

RICARDO RIBEIRO DE CASTRO SOLAR

**EFFECTS OF LAND-USE CHANGE ON TROPICAL FOREST
BIODIVERSITY: A MULTI-SCALE ASSESSMENT IN THE BRAZILIAN
AMAZON**

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Entomologia, para a obtenção do título de *Doctor Scientiae*.

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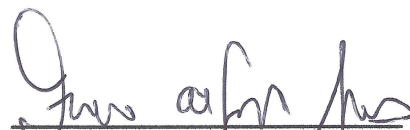
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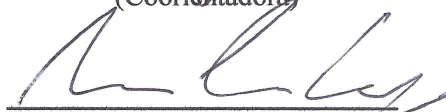
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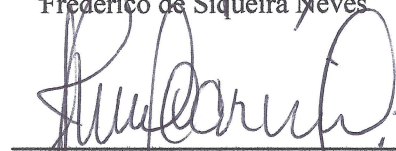
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À minha mãe novamente dedico, pelo eterno exemplo de perseverança e dedicação.

“Do not go where the path may lead; go instead
where there is no path and leave a trail.”
Ralph Waldo Emerson

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RESUMO

SOLAR, Ricardo Ribeiro de Castro, D.Sc., Universidade Federal de Viçosa, março de 2014. **Efeitos de mudanças no uso da terra sobre a biodiversidade de florestas tropicais: uma avaliação em múltiplas escalas na Amazônia Brasileira.** Orientador: José Henrique Schoereder. Coorientadores: Tathiana Guerra Sobrinho e Carlos Frankl Sperber.

A Amazônia Brasileira compreende cerca de 40% das florestas tropicais do globo, abrigando uma enorme parte da biodiversidade mundial. Todavia, taxas alarmantes de desmatamento são encontradas por toda a região amazônica. Demandas cada vez mais altas por recursos naturais são uma das maiores ameaças a este ecossistema e portanto conservacionistas necessitam de informações precisas sobre a biodiversidade e processos do ecossistema, bem como dados da esfera socioeconômica. Dentro das necessidades desta agenda, uma iniciativa de pesquisa denominada Rede Amazônia Sustentável foi desenvolvida. O objetivo desta rede é gerar dados que possam subsidiar planos de conservação para a região. Esta tese traz os resultados de alguns dos objetivos ligados à biodiversidade componentes desta rede. No primeiro capítulo nosso objetivo é fornecer a mais completa lista de espécies até o momento de formigas, abelhas de orquídeas e besouros rola-bostas para a região de Paragominas, bem como descrever os padrões de diversidade de espécies ao longo do gradiente de uso da terra da região. No segundo capítulo, nosso objetivo é responder à pergunta de como as mudanças no uso da terra alteram a composição e a riqueza da comunidade de formigas em Paragominas? Também é nosso objetivo explorar quais os fatores ambientais regula a riqueza de espécies de formigas em escalas local e regional. Por fim, para o terceiro capítulo nossa pergunta é até que ponto existe um processo em andamento de homogeneização biótica acontecendo em consequência do processo de desflorestamento e degradação florestal? Para tal, pesquisamos cinco taxa (plantas, aves, besouros rola-bostas, formigas e abelhas de orquídeas), nos municípios de Paragominas e Santarém. Os resultados do primeiro capítulo incluem a lista de espécies, a qual esperamos possa ser uma referência para estudos de monitoramento do estado de conservação, bem como iniciativas de recuperação florestal, as quais estão em fase inicial em Paragominas. Ainda, encontramos que a diversidade de espécies dos três grupos (formigas, besouros e abelhas) foi reduzida pelo desflorestamento e degradação florestal. No segundo capítulo, observamos uma clara mudança na composição de

espécies da comunidade de formigas com a mudança no uso da terra, bem como um processo de perda de espécies. Estes padrões de riqueza são principalmente explicados pela cobertura de floresta primária remanescente, que foi uma importante variável na explicação dos padrões encontrados. Por fim, no terceiro capítulo encontramos um padrão geral de perda de espécies em escala local com a intensificação do uso da terra. Por outro lado, em escalas maiores, só observamos perda de espécies quando comparamos áreas florestas versus áreas não florestais. Os padrões de diversidade β só foram afetados pelo uso da terra em escalas menores (entre locais), sendo que a mesma é maior em áreas florestais e menor em áreas desflorestadas. Há entretanto um padrão marcado de maior contribuição de aninhamento para a diversidade β em áreas não florestais em ambas as escalas. Portanto, como conclusão geral, encontramos que as mudanças no uso da terra implementadas pelo uso humano estão depauperando a biodiversidade e que, se nenhuma ação for tomada prontamente para proteger as áreas ainda existentes de floresta primária, podemos testemunhar um processo ainda mais severo de perda de espécies. Como uma rede de pesquisa multidisciplinar, esperamos que os resultados apresentados nesta tese possam compor estratégias conjuntas, considerando as esferas ecológicas e sociais, os quais podem culminar em um processo mais razoável e sensato de planejamento de conservação para a região.

ABSTRACT

SOLAR, Ricardo Ribeiro de Castro, D.Sc., Universidade Federal de Viçosa, March, 2014. **Effects of land-use change on tropical forest biodiversity: a multi-scale assessment in the Brazilian Amazon.** Advisor: José Henrique Schoereder. Co-advisors: Tathiana Guerra Sobrinho and Carlos Frankl Sperber.

The Brazilian Amazon comprises around 40% of all tropical forests in the world, harbouring a gigantic part of the world's biodiversity. Yet, alarming rates of deforestation are spread across the Amazon. Increasing rates of resource demands harm this ecosystem and conservationists need precise information about biodiversity and ecosystem processes, as well as socioeconomic data. Within the needings of this agenda, a research initiative called Sustainable Amazon Network was developed, aiming to generate data that can foster conservation plans for the regions. This thesis brings results regarding some of the biodiversity aims of this research network. In the first chapter we aim to provide the most comprehensive species list of ants, orchid bees and dung beetles to date to the region of Paragominas, as well as describe patterns of species diversity across the different land-use types in the region. In the second chapter, we aimed to answer how land-use changes affect ant species composition and richness in Paragominas? We also aim to explore which environmental variables regulate ant species richness at local and regional scales. Finally, for the third chapter we ask whether there is an ongoing process of biotic homogenization happening with forest degradation and conversion to production landscapes. We surveyed five taxa (plants, birds, dung beetles, ants and orchid bees) in this chapter, across the municipalities of Paragominas and Santarém. In the first chapter we provided the list, which we hope will be a baseline for the monitoring of forest conservation initiatives taking place in the region. We also found that species richness of the three groups is being reduced by deforestation and forest degradation. In the second chapter, we observe a marked shift in species composition with land-use changes, as well as a process of species loss, highly associated with primary forest cover, being this the variable with the highest importance in explaining species richness. Lastly in the third chapter, we found a general pattern of steady decrease in local diversity with land-use intensification whereas at larger scales this loss can only be noticed for forest versus non-forest comparisons. We found that β diversity is affected only at smaller scales, being higher in forests than in non-forest areas. There is, however, a marked increase in the

contribution of nestedness to β diversity in non-forest habitats at both scales. Thus, as a general conclusion, we found that land-use changes are eroding biodiversity and if any action is readily implemented in the region to protect the extant forest patches, we can witness a severe biodiversity loss that is already being observed at the local scale. We do expect as a multidisciplinary network that our results can nurture joint strategies, considering natural and socioeconomic sides, which can culminate in a more wise conservation planning to the region.

GENERAL INTRODUCTION

Around 40% of tropical forests in the world are located in the Brazilian Amazon and it harbours a huge part of the world's biodiversity (Malhi *et al.* 2008; Barlow *et al.* 2011). Therefore, the Brazilian Amazon stands out as having a central role in biological conservation. Yet, the region suffers the most intense absolute rates of deforestation in the last decades (Lindenmayer *et al.* 2004; Hansen *et al.* 2008) and despite since 2004 deforestation rates have been decreasing (Nepstad *et al.* 2009), the region is the most active frontier of land-cover change in the world (Barlow *et al.* 2011). Increasing resource demands keeps pressuring the Amazonian region, which represents a major challenge to conservationists (Gardner *et al.* 2009). Science can thus help with this challenge by identifying proximate problems to be addressed, as well as providing baselines for long-term strategies (Foley *et al.* 2011).

Bearing this context in mind, in the last four years a multidisciplinary research initiative, namely Sustainable Amazon Network (in Portuguese *Rede Amazônia Sustentável*, RAS, Gardner *et al.* 2013). RAS is a multidisciplinary research initiative involving more than 30 institutions and organisations (Fig. 1) that aims to explore both social and ecological aspects of the eastern Brazilian, in order to shed some light on the main challenges faced by the region. While most studies in the Amazon are done either at the scales of the whole region (Asner *et al.* 2006) or in few small-scale intensively studied sites (Peres *et al.* 2010), RAS explored the mesoscale. By exploring this scale (spanning hundreds of kilometres and matching political unities), we expect we can foster local decision within the range of action of political and social decisions. This is especially important if we take into account that the two municipalities surveyed – Paragminas and Santarém

affected by land-use intensification? Finally, we assess which environmental variables best predict the patterns of species richness across the entire gradient at both scales. We work with data from Paragominas.

- For the third chapter we explore whether there is an ongoing process of biotic homogenization in human-modified landscapes. Accordingly, we asked: (1) what is the pattern of species loss at both α - and γ -diversities components as function of land-cover changes in a mosaic landscape? (2) how does β -diversity respond to land-cover changes and to what extent is β -diversity scale dependent? Finally, (3) do the processes underpinning β -diversity contribute equally in different land-use types.

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CHAPTER ONE

ANTS, ORCHID BEES AND DUNG BEETLES DIVERSITY AND DISTRIBUTION IN DIFFERENT LAND-USE TYPES OF PARAGOMINAS, AMAZONIA, PA, BRAZIL

**ANTS, ORCHID BEES AND DUNG BEETLES DIVERSITY AND
DISTRIBUTION IN DIFFERENT LAND-USE TYPES OF
PARAGOMINAS, AMAZONIA, PA, BRAZIL**

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ABSTRACT

The Sustainable Amazon Network (in Portuguese *Rede Amazônia Sustentável*; RAS) is an interdisciplinary research initiative concerned with understanding the social and ecological dimensions of land-use sustainability in the eastern Brazilian Amazonia to better promote land management and conservation actions in that region. Within the scope of this project, we sampled ants, dung beetles and orchid bees to produce a list of species of ants, orchid bees and dung beetles collected in Paragominas, PA, Brazil, as the most complete list of species to date of these groups for the western Amazon. Also we aim to compare diversity of these three taxa between major land-uses in the region. Both aims wrap up towards establishing a baseline of vital biodiversity data for ongoing environmental monitoring. We sampled the insects across several land-use types. In total we sampled 289 species of ants, 85 species of dung beetles and 39 species of orchid bees. Species richness was two times higher in forests than in production landscapes and. For ants, primary forests were richer than secondary forests and for dung beetles undisturbed primary forests were the richest sites, followed by disturbed primary forests and then by secondary forests. Assemblage evenness was generally higher in forests for all groups, with production landscapes being dominated by few over-abundant species, such as the orchid bee *Eulaema nigita* and the dung beetles *Trichillum* sp.1 and *Pseudocanthon aff. xanthurus*. The use of different sampling methods has the potential to feed the list with species not sampled in this study, and we recommend this to the future studies. With the implementation of governance agendas to preserve and restore forests in the region, we suggest this study can be used as a baseline for understanding the

effectiveness of ongoing changes in forest conservation and land management practices.

Keywords: Biodiversity baseline, Conservation, Deforestation, Land-use, Monitoring, Rainforest, Species patterns.

INTRODUCTION

That the Brazilian Amazon harbours a gigantic portion of the Earth's biodiversity is a general fact (Barlow *et al.*, 2011; Laurance *et al.*, 2012). Yet, the region has been suffering intense human-impacts and is indeed the most active frontier of land-cover changes in the world. Governmental efforts are yielding positive results, and deforestation rates – although still high – have decreased since 2004 (Nepstad *et al.*, 2009). Given this scenario, it would be desirable that the scientific knowledge could foster conservation plans and actions in the region. However, due to poor infrastructure and the vast size of the region, our knowledge about Amazonian biodiversity is insignificant and most of the species lists only represent a bare underestimate (Barlow *et al.*, 2011).

Aiming to collaborate with better understanding of the region, some large scale, multidisciplinary research networks have been developed in the Amazon. Among them is the Sustainable Amazon Network (Rede Amazônia Sustentável, RAS, in Portuguese, Gardner *et al.*, 2013). A broad spectrum of sampling campaigns were done in the agricultural frontier of Pará state of northern Brazilian region, including socioeconomic, floristic and faunistic. The region has also been suffering of intense deforestation since the 70's (Lindenmayer *et al.*, 2004), although several governmental and social initiatives have been contributing to minimise and revert this process (Viana *et al.*, 2014). Bearing this context in mind, amongst the faunistic surveys, we performed a comprehensive survey of terrestrial invertebrates groups of ecological importance. Desirable characteristics are easy sampling, be present across the whole system, observable sensitivity to environmental changes and cost-effective (McGeoch, 1998; Gardner, 2010). We therefore selected ants (Hymenoptera: Formicidae), orchid

bees (Hymenoptera: Apidae: Euglossina) and dung beetles (Coleoptera: Scarabeidae: Scarabeinae) (Underwood & Fisher, 2006; Gardner *et al.*, 2008b). Because habitat loss is the most serious threat facing biodiversity (Laurance *et al.*, 2012; Laurance *et al.*, 2014), regional inventories constitute an important tool to conservation of insect communities. Recording patterns of species occurrence in space and time, as well as across human-modified landscapes is a valuable tool for studying population ecology and biodiversity responses to human impacts and so measure to which extent human activities are affecting biodiversity (Lach *et al.*, 2010).

Ants (Hymenoptera: Formicidae) are a ubiquitous group of insects, being numerically and ecologically dominant in tropical forests (Hölldobler & Wilson, 2009; Lach *et al.*, 2010). They play roles as seed dispersers (Christianini *et al.*, 2007), nutrient moving among soil layers (Sousa-Souto *et al.*, 2007) and control of species populations, e.g. due to predation (Folgarait, 1998). Ants are also easy to sample, have a relatively well established taxonomy and are present nearly everywhere in the Neotropics throughout the year (Underwood & Fisher, 2006).

Orchid bees are a group endemic to the Neotropics and have around 250 species (Nemesio & Rasmussen, 2011). Pollination of closely associated plant species is one of the striking characteristics of this group (Janzen, 1971). Their potential to indicate shifts in species composition, as they are sensitive to environmental changes (Nemesio & Vasconcelos, 2013), associated with the easy methodology to sample (Gardner *et al.*, 2008b) means that they also provide a cost-effective ecological disturbance indicator group (Gardner, 2010). Nevertheless, in Brazil the vast majority of the studies are done in the Atlantic Forest (Nemesio & Silveira, 2007b; Nemesio, 2009; Nemesio & Silveira, 2010;

Nemesio, 2013a), and there are few studies in the Amazon (Oliveira & Campos, 1996; Barlow *et al.*, 2007; Storck-Tonon *et al.*, 2009; Nemesio & Ferrari, 2011). Further research is needed on this group if conservation strategies in the Amazon are able to take account of their diversity and distribution (Nemesio, 2013b).

Finally, dung beetles are among the most functionally important insect groups in the tropics (Andersen & Feer, 2005). They play a role in several ecological processes, such as dung removal, seed dispersal, nutrient decomposition and cycling, bioturbation and controlling parasites of vertebrates (Nichols *et al.*, 2007; Nichols *et al.*, 2008). Similarly to ants and orchid bees, dung beetles are relatively easy to sample and identify, as well as well as being sensitive to environmental changes (Gardner *et al.*, 2008b).

Here in this paper, we have two main aims. 1) we present the resulting list of species of ants, orchid bees and dung beetles collected in Paragominas, PA, Brazil, as the most complete list of species to date of these groups for the eastern Amazon. 2) we aim to compare diversity of these three taxa between major land-uses in the region. Both aims wrap up towards establishing a baseline of vital biodiversity data for ongoing environmental monitoring.

MATERIAL AND METHODS

Study site

We sampled the insects in Paragominas, a 2 million ha. municipality in Pará state, north Brazil. The region comprises the Amazonian biome, with evergreen forests and annual average rainfall of 1800mm approximately

(Andrade, 2011) and mean annual temperatures of 26.3°C (Pinto *et al.*, 2009). We took all samples between January-June 2011, during the rainy season.

To perform the sample, we selected 18 catchments (ca. 5.000 ha. each) covering the entire municipality, where we established from 8-12 transects (300m) in each catchment, in a density of 1 transect/400ha (Figure 1). In total, we sampled 192 transects across the major land-use classes present in the region including undisturbed primary forests, varyingly disturbed primary and secondary forests due to logging and fire and production areas (silviculture – *Eucalyptus* and *Schyzolobium amazonicum*, pastures and agricultural fields). We determined age of secondary forests based on satellite imagery of a 22-year image sequence, and the average age of the secondary forests sampled is 17 years old (SD=8.27).

Insect sampling

Within each transect we sampled the three insect groups at the same time. To sample the ants, we employed epigaeic pitfall traps, consisting of plastic containers (8cm diameter), half filled with a solution of water, salt (5%) and soap (5%) and baited with sardine and honey, both unreachable to the ants. In each transect we installed six pitfall traps distanced 50m from each other. We also sampled dung beetles with epigaeic pitfall traps, but in this case we baited then with 50g of dung (80% pig and 20% human, Marsh *et al.*, 2013). We installed three sampling points along the transect with three traps in each dug at the corners of a 3-m side triangle and sampled at three points along the transect. To sample orchid bees, we used four plastic bottles per transect (2L, 10cm diameter, 35cm height), tied to a tree trunk, 1.5m above the ground. Male orchid bees were attracted to four types of scent baits (eugenol, methyl salicylate, vanilla or

eucalyptol), separated by 50 m from each other. We tied the traps to a tree trunk, 1.5 m above the ground. In all cases, we installed traps for any taxa 25m far from each other and all traps remained in field for 48h prior removal. In Fig. 1 there is a graphical representation of our sampling design. We processed and identified the ants to the most precise taxonomic level possible using available taxonomic keys (Fernández, 2003; Bolton, accessed at 02/Jan/2014) and checking against the reference collection of Universidade Federal de Viçosa. Processing and identification of the dung beetles followed the taxonomic key by Vaz-de-Mello *et al.* (2011) and reference collections of Universidade Federal de Lavras and Universidade Federal do Mato Grosso. Finally, we processed and identified orchid bees at EMBRAPA – Amazônia Oriental, adapting available taxonomic keys (Nemesio, 2009) and reference collection of EMBRAPA – Amazônia Oriental. We deposited voucher specimens of ants in the reference collection of the Community Ecology Lab, Universidade Federal de Viçosa. Orchid bees are deposited on the reference collection in EMBRAPA – Amazônia Oriental. Dung beetles are deposited in *Seção de Entomologia da Coleção Zoológica da UFMT* (CEMT), Cuiabá. References used for specific species identification are listed in Table S1.

Statistical analyses

To assess our sampling sufficiency, we built site based species accumulation curves (Colwell *et al.*, 2004) and also estimated the total number of species to be sampled in each taxon using the first order Jackknife richness estimator (Chiarucci *et al.*, 2003).

To understand the effects of land-use change on sampled biota, we analysed how total species richness and evenness change with different land-use classes. For species richness, we performed an ANOVA with number of species/transect as response variable and land-use class as the explanatory variable. We used Poisson errors corrected for overdispersion whenever necessary (Crawley, 2012). For evenness, we opted to use the E_{var} index (Smith & Wilson, 1996; Tuomisto, 2012), as this index fulfils desirable characteristics, such as independence of differences in species richness among the treatments, and symmetry with regards to influence of rare or dominant species (Magurran, 2003).

To estimate ant abundance we used the relative frequency of each species (i.e. number of traps found in) in a transect. For dung beetles and orchid bees, we simply counted the number of individuals sampled in each transect as their relative abundances. We analysed evenness differences using ANOVA. As evenness is expressed between 0 and 1, we used arcsine transformed values. For both models with species richness and evenness we employed generalized linear mixed models (GLMM, Bolker *et al.*, 2009) with catchments set as random factors to account for the hierarchical nature of the sampling design.

All analyses were performed using the R platform (R Core Team 2013). Species accumulation curves and diversity estimators are implemented in the package *vegan* (Oksanen *et al.*, 2013). GLMM procedures used the package *lme4* (Bates *et al.*, 2013).

RESULTS

Ants

We sampled a total of 289 species of ants, placed in 56 ant genera, belonging to 10 subfamilies. We assigned a name to all genera and among them, 112 are identified to species names, 23 are placed in species groups or complexes where exact species identification was impossible. The rest 154 are identified until morphospecies. A list of the species and morphospecies is given in Table 1. Two new species, one for the genus *Oxyepoecus* (*Oxyepoecus* sp.PGM1) and one for the genus *Xenomyrmex* (*Xenomyrmex* sp.PGM1) were sampled (R. Feitosa and L. Prado, personal communication, respectively). The regional species accumulation curve is not asymptotic (Fig. 2a), however we sampled 77.5% of the total species richness estimated by the 1st order Jackknife.

Orchid bees

We sampled 3.769 individuals of orchid bees of 39 species, belonging to four of the five known genera of this group. Thirty-seven species could be identified to species level. Only one species of *Eufrisea* and one of *Eulaema* were assigned to morphospecies. The complete list of species is available in Table 2. Species accumulation curve is near-asymptotic (Fig. 2b), and we sampled 87% of the total species richness estimated by 1st order Jackknife.

Dung beetles

We sampled a total 53.113 individuals of 85 species of dung beetles, belonging to 23 genera and six tribes. From the 85 species, 59 (69.4%) could be identified to species and the remainder (26 species) were assigned to morphospecies. The complete list of species is available in Table 3. A new species of the genus *Deltochilum* (*Deltochilum* sp.PGM1) was sampled (F. Silva, under review). The regional species accumulation curve was nearly asymptotic (Fig. 2c),

stabilising with around 100 randomly sampled transects, and encompassing 93% of the total richness estimated using the 1st order Jackknife.

Patterns of species richness and evenness in different land-uses

There was a general trend of species richness loss from primary forests to production areas with agricultural fields being the most depauperate. For ants, primary forest transects (undisturbed and disturbed) harboured the highest species richness, followed by secondary forests, then reforestation and pastures together and with the fewest number of species in agricultural fields (Fig. 3a, $\chi^2_{3,14}=105$, $P<0.001$). The richest assemblage of Orchid bees was found in secondary forests, primary forests (undisturbed and disturbed) had similar richness but lower than secondary forests, followed by reforestation and pastures and the fewest species in agricultural fields (Fig. 3b, $\chi^2_{1,16}=76.7$, $P<0.001$). Dung beetles had the highest species richness in undisturbed primary forests, followed by disturbed primary forests, than secondary forests and the lowest richness in all production areas (Fig. 3c, $\chi^2_{3,14}=148.8$, $P<0.001$).

Species evenness was similar across all taxa, being higher in forests (primary and secondary) and lower in production areas. In general, evenness was higher for ants, followed by orchid bees and then dung beetles (Fig. 4, $\chi^2_{2,15}=334.3$, $P<0.001$). For ants the general pattern was observed with forests presenting higher evenness than production areas (Fig. 4a, $\chi^2_{1,16}=34.1$, $P<0.001$), as for the dung beetles (Fig. 4c, $\chi^2_{1,16}=10.57$, $P=0.001$). For orchid bees, we found that logged and burnt primary forests and reforestation had higher richness values, followed by undisturbed primary forest, logged primary forest, secondary forest

and pasture and the lowest values in agricultural fields (Fig. 4b, $\chi^2_{1,16}=32$, $P<0.001$).

DISCUSSION

Here we present results of the most comprehensive sampling to date of dung beetles, ants and orchid bees for any area of the eastern Amazon. We provide information about three major important insect groups that will be useful for future studies in that region, and assessments of the impacts of ongoing changes in forest conservation and land management programs.

We consider our sampling effort sufficient for all three taxa at the regional scale, with at least 77% of the estimated diversity sampled for all taxa. For ants, the only previous study we are aware of in Paragominas yielded only 74 species belonging to 30 genera (Kalif *et al.*, 2001). By using a different sampling method (Winkler extractors), the authors managed to sample species not represented in our study, demonstrating the importance of considering the use of complementary methods to survey this region as well as others. Exploring seldom studied habitats such as the forest canopies (Basset *et al.*, 2012) or underground soil layers (Rabeling *et al.*, 2008; Schmidt & Solar, 2010; Schmidt *et al.*, 2014) also offers significant potential to increase the number of species described for the region.

Few other studies have surveyed orchid-bees in the Amazonian region. The number of species we sampled is in agreement with other studies (Oliveira & Campos, 1996; Nemesio & Silveira, 2007b; Storck-Tonon *et al.*, 2009; Abrahamczyk *et al.*, 2011). We sampled in a very diverse range of habitats and in a large area, however species are likely to be sampled by using a greater diversity of bait types (Nemesio & Vasconcelos, 2013).

In the case of dung beetles accumulation curves and richness estimators suggest that we sampled most species attracted to dung in the region, with comparable numbers of species to that reported in other studies (Gardner *et al.*, 2008a; Barlow *et al.*, 2010). Apart from the large scale sampling, we recommend the use of mixed human-pig dung in order to optimise sampling efficiency (Marsh *et al.*, 2013). Even so we still have sampled single or rare individuals, especially those associated with specific habitats, such as canopy species or those individuals preferentially captured by other sampling methods, such as *Anomiopus aff. foveicollis*, *Eurysternus harlequin* Genier, 2009 and *Bdelyrus* sp.1.

Patterns of species richness and evenness in different land-use types

Unsurprisingly forests are more species rich than non-forest habitats. However, we also observed more subtle patterns of diversity within and between the major land-use types. In the case of ants we found fewer species in secondary forests, demonstrating that the recovery of species in these forests is not guaranteed even considering we sampled in relatively mature secondary forests on average (Mazzei *et al.*, 2010). As expected few ant species were sampled in production areas with the lowest numbers in agricultural fields.

By contrast to the other groups orchid bees exhibited similar levels of richness in all forest types. This is an expected result, considering orchid bees have a high vagility, being able to fly several kilometres a day (Janzen, 1971). Therefore, they can rapidly colonize new habitats, also considering orchid bees may be able to sustain viable populations in relatively small forest patches (Nemesio & Silveira, 2007a, 2010). Nevertheless orchid bees are seriously affected by deforestation and forest fragmentation (Nemesio & Silveira, 2010)

and forest-dependent species are seriously threatened, as described by Nemesio (2013a) for the Atlantic forest.

Dung beetles, as they apart from changes in habitat characteristics, rely on mammal dung and carcasses as food and nesting resources (Nichols *et al.*, 2013) are expected to show the most marked patterns of diversity change in different land-uses. Indeed, we found the highest number of species undisturbed primary forests, where also large mammals are more expect to be better surviving (Prist *et al.*, 2012). Primary forests disturbed by logging and fire had fewer dung beetle species, however still sustaining a considerably large dung beetle fauna (Fig. 3c). Other researchers have also found that even logged areas can sustain a large portion of the original fauna (Laurance & Laurance, 1996; Putz *et al.*, 2012). Secondary forests exhibit a substantial drop in species richness, indicating that dung beetles are not being able to colonise or coexist in these areas in the same levels they do in primary forests.

Evenness was generally higher in forest areas for both ants and dung beetles, with evenness only decreasing for orchid bees in agricultural fields. Open areas are often the least hospitable environments (Gascon *et al.*, 1999), and are commonly dominated by generalist species. This is the case of the orchid bee *Eulaema nigrata* Lepeletier de Saint Fargeau, 1841, and the case of the dung beetles *Trichillum* sp.1 and *Pseudocanthon aff. xanthurus*. All these three species are examples of organisms rarely present in forest fragments, which on the other hand became massively abundant in open areas. Individuals of *Trichillum* sp.1 reach huge numbers of 7000 individuals of in a single agricultural transect, with the other species in the same transect not surpassing 2% of this abundance.

Similar for orchid bees, where other species in pasture transects have relative frequency of less than 1% compared to *Eulaema nigrita*.

CONCLUSION

Enhanced documentation of local diversity patterns of insects and other organisms are invaluable in helping to assess conservation priorities and assess management effectiveness. Indeed, it would be highly desirable to develop conservation strategies or conclusions to take into account a more comprehensive understanding of diversity and distribution of the major groups of organisms inhabiting a given locality. We hope this assessment provides the baseline for new community and population studies on these groups of insects in the region. Paragominas is the flagship municipality in the state of Pará for the Green Municipalities Program (in Portuguese, *Programa Municípios Verdes* – <http://municipiosverdes.com.br/>), an initiative aiming to stop deforestation and promote secondary forest recovery and sustainable land-use practices in the region (Viana *et al.*, 2014). We suggest therefore this study and the patterns of species distributions can be used as baselines for future studies of forest changes in that region. Thus, enabling strong conclusions to be drawn upon the evolution of the landscape, given the success of the program.

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Figure legends

- Figure 1 Map of the sampling region and sampling design. We stratified our sampling at: regional, catchment and transect scales.
- Figure 2 Species accumulation curves for the three studied taxonomic groups. Each curve was drawn after 10.000 randomisations of original data and the shaded area represents the standard deviation. In the x axis we have number of sampled transects, in the y axis, accumulated species richness.
- Figure 3 Boxplots of average species richness per transect as response variable plotted against land-use type. Letters above bars represent significant differences among levels within the factor. PFU – undisturbed primary forest, PFL – logged primary forest, PFLB – logged and burnt primary forest, SEF – secondary forest, REF – reforestation (silviculture), PAS – pasture and AGR – mechanised agriculture. We considered significant those probabilities under 5%.
- Figure 4 Boxplots of average species evenness per transect as response variable plotted against land-use type. Evenness was measured as Smith & Wilson (1996) E_{var} . Letters above bars represent significant differences among levels within the factor. PFU – undisturbed primary forest, PFL – logged primary forest, PFLB – logged and burnt primary forest, SEF – secondary forest, REF – reforestation (silviculture), PAS – pasture and AGR – mechanised agriculture. We considered significant those probabilities under 5%.

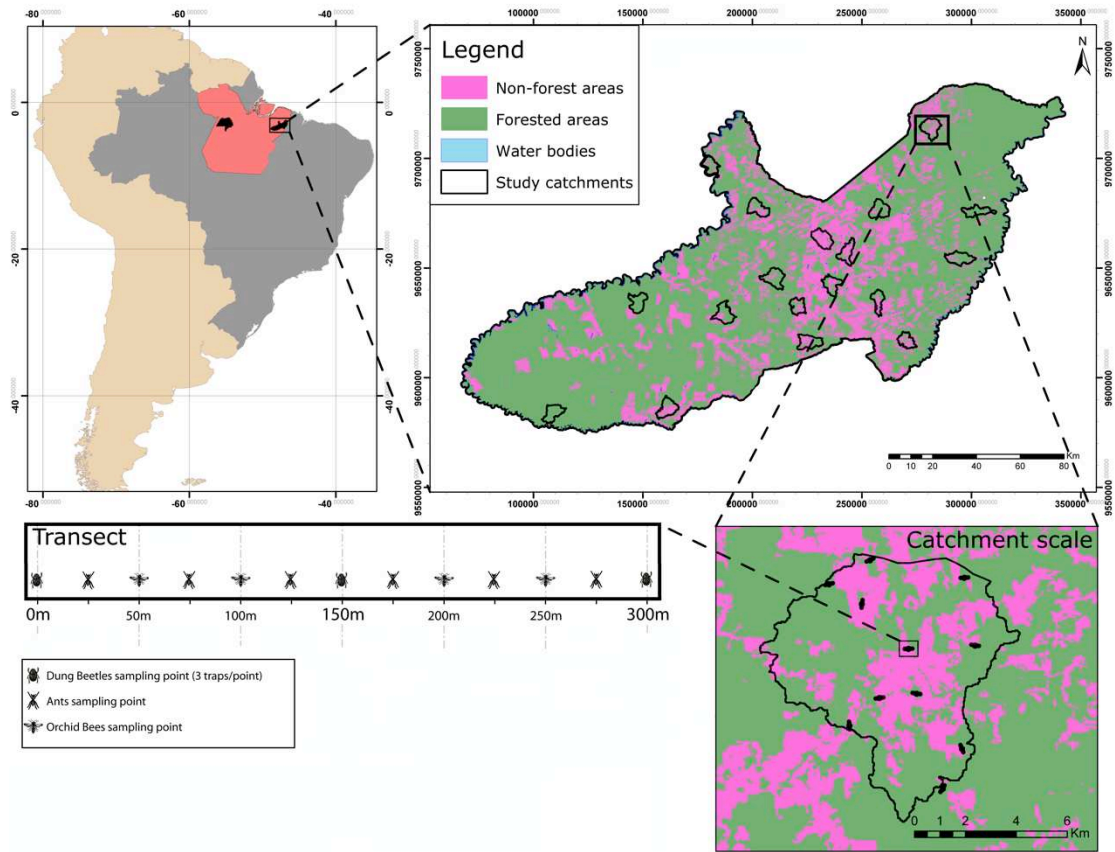


Fig.1

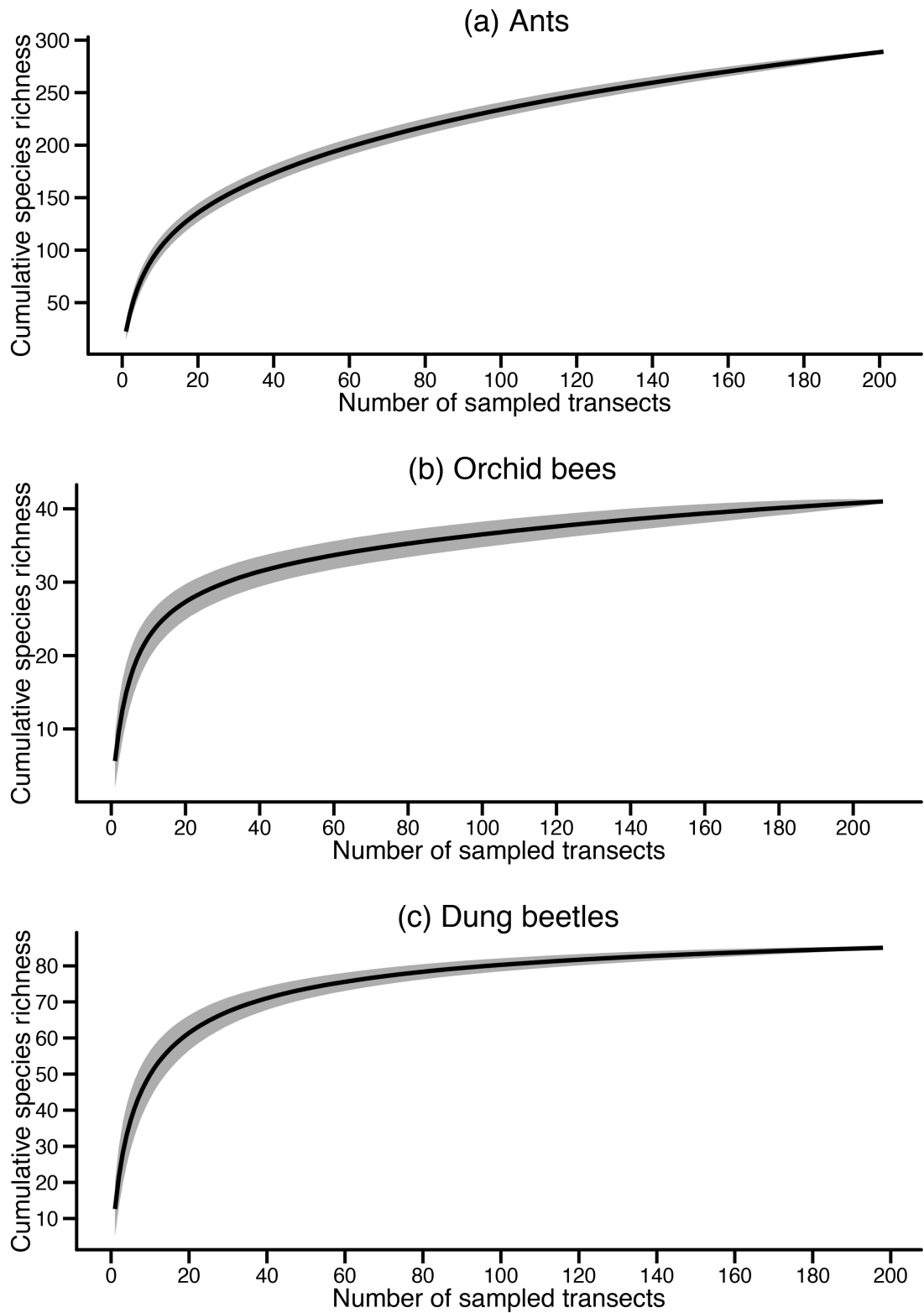


Fig.2

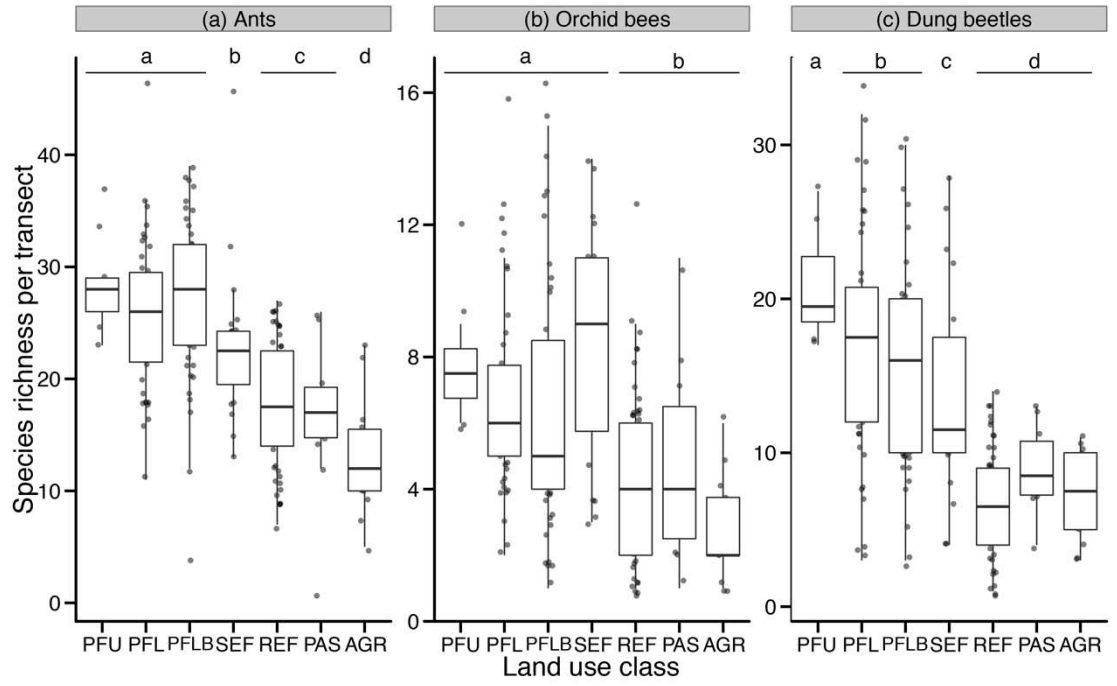


Fig. 3

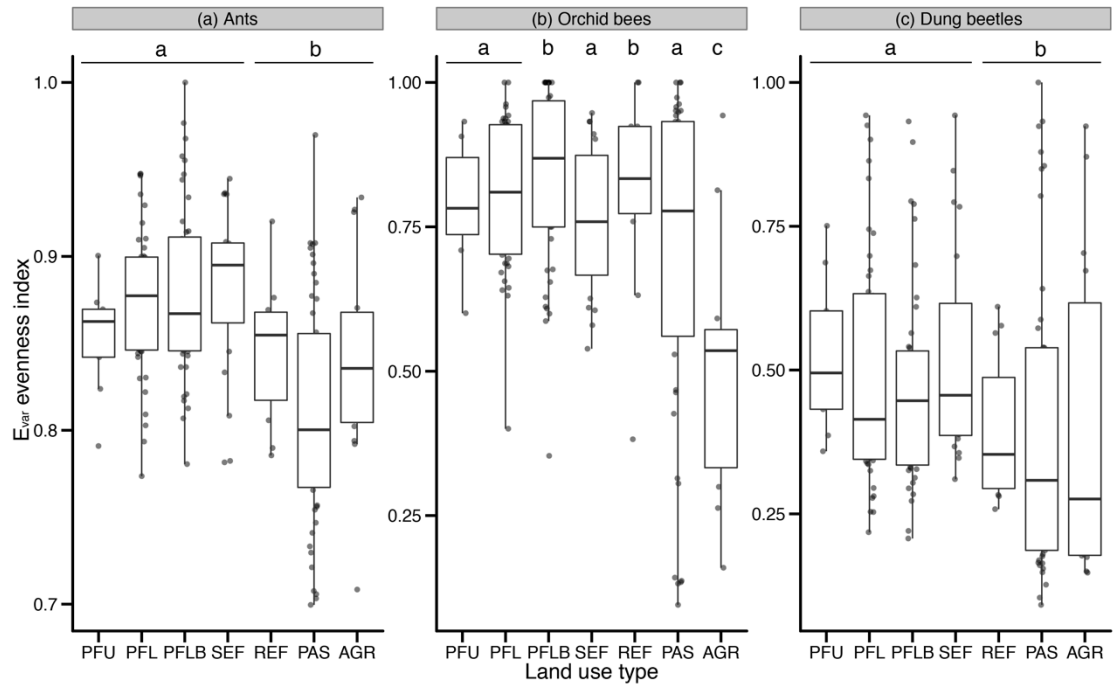


Fig.4

Tables legends

- Table 1 List of ant species collected in this study. Values represent the relative frequencies (%) of each species in each land-use type: PFU – primary forest undisturbed, PFL – primary forest logged, PFLB – primary forest logged and burnt, SEF – secondary forest, REF – reforestation with commercial species, PAS – pasture, AGR – agricultural areas, AP – abandoned plantation, SHA – small holder agriculture. The last land-use type present in the table is not used in analyses, as it was represented by very few transects.
- Table 2 List of orchid bees species collected in this study. Values represent the relative frequencies (number of individuals) of each species in each land-use type: PFU – primary forest undisturbed, PFL – primary forest logged, PFLB – primary forest logged and burnt, SEF – secondary forest, REF – reforestation with commercial species, PAS – pasture, AGR – agricultural areas, AP – abandoned plantation, SHA – small holder agriculture. The last land-use type present in the table is not used in analyses, as it was represented by very few transects.
- Table 3 List of dung beetles species collected in this study. Values represent the relative frequencies (number of individuals) of each species in each land-use type: PFU – primary forest undisturbed, PFL – primary forest logged, PFLB – primary forest logged and burnt, SEF – secondary forest, REF – reforestation with commercial species, PAS – pasture, AGR – agricultural areas, AP – abandoned plantation, SHA – small holder agriculture. The last land-use type present in the table is not used in analyses, as it was represented by very few transects.

Table 1

Species	Author	Land-use type								
		PFU	PFL	PFLB	SEF	PAS	REF	AGR	SHA	
CERAPACHYNAE										
<i>Acanthostichus laticornis</i>	Forel, 1908								1.1	
<i>Cerapachys splendens</i>	Borgmeier, 1957								1.1	
DOLICHODERINAE										
<i>Azteca alfari</i>	Emery, 1893	3.1	1.0							
<i>Azteca</i> sp.1			1.0							
<i>Azteca</i> sp.2			2.0							
<i>Azteca</i> sp.3					1.1					
<i>Azteca</i> sp.4				1.0						
<i>Dolichoderus bispinosus</i>	(Olivier, 1792)				2.2	2.3	1.3			
<i>Dolichoderus decollatus</i>	Smith, 1858		2.0							
<i>Dolichoderus gagates</i>	Emery, 1890									20.0
<i>Dolichoderus imitator</i>	Emery, 1894	3.1								
<i>Dolichoderus lutosus</i>	(Smith, 1858)		1.0							
<i>Dolichoderus varians</i>	Mann, 1916				2.2					
<i>Dorymyrmex pr. goeldii</i>	Forel, 1904						3.9		6.7	20.0
<i>Dorymyrmex</i> sp.1		3.1	1.0			4.7	5.8	50.0	20.0	20.0
<i>Dorymyrmex</i> sp.2							<1	3.3	3.3	
<i>Dorymyrmex spurius</i>	Santschi, 1929		2.0	1.1	7.0	9.7	30.0	33.3	40.0	
<i>Forelius</i> sp.1								3.3		
<i>Gracilidris pombero</i>	Wild & Cuzzo, 2006				1.1	2.3	26.6	20.0	10.0	
<i>Linepithema neotropicum</i>	Wild, 2007		2.0	13.3				3.3		
<i>Tapinoma melanocephalum</i>	(Fabricius, 1793)	3.1	4.0	2.2	4.7	<1	3.3			
<i>Tapinoma</i> sp.1		3.1				<1				

Table 1 continues on the next page

ECITONINAE											
<i>Eciton</i>	<i>burchellii</i>		(Westwood, 1842)		1.0		2.3		20.0		
<i>Eciton</i>	<i>mexicanum</i>		Roger, 1863		1.0						
<i>Eciton</i>	<i>rapax</i>		Smith, 1855			1.1					
<i>Labidus</i>	<i>coecus</i>		(Latreille, 1802)	3.1	5.0	10.0	4.7	11.7	13.3		
<i>Labidus</i>	<i>mars</i>		(Forel, 1912)		1.0				6.7		
<i>Labidus</i>	<i>praedator</i>		(Smith, 1858)			2.2	2.3	1.3			
<i>Labidus</i>	<i>spininodis</i>		(Emery, 1890)		3.0		4.7				
<i>Neivamyrmex</i>	<i>gibbatus</i>		Borgmeier, 1953		1.0						
<i>Neivamyrmex</i>	sp.1			3.1							
<i>Neivamyrmex</i>	sp.2					1.1			3.3		
<i>Nomamyrmex</i>	<i>esenbecki</i>		(Westwood, 1842)			1.1		<1			
ECTATOMMINAE											
<i>Ectatomma</i>	<i>brunneum</i>		Smith, 1858		7.0	35.6	74.4	100.0	100.0	50.0	80.0
<i>Ectatomma</i>	<i>edentatum</i>		Roger, 1863	3.1	4.0	8.9	2.3	3.9			
<i>Ectatomma</i>	<i>lugens</i>		Emery, 1894	90.6	88.0	97.8	30.2	<1			
<i>Ectatomma</i>	<i>tuberculatum</i>		(Olivier, 1792)		6.0	12.2	4.7			6.7	
<i>Gnamptogenys</i>	gr. Rastrata	sp.1			1.0						
<i>Gnamptogenys</i>	gr. Striatula	<i>moelleri</i>	(Forel, 1912)	15.6	18.0	12.2	2.3				
<i>Gnamptogenys</i>	gr. Striatula	sp.1		31.3	16.0	14.4	2.3				
<i>Gnamptogenys</i>	gr. Striatula	sp.2				3.3					
<i>Gnamptogenys</i>	gr. Sulcata	sp.1				1.1		<1			
<i>Gnamptogenys</i>	gr. Sulcata	sp.2			1.0	5.6					
<i>Gnamptogenys</i>	gr. Sulcata	sp.3		9.4	6.0	6.7					
<i>Gnamptogenys</i>	gr. Sulcata	sp.4		3.1		1.1					
<i>Gnamptogenys</i>	<i>haenschi</i>		(Emery, 1902)		1.0	1.1					
<i>Gnamptogenys</i>	sp.5							<1			

Table 1 continues on the next page

FORMICINAE									
<i>Acropyga</i>	<i>goeldii</i>	Forel, 1893					<1		
<i>Brachymyrmex</i>	sp.1					2.3	1.9	3.3	
<i>Brachymyrmex</i>	sp.2				3.3	23.3	27.3	36.7	76.7 40.0
<i>Brachymyrmex</i>	sp.3		3.1						
<i>Brachymyrmex</i>	sp.4			1.0	10.0	16.3	<1		
<i>Brachymyrmex</i>	sp.5				1.1	2.3			
<i>Brachymyrmex</i>	sp.6				1.1				
<i>Brachymyrmex</i>	sp.7			1.0					
<i>Camponotus</i>	<i>atriceps</i>	(Smith, 1858)	15.6	36.0	43.3	48.8			
<i>Camponotus</i>	<i>blandus</i>	(Smith, 1858)			1.1	18.6	33.8	23.3	16.7 100.0
<i>Camponotus</i>	<i>crassus</i>	Mayr, 1862			1.1		1.3		
<i>Camponotus</i>	<i>femoratus</i>	(Fabricius, 1804)		10.0		2.3			
<i>Camponotus</i>	<i>novogranadensis</i>	Mayr, 1870	6.3	1.0	4.4	14.0			
<i>Camponotus</i>	<i>renggeri</i>	Emery, 1894		1.0	3.3	18.6	13.6	6.7	20.0
<i>Camponotus</i>	<i>senex</i>	(Smith, 1858)		1.0	5.6	23.3	37.7	6.7	6.7 40.0
<i>Camponotus</i>	sp.1				1.1		3.2		
<i>Camponotus</i>	sp.2			1.0	2.2	2.3			
<i>Camponotus</i>	sp.3			10.0	26.7	16.3			
<i>Camponotus</i>	sp.4			14.0	18.9	25.6	<1		
<i>Camponotus</i>	sp.5				2.2	2.3			
<i>Camponotus</i>	sp.6				1.1		1.9		3.3
<i>Camponotus</i>	sp.7			1.0	1.1				
<i>Camponotus</i>	sp.8			2.0	13.3	30.2	26.0	40.0	10.0 80.0
<i>Camponotus</i>	sp.12			1.0					
<i>Camponotus</i>	sp.14			1.0	1.1				
<i>Camponotus</i>	sp.15					2.3			

Table 1 continues on the next page

<i>Gigantiops</i>	<i>destructor</i>	(Fabricius, 1804)		5.0	12.2	2.3				
<i>Nylanderia</i>	sp.1			1.0						
<i>Nylanderia</i>	sp.10			1.0	1.1					
<i>Nylanderia</i>	sp.11		3.1	1.0						
<i>Nylanderia</i>	sp.2			10.0	24.4	55.8	26.0	40.0	3.3	40.0
<i>Nylanderia</i>	sp.3		21.9	12.0	7.8	23.3				
<i>Nylanderia</i>	sp.4			2.0	11.1	14.0	35.7	10.0	3.3	40.0
<i>Nylanderia</i>	sp.5		40.6	63.0	76.7	51.2	2.6	3.3	6.7	
<i>Nylanderia</i>	sp.6						1.9			
<i>Nylanderia</i>	sp.7		15.6	5.0	6.7	2.3				
<i>Nylanderia</i>	sp.8				3.3	4.7	1.9	6.7	3.3	
<i>Nylanderia</i>	sp.9				1.1					
<i>Paratrechina</i>	<i>longicornis</i>	(Latreille, 1802)		2.0			1.9			
MYRMICINAE										
<i>Acromyrmex</i>	<i>coronatus</i>	(Fabricius, 1804)		1.0						
<i>Acromyrmex</i>	<i>laticeps</i>	(Emery, 1905)				1.1				
<i>Apterostigma</i>	sp.1		6.3	6.0	5.6	4.7	<1			
<i>Apterostigma</i>	sp.2				1.1					
<i>Apterostigma</i>	sp.3			1.0	1.1					
<i>Atta</i>	<i>cephalotes</i>	(Linnaeus, 1758)			7.8		2.6			
<i>Atta</i>	<i>sexdens</i>	(Linnaeus, 1758)		2.0	1.1	9.3	3.2		23.3	
<i>Cardiocondyla</i>	<i>emeryi</i>	Forel, 1881			1.1		<1	26.7		
<i>Cardiocondyla</i>	<i>minutior</i>	Forel, 1899			1.1		1.9	3.3		
<i>Carebara</i>	<i>brevipilosa</i>	Fernández, 2004	3.1	4.0	2.2	2.3				
<i>Carebara</i>	<i>urichi</i>	(Wheeler, 1922)	9.4	4.0	8.9	2.3		3.3	3.3	
<i>Carebara</i>	comp. Escherichi	sp.2		1.0						
<i>Carebara</i>	comp. Escherichi	sp.3	6.3	2.0	4.4	9.3				

Table 1 continues on the next page

<i>Carebara</i>	comp. Lignata	sp.1			2.0	1.1	7.0					
<i>Carebara</i>	comp. Lignata	sp.2			3.1							
<i>Carebara</i>	comp. Lignata	sp.3					1.1					
<i>Cephalotes</i>	<i>atratus</i>		(Linnaeus, 1758)		2.0	1.1						
<i>Cephalotes</i>	<i>cordatus</i>		(Smith, 1853)					2.3				
<i>Cephalotes</i>	<i>maculatus</i>		(Smith, 1876)		1.0							
<i>Cephalotes</i>	<i>oculatus</i>		(Spinola, 1851)				3.3					
<i>Cephalotes</i>	<i>pusillus</i>		(Klug, 1824)				1.1			1.9		
<i>Crematogaster</i>	<i>brasiliensis</i>		Mayr, 1878	3.1	28.0	47.8	9.3	1.3				
<i>Crematogaster</i>	<i>curvispinosa</i>		Mayr, 1862		1.0							
<i>Crematogaster</i>	<i>erecta</i>		Mayr, 1866		2.0	2.2	14.0					
<i>Crematogaster</i>	<i>flavosensitiva</i>		Longino, 2003		1.0	6.7	2.3					
<i>Crematogaster</i>	<i>levior</i>		Longino, 2003		4.0							
<i>Crematogaster</i>	<i>limata</i>		Smith, 1858	3.1	5.0	16.7	16.3			3.3		
<i>Crematogaster</i>	<i>pr. victima</i>		Smith, 1858						<1			
<i>Crematogaster</i>	<i>sotobosque</i>		Longino, 2003	6.3		2.2	4.7					
<i>Crematogaster</i>	sp.1						1.1					
<i>Crematogaster</i>	sp.2			3.1								
<i>Crematogaster</i>	sp.3				3.0	5.6	14.0	63.6	56.7	76.7	40.0	
<i>Crematogaster</i>	sp.4				1.0							
<i>Crematogaster</i>	sp.5				1.0	1.1	11.6	19.5		23.3	80.0	
<i>Crematogaster</i>	sp.6							7.8	6.7			
<i>Crematogaster</i>	<i>tenuicula</i>		Forel, 1904	100.0	55.0	14.4	16.3	<1		3.3		
<i>Cyphomyrmex</i>	gr. Rimosus	sp.2		3.1	2.0		2.3					
<i>Cyphomyrmex</i>	gr. Rimosus	sp.3					1.1	<1	3.3			
<i>Cyphomyrmex</i>	<i>laevigatus</i>		Weber, 1938	3.1			1.1	2.3				
<i>Cyphomyrmex</i>	<i>rimosus</i>		(Spinola, 1851)	3.1	1.0	10.0	7.0	11.0	6.7	10.0		

Table 1 continues on the next page

<i>Cyphomyrmex</i>	sp.1				2.2	2.3				20.0
<i>Hylomyrma</i>	<i>reitteri</i>		(Mayr, 1887)		1.0					
<i>Megalomyrmex</i>	gr. Leoninus	sp.1				5.6				
<i>Megalomyrmex</i>	gr. Silvestrii	sp.2						<1	3.3	
<i>Megalomyrmex</i>	gr. Silvestrii	sp.3			1.0					
<i>Monomorium</i>	<i>floricola</i>		(Jerdon, 1851)		1.0			<1	3.3	
<i>Mycocepurus</i>	<i>smithii</i>		(Forel, 1893)	3.1	1.0	8.9	9.3	1.9	6.7	10.0
<i>Myrmicocrypta</i>	<i>bucky</i>		Sosa-Calvo & Schultz, 2010			1.1				
<i>Myrmicocrypta</i>	sp.1					2.2	2.3			
<i>Nesomyrmex</i>	<i>spininodis</i>		(Mayr, 1887)						3.3	
<i>Ochetomyrmex</i>	<i>neopolitus</i>		Fernández, 2003	6.3	10.0	11.1	7.0			
<i>Ochetomyrmex</i>	<i>semipolitus</i>		Mayr, 1878	3.1	15.0	3.3	4.7			
<i>Octostruma</i>	sp.1				2.0					
<i>Octostruma</i>	sp.2						2.3			
<i>Oxyepoecus</i>	sp.PGM1*							1.3		
<i>Pheidole</i>	sp.1			6.3	35.0	36.7	69.8	63.0	46.7	90.0
<i>Pheidole</i>	sp.2				2.0	10.0	7.0	24.7	36.7	46.7
<i>Pheidole</i>	sp.3			6.3	1.0	1.1				
<i>Pheidole</i>	sp.4			31.3	4.0	10.0	2.3	<1		
<i>Pheidole</i>	sp.5			9.4	10.0	14.4				
<i>Pheidole</i>	sp.6			34.4	17.0	5.6	14.0	1.9	3.3	
<i>Pheidole</i>	sp.7			6.3	12.0	14.4	20.9	3.2	10.0	3.3
<i>Pheidole</i>	sp.8				5.0	5.6	16.3	17.5	30.0	30.0
<i>Pheidole</i>	sp.9			3.1						
<i>Pheidole</i>	sp.10				1.0	2.2	2.3		3.3	
<i>Pheidole</i>	sp.11			3.1	14.0	12.2	4.7			
<i>Pheidole</i>	sp.12			12.5	7.0					

Table 1 continues on the next page

<i>Pheidole</i>	sp.13	3.1	14.0	28.9	16.3	39.0	23.3	36.7	60.0
<i>Pheidole</i>	sp.14	6.3	7.0	3.3					
<i>Pheidole</i>	sp.15	25.0	21.0	17.8	14.0		3.3		
<i>Pheidole</i>	sp.16	15.6	6.0	2.2	14.0	<1			
<i>Pheidole</i>	sp.17			1.1	4.7	2.6	3.3		
<i>Pheidole</i>	sp.18			1.1					
<i>Pheidole</i>	sp.19	9.4	11.0	7.8					
<i>Pheidole</i>	sp.20	6.3	18.0	6.7	11.6	<1			
<i>Pheidole</i>	sp.21	3.1							
<i>Pheidole</i>	sp.22		3.0	2.2					
<i>Pheidole</i>	sp.23		1.0	2.2					
<i>Pheidole</i>	sp.24		1.0	2.2	7.0				
<i>Pheidole</i>	sp.25	18.8	7.0	10.0	4.7	<1			
<i>Pheidole</i>	sp.26			2.2					
<i>Pheidole</i>	sp.27	9.4	13.0	11.1	9.3				
<i>Pheidole</i>	sp.28	3.1			2.3				
<i>Pheidole</i>	sp.29	3.1			2.3				
<i>Pheidole</i>	sp.30	9.4	13.0	3.3	7.0				
<i>Pheidole</i>	sp.31		3.0	4.4	7.0				
<i>Pheidole</i>	sp.32	18.8	14.0	35.6	18.6	1.3	6.7		
<i>Pheidole</i>	sp.33	25.0	34.0	70.0	60.5	14.9	36.7	40.0	20.0
<i>Pheidole</i>	sp.34	71.9	100.0	100.0	62.8	5.8	23.3	6.7	20.0
<i>Pheidole</i>	sp.35				4.7				
<i>Pheidole</i>	sp.36		1.0						
<i>Pheidole</i>	sp.37		2.0						
<i>Pheidole</i>	sp.38		2.0						
<i>Pheidole</i>	sp.39		1.0						

Table 1 continues on the next page

<i>Pheidole</i>	sp.40		1.0	2.2	4.7	10.4	6.7	13.3	40.0
<i>Pheidole</i>	sp.41		1.0	1.1					
<i>Pheidole</i>	sp.42					<1			
<i>Pheidole</i>	sp.43	3.1	1.0	10.0	9.3	11.7	6.7	16.7	
<i>Pheidole</i>	sp.44		1.0						
<i>Pheidole</i>	sp.45				2.3				
<i>Pheidole</i>	sp.46		1.0						
<i>Pheidole</i>	sp.47	6.3		1.1					
<i>Pheidole</i>	sp.48		1.0						
<i>Pheidole</i>	sp.49	3.1	6.0	23.3	30.2	12.3	26.7	20.0	40.0
<i>Pheidole</i>	sp.50		3.0	5.6	2.3			3.3	
<i>Pheidole</i>	sp.51		2.0	2.2					
<i>Pheidole</i>	sp.52	3.1	7.0	3.3	7.0	4.5			
<i>Pheidole</i>	sp.53		1.0						
<i>Pheidole</i>	sp.54		1.0	3.3	2.3				
<i>Pheidole</i>	sp.55		1.0	2.2	2.3				
<i>Pheidole</i>	sp.56		1.0		2.3				
<i>Pheidole</i>	sp.57				2.3				
<i>Pheidole</i>	sp.58		9.0	5.6	34.9				
<i>Pheidole</i>	sp.59		3.0	3.3					
<i>Pheidole</i>	sp.60			1.1					
<i>Pheidole</i>	sp.61		1.0	1.1		1.3			
<i>Pheidole</i>	sp.62		1.0						
<i>Pheidole</i>	sp.63		3.0	3.3	2.3				
<i>Pheidole</i>	sp.64	3.1	2.0						
<i>Pheidole</i>	sp.65					<1			
<i>Pogonomyrmex</i>	<i>naegelii</i>					16.9	10.0		

Emery, 1878

Table 1 continues on the next page

<i>Sericomyrmex</i>	<i>pr. parvulus</i>	Forel, 1912	6.3	6.0	3.3	14.0				
<i>Sericomyrmex</i>	sp.1		6.3	17.0	50.0	20.9	<1			
<i>Sericomyrmex</i>	sp.2		3.1	3.0	1.1					
<i>Sericomyrmex</i>	sp.3		3.1		2.2	2.3				
<i>Solenopsis</i>	<i>geminata</i>	(Fabricius, 1804)		8.0	36.7	100.0	31.8	90.0	70.0	20.0
<i>Solenopsis</i>	<i>globularia</i>	(Smith, 1858)	3.1	2.0	5.6	7.0	39.6	50.0	100.0	60.0
<i>Solenopsis</i>	<i>invicta</i>	Buren, 1972		8.0	22.2	51.2	61.7	26.7	56.7	80.0
<i>Solenopsis</i>	sp.1					4.7				
<i>Solenopsis</i>	sp.2		18.8	42.0	50.0	25.6	3.9	20.0	16.7	
<i>Solenopsis</i>	sp.3			2.0	3.3	4.7	28.6	33.3	33.3	20.0
<i>Solenopsis</i>	sp.4		21.9	44.0	41.1	27.9	2.6			
<i>Solenopsis</i>	sp.5		6.3	1.0	4.4					
<i>Solenopsis</i>	sp.6		31.3	22.0	23.3	20.9	<1		3.3	
<i>Solenopsis</i>	sp.7		9.4	8.0	26.7	14.0				
<i>Solenopsis</i>	sp.8		25.0	12.0	18.9	9.3	1.3			
<i>Solenopsis</i>	sp.9		15.6	22.0	41.1	41.9	16.9	10.0	3.3	40.0
<i>Solenopsis</i>	sp.10		3.1			2.3		3.3		20.0
<i>Solenopsis</i>	sp.11			4.0	4.4	2.3				
<i>Solenopsis</i>	sp.12				3.3	2.3				
<i>Solenopsis</i>	sp.13		12.5	44.0	34.4	14.0	2.6		6.7	
<i>Solenopsis</i>	sp.14			5.0	3.3	2.3	9.7	6.7		
<i>Solenopsis</i>	sp.15				1.1					
<i>Solenopsis</i>	sp.16		9.4	5.0	13.3	7.0	3.2	10.0	13.3	
<i>Solenopsis</i>	sp.17						1.9			
<i>Solenopsis</i>	sp.19		3.1	13.0	16.7	14.0	3.2	6.7		
<i>Solenopsis</i>	sp.20					2.3	<1			
<i>Solenopsis</i>	sp.21			3.0						

Table 1 continues on the next page

<i>Solenopsis</i>	sp.22		4.0						<1
<i>Solenopsis</i>	sp.23		3.1						
<i>Solenopsis</i>	<i>virulens</i>	(Smith, 1858)	6.3	4.0	6.7				
<i>Strumigenys</i>	<i>denticulata</i>	Mayr, 1887	6.3	3.0	4.4	4.7			
<i>Strumigenys</i>	sp.1			1.0					
<i>Strumigenys</i>	sp.10		3.1						
<i>Strumigenys</i>	sp.11				1.1				
<i>Strumigenys</i>	sp.2				2.2	4.7	1.9	3.3	20.0
<i>Strumigenys</i>	sp.3				1.1				
<i>Strumigenys</i>	sp.4					2.3			
<i>Strumigenys</i>	sp.5					2.3		3.3	3.3
<i>Strumigenys</i>	sp.6						2.6		40.0
<i>Strumigenys</i>	sp.7						1.9		
<i>Strumigenys</i>	sp.8					1.1			
<i>Strumigenys</i>	sp.9							2.3	
<i>Strumigenys</i>	<i>zeteki</i>	(Brown, 1959)		2.0	2.2				
<i>Trachymyrmex</i>	<i>bugnioni</i>	(Forel, 1912)		9.0	14.4	11.6			
<i>Trachymyrmex</i>	sp.1		15.6	43.0	37.8	11.6			3.3
<i>Trachymyrmex</i>	sp.2		3.1	7.0	13.3	7.0			
<i>Trachymyrmex</i>	sp.3			1.0	1.1				
<i>Wasmannia</i>	<i>auropunctata</i>	(Roger, 1863)	37.5	52.0	100.0	83.7	52.6	36.7	20.0
<i>Xenomyrmex</i>	sp.PGM1*				1.1				
PARAPONERINAE									
<i>Paraponera</i>	<i>clavata</i>	Smith, 1858		2.0					
PONERINAE									
<i>Anochetus</i>	<i>horridus</i>	Kempf, 1964		1.0		2.3			
<i>Anochetus</i>	<i>mayri</i>	Emery, 1884		1.0					

Table 1 continues on the next page

<i>Dinoponera</i>	<i>gigantea</i>		(Perty, 1833)	34.4	52.0	72.2	20.9			3.3
<i>Hypoponera</i>	sp.1			3.1	2.0		2.3			
<i>Hypoponera</i>	sp.2							1.3		
<i>Hypoponera</i>	sp.3							<1		
<i>Hypoponera</i>	sp.4					1.1				
<i>Leptogenys</i>	<i>gaigei</i>		Wheeler, 1923		1.0	4.4				
<i>Odontomachus</i>	<i>bauri</i>		Emery, 1892		7.0	23.3	4.7	7.1	23.3	3.3 20.0
<i>Odontomachus</i>	<i>brunneus</i>		(Patton, 1894)	6.3	4.0	8.9	2.3	1.3	3.3	
<i>Odontomachus</i>	<i>caelatus</i>		Brown, 1976			1.1				
<i>Odontomachus</i>	<i>haematodus</i>		(Linnaeus, 1758)		6.0	5.6	2.3			
<i>Odontomachus</i>	<i>meinerti</i>		Forel, 1905		8.0	2.2	2.3			
<i>Odontomachus</i>	sp.1				1.0					
<i>Odontomachus</i>	<i>yucatecus</i>		Brown, 1976			1.1				
<i>Pachycondyla</i>	<i>apicalis</i>		(Latreille, 1802)	37.5	68.0	56.7				
<i>Pachycondyla</i>	<i>arhuaca</i>		(Forel, 1901)	3.1						
<i>Pachycondyla</i>	<i>commutata</i>		(Roger, 1860)	6.3						
<i>Pachycondyla</i>	<i>constricta</i>		(Mayr, 1884)	18.8	13.0	28.9	16.3	1.3	10.0	
<i>Pachycondyla</i>	<i>crassinoda</i>		(Latreille, 1802)	59.4	48.0	43.3	11.6			
<i>Pachycondyla</i>	<i>harpax</i>		(Fabricius, 1804)	62.5	65.0	75.6	27.9		3.3	
<i>Pachycondyla</i>	<i>purpurascens</i>		Forel, 1899			1.1				
<i>Pachycondyla</i>	<i>striata</i>		Smith, 1858			5.6				
<i>Pachycondyla</i>	<i>verenae</i>		(Forel, 1922)	12.5	50.0	62.2	16.3		3.3	
<i>Plathytyrhea</i>	<i>sinuata</i>		(Roger, 1860)			1.1				
PSEUDOMYRMECINAE										
<i>Pseudomyrmex</i>	gr. <i>Gracillis</i>	<i>pr. alvarengai</i>	Kempf, 1961				2.3			
<i>Pseudomyrmex</i>	gr. <i>Ocullatus</i>	sp.3			10.0	6.7	4.7			
<i>Pseudomyrmex</i>	gr. <i>Ocullatus</i>	sp.4			2.0					

Table 1 continues on the next page

<i>Pseudomyrmex</i>	gr. Pallidus	sp.2					1.3			
<i>Pseudomyrmex</i>		sp.1			1.1	2.3				
<i>Pseudomyrmex</i>	<i>termitarius</i>		(Smith, 1855)	2.0	4.4	25.6	86.4	23.3	20.0	60.0

**sp.n*

Table 2

Species	Author	Land-use type							
		PFU	PFL	PFLB	SEF	REF	PAS	AGR	SHA
<i>Eufriesea auripes</i>	(Gribodo, 1882)		2				1		
<i>Eufriesea ornata</i>	(Mocsáry, 1896)			6					
<i>Eufriesea pulchra</i>	(Smith, 1854)			1	4	1	3		
<i>Eufriesea</i> sp.1					1		2		
<i>Eufriesea surinamensis</i>	(Linnaeus, 1758)		2	1	5		4		
<i>Euglossa amazonica</i>	Dressler, 1982	14	59	106	33	19	36	2	
<i>Euglossa augaspis</i>	Dressler, 1982	7	24	15	8	3	8		
<i>Euglossa bidentata</i>	Dressler, 1982	1	3	3	2		1		
<i>Euglossa carolina</i>	Nemésio, 2009	6	16	20	8	5	30	2	
<i>Euglossa chalybeata</i>	Friese, 1925	6	16	23	6	1	2	1	
<i>Euglossa cognata</i>	Moure, 1970		4	4	10				
<i>Euglossa crassipunctata</i>	Moure, 1968	3	7		3	1	1	1	
<i>Euglossa decorata</i>	Smith, 1874				1				
<i>Euglossa despecta</i>	Moure, 1968	1	6	30	24	1	17		
<i>Euglossa ignita</i>	Smith, 1874		15	23	1		1	1	
<i>Euglossa imperialis</i>	Cockerell, 1922	16	77	102	16	6	8	4	2
<i>Euglossa intersecta</i>	Audouin, 1824	1	16	19	7	2	1		
<i>Euglossa laevicincta</i>	Dressler, 1982		1		1				
<i>Euglossa liopoda</i>	Dressler, 1982		6	20	21	4	16	5	1
<i>Euglossa marianae</i>	Nemésio, 2011		2						
<i>Euglossa mixta</i>	Friese, 1899	4	29	36	21	2	3		
<i>Euglossa modestior</i>	Dressler, 1982	6	12	17	12	5	40	6	
<i>Euglossa nigriscens</i>	(Friese, 1923)						1		
<i>Euglossa orellana</i>	Roubik, 2004	5	30	12	8	1	1		

Table 2 continues on the next page

<i>Euglossa</i>	<i>parvula</i>	Dressler, 1982		2	17	1			
<i>Euglossa</i>	sp.1			1	3	4		1	
<i>Euglossa</i>	<i>townsendi</i>	Cockerell, 1904	26	84	113	109	3	7	3
<i>Euglossa</i>	<i>variabilis</i>	Friese, 1899		10		2	1	5	
<i>Eulaema</i>	<i>bombiformis</i>	(Packard, 1869)	20	26	28	14	6	10	2
<i>Eulaema</i>	<i>cingulata</i>	(Fabricius, 1804)		5	16	27	2	40	1
<i>Eulaema</i>	<i>marcii</i>	Nemésio, 2009		4	9	14	2	13	1
<i>Eulaema</i>	<i>meriana</i>	(Olivier, 1789)	19	81	65	38	6	44	17
<i>Eulaema</i>	<i>mocsaryi</i>	(Friese, 1899)		3	8	10			
<i>Euglossa</i>	<i>modestior</i>	Dressler, 1982						1	
<i>Eulaema</i>	<i>nigrita</i>	Lepelletier de Saint Fargeau, 1841		24	16	29	35	1009	227
<i>Eulaema</i>	<i>pseudocingulata</i>	Oliveira, 2006					1		
<i>Exaerete</i>	<i>frontalis</i>	(Guérin-Méneville, 1844)	13	24	13	5	2	2	
<i>Exaerete</i>	<i>lepeletieri</i>	Oliveira & Nemésio, 2003		1		4			
<i>Exaerete</i>	<i>smaragdina</i>	(Guérin-Méneville, 1844)	1	11	15	2		3	

Table 3

Species	Author	Land-use type								
		PFU	PFL	PFLB	SEF	PAS	REF	AGR	SHA	
<i>Anomiopus</i>	<i>aff. foveicollis</i>	Canhedo, 2006		1		1				
<i>Ateuchus</i>	sp.1		49	5		2				
<i>Ateuchus</i>	sp.2		3	11		1				
<i>Ateuchus</i>	sp.3		19	485	393	77				
<i>Ateuchus</i>	sp.4		3							
<i>Ateuchus</i>	sp.5		12	10	20	1				
<i>Bdelyrus</i>	sp.1			1						
<i>Canthidium</i>	<i>aff. lentum</i>	Erichson, 1847	11	104	335	97	26	1	1	29
<i>Canthidium</i>	<i>funebre</i>	Balthasar, 1939	2	1						
<i>Canthidium</i>	<i>gerstaeckeri</i>	Harold, 1867	13	45	104	8	1			
<i>Canthidium</i>	<i>humerale</i>	(Germar, 1813)		1	6	18	182	20		30
<i>Canthidium</i>	<i>semicupreum</i>	Harold, 1868	5	25	13	1	1			
<i>Canthidium</i>	sp.1		15	14	32	26	3	1		
<i>Canthidium</i>	sp.2		5	1		1		1		
<i>Canthidium</i>	sp.3				1		2		2	
<i>Canthidium</i>	sp.4					59				
<i>Canthidium</i>	sp.5			7	24	3				
<i>Canthidium</i>	sp.6		1							
<i>Canthidium</i>	sp.7		46	99	7	15				
<i>Canthidium</i>	sp.8		13	566	739	161	4	47	1	
<i>Canthidium</i>	sp.9		2	20		9				
<i>Canthidium</i>	sp.10		1	1						
<i>Canthidium</i>	sp.11		1							
<i>Canthidium</i>	sp.12		24							

Table 3 continues on the next page

<i>Canthon</i>	<i>aff. octodentatus</i>	Schmidt, 1920				8	6		
<i>Canthon</i>	<i>aff. sericatus</i>	Schmidt, 1922	1	1	1	13			
<i>Canthon</i>	<i>aff. simulans</i>	(Martínez, 1950)	2	16	112	340	4		
<i>Canthon</i>	<i>rufocoeruleus</i>	(Martínez, 1947)	45	35	16	6			
<i>Canthon</i>	<i>histrion</i>	(LePeletier de St-Fargeau & Audinet-Serville, 1828)		54	32	113	15	8	2
<i>Canthon</i>	<i>lituratus</i>	(Germar 1813)		90	126	681	392	212	59
<i>Canthon</i>	<i>proseni</i>	(Martínez 1949)	2	119	47	5			
<i>Canthon</i>	<i>scrutator</i>	Balthasar, 1939		35	53	239	138	174	92
<i>Canthon</i>	sp.1					1	12	23	3
<i>Canthonella</i>	sp.1		1	1					
<i>Coprophanaeus</i>	<i>dardanus</i>	(MacLeay, 1819)	6		3	3	1		
<i>Coprophanaeus</i>	<i>degallieri</i>	Arnaud, 1997	9	6	4		49	1	4
<i>Coprophanaeus</i>	<i>jasius</i>	(Oliver, 1789)	5	1		2			1
<i>Coprophanaeus</i>	<i>lancifer</i>	(Linnaeus, 1767)		63	40	29		2	2
<i>Cryptocanthon</i>	<i>campbellorum</i>	Howden, 1973		58	20	4			
<i>Deltochilum</i>	<i>aff. sextuberculatum</i>	Bates, 1870	3	18	74	8			
<i>Deltochilum</i>	<i>carinatus</i>	(Westwood, 1837)		4	1				
<i>Deltochilum</i>	<i>enceladus</i>	Kolbe, 1893		42	47	10			
<i>Deltochilum</i>	<i>icarus</i>	(Oliver, 1789)	3	10	24	3			
<i>Deltochilum</i>	<i>orbiculare</i>	van Lansberge, 1874		99	47	9			
<i>Deltochilum</i>	sp.PGM1*			5					
<i>Deltochilum</i>	sp.1		10	119	227	14			
<i>Diabroctes</i>	<i>mimas</i>	(Linnaeus, 1758)		5	67	53	1217	132	148
<i>Dichotomius</i>	<i>aff. globulus</i>	(Felsche, 1901)	3	1540	554	299	4		
<i>Dichotomius</i>	<i>aff. lucasi</i>	(Harold, 1869)	26	16	28	22	1	2	
<i>Dichotomius</i>	<i>boreus</i>	(Oliver, 1789)	13	145	147	32			

Table 3 continues on the next page

<i>Dichotomius</i>	<i>imitator</i>	(Felsche, 1901)		4	6	1				
<i>Dichotomius</i>	<i>aff. inachus</i>	(Erichson, 1847)		85	49	54	1			
<i>Dichotomius</i>	<i>longiceps</i>	(Taschenberg, 1870)					1			
<i>Dichotomius</i>	<i>melzeri</i>	(Luederwaldt, 1925)	1	36	108	18			4	
<i>Dichotomius</i>	<i>telamon</i>	(Harold, 1869)	1	23	42	15				
<i>Dichotomius</i>	<i>worontzowi</i>	(Pereira, 1942)	1	16	14	2				
<i>Digitontophagus</i>	<i>gazella</i>	(Fabricius, 1787)		7	1		856	7	117	
<i>Eurysternus</i>	<i>atrosericus</i>	Génier, 2009		9	1	1				
<i>Eurysternus</i>	<i>caribaeus</i>	(Herbst, 1789)	11	469	673	71	1			
<i>Eurysternus</i>	<i>cavatus</i>	Génier, 2009	9	88	110	5				
<i>Eurysternus</i>	<i>foedus</i>	Guérin-Méneville, 1844	5	45	27	5				
<i>Eurysternus</i>	<i>hamaticollis</i>	Balthasar, 1939	1	37	2	5				
<i>Eurysternus</i>	<i>harlequin</i>	Génier, 2009		1						
<i>Eurysternus</i>	<i>howdeni</i>	Génier, 2009		3	1					
<i>Eurysternus</i>	<i>hypocrita</i>	Balthasar, 1939	1	4	7					
<i>Eurysternus</i>	<i>ventricosus</i>	Gill, 1990		13	5	2			1	
<i>Eurysternus</i>	<i>wittmerorum</i>	Martínez, 1988	3	76	27	2				
<i>Eutrichillum</i>	sp.1		1	2	1	2				
<i>Hansreia</i>	<i>affinis</i>	(Fabricius, 1801)	16	152	5	17				
<i>Ontherus</i>	<i>sulcator</i>	(Fabricius, 1775)	1	12	301	178	287	103	59	9
<i>Ontophagus</i>	<i>aff. hirculus</i>	Mannerheim, 1829		259	121	112	486	229	257	9
<i>Ontophagus</i>	<i>onthochromus</i>	Arrow, 1913		23	7	4	9			
<i>Ontophagus</i>	<i>ophion</i>	Erichson, 1847	26	365	279	26	11	17	2	1
<i>Ontophagus</i>	<i>rubrescens</i>	Blanchard, 1846	153	1864	850	194	48		4	
<i>Oxysternon</i>	<i>mackleayi</i>	Nevison, 1892	308	144	155	11				
<i>Oxysternon</i>	<i>silenus</i>	Castelnau, 1840	6	35	34	1				
<i>Phanaeus</i>	<i>chalcomelas</i>	(Perty, 1830)	41	8	5	1				

Table 3 continues on the next page

<i>Pseudocanthon</i>	<i>aff. xanthurus</i>	(Blanchard, 1846)	1	12	37	3335	159	940	27
<i>Sulcophaneus</i>	<i>faunus</i>	(Fabricius, 1775)	1	2	1	4			
<i>Trichillum</i>	<i>externepunctatum</i>	Preudhomme de Borre, 1880		7	3	1	1		
<i>Trichillum</i>	<i>pauliani</i>	Balthasar, 1939	3	3	21	13			
<i>Trichillum</i>	sp.1		42	15	1428	236	19563	174	3480
<i>Uroxys</i>	sp.1		1	16	10	3			
<i>Uroxys</i>	sp.2			11			2		
<i>Uroxys</i>	sp.3			6	3	2			

*sp.n

CHAPTER TWO

LAND-USE ERODES REGIONAL DIVERSITY AND SHIFTS COMPOSITION OF ANT COMMUNITIES IN THE BRAZILIAN AMAZON

**LAND-USE ERODES REGIONAL DIVERSITY AND SHIFTS
COMPOSITION OF ANT COMMUNITIES IN THE BRAZILIAN
AMAZON**

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ABSTRACT

Tropical forests are being rapidly degraded by fragmentation, logging, fire, and hunting. Quantifying and understanding how biodiversity responds to such disturbances is key to designing more effective conservation strategies for human-modified landscapes. With this in mind, the aim of the present study is to examine (1) how ant species composition at transect scale responds to forest disturbance and conversion to production landscapes? We then ask (2) how species richness at transects and catchment scales are affected by land-use intensification? Finally, we assess (3) which environmental variables best predict the patterns of species richness across the entire gradient at both scales. We sampled 192 transects distributed across 18 catchments (5000ha each) in the municipality of Paragominas (Eastern Brazilian Amazon), encompassing a full gradient of land-cover intensification from undisturbed primary forest through varyingly disturbed primary forests, old and young secondary forests, mechanised agriculture and pastures. Variables measured to capture natural patterns of environmental heterogeneity included tree species richness, forest canopy cover, aboveground biomass (total, leaf-litter, fine-woody debris) and soil physical characteristics. Variables used to measure anthropogenic disturbances included the percentage of primary forest in the surrounding landscape, the trajectory of forest loss in the last two decades. We found a clear shift in species composition with land-use change, as well as we found that species richness at transect level decreases almost two-fold from forests to production landscapes. Primary forest cover is an important variable explaining ant species richness at both transect and catchment scales. We also found that litter is an important predictor variable, with species richness at transect level increasing with it in production landscapes. We

conclude that the maintenance of larger portions of primary forests can maintain and enrich the regional pool of species which is beneficial for a landscape-wise conservational act, as it works facilitating species recovery.

Keywords: Amazon forest, Biodiversity patterns, Conservation, Human-induced impacts.

INTRODUCTION

Human induced changes to the biosphere have led to widespread biodiversity loss across the world (Laliberte & Tylianakis 2010; Gibson *et al.* 2011; Tabarelli *et al.* 2012; Arroyo-Rodriguez *et al.* 2013; Melo *et al.* 2013). Tropical forests are at the forefront of conservation concerns as they harbour two-thirds of global terrestrial biodiversity (Pimm & Raven 2000) yet are subject to high levels of selective logging, deforestation, fragmentation, and other impacts (Asner *et al.* 2005; Asner *et al.* 2006; Malhi *et al.* 2008; Hansen *et al.* 2013). As a result, many modern tropical forest landscapes are a mosaic of different levels of forest disturbance and land-use intensity (Chazdon 2008; Gardner *et al.* 2009). Such landscapes are of high interest for conservation, but are poorly understood as the biotic communities are often novel.

Two important methodological issues with current studies limit to our current understanding of how biotic communities respond within human-modified landscapes. First, many studies only examine a relatively short section of the full disturbance gradient (Vasconcelos *et al.* 2000; Vasconcelos *et al.* 2006; Silveira *et al.* 2010; Silveira *et al.* 2012). Second, many studies are restricted to small geographic areas with little or no replication at landscape scale (Oliveira *et al.* 2011). As such, these studies could be systematically failing to capture the importance of changes in landscape scale properties, such as forest cover changes, or to identify different interactions between human disturbance and underlying environmental gradients (Gardner *et al.* 2009). In addition, where studies have attempted a broader scale assessment, these tend to focus on plants (Coronado *et al.* 2009; Koltunov *et al.* 2009; Dexter *et al.* 2012; Arroyo-Rodriguez *et al.* 2013) rather than animal communities (Barlow *et al.* 2007; Prist *et al.* 2012). Therefore,

faunal studies exploring multiple human impacts at variable spatial scales are highly desirable for assessing the conservation value of complex human modified tropical forest landscapes.

Arthropods are by far the most numerically and functionally dominant faunal group in tropical environments and are therefore essential for understanding how ecological processes respond to human induced disturbances (Gardner *et al.* 2008; Vasconcelos & Bruna 2012). Among them, ants are a ubiquitous group of insects, outweighing in number and biomass many other arthropods (Lach *et al.* 2010) and by far the vertebrates (Hölldobler & Wilson 2009), occupying virtually all strata of the forest (Blüthgen & Feldhaar 2010), and playing a wide variety of key functional roles from herbivory, seed dispersal, bioturbation among others (Del Toro *et al.* 2012). They have the additional advantages of being easily sampled and having a relatively well understood taxonomy and ecology (Underwood & Fisher 2006). Yet despite their importance, very few large-scale studies have assessed ants in tropical forests (but see Vasconcelos *et al.* 2006; Vasconcelos *et al.* 2010) and none have explored a comprehensive gradient of human impacts across a whole landscape.

To address these knowledge gaps, we undertook the most comprehensive survey on the effects of land-use changes on tropical forest ants to date. We sampled ants and environmental variables in a total of 192 transects in the eastern Brazilian Amazon, grouped within 18 catchments across 2 million hectares and encompassing seven different land-cover classes (from undisturbed forests, through varying levels of disturbed primary forests (logged and burned), secondary forests and production landscapes). Specifically, we draw upon the strengths of this study to examine (1) how ant species composition at transect

scale responds to forest disturbance and conversion to production landscapes? We expect composition to shift drastically from forest to non-forest habitats along a gradient of land-use. We then ask (2) how species richness at transects and catchment scales are affected by land-use intensification? We expect that species richness at both scales will decline with the land-use intensification gradient. Finally, we assess (3) which environmental variables best predict the patterns of species richness across the entire gradient at both scales. We expect that transect and catchment species richness to have a positive relationship with variables linked to higher forest dominance in the landscape, such as primary forest cover, soil and vegetation characteristics.

MATERIAL AND METHODS

Study region

We conducted our study in Paragominas (hereafter PGM), a municipality of the eastern Brazilian Amazon in Pará state (Figure 1). The municipality used to be covered with a tropical evergreen forest but have suffered significant forest loss in recent decades, especially due to understorey fires, heavy logging process and conversion to pastures and mechanised agriculture (for more details, see Gardner *et al.* 2013; Viana *et al.* 2013). We sampled two major land-use categories in this study (Production landscapes and forests), divided in seven different classes of land cover. Production land covers consisted of mechanized agriculture, cattle pastures, and silviculture (monocultures of *Eucalyptus* and *Schyzolobium amazonicum*). Forest classes were secondary forests, logged primary forests, logged and burnt primary forests and undisturbed primary forests. Secondary forests are patches of forest that have been cleared at some point in time and are under recovery. Primary forests were classified as Undisturbed,

Logged, or Logged and Burnt based on evidence from either field observations (fire and logging scars) or manual interpretation of satellite images. We adopted forest disturbance nomenclature and definitions following Putz & Redford (2010). Finally, we assessed how well our *a priori* land-use categories are matched by the total aboveground biomass (AGB, for details on how it was sampled, see SOM), so we can use AGB as a proxy for our land-use categories. AGB explained almost all the variance in land-use intensification at the transect scale ($F_{6,11}=117.2$, $p<0.001$, $R^2=0.93$). It only could not distinguish between undisturbed and logged forests and pastures and agriculture at the transect level.

Ant sampling

We divided the municipality in 182 roughly evenly sized sub-catchments (ca 5 000 ha, hereafter ‘catchments’), from which we selected 18 catchments for the survey. Catchments were selected to cover a gradient of primary forest cover (6-100%) observed in the region. Within each catchment, we allocated 8–12 transects (each 300 m in length), at a density of 1 transect/400 ha and transects were separated by > 1.5 km. Numbers of transects were distributed in proportion to the percentage occupied by a given land use in a given catchment. We sampled some 192 transects and the total area was ca. 1 million ha (Fig. 1; details about the methods and definitions of land-use classes can be found in Gardner *et al.* 2013).

Within each transect we sampled the ants using epigaeic baited pitfall traps. Traps consisted of plastic containers half filled with a solution of water, salt (5%) and soap (5%) and baited with sardine and honey, both unreachable to the ants. In each transect we installed six pitfall traps distanced 50m from each other, which remained in the field for 48h prior to collection and processing. We processed and identified the ants to the most precise taxonomic level possible

using available taxonomic keys (Bolton 1994; Fernández 2003) and the reference collection of the Community Ecology Lab, Federal University of Viçosa. The nomenclature was checked and revised against Bolton's online catalogue (accessed at 02/Jan/2014).

Environmental variables

In order to better explain the patterns we are trying to describe in this study, we sampled several environmental variables. These variables are directly or indirectly linked to conditions and resources that are important to the ants' establishment and persistence in a given habitat (Blüthgen & Feldhaar 2010), as well as represent the degree by which the transect has been disturbed. The variables we sampled are presented in the Table 1. A detailed methodological description of their sampling is reported in Gardner *et al.* (2013) and in the Supplementary Online Material.

Statistical analyses

To answer the first question, if there is a shift in species composition with land-use intensification we performed a non-metric multidimensional scaling (NMDS) ordination of our community data. As any social insect, ants' abundance in a trap may represent many individuals from the same nest, we opted to use presence/absence data and the Jaccard's dissimilarity index. As well as grouping points according our land cover categories, we also weighed the size of the points relative to the AGB recorded in each transect, which provides a useful overview of land-use intensification in forested catchments. Specifically for forest transects, AGB is a better descriptor of the multiple impacts of human use that are difficult to assess in categories (Berenguer 2014). To test for the significance of the relationship, we performed a PERMANOVA test (Anderson 2001) using the

community data as response variable and land-use classes as explanatory variable, once AGB and land-use classes are too collinear to be kept in the same model. Same as the NMDS, we also used Jaccard distance and we computed 999 permutations to get significance values. As we are aware of some caveats of using PERMANOVA pointed out by Warton *et al.* (2012), we also ran Generalized Linear Models tests, with negative binomial distribution. In this case, we used AGB as explanatory variable as the model yields stronger results with continuous variables. However, both methods yielded the same results, and we opted to show just results for PERMANOVA as they match the graphical representation for the NMDS.

To examine whether there is an effect of land-cover changes on transect and catchment diversities, we analysed the species richness at local and regional scales as response variables. We calculated transect diversity as the number of species sampled in a 300m transect. We fitted generalized linear mixed models, to account for the nested sampling design, (GLMM, Bolker *et al.* 2009) with land-use class as explanatory variable. To get which levels are significant, we performed model simplification via contrasts, lumping similar levels and analysing the contrasts (Crawley 2012). To compare regional diversity across land-use classes we used rarefied species accumulation curves (rarefied to eight transects in each land-use), with confidence intervals generated after 1.000 randomisations (Colwell *et al.* 2004). We considered non-overlapping levels as having different accumulated number of species. As richness is a form of count data, we used Poisson distribution, corrected for overdispersion when necessary (Crawley 2012). Finally, we calculated catchment diversity as the rarefied number of species within a catchment for all transects within it, regardless land-use class.

The rarefied number was achieved as the average species richness for 8 transects (the minimum number of transects/catchment) after 1000 resampling rounds. This metric will be used for the next session.

For the third question, about what variables better predict diversity in human-modified landscapes, we used species richness at transect and catchment scales as response variables. We selected the following set of *a priori* as explanatory variables: above-ground biomass (AGB), fine wood debris (FWD), litter biomass (LB), tree species richness (TSR), primary forest percentage at both transect (500m buffer, PFPT) and catchment area (PFPC), canopy cover (CC), soil bulk density (SBD), clay percentage (CP) and deforestation trajectory (FCCP, Ferraz *et al.* 2009) as explanatory variables. We also included land-use class (LUC) as explanatory for transect diversity. We performed correlation tests for all variables and those ones with high correlation values (>0.7) were removed from the models where their effects could not be disentangled (Zuur *et al.* 2010). In general we had to remove AGB, TSR and CC, as they were frequently correlated with PFP at both scales (transect and catchment). Variables were standardised, ranging between 0 and 1, however we checked it did not influence the results, so we opted to use raw values.

For transect diversity as response, average value per transect was used for each variable. For catchment diversity as response, we averaged values of all variables per catchment, with exception of PFP that was possible to be calculated at the catchment scale. We fitted GLMMs (Bolker *et al.* 2009) and as we hypothesise all variables can have an effect on ant diversity, given they play a role on the ants' biology (Blüthgen & Feldhaar 2010), we fit models starting of from the complete model with all the variables mentioned above. Same as above, we

used Poisson distribution. We checked for global (full) model overdispersion using a likelihood ratio test procedure, which allows computing the deviance between the saturated model and the full model. The deviance is then divided by the residual degrees of freedom to assess potential overdispersion (Vierling *et al.* 2013).

We evaluated relative model performance using Akaike's Information Criterion corrected for small sample size (AICc) (Burnham & Anderson 2004; Burnham *et al.* 2011). We simplified global models via multimodel inference (Burnham & Anderson 2004). Although most studies adopt a cutoff of $\Delta\text{AICc} < 2$ for the model averaging (McCarthy & Masters 2005), we preferred to adopt an approach that conserve more models to be averaged, with $\Delta\text{AICc} < 4$ for the final model selection averaging. As by allowing a more conservative subset of models, uncertainty is increased and therefore we averaged models within the range of $\Delta\text{AICc} < 4$. Model averaging generates a new subset of parameters to determine which explanatory variables have the most important effects on the response variable (Nakagawa & Freckleton 2011). This procedure is recommended when strong support is lacking for a single best model and when all-subset modelling is done (Lukacs *et al.* 2010; Burnham *et al.* 2011).

We performed all analyses in the platform R (R-Core-Team 2013). NMDS, PERMANOVA and rarefaction curves were computed using the package *vegan* (Oksanen *et al.* 2013). GLM tests for species composition are implemented in package *mvabund* (Wang *et al.* 2012). We computed GLMM procedures using the package *lme4* (Bates *et al.* 2013) and model inference with the package *MuMIn* (Barton 2013). Correlation panels among variables are available in the package *psych* (Revelle 2013).

RESULTS

Considering all land-use classes, we sampled a total of 282 ant species and morphospecies, belonging to ten subfamilies and 56 genera. A list with the species found in each land-use per subfamily is given in Table 1 of the 1st chapter.

Question 1: Species composition

There was a clear and significant shift in species composition across land-uses (Fig 2, PERMANOVA $F_{2,182}=29.88$, $P<0.001$). The shift follows a AGB gradient, although this is not clear for production landscapes.

Question 2: How does species richness and diversity respond to land-use changes?

We found that transect species richness is different between forests and production landscapes ($\chi^2_{2,16}= 104.97$, $P<0.001$, Fig 3a), but has no relationship with ABG within each of these categories. Contrasts revealed that forests are not different among each other ($\chi^2_{2,16}= 0.04$, $P=0.83$) and that pastures are not different from silviculture ($\chi^2_{2,16}= 0.961$, $P=0.32$). To the rarefied species accumulation curves (Fig 3b), we cannot distinguish among forest types by the accumulated number of species. However forests have twice as more species than pastures and silviculture. Agriculture is the poorest habitat in number of accumulated species.

Question 3: What variables are better predictors of ant diversity in human-modified tropical forest landscapes?

After model selection, 19 other models remained in the top models ($\Delta AICc<4$) to explain transect species richness within forest landscapes (Table S1). The null models was the top model, and in model averaging we can see that none of the averaged variables have acceptable confidence, as confidence

intervals for them always included zero (Table 2a). Transect species richness in production landscapes (i.e. silviculture, Pasture and agriculture), was explained by a wider range of variables (Table S2). After model averaging, none of the variables have acceptable confidence, as confidence intervals always included zero. However, LB, SBD, LUC and PFP(t) presented high importance values (Table 2b). For catchment species richness, we found that only PFP(c) remained in the top model and have support through model averaging to be considered a acceptable predictor variable (Table 3). There is a positive effect of PFP(c) on the species richness in the catchment level (Fig 4). The complete list of models generated is available in Table S3.

DISCUSSION

The importance of human induced disturbances on tropical forests is a priority topic on the conservationists' agenda (Laurance *et al.* 2012; Laurance *et al.* 2014). Yet, relatively little is known on how major numeric and functional groups (e.g. ants) are responding to this. Indeed, many hypotheses remain unknown on what promotes ant's diversity, composition and coexistence (Andersen 2008). In this study we present evidence that land-use changes (as also shown by AGB) have a strong effect on local species composition. Furthermore, land-use changes reduces the number of species of ants at both local and regional scales. From the variables that influence diversity of ants at both transect and catchment scales, it is noticeable that the amount of primary forest cover is an important factor for keeping ant diversity. At transect scale, and especially in more degraded habitats we found a high importance of the litter layer, as already reported by other authors (Carvalho & Vasconcelos 1999; Campos *et al.* 2003; Blüthgen & Feldhaar 2010; Paolucci *et al.* 2010).

We confirmed our prediction that species composition would present a shift from production landscapes to forests. Furthermore, this change is gradually higher from very low AGB pastures and agriculture, through degraded secondary forests until high AGB primary forests. We found that the higher is the difference in the amount of biomass in a given site, the more dissimilar they are. Nevertheless, distinction between deforested transects via AGB is very rough as they have an overall low biomass (Berenguer 2014). Responses of ant species composition to human induced impacts have already been reported on the literature (Silveira *et al.* 2010; Silveira *et al.* 2012; Silveira *et al.* 2013; Woodcock *et al.* 2013). Schmidt *et al.* (2013) have shown that ants respond gradually to secondary forests recovery time in south-eastern Brazilian forests and Yates & Andrew (2011) showed a shift in species composition of ants in different land-use types. Another study has already shown that primary and secondary forests in the Ecuadorian Amazon have different ant species composition (Wilkie *et al.* 2009). However, despite describing changes in composition, these studies fail to encompass the complexity of human-modified landscapes, specially in the Amazon (Gardner *et al.* 2009). In our study we show this shift is linked to a loss in AGB (and therefore primary forest cover, once there is a high correlation) in degraded forests and production landscapes. Thus, we can conclude that even considering a highly variegated landscape with several land-use types, which could be considered heterogeneous, it is hugely important to prioritise the reestablishment of mature forests. The new species gained in secondary forests and production landscapes may not necessarily be beneficial in terms of conservation value (Gardner *et al.* 2009; Tabarelli *et al.* 2012) and cannot be assumed as an increase in functional diversity, for example. However, one should

consider regional contexts of forest disturbance and also the amounts of remaining primary forests left behind to take a decision.

For the second question, on how transect and catchment species richness are affected by land-use intensification, we expected both would decline with more severe disturbance. Our expectation was confirmed, and both transect and regional diversities presented a decrease with higher levels of disturbance. However in both cases, there is no difference in species richness within forest transects, regardless degradation status. It is already widely known that species richness is a very rough measure to measure any impact on ant communities (Ribas *et al.* 2012; Schmidt *et al.* 2013). Even so, we were able to detect differences in species richness. The most obvious is the reduction from forests to production landscapes. Moreover, within production landscapes pastures and silviculture are richer in species than agricultural fields. Linking results of richness and composition, we can see that despite forests have statistically the same richness, they are strikingly different in composition. This is especially true for the gradient of composition formed by the secondary forests, which comprise a transition in species composition from production landscapes and primary forests. Therefore, there is an enormous potential for conservation if we take into account that forest aboveground biomass present a considerable recovery in around 17 years (West *et al.* 2014), which can represent an increase in forest quality. With the recovery of disturbed primary and secondary forests, we could therefore expect a reclaim of both species richness and species composition of undisturbed and mature forests.

In our third question we asked what environmental variables better predict the patterns of species richness at transect and catchment scales. Percentage of

primary forest cover at both transects and catchment scales had positive influence species richness. However, historical changes (FCCP) did not have any effect on present diversity. At transect scale, forest transects were not better explained than the null model by none of the variables. However for production landscapes we found that there is some support to the fact that with a higher persistence of the litter layer, the ant community is richer. This is expectable as this layer is an important nesting resources for ground dwelling ants and can be a suitable habitat for a very wide range of ant prey (e.g. springtails, other arthropods, molluscs) (Blüthgen & Feldhaar 2010). SBD appeared as an important variable in the model, however we feel that this is due to the fact that poorer agricultural sites are often managed, ploughed and tilled, presenting lower SBD but harbouring few species. Finally, PFP(t) was an important variable associated with higher species richness in production landscapes. This might be explained as primary forests can act as sources of colonisers (Ottonetti *et al.* 2006; Graham *et al.* 2009; Pais & Varanda 2010). At catchment scale, only the amount of primary forest explained higher species richness and this result was already found by Pacheco *et al.* (2013) studying savannahs. This is expected as forests harboured the higher number of species, and therefore can also be sources of new colonisers to newly formed secondary forests and weakly managed pastures. Thus, the maintenance of larger portions of primary forests can maintain and enrich the regional pool of species which is beneficial for a landscape-wise conservational act, as it works facilitating species recovery.

CONCLUSIONS

In this study we show that land-use changes affect both species richness and composition of ants. We found that species richness of ants at both local and

regional scales is associated with the maintenance of high primary forest cover in the landscape. We also could show that secondary forests are an excellent opportunity for conservation, once as they are getting older, their species composition start resembling the primary forests composition. On production landscapes, the persistence of the litter layer can influence positively species richness, as well as keeping forest areas nearby them. On a catchment scale, only the amount of primary forest remaining explains higher levels of species richness. This is important to show that the maintenance of forests should be done at the whole landscape, and not concentrated in one single large area.

As we already know, ants are a dominant group in forests numerically and functionally (Hölldobler & Wilson 2009; Lach *et al.* 2010). It has been argued that not all species play the same role in ecosystem functioning (Loreau 2004; Loreau & de Mazancourt 2013). Hence it is very likely this compositional shift can also incur in a functional diversity loss (Crist 2009; Bihn *et al.* 2010; Leal *et al.* 2012; Arnan *et al.* 2013). Despite this sounds plausible, this hypothesis needs further investigation, as well as if there is a loss in phylogenetic diversity (Srivastava *et al.* 2012).

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Table 1: Variables sampled in this study, followed by the acronym adopted, scale they were sampled and brief description of methods. Details about each variable sampling can be found in Gardner *et al.* (2013).

Variable sampled	Acronym	Proxy for	Scale of sampling	Brief description
Total Above ground Biomass (Mg.ha ⁻¹)	AGB	Land-use intensification (conditions)	Transect	Aboveground biomass of carbon estimates were made based on field measurements and allometric equations.
Fine wood debris biomass (Mg.ha ⁻¹)	FWD	Nesting resources	Transect	Fine woody debris consist of fragments between 2 to 10 cm diameter were sampled in five 2x5m sections.
Litter biomass (Mg.ha ⁻¹)	LB	Conditions and resources	Transect	Leaf litter samples were taken every 50 m along the transect using 50x50cm quadrats.
Tree species richness (Number of species)	TSR	Conditions and resources	Transect	All trees and palms above 10 cm of diameter at 1.3m height were measured in 10 x 250 m plots. Smaller individuals (2 to 10 cm diameter) were sampled in five subplots of 5 x 20 m
Primary Forest cover (Percentage)	PFC	Forest condition	Transect (500m buffer) and Catchment	Satellite imagery (LANDSAT) was used to determine primary forest cover.
Canopy cover (Percentage)	CC	Conditions	Transect	In each transect, five hemispherical photos were taken at a 50m interval
Soil bulk density (g.cm ⁻³)	SBD	Conditions	Transect	Soil bulk density was calculated by the volumetric cylinder method
Clay percentage	CP	Conditions	Transect	Soil granulometric determination was done by the densimeter method
Deforestation Trajectory	FCCP	Historic	Transect	Forest Change Curvature Profile, calculated by the LUCAT tool for ArcGIS (Ferraz <i>et al.</i> 2009).

Table 2 – Model averaging results for transect scale species richness. All candidate models within $\Delta AIC_c < 4$ had their coefficients and relative importance values averaged and estimates of all parameters is provided, as well as standard error (SE) and confidence intervals (CI). Relative importance values are also shown (RIV). CC – canopy cover, FWD – fine wood debris, LB – litter biomass, PFP(t) – primary forest percentage at transect scale, SBD – soil bulk density, FCCP(t) – deforestation trajectory at transect scale, LUC – Land-use class, df – degrees of freedom.

a) Forest Transects

Parameters	Estimate	SE	Lower CI	Upper CI	RIV
Intercept	3.19	0.14	2.93	3.46	
CC	0.15	0.18	-0.19	0.49	0.26
FWD	0.01	0.01	-0.01	0.02	0.25
LB	0.00	0.01	-0.01	0.02	0.23
PFP(t)	0.03	0.09	-0.14	0.20	0.16
SBD	-0.03	0.13	-0.29	0.22	0.15
FCCP(t)	0.04	0.29	-0.52	0.60	0.15

b) Production landscape transects

Parameters	Estimate	SE	Lower CI	Upper CI	RIV
Intercept	2.40	0.37	1.68	3.13	
LB	0.02	0.01	0.00	0.04	0.66
PFP(t)	0.35	0.22	-0.09	0.79	0.47
SBD	0.37	0.21	-0.04	0.77	0.59
LUC (PAS)	0.05	0.14	-0.22	0.32	
LUC (AGR)	-0.22	0.18	-0.57	0.12	0.57
CC	-0.01	0.35	-0.70	0.68	0.16
FWD	0.02	0.03	-0.05	0.09	0.21

Table 3 – Model averaging results for catchment scale species richness. All candidate models within $\Delta AIC_c < 4$ had their coefficients and relative importance values averaged and estimates of all parameters is provided, as well as standard error (SE) and confidence intervals (CI). Relative importance values are also shown (RIV). PFP(c) – primary forest percentage at catchment scale, SBD – soil bulk density, FCCP – deforestation trajectory.

Parameters	Estimate	SE	Lower CI	Upper CI	RIV
Intercept	73.31	14.44	42.82	103.79	
PFP(c)	0.33	0.12	0.07	0.60	1.00
SBD	-10.06	22.06	-57.08	36.96	0.13
FCCP(c)	-13.60	43.98	-107.35	80.14	0.12
LB	-0.01	1.76	-3.76	3.74	0.12

FIGURES LEGENDS

- Figure 1 Map of Paragominas region and sampling design representation. The region is located in Para state, north Brazil. In the map, the pink colours represent non-forest habitats, while the green colour represent forests of any kind (Primary or secondary). A detail of a catchment sampled and the transect design are represented in the boxes.
- Figure 2 NMDS map of species composition according aboveground biomass (point sizes) and land-use types (point colours). We analysed significance PERMANOVA.
- Figure 3 Relationship between species richness and land-use class. In (A) we provide boxplots with results for transect scale species richness. Colours are only to distinguish between forest transects and production landscapes. On the top of the bars, those grouped under the same letter code are statistically similar. In (B) we present species accumulation curves per land-use, rarefied to eight as the minimum comparable sampling effort. Shaded polygons around each curve represent 95% confidence intervals. Significant relationships were considered with $P < 0.05$.
- Figure 4 Positive relationship between catchment species richness and primary forest cover at catchment scale (PFP(c)), as depicted in model averaging. There is a positive trend between the variables and PFP(c) have the highest relative importance value.

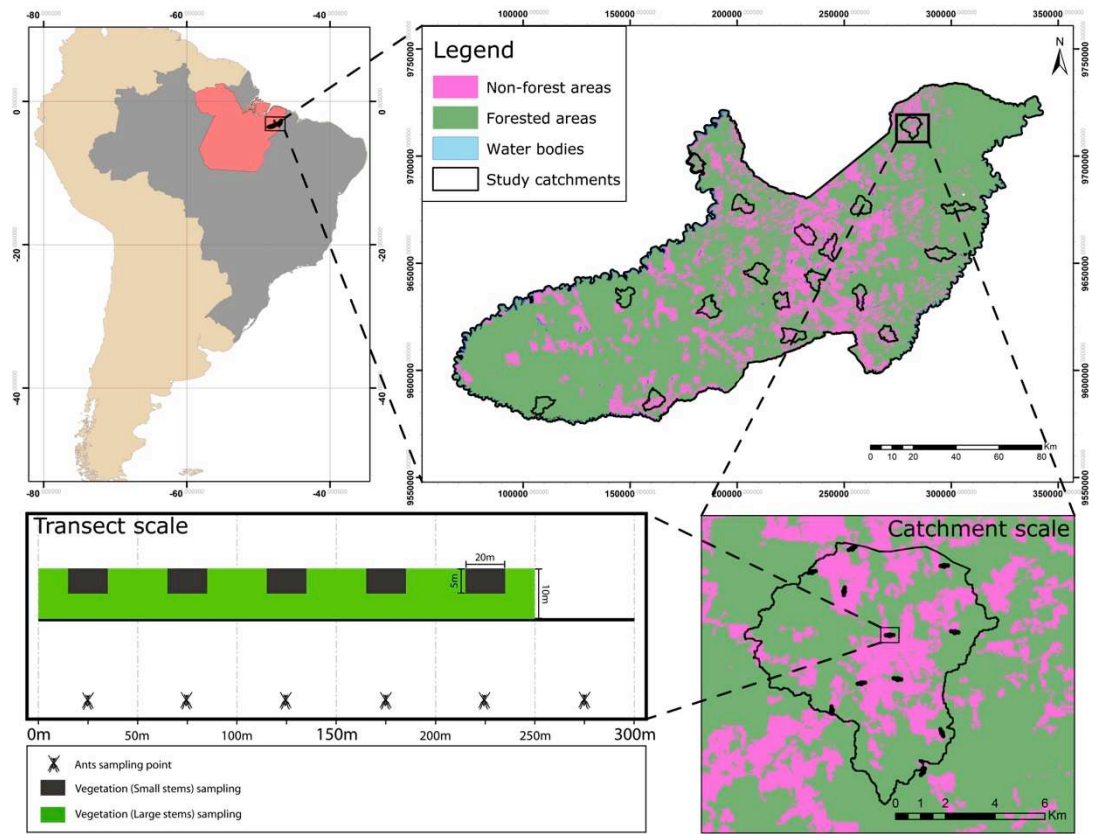


Figure 1

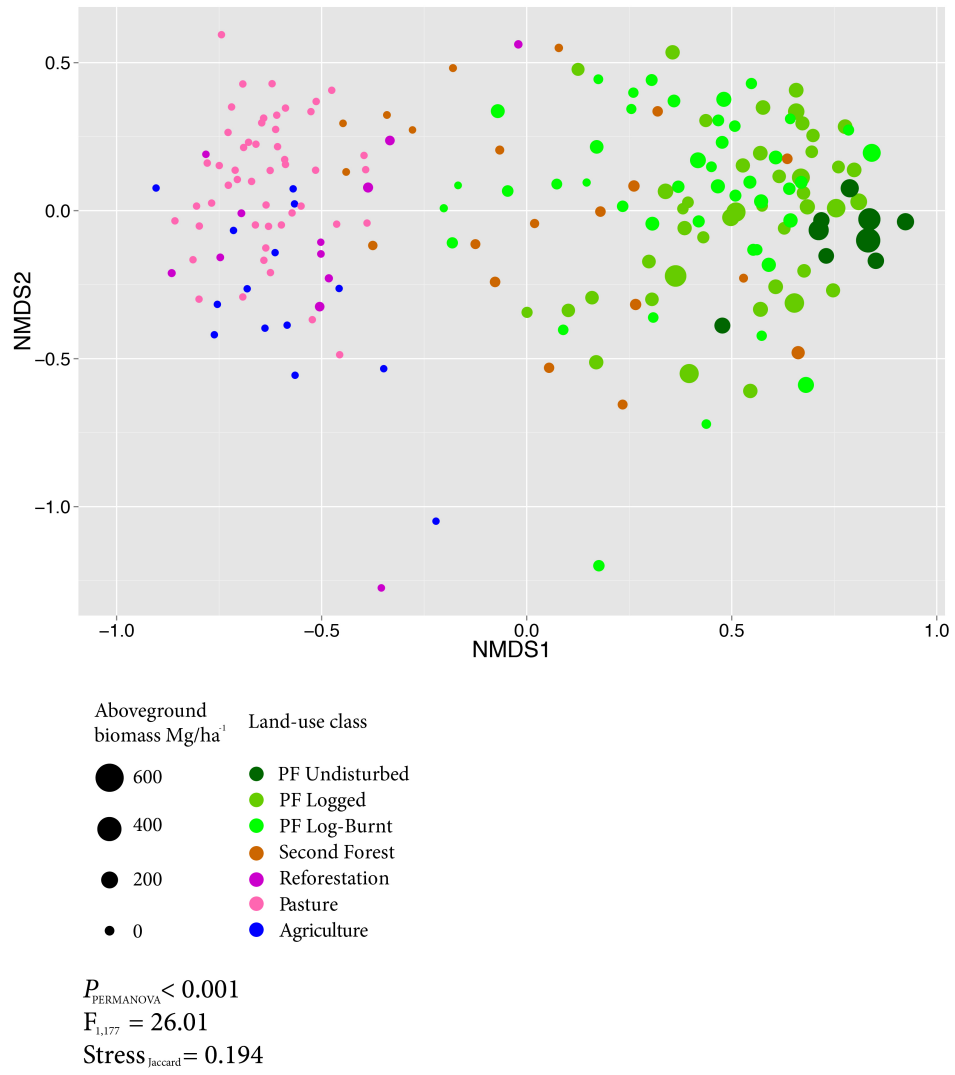


Figure 2

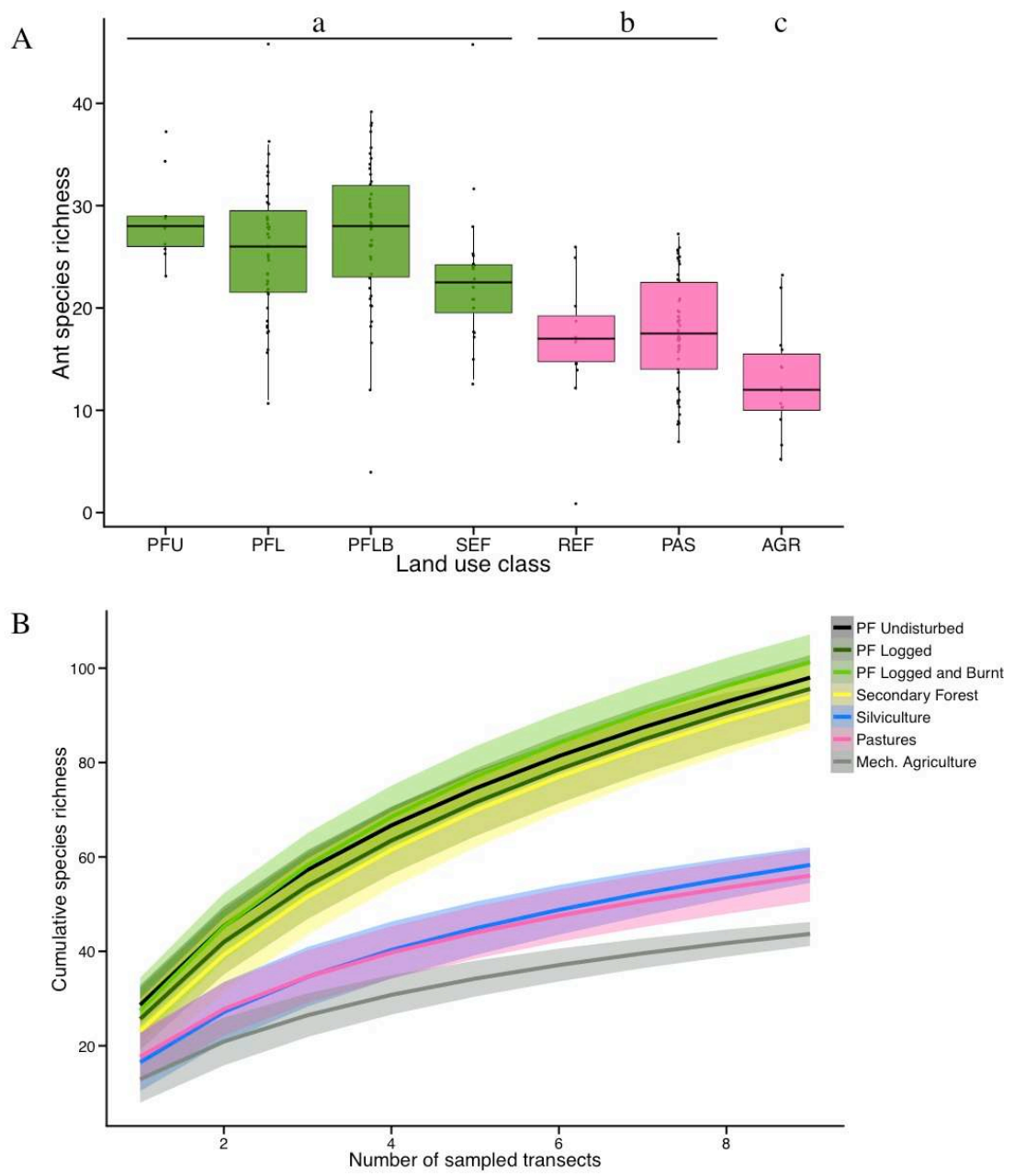


Figure 3

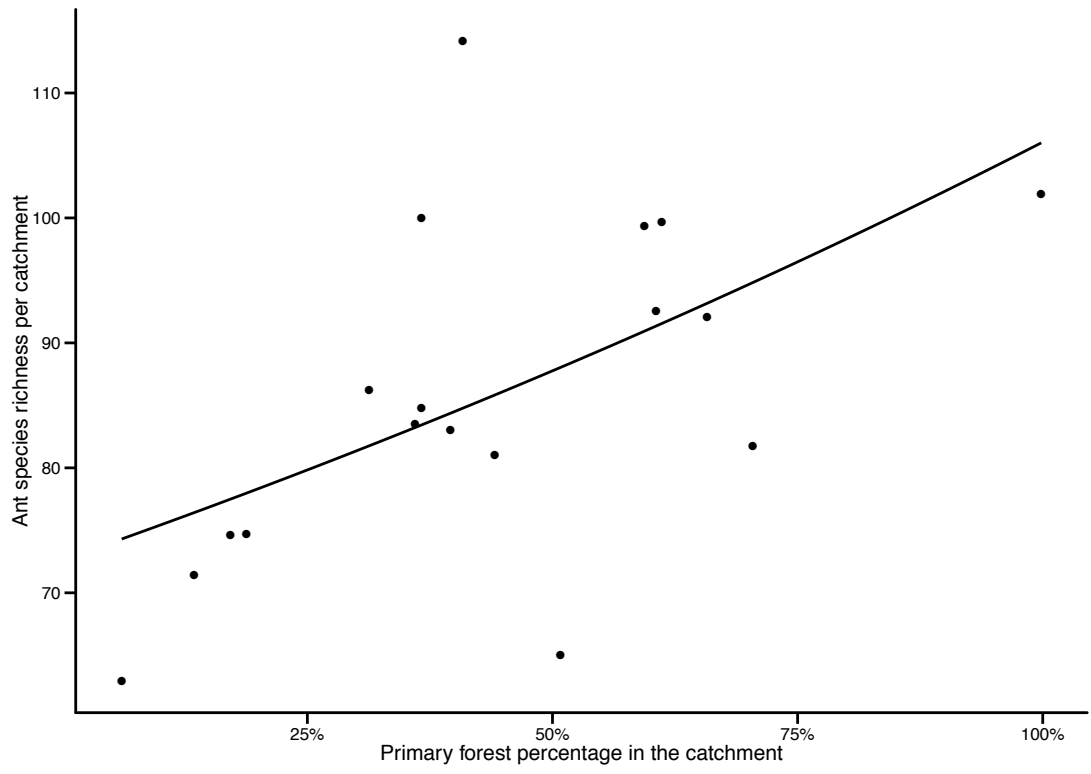


Figure 4

Table S1 – Complete set of models generated by multimodel selection procedure for transect species richness in forest transects. Here a listed all possible variables in the models, followed by model R^2 , degrees of freedom (df), model log-likelihood (logLik), AICc and $\Delta AICc$ and finally model weight (ω). FWD – fine wood debris, LB – litter biomass, CC – canopy cover, FCCP – deforestation profile, PFP(t) – primary forest percentage in a 500m buffer, SBD – soil bulk density.

	Intercept	FWD	LB	CC	FCCP	PFP(t)	SBD	R^2	df	logLik	AICc	$\Delta AICc$	ω
1	3.25	NA	NA	NA	NA	NA	NA	0.29	3.00	-383.95	774.12	0.00	0.13
5	3.13	NA	NA	0.15	NA	NA	NA	0.29	4.00	-383.56	775.48	1.36	0.07
2	3.22	0.01	NA	NA	NA	NA	NA	0.29	4.00	-383.64	775.64	1.52	0.06
3	3.19	NA	0.00	NA	NA	NA	NA	0.29	4.00	-383.74	775.84	1.72	0.06
17	3.23	NA	NA	NA	NA	0.03	NA	0.29	4.00	-383.89	776.13	2.01	0.05
33	3.30	NA	NA	NA	NA	NA	-0.03	0.29	4.00	-383.92	776.19	2.08	0.05
9	3.25	NA	NA	NA	0.04	NA	NA	0.29	4.00	-383.94	776.25	2.13	0.05
6	3.12	0.00	NA	0.13	NA	NA	NA	0.29	5.00	-383.34	777.23	3.12	0.03
4	3.16	0.01	0.00	NA	NA	NA	NA	0.29	5.00	-383.38	777.31	3.20	0.03
7	3.10	NA	0.00	0.14	NA	NA	NA	0.29	5.00	-383.43	777.41	3.29	0.03
37	3.18	NA	NA	0.16	NA	NA	-0.04	0.29	5.00	-383.51	777.57	3.45	0.02
21	3.13	NA	NA	0.15	NA	0.01	NA	0.29	5.00	-383.55	777.65	3.53	0.02
13	3.13	NA	NA	0.15	0.02	NA	NA	0.29	5.00	-383.56	777.66	3.54	0.02
18	3.21	0.01	NA	NA	NA	0.02	NA	0.29	5.00	-383.60	777.75	3.63	0.02
10	3.22	0.01	NA	NA	0.06	NA	NA	0.29	5.00	-383.61	777.77	3.66	0.02
34	3.25	0.01	NA	NA	NA	NA	-0.02	0.29	5.00	-383.62	777.79	3.67	0.02
19	3.16	NA	0.00	NA	NA	0.04	NA	0.29	5.00	-383.64	777.83	3.71	0.02
35	3.24	NA	0.00	NA	NA	NA	-0.03	0.29	5.00	-383.71	777.96	3.85	0.02
11	3.19	NA	0.00	NA	0.04	NA	NA	0.29	5.00	-383.73	778.01	3.89	0.02
49	3.27	NA	NA	NA	NA	0.03	-0.03	0.29	5.00	-383.85	778.25	4.13	0.02
25	3.23	NA	NA	NA	0.05	0.04	NA	0.29	5.00	-383.87	778.28	4.16	0.02
41	3.29	NA	NA	NA	0.03	NA	-0.03	0.29	5.00	-383.91	778.37	4.25	0.02

8	3.08	0.01	0.00	0.12	NA	NA	NA	0.30	6.00	-383.18	779.12	5.00	0.01
38	3.16	0.00	NA	0.14	NA	NA	-0.03	0.29	6.00	-383.32	779.40	5.28	0.01
20	3.13	0.01	0.00	NA	NA	0.03	NA	0.29	6.00	-383.32	779.41	5.30	0.01
14	3.12	0.00	NA	0.13	0.04	NA	NA	0.29	6.00	-383.33	779.44	5.32	0.01
22	3.12	0.00	NA	0.13	NA	0.00	NA	0.29	6.00	-383.34	779.46	5.34	0.01
12	3.15	0.01	0.00	NA	0.07	NA	NA	0.29	6.00	-383.35	779.48	5.36	0.01
36	3.18	0.01	0.00	NA	NA	NA	-0.02	0.29	6.00	-383.37	779.51	5.39	0.01
39	3.14	NA	0.00	0.14	NA	NA	-0.04	0.29	6.00	-383.39	779.55	5.43	0.01
23	3.09	NA	0.00	0.13	NA	0.02	NA	0.29	6.00	-383.41	779.60	5.48	0.01
15	3.10	NA	0.00	0.14	0.02	NA	NA	0.29	6.00	-383.43	779.62	5.51	0.01
53	3.18	NA	NA	0.15	NA	0.01	-0.04	0.29	6.00	-383.51	779.79	5.67	0.01
45	3.18	NA	NA	0.16	0.01	NA	-0.04	0.29	6.00	-383.51	779.79	5.67	0.01
29	3.13	NA	NA	0.15	0.02	0.01	NA	0.29	6.00	-383.55	779.87	5.75	0.01
26	3.20	0.01	NA	NA	0.08	0.03	NA	0.29	6.00	-383.57	779.91	5.79	0.01
50	3.24	0.01	NA	NA	NA	0.02	-0.02	0.29	6.00	-383.59	779.94	5.83	0.01
42	3.25	0.01	NA	NA	0.06	NA	-0.02	0.29	6.00	-383.60	779.97	5.85	0.01
51	3.20	NA	0.00	NA	NA	0.04	-0.03	0.29	6.00	-383.61	780.00	5.88	0.01
27	3.16	NA	0.00	NA	0.06	0.04	NA	0.29	6.00	-383.62	780.01	5.89	0.01
43	3.23	NA	0.00	NA	0.04	NA	-0.03	0.29	6.00	-383.70	780.17	6.05	0.01
57	3.27	NA	NA	NA	0.05	0.04	-0.03	0.29	6.00	-383.84	780.45	6.33	0.01
40	3.11	0.01	0.00	0.12	NA	NA	-0.03	0.30	7.00	-383.15	781.34	7.23	0.00
16	3.08	0.01	0.00	0.11	0.05	NA	NA	0.30	7.00	-383.16	781.36	7.24	0.00
24	3.07	0.01	0.00	0.11	NA	0.01	NA	0.30	7.00	-383.17	781.37	7.25	0.00
28	3.13	0.01	0.01	NA	0.09	0.04	NA	0.29	7.00	-383.28	781.59	7.47	0.00
46	3.16	0.00	NA	0.13	0.04	NA	-0.03	0.29	7.00	-383.31	781.65	7.53	0.00
52	3.16	0.01	0.00	NA	NA	0.03	-0.02	0.29	7.00	-383.31	781.66	7.54	0.00
54	3.16	0.00	NA	0.14	NA	0.00	-0.03	0.29	7.00	-383.32	781.67	7.55	0.00

30	3.12	0.00	NA	0.13	0.05	0.01	NA	0.29	7.00	-383.33	781.70	7.58	0.00
44	3.18	0.01	0.00	NA	0.07	NA	-0.02	0.29	7.00	-383.34	781.72	7.60	0.00
55	3.14	NA	0.00	0.13	NA	0.02	-0.04	0.29	7.00	-383.37	781.79	7.67	0.00
47	3.14	NA	0.00	0.14	0.02	NA	-0.04	0.29	7.00	-383.39	781.81	7.69	0.00
31	3.09	NA	0.00	0.12	0.03	0.02	NA	0.29	7.00	-383.41	781.85	7.73	0.00
61	3.18	NA	NA	0.15	0.02	0.01	-0.04	0.29	7.00	-383.51	782.05	7.93	0.00
58	3.23	0.01	NA	NA	0.07	0.03	-0.02	0.29	7.00	-383.56	782.15	8.03	0.00
59	3.20	NA	0.00	NA	0.06	0.04	-0.03	0.29	7.00	-383.59	782.22	8.11	0.00
48	3.11	0.01	0.00	0.11	0.05	NA	-0.03	0.30	8.00	-383.14	783.63	9.51	0.00
32	3.08	0.01	0.00	0.10	0.06	0.02	NA	0.30	8.00	-383.14	783.63	9.51	0.00
56	3.11	0.01	0.00	0.11	NA	0.01	-0.03	0.30	8.00	-383.14	783.64	9.52	0.00
60	3.15	0.01	0.01	NA	0.09	0.04	-0.02	0.29	8.00	-383.27	783.88	9.76	0.00
62	3.15	0.00	NA	0.13	0.04	0.00	-0.03	0.29	8.00	-383.31	783.96	9.84	0.00
63	3.13	NA	0.00	0.13	0.03	0.02	-0.04	0.29	8.00	-383.37	784.09	9.97	0.00
64	3.11	0.01	0.00	0.10	0.06	0.02	-0.02	0.30	9.00	-383.13	785.95	11.83	0.00

Table S2 - Complete set of models generated by multimodel selection procedure in production landscapes transects. Here a listed all possible variables in the models, followed by model R^2 , degrees of freedom (df), model log-likelihood (logLik), AICc and $\Delta AICc$ and finally model weight (ω). FWD – fine wood debris, LB – litter biomass, CC – canopy cover, FCCP – deforestation profile, PFP(t) – primary forest percentage at a 500m buffer, SBD – soil bulk density.

	Intercept	FWD	LB	CC	LUC	PFP(t)	SBD	R^2	df	logLik	AICc	$\Delta AICc$	ω
51	2.13	NA	0.02	NA	NA	0.38	0.37	0.46	6.00	-233.04	479.29	0.00	0.07
35	2.12	NA	0.02	NA	NA	NA	0.42	0.44	5.00	-234.48	479.81	0.52	0.06
27	2.65	NA	0.02	NA	+	0.37	NA	0.48	7.00	-232.11	479.86	0.57	0.06
11	2.70	NA	0.02	NA	+	NA	NA	0.46	6.00	-233.54	480.30	1.01	0.04
41	2.35	NA	NA	NA	+	NA	0.32	0.45	6.00	-233.55	480.32	1.03	0.04
9	2.84	NA	NA	NA	+	NA	NA	0.44	5.00	-234.79	480.45	1.16	0.04
43	2.27	NA	0.01	NA	+	NA	0.29	0.47	7.00	-232.51	480.66	1.37	0.04
59	2.28	NA	0.02	NA	+	0.34	0.25	0.49	8.00	-231.29	480.72	1.43	0.04
19	2.63	NA	0.03	NA	NA	0.44	NA	0.43	5.00	-234.97	480.80	1.50	0.03
33	2.04	NA	NA	NA	NA	NA	0.52	0.42	4.00	-236.17	480.91	1.62	0.03
25	2.82	NA	NA	NA	+	0.28	NA	0.45	6.00	-233.96	481.13	1.84	0.03
57	2.36	NA	NA	NA	+	0.26	0.30	0.46	7.00	-232.85	481.35	2.06	0.03
55	2.13	NA	0.02	-0.12	NA	0.39	0.37	0.46	7.00	-232.92	481.49	2.20	0.02
52	2.13	0.01	0.02	NA	NA	0.36	0.36	0.46	7.00	-232.97	481.58	2.29	0.02
36	2.12	0.03	0.02	NA	NA	NA	0.40	0.45	6.00	-234.22	481.66	2.37	0.02
49	2.03	NA	NA	NA	NA	0.27	0.50	0.43	5.00	-235.46	481.78	2.49	0.02
10	2.82	0.03	NA	NA	+	NA	NA	0.44	6.00	-234.36	481.95	2.66	0.02
12	2.70	0.03	0.02	NA	+	NA	NA	0.46	7.00	-233.17	481.99	2.70	0.02
39	2.11	NA	0.02	-0.09	NA	NA	0.42	0.44	6.00	-234.42	482.06	2.77	0.02
28	2.65	0.02	0.02	NA	+	0.35	NA	0.48	8.00	-231.99	482.12	2.83	0.02
42	2.37	0.03	NA	NA	+	NA	0.30	0.46	7.00	-233.27	482.18	2.89	0.02
3	2.69	NA	0.02	NA	NA	NA	NA	0.41	4.00	-236.82	482.21	2.92	0.02

31	2.70	NA	0.02	-0.12	+	0.38	NA	0.48	8.00	-232.06	482.27	2.98	0.02
45	2.24	NA	NA	0.21	+	NA	0.33	0.46	7.00	-233.41	482.46	3.17	0.02
34	2.05	0.03	NA	NA	NA	NA	0.50	0.42	5.00	-235.90	482.65	3.36	0.01
44	2.29	0.02	0.01	NA	+	NA	0.27	0.47	8.00	-232.25	482.66	3.37	0.01
15	2.71	NA	0.02	-0.03	+	NA	NA	0.46	7.00	-233.54	482.72	3.43	0.01
13	2.79	NA	NA	0.11	+	NA	NA	0.44	6.00	-234.75	482.73	3.44	0.01
20	2.62	0.02	0.03	NA	NA	0.41	NA	0.44	6.00	-234.85	482.92	3.63	0.01
23	2.63	NA	0.03	-0.12	NA	0.45	NA	0.44	6.00	-234.85	482.93	3.64	0.01
37	2.05	NA	NA	0.13	NA	NA	0.50	0.42	5.00	-236.04	482.93	3.64	0.01
26	2.81	0.02	NA	NA	+	0.25	NA	0.45	7.00	-233.74	483.12	3.83	0.01
47	2.23	NA	0.01	0.08	+	NA	0.30	0.47	8.00	-232.49	483.13	3.84	0.01
60	2.28	0.01	0.02	NA	+	0.32	0.25	0.49	9.00	-231.22	483.16	3.87	0.01
63	2.29	NA	0.02	-0.02	+	0.34	0.25	0.49	9.00	-231.28	483.30	4.01	0.01
29	2.79	NA	NA	0.06	+	0.28	NA	0.45	7.00	-233.94	483.54	4.25	0.01
58	2.37	0.02	NA	NA	+	0.23	0.29	0.47	8.00	-232.72	483.59	4.30	0.01
61	2.28	NA	NA	0.16	+	0.25	0.31	0.47	8.00	-232.76	483.68	4.39	0.01
4	2.67	0.03	0.02	NA	NA	NA	NA	0.41	5.00	-236.44	483.74	4.45	0.01
56	2.13	0.01	0.02	-0.13	NA	0.37	0.36	0.46	8.00	-232.84	483.83	4.54	0.01
53	2.04	NA	NA	0.13	NA	0.27	0.49	0.43	6.00	-235.31	483.84	4.55	0.01
50	2.04	0.02	NA	NA	NA	0.24	0.49	0.43	6.00	-235.33	483.88	4.59	0.01
40	2.12	0.03	0.02	-0.10	NA	NA	0.40	0.45	7.00	-234.15	483.95	4.66	0.01
14	2.79	0.03	NA	0.07	+	NA	NA	0.44	7.00	-234.35	484.34	5.05	0.01
7	2.69	NA	0.02	-0.08	NA	NA	NA	0.41	5.00	-236.78	484.41	5.12	0.01
16	2.72	0.03	0.02	-0.06	+	NA	NA	0.46	8.00	-233.16	484.47	5.18	0.01
46	2.27	0.02	NA	0.17	+	NA	0.31	0.46	8.00	-233.17	484.48	5.19	0.01
32	2.70	0.02	0.02	-0.14	+	0.35	NA	0.48	9.00	-231.93	484.58	5.29	0.01
38	2.06	0.03	NA	0.12	NA	NA	0.49	0.42	6.00	-235.78	484.78	5.49	0.00

24	2.62	0.02	0.03	-0.13	NA	0.42	NA	0.44	7.00	-234.73	485.11	5.82	0.00
48	2.26	0.02	0.01	0.05	+	NA	0.28	0.47	9.00	-232.25	485.22	5.93	0.00
30	2.80	0.02	NA	0.04	+	0.25	NA	0.45	8.00	-233.73	485.62	6.33	0.00
64	2.30	0.01	0.02	-0.04	+	0.32	0.24	0.49	10.00	-231.21	485.81	6.52	0.00
8	2.67	0.03	0.02	-0.09	NA	NA	NA	0.41	6.00	-236.39	485.99	6.70	0.00
62	2.30	0.02	NA	0.14	+	0.23	0.30	0.47	9.00	-232.66	486.04	6.75	0.00
54	2.05	0.02	NA	0.12	NA	0.25	0.48	0.43	7.00	-235.20	486.04	6.75	0.00
1	2.77	NA	NA	NA	NA	NA	NA	0.36	3.00	-239.90	486.12	6.83	0.00
17	2.74	NA	NA	NA	NA	0.31	NA	0.37	4.00	-239.01	486.58	7.29	0.00
2	2.75	0.04	NA	NA	NA	NA	NA	0.36	4.00	-239.41	487.39	8.10	0.00
5	2.76	NA	NA	0.20	NA	NA	NA	0.36	4.00	-239.55	487.67	8.38	0.00
21	2.73	NA	NA	0.20	NA	0.32	NA	0.38	5.00	-238.66	488.17	8.88	0.00
18	2.73	0.03	NA	NA	NA	0.28	NA	0.38	5.00	-238.73	488.31	9.02	0.00
6	2.74	0.04	NA	0.19	NA	NA	NA	0.37	5.00	-239.12	489.09	9.80	0.00
22	2.72	0.03	NA	0.19	NA	0.28	NA	0.38	6.00	-238.41	490.04	10.75	0.00

Table S3 Complete set of models generated by multimodel selection procedure for catchment species richness. Here a listed all possible variables in the models, followed by model R^2 , degrees of freedom (df), model log-likelihood (logLik), AICc and $\Delta AICc$ and finally model weight (ω). LB – litter biomass, FCCP_Catch – deforestation profile at the catchment scale, PFP(c) – primary forest percentage in a catchment, SBD – soil bulk density.

	Intercept	LB	FCCP_Catch	PFP(c)	SBD	R^2	df	logLik	AICc	$\Delta AICc$	ω
5	71.53	NA	NA	0.33	NA	0.32	3.00	-68.49	144.69	0.00	0.50
13	85.34	NA	NA	0.32	-9.79	0.33	4.00	-68.37	147.82	3.13	0.10
7	71.13	NA	-13.58	0.34	NA	0.33	4.00	-68.43	147.94	3.25	0.10
6	71.83	-0.04	NA	0.33	NA	0.32	4.00	-68.49	148.05	3.36	0.09
1	86.04	NA	NA	NA	NA	0.00	2.00	-72.00	148.79	4.10	0.06
2	66.76	2.04	NA	NA	NA	0.08	3.00	-71.23	150.17	5.48	0.03
9	117.57	NA	NA	NA	-23.38	0.05	3.00	-71.50	150.72	6.03	0.02
15	101.77	NA	-40.63	0.32	-22.29	0.36	5.00	-68.04	151.08	6.39	0.02
3	86.09	NA	4.16	NA	NA	0.00	3.00	-71.99	151.70	7.01	0.01
14	88.99	-0.29	NA	0.33	-10.83	0.33	5.00	-68.36	151.71	7.02	0.01
8	71.44	-0.04	-13.58	0.34	NA	0.33	5.00	-68.43	151.86	7.17	0.01
10	90.26	1.66	NA	NA	-14.77	0.10	4.00	-71.04	153.17	8.48	0.01
4	66.76	2.04	-0.21	NA	NA	0.08	4.00	-71.23	153.53	8.84	0.01
11	134.24	NA	-41.33	NA	-36.07	0.08	4.00	-71.26	153.61	8.92	0.01
16	111.68	-0.63	-45.14	0.34	-25.98	0.36	6.00	-67.97	155.57	10.89	0.00
12	105.76	1.47	-30.77	NA	-25.19	0.11	5.00	-70.91	156.82	12.13	0.00

CHAPTER THREE

IS BIOTIC HOMOGENIZATION WIDESPREAD IN HUMAN-MODIFIED TROPICAL FORESTS?

IS BIOTIC HOMOGENIZATION WIDESPREAD IN HUMAN-MODIFIED TROPICAL FORESTS?

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ABSTRACT

Land-use changes and forest degradation processes are still an ongoing threat in tropical forests and understand how species diversity responds to that changes have crucial importance for effective conservation plans. Partitioning regional species diversity in component spatial scales is an effective method, despite practical applications has lagged behind theoretical discussions. Accordingly, we asked: (1) what is the pattern of species loss at both α - and γ -diversities components as function of land-cover changes in a mosaic landscape? (2) how does β -diversity respond to land-cover changes and to what extent is β -diversity scale dependent? Finally, (3) do the processes underpinning β -diversity contribute equally in different land-use types. We surveyed 2.9 million hectares in two municipalities (Paragominas and Santarém) in the Eastern Brazilian Amazon, sapling 36 catchments (5.000ha each) and 10-12 transects in each catchment (300m each), totalising 377 transects encompassing all major landscapes in the region. In each transect we sampled five taxa; plants, birds, dung beetles, ants and orchid bees using specific methodologies. To analyse data, we used multiplicative partitioning of diversity to assess how diversity is partitioned within each land use class and decomposed components of β -diversity in nestedness and turnover. We used generalized linear mixed models to analyse the influence of land-use changes in the patterns of diversity. We found that α diversity have a general steady decline with land-use intensification, whereas γ diversity is equal among forest classes, then drops in production landscapes. β -diversity patterns are scale dependent and while among transects β is higher in forests than in non-forest habitats, among catchments β -diversity is the same across all land-use types. There is however, for both scales an increase of the contribution of nestedness to

β -diversity with land-use intensification. In this study we could observe that deterministic disturbance filters are reducing species diversity at local and regional scales. However, with other spatially stochastic and of different strengths filters taking place at different scales, we observe high β diversity values in disturbed and secondary forests, which can explain the high values of regional diversity, even in disturbed forests. More subtle changes, such as increasing nestedness are an alarming claim for a more landscape-wise conservation planning in the regions.

Keywords: Amazon forest, β -diversity, Diversity partitioning, Land-use changes, Nestedness, Turnover.

INTRODUCTION

Across the world, human activities have led to the modification of entire landscapes, resulting in an overall process of biodiversity loss (Gibson *et al.* 2011; Tabarelli *et al.* 2012; Arroyo-Rodriguez *et al.* 2013), changes in species interaction networks (Laliberte & Tylianakis 2010) and losses in ecosystem function and the provision of ecosystem services (Lewis 2009). Human impacts have led to the genetic, taxonomic or functional simplification and convergence of regional biotas (McKinney & Lockwood 1999; Olden & Rooney 2006). This process, termed biotic homogenization, is a particular concern in the exceptionally biodiverse humid tropics which are undergoing very high rates of land-use change and habitat degradation (Gibson *et al.* 2011; Tabarelli *et al.* 2012; Arroyo-Rodriguez *et al.* 2013). However, the ecological processes that lead to homogenization in complex multiple-use landscapes, and at multiple spatial scales, remain poorly understood (Tabarelli *et al.* 2012).

Tropical forest frontier regions are typically a mosaic of human modified landscapes, resulting from diverse agricultural and extractive activities of varying intensity (Chazdon 2008; Gardner *et al.* 2009). Such human-modified landscapes are highly dynamic, characterized by multiple land-use types and having forests fragments in differing stages of degradation or recovery (Laurance 2002; Gardner *et al.* 2009; Putz & Redford 2010; Gardner *et al.* 2013). Many landscape- and regional-scale factors, combined with the legacy effects of past historical land-use changes, play important roles in determining extant patterns of species distribution and abundance (Gardner *et al.* 2013). Deforestation and land-use change are key drivers of biotic homogenization, which are widespread across the

planet and particularly marked in the tropics (Rockstrom *et al.* 2009; Hansen *et al.* 2010).

Many studies have investigated the local effects of land-use change on tropical forest biotas, yet drawing generalizable inferences from most of these is complicated by a failure to consider the aforementioned characteristics that are inherent to the process of landscape modification. For example, most studies are limited to a single spatial scale, comprising either a detailed analysis of single field sites, which encompass little of the heterogeneity inherent in tropical ecosystems (Peres *et al.* 2010). Large-scale (e.g. whole biome) modelling studies lie at the other extreme, but these are limited in data quality and the ability to deal with important differences in regional context (Gardner *et al.* 2013). Also, most studies are focused on single taxa (eg. Emilio *et al.* 2010; Dexter *et al.* 2012; Karp *et al.* 2012; Myers *et al.* 2013), limiting our ability to distinguish taxon-specific phenomena from potentially general responses. Furthermore, few land-use types or forest disturbance and landscape contexts are considered, which limits our understanding of how biodiversity processes play out across the complex and dynamic land use mosaics that characterize much of the tropics (Asner *et al.* 2009; Gardner *et al.* 2009; Gardner *et al.* 2013). Finally, despite a growing research interest in β diversity (i.e. turnover of species among sites), few other studies have analysed the scale dependency of β diversity response to land-use changes and the different processes underpinning it (i.e. species turnover or richness – Baselga 2010) can change in disturbed tropical habitats.

Here we present the most comprehensive assessment of biotic-homogenization to date, examining the processes of species loss and biological simplification at both site and landscapes scales using a database that

encompasses 5 taxonomic groups sampled across 335 sites in two agricultural frontier municipalities of the Brazilian Amazon. The sites cover most of the Amazonian land-use types that dominate in the arc of deforestation and other frontier zones. This study was novel in sampling the biota at multiple scales, including at the ‘mesocale’ (hundreds of km) relevant to municipal and political contexts in tropical countries (Gardner *et al.* 2013). We analysed how the diversities of five different taxonomic groups (plants, birds, dung beetles, ants, orchid bees) were partitioned across multiple spatial scales across a diverse land-use and forest disturbance gradient, sampled at both local (300 m transects) and landscape (c. 5 000 ha catchments) scales.

We draw upon the strengths of this study to further our understanding of biotic homogenization in human modified tropical forests by asking: (1) what is the pattern of species loss at both α - and γ -diversities components as function of land-cover changes in a mosaic landscape? We anticipated that α - and γ -diversity would steadily decline with increasing human disturbance (from undisturbed forests to mechanized agriculture); and (2) how does β -diversity respond to land-cover changes and to what extent is β -diversity scale dependent? We expected β -diversity to be higher in forests, especially in undisturbed forests. We anticipated that diversity will have a scale dependent response given that at larger scales, different extinction filters (Hillebrand & Blenckner 2002) can act to increase divergence in species composition even in disturbed land-cover types. Last, we asked: (3) do the processes underpinning β -diversity contribute equally in different land-use types. We expected that species loss (nestedness) would have increasing importance in generating β -diversity with increasing disturbance. This is, to our knowledge, the first study to approach biotic homogenization from the

perspective of processes underpinning β -diversity in the tropics (but see Baeten *et al.* 2012 for the use of β -diversity decomposition in temperate reserves).

MATERIAL AND METHODS

Sampling region

We conducted our study in two municipalities of Pará state, in the central and eastern Brazilian Amazon: Paragominas (hereafter PGM) and Santarém/Belterra (hereafter STM) (Figure 1). The two municipalities are ca. 3 million ha., have similar climates and historically were covered in forest of similar physiognomies. Both have suffered significant forest loss in recent decades, but they differ markedly in their historical trajectory of colonization and both past and present land-uses (Lees *et al.* 2012; Lees *et al.* 2013; Viana *et al.* 2014).

Sampling design

We divided each municipality in roughly evenly sized catchments (ca 5 000 ha) using SWAT (Soil and Water Assessment Tool) for ARCGIS, and selected 18 in each municipality for sampling. The sampled catchments covered the gradient of primary forest cover (6-100%) and the major land-use types in each municipality (Table 1). The design includes the major land-use and forest-degradation classes in the Amazon region. Within each catchment, we allocated 8–12 transects (each 300 m in length), at a density of 1 transect/400 ha; transects were separated by > 1.5 km. Transects were distributed in proportion to the area occupied by a given land use in a given catchment (e.g. if pastures comprised 40% of the land use in a catchment, then c. 40% of the transects were in pastures). A total of 335 transects were sampled for plants, birds, dung-beetles, ants and orchid-bees. Details of sampling techniques for each taxonomic group can be found in Supplementary

Material. Details about the methods and definitions of land-use classes can be found in Gardner *et al.* (2013).

DATA ANALYSES

We checked whether there is spatial autocorrelation we performed Mantel tests with species Bray-Curtis dissimilarities versus geographical distances matrices within both regions with randomizations stratified by catchments. We found no evidence of spatial autocorrelation within catchments (Table S1).

Diversity Partitioning.

We defined α_{transect} -diversity as the average number of species per transect sampled in each land use. Moving up scale, $\alpha_{\text{catchment}}$ -diversity is the number of species in per catchment for each land-use. Finally, γ_{region} -diversity is the total number of species in each municipality per land-use class. We use the definition of β -diversity as a measure of the effective number of distinct assemblages or samples in a region, and is dependent on sample size (Jost 2007). Multiplicative partition of diversity (Whittaker 1972) in our study follows the formula $\gamma_{\text{region}} = \alpha_{\text{transect}} \times \beta_{\text{among transects}} \times \beta_{\text{among catchments}}$, where $\beta_{\text{among transects}}$ is the relative differentiation from transects to the total catchment and $\beta_{\text{among catchments}}$ is the relative differentiation from catchments to the entire region. We calculated all values for each land-use and used multiplicative partitioning as it is a measure of the magnitude of differentiation, independent of α -diversity (and therefore species loss), and indicates the amount by which diversity (e.g. species richness) increases from local to regional scales. We calculated β -diversity using species richness (Hill numbers of order 0, Hill 1973; Jost 2007; Chao *et al.* 2012).

Once we undertook proportional sampling and we had different sample sizes for different land-use classes, which would cause biased results for β -

diversity. We therefore resampled the data to obtain comparable values of β -diversity (Baselga 2010). We first resampled for each land-use 3 transects/catchment to get $\beta_{\text{among-transects}}$, and then we took the average value per land-use among all catchments that had at least three transects of a given land-use. In this case we had γ_{catch} as the total richness of the three transects divided by α_{transect} as the average species richness per transect. To calculate $\beta_{\text{among-catchments}}$, we resampled the data now sampling three catchments with three transects each, so we computed. Here we have γ_{region} as the total species richness of the three catchments divided by α_{catch} as the average species richness per catchment. This procedure was replicated 5000 times for each taxon and each land-use.

Decomposition of the β -diversity

We decomposed $\beta_{\text{among transects}}$ and $\beta_{\text{among catchments}}$ diversities into components due to species loss (resulting in nestedness) and due to species replacement (resulting in turnover), by calculating the multi-site Sørensen (β_{SOR}) and Simpson (β_{SIM}) indices (Baselga 2010). β_{SOR} incorporates variation in species composition caused by both turnover and nestedness, whereas β_{SIM} is independent of variation in species richness (therefore, only turnover). Thus, any difference between values is representative of the species loss (nestedness) component of β -diversity: $\beta_{\text{NES}} = \beta_{\text{SOR}} - \beta_{\text{SIM}}$ (Baselga 2010, 2012). Multi-site β calculations based on the Sørensen index are sensitive to sample size, so we calculated β -values for all land-uses using a resampling procedure. This involved taking 5.000 random samples from the total number of transects of each land use class (Table 1) and reducing the sample to the number of sampled transects of undisturbed primary forest to compute average β_{SOR} and β_{SIM} diversities, same as above. The

percentage importance of the nestedness component ($\beta_{\text{NES}}/\beta_{\text{SOR}}$) was then used as response variable for analyses.

Statistical analyses

To address our first objective, we tested whether α_{transect} and γ_{region} diversities (richness/site) differed among land-use classes using generalized linear mixed models (GLMM, Bolker *et al.* 2009) with Poisson errors corrected for over-dispersion when necessary (Crawley 2012). We did an ANOVA and for α -diversity we considered species richness per transect of all combined taxa and for individual taxa as the response variable, land-use classes as explanatory variable and taxonomic group, catchment and municipality as random factors. For γ -diversity, we considered the total number of species in each taxon within each land-use class as response variable and land-use classes as explanatory variable, with municipality as a random factor. To get which land-use levels are different once we got a significant difference with the ANOVA, we performed pairwise contrasts analyses, lumping the most similar levels and comparing models (Crawley 2012).

For the second objective, we tested how β -diversity at two scales (among-transects and among-catchments) responds to land-use changes by using GLMM. In both cases, we used the values of β -diversity for each taxon within each land-use as a response variable and land-use classes as explanatory variable. The random factors for among-transects β -diversity were catchment and municipality and random factors for among-catchments β -diversity was only municipality. Whenever necessary, we also performed contrasts analysis to separate between-levels significance.

Finally, for the third objective, about whether there is a predominance of either turnover or nestedness in more disturbed habitats, we tested differences among land-use classes for all diversity components were analysed using GLMM. Land-use class was used explanatory variable and percentage importance of nestedness for each taxon within each land use. We did this for among-transect and among catchment scales. Random factors included were catchment and municipality for among-transects β -diversity and only municipality for among-catchments β -diversity. We used binomial error distributions, corrected for overdispersion when necessary, and contrast-analysis to discern among levels significance (Crawley 2012).

All analyses were performed in the R platform (R Core Team 2013). We performed residual analyses in all models and checked for distribution of errors and overdispersion in data. We adjusted p-values according Benjamini & Yekutieli (2001), controlling for the probability of false discovery rate in multiple tests. Diversity partitioning, Mantel and correlation analyses were conducted using the *vegan* package v2.0-9 (Oksanen *et al.* 2013). β -diversity decomposition was undertaken using the *betapart* package v1.2 (Baselga & Orme 2012), and GLMMs by using the *lme4* package v1.0-5 (Bates *et al.* 2013).

RESULTS

Patterns of species richness (α and γ diversities) across land-use classes:

We found that pan-taxa α_{transect} -diversity declined steadily from undisturbed forests, through disturbed primary forests, secondary forests and production landscapes (cattle pastures and mechanized agriculture), significant for all pairwise combinations ($\chi^2 = 398.92$, DF=185, $P < 0.001$, Fig. 2a). Species richness at catchment level (i.e. $\alpha_{\text{catchment}}$) was higher at PFU and PFL, decreasing in PFLB and SEF and then smaller at PAS and even smaller at AGR ($\chi^2 = 202.86$,

DF=8 $P < 0.001$, Figure 2b). Species richness at municipality scale (i.e. γ -diversity) was only significantly different between forest transects and production landscapes ($\chi^2 = 42.27$, DF=5 $P < 0.001$, Figure 2c). These trends were broadly similar across individual taxa, however we found particularities within each taxon (Fig 3 a and d).

Patterns of species β -diversity:

Among transect pan-taxa β -diversity showed a similar pattern to γ -diversity, with higher β_{transect} -diversity in forested habitats and lower β_{transect} -diversity in production landscapes ($\chi^2_{1,8} = 12.37$, DF=10, $P \sim 0.005$, Figure 4a). We did not find evidence for significant differences in β diversity among catchments ($\beta_{\text{catchment}}$) characterized by different levels of historical deforestation ($\chi^2 = 9.24$, DF=6, $P \sim 0.09$, Fig. 4b). Trends were broadly similar across individual taxa, however we observe some peculiarities (e.g. β_{transect} is uncommonly higher in agricultural fields for birds, Fig. 3 b and c).

Relative importance of processes underlying β diversity:

In non-forested land-cover, nestedness (species loss) accounted for a significantly higher proportion of all variation in β -diversity, on the other hand in forest transects turnover accounted for almost all variation. The contribution of nestedness to β_{transect} -diversity was significantly higher with up to a three-fold increase in the percentage contribution in production landscapes relative to forest transects ($\chi^2 = 70.22$, DF=10, $P < 0.001$, Fig. 4a). When it comes to $\beta_{\text{catchment}}$ -diversity, differences were also between forest transects and production landscapes ($\chi^2 = 44.163$, DF=6, $P < 0.001$, Fig. 4b). However for the larger scale (i.e. among catchments), turnover accounted with a much larger contribution.

Results for individual taxa followed these patterns, although individual taxa had their particularities (Figure 5 a and b)

DISCUSSION

Our comprehensive analysis of Amazonian biodiversity across large human-modified landscapes provides us with a novel understanding of the processes underlying biotic homogenization in the world's most biodiverse terrestrial ecosystem. We first examine how these results confirm our current understanding (i.e. α and g diversities), before focussing on how β -diversity patterns can be shaped by different levels of forest disturbance and by forest conversion to production landscapes. We found that local diversity (i.e. α diversity) responded directly to the disturbance gradient. Catchment species richness (i.e. $\alpha_{\text{catchment}}$) and municipality species richness (i.e. γ diversity) did not change significantly in moving from undisturbed forests to disturbed primary or regenerating secondary forest, but then it undergoes a significant three-fold decrease when comparing with production landscapes, suggesting a lagged effect of disturbance. The link between these two scales different response is therefore through β diversity. We found that the response of β diversity to the gradient of disturbance is also scale dependent, but bridges the lagged effect observed for g diversity. Behind this maintenance of β diversity in forests at smaller scales (among transects) and no significant response to disturbance at larger scales (among catchments) lies a subtle but important process. β diversity among communities in more disturbed landscapes are significantly more dominated by nestedness than it is by turnover, indicating that the apparent diversity is actually due to the loss of species in the more severely disturbed areas.

These trends should be taken in the regional context of the rarity of truly ‘undisturbed’ forests, as very few areas have not been subject to logging or fire at least historically (Barlow *et al.* 2012). As logging and burning were a widespread process in the recent past years, only a small portion of the regions remained as what can be named undisturbed forests and could be only represented by one catchment in PGM and three catchments in STM. However, these study regions can be considered representative of most *terra firme* forests habitats in frontier regions of Central and Eastern Amazonia.

Scale-dependent responses of species loss and β diversity in human-modified tropical forests:

Reduction of α diversity due to land-use changes is not a new topic, and has been documented by several authors (reviewed by Gibson *et al.* 2011). In an event of forest disturbance or conversion, a drop in its species richness is expected, once the impact source is acting straight on the species pool of that local. Mestre *et al.* (2013) found that local avian diversity responded negatively to wildfires disturbance in the Brazilian Amazonia, as did Arnan *et al.* (2013), studying effects of fire in functional diversity of ants, also found a local scale decrease in diversity due to the disturbance. It is also widely reported that plant diversity is hardly reduced when there is logging, burning or conversion to production lands (Barlow & Peres 2008; Koltunov *et al.* 2009; Karp *et al.* 2012; Arroyo-Rodriguez *et al.* 2013). Powell & Powell (1987) studying orchid-bees also have found that forest fragmentation have a profound effect on orchid-bees visitation on scent baits. Dung beetles also show sensitivity to land-use changes, usually presenting a marked decline in diversity between forest and non-forest habitats, as well as secondary forests (Gardner *et al.* 2008; Ros *et al.* 2012).

Despite most of these studies did not cover the same range of land-use classes, these are consistent with our findings that with increasing levels of disturbance cause a general pattern of decrease in α diversity. Therefore, at a local scale just a minimum impact is able to disrupt communities and effects can be detected measuring species loss.

Unlike the more predictable patterns of impoverishment noted for α diversity, the impact of disturbance on patterns of γ diversity are not consistent (Gibson *et al.* 2011). Processes governing γ diversity take place at scales where spatial heterogeneity of environmental conditions and sources and strength of impacts may compensate for local losses in species richness, accumulating an unexpected high value of γ diversity (Soininen *et al.* 2007). Despite a steady decrease in α diversity, we found that γ diversity is only reduced when forests are replaced by agricultural habitat. At this large scale, sources of variation are much higher and different local extinction filters of species diversity (Hillebrand & Blenckner 2002) may act to influence γ diversity. Synergistically with natural variation in history and topography, primary disturbed forest and secondary forests under regeneration can suffer various degrees of impact strengths, stochastic variations and different disturbance and evolutionary historic trajectories. All these sum up that potentially creates a mosaic of different local communities contributing to the regional pool. However, when we observe open areas, the forest clearance filter is strong enough to reduce diversity and overcome regional heterogeneity and dynamism.

Patterns of β diversity are rather different from expected. Among transects, β diversity is not statistically different between all primary forest types, however it is highest at secondary forests and drops in the open areas. At a larger

scale (among catchments) no statistical difference in β is observed. Hence, one would argue that there is very few or little biotic homogenization in these regions. Indeed, secondary forests are actually heterogenized, compared to the other land-uses. In this study we sampled in secondary forests of several ages, ranging from around five years after recovery to more than 25 years, which is the largest time we could follow the age of secondary forests via satellite imagery. However, despite secondary forests and production landscapes can maintain high β diversity, for some taxa like plants, γ diversity in these areas is still smaller than primary forests. Even stronger is the case of production landscapes, which also have high β diversity, but have very low γ diversity for every taxa, this will be discussed in the next session.

Relative contribution of species loss and turnover in determining patterns of biotic homogenization

One might think that we could discard the hypothesis of biotic homogenization, once β diversity is being maintained high and is indeed statistically the same across all land-uses at larger scales. However, as pointed out by Baselga (2010, 2012), same values of β diversity can be generated due to two antithetic processes with very different consequences. The first and most claimed is species turnover, or the actual change in species composition from place to place. The second and less obvious is nestedness, or the β diversity due to differences in species composition when no species is replaced, therefore due to species loss. Nestedness for instance can be considered as a strong sign of homogenization, once it reflects similar biotas with compositional shifts derived from the same set of (vulnerable) species being lost in the poorer sites (Baeten *et al.* 2012). In this study we found that despite not being able to detect some major

changes in β diversity, the mechanisms underlying it change more dramatically, revealing an ongoing process of homogenization. At both scales, we observed that the contribution of nestedness increase up to four-fold from forests to open areas. Still, decomposing $\beta_{\text{among transects}}$ revealed that all forests have similar values and turnover happens to be the most important process and there is virtually no nestedness. This result may suggest that a widespread biotic homogenization process is very likely to occur if the disturbance process continues through time. Then, a large scale biotic homogenization just lags behind more obvious local immediate effects, that if not stopped and mitigated, will become evident as the process keeps going.

Thus, from a conservation point of view, we can summarize the current situation of tropical biodiversity homogenization. We have a marked species loss with increasing forest disturbance and conversion. At a large scale, no significant effect is observed for forest diversity, being only open areas biodiversity depleted. When we observe β diversity, we see that β is statistically similar among all forest types and only reduced for the among-transects scale in open areas. This framework could lead to the wrong conclusion that all forest conditions are good for biodiversity and that at a large scale there is no biotic homogenization. Nevertheless, depicting the mechanisms generating of the observed β diversity across the scales, we can see that it is markedly more originated by nestedness in converted lands and in undisturbed forests, nestedness plays a negligible role. Therefore, despite we still see that any type of forest cover can enhance biodiversity in tropical forests, we claim for the needing of a well structured landscape planning to achieve effective conservation goals. The main recommendations based in our results are a) to keep all UPF in an intact state, b)

to prevent further degradation of already degraded ones and c) to retain a widespread distribution of (even disturbed) primary forest sites.

CONCLUSION

In this study we could observe that deterministic disturbance filters are reducing species diversity at local and regional scales. However, with other spatially stochastic and of different strengths filters taking place at different scales, we observe high β diversity values in disturbed and secondary forests, which can explain the high values of regional diversity, even in disturbed forests.

Accordingly what we see is that the process of biotic homogenization that takes place subtly at different spatial scales in tropical forests. We propose that there is a lagged effect between what we observe in local scales to propagate to larger scales. However, a series of environmental filters can also be enabling maintenance of high diversity in disturbed forests, which claims for a more wide conservation planning in large scale regions, as the Brazilian Amazonia.

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Table 1: List of sampled land-uses in both municipalities. Acronyms for each land-use are also clarified here, as well as the maximum number of transects of each land-use class sampled in each region. PGM states for Paragominas and STM states for Santarém.

Land-use class	Number of transects sampled	
	PGM	STM
Primary forests		
• Undisturbed (PFU)	13	17
• Logged (PFL)	44	26
• Logged and Burnt (PFLB)	44	24
Secondary Forests (SEF)	20	39
Pastures (PAS)	51	23
Agriculture (AGR)	15	19
Total number of transects	187	148

Figure Legends

- Figure 1 Map of the sampling region and sampling design. In the map, the pink colours represent non-forest habitats, while the green colour represent forests of any kind (Primary or secondary). We stratified our sampling within three spatial scales that are: regional, catchment and transect. In each transect all five taxa were sampled according the figure.
- Figure 2 α and γ components of diversity. Diversity is expressed as average species richness per taxon and within each land use class. In a) α diversity, as the species richness at the transect scale and in b) γ diversity, as the pooled species richness at the regional scale. Different colours express forest and non-forest land-uses, we used $P < 0.05$ as significant and errors bars are standard errors.
- Figure 3 Panel with diversity components shown to all taxa across all land-use classes after resampling. First row (a), shows α diversity (i.e. average number of species per transect). The second and third rows (b and c) are β -diversity at among-transects and among-catchments, respectively. Finally, γ -diversity is in the fourth line (d). Different colours express forest and non-forest land-uses, we used $P < 0.05$ as significant and error bars represent standard errors and when they are missing we could only calculate a single value.
- Figure 4 β diversity at among transects and among catchment scales. β diversity was calculated as the multiplicative Wittaker's β and sampling size is standardized through the data via resampling all land use classes to the same sample size. Data is presented as average β

diversity per taxon and within each land use class. a) is β diversity among transects in a catchment and b) is the β diversity among catchments in a region. Different colours express forest and non-forest land-uses, we used $P < 0.05$ as significant and in the values and errors bars are standard errors.

Figure 5 Percentage contribution of the nestedness component to the total beta diversity observed at among transects and among catchment scales. Decomposition was computed following Baselga (2010) procedure ($\beta_{NES} = \beta_{SOR} - \beta_{SIM}$) and standardized through the data via resampling all land use classes to the same sample size. Data is presented as average percentage contribution of the nestedness component per taxon and within each land use class. (a) is the decomposition of beta diversity among transects in a catchment and (b) is the decomposition of beta diversity among catchments in a region. Different colours express forest and non-forest land-uses, we used $P < 0.05$ as significant and in the values and errors bars are standard errors.

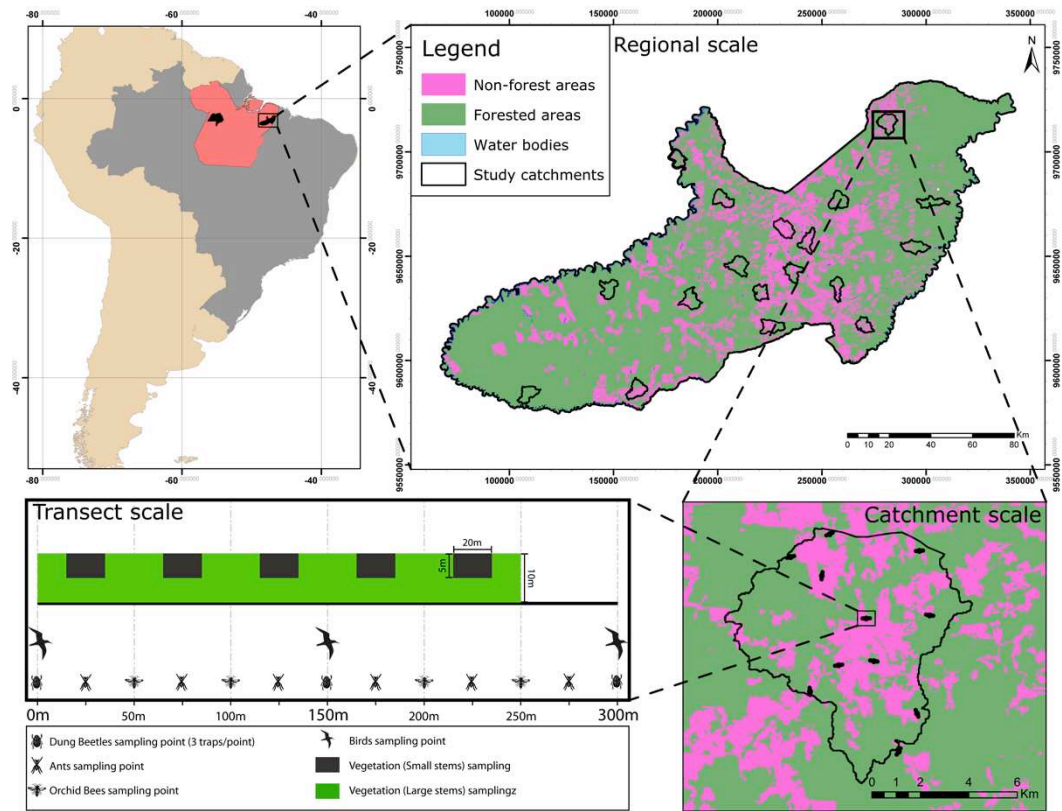


Fig. 1

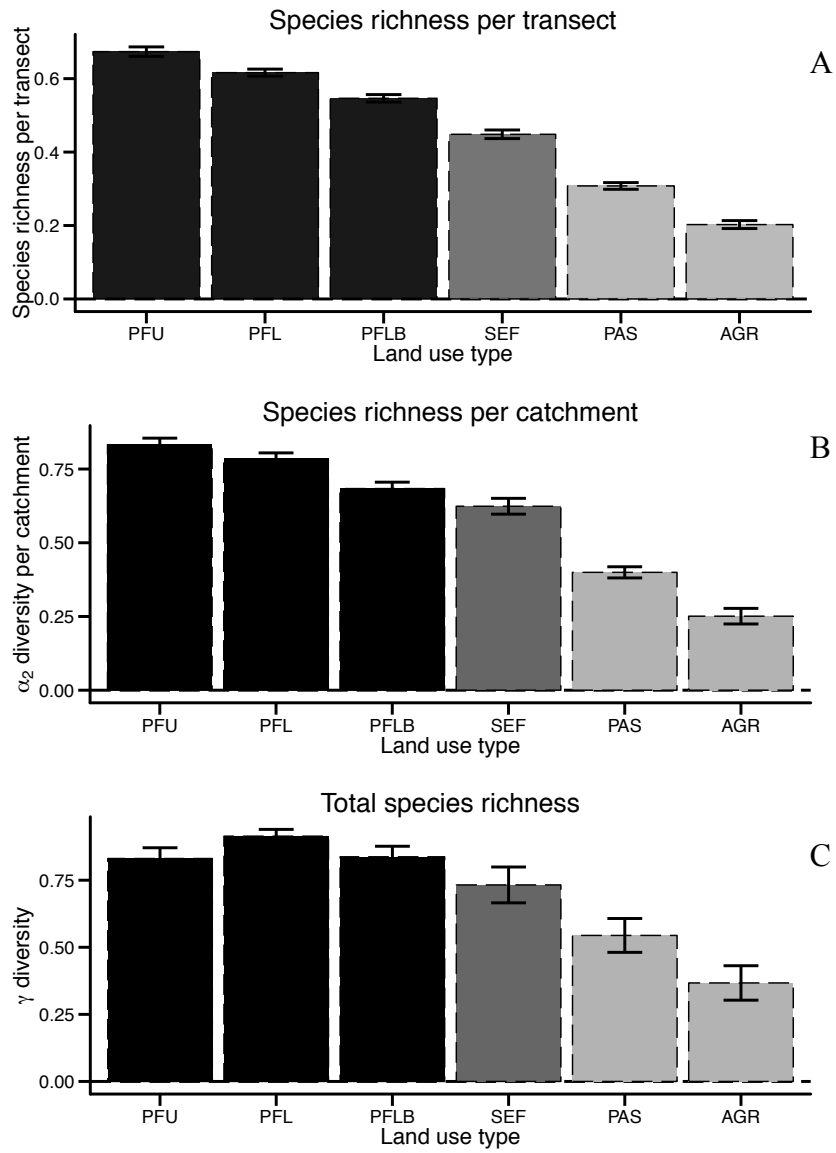


Fig. 2

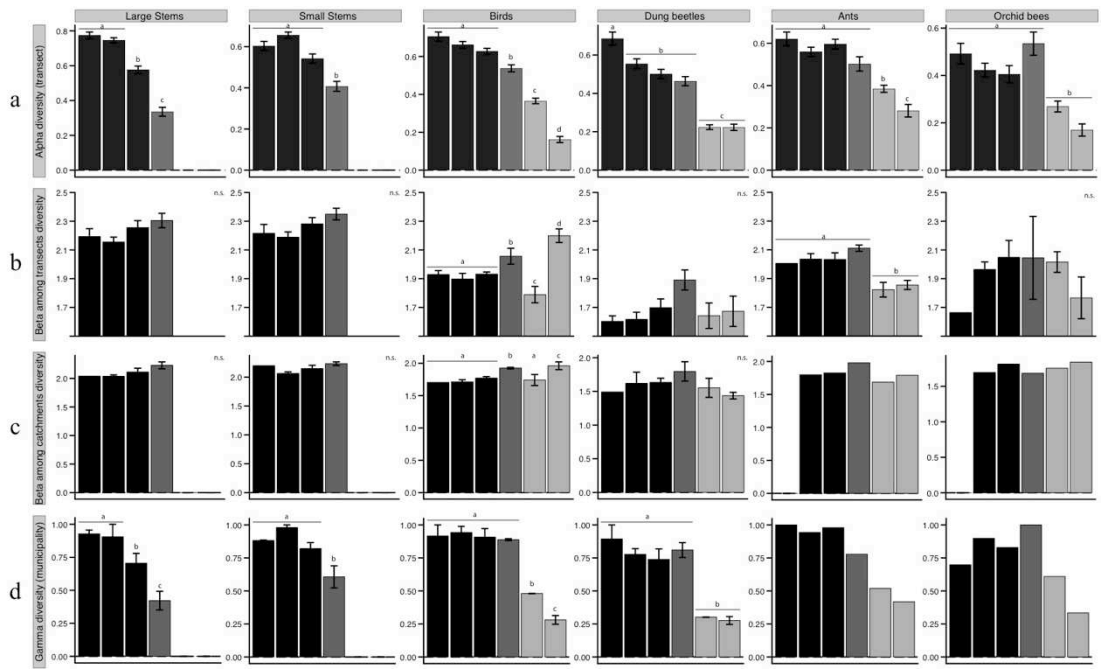


Fig. 3

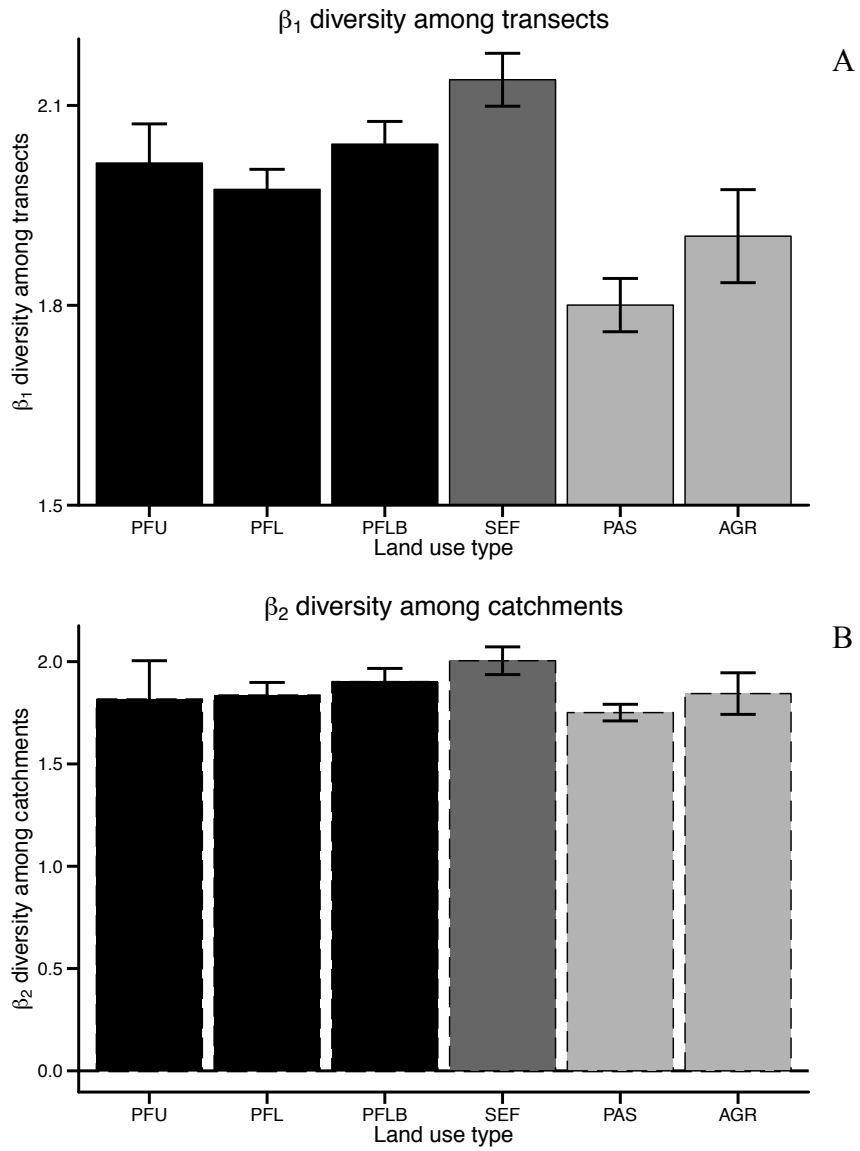


Fig. 4

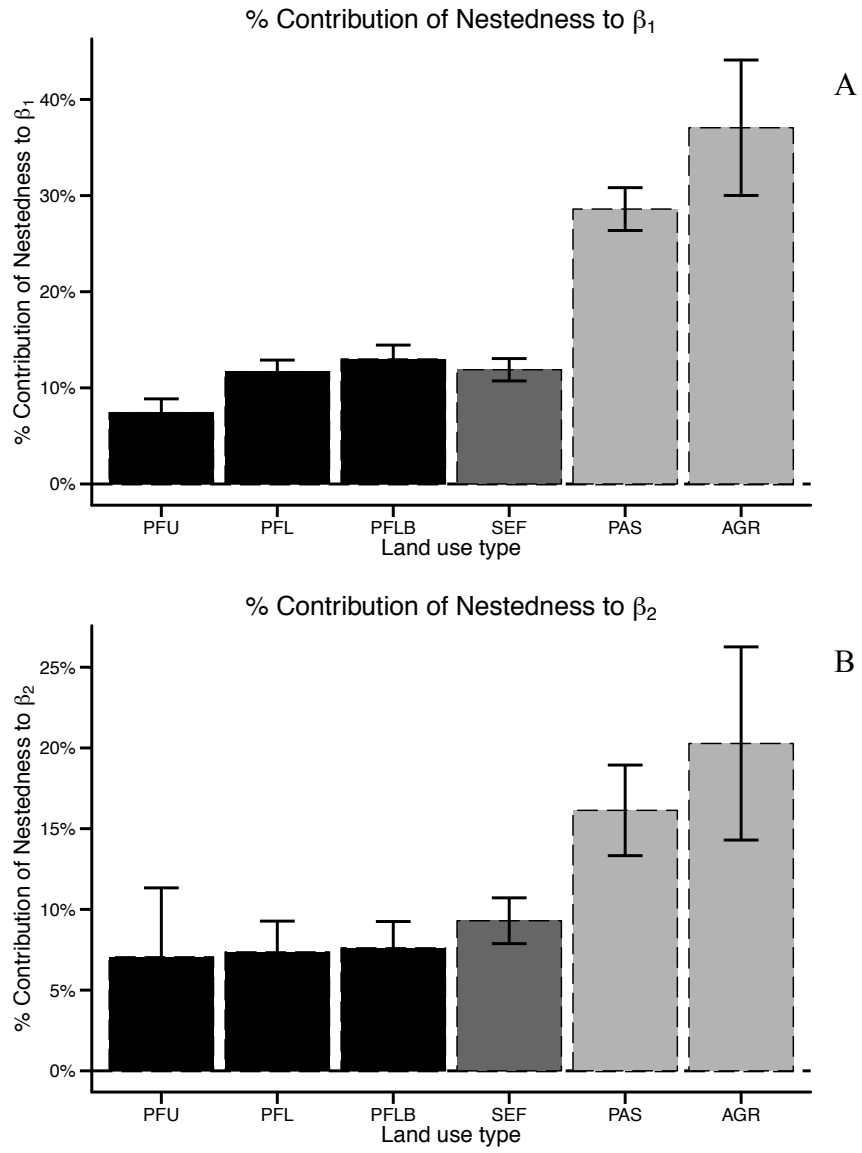


Fig. 5

Supplementary material for Solar et al. Is biotic homogenization widespread in human-modified tropical forests?

Biodiversity sampling

We sampled five taxa: dung beetles, orchid bees, ants, birds and plants.

Large and small stems

All trees and palms (alive or dead) ≥ 10 cm of diameter at 1.3 m height were identified in 10 x 250 m plots. Smaller individuals (2 to 10 cm diameter) were sampled in five subplots of 5 x 20 m. Lianas (woody vines) were also sampled in the same manner with the exception that the diameter was measured at 1.3 m from its main root, located inside the plot (for large individuals) or inside the subplots (for smaller individuals).

Birds

Birds were surveyed with 15-min point counts collected at three sampling points (0, 150 and 300 m); there were two repeat surveys. Sampling was conducted between 15 min before dawn up until 09:30 at the latest (but usually finishing by 08:30) and all point counts were sound-recorded to facilitate error-checking. For a full description of the avian sampling protocol and lists of voucher sound-recordings and images see Lees *et al.* (2012, 2013).

Dung beetles:

Dung beetles were sampled using pitfall traps (1 litre plastic containers, 14 cm radius, 9 cm height) baited with 50 g of dung (80% pig and 20% human, Marsh *et al.* 2013) and half filled with a killing solution (5% detergent and 2% salt). Three traps were dug at the corners of a 3-m side triangle and sampled at three point along the transect (0, 150 and 300 m) and left for 48 hr prior to collection and removal.

Ants

Ants were sampled only in PGM; six epigeic pitfall traps baited with sardine and honey (15 g of each), were located along each transect, separated by 50 m. Traps were left in the field for 48 hr prior to collection and removal and consisted of 12 cm height and 8 cm diameter plastic pots, half filled with a mixture of water, salt (2%) and detergent (5%) to kill the ants.

Orchid bees

To sample orchid bees, which were only sampled in PGM, we used plastic bottles (2L, 10cm diameter, 35cm height) as traps. Each bottle had three radial holes (2 cm diameter) at the height of 20 cm, where a flower-like structure was inserted (the tips of three other bottles). These flower-like structures were impregnated with coarse sand on the inner side to give support to the bees. Male orchid bees were attracted to four types of scent baits distributed along the transect (eugenol, methyl salicylate, vanilla or eucalyptol), separated by 50 m from each other. We tied the traps to a tree trunk, 1.5 m above the ground and remained in the field for 48h.

Table S1 – Mantel tests results detailed for each taxon. Mantel statistic is result of species Bray-Curtis dissimilarities against geographical distances matrix. P-values are obtained via randomisation procedure.

Taxon	Municipality	Mantel statistic	p-value
Large stems	PGM	0.272431638	0.294
Small stems	PGM	0.341640391	0.433
Birds	PGM	0.086218759	0.58
Dung Beetles	PGM	0.165379694	0.903
Ants	PGM	0.064976827	0.98
Orchid bees	PGM	0.007658559	0.924
Large stems	STM	0.200829726	0.509
Small stems	STM	0.139729711	0.396
Birds	STM	0.131078254	0.491
Dung beetles	STM	0.043595061	0.85

GENERAL CONCLUSION

In this thesis we outlined the main aspects regarding the effects of land-use and land-cover changes on insects, plants and birds. We generally found that the conversions of forests to non-forest habitats are the main threats to biodiversity. There are however major changes in species richness at a local scale, as well as shifts in species composition. At regional scales, primary forest appears to be an important variable regulating ant diversity. In the first chapter we present a comprehensive species list, as well as patterns of diversity, which we hope can be strong baselines for future studies. With the development of conservation initiatives in Paragominas, future monitoring based on strong data is vital to direct the actions towards an effective planning. In the second chapter, we found a clear shift in species composition with land-use change, as well as we found that species richness at transect level decreases almost two-fold from forests to production landscapes. Primary forest cover is an important variable explaining ant species richness at both transect and catchment scales. We also found that litter is an important predictor variable, with species richness at transect level increasing with it in production landscapes. We conclude that the maintenance of larger portions of primary forests can maintain and enrich the regional pool of species which is beneficial for a landscape-wise conservational act, as it works facilitating species recovery. Finally, in the third chapter we found that α diversity have a general steady decline with land-use intensification, whereas γ diversity is equal among forest classes, then drops in production landscapes. β -diversity patterns are scale dependent and while among transects β is higher in forests than in non-forest habitats, among catchments β -diversity is the same across all land-use types. There is however, for both scales an increase of the contribution of nestedness to β -diversity with land-use intensification. In this study we could observe that deterministic disturbance filters are reducing species diversity at local and regional scales. However, with other spatially stochastic and of different strengths filters taking place at different scales, we observe high beta diversity values in disturbed and secondary forests, which can explain the high values of regional diversity, even in disturbed forests. More subtle changes, such as increasing nestedness are an alarming claim for a more landscape-wise conservation planning in the regions.

Thus, we believe that the perspectives now open by discussion on this thesis have the potential to offer satisfactory explanations of the processes underpinning responses of biodiversity to land-use and land-cover changes. We strongly believe the furtherance of the monitoring initiative here presented, coupled with governmental and society programs have an enormous potential to revert the pessimistic framework that have been built around conservation of the Amazonian forests. Finally, as a multidisciplinary network, we hope with this contribution to provide answers to important questions that will one day enable awareness and sustainable use of the natural resources of the Amazon.

APÊNDICE I - Gardner et al. 2013 - Philosophical Transactions of the Royal Society B.

A social and ecological assessment of tropical land uses at multiple scales: the Sustainable Amazon Network

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A social and ecological assessment of tropical land uses at multiple scales: the Sustainable Amazon Network

Toby A. Gardner^{1,2}, Joice Ferreira³, Jos Barlow², Alexander C. Lees⁴, Luke Parry², Ima Célia Guimarães Vieira⁴, Erika Berenguer², Ricardo Abramovay⁵, Alexandre Aleixo⁴, Christian Andretti⁶, Luiz E. O. C. Aragão⁷, Ivanei Araújo⁴, Williams Souza de Ávila⁸, Richard D. Bardgett², Mateus Batistella⁹, Rodrigo Anzolin Begotti¹⁰, Troy Beldini¹¹, Driss Ezzine de Blas¹², Rodrigo Fagundes Braga¹³, Danielle de Lima Braga¹³, Janaína Gomes de Brito⁶, Plínio Barbosa de Camargo¹⁴, Fabiane Campos dos Santos¹¹, Vívian Campos de Oliveira⁶, Amanda Cardoso Nunes Cordeiro¹⁵, Thiago Moreira Cardoso³, Déborah Reis de Carvalho¹³, Sergio André Castelan¹⁵, Júlio César Mário Chaul¹⁶, Carlos Eduardo Cerri¹⁰, Francisco de Assis Costa¹⁷, Carla Daniele Furtado da Costa¹⁵, Emilie Coudel^{3,12}, Alexandre Camargo Coutinho¹⁸, Dênis Cunha¹⁶, Álvaro D'Antona¹⁹, Joelma Dezincourt⁴, Karina Dias-Silva²⁰, Mariana Durigan¹⁰, Júlio César Dalla Mora Esquerdo¹⁸, José Feres²¹, Silvio Frosini de Barros Ferraz¹⁰, Amanda Estefânia de Melo Ferreira⁴, Ana Carolina Fiorini²², Lenise Vargas Flores da Silva¹¹, Fábio Soares Frazão¹³, Rachel Garrett²³, Alessandra dos Santos Gomes⁴, Karoline da Silva Gonçalves⁴, José Benito Guerrero²⁴, Neusa Hamada⁶, Robert M. Hughes²⁵, Danilo Carmago Iglioni⁵, Ederson da Conceição Jesus²⁶, Leandro Juen¹⁷, Miércio Junior¹¹, José Max Barbosa de Oliveira Junior²⁷, Raimundo Cosme de Oliveira Junior³, Carlos Souza Junior²⁸, Phil Kaufmann²⁹, Vanesca Korasaki¹³, Cecília Gontijo Leal¹³, Rafael Leitão⁶, Natália Lima¹⁵, Maria de Fátima Lopes Almeida¹⁵, Reinaldo Lourival³⁰, Júlio Louzada¹³, Ralph Mac Nally³¹, Sébastien Marchand¹⁶, Márcia Motta Maués³, Fátima M. S. Moreira¹³, Carla Morsello³², Nárgila Moura⁴, Jorge Nessimian²², Sâmia Nunes²⁸, Victor Hugo Fonseca Oliveira¹³, Renata Pardini³³, Heloisa Correia Pereira¹⁹, Paulo Santos Pompeu¹³, Carla Rodrigues Ribas¹³, Felipe Rossetti¹⁰, Fernando Augusto Schmidt¹³, Rodrigo da Silva¹¹, Regina Célia Viana Martins da Silva³, Thiago Fonseca Morello Ramalho da Silva⁵, Juliana Silveira¹³, João Victor Siqueira²⁸, Teotônio Soares de Carvalho¹³, Ricardo R. C. Solar^{2,17}, Nicola Savério Holanda Tancredi¹⁷, James R. Thomson³¹, Patrícia Carignano Torres³³, Fernando Zagury Vaz-de-Mello³⁴, Ruan Carlo Stulpen Veiga³⁵, Adriano Venturieri³, Cecília Viana⁴, Diana Weinholt³⁶, Ronald Zanetti¹³ and Jansen Zuanon⁶

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Science has a critical role to play in guiding more sustainable development trajectories. Here, we present the Sustainable Amazon Network (*Rede Amazônia Sustentável*, RAS): a multidisciplinary research initiative involving more than 30 partner organizations working to assess both social and ecological dimensions of land-use sustainability in eastern Brazilian Amazonia. The research approach adopted by RAS offers three advantages for addressing land-use sustainability problems: (i) the collection of synchronized and co-located ecological and socioeconomic data across broad gradients of past and

present human use; (ii) a nested sampling design to aid comparison of ecological and socioeconomic conditions associated with different land uses across local, landscape and regional scales; and (iii) a strong engagement with a wide variety of actors and non-research institutions. Here, we elaborate on these key features, and identify the ways in which RAS can help in highlighting those problems in most urgent need of attention, and in guiding improvements in land-use sustainability in Amazonia and elsewhere in the tropics. We also discuss some of the practical lessons, limitations and realities faced during the development of the RAS initiative so far.

1. Introduction

Land-use and land-cover change associated with agricultural expansion and intensification is the most visible indicator of the human footprint on the biosphere [1–3]. Ongoing land-use change is most acute in the tropics [4], with *ca* 50 000 km² p.a. of native vegetation being cleared [5]. These changes are driven by increasing resource demands from a larger and wealthier human population, coupled with the effects of increasing economic globalization and land scarcity [6]. The creation and strengthening of more sustainable development trajectories in the twenty-first century depends on our ability to balance rising demands for food, energy, natural resources and the alleviation of hunger and poverty with the protection and restoration of natural ecosystems, and the critical ecosystem services they provide [7,8].

Amazonia represents a major sustainability challenge: as well as being the world's largest remaining tropical forest, the entire Amazon biome is home to more than 30 million people and provides locally, regionally and globally significant human-welfare benefits, including economic goods (e.g. timber and agricultural products) and non-market ecosystem services, such as climatic regulation and biodiversity conservation [4,9,10]. Rapid social and ecological change has left the future of the Amazon region uncertain [11–13]. In the Brazilian Amazon, in particular, recent reductions in the rate of deforestation, expansion of protected areas, increased market-based demand for more responsible land-use practices, and a strengthening of local and regional governments and civil society organizations provide some cause for guarded optimism that the Amazon economy can be set on a sustainable footing [14–16]. However, we need to ensure the right choices are made as soon as possible, thereby reducing the likelihood of costly or potentially irreversible damage to both social and ecological systems in the region [12,17]. Science can help this process by identifying the problems that need to be addressed first, and assessing the long-term social and ecological implications of land-use alternatives in planning for both regional development and ecological conservation [2,18,19].

While there is already a substantial body of social and ecological knowledge on the Amazon [11,20–22], scientists are often criticized for failing to deliver the evidence most needed to foster sustainability [23]. Criticisms include the fragmented and disciplinary nature of many research projects, a narrow focus on specific ecological or social problems and spatial scales, and a weak connection to local actors and

institutions that are ultimately responsible for implementing changes in land-use policy and management [22–25].

Here, we present the work of the Sustainable Amazon Network (RAS; *Rede Amazônia Sustentável* in Portuguese), which is a multidisciplinary research initiative involving more than 30 research institutions and partner organizations. The overall aim of this paper is to present the conceptual and methodological basis of the RAS initiative while also discussing many fundamental challenges that confront research on land-use sustainability across the tropics. Building on the work of a number of earlier and groundbreaking interdisciplinary assessments in the Amazon, including the LBA (Programa de Grande Escala da Biosfera-Atmosfera na Amazônia) and GEOMA (Pesquisas de Desenvolvimento de Métodos, Modelos e Geoinformação para Gestão Ambiental) research programmes [11,21,26], RAS seeks to address some of the limitations listed above by assessing the sustainability of land-use systems in two dynamic regions of eastern Brazilian Amazonia. The research approach adopted by RAS offers three advantages for addressing this overarching goal: (i) the collection of synchronized and co-located ecological and socioeconomic data across broad gradients of past and present human use and exploitation of natural resources; (ii) a nested sampling design that allows comparisons of the ecological and socioeconomic conditions associated with different land uses to be made across local, landscape and regional scales; and (iii) a strong engagement with a wide variety of actors and non-research institutions.

Drawing upon the strengths of our approach, RAS aims to make important advances in understanding the sustainability challenges facing Amazonia with regards to four broad objectives. First, we aim to quantify and better understand the ecological consequences of forest clearance, forest degradation and exploitation, and agricultural change (including cattle farming and silviculture) at several spatial scales. We are particularly interested in assessing the relative importance of local- and landscape-scale variables, as well as the extent to which past human impacts can help explain observed patterns in current ecological condition. Our measures of ecological condition include changes in terrestrial and aquatic biodiversity, carbon stocks, soil chemical and physical condition and aquatic condition. Our second objective is to examine the factors that determine patterns of land use, management choice, agricultural productivity and profits (and hence opportunity costs for conservation) and patterns of farmer well-being. Beyond input cost, geophysical (e.g. soil type, topography) and location (e.g. road and market access) factors, we recognize the potential importance of social-cultural factors in influencing land-use behaviours, including geographical origin, technical support, credit access, social capital and the importance of supply chains. Third, we plan to use our multidisciplinary assessment to evaluate the relationships between conservation and development objectives and identify potential trade-offs and synergies. Here, we are interested in the relative ecological and socioeconomic costs and benefits of alternative land-use and management choices, and the potential for feedbacks, multiple scale interactions and dependencies and unintended ('perverse') outcomes. Last, RAS seeks to help enable future research initiatives to maximize their cost-effectiveness by examining the implications of choices made with respect to variable selection, sampling design, prioritization of research questions and analyses, and approaches for engaging with local actors and institutions and disseminating results.

The remainder of this paper focuses on describing the key methodological components and novel features of our research design. We highlight some of the practical lessons and realities faced during the development of the RAS initiative so far, and identify the possible ways in which RAS could have a lasting impact in guiding improvements in land-use sustainability in Amazonia and elsewhere in the tropics.

2. The Sustainable Amazon Network: research design

(a) A conceptual framework for assessing land-use sustainability

RAS is inspired by the now well-established paradigm of 'sustainability science'—a science that is focused explicitly on the dynamic interactions between nature and society and is committed to place-based and solution-driven research across multiple scales [27,28]. Making explicit our understanding of the interactions among and between social and ecological phenomena, and their relationship to an overarching sustainability agenda is critical to the effectiveness and transparency of such a research programme.

The challenge of realizing a more sustainable development trajectory for the Amazon region lies in identifying, protecting and restoring the balance of ecological and socioeconomic values necessary to maintain the flow of critical ecosystem services and adapt to changing conditions, while also safeguarding the ability to exploit new opportunities for human development. The starting point for any research programme on sustainability is the selection of a set of socio-ecological values that can provide a basis for assessment. Our focus in RAS is on the conservation of forest-dependent biodiversity (terrestrial and aquatic), the conservation and enhancement of carbon stocks, soil and water quality, the provision of agricultural, silvicultural, timber and non-timber forest products, and the protection and betterment of human well-being.

From this basis, the RAS research process can then address our primary objectives in helping to quantify and understand some of the social and ecological problems and trajectories faced by the Amazon region, examine interactions and the potential for costly or potentially irreversible impacts, and evaluate the social and ecological costs, benefits and trade-offs associated with proposed management interventions. We view the transition towards sustainability as a guiding vision for continuous improvements in management practices rather than a search for a static blueprint of best practice techniques. Within this framework, we see the role of research as providing both an ongoing measure of management performance and a laboratory for testing new ideas for positive change.

Building on earlier work by Collins *et al.* [19], we present a simple framework of how we view the interacting components of our social-ecological study system, and the hypothesized cause-effect relationships, assumptions and feedbacks that provide a foundation for setting specific research objectives (figure 1). Outcomes measures (i.e. changes in valued attributes, such as native biodiversity, ecosystem service provision and human well-being) are captured in both the social and the ecological dimensions, and through changes in the stocks and flows of ecosystem services. Effects on these measures are felt through the cascading effects of changes in human behaviour

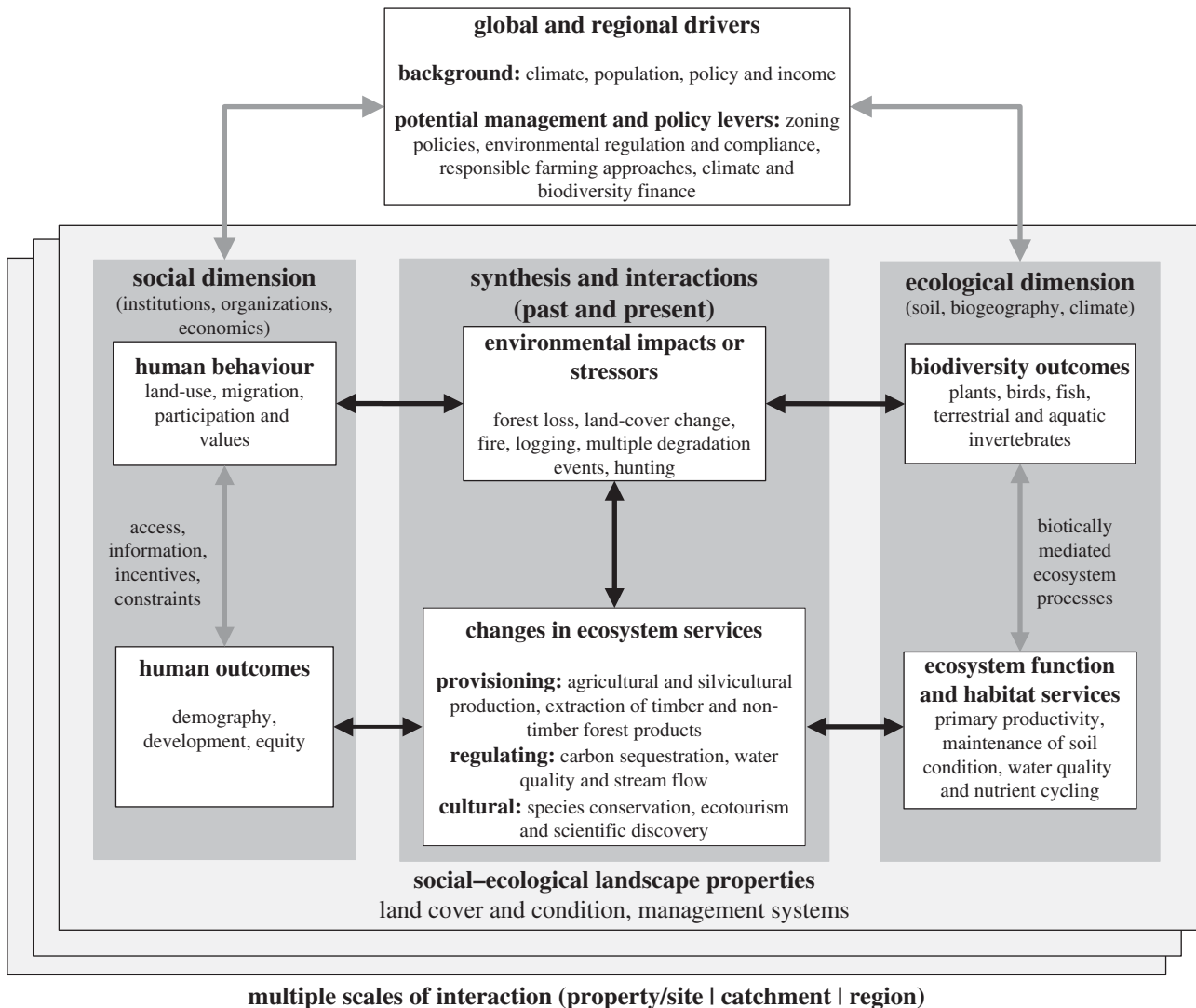


Figure 1. Conceptual model of study system under investigation by the Sustainable Amazon Network. Adapted from a generic framework presented in Collins *et al.* [19] to illustrate how we view the interacting components of our social–ecological study system, and the hypothesized cause–effect relationships, contexts (social and ecological dimensions and social–ecological interactions), assumptions and feedbacks between outcome measures (e.g. related to human well-being, biodiversity and ecosystem service provision), impacts and social and ecological processes, which together provide a foundation for setting specific research objectives. Not all influences and feedbacks are of equal importance and no attempt is made in the model to distinguish relative effect sizes. Social–ecological landscape properties are emergent and dynamic changes in landscape features that mediate relationships between social and ecological phenomena. System dynamics play out across multiple spatial scales. Variables listed are those that have been studied by RAS.

and associated environmental impacts on landscape properties and ecosystem functions. Each one of the influence arrows in figure 1 encompasses a set of specific, disciplinary research questions. The importance of diverse human impacts (both faster dynamics (such as fire and logging) and slower dynamics (such as cumulative land-use change and repeated degradation events)) in determining changes in outcome variables is examined using a space-for-time substitution across a highly replicated network of sampling locations and landholdings, coupled with detailed remotely sensed time-series analysis of past land-cover change and forest degradation. A focus of our work is understanding the extent to which landscape properties (often measurable from satellite and secondary data alone and used to compare multiple landscapes) can provide adequate proxies for understanding changes in the sustainability trajectory of the system as a whole. As much as possible, we try to ensure that the interpretation of our results takes account of the spatial scale of observation, and unmeasured factors, including the effects of external drivers such as climate change and global markets, on the study system. Last, we seek to characterize the effects

of a set of potential management and policy levers on the long-term dynamics and outcomes of the study system (figure 1).

(b) Key RAS design features

RAS is an example of a research initiative that collects matched social and ecological data at multiple scales and of relevance to multiple sustainability problems (see also [29]). A number of features of the research design adopted by RAS offer clear advantages for addressing questions about land-use sustainability and management.

(i) Spatial scale of assessment

Much of the existing social and ecological research in the Amazon (and elsewhere) has not been conducted at the most relevant spatial scales for assessing and guiding the development of more sustainable land-use strategies. Research has concentrated either on the entire Amazon basin, which often depends upon very coarse-scale data and obscures critically important inter- and intra-regional processes and interactions

[30], or on detailed work on a few intensively studied research sites, which captures only a tiny fraction of the variability in environmental and land-use gradients that drive much social and ecological change (see [10] in the case of biodiversity research). While both large- and small-scale research is necessary, much more work is needed at the 'mesoscale' level (i.e. spanning hundreds of kilometres and coincident with the scale of individual municipalities in Brazil). The RAS assessment was conducted in two study regions in the Brazilian state of Pará: the municipality of Paragominas (1.9 million hectares) and part of the municipalities of Santarém and Belterra (ca 1 million hectares) (figure 2). There are several important advantages to working at this spatial scale. The socioeconomic and ecological data collected by RAS cover broad gradients of change in both ecological (e.g. natural factors, such as soil type and the extent of forest loss, degradation and land-use intensification) and socioeconomic variables (e.g. rural population density, property size, wealth and market access), thereby affording more confidence in the general relevance of the patterns, drivers and trade-offs inferred from sample data [31]. In addition, a focus at the mesoscale facilitates assessment of the importance of both local (farm) and regional (state and biome) processes and objectives in a way that work focused on either smaller or larger scales cannot readily achieve. Finally, municipalities (or the equivalent scale of administration elsewhere) are also the administrative unit with arguably the greatest awareness of local pressures on natural resources and social services, and the greatest responsibility for institutional linkages between local communities and states or regions [30].

(ii) Choice of study regions

The RAS study regions of Paragominas and Santarém–Belterra differ both biophysically and in their histories of human occupation and use. By collecting data from two distinct regions of eastern Amazonia, we have a rare opportunity to better understand the extent to which inferences derived from one region can be generalized to another.

The modern city of Santarém, once a centre of pre-Colombian civilization, was founded in 1661, whereas Paragominas was founded as recently as 1959. Recent development of both regions has been closely associated with the construction of federal highways. Northern Santarém and neighbouring Belterra have been densely settled by small-scale farmers for more than a century. By contrast, Paragominas had a very low population density prior to its colonization by cattle ranchers from southern Brazilian states in the 1950s and 1960s, and the boom in the timber industry during the 1980s and 1990s. Both regions are relatively consolidated, with decreasing rates of deforestation of primary vegetation, although on-going paving of the highway means southern Santarém will probably experience both increased human colonization and agricultural expansion in the near future. Large-scale, mechanized agriculture became established in both regions only in the early 2000s and has increased rapidly in recent years (usually at the expense of both pastures and secondary forest), currently occupying approximately 40 000 and 60 000 ha in Santarém and Paragominas, respectively. Paragominas has also witnessed a rapid recent expansion of silviculture (mostly *Eucalyptus* spp. and *Schizobium amazonicum*). Both regions are distinct from the agro-industrial frontier in Mato Grosso which is dominated by large-scale mechanized farming primarily for export [32,33]. Although mechanized farming is expanding rapidly in both

study regions, in contrast to Mato Grosso, the majority of properties are less than 1000 ha. Moreover, local and regional urban centres still provide significant markets for cattle, and landscapes are interspersed with a diverse array of densely populated small-holder colonies and agrarian reform settlements.

Both Santarém and Paragominas have recently embarked upon high-visibility, multi-sectoral sustainability initiatives; specifically, a moratorium on expansion of soya bean from deforested areas in Santarém, and the foundation of the *Município Verde* (Green County) initiative for promoting sustainable land-use systems in Paragominas. These processes have strong support from non-governmental organizations, farmer's unions and local government, and have facilitated the development of RAS by helping us gain trust with local actors and institutions, tailoring the research planning and design towards local priorities and needs, and increasing receptivity towards project results and recommendations.

It is not viable to repeat the scale of assessment of the RAS initiative in every tropical forest region around the world. However, by working at multiple scales and in two differing municipalities that encompass many characteristics of eastern Amazonia and elsewhere, such as large areas of extensive cattle pasture, emergent mechanized agriculture and a population that is highly mobile and dominated by small-holder farmers, we believe that our results provide a suitable laboratory for better understanding many of the risks and opportunities facing the development of more sustainable landscapes across the wider region. By concentrating our efforts in two regions that have received particular attention from existing initiatives in sustainable land use, our results almost certainly will receive greater exposure to, and engagement with, a wide range of decision makers. Last, a key focus of our work is to employ our uniquely comparable and diverse datasets to identify a subset of cost-effective ecological and social indicators that can help guide applied research and monitoring work in other study regions.

(iii) Sampling design

The RAS sampling design is based on a sample of 18 third- or fourth-order hydrological catchments (ca 5000 ha) in each region. Catchments are distributed over a gradient of forest cover in 2009 (10–100% in Santarém; 6–100% in Paragominas; figure 2), with detailed ecological and socioeconomic information being collected from study transects and individual farms within each catchment (figure 2; electronic supplementary material). Advantages to this nested design include the potential for determining the relative importance of drivers and constraints that operate at different spatial scales, and the capacity to make connections between local/individual (farm) and larger scale/public (municipality and state) conservation and development objectives (table 1). Sampling at the catchment scale also permits the integration of terrestrial and aquatic information, and the assessment of changes in ecological and socioeconomic variables that are highly correlated at local scales, such as cumulative deforestation, economic activities and human population density. The 36 study catchments (figure 2; electronic supplementary material, figures S1 and S2) were selected to capture the full deforestation gradient, while incorporating priority areas identified by members of the municipal governments and farming communities (e.g. agrarian reform settlements, traditional rural communities and areas of recent agricultural expansion and development).

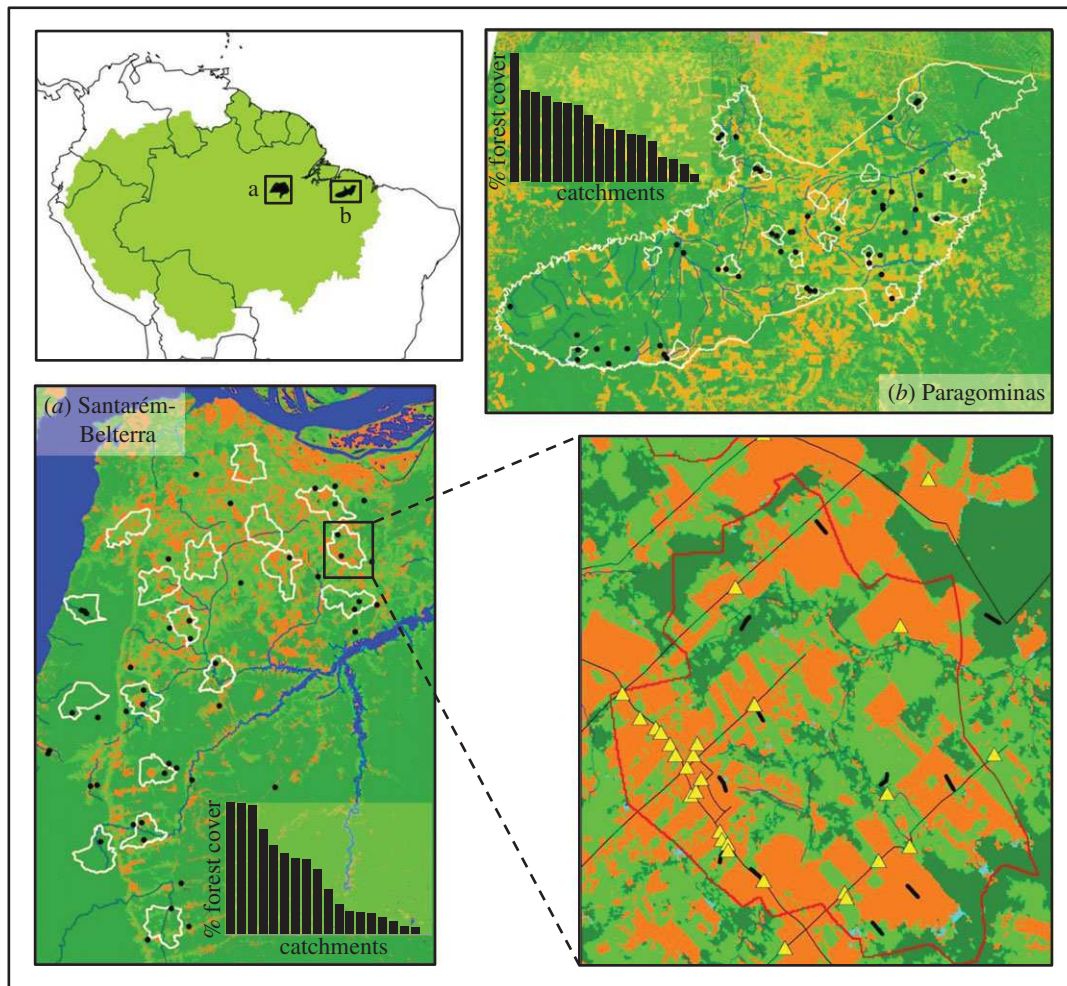


Figure 2. The Sustainable Amazon Network nested sampling design. Distribution of study catchments (white) is shown within both Paragominas (*a*) and Santarém-Belterra (*b*). Black circles show location of streams sampled during the aquatic assessment. Black bar charts show distribution of remnant forest cover across catchments. (*c*) The distribution of study transects (black lines) and the principal household of producer landowners (triangles) in the catchment of Boa Esperança in Santarém. Land-use classification derived from Landsat 2010 image, showing primary forest (grey), secondary forest (light grey), deforested areas (white) and major water bodies (dark grey). (Online version in colour.)

Ecological data were collected from a sample of 300 m study transects in every catchment, distributed using a stratified-random sampling design, where a standard density of transects (1 per 400 ha) was distributed across the catchment in proportion to the percentage cover of total forest and production areas (encompassing agriculture, pasture, fructiculture and silviculture; figure 2). For example, if half of the landscape was covered by forest, then half of the transects were allocated to forest. In catchments with very low levels of forest cover we sampled additional forest transects to ensure a minimum sample of three transects in all catchments. Within each of these two land-use categories (forest and non-forest), sample transects were distributed randomly with a minimum separation of 1500 m to minimize spatial dependence. The use of this stratified-random sampling design provided a balance between the need for: (i) proportional sampling of forest and non-forest areas, and a sufficient density and coverage of sample points to capture major differences in landscape structure and composition among different catchments; and (ii) a well-dispersed set of sampling points across forest and non-forest areas that captured important environmental heterogeneities within each catchment and across the region as a whole, helping to minimize problems of pseudo-replication. Aquatic sampling was conducted across 50 stream sites, each 150 m long in each region, with samples distributed

along a gradient of prior human impact based primarily on the amount of remnant forest cover in the upstream catchment (and not constrained to terrestrial study catchments).

Socioeconomic data were collected from all rural properties with an ecological study transect. Owing to the stratified design, transects tended to be in larger properties and under-represent smaller farms. Therefore, we mapped all rural producers in each catchment and sub-sampled a maximum of 20 randomly selected properties (with at least 1 ha and producing in 2009). Given our focus on the producer community, this sample excluded urban and periurban areas, but could include some of the same farms in the transect-based sample. This combination of sampling techniques enables us to describe the dominant socioeconomic and demographic characteristics of different producers, and to provide a detailed socioeconomic profile of the farming population in each catchment (figure 2). Where rural properties had more than one household (e.g. where there are workers or relatives living on the property), additional surveys on household demography, origins and well-being were made according to the total number of residences (table 1).

(iv) Social and ecological field sampling

RAS project members conducted a detailed assessment of ecological and socioeconomic patterns and processes in

Table 1. Remote-sensing, socioeconomic and environmental data sampled by the Sustainable Amazon Network.

variable type	variables	summary characteristics			
		Paragominas		Santarém	
remote sensing	biannual land-use classification (since 1988 in Paragominas and 1990 in Santarém-Belterra); age of deforestation; frequency and timing of forest degradation events; age and frequency of secondary forest regeneration; mapping of fire and logging scars; indices of deforestation and forest regeneration trajectories; cover of mechanized agriculture since 2000 (MODIS images); land-use intensity by hydrological distances between stream networks and forest remnants				
socioeconomic	property sizes in socioeconomic survey	number	area surveyed (ha)	number	area surveyed (ha)
	0–25 ha	44	936	150	1656
	25–100 ha	47	3030	110	7587
	100–300 ha	20	3577	20	3837
	300–1000 ha	16	9222	21	12 397
	over 1000 ha	44	238 979	16	62 978
	total number of properties	171	255 744	317	88 455
	total number of households	223		400	
	survey modules	property characteristics; household characteristics, demography and well being; productivity and inputs of different production systems; fire use and impacts; forest use (and hunting)			
soil	physical structure, soil fertility, total C and N, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, phospholipid fatty acids (PLFA) analysis of soil microbes, microbial biomass, soil water soluble nutrients, soil emissions of CO_2 , NH_4 , N_2O	3120 and 2580 soil samples from Paragominas and Santarém, respectively. Five replicates from each transect and at three depths (0–10, 10–20, 20–30 cm). Microbial and PLFA data, soil water soluble nutrients and soil gases emissions for selected catchments from Santarém only.			
vegetation and carbon stocks	biomass and vegetation structure (including dead wood, leaf litter and structural measurements)	44 359 stems measured and identified		38 584 stems measured and identified	
	tree, liana and palm diversity	1052 species		1118 species	
	disturbance	observations of fire and logging scars and other damage on all stems			
terrestrial fauna	birds	364 species		377 species	
	dung beetles	85 species		99 species	
		53 113 specimens		40 664 specimens	
	ants	ca 300 species		430 species	
	orchid bees	28 species		34 species	
	ecosystem functions	n.a.		dung removal, soil turbation, and seed dispersal by dung beetles, and seed predation by ants	
aquatic system	physical habitat	237 measurements relating to channel morphology, substrate, habitat complexity and cover, riparian vegetation, channel–riparian interactions and disturbance			
	aquatic quality	physical and chemical parameters of water (dissolved oxygen, conductivity, pH, temperature, nitrate and ammonia)			

(Continued.)

Table 1. (Continued.)

variable type	variables	summary characteristics	
		Paragominas	Santarém
	fish	112 species	71 species
		18 669 individuals	7990 individuals
	Ephemeroptera, Plecoptera and Trichoptera	49 genera	54 genera
		14 113 individuals	7937 individuals
	Heteroptera	9 genera	14 genera
		1847 individuals	543 individuals
	Odonata	97 species	68 species
		1990 individuals	1849 individuals

both study regions between April 2010 and August 2011 (table 1 and figure 2; electronic supplementary material). Choices of sample variables and methods were based on our research priorities, cost-effectiveness and the need to collect a large number of representative samples [34] (table 1). Sampling of terrestrial biodiversity focused on trees and lianas, birds, dung beetles, ants, orchid bees and soil microbes. In a subset of catchments, additional measurements were made of ecosystem functions mediated by beetles and ants (including dung burial, seed dispersal and seed predation). Aquatic biodiversity (and metrics of aquatic condition) consisted of fish and macroinvertebrate assemblages (table 1). Ecosystem service supply was measured for carbon stocks (above- and below-ground) and the maintenance of soil condition (physical and chemical properties). The habitat structure of both terrestrial and aquatic environments was assessed using a combination of measures of canopy openness, vegetation structure, dead wood and leaf litter, and the morphology and substrate of stream channels. Socioeconomic data were collected on the characteristics of study properties (such as land cover, legal status) and producer households (including household demography, producer origins, income, access to services, subjective measures of well-being), costs and productivity of different production systems (livestock, arable and perennial crops, silviculture and timber harvesting), fire use and effects, and the benefits and costs of maintaining forest reserves (including the extraction of timber and non-timber forest products, and risks of invasion and theft) (table 1).

Legacy effects of past human impacts are known to be important for both ecological and social systems, but have been poorly studied to date [35,36]. Remote-sensing analyses were based on a 22-year time series and provide information on changes in land use, forest extent, timing and frequency of forest degradation and age of regeneration (see the electronic supplementary material, table S2). These data provide the basis for validating remotely sensed indicators of ecological and land-use change with direct field observations (e.g. retention and loss of forest biodiversity, forest fires and land-mechanization).

3. Practical lessons and realities from the field

The acquisition of extensive and reliable knowledge about the Amazon is dependent on research networks that can

effectively exploit economies of scale in shared resources and technical expertise, recognize and make explicit interconnections and feedbacks among sub-disciplines, and increase the temporal and spatial scale of existing studies [22]. However, building effective multi-sector and interdisciplinary research programmes at large spatial scales remains one of the most difficult challenges facing sustainability science [37].

One of the greatest challenges of the RAS project has been developing and maintaining engagement with partners from multiple sectors, institutions, local governments, civil society organizations and farmer associations. More than half of the remaining forest in the Amazon lies within private land [25], and one of the novel aspects of RAS is the collection of data from complex landscapes with multiple owners that encompass a broad spectrum of culture, wealth and education. Establishing contact, building a minimum level of trust, and securing permissions from more than 200 private landowners across the 36 study catchments incurred significant costs in time and resources. This was especially difficult in areas with a legacy of conflict over deforestation and the exploitation of natural resources. Such 'transaction costs' are rarely factored into or supported by funders of major research programmes.

Despite the challenges, most landowners recognized the value of research in strengthening the evidence basis for what are otherwise largely rhetorical and highly politicized debates regarding the effects and drivers of land-use change. The diversity of institutional partners that make up RAS, including local organizations, and those directly concerned with agricultural development and local conservation initiatives, was critically important in building trust. While the establishment of meaningful partnerships with very different types of landowners (including some of the poorest and richest farmers in the study regions) was critical for the success of RAS, it was also important to avoid over-promising and over-committing on the benefits to individual land owners from project outcomes. Considerable care was taken to manage expectations by distinguishing clearly the purpose of research from rural development and agricultural extension, and presenting realistic timetables for project participation and the dissemination of results.

Maintaining a meaningful level of engagement with our network of local partners is critical to help maximize the relevance of our analyses of project data to local sustainability problems [23]. We are keenly aware that the difficulties inherent in giving adequate attention to the needs and problems facing

local communities can increase the chance of drawing inappropriate conservation and development recommendations from our work. We are wary of presenting and interpreting trade-offs too simply, and we acknowledge that simplified quantitative analyses and narratives that only take account of a limited set of attributes can obscure important dynamics and dimensions of value, often resulting in the marginalization of some interest groups [38]. Although commonplace in research projects such risks are rarely made explicit.

Within the RAS research network, we encountered many of the problems faced by other multidisciplinary projects, including the need to overcome differences in values, language and modes of thinking among disciplines [22,24]. There are no easy answers to such challenges, though we have found that co-location of researchers from different disciplines within the same field teams, use of a shared online management platform and group exercises (such as participation in conference symposia and writing this paper) have all helped promote constructive dialogue. RAS has its origins in three previously independent research projects that were amalgamated together with more partners and funding sources into a single initiative with shared goals, budget and management structure. While this historical trajectory led inevitably to a more complex funding and communication system, the resulting strong sense of ownership shared by many project members often led to a more open, interactive and democratic decision making process during project planning and execution.

Many of the greatest challenges in developing RAS arose from mundane problems of coordinating the collection, processing and analysis of data. There is a need for continual reassessment of the value and purpose of new measurements or additional samples, and the extent to which more data are necessary to address the priority questions. Cost-effectiveness in time and resources are often ignored in conservation research (e.g. in biodiversity surveys [34,39]), yet the effectiveness of research would be significantly improved if these considerations were consistently taken into account in project planning and development. We suggest that complex projects such as RAS establish 'stopping rules', both in the collection of more field samples and in cutting losses in areas where progress is slow or negligible. The marginal costs of more field data may appear to be little, but they must take account the costs of laboratory and analysis work, and the transaction costs of managing increasing project complexity.

4. Next steps: guiding improvements in land-use sustainability

Work to address our first two objectives is ongoing in many disciplines in RAS to assess and better understand the ecological and socioeconomic consequences of land-use and landscape changes, with synthesis analyses of trade-offs and scenarios scheduled from 2013. We hope that the outcomes from RAS can help guide improvements in land-use policy and management in several ways. At the simplest level, the quantification of deleterious trends in valued attributes (e.g. declines in forest biodiversity, ecosystem service production and socioeconomic values) and the identification of key stressors can both help to identify management priorities. A clearer understanding of spatial patterns of ecological and socioeconomic condition is fundamental for

understanding the appropriate locations, scale, starting conditions and potential constraints associated with any future changes in management actions [40]. Such basic information is still lacking for much of the Amazon region.

RAS datasets can help reconcile social–ecological objectives and reveal trade-offs between farming and conservation at multiple spatial scales by combining data on socioeconomic and ecological values. One prominent debate concerns the effectiveness of alternative approaches for attempting to balance conservation and agricultural activities through changes in agricultural productivity and farming techniques, often referred to as land-sparing versus land-sharing [41]. Understanding of this general problem is limited by a lack of data on the conservation value of areas of remaining native vegetation available for conservation investment that are in differing stages of degradation or regeneration, farm-scale differences in agricultural productivity and other socioeconomic variables related to human well-being and poverty, and landscape-scale influences on local ecological and socioeconomic properties. RAS data can make a potentially important contribution to the development of Reducing Emissions from Deforestation and Degradation (REDD+) initiatives [42], recognizing that we currently have a very poor understanding of the relative ecological and socioeconomic costs and benefits of alternative forest conservation policies (e.g. avoided deforestation versus avoided degradation and forest restoration activities) and the interaction between such policies and the agricultural sector [43].

Data and results from RAS ultimately aim to contribute towards more sustainable land-use systems in Amazonia in five overlapping areas, namely the development of: (i) best practice recommendations for sustainable intensification and responsible agriculture, particularly in the cattle-ranching sector; (ii) cost-effective approaches to achieving compliance with environmental legislation, especially in Brazilian Forest Law; (iii) strategies for investment in forest conservation and restoration through payment for ecosystem service schemes, and particularly carbon finance; (iv) strategies for promoting fire-free agriculture; and (v) municipal-level ecological–economic zoning processes. We seek to identify potential opportunities and motivations for more sustainable development strategies in eastern Amazonia and elsewhere by combining the quantitative foundation of our sustainability assessment with input from stakeholders and work in the political and social sciences [44].

We hope that our data will be helpful to assess how changes in management incentives or regulatory conditions will influence relative ecological and socioeconomic costs and benefits. However, we also recognize that win–win solutions are rare and often misleading. Given this, our work seeks to give explicit consideration to possible conflicts, compromises and synergies among multiple objectives, unexpected interactions and feedbacks, and the broader political and institutional context [45].

Ensuring that the work being undertaken by RAS goes beyond science and successfully bridges the science–policy divide is both extremely challenging and unpredictable. There are at least three areas where we hope that our approach can help to increase opportunities for informing development and conservation decision makers. First, our interdisciplinary, mesoscale and place-based research approach increases the likelihood that our results are relevant and applicable to regional problems. Second, we believe that to be most effective

the process of knowledge exchange should occur across a broad and diverse set of actors as possible. Here, the participation of such a large group of (mostly Brazilian) students and researchers on the one hand, with a large and diverse array of non-research partners and associates (including conservation organizations, farmers groups, government agencies and individual landowners) on the other has provided the basis for multiple ongoing dialogues about our research objectives and preliminary findings. Knowledge exchange should not be limited to high-level executive summaries for policy makers but must exploit opportunities for shared learning and dissemination of ideas at all levels. Last, we are developing an impact strategy that can help to target the presentation and discussion of key results through appropriate media to specific audiences and demands at local, regional and national levels.

Sustainability science needs to balance the often-conflicting timetables of research and policy processes. As scientists we strive to ensure the reliability, intellectual credit and independence of our work; a process that often requires a lot of time. However, to influence the policy process effectively, our experience is that the research process also needs to be able to respond to limited and often unpredictable opportunities for contributing to decisions on management and policy. Engaging in this process requires innovative methods for interacting with

different sectors and contributing not only to the delivery of policy-relevant research outputs as outlined in this paper, but also to broader efforts to build the capacity and understanding necessary to create a more sustainable development trajectory for the Amazon region. We hope that the work of RAS can make a small contribution towards this enormous challenge.

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A social and ecological assessment of tropical land uses at multiple scales: the Sustainable Amazon Network

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APÊNDICE 2 - Moura et al. 2013 - Biological Conservation

Avian biodiversity in multiple-use landscapes of the Brazilian Amazon



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ABSTRACT

Habitat loss and degradation is the most pervasive threat to tropical biodiversity worldwide. Amazonia sits at the frontline of efforts to both improve the productivity of tropical agriculture and prevent the loss of biodiversity. To date our understanding of the biodiversity impacts of agricultural expansion in Amazonia is restricted to findings from small scale studies that typically assess the importance of a limited number of land-use types. Here we investigate local and landscape-scale responses of Amazonian avian assemblages to land-cover changes across a gradient of land-use intensity ranging from undisturbed primary forest to mechanised agriculture in 36 drainage catchments distributed across two large regions of the eastern Brazilian Amazon. We found that species richness of forest-associated birds declined progressively along this gradient, accompanied by marked shifts in assemblage composition. We found significant changes in species composition, but not richness, between primary forests that had been subject to different levels of disturbance from logging and fire. Secondary forests retained levels of species richness intermediate between primary forests and production areas, but lacked many forest-dependent species. Production areas (arable crops, cattle pastures and plantation forests) all retained far fewer species than any forest habitat, and were largely dominated by taxa commonly associated with open areas. Diversity partitioning revealed that species composition varied the most among undisturbed forest transects, and steadily decreased with increasing forest degradation and land-use intensity. Our results emphasise the importance of protecting both remaining areas of primary forest in private lands, as well as protecting the same forests from further disturbance events.

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1. Introduction

In the tropics, land-use change has been the principal driver of biodiversity loss (Sala et al., 2000; Hooper et al., 2012) and ecosystem function impairment (Cardinale et al., 2012). Understanding the impacts of land-use change on patterns of species occurrence and abundance is of fundamental importance for developing effective conservation strategies (Gardner et al., 2009; Waltert et al., 2011; Balmford et al., 2012).

In the Brazilian Amazon, despite significant reductions in deforestation, 4656 km² of forest were still lost in 2012 (INPE, 2013). The loss and degradation (e.g. from timber extraction, fire and over-exploitation of non-timber forest products) of primary forest

remains the most important threat facing the biodiversity of the region (Peres et al., 2010), and is being driven by agricultural expansion (Davidson et al., 2012) and catalysed by major infrastructure improvements including road building and paving projects (Fearnside, 2007; Fearnside et al., 2012).

Although the impacts of forest loss, fragmentation and degradation on Amazonian biota are now increasingly understood, the majority of existing studies are limited in their spatial scale, concentrated in well-studied areas of the region, and have tended to focus on either fragmentation, forestry or fire impacts over a narrow range of land-uses (see reviews in Gardner et al., 2009; Peres et al., 2010; Laurance et al., 2011). In addition the vast majority of studies assessing the impacts of land-use change on biodiversity across the tropics have been limited to site-based assessments, despite increasing evidence indicating that landscape scale characteristics (such as the loss of total forest cover) can have a major

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influence on local species distribution patterns (e.g. Bennett et al., 2006; Pardini et al., 2010). As a consequence, insights into the impacts of multiple land-uses on Amazonian biota have up until now remained largely within the domain of meta-analyses (e.g. Barlow et al., 2006), which do not account for important differences in landscape context.

Here we evaluate avian responses to changes in forest disturbance and land-use across nearly 400 study sites distributed across 36 catchments in two different regions of the Brazilian Amazon, encompassing the full gradient of dominant Amazonian land-use types. Birds are excellent indicators of the ecological consequences of disturbance because their ecology is relatively well known, they are relatively easy to identify and cheap to survey (provided expert field observers can be sourced), and they exhibit a broad range of interspecific responses to human impacts at spatial and temporal scales that can be readily interpreted by snap-shot field assessments (Howard et al., 1998; Lees and Peres, 2006; Gardner et al., 2008).

We have three main aims. First we assess the loss of bird species (total number of species and number of primary forest-associated species separately) along a gradient of human impact from undisturbed primary forest through primary forest that has been varyingly disturbed by logging and fire, secondary re-growth, plantation forests, pastures and mechanised agriculture. This assessment contributes important information towards debates regarding the relative biodiversity value (compared to a primary forest baseline) of production areas (Peres et al., 2010; Mahood et al., 2012), secondary forests (Dent and Wright, 2009), and forests

degraded by fire and logging compared to relatively undisturbed primary forest (Barlow et al., 2006). Second, we compare patterns of avian species richness across catchments (separate landscapes) distributed along a gradient of deforestation in each study region, providing the first assessment of how changes in total forest cover can influence landscape-scale patterns of diversity in multiple-use tropical forest regions. Third, we investigate how patterns of avian diversity are partitioned across multiple spatial scales and within each major land-use type, from point counts to transects to landscapes, and ask whether differences in total forest cover explain these patterns through relative contributions of the α , and β diversity components (Tylianakis et al., 2006).

2. Methods

2.1. Study regions and experimental design

This study was conducted in two regions of eastern and central Pará state (Fig. 1), Brazilian Amazonia, in the municipalities of Paragominas (PGM) between 28 July and 20 November 2010 and 18–29 May 2011 (NGM and ACL) and in Santarém/Beltterra (STM) between 16 October 2010 and 8 February 2011 (NGM, ACL, CBA and BJWD). Both regions have been heavily impacted by deforestation but have significant differences in their historical trajectory of colonization and both past and present land-uses (Gardner et al., 2013). The municipality of Paragominas (1.9 Mha) is located in north-east Pará state, 300 km south-east of Belém. The average

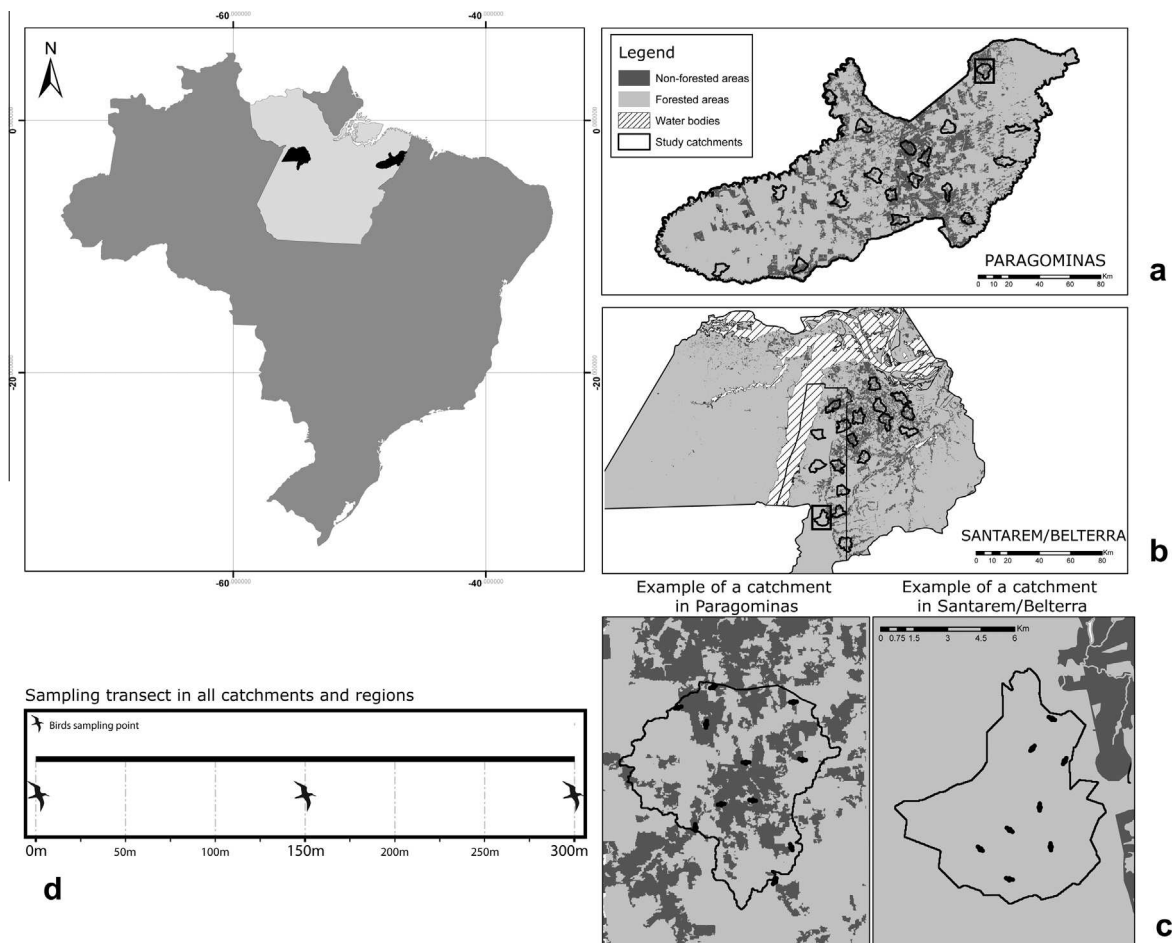


Fig. 1. Map of Paragominas (a) and Santarém/Beltterra (b) showing the location of the 18 catchments surveyed in each municipality. Two example catchments are presented for each municipality in (c) showing the location of transects and transects design and positioning of point count stations (d).

annual temperature is 27 °C, with an average humidity of 81% and annual rainfall averaging 1766 mm (Watrín and Rocha, 1992). The municipalities of Santarém/Belterra (ca 1 Mha) lie south-east of the confluence of the Amazonas and Tapajós rivers, and have an average annual temperature of 25 °C, with an average humidity of 86%, with annual rainfall averaging 1920 mm (Parrotta et al., 1995; Nepstad et al., 2002).

Both regions were divided into approximately evenly-sized catchments, which were delineated using a digital elevation model and SWAT (Soil and Water Assessment Tool) for ARCGIS 9.3. Eighteen catchments (of ca 5000 ha) were selected for each region capturing the full gradient of deforestation in 2009 (10–100% forest cover in Santarém; 6–100% forest cover in Paragominas), whilst also ensuring adequate representation of current land-use practices, the spatial distribution of the rural population, and major soil types. Between eight and twelve 300 m transects were allocated to each catchment, distributed using a stratified-random sampling design across each catchment to increase the likelihood that they would capture important internal heterogeneities in forest and/or production systems (depending on catchment size with an even density of 1 transect per 400 ha). To reduce the dependency between transects within each catchment transects were separated by a minimum distance of 1.5 km. In total we sampled 196 transects in PGM and 165 in STM. All landowners in each catchment were visited prior to any fieldwork to introduce the project and secure permissions for surveys in private properties. Land-use classification was made using 2010 Landsat images and a decision tree classification algorithm (Gardner et al., 2013).

In each transect three point count (PC) stations were located at 0, 150 and 300 m. A total of 1083 PCs were conducted across both regions. For further details on site-selection see Lees et al. (2012, 2013a) and Gardner et al. (2013). We carried out two repetitions of three 15 min, 75 m fixed width PCs per transect, recording all species seen or heard. Repetitions ensured that temporal variation in avian vocal activity was minimized, and PCs were recorded using solid state recorders – for more details on survey methodology, full species lists and links to digital vouchers see Lees et al. (2012, 2013a).

We classified land-use types into six broad groups (see Table 1), namely: 'primary forest': the region's original climax physiognomy that has never been clear-felled for agriculture (although may have been extensively degraded by disturbance and human exploitation); secondary forests: forests that developed after complete clearance (Putz and Redford, 2010); tree plantations – in this case commercial plantations, typically of *Eucalyptus* sp., teak (*Tectona grandis*) or paricá (*Schizolobium parahyba* var. *amazonicum*); cattle pasture; mechanised agriculture: typically soybean fields or rice;

and small-holder agriculture: farms typically smaller than 100 ha and consisting of small-scale manioc plantations and/or fruit trees. Primary forest transects were further sub-classified by disturbance type. These classifications were based on ground-truthed observations of past disturbance events (Gardner et al., 2013), resulting in four types of primary forest: 'undisturbed' for which no evidence of recent human-induced degradation was apparent, 'selectively logged' for forest which have undergone detectable logging, 'burnt' for forests in which fire scars were found on trees and charcoal deposits detected on the ground and logged&burnt for those forests exposed to both of these stressors. We also subdivided secondary forests into three age classes: old (>20 years old), intermediate (5–20 years old) and young (<5 years old). Ageing of secondary forests was done through visual inspection of a 20 year time-series of Landsat images for each transect, calibrated by interviews with local farmers.

2.2. Data analyses

We analysed the responses of total species richness as well as richness and turnover for the subset of 'primary forest-associated birds' (hereafter termed 'forest birds'). These forest birds represent the core avifauna of undisturbed *terra firme* forests but not necessarily birds restricted to those habitats, as some core primary forest species also occur (or indeed proliferate) in human-modified forest and non-forest habitats (e.g. Palm Tanager *Tangara palmarum* and Bananaquit *Coereba flaveola*). These categorizations were based on previously published classification of birds from the region (e.g. Parker et al., 1996; Henriques et al., 2003; Lees et al., 2013b).

To compare avian responses between different land-use systems and catchments we used sample-based rarefaction curves, with 95% confidence intervals (Colwell et al., 2004). The rarefaction curves between bird richness and total forest cover were constructed in EstimateS 7.5 (Colwell, 2004). Comparisons between species richness in each land-use type were also made using a non-parametric Kruskal–Wallis test with 95% confidence intervals followed by the Mann–Whitney U test to check for significant pairwise differences. These were performed in Statistica V.7.1 (Statsoft, 2005).

To explore relationships between forest cover and forest bird species richness we performed linear regressions using percentage of total forest cover (primary and old secondary forests combined) and the percentage of primary forest cover only in a 10 km buffer around the centroid of each catchment (to standardise comparisons of landscape context) as predictor variables for avian species richness.

To assess the variation in species composition between land-use systems and different primary forest disturbance classes we produced non-metric multi-dimensional scaling ordinations (NMDS; Clarke and Green, 1988) using the Bray–Curtis similarity matrix for species presence-absence data. To assess the statistical significance of observed differences in assemblage composition between different land-use types and forest degradation classes we conducted a one-way PERMANOVA which uses pseudo-*F* values to compare among-group to within-group similarity and assesses significance by permutation. All multivariate assemblage analyses were carried out in Primer v.6 (PRIMER-E Ltd., Plymouth, UK, Clarke and Gorley, 2006).

To describe the relative contribution of diversity components α (alpha – total species per point count), $\beta_{\text{among points}}$ (beta diversity among points within a transect) and $\beta_{\text{among transects}}$ (beta diversity among transects in a catchment) in the total diversity per catchment (γ ; gamma diversity), we used additive partitioning of diversity (Lande, 1996), where $\gamma = \alpha + \beta$. This approach allows the additive partitioning of the total diversity in a region to be broken down into scale-specific diversity components, which can be

Table 1
Total number of transects allocated to each land-use type in both study regions.

Land-use type	Paragominas	Santarém
Primary forest		
Undisturbed	9	17
Logged only	44	25
Burnt only	0	9
Logged&burnt	44	23
Secondary forest		
Old	5	21
Intermediate	12	18
Young	8	4
Reforestation	9	0
Pasture	53	25
Mechanised agriculture	12	16
Small-holder agriculture	0	7
Total	196	165

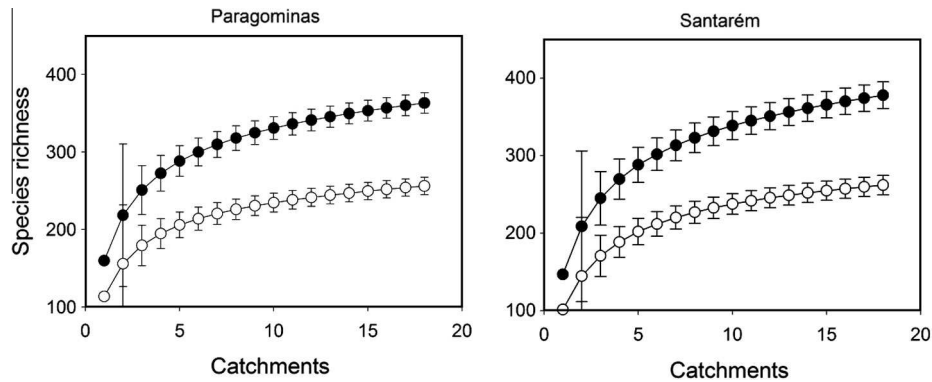
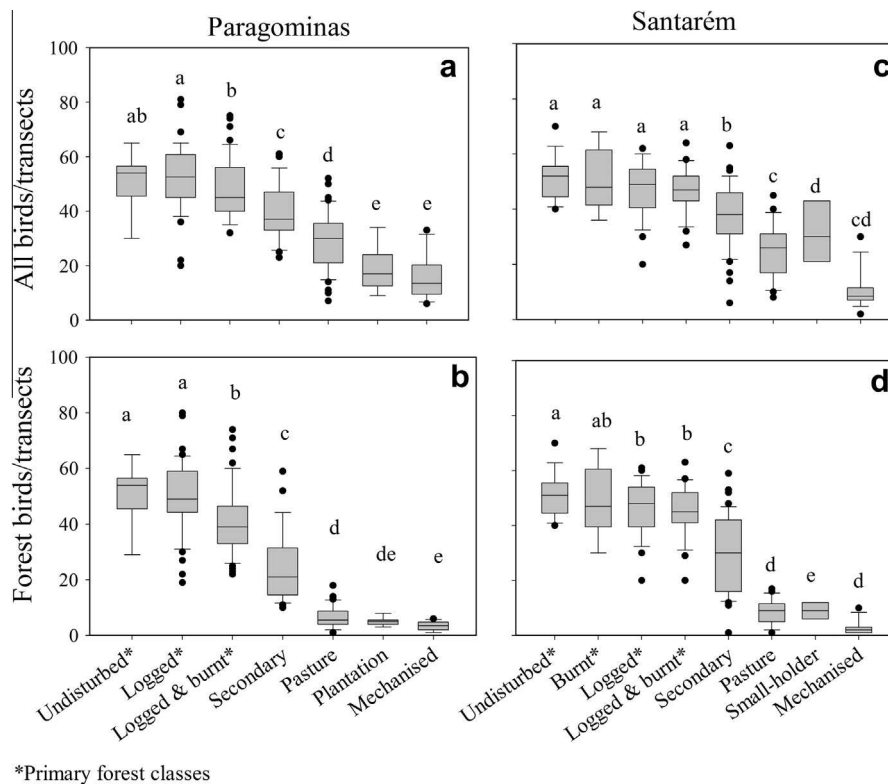


Fig. 2. Species rarefaction curves per catchment in PGM and STM, considering the entire avian assemblage (filled circles) and forest birds (empty circles).



*Primary forest classes

Fig. 3. Box plots comparing avian species richness between land-use types and degradation forest classes in PGM and STM, using the entire avian assemblage (a and c) and just forest birds (b and d). Non-significant pairwise differences between land-use types are indicated by the presence of the same letter (according to Mann-Whitney U).

directly compared (Veech et al., 2002; Gering et al., 2003). In addition, this approach can be important to help understand what factors are controlling the spatial distribution of biodiversity (Veech et al., 2002). In the context of our study, the overall forest bird diversity can be described by the following formula: $\gamma_{\text{Region}} = \alpha_{\text{points count}} + \beta_{\text{Points}} + \beta_{\text{transsects}}$. We omitted plantations and small-holder agriculture from these analyses as our sample size was too small to make reliable inferences. The additive partitioning was performed using the *adipart* function of the *vegan* package (Oksanen et al., 2011) in R software v.2.13.1 (R Development Core Team, 2011).

3. Results

We recorded 24,449 detections of 467 bird species, of which 336 were forest birds, with 359 species (252 forest birds) in PGM and 377 (286 forest birds) in STM (full species lists can be found

in Lees et al., 2012, 2013b). The species accumulation curves indicated that surveys in most land-use types were near asymptotic (Figs. A.1 and A.2). The cumulative richness across catchments (Fig. 2) illustrates a steady accumulation of species as new catchments were inventoried. Ten catchments, distributed throughout each region, were necessary to capture 90% of total species and 91% of forest bird species in PGM and 89% of total species and 90% of forest birds in STM (Fig. 2).

3.1. Species richness responses

In PGM, avian richness (all species) in primary (mean = 50, $sd = 12$) and secondary (mean = 40, $sd = 10$) forests was found to be significantly higher than all other land-uses (Fig. 3a, $H = 116$, $df = 6$, $N = 196$; $p < 0.001$) and secondary forest was statistically less species rich than all primary forest disturbance classes. Agricultural (mean = 16, $sd = 8$) and plantation forest (mean = 19,

sd = 8) areas had similar avian species richness. When the secondary forests were split by age category all three were significantly lower in richness than all primary forest disturbance classes ($H = 116$, $df = 8$, $N = 196$; $p < 0.001$, Fig. A.3). Considering only richness of forest birds, there was no significant difference between undisturbed (mean = 51, *sd* = 10) and logged (mean = 50, *sd* = 13) forest Fig. 3b ($H = 155$, $df = 6$, $N = 195$; $p < 0.001$), whereas both were distinct from logged&burnt (mean = 41, *sd* = 13) and secondary forests (mean = 12, *sd* = 24); (Fig. 3b). After being subdivided by age category ($H = 156$, $df = 8$, $N = 195$; $p < 0.01$) the different secondary forest ages classes remained distinct from all primary forest classes.

In STM considering all birds, the undisturbed forest (mean = 51, *sd* = 8) was statistically indistinguishable from all the primary forest disturbance classes (burnt [mean = 51, *sd* = 11], logged [mean = 47, *sd* = 10] and logged&burnt [mean = 46, *sd* = 8]); Fig. 3c ($H = 93$, $df = 7$, $N = 165$; $p < 0.001$). Secondary forests (mean = 38, *sd* = 12) were distinct from all other land-use types, and mechanised agriculture (mean = 10, *sd* = 7) was indistinguishable from pasture (mean = 25, *sd* = 10) and small-holder agriculture (mean = 31, *sd* = 10). We were unable to demonstrate significant differences between individual secondary forest age classes and most forest and non-forest land-uses, likely due to the small sample sizes (Fig. A.3; $H = 96$, $df = 9$, $N = 165$; $p < 0.001$).

Considering only forest birds in STM, Fig. 3d ($H = 154$, $df = 6$, $N = 195$; $p < 0.001$), undisturbed forest (mean = 51, *sd* = 8) was

indistinguishable from burnt forest (mean = 49, *sd* = 13), but distinct from both logged (mean = 46, *sd* = 10) and logged&burnt forest (mean = 45, *sd* = 10). Secondary forests (mean = 30, *sd* = 14) and small-holder agriculture (mean = 9, *sd* = 4) had intermediate species richness and were distinct from all other land-uses, but pastures (mean = 8, *sd* = 4) and mechanised agriculture (mean = 3, *sd* = 3) had similarly low species richness. Splitting the secondary forest into different ages categories ($H = 156$, $df = 8$, $N = 195$; $p < 0.001$, Fig. A.3) the species richness of old secondary forest (mean = 36, *sd* = 13) was statistically distinct from all other land-uses (including all primary forest classes), whereas young (mean = 126, *sd* = 12) and intermediate (mean = 25, *sd* = 11) secondary forests hosted similar numbers of forest species to pasture and areas of small-holder agriculture.

3.2. Differences in species composition

Species composition of forest birds changed consistently along a gradient of human impacts between primary forests, secondary forests, plantations, pastures and mechanised agriculture (Fig. 4, Table 2, PERMANOVA, Pseudo- $F = 26.152$, $p < 0.001$ and Pseudo- $F = 16.372$, $p < 0.001$ for PGM and STM respectively). All species assemblages were significantly different from each other with the exception of pastures and plantations in PGM ($p = 0.573$; Table 2) and small-holder agriculture and pastures in STM ($p = 0.271$; Table 2). Considering each secondary forest age class

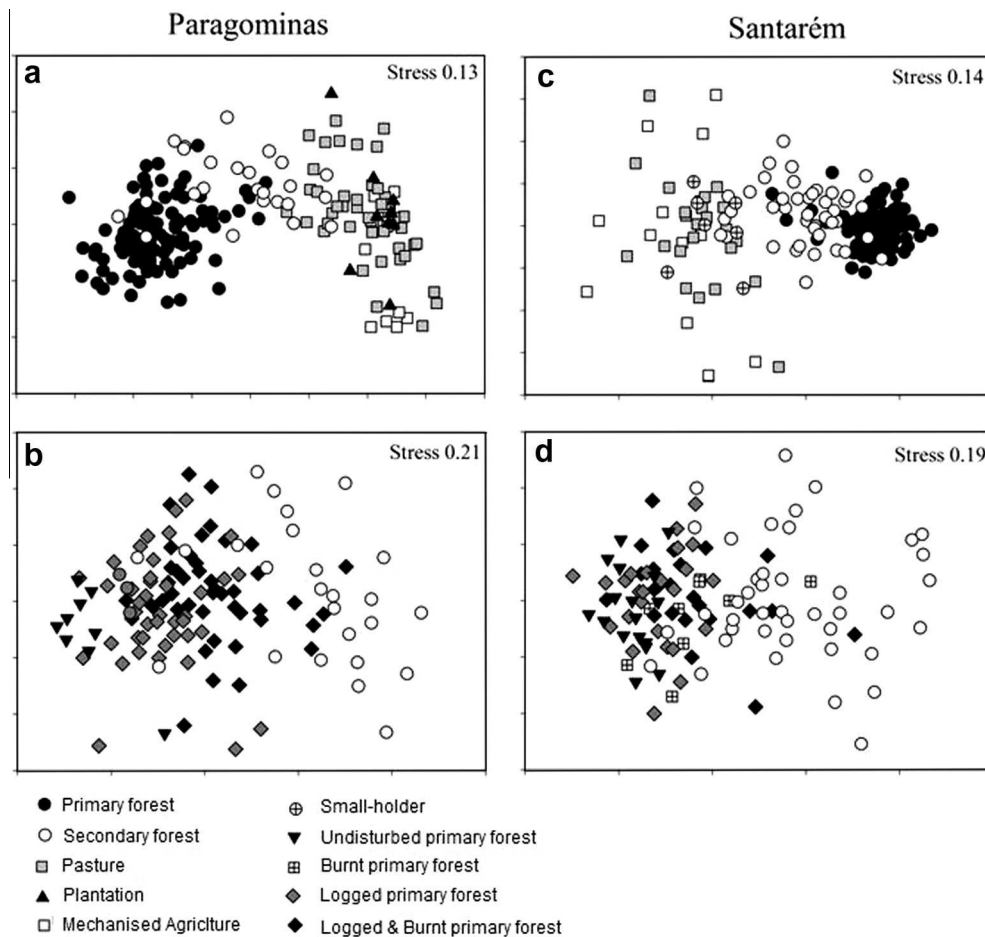


Fig. 4. NMDS plots of community structure of forest birds in all land-use types (a and c) and between different primary forest disturbance classes (b and d) in PGM and STM. Considering all land-use types (a and c) black circles = primary forest; empty circles = secondary forest; grey squares = pasture; empty squares = mechanised agriculture and black triangles = small-holder. For different primary forest disturbance classes (b and d) black triangles = undisturbed; grey hexagons = secondary forest; crossed squares = burnt forest; empty hexagons = logged&burnt forest; grey hexagons = logged forest; empty circles = secondary forest.

Table 2

PERMANOVA Pseudo-*F* statistic values of global test (*p*-values in parenthesis) and *t* values of pair-wise comparison (*p*-values in parenthesis) for forest birds composition in different land-use types and forest disturbance classes in two regions, PGM and STM, of the Brazilian Amazon. NA indicates that the comparison is not valid as the land use in question is unsampled in the respective municipality.

Land uses	PGM	STM
Global test land use	28.122 (<0.001)	17.361 (<0.001)
Mechanised agriculture, pasture	1.960 (<0.05)	1.539 (<0.001)
Mechanised agriculture, primary forest	5.448 (<0.001)	4.671 (<0.001)
Mechanised agriculture, secondary forest	3.783 (<0.001)	3.336 (<0.001)
Pasture, primary forest	8.984 (<0.001)	6.448 (<0.001)
Pasture, secondary forest	4.458 (<0.001)	3.962 (<0.001)
Primary forest, secondary forest	3.792 (<0.001)	4.339 (<0.001)
Plantation, pasture	0.891 (0.57)	NA
Plantation, primary forest	4.698 (<0.001)	NA
Plantation, mechanised agriculture	1.693 (<0.001)	NA
Plantation, secondary forest	3.04 (<0.001)	NA
Small-holders, secondary forest	NA	2.604 (<0.001)
Small-holders, mechanised agriculture	NA	1.689 (0.05)
Small-holders, pasture	NA	1.142 (0.238)
Small-holders, primary forest	NA	4.171 (<0.001)
<i>Forest disturbance classes</i>		
Global test	9.029 (<0.001)	6.1774 (<0.001)
Logged&burnt, logged	2.322 (<0.001)	1.617 (<0.001)
Logged&burnt, secondary forest	2.929 (<0.001)	2.747 (<0.001)
Logged&burnt, undisturbed	2.952 (<0.001)	1.741 (0.001)
Logged, secondary forest	3.904 (<0.001)	3.672 (<0.001)
Logged, undisturbed	2.159 (<0.001)	1.169 (<0.001)
Secondary forest, undisturbed	3.518 (<0.001)	3.48 (<0.001)
Burnt, logged&burnt	NA	0.947 (0.586)
Burnt, logged	NA	1.416 (<0.05)
Burnt, undisturbed	NA	1.365 (<0.001)
Burnt, secondary forest	NA	1.855 (<0.001)

(Fig. A.6), the forest bird assemblage composition was different from all primary forests disturbance classes in both regions (PERMANOVA, Pseudo-*F* = 26.152, *p* < 0.001 and Pseudo-*F* = 16.372, *p* < 0.001 for PGM and STM respectively, Table A.2). The species composition was not significantly different between old and intermediate secondary forest (*p* = 0.42) in PGM although it was different in STM (*p* < 0.05).

Forest disturbance classes were also distinct in their species composition (PERMANOVA, Pseudo-*F* = 9.062, *p* < 0.001 and Pseudo-*F* = 6.18, *p* < 0.001 for PGM and STM respectively; Table 2, Fig. 4b and d). In PGM the avian assemblages of all forest disturbance classes were significantly different from each other (Table 2), whilst in STM burnt and logged&burnt forests appear to be similar (*p* = 0.623; Table 2). Considering all species (rather than just forest

species) the NMDS plots (Fig. A.5) exhibited the same broad gradient pattern, but assemblages were less tightly aggregated (Table A.1).

3.3. Differences in species richness with changes in landscape-scale total forest cover

We found a significant positive and broadly linear relationship (Figs. 5 and A.4) between richness of forest birds and primary forest cover (aggregating all forest disturbance classes) and total forest cover within each catchment in both regions. These relationships were weaker in PGM than in STM for both primary forest cover and total forest cover (primary forest cover: adj.*r*² = 0.46, *p* < 0.001 and adj.*r*² = 0.79, *p* < 0.001 for PGM and STM respectively; total forest cover: adj.*r*² = 0.4, *p* < 0.001 and adj.*r*² = 0.75, *p* < 0.001 for PGM and STM respectively).

3.4. Additive partitioning of diversity

Additive partitioning indicated an increasingly higher percentage contribution for alpha (point count) diversity in more intensively used areas, with this trend being especially marked in STM. The $\beta_{\text{Among points}}$ component (species turnover among points in a transect) did not vary markedly across land uses. In contrast, $\beta_{\text{Among transects}}$ (species turnover among transects in a catchment) had a greater influence on gamma diversity in both regions, with turnover in species composition among transects being higher in primary forest than either secondary forest or production areas (Fig. 6).

4. Discussion

We found that Amazonian bird assemblages in multiple-use agricultural landscapes change markedly along a gradient of human impacts and land-use intensity in a predictable fashion. We observed a decrease in total species richness and an increasing shift in species composition when comparing undisturbed primary forest to increasingly degraded primary forest, secondary forest, plantations, pastures and arable fields. This general conclusion is supported by results from similar studies of land-use intensity gradients elsewhere in the humid tropics, including Indonesia (Waltert et al., 2004), Mexico (Pineda and Halffter, 2004) and Ecuador (Tyllianakis et al., 2006). In the following sections we draw on our results to assess in more detail the relative biodiversity conservation value of production systems, secondary forests and varying (un)degraded primary forests.

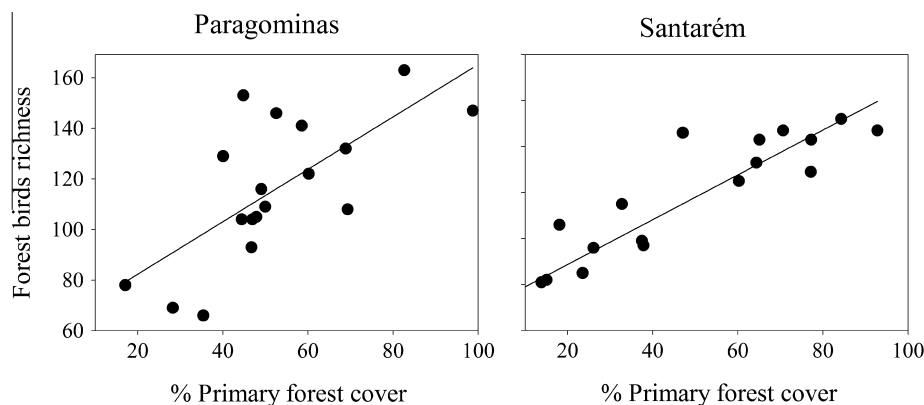


Fig. 5. Linear regressions between percentage of primary forest cover (aggregating all disturbance classes within a 10 km radius of each catchment) and richness of forest birds in PGM adj.*r*² = 0.46 and STM adj.*r*² = 0.79 (*p*-values significant at 0.001).

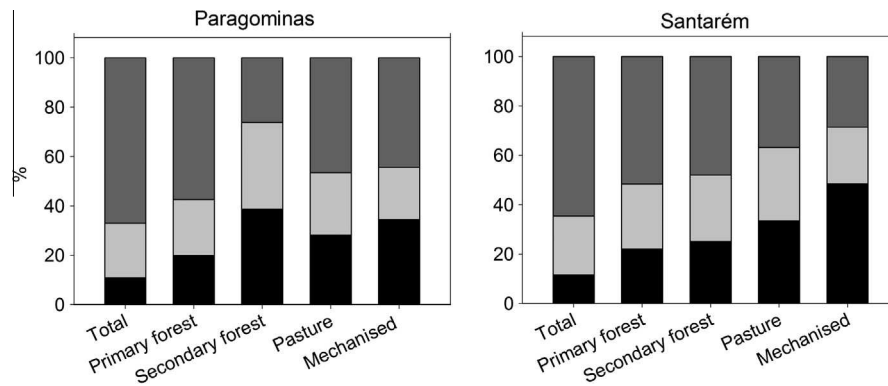


Fig. 6. Additive diversity partitioning (in%) in different land-use systems in PGM and STM, using forest birds. Black = Alpha (point counts); light grey = Beta (among point counts) and dark grey = Beta (among transects).

4.1. Production areas

The conservation value of production areas in the Neotropics has been the subject of considerable debate, with some studies from Central America indicating that non-forest production areas – the tropical ‘countryside’ – may host a significant proportion of the baseline avifauna community (e.g. 70% of native forest birds sampled in pastures and coffee plantations in Costa Rica; Lindell et al., 2004). However, comparable studies from South American production landscapes have found much lower levels of diversity (e.g. 32% of native forest birds sampled in cattle pastures and scrub in the Brazilian Amazon; Mahood et al., 2012). In part, the difference between the Amazon and Central America may reflect the more heterogeneous and structurally diverse old agricultural landscapes that characterise parts of Central America (Lindell et al., 2004).

The results from our study indicate that production areas typical of much of eastern Amazonia (i.e. degraded cattle pastures and mechanised agriculture) may harbour only slightly more than one third of the regional avifauna (43% and 38% in PGM and STM respectively). Cattle pastures provided some habitat for forest species (27% and 17% of species shared with primary and secondary forest habitats in PGM and STM respectively), but the majority of cattle pastures in our sample are unimproved and often contain large numbers of shrubs and scattered trees providing habitat resources and cover for birds. On the other hand, plantations forestry in Paragominas retained very little avian biodiversity harbouring just 7% of the regional pool of forest species.

Interpretation of simple percentages of shared species should be treated with caution (Barlow et al., 2010) as the frequency of occurrence of these forest birds in any given production area was also very low: 15% of all forest species from PGM and STM were recorded on less than five occasions across all agricultural areas. Occasional detections of nominally forest species, such as Black-and-white – Hawk-eagle (*Spizaetus melanoleucus*) utilising non-forest habitats, does not necessarily indicate that these species can persist in the absence of neighbouring forest patches, and many such detections might be better considered to be the result of gap-crossing events (Lees and Peres, 2009) or occasional foraging sorties. However, even such rare events may have important implications for landscape dynamics given the importance of birds as seed dispersers assisting in regeneration processes (Silva et al., 1996; Cole et al., 2010).

4.2. Secondary forests

Secondary or regenerating forests are becoming an increasingly dominant type of land cover in the tropics (Neeff et al., 2006; FAO,

2012) and as such are likely to have a very important future role in safeguarding the persistence of forest species in some regions (Chazdon et al., 2009; Gardner et al., 2009). Combining all secondary forests age groups together, this land cover harboured intermediate levels of forest species richness (242 species, 73% of all forest birds recorded in both regions) and species composition between that of primary forests (332 species in total, 70% overlap with secondary forests) (Fig. 3 and Tables A.3 and A.4) and production land-use systems (88 species, 26% forest species).

However, it is also clear that secondary forests do not provide adequate habitat for many forest-associated species. For example, 18% of forest species were absent from secondary forests in PGM and 23% were absent from secondary forests in STM, including the Great Jacamar (*Jacamerops aureus*) and Uniform Woodcreeper (*Hylexetastes uniformis*), which were only found in primary forest. Although we recorded many of the species listed by Parker et al. (1996) as disturbance-sensitive in secondary forests, many of these species were much more infrequently recorded in primary than secondary forests. For instance, the nuclear understorey flock-leading Cinereous Antshrike (*Thamnomanes caesius*) was recorded in 66% of primary forest transects and just 23% of secondary forest transects and the canopy-dwelling Red-billed Pied Tanager (*Lamprospiza melanoleuca*) was recorded in 28% of primary forest transects and 1.5% of secondary forest transects. This reduction in species richness is especially pronounced in relatively young secondary forests which dominate much of the eastern Amazon, Fig. 3), and these are often returned to agricultural production within less than 10 years in the Amazon region (Neeff et al., 2006).

4.3. Disturbed primary forests

Like other studies, we found consistently more species in undisturbed primary forest than in forests disturbed by logging and burning (e.g. Barlow et al., 2007; Gibson et al., 2011). Nevertheless, we also found that primary forests disturbed by fire and logging retained relatively high numbers of forest species (86% of the total regional species pool were found in logged forest and 78% in logged&burnt forests in PGM; with 59% of species in burnt, 74% in logged&burnt and 74% in logged forests in STM). Despite these differences in species totals, we did not find statistically significant differences in the average number of species per site when comparing between primary forests characterised by different levels of historical disturbance. This may be partly because of the high level of natural environmental variation (due to factors such as soil type and topography) or because forests are grouped within the same degradation class that may mask differences in the time-since or severity of disturbance event(s) or distance to source populations (Dunn, 2004; Barlow et al., 2006; Edwards et al., 2012;

Mestre et al., 2013). Finally, our comparisons may also be biased because areas selected for timber harvesting are often of higher than average tree basal area (and thus perhaps higher faunal species richness) (Henriques et al., 2008; Barlow et al., 2006). These kinds of difficulties in interpretation highlight the limitations of using species richness, rather than species composition to understand the ecological effects of land-use and landscape change (Barlow et al., 2007; Devictor et al., 2010).

Species richness was similar in all types of primary forest irrespective of the level of disturbance, yet some species (4% in PGM and STM) were entirely restricted to the relatively few undisturbed forest transects. These included Brown-winged (*Psophia dextralis*) and Dark-winged (*P. obscura*) Trumpeters, Variegated Antpitta (*Grallaria varia*) and Musician Wren (*Cyphorhinus arada*). Even small canopy disturbance events, such as the felling of a single tree, may alter understorey microclimatic conditions and hence ground cover of the forest floor rendering it unsuitable for some terrestrial species (Lees and Peres, 2010). Although some disturbance sensitive understorey species, such as Bare-eyed Antbird (*Rhegmatorhina gymnops*), Rufous-capped Antthrush (*Formicarius colma*) and Black-tailed Leaf-tosser (*Sclerurus caudacutus*), were occasionally detected in some burnt forest transects, our data support the conclusion by Barlow et al. (2006) in suggesting that areas exposed to fire are more dissimilar to primary forests regarding their avian biota compared to those that have only been logged (see also Fig. 4). Our findings also reinforce the conclusions of other studies from elsewhere in the tropics that disturbed primary forests are able to effectively conserve many forest-dependent species (Putz and Redford, 2010; Edwards et al., 2012; Gibson et al., 2011), at least in Amazonian landscapes that maintain high forest land-cover.

4.4. Effects of landscape scale forest loss on avian diversity

The total amount of remaining primary forest at the catchment (landscape) scale was an important predictor of forest species richness, confirming the conclusions of the small number of previous landscape-scale studies (e.g. Bennett et al., 2006 in Australia and Pardini et al., 2010 in the Atlantic forest of Brazil). We were not able to detect any meaningful thresholds in the relationship between changes in forest cover and changes in avian diversity in either region. Nevertheless, these results point strongly to the importance of adopting a landscape-scale (as opposed to property-level) approach to maintaining and enhancing the conservation status of multiple use landscapes in tropical forest regions.

We found that rates of species turnover changed consistently along a gradient of increasing forest disturbance and land-use intensity. Alpha diversity became increasingly important in explaining total levels of diversity as land was subject to more intensive human use (see Fig. 6); indicating lower levels of turnover as a result of an impoverished species pool characterised by a smaller number of species that can survive or proliferate in anthropogenic habitats; i.e. the process of biotic homogenisation which is already characterising many Neotropical forest habitats (e.g. Lôbo et al., 2011; Melo et al., 2013). In comparison, transect-scale beta diversity made a more important contribution to landscape diversity in forest areas, and to undisturbed forest sites in particular – where the avian assemblage is composed of a large number of habitat specialists that are often found at low densities (Terborgh et al., 1990; Tylianakis et al., 2006).

5. Conclusions

The data presented in this paper represent what is arguably the largest-scale field assessment of the impacts of land-use change on

tropical avifaunas to date. We found that (1) there is no evidence for a significant role of production areas in conserving Amazonian forest bird biodiversity; (2) secondary forest landscapes conserve significant bird biodiversity but differ markedly in assemblage composition from primary forests; (3) primary forests disturbed by fragmentation, logging and fire retain a high proportion of forest bird species but still lack some of the most sensitive taxa, with burnt forests appearing more affected than forests that have been logged but not burnt; (4) primary forest cover is an important predictor of total diversity for each catchment; and (5) that the distribution of species diversity across multiple spatial scales is highly influenced by the level of habitat modification, with beta-diversity consistently declining with increasing land-use intensity. The broad patterns of species richness and loss across the gradient of land-use between these two regions located 800 km apart in biogeographically different Amazonian interfluvial regions were similar, suggesting that conclusions on responses of Amazonian avifaunal communities to forest loss and degradation can be generalised.

As most of our fieldwork was conducted on private lands, our results reinforce the importance of conservation through private forest reserves in Brazil and the need to enforce current forest legislation and promote coordinated conservation strategies across neighbouring properties to safeguard regional biodiversity in the Amazon. In considering priorities for the protection of regional forest avifauna in eastern Amazonia, perhaps the most important implication of our results is the urgent need (ahead of costly investments in the restoration of cleared land) to protect and restore the varyingly disturbed and degraded primary forests that dominate much of eastern Amazonia, and which remain vulnerable to further timber extraction and recurrent fire events.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2013.08.023>.

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