calculations, the forests sampled might never actually be intensely logged or cleared for agriculture, although long term projections for the study area indicate that is plausible in a few decades under a business-as-usual scenario (Soares-Filho et al., 2006). Nine of the sampling points are also within a protected area, which is an additional safeguard, although again it is not necessarily a guarantee of protection on the long-term (Bernard et al., 2014).

The multiple dimensions of the concepts of biodiversity and ecosystem services, as well as their layered relationship, make studying ES-biodiversity links a challenging endeavour (Mace et al., 2012; Ricketts et al., 2016). Ecosystem service provision is a complex and interlinked process, from underlying ecological processes to the benefits that people value (UK NEA, 2011), which is influenced by biodiversity at different trophic levels (Soliveres et al., 2016). The approach used here includes two different indicators of biodiversity that aim to account for the relationship between biodiversity and ES at two distinct stages of that process. Tree richness was selected for its structural function and impact on ecological processes (Hooper et al., 2012; Liang et al., 2016; Loreau, 2010; Quijas et al., 2010), and for being a frequently used metric in multifunctionality studies (Fanin et al., 2018; Gamfeldt et al., 2013; Allan et al., 2015). On the other hand, the insect richness index developed aims to capture the cultural value attributed by people to species richness in tropical forests, particularly those sharing a more biocentric view on nature (Chan et al., 2012).

Finally, while methods to measure multifunctionality have been recently reviewed and consolidated (Manning et al., 2018), comparability between studies is still problematic. This would require, for example, a broad consensus on what services and indicators should be included in each ecosystem or biome, which seems unfeasible considering the context specificity of ES assessments (Costanza, 2008). The conclusions reached in this research reflect the conditions of the sampled area and are bounded by the methodological approach selected. Nevertheless, there are ongoing efforts for a better standardisation of biodiversity monitoring (Pereira et al., 2013), which might also benefit multifunctionality studies or at least provide a foundation for future standardisation.

5.5.4. Implications for forest management

Multifunctionality loss, as defined by the approach used here, indicates a diminished capacity of the ecosystem to provide multiple ES above a certain threshold in relation to the maximum possible output. The threshold levels aim to reflect minimum acceptable levels of provision. However, specific levels of service demand will vary between services and depend on which stakeholders are being considered (Martín-López et al., 2012). By including provisioning, cultural, and regulating services in the measurement of multifunctionality, results highlight the versatility of tropical forests (Fearnside, 2008). While moderate forest uses are able to keep similar multifunctionality levels to undisturbed forests, both higher than under intensified use, it is important to stress that the services included here capture changes in ecological functions but say nothing about the monetary value of the goods extracted from each forest use analysed. In fact, the plantations that have the lowest mean multifunctionality are also likely to provide the highest returns per area unit.

Despite its simplified categorisation of the interests of different social actors into nature-focus, production-focus, or equal weight between all ES, and also restricted by the low number of ES measured, this research provides additional evidence of how conclusions might differ depending on which benefits are prioritised, which in turn might favour certain social actors over others (Daw et al., 2011; Wieland et al., 2016).

Taking the results found here as starting point, it would be interesting to further research what might be the consequences on forest landscape configuration of changes in current levels of ES provision (e.g., Law et al., 2017), for example to meet certain rates of increased ES output and which might mirror what is demanded of forest managers in real-world situations. It would also be interesting to focus on how those changes in forest landscape configuration might affect biodiversity (e.g., Edwards et al., 2014a).

The compromises reached on forest management between conflicting objectives depend on social demands that can vary spatially and temporally and between social actors (Daw et al., 2011; Sayer et al., 2013; Wieland et al., 2016). In Eastern Amazonia, while biodiversity-friendly landscapes prevail for now, there are indications that industrialised land uses will add pressure on these natural forests, which on the long term can lead to a repetition of the deforestation patterns currently seen in other Amazonian regions (Soares-Filho et al., 2006). Unlocking trade-offs requires effective landscape-level decision making that acknowledges the multidimensionality of coupled socio-ecological systems (Cordingley et al., 2015; Fedele et al., 2018; Gardner et al., 2009; Reyers et al., 2013; Tscharntke et al., 2005). Sustainable landscape configurations seem able to integrate a certain share of intensified use, as long as a well-connected matrix of large undisturbed areas is maintained (Cordingley et al., 2015; Melo et al., 2013). Finding better ways to incentive decision makers to account for both the benefits of moderate forest uses common in the Amazonian context and the interests of global beneficiaries, by for example financially rewarding local actors that maintain ES provision (Grima et al., 2016), can also help shifting power balances in favour of the maintenance of forest multifunctionality on the long term (Brockhaus et al., 2013).

5.6. Conclusions

This chapter explored the relationship between forest use intensification, biodiversity loss, and forest multifunctionality in a tropical socio-ecological system with high levels of forest cover. The synergetic link found between tree richness and forest multifunctionality indicates that, in the context of tropical forests, it is counterproductive to disregard biodiversity conservation in forest management decisions at landscape scale. It also demonstrated the paths through which use intensification impacts on multifunctionality showing the significant role of mediation by biodiversity loss. Low and moderate forest uses maintain higher multifunctionality levels, indicating stronger trade-offs in ecosystem service provision under intensified uses. Nevertheless, the integration of different forest management regimes, including intensive ones, within multifaceted landscape configurations, has the potential to reconcile economic and conservation priorities.

Data availability

The dataset used in this chapter is available at http://discovery.ucl.ac.uk/10070655

Chapter 6: Discussion

6.1. Main findings

The aim of this thesis was to better understand the multi-layered relationship between biodiversity and ecosystem services in the human-modified forest landscapes of Eastern Amazonia. My empirical research centred on the basin of Jari River, which delineates the east-west border between the Brazilian states of Amapá and Pará, because this region maintains high levels of forest cover and biodiversity within a rich matrix of forest uses. In Amazonia, the preservation of pristine areas shielded from direct anthropogenic disturbances is also dependent on finding solutions for the long-term sustainable management of these forests where people and nature more closely interact, which implies finding policy solutions that incentivise sustainable use of forests over deforested land uses. These solutions require that relationships between biodiversity and ecosystem services are considered in a way that acknowledges the complexity of the socioecological systems they are inserted in (Díaz et al. 2006).

In addressing the overall aim of this thesis, I used a variety of methodologies that approached the multi-layered relationship between biodiversity and ecosystem services from different perspectives. In Chapter 2 I provide a comprehensive overview of ES provision at the scale of the state of Amapá. This is a high forest cover, low deforestation region with low data availability, so I developed a simple set of indicators to measure a balanced number of provisioning, cultural, and regulating services, that can be applied at low cost in regions with similar conditions. This allowed me to identify forests as one of the land uses in the state with highest ES provision and show that forests closer to edges, which might be more at risk of conversion, also provide more benefits to local communities. In Chapter 3, using surveys, I showed that in general local communities living in or near forests are able to link that provision to high biodiversity levels. This awareness also influences attitudes towards conservation measures and can lead to more biodiversity-friendly behaviours. Chapter 4 involved the collection of data on three different taxa along a gradient of forest use intensity to assess how biodiversity is impacted by forest management. It found a trade-off between different metrics of biodiversity and the intensification of forest use, which indicates that impacts of forest use are unavoidable at site scale but can be minimised under management strategies at landscape scale that integrate different use intensities, including intact areas. After analysing the link between forest use and biodiversity, in Chapter 5 I focused instead on the link between biodiversity and the capacity of forests to provide multiple services. By measuring ecosystem services based on ecological data I collected and by using a standard protocol for calculating multifunctionality, I was able, not only to confirm some of the associations found in Chapter 2, but especially to demonstrate that more diverse forests are also more multifunctional, a conclusion that was not possible to establish with the broader but also coarser analysis of Chapter 2.

6.1.1. The multifunctionality of Eastern Amazonia forests

This thesis presented empirical data on the multifunctionality levels, measured by the simultaneous provision of five ecosystem services, found in four different forests uses: old-growth forest, forest under reduced impact logging, forest under Brazil nut extraction, and eucalyptus plantations. To my knowledge this is the first study that compares multifunctionality between these four regionally expressive forest uses. Either plantations fit within the definition of forest, depends on which of the more than 800 official definitions is being used (Sexton et al., 2016). But regardless of that categorisation, they are still appropriate for comparative studies on the effect of biodiversity on multifunctionality. As Cardinale et al. (2012) illustrate, the role of biodiversity in ecosystem service provision in forests should be assessed by comparing more and less diverse habitats, rather than comparing diverse habitats and areas where that habitat was destroyed. Since plantations are tree monocultures, their structure can be considered the extreme simplification of a forest ecosystem.

Results show that, on the broader scale used in Chapter 2, the natural forests of Amapá are highly multifunctional relatively to other land uses, although mean ES output from agricultural areas is also high, due to higher provision of provisioning services at the expense of regulating and cultural services. And, on the finer scale used in Chapter 5, multifunctionality levels are higher under moderate or low use regimes than under intensive use. Ecosystem capacity to provide multiple ES was measured by ecological functions, meaning that the multifunctionality metric used here is disassociated from monetary returns. In fact, the forest use with lowest mean multifunctionality (plantation) is likely to have the highest monetary return per area unit. This disassociation only confirms why ES approaches can be relevant in policy making, as they provide a more comprehensive basis for decisions that is not restricted to monetary valuations and is more representative of the actual social value of natural areas to multiple stakeholders (Carpenter et al., 2009).

Trade-offs need to be explicitly acknowledged in conservation strategies (McShane et al., 2011), as this is a first step towards resolving, or at least minimising, conflicts between different land use priorities in landscape management (Sayer et al., 2013).

This thesis identifies significant trade-offs both at the broader scale of Chapter 2, where 84.2% pairwise associations involving at least one provisioning service were negative, and at the finer scale of Chapter 5, where higher multifunctionality is associated with more tree richness and less use intensification, again driven by our need for provisioning services, in this case timber from eucalyptus plantations. However, Chapter 5 also suggests why areas of intensified use, if not too dominant and suppressive of other forest uses at landscape scale, can also play a part in the conservation of natural forests by reducing pressure on them (Green et al., 2005). In order to reach the same levels of volume extracted in plantations per area unit, it would be necessary to cut all commercial trees found in a natural forest area of roughly the same size per rotation cycle, with devastating effects.

The multifunctional forests of Eastern Amazonia inserted in human-modified landscapes are highly important for conservation, for maintaining high biodiversity levels and providing a buffer against disturbance for some of the last remaining intact forests in the world, and also highly important for beneficiaries at different scales, particularly local due to their greater accessibility. This thesis argues that the preservation of these forests on the long term is fundamental for both biodiversity conservation in Amazonia and for the livelihood of local communities.

6.1.2. Effects of forest use intensity on biodiversity

The results of this thesis clearly show that biodiversity, measured using different metrics and taxa, is affected by changes in forest use intensity. While the responses of butterflies, dung beetles, and trees were not always congruent, results generally point to Brazil nut extraction areas and reduced impact logging areas being able to hold similar, albeit slightly lower, diversity levels in relation to undisturbed areas. Communities in eucalyptus plantations were distinctly less diverse and were consistently the forest use that shared less species with old-growth areas. Nevertheless, plantations were still able to retain considerable conservation value for the insect taxa sampled, indicating that some species are adapted to the conditions found in that more open habitat (Gardner et al., 2008; Hamer et al., 2003). Of the four forest uses considered, the Brazil nut tree groves used by local communities, locally called *"castanhais"*, has received the least attention from researchers up to now. Results here confirm that these areas had levels of diversity for the three taxa sampled similar to reduced-impact logging, in contrast to previous research suggesting that this use can be relatively more prejudicial to biodiversity (Gibson et al., 2011).

These results apply to a landscape context that can be considered “biodiversity-friendly” (Melo et al., 2013), due to the large pools of intact forest that remain part of the matrix of forest uses. Therefore, as I state in Chapter 4, extrapolation to other contexts require caution, because of potentially differentiated impacts of fragmentation and spill-over effects (Gardner et al., 2008; Korasaki et al., 2013; Nichols et al., 2007).

While Chapter 4 provided a more detailed analysis focusing only on forest management regimes under different use intensities, Chapter 2 had already shown that spatial associations between biodiversity and other ES were mostly synergetic, except for provisioning services, where trade-offs were more likely. Those results were obtained through an analysis at larger scale and including land uses besides forests, but already indicated that intensification of land use for the benefit of provisioning services is achieved at a cost to biodiversity (Chan et al., 2006; Cimon-Morin et al., 2013; Howe et al., 2014).

6.1.3. Perception of the relationship between biodiversity and ecosystem services

The findings of Chapter 3 show that on average each respondent was able to identify most (75%) of the causal relationships, supported by the literature, between biodiversity and ecosystem services that were presented to them. This perception varied between ES category, which showed that awareness levels were relatively lower for regulating ES. Higher income levels, which might reflect access to more ES, and particularly participation in Brazil nut extraction, an activity deeply linked with the forest, were both linked to higher awareness levels. This shows that the sampled population, which lives in a region of high forest cover, is generally aware of the role of biodiversity in ES provision. However, more interesting for the role of the ecosystem service framework in conservation is the finding that higher awareness of these biodiversity-ES links was in turn associated with more positive attitudes towards conservation, which suggests that highlighting the role of species, or healthy ecosystems, on the processes that lead to benefits cherished by society for their impact on well-being might be an effective strategy in the promotion of pro-conservation behaviour.

Since the foundation of the ES concept ecologists have lamented how decision makers are often unaware of the services natural ecosystems provide to society and their failure in communicating them to the general public (Daily, 1997). While significant improvements have occurred since then (e.g. the creation of IPBES), much remains to be done to increase ES awareness and knowledge (e.g., Zhang et al., 2016). Furthermore, there is a danger that, despite research advancements, people fail to consciously connect the benefits gained from nature to biodiversity per se (Pett et al., 2016), when that relation exists, which is not always the case (Anderson et al., 2009). This, linked to a concern that ES solely promotes a utilitarian view of nature, has led to questioning of the effectiveness of ES as a communication tool (Bekessy et al., 2018).

I argue that the ES framework is flexible and comprehensive enough to also integrate intangible values linked to nature (Chan et al., 2012; Reyers et al., 2013). The results of Chapter 3 have implications for the communication of conservation messages to the public, at least in the context of Eastern Amazonia, a region of high conservation value. An example easily relatable to people in that region, which has been explored by NGOs such as WWF (2007), is Brazil nut extraction. Their trees are highly dependent on local fauna for seed dispersal (Peres et al., 1997) and pollination (Maués, 2002), and are also a symbol of the benefits of standing forests. Due to the regional prominence of this activity, it seems a suitable flagship for communicational purposes, in pro-conservation campaigns or environmental education, to promote the importance of biodiversity for local livelihoods and well-being. Pro-environmental behaviour entails a mixture of self-interest and pro-social motives (Bamberg and Moser, 2007). Celebrating nature within the ES framework, while emphatically putting the role of biodiversity on the spotlight, might offer a route to reduce conflict between egoistic, altruistic, and biospheric individual values and therefore making pro-environmental behaviours more likely (De Groot and Steg, 2009).

6.2. Future directions

6.2.1. Forest management in the tropics

One of the greatest challenges of our time is to find solutions that enable feeding a growing population while preserving global forests (FAO, 2018; Watson et al., 2018). Forests provide vital resources for over a billion people, including many of world’s poorest, while also harbouring more species than any other biome in the planet (FAO, 2018; MEA, 2003). Improved forest management practices should reflect their crucial role both for biodiversity and for the livelihoods of people (Ostrom and Nagendra, 2006). However, vast areas of forest, such as the Amazon, are unlikely to be able to rely simply on self-organisation to reach sustainable outcomes (Ostrom, 2009). And since slightly more than half of the Brazilian Amazon is not covered by a protected area (Walker et al., 2009), effective governance strategies require going beyond protected area management.

In north-eastern Amazonia, while biodiversity-friendly landscapes prevail for now, there are indications that industrialised land uses will add pressure on these natural forests, which on the long term can lead to a repetition of the deforestation patterns observed in other Amazonian regions (Soares-Filho et al., 2006). Current land-use dynamics put forests at risk of conversion to more profitable uses, mainly agriculture in large rural properties (De Sy et al., 2015; Godar et al., 2014). Thus, there is no guarantee the region will not progress to more degraded states, in the absence of effective regulations and incentives that accommodate both small and large-scale stakeholders (Melo et al., 2013). With more than two thirds of its territory protected, Amapá is in a good position to champion an alternative model of development better suited to conciliate economic and conservation priorities through the prioritisation of biodiversity-based product value chains (Nobre et al., 2016). However, this requires landscape-level decision making that acknowledges the multidimensionality of coupled socio-ecological systems (Cordingley et al., 2015; Fedele et al., 2018; Gardner et al., 2009; Reyers et al., 2013; Tscharntke et al., 2005).

This thesis indicates that sustainable landscape configurations might be able to integrate a certain share of intensified use, as long as a well-connected matrix of large undisturbed areas is maintained (Cordingley et al., 2015; Melo et al., 2013). However, more research is needed on how specific goals for ecosystem service supply in forests might affect landscape configurations (Law et al., 2017). Further empirical research on how the effect of fragmentation on biodiversity interlinks, at landscape scale, with the flow of multiple services to people can also help inform better forest management strategies.

A broader use of forest multifunctionality measures can increase the integration of interdisciplinary perspectives in policy making. This approach, as demonstrated in Chapter 5, can potentially result in valuable information for the governance of forests at large scales by feeding analytic deliberations and providing a common link between distinct institutions (Dietz, Ostrom and Stern, 2003). In overall, it provides an analytical foundation to measure relationships between people and nature, which is relevant because compromises between conflicting objectives in forest management require the consideration of social demands that can vary spatially and temporally and between social actors (Daw et al., 2011; Sayer et al., 2013; Wieland et al., 2016).

If the preservation of forest-rich landscapes is to be achieved in the region, institutions need to provide clear incentives with impacts both on ecosystem function and rural livelihoods (Ashley et al., 2006). These rules need to be congruent with the local socioecological context for their long-term sustainability (Ostrom, 2009). Fiscal support, payment for ecosystem services, easier access to credit and markets, or certification schemes, are measures that can incentivise moderate forest use in forest-rich landscapes (Bhagwat et al., 2008). Tenure security is also an influential factor in land use decisions (Robinson et al., 2013).

There is evidence that a combination of punitive measures and positive incentives can be effective in the Amazonian context (Arima et al., 2014; Nepstad et al., 2014), but more research is needed on how to fine-tune these policy tools to specific land use contexts and goals. Regarding land tenure, the creation of a land registry in Brazil by Law 12.651/12 was a key recent development. As of 2018 the area declared by owners in the registry already surpasses 100% of the territory, with the highest gap found in the Amazonian region (MMA, 2018), indicating ongoing land conflicts that if left unresolved can threaten both local communities and conservation goals (Robinson et al., 2013). Both Chapters 2 and 5 support the existence of a synergetic link between carbon stocks and biodiversity in the region, suggesting that payment for ecosystem services can lead to beneficial forest conservation outcomes in the region, although the effectiveness of that measure is dependent on addressing known constrains and following scientific guidelines (Naeem et al., 2015; Wunder, 2007).

Finding better ways to incentivise decision makers to account for both the benefits of moderate forest uses common in the Amazonian context and the interests of global beneficiaries, by for example financially rewarding local actors that maintain ES provision (Grima et al., 2016), can help shifting power balances in favour of the maintenance of forest multifunctionality on the long term (Brockhaus et al., 2013). Furthermore, effective long-term solutions are dependent on the engagement of local communities, so equity considerations in forest access and benefit distribution are also crucial (Ashley et al., 2006; Daw et al., 2011; Ostrom and Nagendra, 2006; Sheil et al., 2004).

6.2.2. Biodiversity conservation in forest-rich human-modified landscapes

An ambitious plan of action is needed for the conservation of global biodiversity (Mace et al., 2018). Protected areas are essential for biodiversity conservation but on their own also unlikely to be sufficient for the complete preservation of global ecosystems and species, even when the current objective, set on the Convention on Biological Diversity Aichi Targets, of protecting 17% of terrestrial land surface, is achieved (Joppa et al., 2013; Putz et al., 2001). While integral protection areas should be a priority in conservation to help protect the irreplaceability of pristine forests (Gibson et al., 2011), additional measures are required to safeguard biodiversity beyond those restricted boundaries, in areas where people and nature coexist, which also include all protected areas with sustainable use goals. This makes the improvement of sustainable forest management and the promotion of biodiversity-friendly human-modified landscapes worthy objectives in conservation science (Melo et al., 2013; Putz et al., 2001). It also presents some challenges because these areas might be more susceptible to anthropogenic disturbance, such as fire and hunting, and to deforestation pressures that increase fragmentation and loss of forest cover (Barlow et al., 2016; Laurance et al., 2002b). They also increase chances of human-wildlife conflict, which are complex problems better addressed by holistic conflict management strategies (Marcini and Crawshaw, 2015; Mason et al., 2018).

As shown by Chapter 4, while most species are resilient to low use intensities (Burivalova et al., 2014), there are others that decline even under those conditions (França et al., 2017). So framing discussions on the sustainable management of forest-rich landscapes as a dichotomy between either maximising the integration or separation between conservation and production might not be a helpful approach. Although use intensification can help alleviate pressure on intact forests (Green et al., 2005), focusing exclusively on that strategy might not always be appropriate and even lead to undesired outcomes, such as intensification at the expense of forests rather than disturbed land (Gutierrez-Velez et al., 2011). Management of forest-rich human-modified landscapes should instead encourage a healthy coexistence of integral protection and sustainable use (Fischer et al., 2014).

It is doubtful that current management orientations in Brazil are adequately equipped to achieve that, suggesting the need for further research and especially policy advancements that support the long-term preservation of natural communities in human-modified landscapes (Arima et al., 2014; Brancalion et al., 2018; Richardson and Peres, 2016; Shearman et al., 2012). Griscom et al. (2018), for example, projected that selective logging had the potential to yield both the best and worst outcomes for conservation of all forestry alternatives considered, depending on whether certification and land tenure were in place. Overall, conflict between different priorities and choices is an inherent problem in forest management that can only be addressed through adaptive institutional arrangements (Dietz, Ostrom and Stern, 2003).

It is relevant to highlight that the achievement of forest conservation goals is an interdisciplinary effort (Reyers et al., 2010) that requires the engagement of local communities (Persha et al., 2011). Chapter 3 provided additional empirical evidence of the potential usefulness of the ecosystem service framework to push forward the conservation agenda with the general public. That approach should be considered by conservationist organisations as an additional element for a multifaceted communicational strategy that can be tailored to specific audiences (Pearson, 2016). Further research into novel approaches, such as conservation marketing (Wright et al., 2015), can provide clearer answers on the best ways to frame biodiversity to convey effective messages that advance conservation goals.

6.3. Concluding remarks

The future prospects of the genetic, species, and ecosystem diversity found on Earth remain uncertain. Efforts from conservationists throughout the years have at best managed to reduce the rates of decline, but in overall have been unable to reverse the negative trends. Current global conservation targets, such as the Aichi targets set in a Conference of the Parties of the Convention on Biological Diversity, while ambitious, are unlikely to be achieved by 2020 (Tittensor et al., 2014). These current trends in part reflect an inadequate valuation of the benefits of biodiversity to human well-being but are also a consequence of trade-offs with other social priorities, such as food production (De Sy et al., 2015).

Conservation science has traditionally focused on challenging the prioritisation of land uses and activities that are destructive to biodiversity, with the implementation of protected areas being the most symbolic wins on that front, but more recently has also started broadening its focus and emphasise the importance of achieving balanced and resilient socioecological systems in all areas where nature and people coexist (Mace, 2014). This latest development allows further integration of elements, such as the perspectives of local communities or analysis of how benefits are shared between social actors, that are fundamental for meeting conservation goals (Bennett et al., 2017). Approaching nature-people relations from different perspectives enable additional tools in conservation science that can be combined in response to specific contexts and therefore increase the likelihood of reaching positive outcomes (Pearson, 2016; Reyers et al., 2010).

In the Amazonian context, it is in the interest of conservationists to champion sustainable forest uses that help prevent further encroachment into some of the last intact forest ecosystems in the planet (Watson et al., 2018). Despite the propagation of anthropogenic disturbances such as hunting and fire that might be associated with forested socioecological systems (Barlow et al., 2016), the preservation of tree cover is still preferable to most alternative land uses and can complement areas under integral protection (Putz et al., 2001). In the human modified forest landscapes of Eastern Amazonia, biodiversity conservation seems attainable, and more likely to be maintained in the longer term, through landscape configurations that reflect the needs and preferences of multiple stakeholders.

Overall, results provided further evidence of the important role of forests in socioecological systems in Amazonia. They are important providers of ecosystem services with beneficiaries at different scales and their multifunctionality is linked with the preservation of biodiversity. Intensification of forest use comes at a cost to biodiversity and in turn to forest multifunctionality. Sustainable forest management strategies are needed for the long-term persistence of high forest multifunctionality at landscape scale. This is more likely to be supported by the public when the multiple benefits of forests are recognised and the role of biodiversity in the delivery of those benefits is highlighted.

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Appendix A

Table A1. Kendall tau correlation coefficients (bottom-left) and the corresponding p-values (top-right). Red represents positive (and blue negative) associations.

	Agb	Agri	Biodiv	Reg.cli	Herit	NTFP	Recr	Loc.cli	Timber
Agb	1	***	***	***	0.946	***	***	***	***
Agri	-0.068	1	***	0.594	***	***	***	***	**
Biodiv	0.725	-0.034	1	***	***	***	***	***	***
Reg.cli	0.206	n.s.	0.234	1	***	***	***	***	***
Herit	n.s.	-0.016	0.038	0.108	1	***	0.526	***	***
NTFP	-0.039	-0.023	0.111	-0.053	-0.126	1	***	***	***
Recr	-0.035	0.017	-0.032	-0.029	n.s.	-0.011	1	***	0.069
Loc.cli	0.669	-0.059	0.668	0.332	0.091	0.051	-0.030	1	***
Timber	-0.149	-0.009	-0.129	-0.054	-0.032	-0.044	n.s.	-0.174	1

Notes: n.s. – Non-significant; * P ≤ 0.05; ** P ≤ 0.01; ***P ≤ 0.001.

Table A2. Direction of the pairwise associations using three validation approaches (bottom-left). Top of table cell: polychoric correlation in original data set. Middle of table cell: Kendall tau correlation on joined 2x2 spatial units. Bottom of table cell: Kendall tau correlation on joined 3x3 spatial units. Red corresponds to positive associations, blue to negative associations. Top-right shows the corresponding p-values.

	Agb	Agri	Biodiv	Reg.cli	Herit	NTFP	Recr	Loc.cli	Timber
Agb	1	*** *** ***	*** *** ***	*** *** ***	0.556 * *	*** *** ***	*** *** ***	*** *** ***	*** *** ***
Agri	- - -	1	*** *** ***	0.717 0.158 *	*** *** *	*** *** ***	*** *** ***	*** *** ***	0.171 * 0.132
Biodiv	+ + +	- - -	1	*** *** ***	*** *** ***	*** *** ***	*** *** ***	*** *** ***	*** *** ***
Reg.cli	+ + +	n.s. n.s. -	+ + +	1	*** *** ***	*** *** ***	*** *** ***	*** *** ***	*** *** ***
Herit	n.s. - -	- - -	+ + +	+ + +	1	*** *** ***	0.348 0.348 0.138	*** *** ***	0.08 *** ***
NTFP	- - -	- - -	+ + +	- - -	- - -	1	*** ** 0.095	*** *** ***	* *** ***
Recr	- - -	+ + +	- - -	- - -	n.s. n.s. n.s.	- - n.s.	1	*** *** ***	0.821 0.056 0.807
Loc.cli	+ + +	- - -	+ + +	+ + +	+ + +	+ + +	- - -	1	*** *** ***
Timber	- - -	n.s. - n.s.	- - -	- - -	n.s. - -	- - -	n.s. n.s. n.s.	- - -	1

Notes: n.s. – Non-significant; * P ≤ 0.05; ** P ≤ 0.01; ***P ≤ 0.001.

Table A3. Direction of the pairwise associations by ES category, in percentage. It applies to the results of the Kendall tau correlations shown in Table A1. Only significant pairwise associations were considered.

<table>
<tr><td></td><td colspan="6"><i>Associations with at least one ES of the following categories (%)</i></td></tr>
<tr><td></td><td colspan="2">P
(n=19)</td><td colspan="2">R
(n=19)</td><td colspan="2">C
(n=18)</td></tr>
<tr><td>Positive (+)</td><td colspan="2">15.8</td><td colspan="2">47.4</td><td colspan="2">44.4</td></tr>
<tr><td>Negative (-)</td><td colspan="2">84.2</td><td colspan="2">52.6</td><td colspan="2">55.6</td></tr>
<tr><td></td><td colspan="6"><i>All associations (%)</i></td></tr>
<tr><td></td><td>P – R
(n=8)</td><td>P – C
(n=8)</td><td>R – C
(n=8)</td><td>P – P
(n=3)</td><td>R – R
(n=3)</td><td>C – C
(n=2)</td></tr>
<tr><td>Positive (+)</td><td>12.5</td><td>25</td><td>62.5</td><td>0</td><td>100</td><td>50</td></tr>
<tr><td>Negative (-)</td><td>87.5</td><td>75</td><td>37.5</td><td>100</td><td>0</td><td>50</td></tr>
</table>

Notes: P= Provisioning; R= Regulating; C= Cultural.

Table A4. Observed plant species richness and indication of sampling effort in each vegetation cover type considered in this study. Data extracted from GBIF and ICMBIO. Vegetation cover map used was developed by Amapá's State Government (SEMA-AP, 2012).

Vegetation cover	Observed species richness	No of sampling sites
Alluvial forest	594	37
Floodplains	509	99
Forest	1727	484
Savannah	348	98
Secondary vegetation	849	120

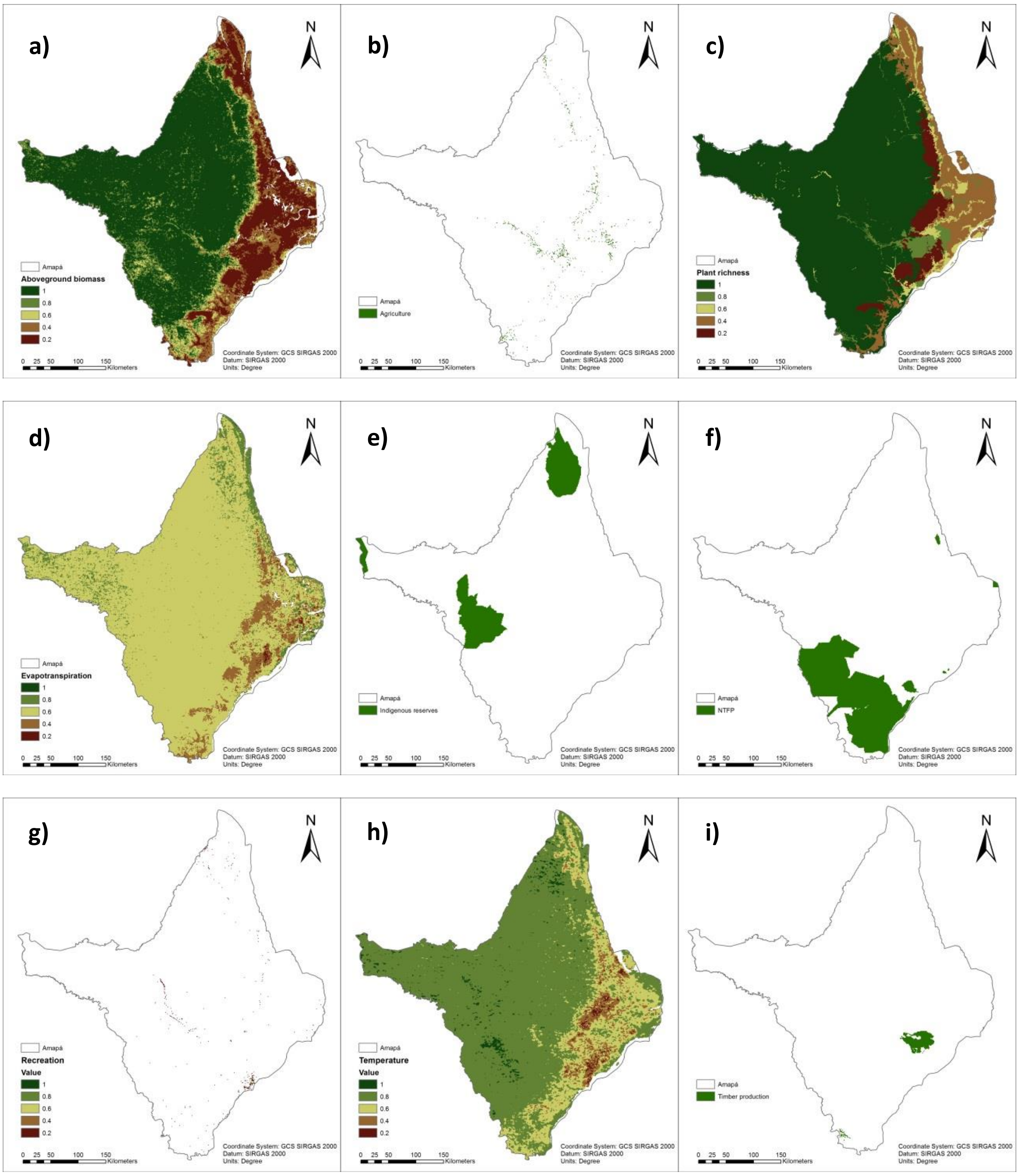


Figure A1. Individual spatial distribution maps for each of the 9 ES analysed. a) Aboveground carbon storage; b) Agricultural production; c) Biodiversity; d) Regional climate regulation; e) Indigenous heritage; f) NTFP extraction; g) Recreation; h) Local climate regulation; i) Timber production. Each ES layer was normalised to a 0-1 scale.

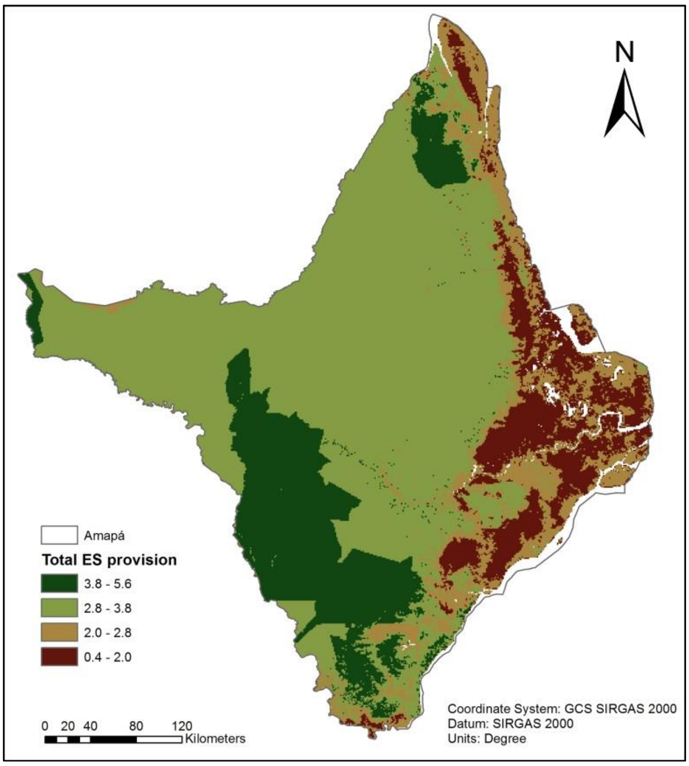


Figure A2. Map of the aggregated provision of 9 ES in the state of Amapá, Brazil. Each ES layer was normalised to a 0-1 scale. The size of each grid cell is 0.01 degrees (approximately 1.1 km). White cells within the state frontier represent areas containing bodies of water with no data available.

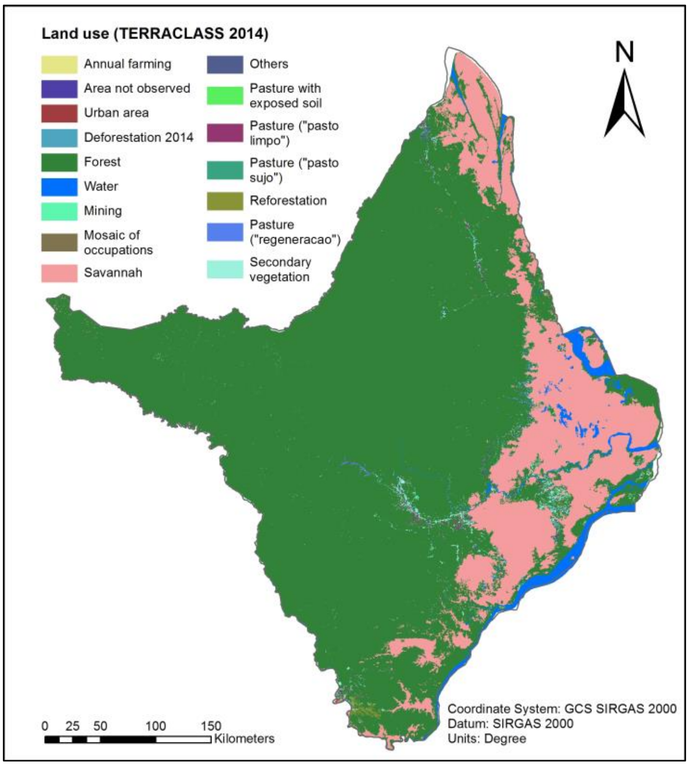


Figure A3. TERRACLASS (INPE) land use map for 2014.

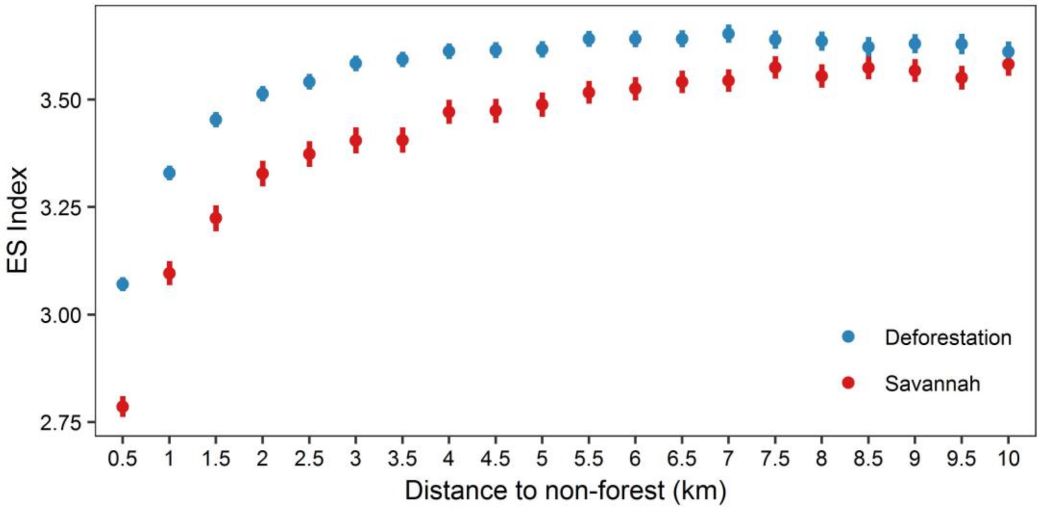


Figure A4. ES provision in forest areas in relation to distance to its edge, up to 10 km, when edges are either caused by deforestation or from natural transition with savannah. Horizontal lines (error bars) correspond to the 95% confidence interval.

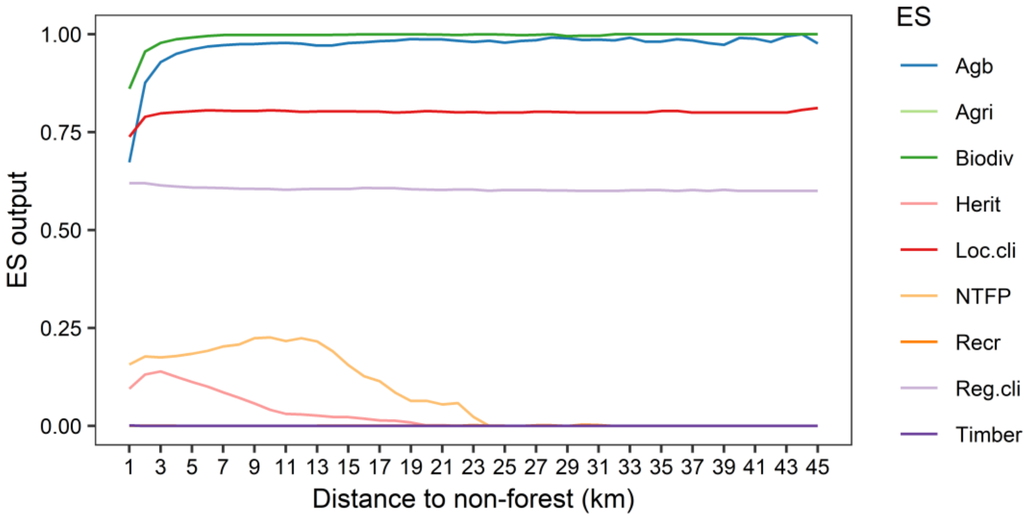


Figure A5. Forest provision of each ES in relation to distance to forest edge. Y-axis represents the mean output for spatial units in the distance interval [x-1,x[. This plot disaggregates by ES the information provided in Figure 2. Timber production and agricultural production in forest were null, as expected, although there was a small spill-over for timber at x=1 (y= 0.001). Recreation had positive mean ES output values close to zero that are not visible in this plot (max= 0.003).

Appendix B

Text B1. Questionnaire Design

Section I

1.1. Do you live in this village? *[Y/N]*
1.1.1. If not, where do you live? *[Open]*
1.2. In the last month, did you use any product sourced directly from the forest? *[Y/N]*
1.3. In the last month, what percentage of the food in your house was obtained, by you or anyone else in your household, through fishing, hunting, or gathering, on forest areas? *[0–10%; 11–40%; 41–70%; 71–100%]*
1.4. Do you or anyone in your household earn income from the sales of forest products or from forest related services? *[Y/N]*
1.5. How often do you enter the forest? *[1+ times per week; 1-3 times per month; a few times per year; never]*
1.6. Which motives might make you go to the forest? *[Open]*

Section II

2. Please tell us whether you agree or disagree with the following sentences, choosing one of the following five options: “Completely agree”, “Slightly agree”, “Neither agree or disagree”, “Slightly disagree”, “Completely disagree”. *[5-point Likert scale]*
2.1. In a native forest bush meat is as easy to find as in a secondary forest.
2.2. The preservation of plant variety is indifferent for agricultural production.
2.3. Living near a river full of different fishes gives me more confidence that the fish yield will always be good.
2.4. In a forest with more variety of trees, wood production is lower.
2.5. A pasture with more variety of plants produces more food for cattle.
2.6. If I need any medicinal plant, I can find it even in a secondary forest.
2.7. Brazil nut production is improved in a forest with more variety of animals.
2.8. In a secondary forest there are less fruits I can eat than in a native forest.
2.9. A forest closer to a village will have as much rattan as a more distant forest.
2.10. Protecting the forest helps poorer communities secure their livelihoods.

Section III

3. Please tell us whether you agree or disagree with the following sentences, choosing one of the following five options: “Completely agree”, “Slightly agree”, “Neither agree or disagree”, “Slightly disagree”, “Completely disagree”. *[5-point Likert scale]*
3.1. More plant variety results in less soil lost due to water action.
3.2. In areas with less variety of living beings, people are less affected by infectious diseases.
3.3. Farms closer to forests are more attacked by herbivorous pests.
3.4. If a farm is in a region with more variety of living beings, it will be less attacked by plant diseases.
3.5. If the forests in (Amapá/Pará) are converted to agriculture, the rainfall regime would remain the same.
3.6. A forest with a greater variety of trees and lianas absorbs more carbon from the atmosphere.
3.7. Areas close to forests are hotter than urban areas.
3.8. If there were less different types of bees that would be bad for agriculture.
3.9. A remote forest (like Tumucumaque) is more resistant to prolonged droughts than a forest close to where people live.
3.10. In a region with more forest, water quality is the same as in a region with less forest.

Section IV

4. Please tell us whether you agree or disagree with the following sentences, choosing one of the following five options: “Completely agree”, “Slightly agree”, “Neither agree or disagree”, “Slightly disagree”, “Completely disagree”. *[5-point Likert scale]*
4.1. A landscape where trees have different colours and shapes is not prettier than a landscape where trees are all the same.

4.2. Living in a region with such richness of animals and plants makes me feel more connected to God.
4.3. Preserving the wildlife of (Amapá/Pará) is indifferent for tourism.
4.4. In a native forest, scientists are more likely to make new discoveries, like new medicines.
4.5. Children learn more about nature if they visit a forest less used by people.
4.6. Nature is not part of my cultural heritage.
4.7. Areas with more nature make me feel stressed.
4.8. If the forests of (Amapá/Pará) lost part of its richness, Brazil would also lose part of what makes it unique.
4.9. Knowing that some places have lots of different animals and plants is indifferent to me.
4.10. I hope future generations can see the same animals and plants that I saw when I was a child.

Section V

5. Please tell us whether you agree or disagree with the following sentences, choosing one of the following five options: “Completely agree”, “Slightly agree”, “Neither agree or disagree”, “Slightly disagree”, “Completely disagree”. *[5-point Likert scale]*
5.1. It is good that a large share of (Amapá/Pará) is part of a protected area.
5.2. The balance of nature is delicate and easily upset.
5.3. It is important to maintain jaguars in the Amazon because they have always been here.
5.4. We have the right to use nature any way we want.
5.5. Protecting economic growth is more important than protecting nature.
5.6. Public money should also be used to protect forests and endangered living beings.
5.7. I would prefer less protected areas because that would increase job creation.
5.8. Hunting and fishing in the Amazon should be unrestricted.
5.9. I would not mind if most forests in Amapá were cleared for agriculture.
5.10. We have to protect nature even if it means that livelihoods will be lower.

Section VI

6. I will now show you pictures of 12 animals and plants. In your opinion, which of them exist in this region? Answer “Yes” if you think the animal/plant shown exists in this region, “No” if you think it does not exist in this region. *[Y/N] [Images shown randomly]*
Present
6.1. *Eperua rubiginosa* (plant)
6.2. *Chelonoidis denticulata* (yellow-footed tortoise)
6.3. *Heliconia bihai* (plant)
6.4. *Tangara chilensis* (paradise tanager)
6.5. *Tamandua tetradactyla* (collared anteater)
6.6. *Alouatta macconnelli* (Guiana red howler monkey)
Absent
6.7. *Araucaria angustifolia* (Paraná pine)
6.8. *Varanus komodoensis* (Komodo dragon)
6.9. *Eryngium amethystinum* (plant)
6.10. *Buceros bicornis* (great hornbill)
6.11. *Papio cynocephalus* (yellow baboon)
6.12. *Neofelis nebulosa* (clouded leopard)

Section VII

7. Lastly, in this section we would like to know a bit more about you.
7.1. Age *[Open]*
7.2. Gender *[F/M]*
7.3. Do you live in the same locality since birth? *[Y/N]*
7.3.1. If not, in what year have you moved in? *[Open]*
7.4. Main occupation? *[Open]*
7.5. What is your average monthly income? *[Less than 937 R$; Between 937 and 1874 R$; More than 1874 R$]*
7.6. What is your educational level? *[None; Up to year 9; Up to year 12; Terciary]*
7.7. Are you a land owner? *[Y/N]*
7.7.1. If yes, what is the size, in hectares or m2, of your land property? *[Open]*
7.8. Do you raise livestock? *[Y/N]*

7.9. Do you plant agricultural products? *[Y/N]*
7.10. Are you a Brazil nut producer? *[Y/N]*

Text B2. References supporting the BES links mentioned in the questionnaire. The numbers highlighted in bold refer to the sentence numbering in the questionnaire.

S2.1. Peres, C.A. (2000) ‘Effects of subsistence hunting on vertebrate community structure in Amazonian forests’, *Conserv. Biol.*, 14, pp. 240–253.

S2.2./ S2.3./ S2.4./ S2.5./ S3.3./ S3.4./ S3.6. Cardinale, B.J. *et al.* (2012) ‘Biodiversity loss and its impact on humanity’, *Nature*, 486, pp. 59–67.

S2.6. Alves, R.R.N., Rosa, I.M.L. (2007) ‘Biodiversity, traditional medicine and public health: where do they meet?’, *J. Ethnobiol. Ethnomed.*, 3(14).

S2.7. Tuck Haugaasen, J.M. *et al.* (2012) ‘Fruit Removal and Natural Seed Dispersal of the Brazil Nut Tree (*Bertholletia excelsa*) in Central Amazonia, Brazil’, *Biotropica*, 44, pp. 205–210.

S2.8. Roe, D. *et al.* (2014) ‘Which components or attributes of biodiversity influence which dimensions of poverty?’, *Environ. Evid.*, 3(3).

S2.9. Siebert, S.F. (2004) ‘Demographic effects of collecting rattan cane and their implications for sustainable harvesting’, *Conserv. Biol.*, 18, pp. 424–431.

S2.10. Daw, T. *et al.* (2011) ‘Applying the ecosystem services concept to poverty alleviation: The need to disaggregate human well-being’, *Environ. Conserv.*, 38, pp. 370–379.

S3.1. Quijas, S., Schmid, B., Balvanera, P. (2010) ‘Plant diversity enhances provision of ecosystem services: A new synthesis’, *Basic Appl. Ecol.*, 11, pp. 582–593.

S3.2. Keesing, F. *et al.* (2010) ‘Impacts of biodiversity on the emergence and transmission of infectious diseases’, *Nature*, 468, pp. 647–652.

S3.5. Spracklen, D. V., Arnold, S.R., Taylor, C.M. (2012) ‘Observations of increased tropical rainfall preceded by air passage over forests’, *Nature*, 489, pp. 282–285.

S3.7. Nobre, C.A., Sellers, P.J., Shukla, J. (1991) ‘Amazonian Deforestation and Regional Climate Change’, *J. Clim.*, 4, pp. 957–988.

S3.8. Garibaldi, L.A. *et al.* (2016) ‘Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms’, *Science*, 351, pp. 388–391.

S3.9. Isbell, F. *et al.* (2015) ‘Biodiversity increases the resistance of ecosystem productivity to climate extremes’, *Nature*, 526, pp. 574–577.

S3.10. Martínez, M.L. *et al.* (2009) ‘Effects of land use change on biodiversity and ecosystem services in tropical montane cloud forests of Mexico’, *For. Ecol. Manage.*, 258, pp. 1856–1863.

S4.1./ S4.3. Daniel, T.C. *et al.* (2012) ‘Contributions of cultural services to the ecosystem services agenda’. *Proc. Natl. Acad. Sci. U. S. A.*, 109, pp. 8812–9.

S4.2./ S4.5./ S4.6./ S4.8. Russell, R. *et al.* (2013) ‘Humans and Nature: How Knowing and Experiencing Nature Affect Well-Being’, *Annu. Rev. Environ. Resour.*, 38, pp. 473–502.

S4.4./ S4.9./ S4.10. Chan, K.M.A., Satterfield, T., and Goldstein, J., (2012) ‘Rethinking ecosystem services to better address and navigate cultural values’, *Ecol. Econ.*, 74, pp. 8–18.

S4.7. Keniger, L.E. *et al.* (2013) ‘What are the benefits of interacting with nature?’, *Int. J. Environ. Res. Public Health*, 10, pp. 913–35.

Table B1. Descriptive summary with absolute frequencies for all questions in Sections I and VII of the questionnaire, plus disaggregation per interviewer and location.

1.1. Lives there	**N:** 9	**Y:** 392				
1.2. Used any forest product last month	**N:** 147	**Y:** 242	**NA:** 12			
1.3. Percentage of food obtained on forest areas	**0–10%:** 250	**11–40%:** 71	**41–70%:** 52	**71–100%:** 23	**NA:** 5	
1.4. Income from forest products last month	**N:** 272	**Y:** 114	**NA:** 15			
1.5. How often enters the forest	**Never:** 105	**Some times per year:** 132	**1-3 times per month:** 74	**1+ times per week:** 90		
1.6. Motives for forest entry	**Provisio.:** 124	**Cultural:** 173	**Others:** 59	**NA:** 109		
7.1. Age	**x̄:** 39.6	**s.d.:** 15.9				
7.2. Gender	**F**: 218	**M**: 183				
7.3. Lives same place since birth	**N:** 190	**Y:** 207	**NA:** 4			
7.4. Main occupation	**Pensioner:** 29	**Primary:** 26	**Unemployed or student:** 115	**Tertiary:** 170	**NA:** 61	
7.5. Monthly income	**< R$937:** 231	**R$937 - R$1874:** 103	**> R$1874:** 67			
7.6. Education level	**No school:** 22	**Primary:** 148	**Second.:** 180	**Tertiary:** 51		
7.7. Land owner	**N:** 325	**Y:** 76				
7.8. Raises livestock	**N:** 395	**Y:** 6				
7.9. Farming	**N:** 255	**Y:** 146				
7.10. Brazil nut production	**N:** 322	**Y:** 79				
Interviewers	**A:** 91	**B:** 53	**C:** 59	**D:** 83	**E:** 48	**F:** 67
Localities	**Açaizal:** 8	**Água Branca:** 17	**Bandeira:** 12	**Braço:** 10	**Dona Maria:** 5	**Laranjal do Jari:** 152
	Macapá: 103	**Marinho:** 11	**Martins:** 14	**Monte Dourado:** 40	**Planalto:** 18	**São Miguel:** 11

Notes: Total of 401 respondents sampled. Unanswered questions (NAs) indicated in table, whenever present. Q1.6: “Provisioning” aggregates motives linked with provisioning services, such as food gathering or material extraction; “Cultural” aggregates motives linked with cultural services, such as hiking or visiting a waterfall; “Others” include all motives that do not fit in the previous two categories; respondents could mention more than one motive. Q7.4: “Unemployed” includes housewifes; “Primary” refers to activities in the primary sector; “Tertiary” to activities in the services sector. Q7.5: The Brazilian minimum salary in 2017 was R$937 (Decree no 8.948/2016). Q7.6: Secondary education refers to 10 to 12 school years; Tertiary education includes professional degrees after 12 school years.

Table B2. Disaggregated percentage of respondents that identified each BES link, or stated a positive attitude, in sections II (perceptions on BpES links), III (perceptions on BrES links), IV (perceptions on BcES links), and V (attitudes towards conservation). N= 401 respondents.

Sentences applied in the questionnaire	%
2.1. In a native forest bush meat is as easy to find as in a secondary forest.	34.9
2.2. The preservation of plant variety is indifferent for agricultural production.	74.6
2.3. Living near a river full of different fishes gives me more confidence that the fish yield will always be good.	92.8
2.4. In a forest with more variety of trees, wood production is lower.	81.3
2.5. A pasture with more variety of plants produces more food for cattle.	62.8
2.6. If I need any medicinal plant, I can find it even in a secondary forest.	49.9
2.7. Brazil nut production is improved in a forest with more variety of animals.	75.3
2.8. In a secondary forest there are less fruits I can eat than in a native forest.	71.1
2.9. A forest closer to a village will have as much rattan as a more distant forest.	81.8
2.10. Protecting the forest helps poorer communities secure their livelihoods.	96.0
3.1. More plant variety results in less soil lost due to water action.	55.4
3.2. In areas with less variety of living beings, people are less affected by infectious diseases.	30.9
3.3. Farms closer to forests are more attacked by herbivorous pests.	29.7
3.4. If a farm is in a region with more variety of living beings, it will be less attacked by plant diseases.	48.4
3.5. If the forests in (Amapá/Pará) are converted to agriculture, the rainfall regime would remain the same.	69.3
3.6. A forest with a greater variety of trees and lianas absorbs more carbon from the atmosphere.	83.3
3.7. Areas close to forests are hotter than urban areas.	94.8
3.8. If there were less different types of bees that would be bad for agriculture.	68.1
3.9. A remote forest (like Tumucumaque) is more resistant to prolonged droughts than a forest close to where people live.	88.5
3.10. In a region with more forest, water quality is the same as in a region with less forest.	84.5
4.1. A landscape where trees have different colours and shapes is not prettier than a landscape where trees are all the same.	71.8
4.2. Living in a region with such richness of animals and plants makes me feel more connected to God.	93.3
4.3. Preserving the wildlife of (Amapá/Pará) is indifferent for tourism.	79.6
4.4. In a native forest, scientists are more likely to make new discoveries, like new medicines.	97.0
4.5. Children learn more about nature if they visit a forest less used by people.	93.0
4.6. Nature is not part of my cultural heritage.	78.3
4.7. Areas with more nature make me feel stressed.	96.5
4.8. If the forests of (Amapá/Pará) lost part of its richness, Brazil would also lose part of what makes it unique.	94.5
4.9. Knowing that some places have lots of different animals and plants is indifferent to me.	77.1
4.10. I hope future generations can see the same animals and plants that I saw when I was a child.	94.5
5.1. It is good that a large share of (Amapá/Pará) is part of a protected area.	95.8
5.2. The balance of nature is delicate and easily upset.	79.6
5.3. It is important to maintain jaguars in the Amazon because they have always been here.	95.8
5.4. We have the right to use nature any way we want.	91.0
5.5. Protecting economic growth is more important than protecting nature.	82.3
5.6. Public money should also be used to protect forests and endangered living beings.	96.5
5.7. I would prefer less protected areas because that would increase job creation.	65.6
5.8. Hunting and fishing in the Amazon should be unrestricted.	78.8
5.9. I would not mind if most forests in Amapá were cleared for agriculture.	75.1
5.10. We have to protect nature even if it means that livelihoods will be lower.	81.5

Table B3. All models for overall BES perceptions with substantial level of empirical support (Δ AICc <2).

	df	**LogLikelihood**	**AICc**	**delta**	**weight**
Brazil nut, Gender, Income	5	-1012.72	2035.59	0	0.23
Brazil nut, Gender, Income, Rural	6	-1012.25	2036.72	1.13	0.13
Brazil nut, Forest use, Gender, Income	6	-1012.29	2036.79	1.2	0.13
Brazil nut, Income	4	-1014.46	2037.03	1.44	0.11
Brazil nut, Gender, Income, Landowner	6	-1012.45	2037.12	1.53	0.11
Brazil nut, Forest nearby, Gender, Income	6	-1012.54	2037.29	1.71	0.10
Age, Brazil nut, Gender, Income	6	-1012.58	2037.37	1.78	0.10
Biodiversity knowledge, Brazil nut, Gender, Income	6	-1012.63	2037.48	1.89	0.09

Table B4. Correlation matrix, using Kendall correlation coefficients, between the explanatory variables used in the perception models.

	Biodiv. know.	Brazil nut	Education	Forest nearby	Forest use	Gender: M	Income	Landowner	Rural
Age	-0.02	0.09	-0.36	0.02	-0.001	0.13	0.10	0.11	0.07
Biodiv. knowledge	1	0.26	-0.09	0.29	0.18	0.02	-0.06	-0.01	0.24
Brazil nut		1	-0.32	0.40	0.42	0.05	-0.18	0.19	0.70
Education			1	-0.27	-0.10	-0.12	0.22	-0.02	-0.34
Forest nearby				1	0.31	0.02	-0.15	0.01	0.55
Forest use					1	0.21	0.04	0.15	0.40
Gender: M						1	0.26	0.03	0.04
Income							1	0.11	-0.19
Landowner								1	0.14

Table B5. Variance Inflation Factors (VIF) calculated for the independent variables in the generalised linear mixed model with overall BES perception as response variable, as described in the data analysis section of Chapter 3.

	Age	Biodiv. know.	Brazil nut	Education	Forest nearby	Forest use	Gender: M	Income	Landowner	Rural
VIF	1.43	1.18	1.25	1.46	1.14	1.25	1.14	1.35	1.04	1.12

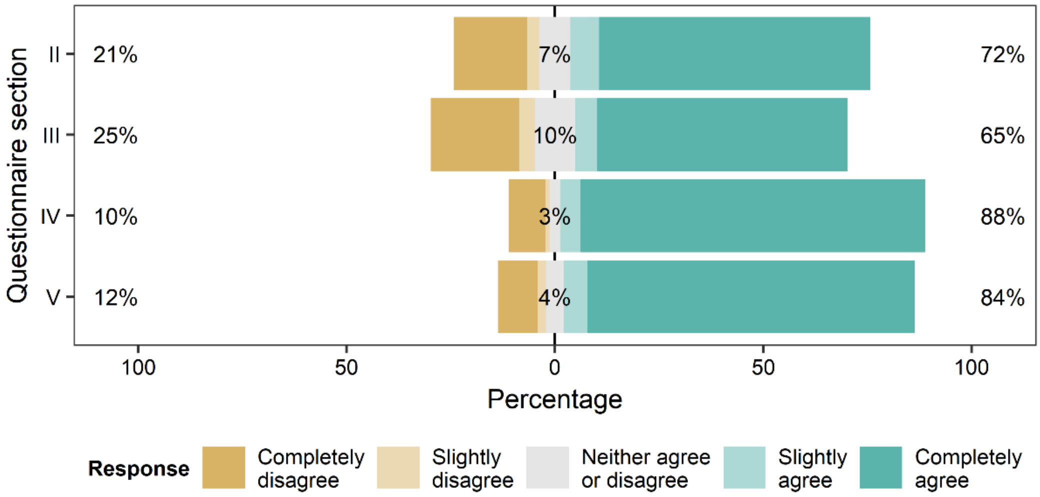


Figure B1. Distribution of the responses in each section of the questionnaire that applied a 5-point Likert scale. The percentages at each side of the plot refer to the sum of responses that strongly/moderately disagreed (left) or agreed (right) with the sentences. The percentages at the middle of the plot indicate “Neither agree or disagree” responses.

Appendix C

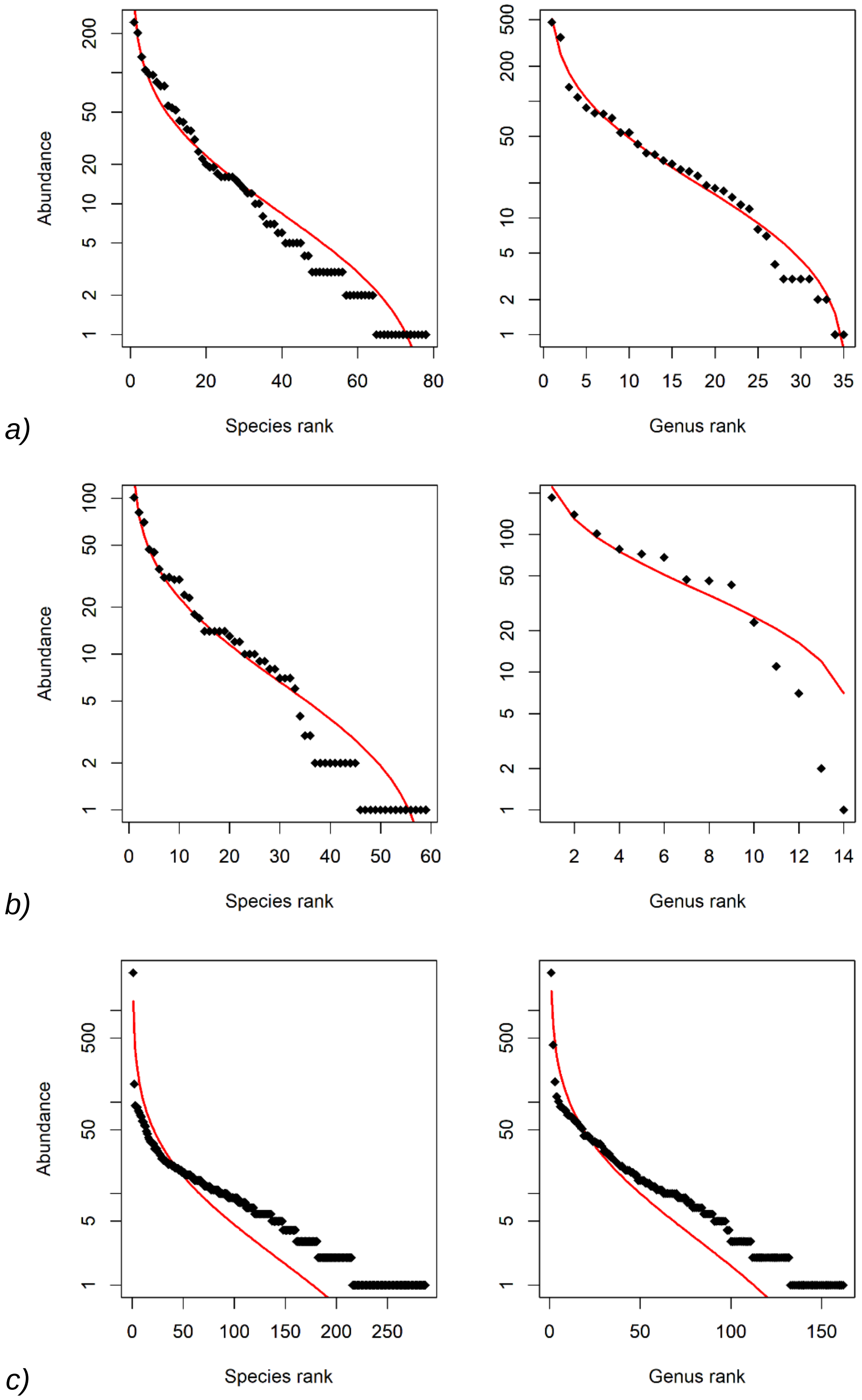


Figure C1. Rank abundance curves (in red), fitted with log-normal models, for butterflies (a), dung beetles (b), and trees (c). The curves on the left side are fitted on species level abundance data, while on the right curves are fitted on genus level data.

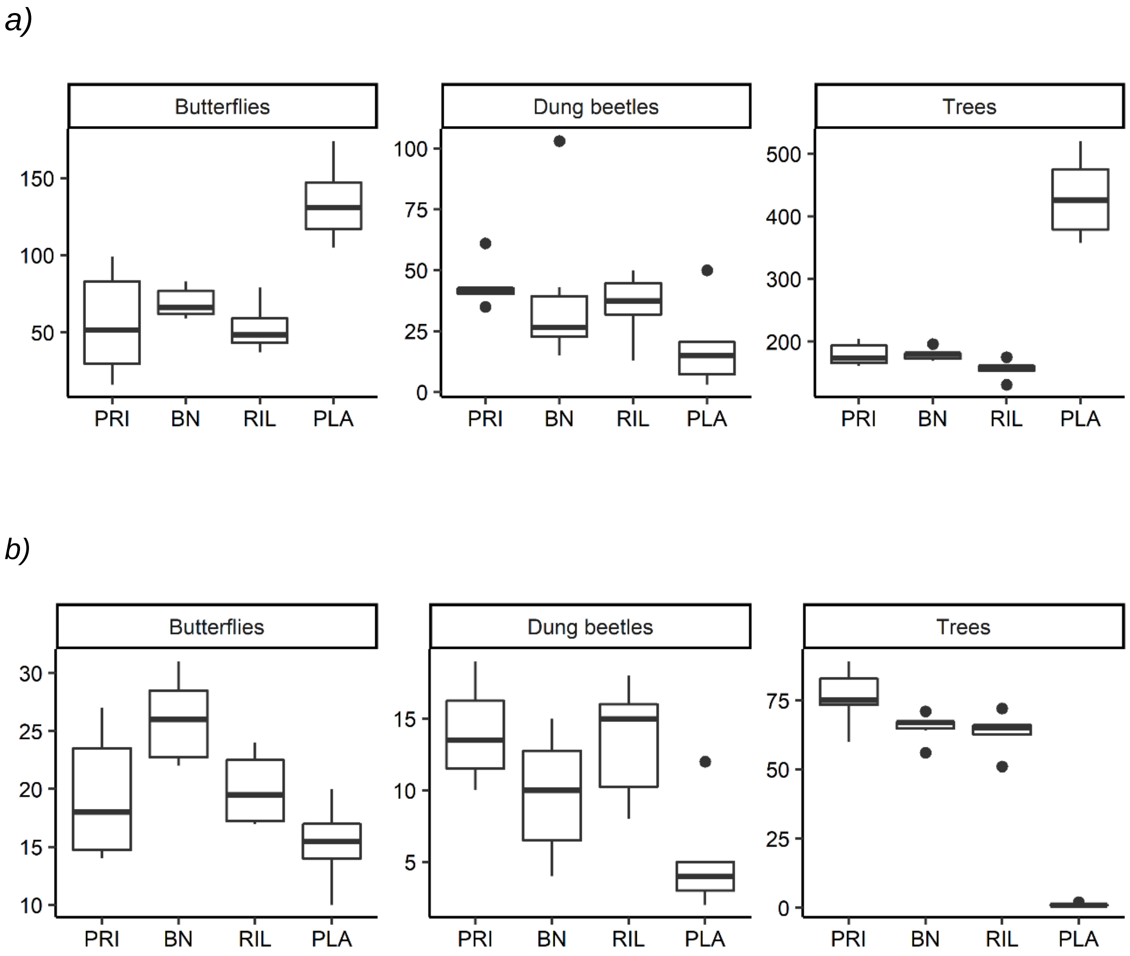
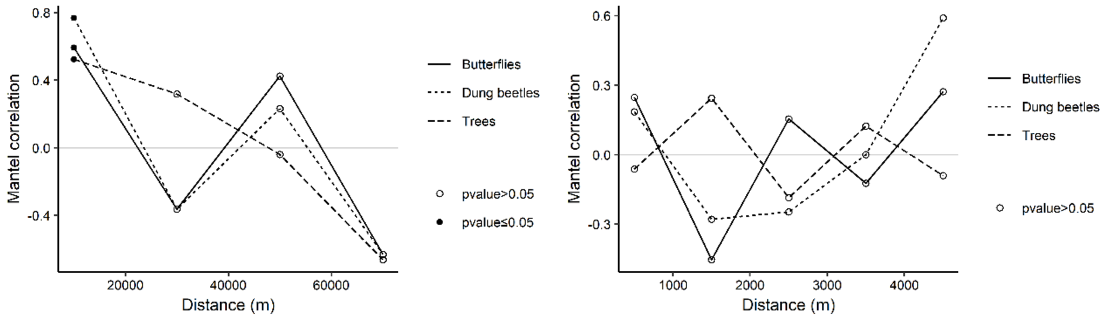
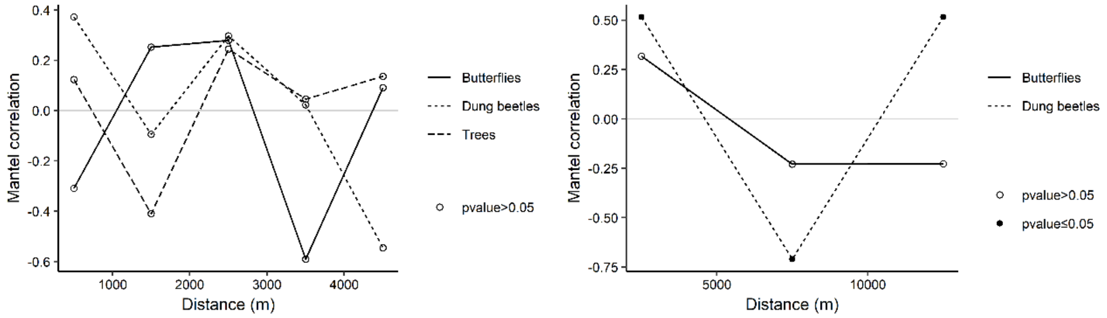


Figure C2. Site level variation in abundance (a) and richness (b) levels for butterflies, dung beetles, and trees, per forest use.



a) Old-growth forest

b) Brazil nut extraction



c) Reduced impact logging

d) Eucalyptus plantation

Figure C3. Correlograms for sampling points within the same forest use. The number of distance groups used varied between forest uses.

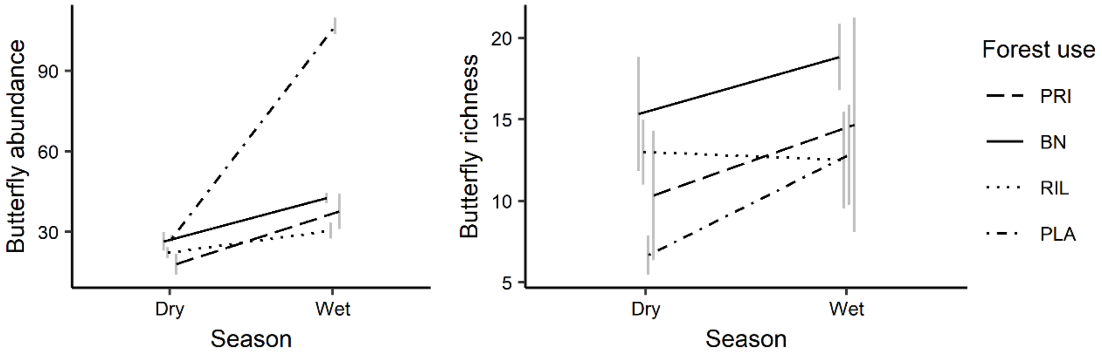


Figure C4. Seasonality of butterfly mean abundance (left) and richness (right) across sites. Grey lines indicate standard deviation.

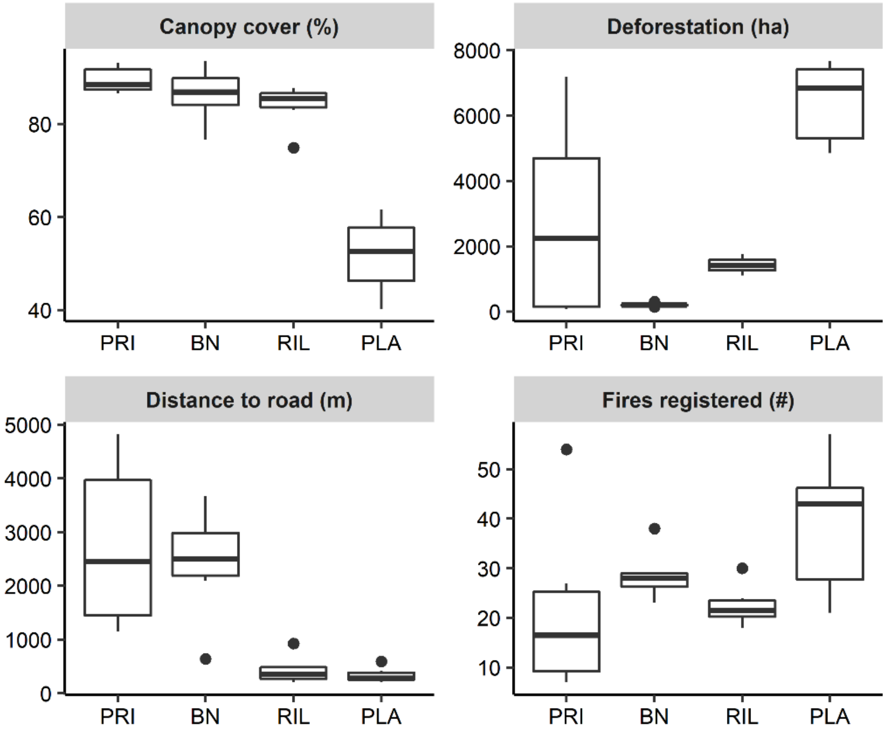


Figure C5. Box plots indicating variation across sampling sites, per forest use, in canopy openness (i.e., vegetation cover fraction), distance to nearest road, deforested area within a 5km radius, and number of registered fires within a 5km radius. Units of the y-axis are indicated in the title of each plot.

Table C1. Analysis of species indicator value (IndVal). Only species with p-values ≤ 0.01 are shown. 'Forest use' column indicates the forest uses associated with each indicator species (PRI: old-growth forest; BN: Brazil nut extraction area; RIL: reduced-impact logging; PLA: eucalyptus plantation).

Taxa	Species	IndVal	p-value	Forest use
SCARAB	*Canthidium sp.4*	0.80	0.01	PRI/ BN
SCARAB	*Deltochilum (Deltohyboma) sp.2*	1	0.001	RIL
SCARAB	*Dichotomius boreus*	0.94	0.001	PRI/RIL
SCARAB	*Uroxys sp.*	0.97	0.001	PRI/ BN
NYMPH	*Archaeoprepona demophon*	0.95	0.003	PRI/ BN/ RIL
NYMPH	*Bia actorion*	0.88	0.005	PRI/ BN/ RIL
NYMPH	*Caligo euphorbus*	0.78	0.004	BN
NYMPH	*Catoblepia berecynthia*	0.89	0.007	PRI/ BN
NYMPH	*Catonephele acontius*	0.92	0.002	PRI/ RIL
NYMPH	*Cissia penelope*	0.91	0.001	PLA
NYMPH	*Eryphanis automedon*	0.88	0.002	PRI/ BN
NYMPH	*Hamadryas februa*	1	0.001	PLA
NYMPH	*Hamadryas feronia*	0.91	0.001	PLA
NYMPH	*Hermeuptychia sp.*	0.90	0.002	PLA
NYMPH	*Magneuptychia libye*	0.91	0.001	PLA
NYMPH	*Magneuptychia newtonii*	0.82	0.004	PLA
NYMPH	*Mesoprepona pheridamas*	0.82	0.01	PRI/ BN
NYMPH	*Nessaea obrinus*	0.95	0.001	PRI/ BN
NYMPH	*Paryphthimoides sp.*	1	0.001	PLA
NYMPH	*Pseudodebis valentina*	0.97	0.001	BN
NYMPH	*Taygetis cleopatra*	0.94	0.001	PRI/ BN/ RIL
NYMPH	*Taygetis echo*	0.94	0.003	PRI/ BN/ RIL
NYMPH	*Taygetis zippora*	1	0.001	PRI/ BN/ RIL
TREES	*Apeiba burchellii*	0.85	0.004	BN/ RIL
TREES	*Aspidosperma sp.*	0.91	0.003	PRI/ BN/ RIL
TREES	*Didymopanax morototoni*	0.87	0.002	PRI/ BN
TREES	*Dinizia excelsa*	0.91	0.001	RIL
TREES	*Eschweilera sp.*	0.88	0.001	RIL
TREES	*Eucalyptus sp.*	1	0.001	PLA
TREES	*Geissospermum sericeum*	0.87	0.001	PRI/ RIL
TREES	*Guatteria sp.*	0.78	0.005	RIL
TREES	*Gustavia augusta*	0.89	0.001	BN
TREES	*Hebepetalum humiriifolium*	0.82	0.005	PRI/ BN
TREES	*Inga cayennensis*	0.87	0.001	PRI/ BN
TREES	*Inga gracilifolia*	0.77	0.01	BN
TREES	*Inga heterophylla*	0.82	0.006	PRI/ BN
TREES	*Iryanthera juruensis*	0.91	0.001	PRI/ BN
TREES	*Lecythis sp.*	0.82	0.005	PRI/ BN
TREES	*Manilkara bidentata*	0.88	0.003	RIL
TREES	*Manilkara huberi*	0.85	0.007	PRI/ RIL
TREES	*Maquira sclerophylla*	0.97	0.001	PRI/ BN/ RIL
TREES	*Ocotea douradensis*	0.9	0.001	PRI/ BN
TREES	*Paraprotium amazonicum*	0.91	0.002	PRI/ BN
TREES	*Pithecellobium racemosum*	0.9	0.001	RIL
TREES	*Pouteria jariensis*	0.96	0.001	RIL
TREES	*Protium decandrum*	0.91	0.003	PRI/ RIL
TREES	*Protium heptaphyllum*	0.82	0.005	PRI/ BN
TREES	*Protium sp.*	0.94	0.001	PRI/ BN/ RIL
TREES	*Rheedia sp.*	0.82	0.004	BN
TREES	*Sterculia pilosa*	0.89	0.001	PRI/ BN
TREES	*Tetragastris panamensis*	0.88	0.01	PRI/ BN/ RIL
TREES	*Theobroma sylvestre*	0.82	0.005	BN
TREES	*Thyrsodium guianense*	0.85	0.004	RIL
TREES	*Vantanea parviflora*	0.82	0.004	RIL
TREES	*Vouacapoua americana*	0.95	0.001	RIL

Table C2. List of the species sampled per taxon and corresponding abundance data disaggregated per forest use. The p-values shown were calculated with a Kruskal-Wallis test to determine if abundance levels between forest uses are significantly different for each species. Significant p-values are shown in bold.

Dung beetles	**BN**	**RIL**	**PLA**	**PRI**	**pvalue**
Ateuchus aff. connexus	11	29	1	6	**0.007**
Ateuchus aff. murrayi	3	21	0	0	0.079
Ateuchus irinus	34	0	0	1	0.065
Ateuchus pauki	0	1	0	0	0.392
Ateuchus sp.1	0	0	0	1	0.392
Ateuchus sp.2	2	0	6	0	0.262
Ateuchus sp.3	1	0	0	0	0.392
Ateuchus sp.4	1	0	0	0	0.392
Ateuchus sp.5	3	4	0	0	**0.033**
Ateuchus sp.6	14	0	0	0	**0.02**
Canthidium aff. deyrollei	1	0	0	13	0.059
Canthidium aff. lentum	0	0	14	0	**0.02**
Canthidium sp.1	2	0	0	1	0.26
Canthidium sp.2	0	0	0	6	0.099
Canthidium sp.3	0	2	0	0	0.392
Canthidium sp.4	21	1	0	8	**0.02**
Canthidium sp.5	1	1	0	0	0.554
Canthidium sp.6	1	0	0	0	0.392
Canthon bicolor	5	0	0	4	0.057
Canthon scrutator	0	0	4	0	0.392
Canthon simulans	0	0	13	0	0.1
Canthon subhyalinus	0	0	2	0	0.392
Canthon triangularis	0	7	1	10	0.108
Coprophanaeus jasius	0	0	1	0	0.392
Coprophanaeus lancifer	0	8	0	2	**0.02**
Deltochilum (Deltohyboma) sp.1	0	1	29	1	**0.032**
Deltochilum (Deltohyboma) sp.2	0	12	0	0	**0**
Deltochilum carinatum	0	0	0	2	0.392
Deltochilum icarus	1	5	0	6	0.09
Deltochilum orbiculare	0	1	0	6	0.235
Deltochilum septemstriatum	7	4	0	3	0.118
Dichotomius aff. lucasi	52	8	2	19	0.056
Dichotomius apicalis	0	0	0	3	0.1
Dichotomius boreus	2	43	1	24	**0.003**
Dichotomius imitator	0	0	1	0	0.392
Dichotomius latilobatus	0	0	1	0	0.392
Dichotomius mamillatus	0	0	0	9	0.392
Dichotomius roberti	0	0	0	2	0.099
Dichotomius subaeneus	0	1	0	0	0.392
Dichotomius worontzowi	4	2	6	5	0.933
Eurysternus atrosericus	0	8	1	5	**0.021**
Eurysternus balachowskyi	0	1	0	1	0.554
Eurysternus caribaeus	1	16	2	12	0.057
Eurysternus foedus	0	1	0	1	0.554
Eurysternus hamaticollis	0	6	0	4	0.098
Eurysternus hypocrita	0	0	0	8	**0.02**
Eurysternus vastiorum	0	0	0	1	0.392
Ontherus carinifrons	0	0	22	1	0.248
Onthophagus aff. bidentatus	1	2	0	7	0.411
Onthophagus aff. clypeatus	0	0	0	1	0.392
Onthophagus aff. haemathopus	4	15	0	11	0.055
Onthophagus aff. hirculus	0	0	0	1	0.392

Onthophagus onthochromus	0	0	1	0	0.392
Oxysternon durantoni	0	0	0	2	0.099
Oxysternon festivum	2	8	2	33	0.168
Phanaeus chalcomelas	0	0	0	7	0.1
Sulcophanaeus faunus	0	1	0	1	0.554
Trichillum pauliani	0	1	0	0	0.392
Uroxys sp.	62	5	0	34	**0.002**

Butterflies	**BN**	**RIL**	**PLA**	**PRI**	**pvalue**
Amphidecta calliomma	2	0	0	0	0.099
Archaeoprepona amphimachus	4	1	1	0	0.477
Archaeoprepona demophon	24	14	2	16	**0.015**
Archaeoprepona licomedes	3	0	0	4	0.207
Archaeoprepona meander	1	2	0	0	0.26
Bia actorion	13	6	0	24	**0.018**
Caeruleuptychia aff. coelestis	0	1	0	0	0.392
Caeruleuptychia brixius	1	0	0	0	0.392
Caeruleuptychia urania	0	1	0	0	0.392
Caligo brasiliensis	4	2	0	1	0.211
Caligo euphorbus	14	2	0	3	**0.009**
Catoblepia berecynthia	20	4	1	12	**0.004**
Catoblepia versitincta	1	0	0	0	0.392
Catoblepia xanthus	10	5	0	1	**0.028**
Catonephele acontius	7	65	0	13	**0.003**
Catonephele numilia	0	2	1	0	0.26
Chloreuptychia agatha	4	0	0	1	0.07
Chloreuptychia chlorimene	0	3	0	0	0.1
Cissia myncea	0	0	1	1	0.554
Cissia penelope	0	0	10	0	**0**
Cissia terrestris	1	7	6	3	0.574
Colobura cf. annulata	4	2	1	5	0.654
Colobura dirce	11	29	41	15	0.115
Erichthodes antonina	0	0	0	3	0.1
Eryphanis automedon	4	1	0	10	**0.001**
Fountainea ryphea	0	0	2	0	0.099
Hamadryas amphinome	0	0	6	0	**0.02**
Hamadryas arinome	0	1	1	0	0.554
Hamadryas chloe	0	0	0	1	0.392
Hamadryas februa	0	1	241	1	**0**
Hamadryas feronia	0	1	96	0	**0.001**
Hamadryas iphthime	0	0	3	0	**0.02**
Hamadryas laodamia	0	0	1	0	0.392
Hermeuptychia sp.	0	0	30	1	**0.002**
Historis odius	0	0	3	0	0.1
Hypna clytemnestra	4	5	0	4	0.223
Junonia evarete	0	0	1	0	0.392
Magneuptychia libye	0	0	22	0	**0**
Magneuptychia newtonii	0	0	8	0	**0.003**
Magneuptychia tricolor	4	0	0	1	0.07
Memphis cf. acidalia	2	5	8	1	0.237
Memphis laertes	2	0	0	0	0.392
Memphis oenomais	1	0	1	0	0.554
Memphis polycarmes	2	0	0	1	0.26
Mesoprepona pheridamas	33	6	0	15	**0.014**
Morpho achilles	4	4	1	5	0.497
Morpho deidamia	1	0	0	0	0.392
Morpho helenor	5	8	1	6	0.067

Morpho menelaus	1	0	0	0	0.392
Nessaea obrinus	45	1	1	32	**0.001**
Opsiphanes cassiae	2	1	1	0	0.513
Opsiphanes cassina	2	0	0	0	0.392
Opsiphanes invirae	3	3	0	1	0.156
Opsiphanes quiteria	1	0	0	4	0.234
Pareuptychia lydia	9	9	0	18	0.071
Pareuptychia ocirrhoe	10	15	2	15	0.113
Paryphthimoides sp.	0	0	131	1	**0**
Posttaygetis penelea	4	0	0	0	**0.02**
Prepona claudina	0	1	0	0	0.392
Prepona narcissus	0	0	0	1	0.392
Prepona rhenea	3	2	0	0	0.088
Pseudodebis celia	1	0	0	0	0.392
Pseudodebis valentina	15	0	0	1	**0**
Taygetina kerea	0	1	0	0	0.392
Taygetis cleopatra	37	46	1	21	**0.003**
Taygetis echo	29	8	0	15	**0.002**
Taygetis laches	12	2	162	26	**0.029**
Taygetis larua	2	0	0	0	0.099
Taygetis leuctra	0	1	0	0	0.392
Taygetis mermeria	4	0	0	6	**0.041**
Taygetis rufomarginata	4	6	5	4	0.88
Taygetis sosis	0	4	1	0	0.248
Taygetis zippora	34	22	0	23	**0.003**
Temenis laothoe	0	1	2	0	0.26
Tigridia acesta	7	5	0	13	**0.01**
Yphthimoides renata	0	2	9	1	0.062
Zaretis isidora	2	0	1	0	0.26
Zaretis itys	2	9	1	4	0.054

Trees	**BN**	**RIL**	**PLA**	**PRI**	**pvalue**
Acosmium nitens	0	3	0	1	0.248
Alexa grandiflora	0	0	0	1	0.392
Amanoa guianensis	1	2	0	3	0.433
Anacardium giganteum	0	1	0	1	0.554
Anaxagorea dolichocarpa	1	0	0	0	0.392
Aniba sp.	4	4	0	8	**0.048**
Antonia ovata	2	3	0	0	0.088
Apeiba burchellii	13	7	0	3	**0.004**
Aspidosperma carapanauba	2	3	0	2	0.295
Aspidosperma desmanthum	0	0	0	1	0.392
Aspidosperma eteanum	10	1	0	6	0.09
Aspidosperma megalocarpon	0	0	0	1	0.392
Aspidosperma sp.	9	17	0	15	**0.013**
Astronium gracile	0	5	0	5	**0.032**
Bagassa guianensis	0	0	0	1	0.392
Batesia floribunda	1	0	0	0	0.392
Bauhinia sp.	1	6	0	0	0.553
Beilschmiedia sp.	3	0	0	6	0.054
Bellucia dichotoma	4	1	0	14	0.409
Bertholletia excelsa	10	0	0	4	**0.024**
Bombacopsis nervosa	0	0	0	1	0.392
Bowdichia nitida	6	3	0	7	0.208
Brosimum parinarioides	5	1	0	4	0.216
Buchenavia grandis	0	2	0	0	0.392
Buchenavia parvifolia	1	0	0	3	0.553

Buchenavia sp.	0	2	0	2	0.286
Byrsonima aerugo	0	0	0	3	0.1
Capirona decorticans	0	1	0	0	0.392
Carapa guianensis	4	0	0	3	0.099
Caryocar glabrum	0	1	0	0	0.392
Caryocar villosum	5	3	0	4	0.172
Casearia javitensis	0	1	0	0	0.392
Cecropia obtusa	5	1	1	4	0.197
Cecropia sp.	2	0	0	4	0.201
Cedrela odorata	0	0	0	2	0.099
Cedrelinga sp.	1	0	0	0	0.392
Ceiba pentandra	1	0	0	2	0.553
Chamaecrista bahiae	3	0	0	3	0.099
Chaunochiton kappleri	0	0	0	1	0.392
Chimarrhis turbinata	6	10	0	4	0.066
Conceveiba guianensis	2	1	0	1	0.776
Conceveiba martiana	6	0	0	4	0.092
Copaifera martii	0	2	0	0	0.099
Couepia robusta	0	1	0	0	0.392
Couma guianensis	0	1	0	1	0.554
Couratari pulchra	3	3	0	2	0.467
Couroupita sp.	0	1	0	0	0.392
Dacryodes nitens	1	0	0	3	0.248
Dialium guianense	3	3	0	0	0.053
Didymopanax morototoni	11	0	0	7	**0.004**
Dimorphandra multiflora	0	0	0	1	0.392
Dinizia excelsa	0	6	0	0	**0**
Diospyros santaremnensis	0	3	0	2	0.205
Diospyros sp.	0	0	0	4	0.099
Diplotropis purpurea	1	1	0	6	0.134
Diplotropis racemosa	1	2	0	1	0.513
Dipteryx magnifica	0	0	0	1	0.392
Dipteryx odorata	10	5	0	13	**0.038**
Drypetes variabilis	0	2	0	1	0.553
Duguetia surinamensis	0	1	0	2	0.26
Duroia macrophylla	1	0	0	4	0.248
Duroia sp.	2	0	0	3	0.274
Dussia discolor	0	2	0	0	0.392
Ecclinusa abbreviata	1	0	0	0	0.392
Endopleura uchi	1	4	0	1	0.477
Enterolobium schomburgkii	1	3	0	0	0.248
Enterolobium sp.	1	0	0	2	0.553
Eriotheca globosa	2	0	0	0	0.099
Erisma laurifolium	0	1	0	0	0.392
Erisma sp.	0	1	0	0	0.392
Eschweilera amazonica	0	3	0	4	0.286
Eschweilera coriacea	0	0	0	1	0.392
Eschweilera obversa	0	1	0	0	0.392
Eschweilera odora	27	8	0	13	**0.011**
Eschweilera sp.	0	13	0	1	**0.002**
Eucalyptus sp.	0	0	2583	0	**0**
Eugenia patrisii	0	0	0	1	0.392
Ferdinandusa paraensis	0	2	0	1	0.26
Ficus nymphaeifolia	0	2	0	1	0.26
Geissospermum sericeum	0	45	0	16	**0.001**
Glycydendron sp.	0	1	0	0	0.392
Goupia glabra	8	8	0	8	0.184
Guarania sp.	0	0	0	1	0.392
Guarea silvatica	0	0	0	12	**0.02**

Guarea sp.	0	0	0	15	**0.02**
Guatteria poeppigiana	9	3	0	9	0.063
Guatteria sp.	0	11	0	1	**0.01**
Guazuma ulmifolia	0	1	0	1	0.554
Gustavia augusta	65	0	0	4	**0.005**
Hebepetalum humiriifolium	12	0	0	10	**0.009**
Helicostylis sp.	0	9	0	5	0.098
Herrania mariae	0	2	0	1	0.553
Hevea brasiliensis	2	0	0	0	0.392
Himatanthus sucuuba	1	0	0	1	0.554
Hirtella bicornis	1	0	0	2	0.553
Hirtella piresii	12	1	0	3	0.051
Hirtella sp.	7	8	0	1	**0.031**
Hymenaea courbaril	1	1	0	0	0.554
Hymenaea intermedia	0	1	0	0	0.392
Hymenaea parvifolia	0	1	0	1	0.554
Hymenolobium excelsum	0	1	0	0	0.392
Hymenolobium sericeum	0	0	0	1	0.392
Inga acrocephala	0	0	0	2	0.099
Inga alba	4	0	0	15	**0.02**
Inga cayennensis	10	0	0	5	**0.003**
Inga gracilifolia	9	0	0	1	**0.012**
Inga heterophylla	6	0	0	15	**0.01**
Inga negrensis	5	0	0	1	0.07
Inga paraensis	0	5	0	2	0.078
Inga rubiginosa	1	2	0	0	0.26
Inga splendens	3	0	0	21	0.054
Inga subsericantha	0	0	0	7	**0.02**
Inga tarapotensis	1	0	0	0	0.392
Iryanthera juruensis	24	0	0	21	**0.001**
Iryanthera sp.	4	0	0	2	0.091
Jacaranda copaia	0	2	0	52	0.205
Jacaratia sp.	0	0	0	1	0.392
Lacmellea gracilis	0	0	0	1	0.392
Lacunaria spruceana	0	0	0	1	0.392
Laetia procera	13	10	0	6	0.158
Lecythis corrugata	0	1	0	0	0.392
Lecythis lurida	0	0	0	2	0.099
Lecythis poiteaui	5	0	0	2	**0.022**
Lecythis sp.	15	0	0	4	**0.004**
Lecythis usitata	10	3	0	1	**0.013**
Licania heteromorpha	3	0	0	3	0.053
Licania laevigata	0	0	0	2	0.392
Licania latifolia	17	11	0	9	**0.027**
Licania micrantha	0	16	0	2	**0.018**
Licania robusta	0	3	0	0	0.1
Licania sp.	1	4	0	1	0.18
Licaria cannella	2	0	0	0	0.392
Luehea speciosa	1	0	0	1	0.554
Macoubea guianensis	6	0	0	3	**0.007**
Manilkara bidentata	0	13	0	1	**0.002**
Manilkara huberi	1	16	0	6	**0.002**
Maquira guianensis	0	3	0	0	0.392
Maquira sclerophylla	44	17	0	19	**0.005**
Mezilaurus itauba	4	0	0	1	0.07
Mezilaurus lindaviana	9	1	0	3	0.064
Miconia guianensis	4	0	0	13	**0.018**
Miconia rosea	2	1	0	10	**0.012**
Miconia sp.	0	0	0	1	0.392

Miconia surinamensis	0	2	0	6	0.077
Micropholis mensalis	1	0	0	1	0.554
Minquartia guianensis	3	2	0	5	0.333
Mouriri brachyanthera	5	5	0	10	**0.045**
Mouriri brevipes	0	1	0	3	0.248
Mouriri collocarpa	9	5	0	5	**0.012**
Mouriri sp.	2	11	0	1	**0.012**
Myrcia fallax	0	1	0	1	0.554
Myrciaria floribunda	0	2	0	0	0.392
Neea constricta	0	1	0	1	0.554
Neea sp.	0	5	0	0	0.1
Nemaluma engleri	0	0	0	2	0.099
Ocotea amazonica	0	0	0	1	0.392
Ocotea douradensis	22	1	0	16	**0.002**
Ocotea sp.	0	1	0	1	0.554
Oenocarpus bacaba	6	16	0	15	0.085
Onychopetalum amazonicum	0	2	0	3	0.553
Ormosia coccinea	1	1	0	0	0.554
Ormosia coutinhoi	1	0	0	0	0.392
Ormosia paraensis	0	1	0	1	0.554
Osteophloeum platyspermum	2	0	0	1	0.26
Ouratea oliviformis	3	1	0	7	0.424
Paraprotium amazonicum	29	0	0	33	**0.001**
Parinari excelsa	5	2	0	11	0.056
Parkia oppositifolia	1	4	0	5	0.139
Parkia pendula	3	3	0	3	0.267
Parkia reticulata	0	0	0	1	0.392
Parkia ulei	0	0	0	2	0.099
Peltogyne paniculata	0	0	0	1	0.392
Peltogyne paradoxa	0	1	0	0	0.392
Pentaclethra macroloba	10	0	0	0	0.392
Persea jariensis	22	3	0	10	0.127
Piptadenia communis	1	6	0	4	0.202
Pithecellobium decandrum	1	6	0	4	**0.033**
Pithecellobium racemosum	0	18	0	4	**0**
Pithecellobium sp.	1	2	0	0	0.553
Platonia insignis	0	0	0	1	0.392
Platymiscium sp.	0	0	0	1	0.392
Pogonophora schomburgkiana	1	3	0	1	0.204
Pourouma sp.	3	1	0	8	0.125
Pourouma villosa	0	1	0	0	0.392
Pouteria amazonica	2	0	0	1	0.26
Pouteria bilocularis	9	10	0	7	0.071
Pouteria cladantha	0	8	0	0	**0.02**
Pouteria elegans	2	0	0	10	0.071
Pouteria jariensis	2	32	0	1	**0**
Pouteria krukovii	1	10	0	3	0.057
Pouteria laurifolia	0	3	0	3	0.099
Pouteria sp.	6	16	0	9	0.08
Pouteria spruceana	7	11	0	2	**0.023**
Pouteria torta	6	3	0	2	0.221
Prieurella sp.	0	1	0	1	0.554
Protium altsonii	6	0	0	3	0.204
Protium apiculatum	0	2	0	3	0.205
Protium decandrum	8	53	0	16	**0.007**
Protium giganteum	0	1	0	0	0.392
Protium heptaphyllum	11	0	0	20	**0.009**
Protium juruense	0	0	0	1	0.392
Protium krukoffii	0	1	0	0	0.392

Protium opacum	1	2	0	3	0.235
Protium pallidum	20	6	0	5	0.061
Protium paniculatum	2	3	0	1	0.513
Protium sagotianum	2	68	0	2	0.051
Protium sp.	83	17	0	57	**0.005**
Protium subserratum	0	16	0	0	**0.02**
Protium tenuifolium	0	5	0	2	0.205
Psychotria mapourioides	1	0	0	2	0.553
Pterocarpus rohrii	0	1	0	0	0.392
Qualea albiflora	2	1	0	8	**0.045**
Qualea sp.	0	6	0	3	0.054
Radlkoferella macrocarpa	2	5	0	2	0.239
Rheedia macrophylla	0	0	0	1	0.392
Rheedia sp.	11	0	0	0	**0.003**
Rinorea amapensis	2	0	0	0	0.392
Rinorea guianensis	0	1	0	8	0.07
Roupala montana	0	0	0	1	0.392
Sacoglottis amazonica	0	1	0	0	0.392
Sacoglottis guianensis	1	2	0	3	0.433
Sclerolobium melanocarpum	1	0	0	1	0.554
Sclerolobium melinonii	0	1	0	0	0.392
Simaba cedron	5	0	0	6	0.207
Simarouba amara	3	2	0	3	0.312
Sloanea grandis	0	2	0	1	0.26
Sloanea obtusa	0	3	0	0	**0.02**
Sloanea sp.	4	0	0	0	**0.02**
Socratea exorrhiza	3	0	0	0	0.392
Spondias mombin	0	0	0	2	0.392
Sterculia amazonica	1	0	0	0	0.392
Sterculia pilosa	11	1	0	11	**0.003**
Sterculia roseiflora	0	0	0	1	0.392
Stryphnodendron paniculatum	4	0	0	0	0.099
Stryphnodendron sp.	0	0	0	1	0.392
Styrax sieberi	0	0	0	1	0.392
Swartzia amazonica	0	0	0	1	0.392
Swartzia grandifolia	0	1	0	0	0.392
Swartzia panacoco	2	4	0	3	0.113
Swartzia polyphylla	0	0	0	1	0.392
Swartzia sp.	0	0	0	1	0.392
Symphonia globulifera	1	0	0	0	0.392
Syzygiopsis oppositifolia	0	0	0	1	0.392
Syzygiopsis sp.	0	4	0	4	**0.023**
Tabebuia impetiginosa	1	1	0	0	0.554
Tabebuia serratifolia	0	1	0	0	0.392
Tachigali alba	0	4	0	0	0.099
Tachigali myrmecophila	19	16	0	21	**0.03**
Tachigali sp.	2	8	0	11	**0.049**
Tapirira sp.	0	2	0	15	0.202
Tapura amazonica	1	0	0	0	0.392
Terminalia amazonia	0	1	0	0	0.392
Terminalia sp.	0	0	0	1	0.392
Tetragastris altissima	1	0	0	0	0.392
Tetragastris panamensis	56	16	0	16	**0.016**
Theobroma subincanum	72	3	0	17	**0.023**
Theobroma sylvestre	8	0	0	2	**0.003**
Thyrsodium guianense	0	7	0	1	**0.002**
Toulicia sp.	6	0	0	4	0.057
Tovomita cephalostigma	0	0	0	1	0.392
Trattinnickia burseraefolia	0	1	0	3	0.248

Trattinnickia rhoifolia	3	0	0	3	0.099
Trattinnickia sp.	0	1	0	1	0.554
Trichilia lecointei	2	0	0	3	0.205
Trichilia septentrionalis	0	4	0	5	0.098
Vantanea guianensis	1	0	0	0	0.392
Vantanea parviflora	0	6	0	0	**0.003**
Vatairea erythrocarpa	1	2	0	3	0.235
Vataireopsis speciosa	0	0	0	1	0.392
Virola calophylla	1	3	0	4	0.513
Virola flexuosa	4	7	0	1	0.072
Virola melinonii	4	5	0	0	**0.005**
Virola michelii	7	3	0	3	0.474
Virola sp.	0	0	0	1	0.392
Vismia cayennensis	3	0	0	0	0.392
Vismia sp.	0	0	0	2	0.099
Vochysia eximia	8	0	0	8	**0.022**
Vochysia guianensis	2	0	0	1	0.553
Vochysia maxima	0	1	0	0	0.392
Vochysia obscura	3	5	0	7	0.123
Vochysia paraensis	0	0	0	2	0.099
Vochysia splendens	5	0	0	0	0.392
Vochysia vismiifolia	1	0	0	0	0.392
Vouacapoua americana	0	79	0	9	**0.001**
Xylopia benthamii	14	0	0	13	0.089
Zanthoxylum regnellianum	1	0	0	0	0.392
Zygia latifolia	0	0	0	1	0.392

Table C3. Results for the models y ~ forest + sand + slope + elevation, where y corresponds to either species richness or abundance of the three taxa sampled. ‘Forest’ is a categorical variable with four levels (PRI, BN, RIL, PLA), with PRI being the reference category. ‘Sand’ refers to the percentage of sand in the soil at each site. Significant p-values are shown in bold.

		Richness				Abundance			
Taxa	**Variables**	**Coef.**	**S.Error**	**t-value**	**p-value**	**Coef.**	**S.Error**	**t-value**	**p-value**
Butterflies	*Intercept*	12.328	6.868	1.795	0.09	6.951	44.652	0.156	0.878
	Forest: BN	4.689	2.201	2.131	**0.048**	3.631	14.309	0.254	0.803
	Forest: RIL	1.913	2.72	0.703	0.491	0.937	17.683	0.053	0.958
	Forest: PLA	-4.457	2.617	-1.703	0.107	69.718	17.014	4.098	**0.001**
	Sand	0.01	0.005	2.004	0.061	0.05	0.033	1.525	0.146
	Slope	0.165	0.206	0.801	0.434	-0.927	1.339	-0.693	0.498
	Elevation	0.012	0.039	0.316	0.756	0.217	0.254	0.855	0.404
Dung beetles	*Intercept*	25.686	7.465	3.441	**0.003**	88.267	38.735	2.279	**0.036**
	Forest: BN	-3.137	2.392	-1.311	0.207	-5.573	12.413	-0.449	0.659
	Forest: RIL	-2.232	2.956	-0.755	0.461	-25.269	15.34	-1.647	0.118
	Forest: PLA	-6.198	2.845	-2.179	**0.044**	-14.556	14.759	-0.986	0.338
	Sand	-0.009	0.005	-1.585	0.131	-0.025	0.028	-0.877	0.393
	Slope	0.142	0.224	0.634	0.535	-1.918	1.161	-1.651	0.117
	Elevation	-0.067	0.042	-1.571	0.135	-0.254	0.22	-1.154	0.264
Trees	*Intercept*	89.397	11.804	7.574	**0**	135.787	61.118	2.222	**0.04**
	Forest: BN	-11.899	3.783	-3.146	**0.006**	15.411	19.586	0.787	0.442
	Forest: RIL	-15.66	4.675	-3.35	**0.004**	0.299	24.204	0.012	0.99
	Forest: PLA	-70.154	4.498	-15.598	**0**	231.092	23.288	9.923	**0**
	Sand	-0.002	0.009	-0.251	0.805	-0.02	0.045	-0.454	0.656
	Slope	0.202	0.354	0.571	0.576	1.697	1.833	0.926	0.367
	Elevation	-0.113	0.067	-1.685	0.11	0.467	0.348	1.342	0.197

Table C4. Analysis of variance (ANOVA) comparing the models indicated below (full model) with a constrained version of the same model where ‘forest’ is the only explanatory variable. DF= degrees of freedom of the constrained model minus degrees of freedom of full model. Deviance= residual sum of squares of constrained model minus residual sum of squares of full model.

Full model	DF	Deviance	F-test	p-value
Butterfly richness ~ forest + sand + slope + elevation	3	118.3	3.188	0.0504
Dung beetle richness ~ forest + sand + slope + elevation	3	54.3	1.237	0.327
Tree richness ~ forest + sand + slope + elevation	3	271.1	2.472	0.0968
Butterfly abundance ~ forest + sand + slope + elevation	3	1762	1.123	0.3676
Dung beetle abundance ~ forest + sand + slope + elevation	3	1331.1	1.127	0.366
Tree abundance ~ forest + sand + slope + elevation	3	8409.5	2.86	0.0676

Appendix D

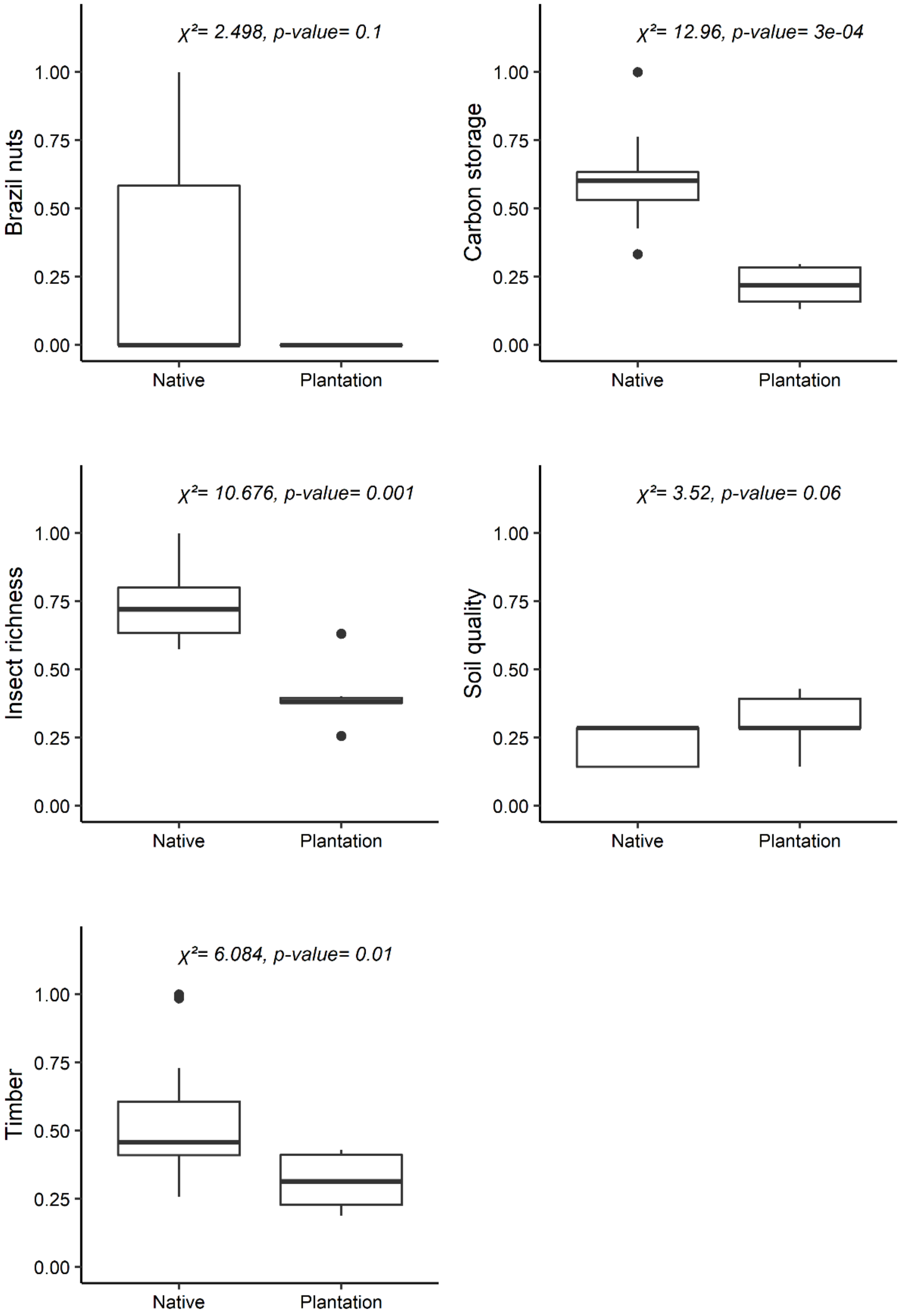


Figure D1. Comparison of the provision of the five ecosystem services measured between native forests (i.e., Brazil nut extraction areas, reduced impact logging, and old-growth) and eucalyptus plantations. The results of a Kruskal-Wallis test (chi-squared statistc and p-value) between the two groups are indicated on the top of the plot. The middle line of the boxplot indicates the median, the upper and lower margins indicate the interquartile range (IQR), the whiskers show values within 1.5xIQR. Data beyond the end of the whiskers are shown as outlying points.

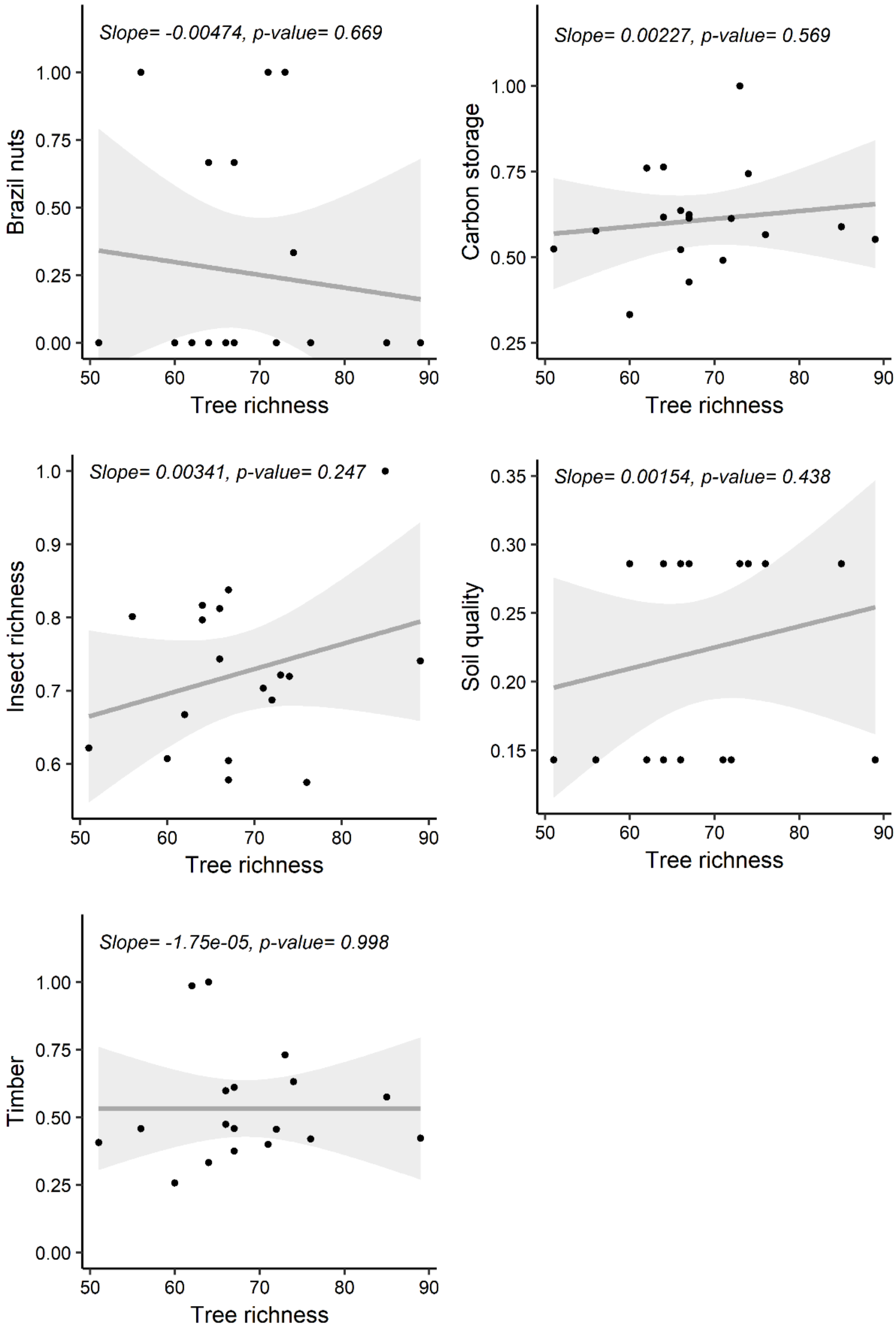


Figure D2. Relationship between the provision of five ecosystem services and tree species richness in native forests (i.e., Brazil nut extraction areas, reduced impact logging, and old-growth). Data from plantations is excluded from these plots. The regression lines were fitted using generalised linear models with a Gaussian error distribution. Light grey areas indicate the 95% confidence intervals of model errors.

Table D1. Spearman rho correlation coefficients (bottom-left) and the corresponding p-values (top-right) between the five ecosystem services measured and tree richness.

	Carbon storage	**Timber**	**Brazil nuts**	**Soil quality**	**Insect richness**	**Tree richness**
Carbon storage		<0.001	0.079	0.249	0.009	0.002
Timber	0.837		0.461	0.984	0.045	0.03
Brazil nuts	0.365	0.158		0.315	0.247	0.226
Soil quality	-0.245	0.004	-0.214		0.279	0.465
Insect richness	0.521	0.413	0.246	-0.23		0.008
Tree richness	0.592	0.443	0.257	-0.157	0.526	

Table D2. GLM coefficients with the multifunctionality scores for the different thresholds and hypothetical stakeholder groups as response variable and tree richness, slope and elevation as independent variables. Stakeholder group 1: nature-focused multifunctionality score; Stakeholder group 2: production-focused multifunctionality score; Stakeholder group 3: multifunctionality score with equal weighting between all five ecosystem services.

Stakeholder	Threshold	Variables	Coefficient	S.Error	t-value	P-value
1	30%	*Intercept*	1.086	0.245	4.441	0
1	30%	*Tree richness*	0.015	0.002	7.648	0
1	30%	*Slope*	0.253	0.143	1.762	0.093
1	30%	*Elevation*	-0.445	0.297	-1.498	0.15
1	60%	*Intercept*	0.483	0.674	0.717	0.482
1	60%	*Tree richness*	0.014	0.005	2.726	0.013
1	60%	*Slope*	0.503	0.395	1.272	0.218
1	60%	*Elevation*	-0.63	0.818	-0.769	0.451
1	90%	*Intercept*	-0.142	0.331	-0.43	0.672
1	90%	*Tree richness*	0.003	0.003	1.166	0.257
1	90%	*Slope*	0.039	0.194	0.199	0.844
1	90%	*Elevation*	0.114	0.402	0.283	0.78
2	30%	*Intercept*	-0.328	0.772	-0.425	0.676
2	30%	*Tree richness*	0.012	0.006	2.059	0.053
2	30%	*Slope*	0.512	0.452	1.133	0.271
2	30%	*Elevation*	1.372	0.937	1.465	0.158
2	60%	*Intercept*	0.175	0.66	0.266	0.793
2	60%	*Tree richness*	0.006	0.005	1.245	0.228
2	60%	*Slope*	-0.041	0.387	-0.105	0.917
2	60%	*Elevation*	-0.158	0.801	-0.197	0.846
2	90%	*Intercept*	0.504	0.477	1.055	0.304
2	90%	*Tree richness*	0	0.004	0.133	0.896
2	90%	*Slope*	0.002	0.28	0.007	0.994
2	90%	*Elevation*	-0.65	0.579	-1.121	0.276
3	30%	*Intercept*	0.759	0.726	1.046	0.308
3	30%	*Tree richness*	0.027	0.006	4.768	0
3	30%	*Slope*	0.765	0.425	1.799	0.087
3	30%	*Elevation*	0.928	0.881	1.053	0.305
3	60%	*Intercept*	0.658	1.165	0.565	0.578
3	60%	*Tree richness*	0.021	0.009	2.283	0.034
3	60%	*Slope*	0.462	0.683	0.677	0.506
3	60%	*Elevation*	-0.787	1.414	-0.557	0.584
3	90%	*Intercept*	0.362	0.629	0.575	0.572
3	90%	*Tree richness*	0.004	0.005	0.714	0.483
3	90%	*Slope*	0.041	0.369	0.11	0.913
3	90%	*Elevation*	-0.536	0.763	-0.702	0.491

Table D3. List of tree species with commercial value used for the measurement of the timber production ecosystem service.

- *Alexa grandiflora*
- *Anacardium giganteum*
- *Astronium gracile*
- *Bagassa guianensis*
- *Batesia floribunda*
- *Bowdichia nitida*
- *Brosimum parinarioides*
- *Buchenavia parvifolia*
- *Carapa guianensis*
- *Caryocar glabrum*
- *Caryocar villosum*
- *Cedrela odorata*
- *Ceiba pentandra*
- *Dialium guianense*
- *Dinizia excelsa*
- *Diplotropis purpurea*
- *Diplotropis racemosa*
- *Dipteryx magnifica*
- *Dipteryx odorata*
- *Endopleura uchi*
- *Enterolobium schomburgkii*
- *Eucalyptus sp.*
- *Ficus nymphaeifolia*
- *Goupia glabra*
- *Guazuma ulmifolia*
- *Hymenaea courbaril*
- *Hymenaea intermedia*
- *Hymenaea parvifolia*
- *Hymenolobium excelsum*
- *Hymenolobium sericeum*
- *Inga alba*
- *Jacaranda copaia*
- *Lecythis lurida*
- *Lecythis poiteaui*
- *Licania heteromorpha*
- *Licaria canella*
- *Macoubea guianensis*
- *Manilkara huberi*
- *Maquira sclerophylla*
- *Mezilaurus itauba*
- *Mezilaurus lindaviana*
- *Minquartia guianensis*
- *Ormosia coccinea*
- *Ormosia coutinhoi*
- *Ormosia paraensis*
- *Osteophloeum platyspermum*
- *Parkia pendula*
- *Parkia ulei*
- *Peltogyne paniculata*
- *Platonia insignis*
- *Pouteria elegans*
- *Pouteria sp.*
- *Protium decandrum*
- *Protium sagotianum*
- *Qualea albiflora*
- *Roupala montana*
- *Sacoglottis guianensis*
- *Sclerolobium melanocarpum*
- *Simarouba amara*
- *Swartzia panacoco*
- *Symphonia globulifera*
- *Tabebuia impetiginosa*
- *Tabebuia serratifolia*
- *Tachigali alba*
- *Tachigali sp.*
- *Terminalia amazonica*
- *Tetragastris altissima*
- *Tetragastris panamensis*
- *Virola calophylla*
- *Virola flexuosa*
- *Virola melinonii*
- *Virola michelii*
- *Virola sp.*
- *Vochysia guianensis*
- *Vochysia maxima*
- *Vochysia obscura*
- *Vochysia vismiifolia*
- *Vouacapoua americana*