



CÁSSIO ALENCAR NUNES

**THE CONSEQUENCES OF TROPICAL FOREST
DISTURBANCES AT THE COMMUNITY AND THE
ECOSYSTEM LEVEL**

LAVRAS – MG

2019

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Tese apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, para obtenção do título de Doutor.

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COMMUNITY AND THE ECOSYSTEM LEVEL**

**AS CONSEQUÊNCIAS DOS DISTÚRBIOS EM FLORESTAS TROPICAIS NOS
NÍVEIS DA COMUNIDADE E DO ECOSISTEMA**

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2019

Dedico esta tese para os/as cientistas que me inspiraram e para os/as cientistas que podem se inspirar nela!

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RESUMO

As florestas tropicais são o bioma mais biodiverso da Terra e desempenham importantes funções nos ciclos globais de água e carbono. Apesar da importância das florestas tropicais na provisão de serviços ecossistêmicos para toda a humanidade, as atividades antrópicas estão impondo mudanças significativas a este bioma. No Antropoceno, as florestas tropicais sofrem impactos da conversão para usos agrícolas do solo, da degradação devido ao corte seletivo, fogo, caça e fragmentação e da regeneração de florestas secundárias. Apesar dos cientistas investigarem esses distúrbios há algum tempo, ainda existem lacunas de conhecimento a serem preenchidas. Nesta tese, eu abordei lacunas de conhecimento no nível de comunidade e de ecossistemas. No capítulo 1, eu investiguei os efeitos da degradação florestal através da perda de espécies raras na diversidade funcional, usando besouros rola-bosta como grupo focal. No segundo capítulo, eu foquei na resposta ecossistêmica a diferentes tipos de distúrbio para investigar qual o componente do ecossistema é mais vulnerável aos distúrbios em florestas tropicais. Nos dois capítulos eu usei dados coletados em centenas de locais na maior floresta tropical do mundo, a Amazônia. Os resultados do capítulo 1 mostraram que as comunidades locais de besouros rola-bosta foram resistentes ao distúrbio tropical devido à redundância funcional do conjunto de espécies regional, que por sua vez é mantido na matriz florestal na paisagem. No capítulo 2, eu descobri que a biodiversidade é o componente do ecossistema mais sensível à ocorrência de diversos tipos de distúrbio. Em conjunto, os resultados dos dois capítulos não apenas demonstram a vulnerabilidade da biodiversidade de florestas tropicais, mas também dão suporte a iniciativas atuais para conservação de áreas de floresta intacta para servir de refúgio para as espécies e fontes de diversidade. Ao final da tese, eu discuto as implicações dos meus resultados no contexto global de conservação de florestas tropicais.

Palavras-chave: Amazônia. Besouros rola-bosta. Biodiversidade. Conversão de florestas. Degradação de florestas. Distúrbios. Diversidade funcional. Floresta secundária. Florestas Tropicais. Raridade.

ABSTRACT

Tropical forests are the most biodiverse biome on Earth and play important roles in global water and carbon cycles. Despite the importance of tropical forest in providing ecosystem services to all humans, anthropogenic activities are imposing significant changes upon this biome. In the Anthropocene, tropical forests suffer impacts from conversion to non-forested land-uses, degradation of remaining forests through logging, fire, hunting and fragmentation, and regeneration of secondary forests. Although scientists have been investigating these disturbances for a long time, there are still some knowledge gaps. In this thesis, I addressed knowledge gaps at both the community and the ecosystem level. In chapter 1, I investigated the effects of tropical forest degradation through rare species loss on functional diversity using dung beetles as focal group. In the second chapter, I focused on the ecosystem-level responses to different types of forest disturbance to question which ecosystem component was more vulnerable to tropical forest disturbance. In both chapters I used data collected in hundreds of sites in the biggest tropical forest on Earth, the Amazon. The results of chapter 1 showed that dung beetle local communities were resistant to tropical forest disturbance due to functional redundancy of the regional pool of species, which in turn is maintained in the forest matrix in the landscape. In the chapter 2, I found that biodiversity was the ecosystem component of tropical forests that was most sensitive to the occurrence of multiple types of disturbance. Taken together the results from both chapters not only demonstrate the vulnerability of tropical forest biodiversity, but also support current initiatives to conserve substantial areas of intact forest to serve as refuges for species and sources of tropical diversity. At the end of the thesis, I discuss the implications of my findings in the context of global conservation of tropical forests.

Keywords: Amazon. Biodiversity. Disturbance. Dung beetles. Forest conversion. Forest degradation. Functional diversity. Rarity. Secondary forest. Tropical forests.

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PRIMEIRA PARTE

GENERAL INTRODUCTION

Tropical forests are believed to have appeared between 50 and 65 million years ago, in the fragments of the continent Gondwanaland. In the present day, they occur mainly in five biogeographical regions in the tropics: Neo- (Americas), Afro- (Africa), Indo-Malayan (Southeast Asia), Australasian (New Guinea) and Madagascar, besides many tropical islands (MALHI et al., 2014). Since tropical forests appeared on our planet, they have played a critical role to the functioning of the Earth as we know it, mainly because they regulate global climate via water transpiration and cloud formation, which in turn affects atmospheric circulation (LAWRENCE; VANDECAR, 2015). Tropical forests exchange more water and carbon with the atmosphere than any other biome on Earth. For instance, they account for one third of terrestrial productivity and evapotranspiration (MALHI, 2012), and store approximately 230 Pg of carbon (BACCINI et al., 2012). Besides their importance to Earth's climate, tropical forests are exceptionally crucial to the world's biodiversity: they harbour around 60% of terrestrial biodiversity and are by far the most diverse biome (PIMM; RAVEN, 2000). Because of this huge contribution to water and carbon cycling, as well as a global repository of biodiversity, tropical forests provide crucial ecosystem services to humans, such as water provision and regulation, food, timber, carbon sequestration, medicines, and many others (VIRA et al., 2015). Around 20% of the human population (~1.5 billion people) rely directly on ecosystem services provided by tropical forests and it would not be an exaggeration to say that all humans indirectly benefit from these services (LEWIS; EDWARDS; GALBRAITH, 2015).

Human beings have lived in tropical forests for the past 60,000 years and since the initial colonization, we have explored the ecosystem services provided by this biome (MALHI et al., 2014). Indeed, this exploration intensified after the development of agriculture in the tropics around 6,000 years before present. However, because of the low population densities and shifting cultivation systems employed, human impacts on tropical forests were relatively low and forest health was maintained in the pre-historic ages. It was only more recently, with industrialization and globalization, that we started to impose significant changes upon these ecosystems (MALHI et al., 2014; LEWIS; EDWARDS; GALBRAITH, 2015). Human activities are now changing the world so extensively that scientists have proposed the start of a new geological period called the Anthropocene (STEFFEN et al., 2011). Tropical forests in the Anthropocene suffer impacts from agriculture, cattle grazing (GIBBS et al., 2010), road networks (AHMED et al., 2014) and urbanization (TREGIDGO et al., 2017), existing in

landscapes composed by a mosaic of primary and secondary forests, agricultural lands and cities.

All these anthropogenic impacts on tropical forests in the recent past led to three major trends of their existence today (LEWIS; EDWARDS; GALBRAITH, 2015): i) conversion to non-forested land-uses, mainly farmland and pastures; ii) degradation of remaining forests through fragmentation, logging, fire and hunting; and iii) regeneration of previously deforested areas as secondary forest regrowth. The destruction of tropical forests was the main source of farmlands in the 1980s and 1990s with more than 100 million ha converted worldwide (GIBBS et al., 2010). The remaining forests are facing high rates of degradation with 20% of all tropical forests affected by logging and fires (MOUILLOT; FIELD, 2005; ASNER et al., 2009). In some regions, such as the Amazon forest, fires have increased in the last decade, especially due to droughts and climate change, even though deforestation decreased (ARAGÃO et al., 2018). Fragmentation of tropical forests is also a major issue; for example, in the Brazilian Atlantic forest, more than 80% of the fragments are smaller than 50 ha, and therefore subjected to edge effects (RIBEIRO et al., 2009). Edge effect is a term that synthesise a variety of abiotic and biotic changes after forest fragmentation. The forest edges exhibit higher temperature, lower humidity and greater wind disturbances (EWERS; BANKS-LEITE, 2013) which in turn affect biodiversity causing, for example, an increase in tree mortality and proliferation of invasive species (LAURANCE et al., 2002). On the other hand, large areas of tropical forests have regenerated after abandonment of farmlands or have even been actively restored. For example, all the forested areas in Costa Rica and Puerto Rico, and almost all of the Brazilian Atlantic Forest are secondary forests (CHAZDON, 2003; LUGO; HELMER, 2004; RIBEIRO et al., 2009). However, secondary forests generally store less carbon, are less diverse and have different communities compared to primary forests (GIBSON et al., 2011), even after a century of recovery (MARTIN; NEWTON; BULLOCK, 2013).

The effects of these disturbances on biological communities and ecosystem services have long been the subject of research. Many studies have focused on the impacts of the main disturbance types (deforestation, forest degradation and secondary regeneration after clear cutting) on individual biological groups or individual ecosystem components. For example, we know that forest conversion has a negative impact on birds (MOURA et al., 2013), ants (SOLAR et al., 2016) and dung beetles (BRAGA et al., 2013). It is also well-established that forest conversion is the second key emitter of greenhouse gases due to the release of carbon in biomass and soils (VAN DER WERF et al., 2009). We also have evidence that logging and fire

in tropical forests can double the biodiversity loss caused by deforestation (BARLOW et al., 2016) and result in 40% lower carbon storage in disturbed forests, compared to intact forests (BERENGUER et al., 2014). Finally, we know that secondary forests have less diverse and different biological communities compared to primary forests (BARLOW et al., 2007; LENNOX et al., 2018) and that carbon pools can recover faster than biodiversity (MARTIN; NEWTON; BULLOCK, 2013). Although we have a lot of evidence for the negative effects of disturbances on individual components of the tropical forest ecosystem, we still need to evaluate the impacts of anthropogenic activities on the ecosystem as a whole. Human activities are the cause of tropical forest destruction, but at the same time we are able to intervene to preserve this biome (e.g., Arima et al. 2014), and consequently, an integrated assessment of the ecosystem-level responses is crucial to understand which components are more vulnerable to forest disturbance and hence where we should focus our conservation efforts.

Studies focusing on the ecosystem level are scarce because it is very difficult to obtain data of the whole ecosystem in individual research projects. We generally use proxies from the community level that can be used to predict impacts on the whole ecosystem, but which are much easier to access in terms of time, effort and budget. We often collect data of species and communities to use metrics of change in species abundance, richness and composition to understand the links between biodiversity and ecosystem functioning. This is based on our understanding that ecosystem functions are driven by the identity of species via their ecological or functional traits, and that the functional structure of communities is both linked to and influences ecosystem functioning as a whole (CADOTTE; CARSCADDEN; MIROTCHEV, 2011). In this sense, including functional diversity in community-level studies may help to evaluate how disturbances alter species assemblages and thus jeopardise ecological processes (MOUILLOT et al., 2013a; BEIROZ et al., 2018; LEITÃO et al., 2018). In addition, more refined data on species characteristics may also help us to disentangle if and how species that are more sensitive to disturbances contribute to the functional structures of communities. For example, rare species are assumed to be more susceptible to local and regional extinctions due to factors such as small population size and limited geographical ranges (DAVIES; MARGULES; LAWRENCE, 2004; HARNIK; SIMPSON; PAYNE, 2012), but rare species can perform unique functions (MOUILLOT et al., 2013b) and contribute disproportionately to functional structure of communities (LEITÃO et al., 2016).

There is an increasing number of studies focusing on community-level responses to tropical forest disturbances using functional approaches, which provide insights into the

vulnerability of different groups of organisms. For example, tropical forest conversion caused negative effects on dung beetle functional diversity (GÓMEZ-CIFUENTES et al., 2017) and after restoration, secondary forests had reduced dung beetle functional diversity compared to primary forests (AUDINO; LOUZADA; COMITA, 2014). In contrast, tropical forest degradation through logging did not affect tree functional diversity (CARREÑO-ROCABADO et al., 2012) and caused minor changes in bird functional structure (CHAPMAN et al., 2018). Although we are advancing in understanding the effects of forest disturbance on functional structure and diversity and the links with ecosystem functioning, there are still some major knowledge gaps. For example, we still do not know whether there is a clear relationship between the magnitude of disturbance effects and the rarity of species, nor how such rarity-dependent effects would influence the functional structure of biological communities. Filling these knowledge gaps may be crucial to understand how different species attributes will be filtered after forest disturbance and how this could affect ecosystem functions and the provision of ecosystem services.

In this PhD thesis, I investigated the effects of tropical forest disturbances both at the community and the ecosystem level. The thesis is separated into two chapters, each being in the format of a manuscript for a scientific article. In the first chapter, the focus is in the community-level responses; here, I wanted to understand the effects of tropical forest degradation on functional diversity and ecological functions, using dung beetles as focal group. Dung beetles (Coleoptera: Scarabaeinae) are considered bioindicators and perform important roles in detritivorous pathways (NICHOLS et al., 2008). I investigated whether the loss of rare dung beetle species would have a disproportionate impact on the functional structure of their communities. In this chapter, I used data collected from more than 100 forested sites in the Brazilian Amazon and also simulated different scenarios of species loss. The forests formed a disturbance gradient ranging from undisturbed primary forests, through degraded primary forests (burned, logged and logged-and-burned) and finally secondary forests. I compared the results based on field assessments and simulated species loss to discuss why and how forest disturbance affects the functional structure of dung beetle communities.

In the second chapter, the focus is in the ecosystem-level responses; I wanted to understand which of three ecosystem components (biodiversity, aboveground structure and soil properties) is more vulnerable to anthropogenic influences on tropical forest. I used data for 39 variables from different ecosystem components collected systematically from more than 300 sites in the Brazilian Amazon to fulfil this objective. I analysed the responses of biodiversity,

aboveground structure and soil properties in response to six disturbances belonging to the three major disturbance classes: conversion to i) pastures and ii) mechanised agriculture, degradation through iii) logging and iv) logging + burning, and regeneration in v) young and vi) established secondary forests. I used the results of this study to highlight the full range of impacts of anthropogenic disturbances in tropical forests and discuss why tropical forests are still being destroyed.

At the end of the thesis, I present a general conclusion section where I discuss the overall implications of the findings from both chapters. I highlight the main messages from both chapters and link them to the wider context of tropical forest ecology and conservation. The work presented in my thesis addresses important gaps in our knowledge of tropical forest responses to human disturbance both at the community and the ecosystem level. As such, it paves the way for new avenues of investigation, which will underpin future conservation efforts.

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SEGUNDA PARTE - ARTIGOS

ARTIGO 1**Functional redundancy of Amazonian dung beetles confers community-level resistance to primary forest disturbance at local and regional scales**

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Functional redundancy of Amazonian dung beetles confers community-level resistance to primary forest disturbance at local and regional scales

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ABSTRACT

Tropical forests are subjected to multiple anthropogenic impacts at different scales. We used data collected in the Amazon to assess the impact of forest disturbance on dung beetle taxonomic and functional diversity and simulated species loss at regional and local scales to evaluate effects of extinction scenarios on the functional structure of dung beetle communities. We found that dung beetle community metrics were largely unaffected by primary forest disturbance although differed between primary and secondary forests. Our extinction scenarios showed that only high proportions of species loss at the local scale would erode functional structure. The functional redundancy of dung beetles at the regional scale buffers the impact of species losses and makes local dung beetle communities functionally resistant to primary forest disturbance. We therefore suggest the importance of maintaining the regional pool of species and traits through the conservation of a forest matrix in the landscape.

Keywords: Extinctions, Tropical forest degradation, Functional metrics, Rare species, Rarity, Resilience, Scarabaeinae

INTRODUCTION

Human activities cause changes in most terrestrial (Newbold *et al.* 2015) and aquatic ecosystems (Halpern *et al.* 2008), leading to a loss of biodiversity and ecosystem functions and services (Vörösmarty *et al.* 2010; Mitchell *et al.* 2015). Despite harbouring more than 60% of the global terrestrial biodiversity (Slik *et al.* 2015), tropical forests are among the most heavily modified ecosystems on Earth, as they are subjected to a multitude of stressors interacting at different scales (Barlow *et al.* 2018). At the regional scale, disturbances are often related to deforestation (Barlow *et al.* 2016), resulting in an increasing number of remaining forested areas being affected by edge effects (Malhi *et al.* 2014; Baccini *et al.* 2017). At the local scale, within-forest disturbances usually result from fires, logging and hunting, and are expected to reduce the conservation value (Barlow *et al.* 2016), as well as the capacity of a forest to supply goods and services (Parrotta *et al.* 2012).

There is a consensus that ecosystem functions and services are at least in part driven by the extent and identity of species ecological traits (Cadotte *et al.* 2011). Taking into account the functional structure of communities could thus accelerate our understanding of the links between biodiversity and ecosystem functioning (Gagic *et al.* 2015). More than this, it may help to elucidate how disturbance-driven changes in species assemblages could impair ecological processes (Cadotte *et al.* 2011; Beiroz *et al.* 2018; Leitão *et al.* 2018). In this context, a critical question to be asked is whether species more sensitive to human activities contribute more or less to the functional structure of communities. Given the combination of small population size, restricted geographic range and narrow environmental tolerances, rare species are more prone to extinctions (Davies *et al.* 2004; Lavergne *et al.* 2005; Harnik *et al.* 2012). Importantly, there is increasing evidence that they can perform unique functional roles, contributing disproportionately to functional diversity of communities, despite their low numeric representation (Mouillot *et al.* 2013a; Jain *et al.* 2014; Leitão *et al.* 2016). Hence, the loss of rare species due to forest disturbance could lead to an erosion of functional diversity and an ultimate threaten of ecosystem functions and services.

The majority of conservation plans and studies of anthropogenic disturbances focusses on vertebrates and plants (Pereira & Cooper 2006). However, invertebrates, especially arthropods, perform a number of irreplaceable ecosystem functions (Hamilton *et al.* 2010; Cardoso *et al.* 2011). Given the enormous diversity of invertebrates in the tropics, we first need to focus on taxa that we know to be important components of the ecosystem and for which we

also have access to well-established taxonomic data and in-situ functional traits. Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) are one such focal taxon, and additionally, they play critical roles in detritivorous pathways (França *et al.* 2018), are abundant and diverse, and their sampling is highly cost-effective (Halffter & Favila 1993; Gardner *et al.* 2008). Due to their feeding and nesting habits, they perform key ecological functions such as dung removal, soil fertilization and aeration and secondary seed dispersal (Nichols *et al.* 2008). Furthermore, they are sensitive to both natural (Beiroz *et al.* 2017) and anthropogenic disturbances (Gómez-Cifuentes *et al.* 2017) and their response traits are relatively well studied (Griffiths *et al.* 2016).

In this study, we aimed to assess the influence of tropical forest disturbance on dung beetle diversity and ecological functions, and to determine whether the loss of rare species has a disproportionate impact on the functional structure of their communities. We used an extensive field dataset (Gardner *et al.* 2013) to test the following hypotheses:

1. Forest disturbance negatively affects dung beetle communities, functional structure and ecological function.
2. The extinction of rare species during forest disturbance results in a greater erosion of functional structure than the loss of common species.

We defined species rarity using data from 356 transects across the Eastern Amazon. We then tested our first hypothesis using a subset of 106 forested sites along a gradient of human disturbance to assess the impact of forest disturbance on dung beetle communities and their key ecological function (dung removal). Finally, we tested our second hypothesis by simulating species loss at local and regional scales to assess the effects of distinct extinction scenarios on the functional structure of dung beetle communities. We defined the functional structure of dung beetle communities using three indices: Functional Richness (FRic) to represent the range of trait combinations within a community, Functional Specialization (FSpe) to represent the distinctiveness of species traits within a community, and Functional Originality (FOri) to represent the isolation of species traits in relation to the community (Mouillot *et al.* 2013b). In combination, these indices provide important information to assess potential functional redundancy and determine the importance of species losses.

MATERIALS AND METHODS

Study Sites

We sampled data in 356 transects located in two regions in the eastern Amazon: Santarém (c. 2.7 million ha) and Paragominas (1.9 million ha). Eighteen hydrological catchments (c. 5000 ha) were selected for sampling in each region, and eight to 12 transects were installed in each catchment. Each transect was 300 m in length and transects within the same catchment were separated by at least 1.5 km (Fig. 1a). Transects were distributed within forest and non-forest land cover. Forested transects included primary (undisturbed, logged, burned, and logged-and-burned) and secondary forests (*i.e.*, those regenerating in previously deforested land). Non-forest transects included pasture, mechanized agriculture, abandoned plantation, fruticulture and tree plantation. To test the influence of time since the occurrence of a disturbance on dung beetle communities, we obtained, for each forest site, time since last disturbance (primary forests) and regeneration age (secondary forests) by combining a visual analysis of Landsat images (1988 to 2010 in two-year intervals) with a visual field assessment (Gardner *et al.* 2013). In the case of undisturbed primary forests, we attributed an arbitrary value of 50 years since last disturbance. For those forests in which we found physical evidence of disturbance, but this happened before the chronosequence (before 1988), we attributed an arbitrary value of 25 years since previous disturbance. We used data from all 356 transects to access species rarity and data from 106 forested sites in the Santarém region to test our first hypothesis (Fig. 1b, Table 1). Additional information on the study design can be found in Gardner *et al.* 2013.

Data Collection

Environmental variables - We used vegetation data and environmental variables collected from each transect to calculate the habitat breadth of dung beetles, a component of our rarity index (see below). Tree species richness and aboveground biomass were determined in a 10-m × 250-m vegetation plot in each transect, by measuring and identifying all individuals with a diameter at breast height (DBH) ≥ 10 cm. Understorey density was determined by measuring all stems ≥ 2 cm DBH within five 5-m × 20-m subplots per plot (number of individuals in the plot). Canopy openness (%) was assessed from five hemispherical photos per transect (50-m apart and at 1-m height) using Gap Light Analyzer 2.0 (Frazer *et al.* 1999). Litter stock (Mg ha⁻¹) was measured with 50-cm × 50-cm quadrats at 10 sampling points per transect. Soil texture (sand, silt and clay content; g kg⁻¹) was determined using the densimeter method

(Camargo *et al.* 1986) on composite soil samples collected at three different depths (0-10, 10-20, and 20-30 cm) on three to five sampling points located 50 m apart within each transect. Mean transect elevation was obtained in a 100 m buffer around the vegetation plot using digital elevation models. Full details of all measurements are given in Gardner *et al.* 2013 and Berenguer *et al.* 2014.

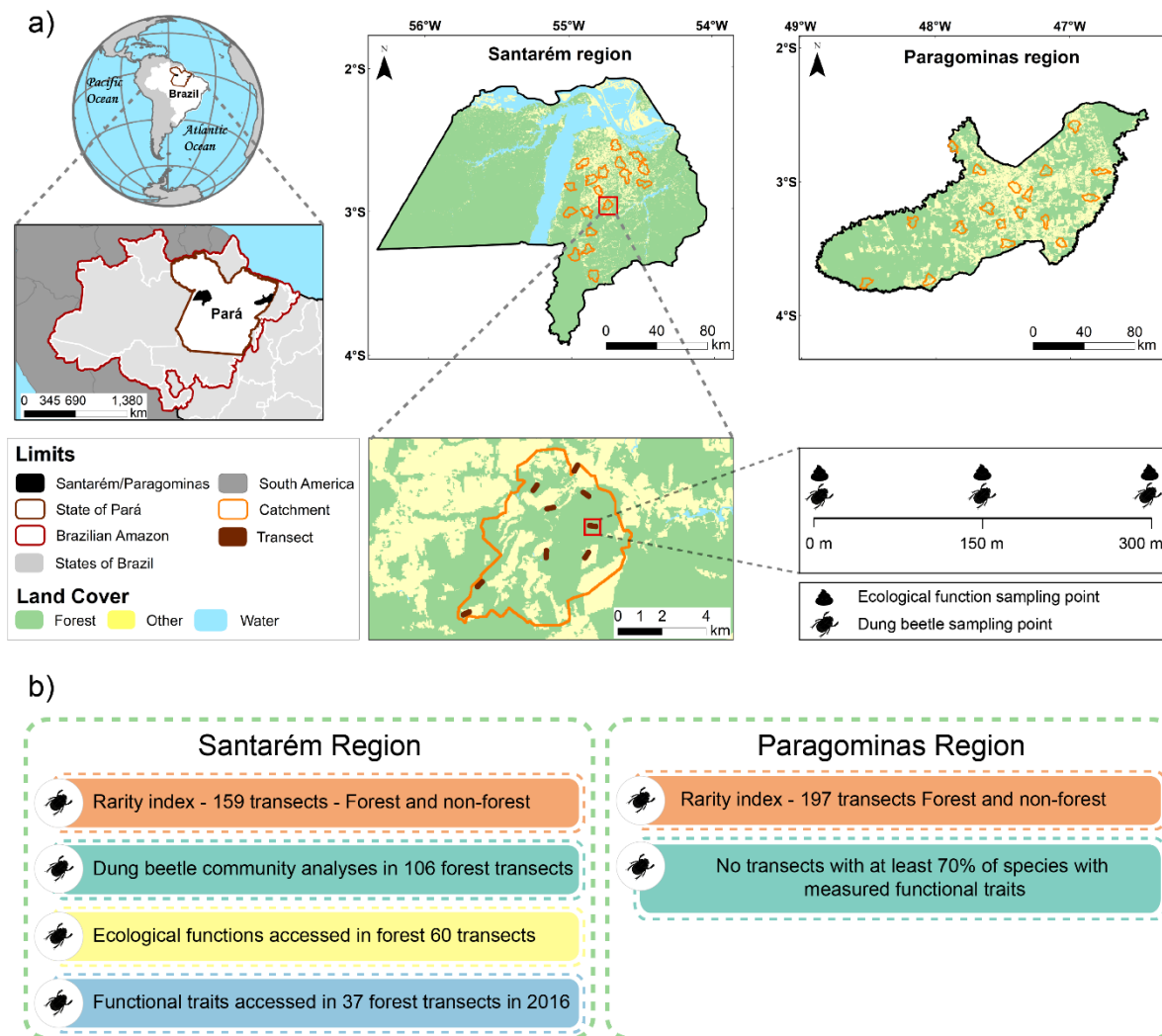


Figure 1 Map of study site and design. **a)** Dung beetles were collected in two regions of eastern Amazon, in the Brazilian state of Pará – Santarém and Paragominas regions. **b)** We accessed dung beetle rarity using data from both regions. We measured functions and functional traits of dung beetles collected in subsets of transects in Santarém region. We used data from dung beetles collected from Santarém region to test our hypotheses.

Dung beetle sampling - Dung beetles were sampled in all transects between April 2010 and August 2011 using pitfall traps (14-cm diameter and 9-cm height) baited with 50 g of dung (80% pig and 20% human). Traps were installed at three points along each transect (0, 150 and 300 m) and at each of the three points there were three traps at the corners of a triangle with 3-

m sides. Traps were left in the field for 48 h and then collected and stored in ethanol. Dung beetles were taken to the lab where they were dried and identified to species level or the lowest possible taxon. Voucher specimens were deposited in the Zoological Collections at the Universidade Federal de Mato Grosso, Universidade Federal de Lavras and Universidade Federal de Viçosa, Brazil.

Since we were interested in testing hypotheses that were related to species rarity, we excluded from the analyses species that are well known to be undersampled by baited pitfall traps, *i.e.* dung beetles that are not attracted by mammal dung (F. Z. Vaz-de-Mello, personal communication).

Dung beetle functional traits - We assessed dung beetle functional traits in a subset of transects in the Santarém region: five undisturbed primary forest, five logged primary forest, five burned primary forest, 15 logged-and-burned primary forest and seven secondary forest sites (Fig. 1b, Table 1). Dung beetles were collected in July 2016 as described above. To obtain trait data that accurately predict ecological functions, we recorded a suite of measurements on all individuals for species with <50 individuals and at least 50 individuals of all other collected species (Griffiths *et al.* 2016). Individuals were dried in the lab and weighed with a precision balance (0.0001 g). We then used digital callipers to measure: i) front leg length, ii) back leg length, and iii) pronotum width. The combined measurements gave the following functional traits: i) body mass (BM), ii) front leg length/BM, iii) pronotum width/BM, iv) back leg length/first leg length (Griffiths *et al.* 2015). We calculated the median value of each trait for each species, pooling together data of traits from all forest classes. We also obtained information on v) dietary habit (coprophagous, necrophagous and generalist) and vi) the functional guild of dung beetles (roller, dweller or tunneler) following Halfpter & Edmonds 1982, Griffiths *et al.* 2015 and Beiroz *et al.* 2017. The functional meaning and the relationship of each trait to dung beetle ecological functions is described in Table 1.

The trait measurements from the 37 transects (sampled in 2016) gave functional trait data for 67.8% of all species collected in the 106 forest transects in 2010 (61 out of 90 species), representing 87.6% of the total abundance of dung beetles. As functional trait data was lacking for some species, we completed the dataset by extracting additional information on functional traits from the literature (Griffiths *et al.* 2015; Beiroz *et al.* 2017) and also by estimating traits based on species body mass. For the trait estimates, we used linear regressions of each measured trait against body mass, using subsets of functional data for genera, or tribes when the number

of species in the genera was too low. We then used the equation of the linear regression to estimate the value of each trait for a given species using its mean body mass. In total we measured body mass of 83 species (3,658 individuals) and functional traits of 61 species (2,482 individuals). We estimated traits for 22 species based on measured body mass, estimated traits based on body mass extracted from the literature for four species and excluded three species for which we could find no functional trait data.

Table 1 Dung beetle functional traits used in the analyses with their related functional meaning and relationship with dung beetle ecological function.

Functional traits	Functional meaning	Relationship with ecological function *
Body mass (BM)	Size	Amount of resource removed and buried
Front leg length / BM	Robustness of front leg	Digging capability and dung burial
Pronotum width / BM	Robustness of prothorax	Muscle tissue accommodation - digging strength
Back leg length / first leg length	Dung manipulation capability	Ability of dung ball construction and rolling
Functional guild	Resource allocation strategy	How resource is removed and soil is excavated
Dietary habitat	Diet specialisation	Which kind of resource is removed

* (Halffter & Edmonds 1982)

Dung beetle ecological function - To quantify dung beetle ecological function, we used a “function arena”, which consisted of a 1-m diameter circular plot, delimited by a nylon fence (20-cm height), with 200 g of dung (80% human, 20% pig) deposited in the centre (Braga *et al.* 2013). To calculate the amount of dung removed (i.e., the ecological function), we weighed the remaining mass of the dung after 24 hours of exposure in the function arena. In 60 transects distributed in the Santarém region we installed the arenas between April and August 2010: 12 in undisturbed, 13 in logged, 5 in burned and 13 in logged-and-burned primary forests, and 17 in secondary forests (Fig. 1b, Table 2). Per transect, we placed three function arenas, located at 0, 150 and 300 m.

Data Analyses

All calculations of functional indices, estimation of traits, statistical analyses, and simulations were done in R version 3.4.2 (R Core Team 2017), using the following packages: “vegan” for multivariate analyses (Oksanen *et al.* 2013), “lme4” for linear mixed effects models

(LMMs, Bates *et al.* 2013), “phia” for post-hoc analysis of LMMs (De Rosario-Martinez 2015), “ape” for PCoA analysis (Paradis *et al.* 2004), “cluster” for functional distance matrix calculation (Maechler *et al.* 2017) and “ade4” for Outlying Mean Index analysis (Dray & Dufour 2007). We built R scripts based on Leitão *et al.* 2016 to calculate functional indices and run the simulations.

Rarity assessment - To define species rarity, we combined estimates of local abundance, geographical range, and habitat breadth of each dung beetle species. We used the full dataset (*i.e.*, data from 356 transects) to calculate these metrics, unless a species was only collected in 2016 (six species), in which case we used the data from the subset of transects. The local abundance of a dung beetle species i (LA_i) was calculated as the mean number of individuals in all transects where the species occurred. The geographical range (GR_i) was estimated as the area (ha) inside the smallest polygon joining the outermost sites in which the species occurred using QGIS software (QGIS Development Team 2017). If the species only occurred in < 3 transects, the GR_i was considered as the sum of the buffer area within a 1-km radius of the central point of each transect. To estimate the habitat breadth (HB) of a dung beetle species i , we used the “tolerance” metric from Outlying Mean Index analysis. The Outlying Mean Index is a measure of the species’ niche breadth relative to the niche space of the region, and the tolerance metric describes the spatial variance of the niche across measured environmental conditions or resources (Dolédec *et al.* 2000). We used the environmental variables described above to estimate the habitat breadth of each dung beetle species.

We calculated a rarity index for each species using LA, GR and HB, following Leitão *et al.* 2016. We first log-transformed each metric and then standardized the data by dividing each value by the maximum value across all species, to give values between 0 and 1 for each metric. We also accounted for the degree of dependence among the three metrics by weighting each by its correlation with the other two.

The rarity index for a species i (RI_i) was calculated by the following formula:

$$RI_i = \frac{[(LA_i \times w_{la}) + (GR_i \times w_{gr}) + (HB_i \times w_{hb})]}{(w_{la} + w_{gr} + w_{hb})}$$

where w_{la} , w_{gr} and w_{hb} are the weighting parameters for local abundance, geographical range and habitat breadth, respectively. The weighing parameter for each metric x was calculated by the following formula:

$$w_x = \frac{1}{2} + \left[\left(\frac{1 - |r_{x1}|}{2} \right) + \left(\frac{1 - |r_{x2}|}{2} \right) \right]$$

where r_{x1} and r_{x2} are the Pearson's correlation coefficients between the given metric x and each of the other two metrics. Values of RI_i range from 0-1, whereby 0 represents the potential value of the rarest species, and 1 is the potential value of the most common species.

Functional structure of dung beetle communities - To define the multidimensional functional space of dung beetle communities, we ran a principal coordinate analysis ('pcoa' function) using a functional distance matrix. As not all dung beetle functional traits were continuous, we used Gower distance to compute the functional distances between pairs of species given in the matrix ('daisy' function). We then chose three PCoA axes to construct the functional space, based on the mean squared-deviation index (mSD), which provides a measure of the functional space quality (Maire *et al.* 2015; Leitão *et al.* 2016).

To assess the functional structure of dung beetle communities, we calculated Functional Richness (FRic), Functional Specialization (FSpe) and Functional Originality (FOri) following Mouillot *et al.* 2013b. FRic is defined as the convex hull volume of the functional space (the PCoA axes) filled by all species of a given community, FSpe is calculated from the mean Euclidean distance between each species and the centroid of the species pool in the functional space, and FOri is expressed as the mean distance between each species and its nearest neighbour in functional space (Mouillot *et al.* 2013b). We standardized all three indices between 0 and 1 using the data from the subset of transects by (106 transects): i) expressing FRic as a proportion of the volume filled by the total pool of species in the dataset, ii) dividing FSpe by the maximum distance to the rest of the species pool in functional space across the whole dataset, iii) dividing FOri by the maximum nearest-neighbour distance observed across all species in the dataset.

Simulations of species loss - We simulated scenarios of species loss to assess the consequences of possible extinctions on the functional structure of dung beetle communities. We ran simulations for extinction scenarios at a local (transects) and a regional scale (pool of species), using dung beetle assemblages from undisturbed primary forest (12 transects), and assessing the outcomes of the scenarios from the change in the three functional indices.

For the regional simulations, we assessed three scenarios: 1) "rarest first" in which we sequentially removed species from the pool, from the rarest to the most common species, and recalculated the three indices after each removal; 2) "common first" in which we sequentially

removed species from the most common to the rarest; 3) “null scenario” in which we randomly removed species from the pool by shuffling the order of species removal 1000 times. We then evaluated the level of functional erosion (the change in the values of the three functional indices) for each scenario, comparing the outcome of the first two scenarios against the null scenario.

The local simulations also included the same three scenarios, but we calculated FSpe and FOr_i indices for nine levels of species loss (from 10% to 90%), and we calculated FR_{ic} for seven levels (10% to 70%), to ensure there was sufficient species per transect in all scenarios to calculate the convex hull volume of the functional space (four species minimum, representing the number of functional dimensions plus one; Mouillot *et al.* 2013b). We compared the values of functional indices resulting from the three scenarios using Friedman paired tests.

Response to forest disturbance - To assess whether forest disturbance promotes local species loss and consequently functional erosion (diversity and function), we performed generalized linear mixed models (GLMM) for richness and abundance of dung beetles, using a *negative binomial* error distribution (‘nb.glm_{er}’ function) and linear mixed models (LMM) for the three functional indices and the amount of dung removed as a measure of ecological function of dung beetle communities (‘lmer’ function). As the amount of dung removed was expressed as a proportion of the initial amount, we log-transformed the data before the analysis. For all models, we considered Santarém forest transects as sampling units because no forest transects in Paragominas region had more than 70% of species with measured traits (106 transects, Fig. 1b, Table 2). In these models, we used dung beetle species richness, FR_{ic}, FSpe, FOr_i, or the log-transformed proportion of dung removed as response variables, and catchments as a random effect. We ran separate models using forest type, time since last disturbance (for primary forests) or regeneration time (for secondary forests) and aboveground biomass as explanatory variables. We also assessed the effect of forest disturbance on mean species rarity using linear models. We used the mean rarity index for the local communities as the response variable, forest type, time since last disturbance/regeneration time and aboveground biomass as explanatory variables, and catchment as a random effect. We ran the models of functional indices using transects that had at least 70% species with measured traits even in Santarém region, which ended in 101 forest transects in these models (Table 2). Finally, to assess the potential influence of estimated trait data on our results, we also ran extinction scenarios and models of functional indices using only measured data from the 37 transects sampled in 2016 (see Appendix S1 – B).

Table 2 Overview of the field data used to assess changes in the functional structure and ecological function of dung beetle communities in different forest habitats along a disturbance gradient, showing the number of transects and year of sampling in undisturbed primary forest (UF), logged primary forest (LF); burned primary forest (BF), logged and burned primary forest (LBF) secondary forest (SF) and non-forest (NF) sites in each of two regions in the eastern Amazon; where FRic is functional richness, FSpe is functional specialisation, and FOr is functional originality.

Analysis	Santarém						Paragominas						Total	Year
	UF	LF	BF	LBF	SF	NF	UF	LF	BF	LBF	SF	NF		
Rarity Index	12	25	7	23	39	53	9	44	-	44	20	80	356	2010
Species richness, abundance and rarity index	12	25	7	23	39	-	-	-	-	-	-	-	106	2010
FRic, FSpe and FOr	12	25	7	23	34	-	-	-	-	-	-	-	101	2010
Dung removal	12	13	5	13	17	-	-	-	-	-	-	-	60	2010
Simulations of extinction scenarios	12	-	-	-	-	-	-	-	-	-	-	-	12	2010
Measurements of functional traits	5	5	5	15	7	-	-	-	-	-	-	-	37*	2016

* 16 of these plots burned during the 2015-16 El Niño, thus changed category compared to 2010.

RESULTS

Across all forest transects (106 in 2010 + 37 in 2016), we collected 31,592 individuals of dung beetles from 96 species. Of those, 26,339 individuals of 90 species were collected in 2010 and 5,253 individuals of 63 species in the subset of transects sampled in 2016. The most common species (*Trichillum* sp. 1) exhibited a Rarity Index (RI) of 0.81 and the rarest species had an RI of 0.15 (*Onthophagus* aff. *clypeatus*), with a mean RI and standard deviation of 0.55 ± 0.13 across all species.

The four primary forest classes (*i.e.* undisturbed, burned, logged, logged-and-burned) had similar dung beetle richness, abundance and mean RI, whereas secondary forests had significantly fewer individuals ($\chi^2 = 11.17$, $p = 0.024$), species ($\chi^2 = 26.42$, $p < 0.001$), and rare species ($\chi^2 = 13.21$, $p = 0.010$, Fig. 2). Neither the abundance and mean RI of logged-and-burned primary forests, nor the mean RI of burned forests differed from secondary forests (Fig. 2a and c).

Dung beetle richness, abundance and mean RI were not influenced by the time since last disturbance in primary forests or by regeneration time in secondary forests (Fig. S1, and Table S1 and S2 in Appendix A1). Dung beetle richness was positively and RI was negatively related to aboveground biomass, which was largely attributed to the lower biomass of secondary forests, which had fewer rare species, and hence the effect was weak ($R^2 = 0.17$ for richness and $R^2 = 0.11$ for RI; Fig. S1, and Table S3 in Appendix A1).

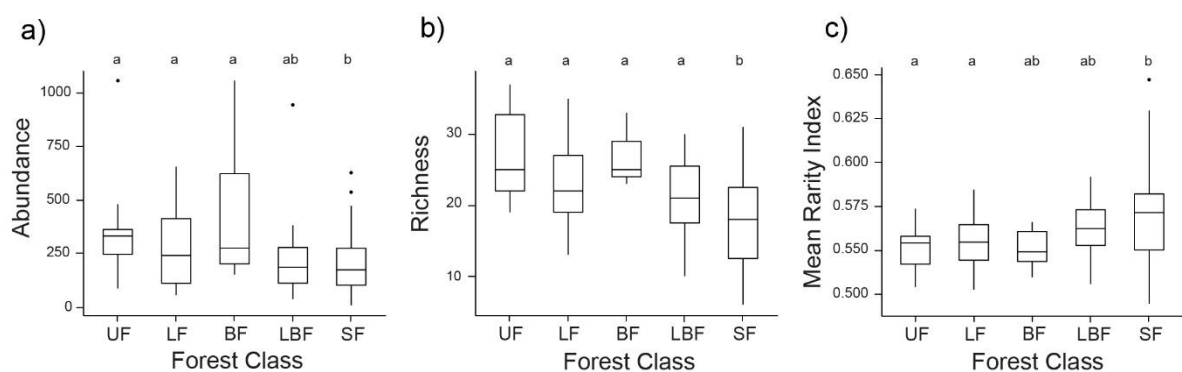


Figure 2 a) Richness, b) abundance and c) mean Rarity Index of dung beetle communities in 106 transects along an Amazon forest disturbance gradient. Different letters represent statistical differences among forest classes at $p < 0.05$; black dots are outliers and lines inside boxplots represent median values. UF is primary undisturbed forest ($n = 12$), LF is primary logged forest ($n = 25$), BF is primary burned forest ($n = 7$), LBF is primary logged-and-burned forest ($n = 23$), and SF is secondary forest ($n = 39$).

There was variation in the functional structure of dung beetle communities across transects: the values of the three functional structure indices ranged between 4.4×10^{-6} and 0.03 for FRic, 0.24 and 0.43 for FSpe, and 0.01 and 0.14 for FOr*i* across all forest transects. Dung beetle functional richness largely mirrored the pattern of taxonomic richness, with similar values in the four primary forest classes, but lower values in secondary forests ($\chi^2 = 10.83$, $p = 0.028$; Fig. 3a), although the FRic of burned primary forests and secondary forests were similar. Neither FSpe nor FOr*i* differed among forest classes (Fig. 3b and c). None of the three indices were influenced by time since last disturbance in primary forests, and only FRic increased with regeneration time in secondary forests (Fig. S2 and Table S1 and S2 in Appendix A1). Only FRic increased with aboveground biomass, but the relationship was very weak (Figure S2 and Table S3 in Appendix A1; $R^2 = 0.07$).

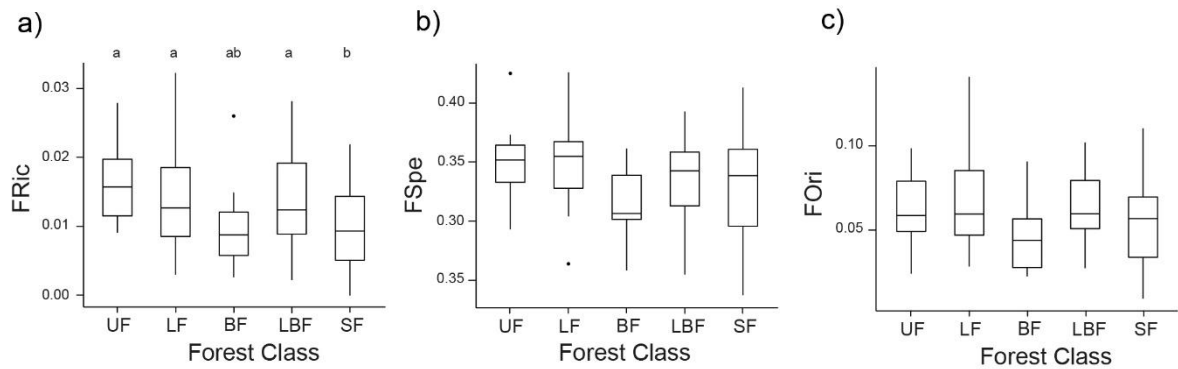


Figure 3 a) Functional richness (FRic), **b)** specialization (FSpe) and **c)** originality (FOr*i*) of dung beetle communities in 106 transects along an Amazon forest disturbance gradient. Different letters represent statistical differences among forest classes at $p < 0.05$; black dots are potential outliers and lines inside boxplots represent median values. UF is primary undisturbed forest ($n = 12$), LF is primary logged forest ($n = 25$), BF is primary burned forest ($n = 7$), LBF is primary logged-and-burned forest ($n = 23$), and SF is secondary forest ($n = 34$).

Dung removal by dung beetles was not influenced by disturbance, as a similar proportion of dung was removed in all forest classes ($\chi^2 = 1.56$, $p = 0.81$, Fig. 4, Table 1). Across all forest types, the proportion of dung removed ranged from 40.8% to 100%, with a mean of 74.2%. Dung removal was not influenced by time since last disturbance, regeneration time or aboveground biomass (Fig. S3 and Table S1, S2 and S3, Appendix A1).

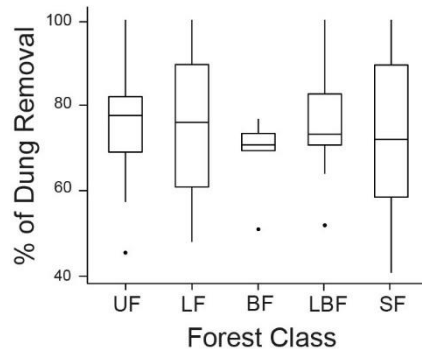


Figure 4 Dung removal in a subset of 54 transects along an Amazonian forest disturbance gradient. Black dots are outliers and lines inside boxplots represent median values. UF is primary undisturbed forest ($n = 12$), LF is primary logged forest ($n = 13$), BF is primary burned forest ($n = 5$), LBF is primary logged-and-burned forest ($n = 13$), and SF is secondary forest ($n = 17$).

At the regional scale, the results of the extinction scenarios were similar, regardless of whether the rarest or most common dung beetle species were lost first. The simulated changes in the values of functional structure indices did not differ from those obtained under a null scenario (random species loss; Fig. 5a, b and c). However, at the local scale a 50% and 60% loss of the rarest dung beetle species resulted in a greater decline in FRic and FSpe, respectively, than the null scenario (Fig. 5d and e). A 50% loss of the rarest species more than halved dung beetle functional richness, and the declines in FRic were also greater with the loss of rare species compared to the null scenario for 60-70% of total local species loss. FOr_i initially increased with a rare species loss of up to 30%, but then declined once 80-90% of the rarest species were lost (Fig. 5f). A 10%, 20% or 40% loss of the most common species resulted in a smaller decline in FRic compared to the null model (Fig. 5d) and FSpe and FOr_i increased relative to the null scenario with common species losses of 30-40% and 10-20%, respectively (Fig. 5e and f). The simulations using measured functional traits only (*i.e.* excluding species for which we estimated traits) produced very similar results, except that there was a greater decrease in FRic compared to the null scenario at the regional scale when rarest species were lost first (30% - 55% species loss; Fig. S6a in Appendix A1 – B). At the local scale the results of the models using only measured traits were also very similar, except that there was no difference in the decrease of FSpe among the three scenarios (Fig. 6e in Appendix A1 – B) and a decrease in FOr_i with a 40% loss of the rarest species.

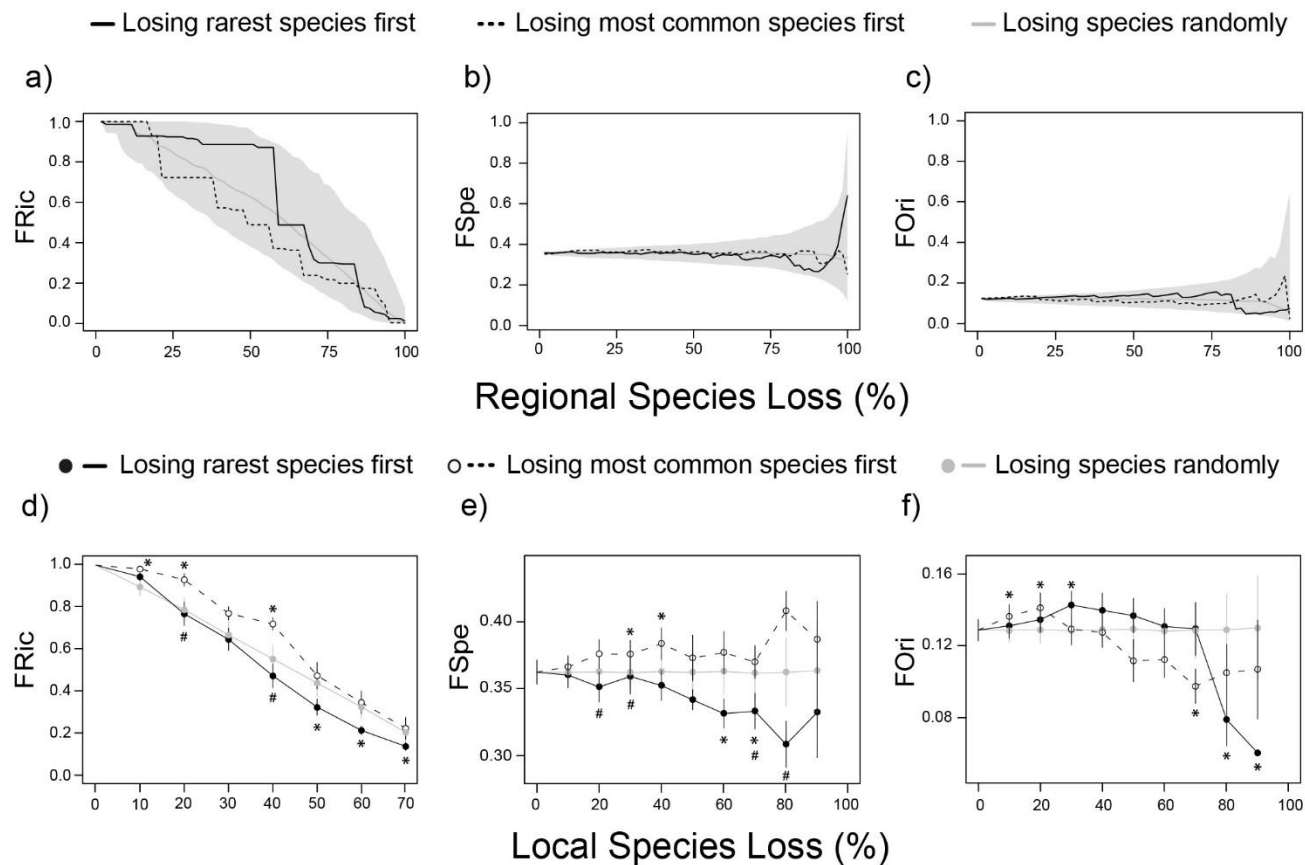


Figure 5 Simulations of regional (a-c) and local (d-e) dung beetle species extinction in undisturbed Brazilian Amazon Forest, showing the effects of species loss on functional richness (FRic, a and d), specialization (FSpe, b and e) and originality (FOri, c and f); scenarios were based on losing the rarest species first (solid black line) and losing the most common species first (dashed black line), compared to a null scenario of random species loss (solid grey line); mean values and confidence intervals based on 1000 random simulations (shading) are shown for undisturbed primary forests for the regional scenarios and error bars (standard error) are given for $n = 12$ transects for the local scenarios; an asterisk denotes a significant difference compared to the null scenario and a hash denotes a significant difference between “rare vs common” scenarios at $p < 0.05$.

DISCUSSION

Functional metrics of dung beetle communities did not differ among any of the forest classes, with the exception of reduced functional richness in secondary forests. Furthermore, although we measured lower dung beetle species richness, abundance and fewer rare species in secondary forests, functional specialisation, functional originality and percentage of dung removal did not differ from primary forests, which suggests that these dung beetle communities have high functional redundancy. Importantly, we found limited evidence that the loss of rare species will disproportionately affect dung beetle community function: our extinction scenarios demonstrate that only a high proportion of rare species loss ($\geq 50\%$) at the local scale will result in an erosion of functional structure. Accordingly, we propose that high functional redundancy at the regional scale mitigates the impact of rare species losses and makes dung beetle communities functionally resistant to primary forest disturbance at local scales.

Functional resistance and resilience to forest disturbance

The level of primary forest disturbance in our study did not substantially affect dung beetle diversity or functional metrics as we detected no change in community structure or function in response to logging, burning, or time since last disturbance. It is possible that high variability among sites made it harder to detect changes, because our disturbance classes were broad and included sites with different levels of disturbance and recovery times. Nonetheless, our extinction scenarios suggest that the extent of species loss in disturbed primary forests was indeed too low to result in a substantial reduction in dung beetle community function: we measured a 21% decline in species richness in the most disturbed primary forests (logged-and-burned), whereas our regional extinction scenarios indicated that functional richness would only decline with a species loss $>50\%$ (Fig. 5). Dung beetle communities are mainly composed of generalist species (Hanski & Cambefort 1991) and previous studies have revealed functional redundancy in dung beetle communities in undisturbed forests (Beiroz *et al.* 2018), fragmented forests (Barragán *et al.* 2011) and across environmental gradients (Nunes *et al.* 2016). Shared traits across generalist species explain the low levels of functional originality (a measure of uniqueness) in our study, which provides further evidence of functional redundancy of dung beetle communities (Mouillot *et al.* 2013b).

In addition to the potential resistance of dung beetle communities, it is also possible that the life-cycle and nesting habits of dung beetles confer high resilience to a certain level of primary forest disturbance. Dung beetles spend most of their life-cycle beneath the soil surface

(both during larval and adult life stages), which could allow them to persist during infrequent or low-intensity disturbances if the impacts belowground are buffered. Furthermore, some species reproduce more than once a year (Scholtz *et al.* 2009), which would allow communities to recover rapidly after forest disturbance. In our study, the shortest time since last disturbance in a primary forest was eight years, and it is therefore conceivable that dung beetle communities had already recovered from the disturbances.

Although our study demonstrates resistance of dung beetle community structure to primary forest disturbance, deforestation can still have a major impact on dung beetle community composition and function (Figs. 1 and 2a). Since secondary forests establish after forest clearance and subsequent abandonment, which usually occur after some form of agricultural use, the properties of soil, vegetation and mammal communities of these areas are highly variable (Parry *et al.* 2007; Berenguer *et al.* 2014; Lennox *et al.* 2018), resulting in major changes in dung beetle communities (Solar *et al.* 2015). Furthermore, in secondary forests, dung beetle communities need to re-establish after the forest starts to regenerate, and it will depend on species arrival (dispersal) and colonization in the new patches of forest, through metacommunity processes. Nonetheless, the similar levels of dung removal, despite lower dung beetle abundance, species richness and functional richness in secondary forests, suggest that less diverse dung beetle communities can maintain functionality in these forests.

Species loss at different scales

Our simulated extinction scenarios provide further evidence of the high functional redundancy of dung beetle communities, but they also demonstrate that the effect of species losses on functional structure is scale-dependent, whereby higher-level processes can at least temporarily offset losses at a local scale. At the regional scale, the functional structure of dung beetle communities did not differ among the three species-loss scenarios – rarest first, most common first, or random loss of species. It is noteworthy that the values of FSpe and FOr hardly declined, even with 75% of species loss in all scenarios (Fig. 5), as this indicates that the regional species pool is functionally redundant and ecological function is highly resistant to species losses. Our results also imply that rare dung beetles are not necessarily highly specialized and consequently do not contribute unique traits or functions to the community; this can be explained by the high nestedness of mammal – dung beetle networks (Raine *et al.* 2018), whereby common species feed in a wide range of mammal dung types whereas rarer species feed in a subset of these dung types. Hence, as there is a relatively low level of specialisation

within the dung beetle community, there is a high probability that other species will share the same functional traits, regardless of whether rare or common species are lost from the community.

Despite the high resistance of community functional structure at the regional scale, we observed a greater erosion of functional structure with the loss of rare species at the local scale, although only at a high percentage of loss ($\geq 50\%$). Functional richness, specialisation and originality declined more than expected based on the random loss scenario when 50%, 60% or 80% of the rarest species were lost, respectively. Because the rarest species have low local abundance, as well as limited geographical range and habitat breadth, they are more vulnerable to extinctions (Davies *et al.* 2004; Harnik *et al.* 2012) and therefore our scenario predicting that rare species will be lost first is likely to be realistic. The 50% rare species loss threshold at a local scale also explains why we found no significant effect of primary forest disturbance on dung beetle community structure and function, as the overall decline in species richness relative to undisturbed forests was generally $<20\%$. By contrast, dung beetle species richness in secondary forests was 16-68% lower than in undisturbed primary forests, which likely contributed to the lower values of functional richness in secondary forest sites. Indeed, for the range of species loss we observed in our field data in secondary forests, the random extinction scenario predicted a decline of 11-79% in FRic and the rare species loss scenario predicted a decline of 6-87% , which is comparable to the measured decline in FRic (20-99%, Fig. 5d).

Although we found no evidence for substantial loss of species in our primary disturbed forests, more intense disturbance, frequent logging (França *et al.* 2017), fires (de Andrade *et al.* 2014) and other types of forest degradation such as hunting (Nichols *et al.* 2013), can exacerbate species loss and compositional changes in dung beetle communities. Furthermore, dung beetle community structure and function could decline rapidly with minor primary forest disturbance in fragmented landscapes with an eroded regional species pool. Under these scenarios, a local loss of 50% of rare species is plausible, which would lead to the erosion of functional structure and could jeopardize ecological functions of dung beetle communities.

Implications for conservation

Taken together, our results from field data and simulations of extinction scenarios suggest that local resistance of dung beetles to forest disturbance is supported by the functional redundancy of the regional species pool. Species dispersal can stabilize ecosystem functioning at larger spatial scales (Loreau *et al.* 2003; Pasari *et al.* 2013; Wang & Loreau 2014) and dung

beetles have a great dispersal capability (da Silva & Hernández 2015). Accordingly, communities from disturbed forests could be supplemented by immigration from nearby undisturbed forests through metacommunity dynamics, as has been shown after fires in open habitats (Brotons *et al.* 2005; Nunes *et al.* 2019). Here, the resistance of local dung beetle communities would be highly dependent on metacommunity processes and the maintenance of species and trait diversity in undisturbed forests at the regional scale. Maintaining the regional pool of species and traits and assuring that there is dispersal among local communities (i.e. ensuring the preservation of metacommunities), will increase the so-called ‘functional insurance’ at both local and regional scales (Yachi & Loreau 1999; Wang & Loreau 2014).

Although we found no evidence that primary forest disturbance affects dung beetle community function, our study is clearly not an incitement for indiscriminate logging, fires, or other within-forest disturbances. It is important to highlight that our study was conducted in forests that were subject to one or only few disturbances and that our study is based on a space-for-time approach, which can underestimate disturbance effects compared to a before-and-after approach (França *et al.* 2016). In conclusion, our study indicates that the local resistance of dung beetle communities to forest disturbance is supported by the functional redundancy of the regional species pool and therefore the conservation of an undisturbed forest matrix at the landscape scale could be crucial for maintaining the species, trait and functional diversity of regional and local biological communities.

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SUPPORTING INFORMATION

Appendix A1 - Supplementary results

Appendix A2 – Dung beetle species and their functional traits

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APPENDIX A1 – Supplementary results

A) Results of dung beetle community metrics in relation to aboveground biomass, time since last disturbance (primary forests) and regeneration time (secondary forests).

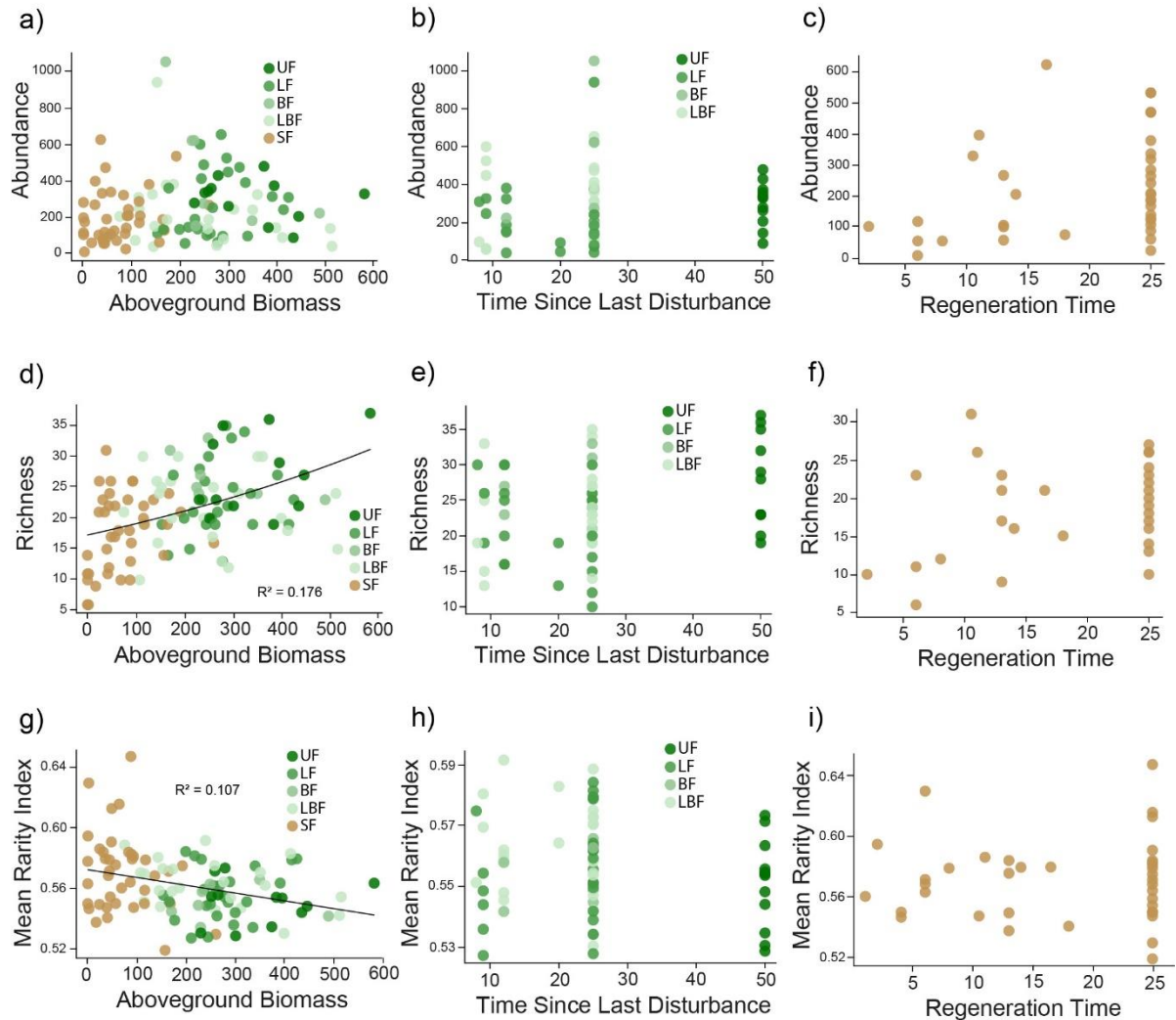


Figure S1 Abundance, richness and mean rarity index of dung beetle communities in relation to aboveground biomass (a, d and g), time since last disturbance in primary forests (b, e and h) and regeneration time in secondary forests (c, f and i) in the Brazilian Amazon. The aboveground biomass is the biomass of trees with more than 10 cm of diameter at 1.3 m height (Mg ha^{-1}). UF = primary undisturbed forest, LF = primary logged forest, BF = primary burned forest, LBF = primary logged and burned forest, SF = secondary forest. Number of local communities: UF = 12, BF = 7, LF = 25, LBF = 23, SF = 34.

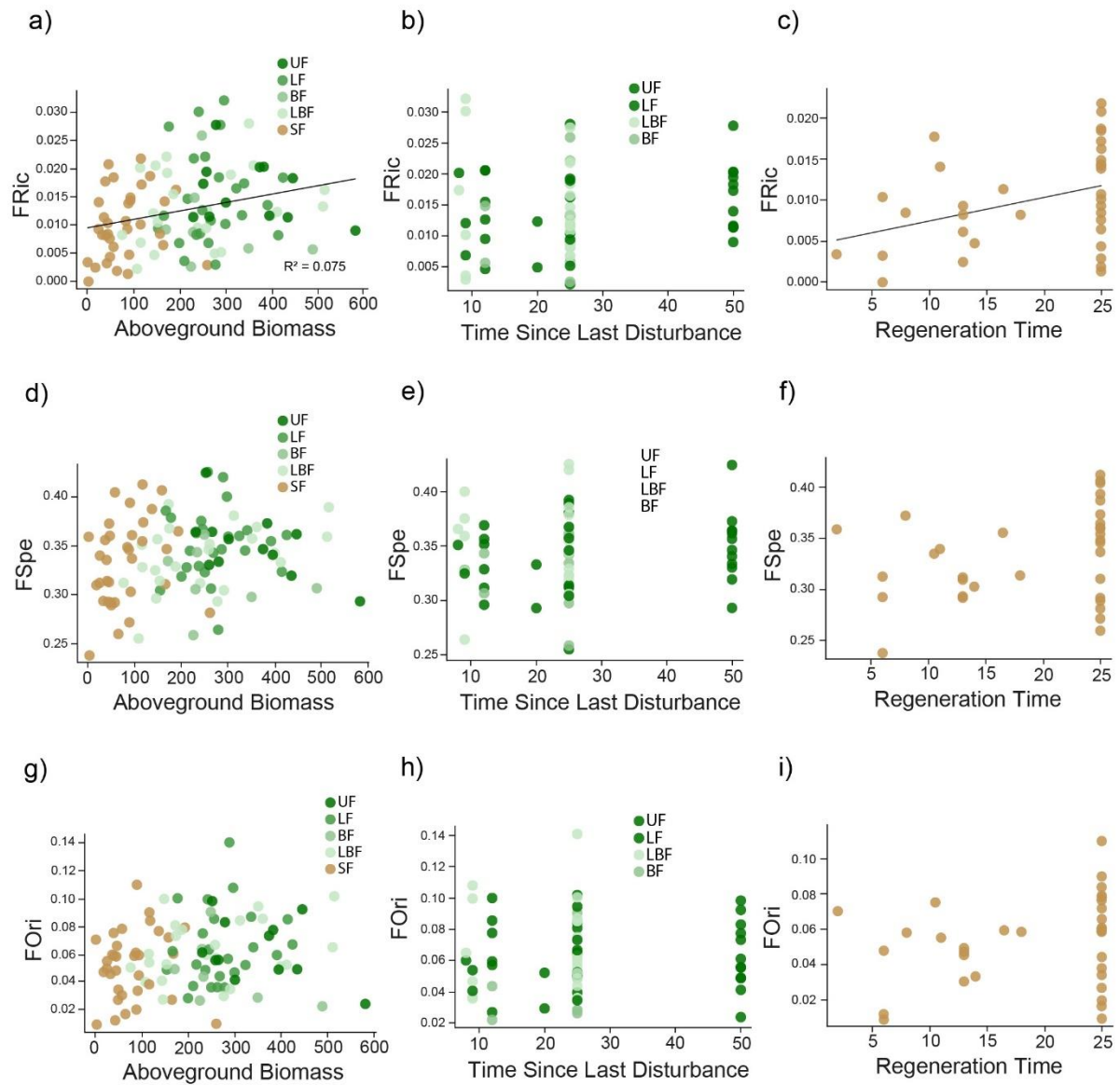


Figure S2 Functional richness (FRic), specialization (FSpE) and originality (FOri) of dung beetle communities in relation to aboveground biomass (a, d and g), time since last disturbance in primary forests (b, e and h) and regeneration time in secondary forests (c, f and i) in the Brazilian Amazon. The aboveground biomass is the biomass of trees with more than 10 cm of diameter at 1.3 m height (Mg ha^{-1}). UF = primary undisturbed forest, LF = primary logged forest, BF = primary burned forest, LBF = primary logged and burned forest, SF = secondary forest. Number of local communities: UF = 12, BF = 7, LF = 25, LBF = 23, SF = 34.

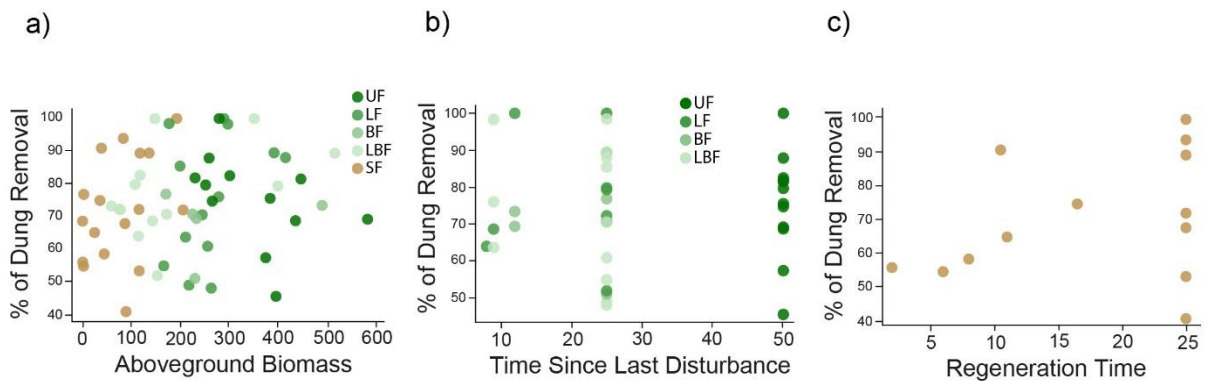


Figure S3 Dung beetle ecological function (dung removal) in relation to aboveground biomass (a), time since last disturbance in primary forests (b) and regeneration time in secondary forests (c) in the Brazilian Amazon. The aboveground biomass is the biomass of trees with more than 10 cm of diameter at 1.3 m height (Mg ha^{-1}). UF = primary undisturbed forest, LF = primary logged forest, BF = primary burned forest, LBF = primary logged and burned forest, SF = secondary forest. Number of local communities: UF = 12, BF = 5, LF = 13, LBF = 10, SF = 14.

Table S1 Results of mixed effect models (GLMMs and LMMs) with each dung beetle response variable in relation to time since last disturbance in primary Amazonian forests (undisturbed, logged, burned, and logged and burned). For richness and abundance we constructed GLMMs with negative binomial distribution of errors. For Rarity Index, FRic, FSpe, FOr and dung beetle ecological function (% of dung removal) we constructed LMMs. D.F.= Degrees of freedom used; Res. D.F.= Residual degrees of freedom; χ^2 = values of Chi-Square tests.

Response Variable	D.F.	Res. D.F.	χ^2	P-value
Richness	4	67	1.88	0.169
Abundance	4	67	0.78	0.375
Rarity Index	4	67	0.22	0.637
FRic	4	63	0.68	0.406
FSpe	4	63	1.14	0.283
FOr	4	63	0.32	0.570
Ecological Function	4	46	7e-04	0.979

Table S2 Results of mixed effect models (GLMMs and LMMs) with each dung beetle response variable in relation to regeneration time in secondary Amazonian forests. For richness and abundance we constructed GLMMs with negative binomial distribution of errors. For Rarity Index, FRic, FSpe, FOri and dung beetle ecological function (% of dung removal) we constructed LMMs. D.F.= Degrees of freedom used; Res. D.F.= Residual degrees of freedom; χ^2 = values of Chi-Square tests. P-value = bold values are significant.

Response Variable	D.F.	Res. D.F.	χ^2	P-value
Richness	4	30	3.60	0.057
Abundance	4	30	2.44	0.117
Rarity Index	4	30	0.001	0.969
FRic	4	30	5.41	0.019
FSpe	4	30	2.32	0.126
FOri	4	30	1.53	0.215
Ecological Function	4	10	1.75	0.185

Table S3 Results of mixed effect models (GLMMs and LMMs) with each dung beetle response variable in relation to aboveground biomass in Amazonian forests. For richness and abundance we constructed GLMMs with negative binomial distribution of errors. For Rarity Index, FRic, FSpe, FOri and dung beetle ecological function (% of dung removal) we constructed LMMs. D.F.= Degrees of freedom used; Res. D.F.= Residual degrees of freedom; χ^2 = values of Chi-Square tests. P-value = bold values are significant.

Response Variable	D.F.	Res. D.F.	χ^2	P-value
Richness	4	102	18.90	< 0.001
Abundance	4	102	1.72	0.188
Rarity Index	4	102	10.91	< 0.001
FRic	4	97	7.12	0.007
FSpe	4	97	3.53	0.060
FOri	4	97	3.80	0.0509
Ecological Function	4	56	1.68	0.194

B) Results of dung beetle functional structure metrics responses to Amazon forest disturbance, using only data with measured functional traits

In this section, we present the results of functional responses to forest disturbance and to simulations of species loss, however using data from the subset of transects, collected in 2016 in Santarém. Here, we used only data with measured functional traits and did not estimate any trait as we presented in the article. The subset has fewer transects (22 compared to 106 – RAS) and one forest class less than the complete dataset (primary burned forest).

The responses of dung beetle functional structure to forest disturbance using only measured traits followed the same pattern when we considered estimated functional traits to run the analyses: no influence of forest disturbance on functional indices (Fig. S4 and Table S4). The only difference was that when using the 106 transects we found that functional richness (FRic) was lower in secondary forests compared to the other classes (Fig. 2 in the article) while here it FRic was equal for all four forest classes.

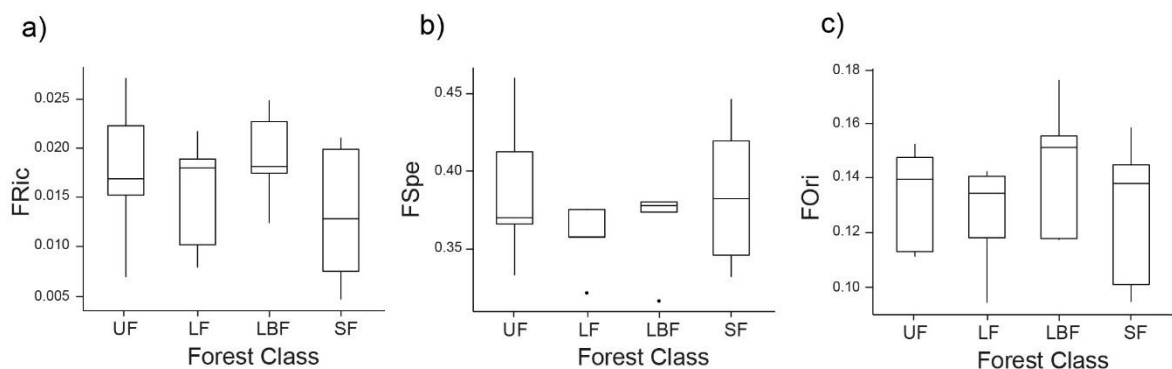


Figure S5 a) Functional richness (FRic), b) specialization (FSpe) and c) originality (FOri) of dung beetle communities in transects along an Amazon forest disturbance gradient. Different letters represent statistical differences among forest classes at $p < 0.05$; black dots are outliers and lines inside boxplots represent median values, where UF is primary undisturbed forest ($n = 5$), LF is primary logged forest ($n = 5$), BF is primary burned forest ($n = 5$), LBF is primary logged-and-burned forest ($n = 5$), and SF is secondary forest ($n = 7$).

The simulations here were made using five undisturbed forest transects, while in the article it was 12. Similar to what was showed using estimated traits and for the 12 transects, at the regional scale the pattern was of no difference between the scenarios losing rarest, most common or random species (Fig. S6 and Fig. 4). The only difference was that, here, FRic presented a greater erosion when losing rarest species first than expected by a random loss at 30% to 60% (Fig. S6 a). At the local scale, the pattern of higher loss of FRic when losing 50%

of rarest species than in a random loss of species was also present here (Fig. S6 d and Fig. 4 d). On the other hand, for functional specialisation the difference between the random scenario and the rare species loss scenario disappeared (FSpe; Fig. S6 e and Fig. 4 e). Another difference was that functional originality (FOri) was lower in the scenario losing rare species first with 40% of species loss, which was verified when using estimated traits with 12 transects only after 70% of species loss (Fig. S6 f and Fig. 4 f).

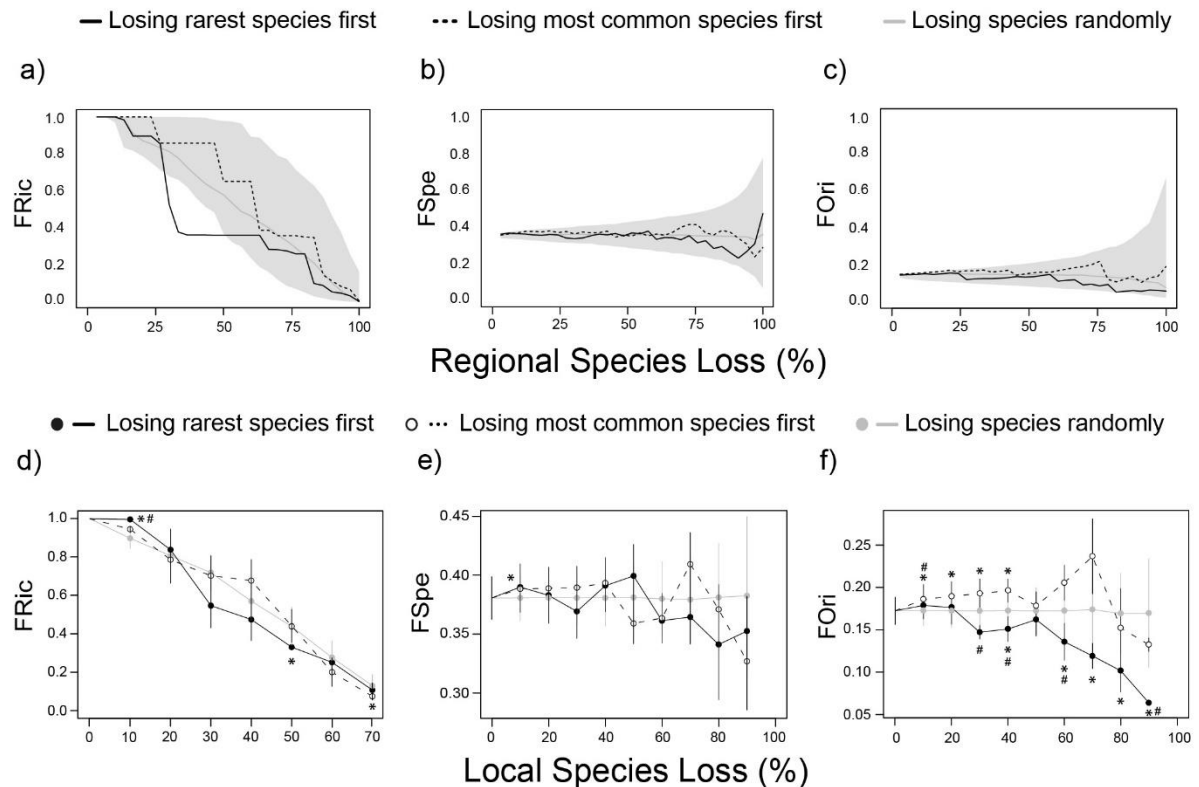


Figure S6 Simulations of regional (a-c) and local (d-e) dung beetle species extinction in undisturbed Brazilian Amazon Forest, showing the effects of species loss on functional richness (FRic, a and d), specialization (FSpe, b and e) and originality (FOri, c and f); scenarios were based on losing the rarest species first (solid black line) and losing the most common species first (dashed black line), compared to a null scenario of random species loss (solid grey line); mean values and confidence intervals based on 1000 random simulations (shading) are shown for undisturbed primary forests for the regional scenarios and error bars (standard error) are given for $n =$ five transects for the local scenarios; an asterisk denotes a significant difference compared to the null scenario and a hash denotes a significant difference between “rare vs common” scenarios at $p < 0.05$.

Table S4 Results of linear mixed effect models (LMMs) with each dung beetle functional index response to forest disturbance in Brazilian Amazon. These results are from the subset of transects using only measured traits (22 transects). D.F.= Degrees of freedom used; Res. D.F.= Residual degrees of freedom; χ^2 = values of Chi-Square tests.

Response Variable	D.F.	Res. D.F.	χ^2	P-value
FRic	6	16	3.08	0.378
FSpe	6	16	2.63	0.451
FOri	6	16	2.28	0.514

APPENDIX A2 – Dung beetle species and their functional traits

Table A1 Dung beetle species and their functional traits. Species for which we had to estimate traits have the row coloured in grey. BM: body mass; NA: not available.

Species names	Trait category	Guild	Diet	Body mass (g)	Front leg/BM	Pronotum/BM	Back/First leg
<i>Ateuchus</i> aff. <i>candezei</i>	Measured	Paracoprid	Coprophagous	0.0234	126	179.2683	1.775701
<i>Ateuchus</i> aff. <i>murrayi</i>	Measured	Paracoprid	Coprophagous	0.0081	232.3244	334.5305	1.357736
<i>Ateuchus</i> aff. <i>romani</i>	Measured	Paracoprid	Coprophagous	0.0031	329.0323	593.5484	1.294118
<i>Ateuchus</i> aff. <i>striatulus</i>	Measured	Paracoprid	Coprophagous	0.016	143.0952	217.3333	1.245766
<i>Ateuchus</i> <i>connexus</i>	Measured	Paracoprid	Coprophagous	0.025	131.3363	172.5578	1.309486
<i>Ateuchus</i> sp.1	Measured	Paracoprid	Coprophagous	0.0115	189.1691	269.5048	1.304613
<i>Ateuchus</i> sp.2	Estimated	Paracoprid	Coprophagous	0.01793	137.2918	200.8422	1.474813
<i>Canthidium</i> (<i>Canthidium</i>) aff. <i>deyrollei</i>	Measured	Paracoprid	Coprophagous	0.011	268.1818	314.5156	1.673974
<i>Canthidium</i> (<i>Canthidium</i>) aff. <i>gerstaeckeri</i>	Measured	Paracoprid	Coprophagous	0.017	207.2539	251.6484	1.674051
<i>Canthidium</i> (<i>Canthidium</i>) aff. <i>lentum</i>	Measured	Paracoprid	Coprophagous	0.0173	212.5828	254.3353	1.561743
<i>Canthidium</i> (<i>Canthidium</i>) <i>barbacenicum</i>	Estimated	Paracoprid	Coprophagous	0.00795	677.4101	815.0146	1.492052
<i>Canthidium</i> (<i>Canthidium</i>) <i>multipunctatum</i>	Estimated	Paracoprid	Coprophagous	0.005	1034.273	1249.165	1.490804
<i>Canthidium</i> (<i>Canthidium</i>) sp.1	Measured	Paracoprid	Coprophagous	0.0171	185.0649	221.5054	1.596045
<i>Canthidium</i> (<i>Canthidium</i>) sp.2	Measured	Paracoprid	Coprophagous	0.005	654	834	1.306254
<i>Canthidium</i> (<i>Canthidium</i>) sp.3	Estimated	Paracoprid	Coprophagous	0.0049	1053.478	1272.582	1.490748
<i>Canthidium</i> (<i>Canthidium</i>) sp.4	Measured	Paracoprid	Coprophagous	0.0052	390.3846	576.9231	1.539568
<i>Canthidium</i> (<i>Canthidium</i>) sp.7	Measured	Paracoprid	Coprophagous	0.011	231.8182	280	1.408072
<i>Canthidium</i> (<i>Eucanthidium</i>) aff. <i>ardens</i>	Measured	Paracoprid	Coprophagous	0.0068	239.2857	382.8947	1.380117
<i>Canthidium</i> (<i>Eucanthidium</i>) aff. <i>collare</i>	Measured	Paracoprid	Coprophagous	0.0022	609.0909	1004.348	1.360656
<i>Canthidium</i> (<i>Eucanthidium</i>) aff. <i>funebre</i>	Measured	Paracoprid	Coprophagous	0.019	173.1579	226.3158	1.282675
<i>Canthidium</i> (<i>Eucanthidium</i>) sp.5	Measured	Paracoprid	Coprophagous	0.0016	706.25	1262.5	1.320292
<i>Canthidium</i> (<i>Eucanthidium</i>) sp.6	Estimated	Paracoprid	Coprophagous	0.00682	432.668	686.4617	1.352958

<i>Canthidium (Eucanthidium) sp.8</i>	Measured	Paracoprid	Coprophagous	0.0045	435.5556	556.25	1.421053
<i>Canthidium humerale</i>	Estimated	Paracoprid	Coprophagous	0.0574	109.719	130.2253	1.496421
<i>Canthon aff. acutus</i>	Estimated	Telecoprid	Coprophagous	0.0116	242.2504	316.9156	1.87845
<i>Canthon aff. angustatus</i>	Estimated	Telecoprid	Coprophagous	0.01805	171.6417	217.0173	1.836147
<i>Canthon aff. chalybaeus</i>	Measured	Telecoprid	Generalist	0.0177	209.322	247.4576	1.677416
<i>Canthon aff. heyrovskyi</i>	Estimated	Telecoprid	Coprophagous	0.0065	397.2864	536.263	1.918579
<i>Canthon aff. quadrimaculatus</i>	Measured	Telecoprid	Coprophagous	0.009	295.5556	366	1.978541
<i>Canthon aff. sericatus</i>	Measured	Telecoprid	Coprophagous	0.00175	1461	2043	1.831809
<i>Canthon aff. simulans</i>	Measured	Telecoprid	Coprophagous	0.005	391.25	589.5833	1.856008
<i>Canthon fulgidus</i>	Measured	Telecoprid	Coprophagous	0.154	60.29414	55.19176	1.516696
<i>Canthon histrio</i>	Measured	Telecoprid	Coprophagous	0.057	89.35361	102.9825	1.802521
<i>Canthon lituratus</i>	Estimated	Telecoprid	Coprophagous	0.005465	464.0701	630.7496	1.927603
<i>Canthon obscuriellus</i>	Estimated	Telecoprid	Coprophagous	0.00545	465.2244	632.3828	1.927736
<i>Canthon proseni</i>	Measured	Telecoprid	Coprophagous	0.1166	60.0299	66.2988	1.617527
<i>Canthon semiopacus</i>	Measured	Telecoprid	Coprophagous	0.04255	98.95159	126.2549	1.868507
<i>Canthonella sp.1</i>	NA	Telecoprid	Coprophagous	NA	NA	NA	NA
<i>Canthonella sp.2</i>	NA	Telecoprid	Coprophagous	NA	NA	NA	NA
<i>Coprophanaeus degallieri</i>	Measured	Paracoprid	Necrophagous	0.328	24.83115	33.05144	1.456712
<i>Coprophanaeus jasius</i>	Measured	Paracoprid	Necrophagous	0.781	15.9431	20.48656	1.409877
<i>Coprophanaeus lancifer</i>	Measured	Paracoprid	Necrophagous	2.696	6.947075	9.468753	1.292929
<i>Cryptocanthon peckorum</i>	Estimated	Telecoprid	Coprophagous	0.00115	2037.786	2857.268	1.956197
<i>Deltochilum amazonicum</i>	Measured	Telecoprid	Necrophagous	0.5448	24.81305	24.44934	1.862012
<i>Deltochilum carinatum</i>	Measured	Telecoprid	Necrophagous	0.341	33.81317	32.15408	1.806856
<i>Deltochilum enceladus</i>	Measured	Telecoprid	Coprophagous	1.219	13.6402	14.087	1.951103
<i>Deltochilum orbiculare</i>	Measured	Telecoprid	Coprophagous	0.56245	22.74514	25.08124	2.108332
<i>Deltochilum sp.1</i>	Measured	Telecoprid	Generalist	0.0765	77.06487	93.26303	1.77659
<i>Deltochilum sp.2</i>	Measured	Telecoprid	Generalist	0.0636	77.49908	89.65053	1.836539
<i>Diabroctis mimas</i>	Estimated	Paracoprid	Coprophagous	0.7583	14.1107	18.16871	1.400227

<i>Dichotomius</i> aff. <i>fortestriatus</i>	Measured	Paracoprid	Coprophagous	0.103	57.5	71.18812	1.690544
<i>Dichotomius</i> aff. <i>lucasi</i>	Measured	Paracoprid	Generalist	0.09425	61.1903	74.45769	1.656479
<i>Dichotomius boreus</i>	Literature/estimated	Paracoprid	Coprophagous	0.847	13.87799	10.42559	1.31338
<i>Dichotomius carinatus</i>	Measured	Paracoprid	Coprophagous	0.44	23.62944	30.40909	1.369877
<i>Dichotomius imitator</i>	Measured	Paracoprid	Coprophagous	0.2421	38.6366	44.41293	1.489601
<i>Dichotomius mamillatus</i>	Estimated	Paracoprid	Coprophagous	0.34465	31.64974	24.30769	1.301698
<i>Dichotomius melzeri</i>	Measured	Paracoprid	Coprophagous	0.49365	21.3818	27.47346	1.351733
<i>Dichotomius nisus</i>	Measured	Paracoprid	Coprophagous	0.414	20.89372	29.7343	1.759538
<i>Dichotomius robustus</i>	Measured	Paracoprid	Coprophagous	0.086	78.13953	101.7442	1.494048
<i>Dichotomius worontzowi</i>	Measured	Paracoprid	Coprophagous	0.107	71.02804	88.28571	1.405204
<i>Eurysternus arnaudi</i>	Measured	Endocoprid	Coprophagous	0.03375	116.6045	125.1585	1.866768
<i>Eurysternus atrosericus</i>	Measured	Endocoprid	Coprophagous	0.0109	230.9167	243.4314	2.562089
<i>Eurysternus balachowskyi</i>	Measured	Endocoprid	Coprophagous	0.0358	105.8824	120.1117	2.029777
<i>Eurysternus caribaeus</i>	Measured	Endocoprid	Coprophagous	0.1045	55.66814	60.37901	2.002651
<i>Eurysternus cayannensis</i>	Measured	Endocoprid	Coprophagous	0.0349	124.3553	124.4444	1.931298
<i>Eurysternus cyclops</i>	Measured	Endocoprid	Coprophagous	0.153	54.20185	63.48827	1.906721
<i>Eurysternus haematicollis</i>	Measured	Endocoprid	Generalist	0.214	30.07851	37.08367	1.898865
<i>Eurysternus howdeni</i>	Literature/estimated	Endocoprid	Coprophagous	0.293	29.53349	34.37227	1.866692
<i>Eurysternus hypocrita</i>	Literature/estimated	Endocoprid	Coprophagous	0.178	46.71716	54.26965	1.871491
<i>Eurysternus plebejus</i>	Measured	Endocoprid	Coprophagous	0.013	206.6225	261.5385	1.913534
<i>Eurysternus vastiorum</i>	Estimated	Endocoprid	Coprophagous	0.0103	619.9054	709.668	1.908671
<i>Eurysternus wittmerorum</i>	Measured	Endocoprid	Coprophagous	0.0291	136.9168	148.1034	1.976413
<i>Eutrichillum</i> sp.1	NA	Endocoprid	Coprophagous	NA	NA	NA	NA
<i>Ontherus appendiculatus</i>	Estimated	Paracoprid	Coprophagous	0.03885	226.5582	286.9451	1.49538
<i>Ontherus carinifrons</i>	Measured	Paracoprid	Coprophagous	0.0394	122.8426	147.2973	1.318982
<i>Onthophagus</i> aff. <i>clypeatus</i>	Literature/estimated	Paracoprid	Coprophagous	0.017	145.0821	205.7674	1.418336
<i>Onthophagus</i> aff. <i>hirculus</i>	Measured	Paracoprid	Coprophagous	0.016	100.5556	168.0672	1.517819
<i>Onthophagus</i> aff. <i>onorei</i>	Measured	Paracoprid	Coprophagous	0.008	280.8989	364.1791	1.377193

<i>Onthophagus onthochromus</i>	Estimated	Paracoprid	Coprophagous	0.052	95.32988	135.7119	1.494082
<i>Onthophagus</i> sp.1	Estimated	Paracoprid	Coprophagous	0.0605	91.93475	130.9313	1.50224
<i>Oxysternon macleayi</i>	Measured	Paracoprid	Coprophagous	0.25905	31.34113	44.16083	1.39788
<i>Oxysternon silenus</i>	Measured	Paracoprid	Coprophagous	0.20055	40.13755	47.63361	1.406447
<i>Phanaeus alvarengai</i>	Estimated	Paracoprid	Coprophagous	0.0872	90.95398	118.7437	1.445567
<i>Pseudocanthon</i> aff. <i>xanthurus</i>	Measured	Telecoprid	Generalist	0.003	566.6667	836.6667	1.570588
<i>Scybalocanthon</i> sp.1	Measured	Telecoprid	Coprophagous	0.0317	121.8519	154.1796	2.120743
<i>Sylvicanthon</i> sp.1	Measured	Telecoprid	Coprophagous	0.0195	238.3889	311.3889	1.878506
<i>Trichillum externepunctatum</i>	Estimated	Endocoprid	Coprophagous	0.0028	519.9502	733.6136	1.313696
<i>Uroxys</i> sp.1	Measured	Paracoprid	Coprophagous	0.0146	185.5769	240.411	1.100719
<i>Uroxys</i> sp.2	Estimated	Paracoprid	Coprophagous	0.03615	105.9252	150.6311	1.471988
<i>Uroxys</i> sp.3	Estimated	Paracoprid	Coprophagous	0.0274	117.0258	166.2616	1.453132

ARTIGO 2**Aboveground structure, biodiversity and soil: who is taking a bigger hit from tropical forest destruction?**

Este artigo está formatado nas normas do periódico *Proceedings of the National Academy of Sciences – PNAS* (Versão preliminar).

Aboveground structure, biodiversity and soil: who is taking a bigger hit from tropical forest destruction?

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ABSTRACT

Human activities are imposing significant changes upon tropical forests worldwide. The future of tropical forests depends on three major classes of disturbance: deforestation, degradation and regeneration of secondary forests. Here, we investigated the effects of these disturbances on three ecosystem components: biodiversity, aboveground structure and soil. We systematically collected data of seven biological groups, nine aboveground structure variables and nine soil variables in 317 sites in Brazilian Amazon to examine which was the most affected ecosystem component in response to tropical forest disturbance. We found that biodiversity was the most affected ecosystem component in response to all disturbances, followed by aboveground structure and the soil was the least affected. Forest conversion was the disturbance type with higher effects on all ecosystem components. Forest degradation did not affect aboveground structure and soil as a whole, but impacted biodiversity. Our analyses showed that even established secondary forests are not substitutes for primary forests, as they exhibited significant changes in all three ecosystem components. We used our results to discuss why tropical forests are still being destroyed despite the huge impact on biodiversity. Activities that are important direct drivers of deforestation and forest degradation do not rely on biodiversity to their development. To achieve global reduction in tropical forest destruction, we need to target both direct and indirect drivers of disturbance and include biodiversity together with carbon in tropical forest conservation initiatives.

Keywords: Agriculture, Carbon, Degradation, Disturbance, Fires, Logging, Pastures, Regeneration, Secondary forests

SIGNIFICANCE STATEMENT

Tropical forests are home of two thirds of all species and stores more carbon than any other biome on Earth. Nevertheless, they are subjected to impacts of anthropogenic disturbances, such as conversion to agricultural lands and degradation by logging and fire, which can impair the ecosystem services tropical forests provide. We used an extensive dataset of tropical forest disturbances collected in the Brazilian Amazon and found that biodiversity is the most affected ecosystem component, followed by aboveground vegetation structure and soil was the least affected. We discuss why tropical forests are still being destroyed despite the huge impact on biodiversity.

INTRODUCTION

Although human beings have interacted with tropical forests for around 60,000 years, it was only more recently that human activities have started to impose significant changes upon these ecosystems (1). Since the start of the Anthropocene, three major classes of anthropogenic disturbance have had particularly profound consequences for tropical forests: i) conversion to non-forested land-uses (mainly farmland or pastures), ii) degradation of remaining forests through selective logging, fires, hunting, and fragmentation and iii) regeneration of secondary forests, *i.e.*, forests regrowing in previously deforested areas (2). In the last 40 years alone, the anthropogenic use of tropical forests led to the conversion of more than 100 million ha worldwide (3, 4). Fires degraded 54 million ha of tropical forests per year in the 1990s (5), around 20% of tropical forests are affected by selective logging (6), and secondary forests now dominate in many regions, such as Costa Rica (7) and the Brazilian Atlantic forest (8). Despite the widespread destruction of tropical forests, these ecosystems still harbour half of all terrestrial biodiversity (9), account for one third of productivity and evapotranspiration (10), and store c. 230 Pg of carbon (11). In addition, 1.5 billion people directly rely on ecosystem services provided by tropical forests, such as food, medicines and water supply (2).

The importance of preserving the ecosystem services provided by tropical forests, and the extent of the threats to this biome, have led to the publication of numerous studies focusing on the consequences of anthropogenic impacts in tropical forests. Many studies have assessed the impacts of the main disturbances affecting tropical forests, but they have often assessed changes in individual components of ecosystems (biodiversity, aboveground structure and soil properties) separately, *e.g.* the impacts of forest conversion on soil carbon stocks (12), forest degradation on biodiversity (13), or forest regeneration on carbon stocks (14). We still need a concerted assessment of tropical forest structure, function and biodiversity to ascertain which of these ecosystem components is the most vulnerable to disturbance. A lot of attention is given to aboveground structure, as it plays an important role in the global carbon cycle and is directly relevant for global initiatives such as REDD+ (15). However, there is some concern that focussing on carbon sequestration (or aboveground structure) does not help conserve the ecosystem as a whole (16). Since the future of tropical forests is largely determined by direct anthropogenic disturbances (1), but also on the intervention policies created to preserve ecosystem services, *e.g.* (17), there is an urgent need to determine the vulnerability of each ecosystem component and quantify their concerted changes in response to tropical forest disturbance and destruction. Filling these knowledge gaps could improve existing policies and

inspire new initiatives. Hence, it is critical to evaluate the impacts of anthropogenic activities across multiple tropical forest ecosystem components simultaneously.

Scientists have mainly synthesised the effects of anthropogenic disturbances on tropical forests using meta-analyses (18); for example, in a global meta-analysis of the effects of forest degradation on biodiversity (19), of forest regeneration on biodiversity and aboveground structure (20) and of land-use change on soil carbon stocks (12). However, previous research has focused either on only one kind of disturbance (21), or only one ecosystem component (22). In addition, although it is possible to identify publication biases in such analyses, there remain numerous data gaps, which limit the conclusions we can draw from the synthesis of published research (18). To address this, we present a unique study comparing tropical forest sites across different disturbance types and covering multiple aspects of three main ecosystem components. Our study incorporates detailed data from the same sites and collected within a discrete period of time to assess the concerted response of tropical forest ecosystems to multiple disturbances.

We investigated the effects of six disturbance types on a range of variables classified within three ecosystem components of tropical forests: biodiversity, aboveground structure, and soil properties. We assessed the impacts of i) forest conversion to pastures and ii) agriculture, iii) degradation with selective logging and iv) logging + burning, as well as regeneration in v) young and vi) established secondary forests using data for 39 variables collected systematically from 317 sites in Brazilian Amazon. Specifically, our study aimed to:

- 1) Determine which component of tropical forest ecosystems (biodiversity, aboveground structure, or soil) is more vulnerable to anthropogenic disturbance.
- 2) Compare the responses of distinct aspects of each ecosystem component (i.e. groups of organisms, structural characteristics and soil properties) to each disturbance type.

We use our results to demonstrate the full extent of human activities on tropical forest ecosystems and discuss the policy implications for the near future.

METHODS

Study sites

We collected data from 317 plots located in two regions of the eastern Amazon, in Brazil: Santarém, Belterra and Mojuí-dos-Campos municipalities (*c.* 2.7 million ha; STM hereafter) and Paragominas municipality (1.9 million ha; PGM hereafter). We separated both

regions in third/fourth order drainage catchments (*c.* 5000 ha) and then selected 18 catchments in each region, each with an anthropogenic disturbance gradient. In each catchment, we installed between eight and 12 transects measuring 300-m \times 10-m (our sampling plots), separated by at least 1.5 km (Fig. 1a). All the data were obtained from the same sampling plots, during 2010 and 2011. For more details on the sites and sampling design, see (23).

Across the 317 transects, there were six distinct disturbance types besides undisturbed primary forests (12 in STM and 9 in PGM): primary logged (25 in STM and 43 in PGM) and primary logged + burned forests (23 in STM and 42 in PGM), established secondary (20 in STM and 5 in PGM) and young secondary forests (18 in STM and 15 in PGM) regenerating from previously deforested land, pastures (23 in STM and 49 in PGM), and mechanised agriculture (16 in STM and 10 in PGM). The disturbed forests were classified using field assessments and time series of satellite images (between 1988 and 2010). Secondary forest ages were calculated using time series of satellite images and we considered forests aged > 20 years as established secondary forest, and those aged 1-20 years as young.

Data collection

- Aboveground structure

Aboveground structure variables were determined in a 0.25-ha plot (250-m \times 10-m) within each transect (Fig. 1b). To calculate the basal area and biomass of large trees and lianas, we measured all trees with a diameter at breast height (DBH) ≥ 10 cm, and then summed the values to obtain total basal area and biomass for each plot. We used wood density data for each tree species to calculate the mean wood density per plot (global wood density database (24)). We estimated understorey density by counting saplings (trees and lianas with DBH > 2 cm and < 10 cm) in five 0.01-ha subplots (5-m \times 20-m). We also calculated the biomass of coarse wood debris (≥ 10 cm diameter in at least one extremity) from measurements taken in the five 0.1-ha sub-plots. We estimated the biomass of fine wood debris (2-10 cm diameter in at least one extremity) from measurements taken in a further five sub-plots of 2-m \times 5-m (Fig. 1b). Finally, we collected and weighed leaf litter in 10 quadrats of 0.5-m \times 0.5-m per plot. We used plot-level means and totals to obtain mean values per hectare; details on biomass estimation can be found in supporting information (Appendix A1) and in (25). We further determined canopy cover (%) from five hemispherical photos per transect (at 50-m intervals and 1-m height) using Gap Light Analyzer 2.0 (26). Hence, we obtained nine variables for aboveground structure:

biomass of trees, lianas, coarse wood debris, fine wood debris, leaf litter, basal area of trees, canopy cover, mean wood density and understorey density.

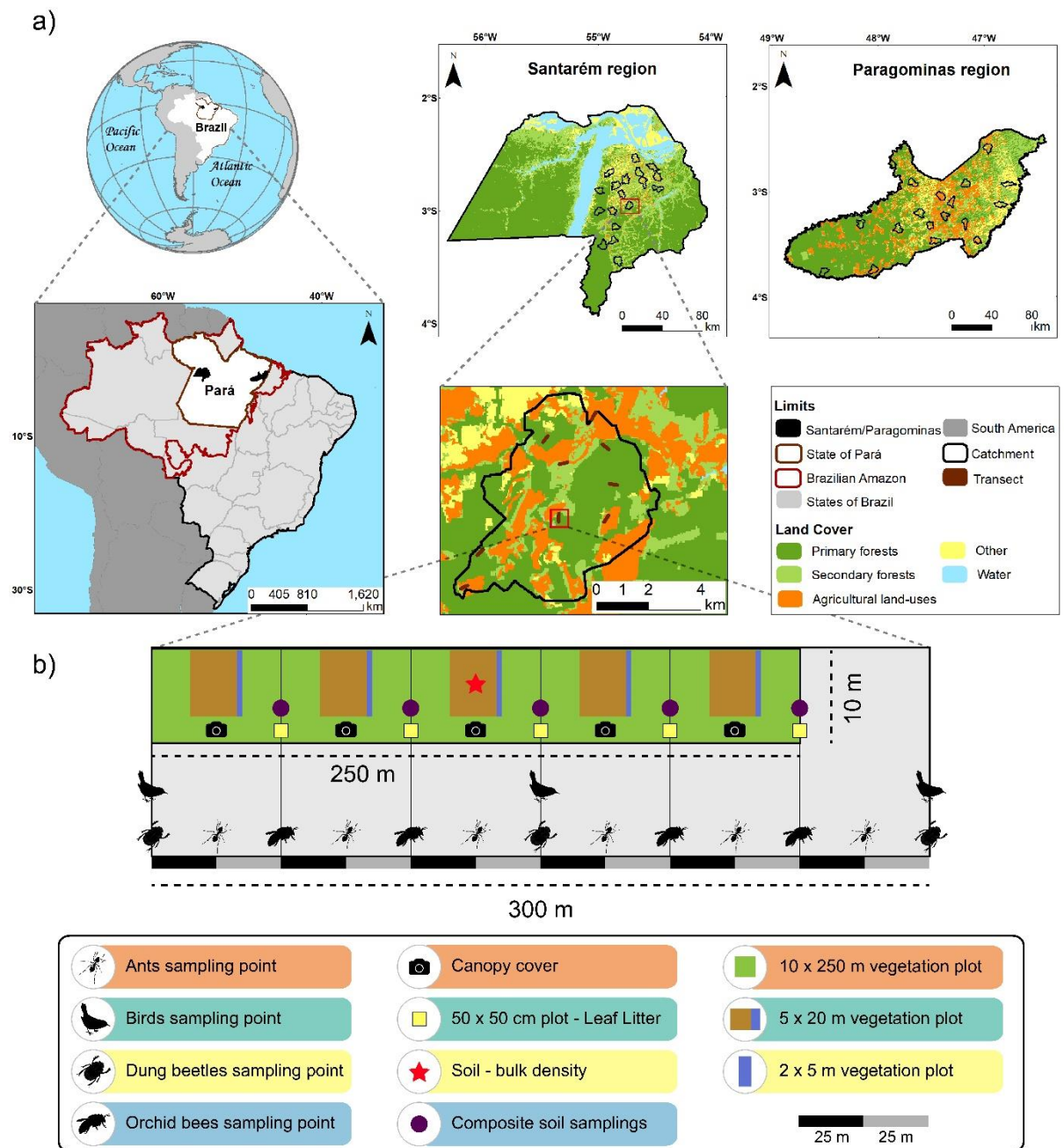


Fig. 1. Map of study site and design. a) All variables were collected in two regions of eastern Amazon, in the Brazilian state of Pará – Santarém and Paragominas regions. b) Sampling design to collect variables from aboveground structure, biodiversity and soil properties. In 10 x 250 m plots we sampled trees and lianas ≥ 10 cm DBH; in 5 x 20 m plots we sampled trees and lianas $2 \leq \text{DBH} < 10$ cm and coarse wood debris; in 2 x 5 m plots we sampled fine wood debris.

- Biodiversity

We assessed seven biological groups in each transect which are considered bioindicators and provide important ecosystem services such as carbon storage, pollination, nutrient cycling and seed dispersion. Birds and dung beetles were sampled at three points separated by 100 m. Ants were sampled in six points separated by 50 m, and orchid bees were sampled at five points, also separated by 50 m. Trees, lianas and saplings were identified during biomass measurements in the plots and subplots (Fig. 1b). More details on sampling techniques for each taxon can be found in supporting information (Appendix A1) and in (23). For trees, saplings, lianas, dung beetles and orchid bees we considered the number of individuals sampled as their abundance, but for birds and ants, the measurement of abundance was the number of point-counts in which each species was recorded at the sampling points. We calculated the richness of each group for each sampling plot, as well as the Simpson inverse index ($1/D$) to consider both richness and abundance. We calculated the mean β -diversity based on Sørensen distance for each sampling plot. Hence, for the biodiversity component we had a total of 21 variables: seven biological groups (ants, birds, dung beetles, lianas, orchid bees, saplings and trees) \times three metrics (composition, diversity and richness).

- Soil

To determine soil properties, composite soil samples were collected at 10-cm increments from 0-30 cm at five sampling points separated by 50 m in each sampling plot. We measured bulk density on two undisturbed soil cores per soil depth, which were collected at the centre of each plot using a volumetric ring. All soil samples were dried and subsequently analysed following the methods described in (27). Carbon and nitrogen were measured by dry combustion and carbon stocks were calculated by multiplying the carbon content of each layer by the layer thickness (10 cm) and soil bulk density. More details on soil sampling can be found in supporting information and in (23). We calculated the mean values for the three depths for all soil properties to obtain nine soil variables: bulk density (g/cm^3), soil pH, carbon stock (C), total nitrogen (% N), phosphorus (P), potassium (K^+), calcium and magnesium ($\text{Ca}^{2+} + \text{Mg}^{2+}$), sodium (Na^+) and aluminium (Al^{3+}).

Data analysis

We worked with 39 variables, for which we calculated the effect sizes of responses to each of the six disturbances (see details below) in each region. Hence, we had 21 variables for

biodiversity (18 in STM because we did not sample orchid bees in this region), nine for aboveground structure and nine for soil properties.

All data analyses were performed in R version 3.5.3 (28). We used the *vegan* package (29) to calculate differences in community composition, *metafor* package (30) to analyse effect sizes and *multcomp* package to run contrast analyses (31).

- *Effect size calculation*

To calculate effect sizes, we used a standardized mean difference with correction to positive bias (using the *escalc* function from *metafor* package). For each variable, we calculated the mean, standard deviation and number of replicates for reference (undisturbed/undegraded) and treatment (disturbed/degraded) classes and then subtracted the mean value of reference forests from disturbed/degraded ecosystems, standardizing the difference with the pooled standard deviation. These effect sizes were used to accomplish our second goal, when we were looking “inside” each ecosystem component. As the effect sizes for variables even within the same ecosystem component included both positive and negative values, to fulfil our first objective, we also calculated the effect sizes based on dissimilarities (Euclidean distance), which is a routine used to assess species compositional changes in meta-analyses, *e.g.* (22, 32). First, we used the *dist* function to construct, for each variable, one matrix of Euclidean distances between all pairs of reference sampling plots (forests) and a set of matrices with pairs of reference sites and disturbed/degraded plots (one for each of the six disturbance types). We then calculated the mean Euclidean distances for each reference sampling and each disturbed/degraded plots and used these to calculate the mean, standard deviation and number of replicates for reference and treatment ecosystems. Hence, the effect sizes represent the dissimilarity between reference and disturbed sites relative to the baseline dissimilarity among reference sites. We considered an increase in dissimilarity compared to the baseline as a negative impact and therefore expressed all effect sizes as negative values for comparison. For changes in species composition, we used the same approach, but created matrices based on Sørensen distance (β -diversity), using the *betadiver* function.

To assess the effect of tropical forest conversion (to pastures and to mechanised agriculture) and regeneration (young and established secondary forests), we considered all primary forests as references sites. However, to investigate the effect of forest degradation (logging and logging + burning), we considered only primary undisturbed forests as references.

- Effect size analyses

We followed a sequence to analyse the effect sizes of each of the six disturbance types. To assess overall changes in the three ecosystem components (our first goal), we used the effect sizes calculated based on Euclidean distances in a Multivariate/Multilevel Linear (mixed-effects) Model using the *rma.mv* function with region as a random effect in all our models. We used the variables' effect sizes as the response terms in the model, and ecosystem component as an explanatory term (moderator). We tested for the significance of the moderator with an omnibus test (Wald-type). We also ran contrast analysis using the *glht* function to assess which ecosystem components differed from each other. We ran these models, considering only the metric of composition to estimate biodiversity, as it has been pointed out as one of the best metrics to summarize cross-taxon responses to environmental changes (33, 34).

To investigate the impact of forest disturbance on variables individually (our second goal), we used the effect sizes calculated from mean values. In this stage, we ran a separate model for each of the three ecosystem components for each disturbance type. We used the variables' effect sizes as response terms in all models. For the biodiversity component, we used metric and biological group as explanatory terms and for aboveground structure and soil components we used the variable identity as explanatory term. Again, we tested for the significance of the moderators. If metric or taxon was not significant in biodiversity component models, we simplified the model by removing the non-significant term.

RESULTS

Biodiversity, represented by species composition, was the ecosystem component most affected by forest disturbance, followed by aboveground structure, and soil was the least affected (Fig. 2). This pattern was consistent across forest conversion types (to pasture or mechanised agriculture) and in young secondary forests, whereas the extent of changes to aboveground structure and soil were similar in logged, logged + burned, and established secondary forests. Primary forest degradation generally did not alter aboveground structure and soil, as the confidence intervals of all estimated means crossed zero for these ecosystem components (see Table 1 for model results and Table S1 for contrast analysis).

As expected, the complete removal of trees during forest conversion resulted in substantial negative effects in all aboveground structure and biodiversity variables (Fig. 3). Basal area, leaf litter biomass, understorey density and wood density were the most affected

variables in aboveground structure. Accordingly, trees, saplings and birds were the most affected taxa after forest conversion to pastures and mechanised agriculture. Composition was the most responsive biodiversity metric, followed by richness and diversity. The changes in soil properties with forest conversion varied, but overall, soil pH and soil fertility increased (P, K and Ca/Mg), and Al concentrations decreased after conversion to both pasture and mechanised agriculture. Bulk density increased in pastures and the percentage of nitrogen decreased but they did not change with conversion to mechanised agriculture. Surprisingly, carbon stocks did not decline significantly after forest conversion (Fig. 3).

Primary forest degradation had a negative impact on tree biomass, total basal area and wood density. Understorey density increased in response to logging, whereas biomass of lianas decreased in response to logging + burning. Primary forest degradation did not affect species richness and diversity, whereas the effect of degradation on species composition was always negative (Fig. 4). For individual taxa, logging had no overall effect (average of the three metrics), and only trees and dung beetles responded negatively to logging + burning. Forest degradation resulted in a decrease in bulk density and increased soil pH, total N and Ca + Mg. The concentrations of Na and K in the soil increased in response to logging, but not to logging + burning (Fig. 4).

Our results showed that even established secondary forests had a distinct structure compared to primary forests. Although leaf litter remained unchanged, almost all aboveground structure variables presented lower values compared to primary forests, with the exception of understorey density in young regenerating forests and canopy cover in established secondary forests (Fig. 5). The same trends were observed for the biodiversity component, where all taxa except orchid bees and ants (in establish forests) were negatively affected. All three biodiversity metrics responded equally in established secondary forests, whereas composition was the most responsive metric in young forests. Of the nine soil properties in established secondary forests, seven were similar to primary forests: only pH and Ca+Mg increased. In the early stages of forest regeneration, pH, Ca/Mg and bulk density increased, whereas Na and Al decreased relative to the primary forest baseline.

Ecosystem responses to anthropogenic disturbances

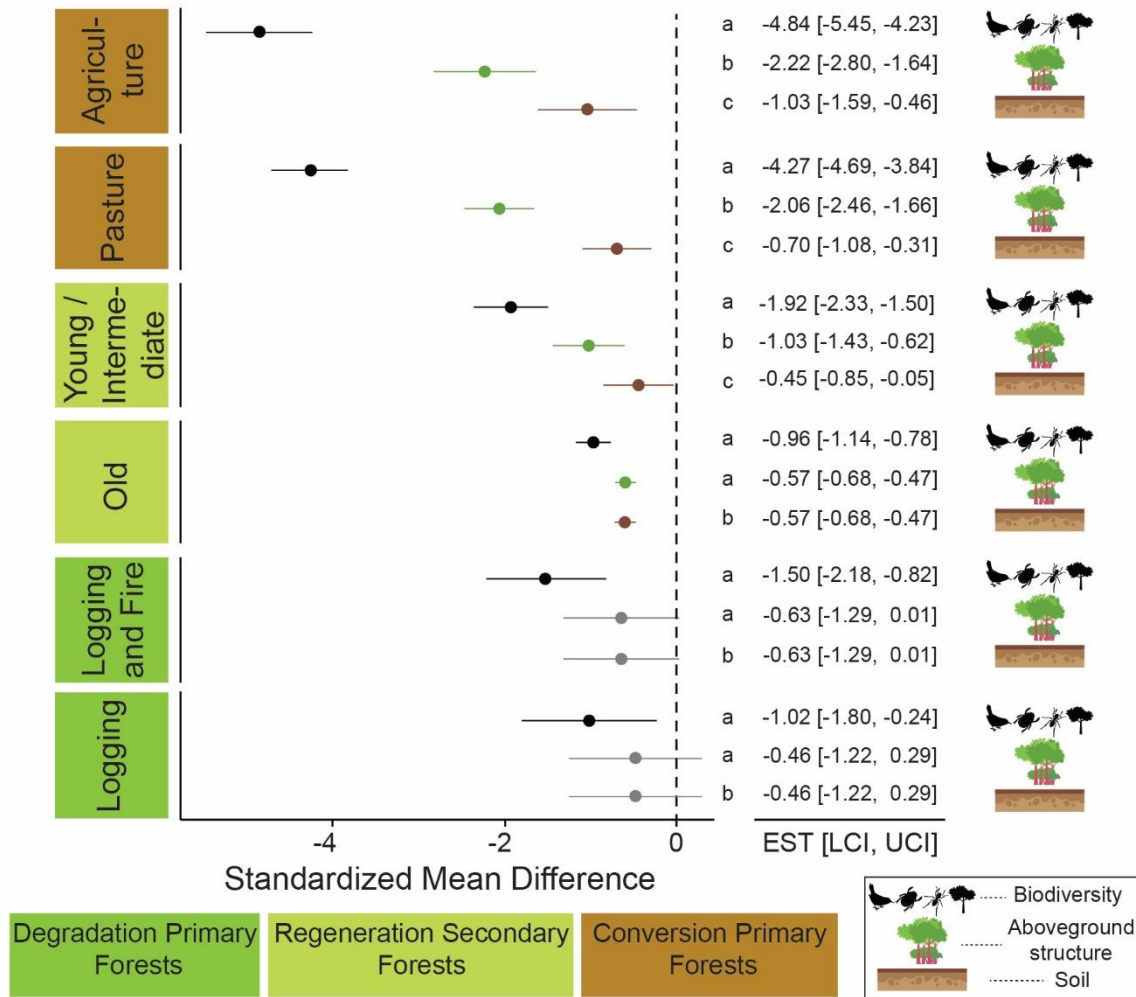


Fig. 2. The overall predicted effect sizes (standardized mean difference) of the impacts of six disturbance types on three ecosystem components in tropical forests. Different letters represent statistical difference. Biodiversity component is represented by species composition of ants, birds, dung beetles, orchid bees, lianas, saplings and trees. Aboveground structure component is represented by the biomass of coarse and fine wood debris, leaf litter, lianas and trees, and the basal area, understory density and mean wood density. Soil component is represented by bulk density, aluminium, calcium/magnesium, carbon stock, nitrogen, potassium, phosphorus, sodium and pH. EST = estimated value, LCI = lower bound of confidence interval, UCI = upper bound of confidence interval. Different colours in the dots represent different ecosystem components. Grey dots represent estimated values and confidence intervals that cross zero.

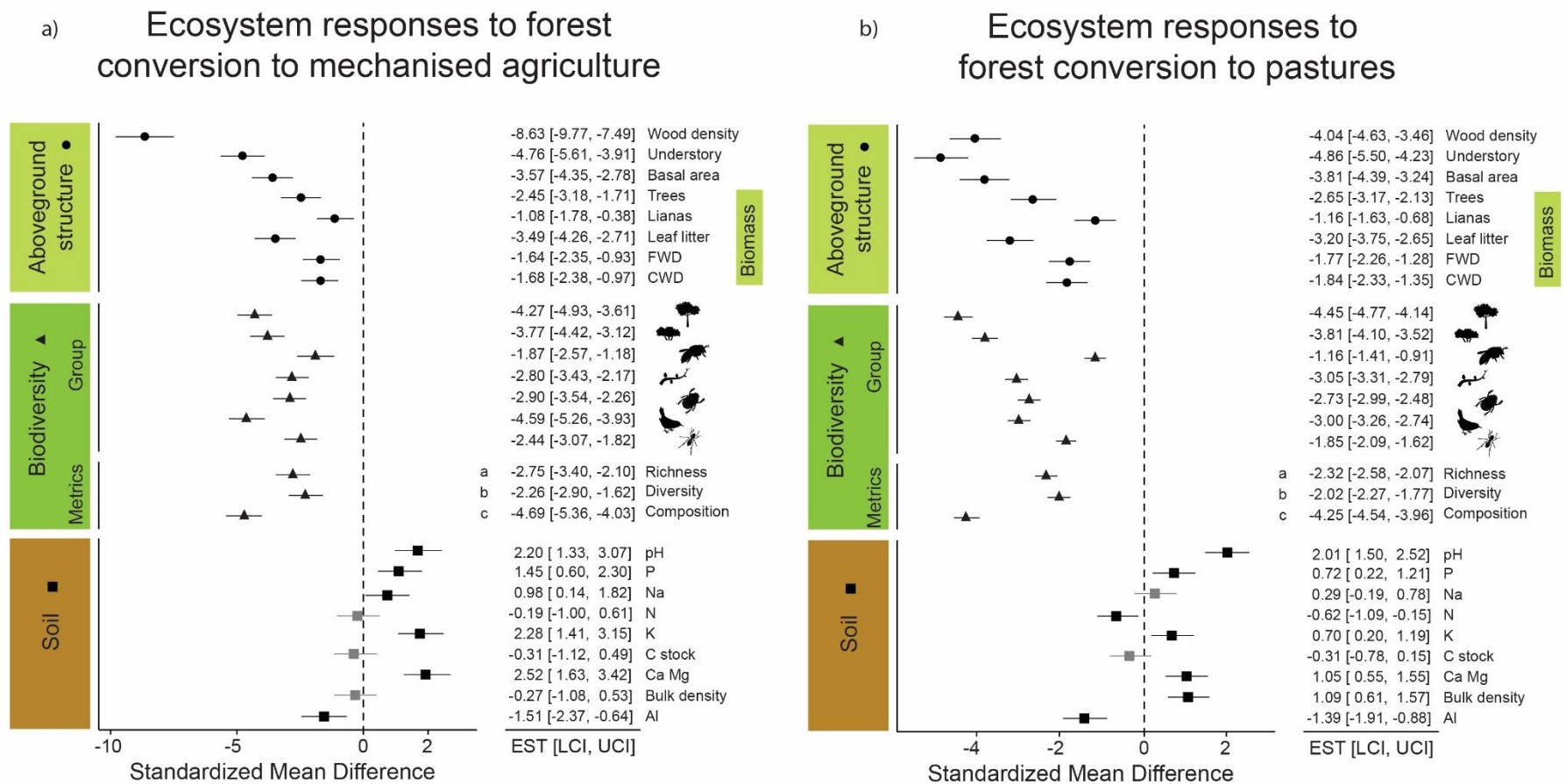


Fig. 3. Predicted effect sizes (standardized mean difference) of the impacts of tropical forest conversion to a) mechanised agriculture and b) pastures. Different letters represent statistical difference between metrics of biodiversity. Different shapes represent variables from different ecosystem components. Biological groups are displayed in the order: trees, saplings, orchid bees, lianas, dung beetles, birds, ants. EST = estimated value, LCI = lower bound of confidence interval, UCI = upper bound of confidence interval. Grey shapes represent estimated values and confidence intervals that cross zero.

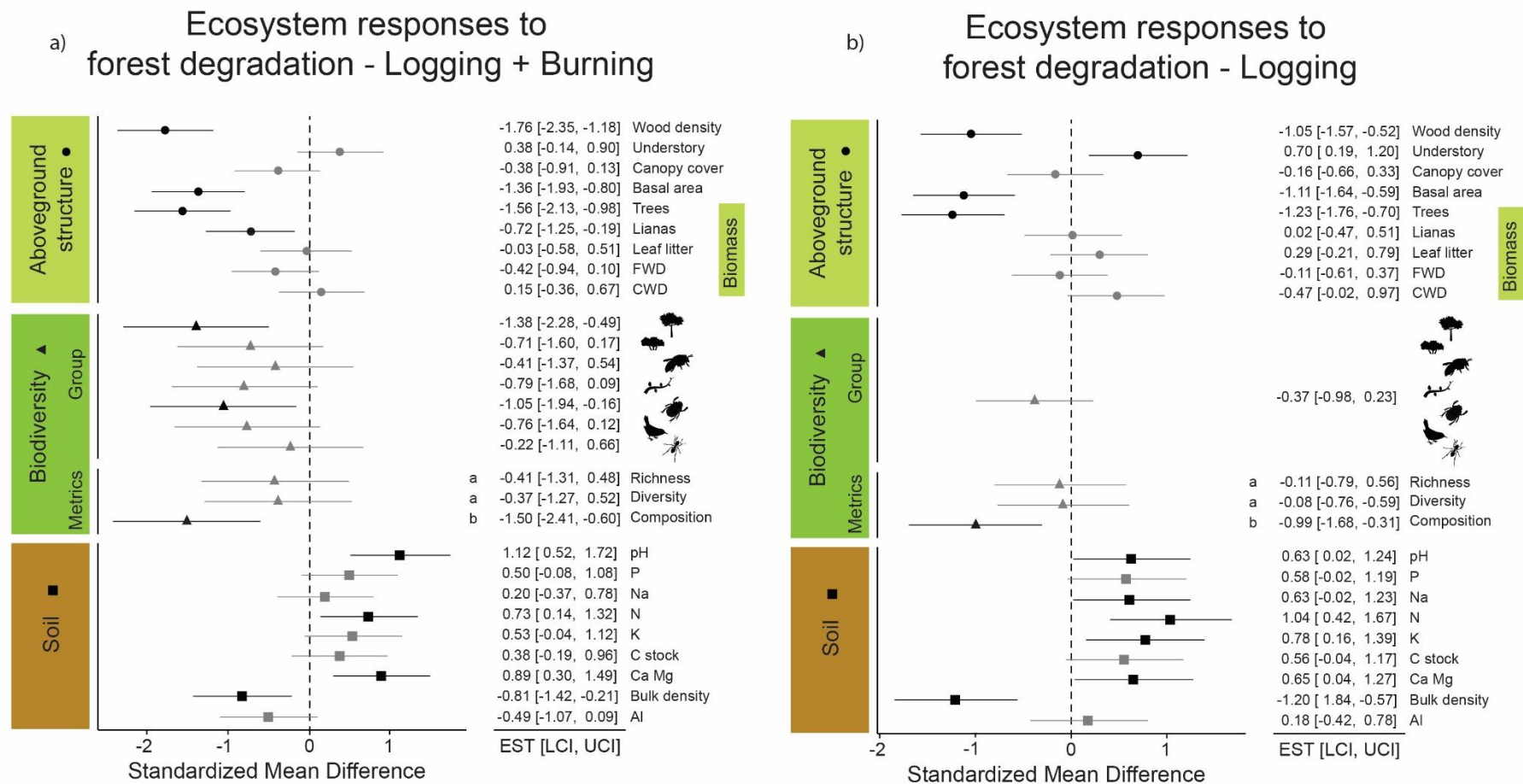


Fig. 4. Predicted effect sizes (standardized mean difference) of the impacts of tropical forest degradation through a) logging and burning and b) logging. Different letters represent statistical difference between metrics of biodiversity. Different shapes represent variables from different ecosystem components. Biological groups are displayed in the order: trees, saplings, orchid bees, lianas, dung beetles, birds, ants. In Fig. 4b. there is only one value for biological groups, because this term was not significant (all equal). EST = estimated value, LCI = lower bound of confidence interval, UCI = upper bound of confidence interval. Grey shapes represent estimated values and confidence intervals that cross zero.

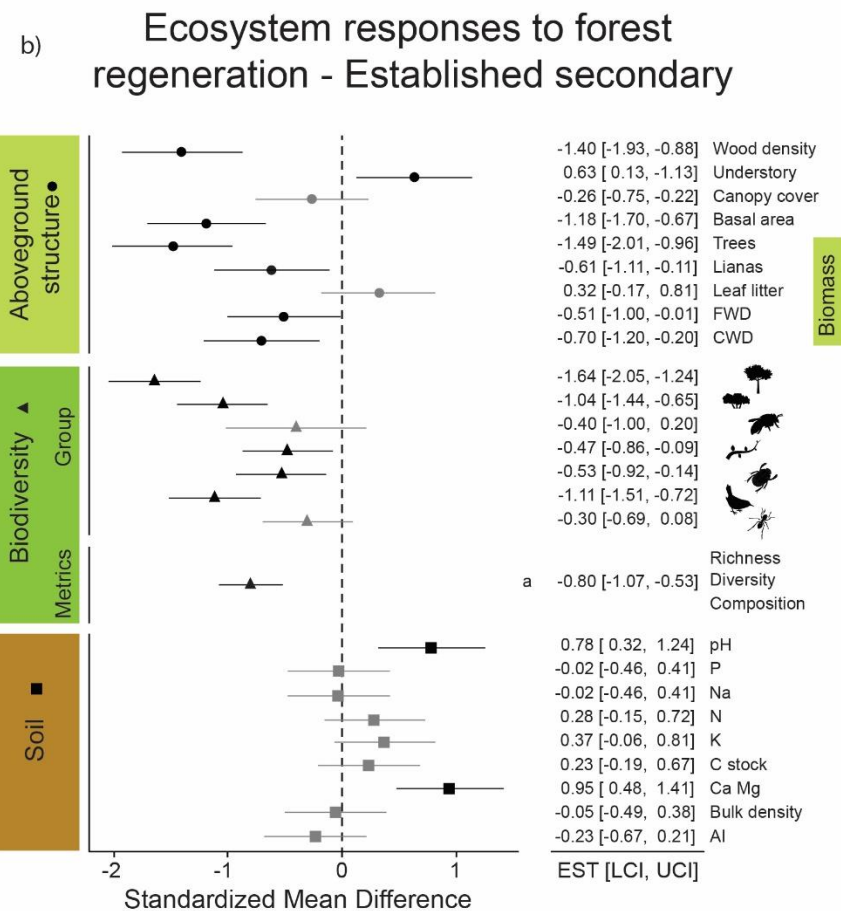
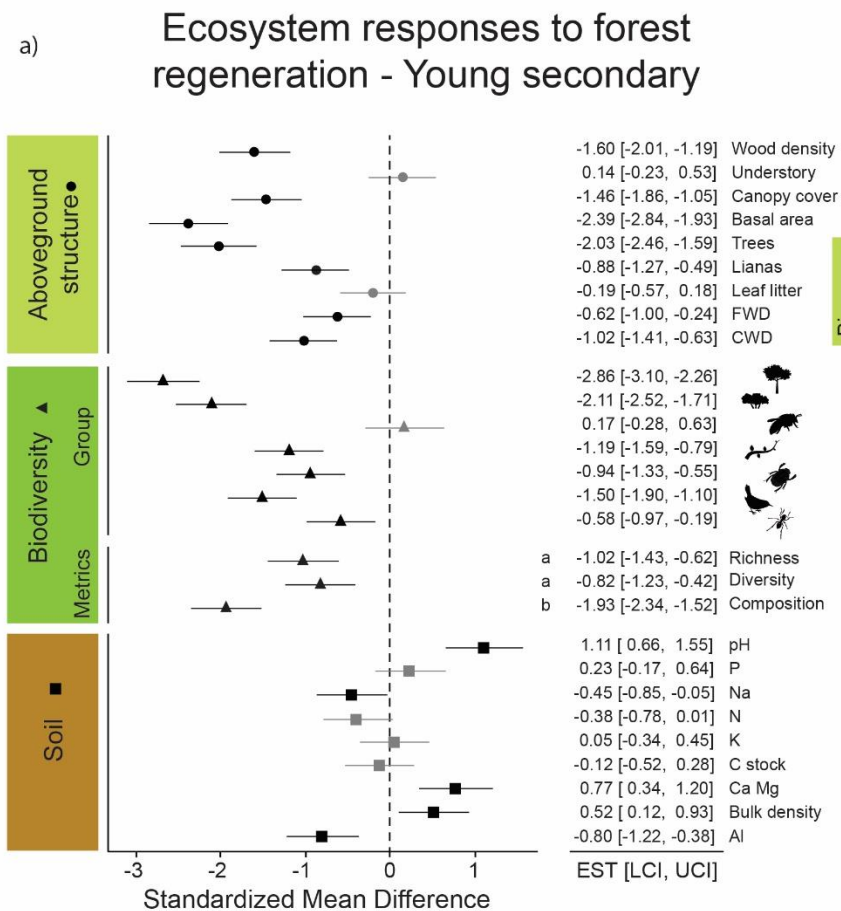


Fig. 5. Predicted effect sizes (standardized mean difference) of the ecosystem response to tropical forest regeneration in a) young and b) established secondary forests. Different letters represent statistical difference between metrics of biodiversity. Different shapes represent variables from different ecosystem components. Biological groups are displayed in the order: trees, saplings, orchid bees, lianas, dung beetles, birds, ants. In Fig. 5b. there is only one value for metrics of biodiversity, because this term was not significant (all equal). EST = estimated value, LCI = lower bound of confidence interval, UCI = upper bound of confidence interval. Grey shapes represent estimated values and confidence intervals that cross zero.

Table 1. Results of multivariate mixed-effects models when using ecosystem components as explanatory term (moderator) to effect sizes of the six disturbance types. Number of effect sizes was 49 for all models, except in conversion models which had 47. Df = Degrees of freedom; Res. Df = Residual degrees of freedom; Q_M = Wald-type omnibus test of moderator. PA = pasture, MA = mechanised agriculture, Log. = logging, Log. Burn = logging + burning, Established = established secondary forests, Young = young secondary forests.

Disturbance	Df	Res. Df	Q_M	p-value
Conversion – PA	2	44	1084.0	< 0.001
Conversion – MA	2	44	589.57	< 0.001
Degradation – Log.	2	46	20.54	< 0.001
Degradation – Log. Burn	2	46	45.52	< 0.001
Regeneration – Established	2	46	13.96	< 0.001
Regeneration – Young	2	46	180.36	< 0.001

DISCUSSION

Most studies of anthropogenic impacts in tropical forests have focused on one or few disturbance types and/or one ecosystem component. We present the first large-scale study contrasting the effects of six major types of disturbances on three components of tropical forest ecosystems: aboveground structure, biodiversity, and soil. We showed that biodiversity is the ecosystem component most affected by disturbance, regardless of the disturbance type. Independently of the magnitude of changes, community species composition always significantly changed in response to forest conversion, degradation and regeneration compared to primary forests. The estimated effect sizes of species compositional changes were as high or higher than any other affected variable from aboveground and soil components, which is surprising, given the extent of changes to forest structure incurred by all of the disturbance types we assessed. Individual studies using the biodiversity data from our sites found similar trends (supporting information - Appendix A2). However, our study is the first to make a direct comparison of changes in all key ecosystem components across such an extensive site network.

The effects of biodiversity loss are very well studied and even few changes in species composition can impair ecosystem functioning (35). Deforestation and degradation of tropical forest are driving to taxonomic and functional simplification of communities, so-called biotic homogenization. The homogenized communities lack specialized (rare) species that fulfil unique functions (36) and are more vulnerable to biotic invasions (37). There are numerous examples of how biodiversity loss and changes reduce the efficiency and stability of ecosystem services upon which we rely directly or indirectly (35, 38). For instance, disturbed tropical forest communities may have fewer tree species with high wood density, which affects carbon accumulation (39), smaller dung beetles, which affects detritus pathways (40), and fewer frugivorous birds, which affects seed dispersal (41). The loss of biodiversity in tropical forests can also result in the loss of still unknown medicines and products which would be beneficial to humans, *e.g.* (42).

Aboveground structure is strongly linked to biodiversity, as it is both a consequence and a source of species diversity. Although these two ecosystem components are related, we always found greater effect sizes for biodiversity (represented by community species composition) than aboveground structure. This may be because forest diversity is related to the productivity, availability and heterogeneity of resources, and because changes in forest structure cause change in conditions [habitat heterogeneity hypothesis (43)]. In secondary regenerating forests, for example, trees, saplings, birds and dung beetle diversity were influenced by vegetation biomass and canopy cover more than any other variable (44). Hence, negative effects of forest disturbance on aboveground structure not only directly entail changes in plant diversity and species composition but are also likely to have cascading impacts on the diversity of many other taxa (33). In our study, the aboveground biomass, basal area and mean wood density of trees were always negatively affected by conversion, degradation, and regeneration. Given that trees store ~230 Pg of carbon in tropical forests (11), these changes in forest structure have important implications for the carbon cycle and climate change. Our study provides further evidence of the importance of limiting forest degradation, besides deforestation, to reduce carbon emissions.

Overall, the soil compartment was the least affected ecosystem component, particularly by forest degradation, but our analyses of individual soil properties indicated changes that could influence the trajectory of forest succession during recovery. For example, the concentrations of several soil nutrients increased after disturbance, which would facilitate the establishment of

fast-growing competitive tree species during regeneration. The observed increases in soil nutrients after forest conversion likely reflect fertiliser application or animal dung inputs, whereas increased soil nutrients in degraded forests likely result from substantial inputs of plant litter during harvest, *e.g.* (45). Although soil pH after conversion to mechanised agriculture and forest degradation by logging + burning could indicate liming or ash inputs, respectively, soil pH increased in response to all disturbances, which can in turn affect the availability of nutrients. In addition, the diversity of soil bacteria increases in disturbed soils in tropical forests, while the species composition changes mainly in response to shifts in soil pH (46), which often accompany shifts in tree species composition and plant inputs, *e.g.* (47). Surprisingly, soil carbon stocks were unaffected by any of the forest disturbance types, even mechanised agriculture, which usually entails substantial soil disturbance and release of carbon stored belowground. Although forest degradation appears to have limited effects on soil properties, and soil fertility can be managed by farmers through burning and fertilization (48), we still know very little about soil processes in the tropics and it is unclear how some of the observed changes in physical-chemical properties could cascade through soil microbiota and influence soil functioning.

Our results reinforce the idea that even later stages of regeneration in secondary forests are not substitutes of primary forests (19). Secondary forests (both young and established) had distinct aboveground structure, biodiversity, and soil properties compared to primary forests, even considering the degraded ones. However, aboveground structure generally recovers faster than biodiversity during secondary succession (14). Notwithstanding, the mean effect sizes of all ecosystem components in later stages of secondary regeneration were very similar to the mean effect sizes in response to logging, suggesting that established secondary forests differ from undisturbed primary forest as much as a primary logged forest (on average). It is important to consider that our sample sites only included naturally regenerating forests, and that both study regions retain more than 50% of forest cover (44), which facilitates reestablishment of forest (7). It is possible to accelerate secondary forest regeneration and approximate these forests to primary forests through active restoration programs (49) and initiatives to protect both biodiversity and carbon stocks in tropical forests already attempt to do so through secondary regeneration (50).

Why are tropical forests still being destroyed?

The main direct drivers of tropical forest deforestation and degradation are conversion to agricultural lands and logging activity, respectively (4, 51). We analysed both types of disturbance and found that although these activities have huge impacts on biodiversity, they have a smaller effect on other ecosystem components. In the case of mechanised agriculture and extensive cattle grazing (pastures), the disturbance actors, *i.e.* farmers, do not rely directly on biodiversity or aboveground structure to develop their activities. On the other hand, they rely on soil/land. Our results showed that soil was the less affected ecosystem in all disturbances and after conversion. Indeed, pH, P, K and Ca/Mg (fertility) increased whereas Al decreased after conversion, indicating that farmers can control/improve soils to deliver the ecosystem services they need for production. In the same region of our study site, (48) showed that even smallholders manage soils using fire or fertilizers. Although we did not evaluate for how long they can maintain soil fertility after conversion, losing biodiversity is not a barrier or limitation to the activities that underpin their livelihoods. In the case of logging, the disturbance actors (mainly timber companies) rely on aboveground structure and specifically on certain commercially viable timber species. Again, the loss and change of other species in selectively logged forest does not necessarily impede logging activity. In addition, our results showed that logging did not change the overall aboveground structure in tropical forest (Fig. 2). Although logging alters the biomass, basal area and mean wood density through the removal of large trees, it does not alter the general forest architecture and it remains a primary tropical forest.

Beyond the direct drivers of deforestation and degradation, there are important indirect drivers which can also explain why tropical forests are still being destroyed despite the loss of biodiversity. Such indirect drivers are mainly international demand for commodities (51), but also increasing population, weak law enforcement, corruption and poverty (52). In addition, there is evidence that although the global program of reduction of emissions from deforestation and forest degradation (REDD+) is succeeding in targeting direct local and regional drivers, it has less influence on indirect national and international drivers (52). Moreover, 87% of exports that came from deforestation from 2005 to 2013 were bought by countries that attained decreases in deforestation rates or even increasing in forest cover (53). Therefore, despite the magnitude of current biodiversity loss, it has not yet affected the availability of tropical forest products and worldwide consumers continue to purchase products originating from deforestation or degradation of tropical forests.

Supply-chain governance could also play a critical role in reducing tropical forest degradation. Since voluntary agreements motivated by supply-chain governance worked to reduce deforestation (54), they could help to reduce tropical forest degradation and even encourage forest restoration. Brazil, which contains 60% of the Amazon and all the Atlantic forest, is currently negotiating trade agreements with the EU, its second largest trading partner. This opens the possibility for supply-chain governance motivated by official standards of sustainable trade between these two partners (55). Public policies, supply-chain governance, and positive incentives and financing (for example through REDD+ programmes) could help to reduce both global carbon emissions and biodiversity loss from tropical forest destruction.

We provide sufficient evidence that biodiversity is the most affected ecosystem component in response to several disturbance types. Nevertheless, disturbance actors are still maintaining their activities and product originating from these activities are still being traded worldwide. Therefore, global conservation initiatives must consider both direct and indirect drivers of tropical forest destruction. Not only carbon but also biodiversity markets along with national policies could help to change environmentally degrading activities in tropical forest (56) to support secondary regeneration and reduce deforestation and degradation, with co-benefits for carbon and biodiversity (57).

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SUPPORTING INFORMATION

Appendix A1 – Detailed information on aboveground biomass and biodiversity sampling

Appendix A2 – Main findings of studies that used the same data to answer different questions

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APPENDIX A1 – Detailed information on aboveground biomass and biodiversity sampling

Information on biomass estimation

To estimate tree biomass species-specific wood density were obtained from the Global Wood Density Database (1). If a species-specific wood density was not available, the average of the genus or family was used. For all trees and saplings, the Chave allometric equation was used to calculate biomass based on the DBH and wood density (2), except for the genus *Cecropia* for which Nelson allometric equation was used (3). To estimate the biomass of lianas the Gerwing & Farias equation was used (4).

Biomass estimation of litter components (fine wood debris and leaf litter) was made by weighing the samplings after drying them to a constant weight. For coarse wood debris, every piece of dead wood was classified in terms of its decomposition state and biomass was calculated by multiplying its volume by the density of its decomposition. More details on biomass estimation can be found in (5) and in (6).

Detailed information of animal sampling

Birds

Bird sampling was conducted in three points in each transect separated by 150 m (0, 150 and 300 m). In each of these three points, 15-minute point count samples were collected between 15 minutes before dawn and 9:30 am. These samplings were repeated in each point in the transect, but in reverse order to remove temporal bias. Solid state sound recorders were used to record each point count sampling to facilitate identification of any species not identified in the field. More details on the birds sampling and a list of voucher species collected in Santarém see (7) and in Paragominas see (8).

Ants

Ants were collected with passive (non-baited) pitfall traps in Santarém region, whereas in Paragominas traps were baited with sardine and honey. Traps consisted in plastic containers with 12 cm height and 8 cm diameter. The traps were half-filled with a killing solution with water, salt (2%) and detergent (5%) and were left in the field for 48 hs. In Paragominas, six traps were installed separated by 50 m (between 25 and 275 m in the transect), while in

Santarém 10 traps were installed separated by 10 m (between 50 – 90 and 200 – 240 m in the transect). All specimens collected were kept in ethanol and then were taken to the Universidade Federal de Lavras and Universidade Federal de Viçosa – Minas Gerais – Brazil where they were identified to the lowest taxonomic level. Final identification was checked by the taxonomist Dr. Rodrigo Feitosa at the Museu de Zoologia de São Paulo. For a full list of voucher species collected in Paragominas see (9).

Dung Beetles

Dung beetles were collected using baited pitfall traps. Traps consisted in plastic containers of 1 litre, 14 cm diameter, 9 cm height and were baited with 50 g of dung (80% pig and 20% human). All traps were half-filled with a killing solution with water, salt (2%) and detergent (5%). Dung beetles were sampled in three point in each transect separated by 150 m (0, 150 and 300 m). In each of these three sampling points, 3 pitfalls were installed in the corners of a 3-m side triangle and were left in the field for 48 hs. The individuals were kept in ethanol for preservation and taken to the Universidade Federal de Lavras and Universidade Federal de Viçosa – Minas Gerais – Brazil for identification. Final identification was checked by the taxonomist Dr. Fernando Zagury Vaz-de-Mello at the Universidade Federal do Mato Grosso.

Orchid bees

Orchid bees (males) were collected using baited traps, consisting in plastic bottles of 2 litres, 10 cm diameter and 35 cm height. The bottles were installed in four sampling points in each transect in Paragominas region separated by 50 (50, 100, 150 and 200 m). In each bottle, radial holes at the height of 20 cm were made, where flower-like structures were inserted. The flower-like structures were impregnated with coarse sand on the inner side to give support to the bees. Inside the bottle, a stick with cotton ball was baited with eugenol, methyl salicylate, vanilla or eucalyptol (each trap received only one type of bait). The traps were tied to tree trunks 1.5 m above the ground and were left in the field for 48 hs. Bee specimens were kept frozen before triage and identification at EMBRAPA – Amazônia Oriental where the taxonomist Dr. André Nemésio checked final identification. For a full list of voucher species collected see (9).

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APPENDIX A2 – Main findings of individual studies conducted using the same data used in this study

Table A1. Reference, the ecosystem component focused, and the main findings of individual studies conducted in the same regions of this study.

Article	Ecosystem component	Main finding
Barlow et al. (2016)	Biodiversity	Forest disturbance increases the loss of biodiversity from deforestation
Barlow et al. (2012)	Aboveground structure	Not considering fire in REDD+ programmes may lead to failure in achieving carbon emission reductions
Berenguer et al. (2014)	Aboveground structure	Disturbed forests store less carbon than undisturbed
Berenguer et al. (2018)	Aboveground structure	Wood density of saplings in disturbed and secondary forests are similar
Bregman et al. (2016)	Biodiversity	Forest disturbance reduced functional diversity of bird communities
de Carvalho et al. (2016)	Biodiversity/Soil	Land-use intensification increases diversity of soil bacteria
Durigan et al. (2017)	Soil	Forest conversion do not reduce carbon and nitrogen soil stocks
Ferreira et al. (2018)	Aboveground structure/Biodiversity	Carbon focused conservation may fail to protect biodiversity
Lennox et al. (2018)	Aboveground structure/Biodiversity	High recovery of biomass and biodiversity in secondary forests after 40 years of regeneration
Moura et al. (2013)	Biodiversity	Marked differences in species composition of birds along forest disturbance gradient
Moura et al. (2016)	Biodiversity	Birds present idiosyncratic responses to forest disturbance
Solar et al. (2015)	Biodiversity	High biotic homogenization in production areas but lower in disturbed and regenerating areas
Solar et al. (2016)	Biodiversity	Marked differences in species composition of ants along forest disturbance gradient

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GENERAL CONCLUSION

In this thesis, I address knowledge gaps about the effects of tropical forest disturbances at the community and the ecosystem level. At the community level, I wanted to understand what would happen to the functional structure of communities after forest disturbance occurred and species were lost. At the ecosystem level, I wanted to assess which ecosystem component would be most affected by tropical forest disturbances. Overall, the work presented in my thesis represents an advance towards filling these knowledge gaps and also highlights new avenues of inquiry for future work in this area. Synthesising the findings of both Chapters, my work highlights two key messages. First, in Chapter 1 my results demonstrate that local resistance to forest disturbance is supported by functional redundancy of the regional pool of species, which in turn is maintained due to the existence of a forest matrix in the landscape. These findings are important because my results provide new evidence to understand why and how communities can be functionally resistant to forest disturbances. The second key message emerges from the results from the ecosystem-level study in Chapter 2, which demonstrates that biodiversity is the ecosystem component of tropical forests that is most sensitive to the occurrence of multiple types of disturbance. Whereas previous meta-analyses of published results have largely focussed on changes in one or two ecosystem components, to my knowledge, this work is the first to identify the most vulnerable ecosystem component in response to all major tropical forest disturbances from empirical data in a single large-scale study.

Taken together, the results of the work presented in my thesis suggest that, although we are modifying and negatively affecting tropical forests, the maintenance of biodiversity in disturbed forests depends largely on the pools of species and traits at a regional and landscape level, most of which are present in conserved or intact forests. Hence, my results not only demonstrate the vulnerability of tropical forest biodiversity, but also support current initiatives to conserve substantial areas of intact forest, which can act as a refuge for tropical species and support the regeneration of disturbed or converted areas.

International initiatives for tropical forest conservation, such as the Reducing Emissions from Deforestation and Degradation (REDD+) and the Convention on Biological Diversity (CBD) emerged due to the need for preserving the crucial ecosystem services provided by tropical forests, and that the entire human population rely on, either directly or indirectly. Although there have been advances in stopping or mitigating tropical forest destruction in some

countries, we still have a long way to go in conserving tropical forest diversity and ecosystem services. We have, for example, recently seen the displacement of deforestation from countries that are consuming tropical products to tropical countries that are destroying forests to provide these products (PENDRILL et al., 2019). We have also only recently started to pay attention to the huge importance of degradation by fire in tropical forests (BARLOW et al., 2012); although deforestation has decreased in the Amazon, the extent of fires counteracts the declines in carbon emissions (ARAGÃO et al., 2018). It is clear that preserving one of the most important biomes of our planet requires more than local or even national actions targeting specific disturbance types. If we want to reduce the effects of anthropogenic impacts on tropical forest ecosystems, we urgently need a wider, international, focus.

Governmental guidelines and international policies and pressures acting together can be very effective in reducing the extent of tropical deforestation. A notorious example of success is the joint action of Brazil's government [PPCDAM; (ARIMA et al., 2014)] and international pressure [soy moratorium, cattle agreement; (GIBBS et al., 2015)] to reduce deforestation due to soybean expansion and beef production in the Amazon (NEPSTAD et al., 2014), the biggest continuous tropical forest on Earth. More recently, a moratorium on large-scale land acquisitions was established in Indonesia, which also slowed down the annual deforestation rate by 90 times (CHEN; KENNEDY; XU, 2019). These policies can be very useful to help maintaining a matrix of conserved forests in the landscape and consequently a source of biological diversity. As the results of Chapter 1 indicates, the local resistance of communities to forest degradation is supported by the regional functional redundancy. My results from Chapter 1 also underline that conserving habitats within the landscape may be more important for maintaining ecosystem function than concentrating conservation efforts on individual rare species. In addition, when we achieve decreases in deforestation rates, we are avoiding the loss of functional diversity predicted in the simulated extinctions scenarios I present in Chapter 1. Although forest degradation did not exceed the 50% local species loss at which point functional diversity started to decline in my extinction scenarios, it is likely that this will happen more rapidly in fragmented landscapes that have an impoverished regional pool of species.

Although deforestation has decreased following the conservation initiatives, forest degradation, mainly by logging and fire, have increased in the same regions (ARAGÃO et al., 2018; CHEN; KENNEDY; XU, 2019). The results from Chapter 2 demonstrate that biodiversity is generally the most sensitive ecosystem component to forest disturbance and is

more affected than aboveground and soil components. The sensitivity of biodiversity indirectly affects carbon sequestration, because species diversity supports forest structure and hence carbon stocks. Therefore, the effects on biodiversity could cascade to affect carbon sequestration and storage, which is a concern for the success carbon-focused programmes that neglect the high sensitivity of biodiversity to forest disturbance. REDD+, which is primarily a climate/carbon-focused mechanism, is already including biodiversity as part of its goals, since preserving tropical forest biodiversity might help meet its targets on carbon emissions. However, REDD+ individual programmes usually lack measures to identify, address and monitor the threats to biodiversity, and do not explicitly link their activities to national biodiversity conservation plans (PANFIL; HARVEY, 2016). If we want to optimize the co-benefits of preserving carbon and biodiversity, we need to incorporate biodiversity-specific management in design and implementation of REDD+ programmes and even include other mechanisms such as biodiversity markets (PUTZ; ROMERO, 2012; MURRAY; JONES, 2014). This could be an opportunity to complement punitive measures with positive incentives and financing to reduce tropical forest destruction impacts on biodiversity.

The work presented in my thesis highlights new avenues of investigation. In Chapter 1 the results demonstrated how dung beetle communities can be functionally resistant to forest disturbance in tropical forests. However, we still need to know if communities of other organisms would present similar patterns. This would be even more interesting in the case of organisms that are considered ecological engineers and play important roles in the ecosystem. Another research line would be to investigate thresholds of functional resistance, for example, i) testing if more intense forest degradation would lead to different results and ii) questioning with which amount of surrounding forest in the landscape, regional pool of species starts to be impoverished. Additionally, the results of Chapter 2 showed that species composition is the most sensitive metric for evaluating disturbances in tropical forests, especially of trees and birds. Future research on tropical forest disturbance should focus on compositional metrics rather than only on richness and also on how to optimize sampling of these sensitive groups. Species composition of groups that are sensitive to disturbances in tropical forests could be used as proxies for evaluating the effectiveness of conservation plans and programmes, *e.g.* (IMAI et al., 2014).

Finally, future research about anthropogenic disturbance effects on tropical forests should also focus on how we could reduce the impacts on this ecosystem, especially on

biodiversity. We have a lot of evidence of how biological communities and ecosystem services respond to anthropogenic disturbances [e.g., broad meta-analysis: Dent and Wright (2009), Sodhi et al. (2009), Gibson et al. (2011), Don et al. (2011)] but are only scratching the knowledge of how to reduce and mitigate the negative effects. While the results of this thesis showed that biodiversity is the most affected ecosystem component after anthropogenic disturbances (Chapter 2), it also showed that regional functional redundancy provided community-level resistance to forest disturbance (Chapter 1). Hence, it is possible to manage landscapes to buffer the local and regional effects of disturbances on biodiversity and ecosystem functioning, but we still need to improve our knowledge of how to achieve this. Knowing what our targets are is just the beginning.

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APÊNDICE

UMA AUTOBIOGRAFIA DE UM DOUTORANDO

“Viver não cabe no Lattes!”

Autor Desconhecido

O autor desconhecido da frase tem completa razão: a vida vai muito além de publicações e citações! Desde meados do curso de doutorado eu estive pensando em alguma maneira de contar mais do que as descobertas científicas que fiz durante o doutorado. Decidi fazer isso na forma de uma autobiografia (bem resumida, é verdade), em que, como bom mineiro, conto *causos* dos aprendizados que tive ao longo de quatro anos no processo de doutoramento. À medida que fui trilhando o caminho para me tornar um cientista, vários foram os percalços, dificuldades e dúvidas e sempre me perguntava se eram “normais” ... se outras pessoas se sentiam assim também. É claro que as conversas com os amigos que também escolheram esse caminho e o apoio da família ajudaram e muito. Mas, talvez, se em cada um dos inúmeros artigos que li nesse tempo eu conseguisse perceber tudo que os autores passaram para, por fim, dar à luz oito páginas em inglês com uma singela mensagem científica, saberia que essa ansiedade e angústia fazem parte do processo. E tudo é aprendizado! Então, sendo bastante otimista, pode ser que um dia um curioso estudante procure minha tese no repositório da biblioteca, leia este apêndice e perceba que ele não está sozinho e que de fato existem pedras no caminho, mas que elas são transponíveis. Vou contar alguns acontecimentos marcantes e aprendizados que tive ao longo dos quatro anos e espero passar uma noção otimista.

Essa história começa em meados de julho de 2015, quando o resultado da seleção de estudantes para o curso de doutorado em Ecologia Aplicada da Universidade Federal de Lavras foi divulgado online. Lá estava meu número de matrícula: aprovado! Uma grande felicidade foi me tomando conta. Mas espera aí... em pouco tempo eu percebi que estava muito provavelmente fora da classificação com bolsa de estudos. A felicidade que estava expandindo começou a se contrair e a decepção foi tomando seu lugar. Mas espera aí de novo... Minha pontuação do currículo estava estranha. Após algum tempo remoendo a decepção, resolvi que tentaria

solicitar um recurso para questionar a nota do currículo. Não foi fácil justificar o pedido de recurso, porque o resultado foi liberado com os números de inscrição e não com os nomes dos candidatos. Então, eu tive que calcular todos os currículos de todos os inscritos, já que também não conhecia os candidatos classificados. Realmente havia algum erro no cálculo e assim, enviei o pedido de recurso. Valeu a pena o trabalho! Alguns dias depois, o resultado final pós-recurso: aprovado em uma posição com bolsa. Antes mesmo de entrar no curso de doutorado eu já havia experimentado angústia e ansiedade, mas também o primeiro aprendizado: se existem chances e estamos certos do que queremos, precisamos tentar.

O primeiro semestre do curso foi uma experiência muito diferente das que eu já havia vivido. Mudança de cidade, nova universidade, novo laboratório e novos professores e colegas. Eu estive muito empolgado e aproveitei para fazer muitas disciplinas e ler bastante para pensar um projeto. Já no fim desse primeiro semestre (2/2015) eu tinha um projeto escrito e boa parte dos créditos obrigatórios cumpridos. No segundo semestre (1/2016) eu tentei manter o pique da empolgação. Junto com meu orientador e alguns professores colaboradores, incrementei o projeto tornando-o mais amplo e resolvemos submetê-lo para os editais de financiamento do CNPq e da FAPEMIG. Ainda aproveitando a animação, resolvi preparar meus capítulos do mestrado para publicação.

O primeiro capítulo do mestrado estava mais adiantado e após algumas mudanças e revisões de texto parti para o processo de submissão para periódicos científicos. Ele foi aceito após nada menos do que DEZ rejeições. Usei o primeiro aprendizado (tente, sempre) para não desistir de tentar publicar o trabalho. Eu confiava que era uma mensagem científica importante e que era questão de melhorar o texto, refinar as análises e encontrar o periódico certo. Naturalmente, o processo foi regado a bastante ansiedade. A ansiedade de ser aceito como um jovem cientista. Me perguntava: será que tenho mesmo cacife pra ser aceito pela comunidade científica? Será que esse artigo é de interesse geral ou eu que estou apaixonado pelo meu trabalho? Os revisores questionaram algumas análises e sugeriram mudanças que melhoraram o texto consideravelmente. Foi muito legal poder debater minhas ideias com pessoas de qualquer lugar do mundo e tentar convencê-las que a minha mensagem valia ser publicada. Após seis meses de vai e vem, veio o aceite e a resposta para minhas dúvidas: sim, ainda preciso de ajuda e treinamento, mas fui aceito! 😊

O segundo semestre do curso, então, terminava muito bem. Além do artigo do mestrado, participei como coautor da publicação de um capítulo de livro e de outro artigo oriundo de um trabalho de disciplina do mestrado. Ainda tinha mais um artigo de uma colaboração com professores do mestrado em revisão que viria a ser aceito em meados do terceiro semestre. Não podia imaginar que estaria sendo tão produtivo com tão pouco tempo de curso!

Como diz aquela música clássica do Creedence¹: sempre vem uma calmaria antes da tempestade! O terceiro semestre do curso de doutorado (2/2016) foi uma completa bagunça e talvez o pior período da minha formação de cientista. O resultado do edital de financiamento do CNPq era para ter sido divulgado em julho e não foi, enquanto o resultado da FAPEMIG foi negativo. De repente, eu passei de uma fase cheia de trabalho e rendimento para uma fase em que o máximo que podia fazer era aguardar. Mas e se o projeto não fosse aprovado pelo CNPq, como eu iria fazer a tese de doutorado? Após um ano de doutorado eu só teria mais três para desenvolver o projeto, com coletas, triagem, identificação, análises e escrita. Começaram as dúvidas como e se eu seria capaz de fazer o projeto nesse tempo. Nesse meio tempo, eu decidi fazer um Curso de Campo, para treinar as habilidades como ecólogo e preencher o tempo com algo útil, sem continuar alimentando a ansiedade e a angústia. Em meados de setembro, parti para o Curso de Campo no Parque Estadual do Rio Doce, sem celular e sem internet: completa imersão na ecologia.

O curso de campo foi um acontecimento marcante, de aprendizado, mas também de muitas dúvidas. A primeira coisa que me aconteceu foi boa: meu, hoje, coorientador me propôs trabalhar com o banco de dados que ele havia coletado, para responder a questões que eu havia planejado com meu projeto. Pronto! A ansiedade com o financiamento do projeto diminuía à medida que a parceria se consolidava e ainda ganhei mais um membro para a comissão de orientação. Entretanto, o trabalho no Curso de Campo era bem exaustivo e sempre há uma cobrança bem alta neste tipo de disciplina; que é parte do treinamento, mas ainda assim difícil de lidar. Além disso, eu estava participando como tutor e nessa posição precisava ajudar os outros estudantes a desenvolverem suas atividades e a lidarem com as suas próprias pressões. A carreira de cientista de fato é cheia de cobranças, e acredito que o Curso de Campo foi um bom simulador do que é ser um cientista no Brasil. Mas por já estar em uma fase onde eu mesmo me cobrava bastante, passei a me questionar se era isso mesmo que eu queria para minha vida.

¹ Have You Ever Seen The Rain – Creedence Clearwater Revival

Ao invés de retornar confiante, voltei bastante inseguro com minha carreira. Conversando com amigos e colegas da profissão, hoje percebo que todos passaram por essa fase em algum momento de suas trajetórias.

Ainda no terceiro semestre do doutorado (2/2016), participei de um congresso científico bastante específico para o grupo de organismos que trabalho: os besouros rola-bosta. Eu ainda estava tentando lidar com as dúvidas que me acompanharam desde o Curso de Campo, quando durante o congresso, o artigo do meu primeiro capítulo do mestrado foi questionado por especialistas que admiro. Apesar de ser completamente normal esse debate científico (inclusive acho superinteressante quando isso ocorre), por já estar carregando muitas dúvidas, esse acontecimento foi como uma rasteira no moribundo que tentava se levantar. Mesmo sempre tendo me imaginado um cientista, eu passei a pensar que talvez ciência não fosse mesmo para mim... Será que o diabinho no meu ombro tinha razão? Sem saber na época, recebi a resposta ainda no congresso: o estudante de biologia que orientei durante o meu mestrado recebeu o prêmio de melhor trabalho de graduação do congresso! Somente o tempo e o apoio dos amigos e familiares foi capaz de me fazer entender que isso só podia significar que o diabinho estava errado. Eu sabia, e ainda sei, que não estava pronto, porque isso de fato não existe, mas estava no caminho certo para alcançar a ciência bem-feita.

No final do ano de 2016, realizei a apresentação do meu novo projeto de doutorado, agora baseado no banco de dados em colaboração e ele foi aprovado pela comissão de acompanhamento. Além disso, em dezembro o CNPq publicou o resultado do financiamento do projeto: aprovado! Apesar de não dar mais tempo para que eu realizasse o projeto como parte da minha tese fiquei muito feliz de saber que fui capaz de escrever um projeto suficientemente inovador para ser aprovado em concorrência nacional.

Minha confiança começou a retornar no início do quarto semestre do doutorado, em 2017. Decidi trabalhar no segundo capítulo do meu mestrado para publicá-lo e iniciei todo o processo de submissão novamente. Dessa vez, apesar de ter levado bastante tempo para sair (somente em janeiro de 2018), o artigo foi aceito na segunda submissão. Novamente os revisores foram essenciais para melhorarem o texto e um aprendizado que eu já estava amadurecendo se consolidou. A ciência é, realmente, colaborativa! Os textos publicados já haviam passado pela mão de vários coautores e dos revisores. Eram muitas cabeças ali naquele texto e é assim que tem que ser. Aprendi de uma vez por todas que não se faz ciência sozinho

e que é muito legal colaborar em um trabalho e vê-lo ser recebido por outras pessoas de maneira positiva.

O ano de 2017 foi um pouco mais tranquilo e aproveitei para estudar e aprender a mexer no banco de dados para o projeto do doutorado. Participei também do programa de Docência Voluntária da UFLA, dando aulas de Ecologia Agrícola para os cursos de Agronomia e Engenharia Agrícola. Foi uma experiência extremamente positiva, apesar de ter gerado muita angústia ao longo do processo. Foi a minha primeira experiência com livre docência e aprendi muito sobre como lidar com uma classe, como conquistar a atenção e confiança dos estudantes, como preparar aulas, o que falar e o que não falar em sala, dentre diversas outras habilidades. Mas também foi extremamente angustiante perceber que a disciplina e todos os conhecimentos que eu estudei anos para passar eram para uma porcentagem muito pequena dos estudantes (talvez 10%?). A maioria dos estudantes não estava interessada em aprender. Conversando com professores de longa carreira, eu entendi que é assim mesmo. Não era minha culpa, não eram minhas aulas que eram ruins e talvez nem dos próprios estudantes; era o sistema. Além disso, foi duro perceber o buraco que a educação básica do país está enfiada: uma boa parte dos estudantes não sabia interpretar ou escrever textos. Sobre esses pontos negativos, os tomei como inspiração para tentar fazer minha parte para mudar esse cenário se e quando for um professor universitário. Apesar dessas angústias, considerei o todo da experiência muito positivo e foi realmente um aprendizado muito grande. Recomendei para todos os meus amigos da área acadêmica!

À medida que fui testando o banco de dados, percebi que teria que mudar minhas perguntas do projeto original porque elas não seriam possíveis de serem respondidas com esses dados já coletados. Conteí com muita ajuda do meu orientador e coorientador para pensarmos novas linhas de pesquisa e compor uma tese. O ano de 2017 foi de bastante tentativas e erros até começar a desenvolver o primeiro capítulo da tese. Quando cansava dessas tentativas, aproveitava para trabalhar em colaboração com um amigo, com dados coletados no mestrado, mas que não tinham feito parte da dissertação. Mais uma vez, o trabalho em equipe foi essencial para os frutos!

Ainda ao longo de 2017 e até meados de 2018, eu desempenhei uma função que considero também como um divisor de águas para meu treinamento de jovem cientista: representante discente no colegiado do Programa de Pós-Graduação em Ecologia Aplicada.

Nesse período aprendi muito sobre fazer política no sentido mais amplo da palavra, sendo o relacionamento entre diversas pessoas para atingir objetivos em comum. Dentro do colegiado, todos os membros buscam sempre a melhoria do programa de pós-graduação, mas cada um com sua visão e opinião pessoais. Sendo um membro discente e vários docentes, um dos papéis do representante discente é tentar convencer politicamente os demais membros em prol do melhoramento do programa na esfera dos estudantes. Não é uma tarefa fácil, porque os seres humanos adoram fazer parte de um grupo e assim defendem, cada qual, o seu grupo. Mesmo assim, durante todo o meu período no colegiado tive a sorte de poder debater ideias com pessoas abertas à discussão e que sempre se mostraram muito sensatas nas decisões. É uma experiência que me fez ver várias questões da pós-graduação no Brasil com outros olhos e ter uma visão muito mais ampla de problemas que muitas vezes eu nem considerava. Também sempre recomendo para os amigos da área!

Iniciando o meu antepenúltimo semestre em 2018, tive a oportunidade de tentar uma bolsa de doutorado sanduíche pela CAPES e fazer seis meses do doutorado em uma instituição estrangeira. Essa é uma oportunidade que já foi muito rara num passado distante, passou a ser até corriqueira em um passado próximo e hoje é muito rara de novo. Quem está envolvido na área sabe que a ciência não é prioridade no Brasil, então se a economia do país não vai bem, é uma das primeiras áreas a serem afetadas. Por isso me considero muito, mas muito, sortudo de ter sido premiado com a bolsa. O primeiro semestre de 2018 foi uma correria só: eu queria aproveitar para finalizar o primeiro capítulo da tese e vários projetos paralelos, além de matar a saudade antecipadamente da namorada, amigos e família. Consegui dar uma boa adiantada no capítulo da tese e finalizei a escrita do artigo em colaboração com o amigo, o qual submetemos antes da minha viagem.

O doutorado sanduíche de seis meses foi com certeza a experiência profissional mais incrível da minha, ainda curta, carreira. Eu fui para a Lancaster University, uma das dez melhores universidades do Reino Unido. Chegando lá, eu fiquei extremamente impressionado com a estrutura física da universidade, onde os prédios eram novos e os equipamentos de última geração. Fui recebido pela minha coorientadora que me mostrou o campus (muito bonito por sinal) e me deixou em um escritório com um supercomputador só para mim. Eu tinha acesso a todos os recursos que os alunos regulares da Lancaster University têm, por exemplo, os programas do Office, 2 Tb de armazenamento na nuvem, impressões e acesso à biblioteca. Apesar de achar a estrutura que tive na UFLA excelente, foi bem motivador ter acesso a mais

excelência ainda. Outra coisa impressionante é a maneira como os britânicos trabalham e poder absorver conhecimentos em um dos berços da ciência moderna, foi para mim, de enorme valor, tanto real quanto simbólico. O ambiente de silêncio e concentração do escritório também colaborou bastante para o rendimento, apesar de eu sentir falta das pausas para lanches, tão comuns na UFLA 😊.

Logo nas primeiras semanas eu consegui escrever uma versão do primeiro capítulo da tese (coisa que vinha tentando há seis meses) e o entreguei para a minha coorientadora. Dei muita sorte também dela ser uma exímia redatora e muito boa professora; ela escreveu o manual de escrita científica da British Ecological Society. Sentamos lado a lado para que ela me desse dicas de escrita científica e redação em inglês. Eu só tentava absorver o máximo que podia e realmente vi muita diferença nos meus textos seguintes. Mais para o final do ano, participei do congresso da British Ecological Society apresentando parte dos resultados do primeiro capítulo da tese. Foi muito difícil apresentar em inglês e ainda por cima na frente de grandes referências da ecologia, mas ao final me senti bastante orgulhoso. Os colegas e professores da Lancaster University me ajudaram bastante com treinamentos e apresentações prévias para treinar tanto a mensagem do capítulo quanto a pronúncia do inglês. Também no final do ano e no início de 2019, comecei a trabalhar no segundo capítulo já que faltariam seis meses quando eu retornasse do sanduíche. Para evitar muitas modificações como no primeiro capítulo, nesse segundo fizemos um planejamento mais refinado e que realmente deu bastante resultado. Dentre vários aprendizados que tive no sanduíche, a organização e planejamento minuciosos foram muito importantes.

Mesmo com tanta coisa boa no doutorado sanduíche, o caminho, obviamente, não foi só de flores. O primeiro capítulo foi MUITO difícil de terminar, porque a cada versão, descobríamos novas pontas soltas e novas abordagens para serem feitas. Outra situação que me deixava bastante apreensivo era quando me sentia perdido ao não conseguir expressar exatamente o que queria dizer em inglês. A experiência de viver em outro país com uma cultura muito diferente da nossa é fantástica e aprendi muito com os britânicos, mas confesso que mesmo com todas as partes boas, tanto científicas quanto pessoais, não é nem um pouco fácil. Parece exagero, mas lutar contra o desânimo causado pela falta de sol e pelo frio demandou uma enorme força de vontade. A própria saudade de casa, da namorada, dos amigos e da família foi algo muito presente ao longo dos seis meses. Além disso, o período em que

morei fora foi muito difícil no Brasil com um processo eleitoral marcado por polarização e violência e foi muito angustiante assistir tudo de longe. Ainda no final de 2018 perdi um amigo da UFLA, o que também me trouxe uma grande tristeza. De toda forma, acredito que voltei para Brasil mais fortalecido do que saí, tanto profissional quanto pessoalmente.

O último semestre do curso (1/2019) não podia ser nada menos do que de muito trabalho e desespero para terminar tudo a tempo. No final, deu certo! Consegui finalizar os capítulos da maneira como queria e espero que além de mim, a banca de defesa também goste do resultado final 😊. Mas junto à ansiedade de terminar o curso da melhor forma possível, vem também a ansiedade do depois. Vou ter um emprego? Estou pronto para ser um cientista? Essas e outras questões me tiraram o sono durante várias noites no último semestre. Apesar de serem questões que de fato trazem muita ansiedade, tento colocar na minha própria cabeça que o máximo que eu posso fazer é continuar trabalhando com o que gosto e estar sempre preparado para quando as portas de oportunidades se abrirem. Sorte é estar preparado para uma oportunidade quando ela aparece. E ao final do curso de doutoramento acredito ter, ao menos, aprendido a usar as melhores ferramentas para estar preparado!