VICTOR HUGO FONSECA OLIVEIRA

QUANTIFICANDO RESPOSTAS DE BESOUROS ROLA-BOSTAS A DISTÚRBIOS ANTRÓPICOS EM REGIÕES DE FLORESTAS TROPICAIS

QUANTIFYING DUNG BEETLE RESPONSES TO ANTHROPOGENIC DISTURBANCES IN TROPICAL FOREST REGIONS

LAVRAS – MG
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Orientador
Prof. Dr. Jos Barlow

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Prof. Dr. Julio Louzada

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I dedicate this thesis to my parents.

Dedication

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Above all, I thank The Lord Jesus Christ and His Creation, my family and friends for making me alive and teaching me the power of Love.

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RESUMO

As florestas tropicais sustentam a maior parte da biodiversidade terrestre e proporcionam inúmeros serviços ecossistêmicos. Entretanto, essas florestas têm sido impactadas por atividades humanas, devido às crescentes demandas por recursos para atender às necessidades humanas. Por exemplo, a Amazônia brasileira é a maior floresta tropical remanescente e, atualmente, tem uma área de aproximadamente 60 milhões de hectares convertidos em pastagens, e outros 50 milhões de hectares sob concessão madeireira. No intuito de avançar em direção a usos mais sustentáveis nessa região, devemos compreender as respostas da biodiversidade às atividades humanas, e os mecanimos através dos quais essas respostas são determinadas. Essa tese objetiva abordar essa lacuna de conhecimento através da quantificação da resposta de besouros rola bosta a mudanças antropogênicas no estado do Pará, Amazônia brasileira. No Capítulo 2, meus objetivos foram investigar respostas dos besouros rola bosta a distúrbios como corte seletivo e queimadas, e identificar características ambientais e/ou históricas influenciando os padrões observados. O Capítulo 3 avalia os impactos da conversão florestal em pastagens sobre comunidades de rola bostas, identificando os principais direcionadores da ocorrência de espécies nesse tipo de uso da terra. Finalmente, no Capítulo 4, eu avaliei a escolha de variáveis para estudos sobre besouros rola bosta e mudanças antropogênicas em paisagens tropicais, identificando lacunas entre a importância de variáveis e seu uso na literatura. Para essa tese, eu usei dados de besouros rola bosta amostrados em 273 sítios independentes, ao longo de múltiplas escalas e abrangendo florestas primárias sem distúrbio detectado, florestas primárias sob corte seletivo, florestas primárias sob corte seletivo e com registro de queimadas, florestas secundárias e pastagens introduzidas (Capítulo 2 e Capítulo 3). No total, eu amostrei 74.926 besouros rola bosta pertencentes a 149 espécies. Eu também utilizei dados de uma revisão de literatura e um questionário estruturado aplicado a 25 pesquisadores (Capítulo 4). De forma geral, eu demonstro que distúrbios antropogênicos promovem empobrecimento de comunidades de rola bostas em florestas tropicais, acompanhando as mudanças na abertura de dossel e biomassa das florestas, e também uma forte dependência de hábitats naturais abertos para servir como fontes de populações para as pastagens introduzidas. Eu também mostro que existem algumas discrepâncias em relação à importância de variáveis e seu uso nos estudos de rola bostas sobre as consequências de modificações em florestas tropicais. Por fim, eu uso os resultados dessa tese para discutir os impactos de atividades humanas em florestas tropicais, apresentando alternativas para pesquisa futura e iniciativas de manejo aplicado.

Palavras-chave: Rola bostas. Amazônia. Desmatamento. Distúrbios antropogênicos. Seleção de variáveis. Cerrado. Estocasticidade. Dossel. Biomassa sobre o solo.

ABSTRACT

Tropical forests sustain most of Earth's biodiversity and provide numerous ecosystem services. However, these forests have long been impacted by human activities, following the growing demands for resources to satisfy human needs. For instance, the Brazilian Amazon is the largest tropical forest remaining and currently has approximately 60 million ha of forests converted to pastures, and other 50 million ha under timber concession. In order to move towards a more sustainable use of this tropical forest region, we need to understand biodiversity responses to human activities, and the underlying mechanisms that determine those responses. This thesis aims to address this knowledge gap by quantifying dung beetle responses to anthropogenic changes in the Amazonian state of Pará, Brazil. In Chapter 2, my objectives were to investigate dung beetle responses to disturbances such as selective logging and wildfires, and identify environmental and/or historical characteristics influencing the observed patterns. Chapter 3 assess the impacts of forest conversion to pastures on dung beetle communities, identifying the main drivers of species occurrence in this open land-use. Finally, in Chapter 4 I assess the choice of variables for dung beetle studies on anthropogenic changes in tropical landscapes, identifying gaps between variables importance and use in the literature. For this thesis, I used data on dung beetles sampled across 273 independent sites, across multiple scales and encompassing undisturbed primary forests, logged primary forests, logged and burnt primary forests, secondary forests and introduced pastures (Chapter 2 and Chapter 3). In total, I sampled a total of 74,926 dung beetles belonging 149 species. I also, used data from a literature review and a structured survey of 25 authors (Chapter 4). Overall, this thesis demonstrate that anthropogenic disturbances promote impoverishment of dung beetle communities in tropical forests, following changes in forest canopy openness and biomass, and a strong dependence of natural open habitats to serve as source of populations for the introduced pastures. This work also shows that there are some discrepancies in relation to variables importance and use in the dung beetle studies on consequences of tropical forest modification. I use the findings from this thesis to discuss the impacts of human activities in tropical forests, presenting alternatives for future research and applied management initiatives.

Keywords: Dung beetles. Amazon. Deforestation. Anthropogenic disturbances. Variables selection. Cerrado. Stochasticity. Canopy. Aboveground biomass.

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CHAPTER 1

GENERAL INTRODUCTION

1 BACKGROUND

Tropical forests cover only 7–10% of the global land area, and are located mainly in the Amazon Basin, Congo Basin and Southeast Asia (MAYAUX et al., 2005). These forests are one of the most diverse and important ecosystems on Earth's surface (MAYAUX et al., 2005). They host approximately 50% of described species and are estimated to host an even larger number of undescribed species (DIRZO & RAVEN, 2003), providing essential ecological services to humans across the planet, including biodiversity conservation, carbon sequestration and storage, regulation of water and air quality, provision of freshwater, food and shelter, and pest and disease control (FOLEY, 2005; KLEMICK, 2011; BACCINI et al. 2012; FAO, 2020; BERENGUER et al., 2014).

Nevertheless, despite their importance, tropical forests are being deforested and degraded rapidly as the human population and global consumption levels increase (GEIST & LAMBIN, 2002; WRIGHT, 2005; LEWIS, 2009). The population of tropical regions has grown from 1.8 billion in 1950 to 4.9 billion people in 2000. Moreover, to meet burgeoning demands of a larger and more affluent population in an increasingly globalized world, large areas of rainforest have been cleared and converted to other land use systems (FOLEY et al., 2005). These human-driven land use and cover changes have accelerated over the last three centuries, and particularly in the last three decades (LAMBIN & GEIST, 2006). Indeed, tropical deforestation is one of the primary causes of global environmental change driven mainly by the expansion of agriculture, cattle-ranching and forestry, urbanization and expansion of infrastructure (GEIST & LAMBIN, 2002), and combined with the widespread degradation of remaining forests has severely compromised the provision of ecosystem services at local, regional and global scales (PARROTTA et al., 2012).

1.1 Tropical Forests

Deforestation is a process that occurs when the entire plant biota of an area is cleared (FAHRIG, 2003). The negative environmental effects resulting from deforestation include biodiversity loss (FOLEY et al., 2005; TURNER et al., 2007), reduction of genetic potential, scarcity of timber and firewood, climate change, reduction of soil fertility, increased soil erosion, changes in the water regime (FEARNSIDE, 2005) and exotic species invasions (PUIG, 2009).

In the early twentieth century, almost half of the world´s tropical forests were deforested (WRIGHT, 2005), driven overwhelmingly by agricultural expansion (ACHARD, 2002; GEIST & LAMBIN, 2002; MAYAUX et al., 2005). Between 2000 and 2005, over 27,461,500 ha were lost, representing 1.4% of humid tropical forests in the world (ASNER et al., 2009). Other estimates show that between 2000 and 2012 around 80 millions ha of humid forests were lost across the tropics, half from South America (HANSEN et al., 2013). These changes have altered the identity of landscapes across the tropics (FOLEY et al., 2005; TURNER et al., 2007).

In addition to direct forest clearance a major consequence of deforestation is forest fragmentation (FAHRIG, 2003), which refers to the degree of disruption of an originally continuous landscape unit (METZGER, 2004) and the changes in the habitat configuration as a result of habitat subdivision and isolation (FAHRIG, 2003). Fragmentation of forests has facilitated loggers and settlers to access previously remote forested areas, intensifying the pressure on remaining forests (WRIGHT, 2005; BARLOW et al., 2016)

The combination of deforestation and forest fragmentation has left large swathes of the tropics as human-modified landscape mosaics containing remnants of tropical forest immersed in a matrix of anthropogenic systems, ranging from secondary forests to introduced land uses without canopy cover (WRIGHT, 2005; LEWIS 2009). Many scholars suggest that the combination of these changes is driving a similar number of extinctions as those associated with mass extinction events in Earth's geological history (e.g. DIRZO & RAVEN, 2003; LAURANCE, 2007). In addition to biodiversity loss the clearance of tropical forests has also resulted in massive additions of carbon dioxide to the atmosphere, contributing to the acceleration of climate change (SALA et al., 2000).

1.1.1 Tropical Forest Conversion into Pastures

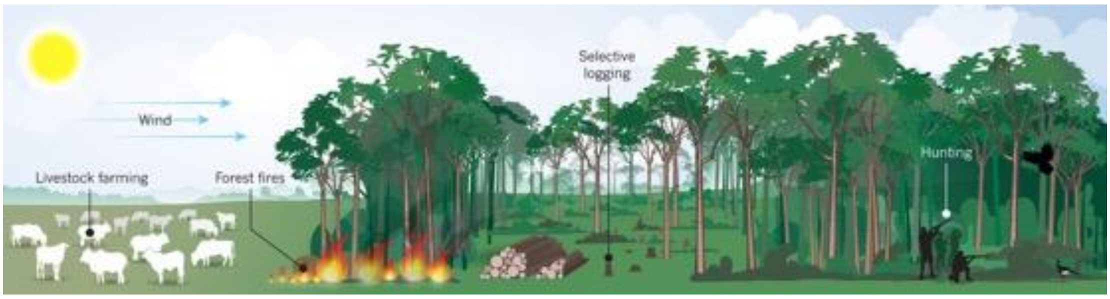
Forest clearance for agriculture is the main driver of tropical deforestation. Only in Brazil, more than 150 million hectares are covered by pastures, from which *ca.* 60 million ha are in the Brazilian Amazon (ALMEIDA et al., 2016). In this fact, Brazil plays a categorical role being responsible for the highest rates of global deforestation, while sustaining the largest and most diverse tropical forest (FAO, 2010). Recently, it has been demonstrated that this country alone could meet world's increasing demands for beef consumption without promoting further forest clearance. This would be achieved by improving its typically lowproductive pasturelands, raising from 32–34% to 49–52% its potential productivity (STRASSBURG et al., 2014). Although land-sparing appears as a practical and intuitive solution for reducing tropical deforestation and improve food security (PHALAN et al., 2011, 2016), it also could make deforestation more economically attractive and result in opposite results (BYERLEE et al., 2014). The undeniable socio-economic and ecological importance of exotic pastures, together with its long-term persistence in tropical landscapes, lead researchers to suggest it as novel ecosystems (HOBBS et al., 2006) that should no longer be neglected or considered a threat to biodiversity. Although it is still a very controversial definition (MURCIA et al., 2014; HOBBS et al., 2014; MORSE et al., 2014), it is fact that understanding the consequences of the tropical forest conversion to pastures is imperative.

1.1.2 Tropical Forest Degradation

Forest degradation can be characterized as the continuing decline or impairment in the delivery of ecosystem services due to increasing levels of unsustainable human impacts (PARROTTA et al., 2012). Degradation is a pervasive process across the tropics, driven by disturbances such as fragmentation, timber extraction, fragmentation and over-hunting, contributing to global anthropogenic carbon emissions (PARROTTA et al., 2012), and reductions in biodiversity (BARLOW et al., 2016; SOLAR et al., 2016). Estimates indicate that 2.3 million hectares of tropical forests were degraded between 1990 and 1997 (ACHARD, 2002). In Borneo, a recent study found that around 80% of forests were disturbed by high-impact logging or clearing operations from 1990 to 2009, while in the Brazilian Amazon, degradation processes impacted twice the area deforested in 2008 (INPE, 2016a, b). The impact of forest disturbance by human activities on biodiversity in one state of the Brazilian Amazon (Pará) corresponds to biodiversity estimated to be lost from the clearance of 13.9 million ha of intact forest (BARLOW et al., 2016), which is also equivalent to all deforestation identified in this state since 1988, the year in which the official monitoring of the National Institute for Space Research (INPE) started (INPE 2016b).

Although natural disturbances such as landslides and hurricanes may also contribute with forest degradation (GARWOOD et al., 1979; TANNER et al., 2014), two of the major causes of forest degradation in the tropics are logging and fire. As can be seen in Figure 1, besides contributing to biodiversity loss, forest degradation makes forests more vulnerable to edge effects, with warmer conditions and more intense winds, facilitating the occurrence of forest fires, which often lead to the spread of wildfires lit on farmlands (EDWARDS, 2016; BARLOW et al., 2016).

Figure 5- Major disturbances driving conservation losses.



Source: Reproduced from Edwards 2016.

Recently a greater focus has been given to conservation programs, such as REDD +, which supports actions such as sustainable forest management (selective and reduced impact logging) trying to avoid the consequences of forest degradation in tropical forests (PANFIL e HARVEY, 2016). However, contrary to deforestation that can be easily recognized in remote sensing imagery, forest degradation is much harder to be detected remotely (Berenguer *et al.* 2014) (Asner *et al.* 2009). For this reason, the degradation of tropical forest ecosystems has historically received much less attention than the deforestation processes, and has subsequently been overlooked by major conservation programmess (PANFIL e HARVEY, 2016).

1.1.3 The Brazilian Amazon

The Amazon is the largest remaining tropical forest in the world, occupying an area of approximately 6.9 million km2 along nine countries (BARTHEM et al., 2004). It is crucial for the conservation of biodiversity (FAO, 2011) and ecosystem services at local, regional and global scales (TRIVEDI et al., 2009). For instance, the Amazon hosts a quarter of the world’s biodiversity (DIRZO & RAVEN, 2003), has a profound influence on Earth’s temperature and rainfall patterns (LAWRENCE & VANDECAR, 2014), and provides substantial amounts of timber and non-timber (e.g. fruits, bush-meat and shelter) products for more than 31 million people (FAO, 2011).

1.2 Dung Beetles

Dung beetles are detritivorous insects from the Scarabaeinae subfamily (Coleoptera: Scarabaeidae) that rely on resources from other organisms for feeding, breeding and nesting (SPECTOR, 2006; HALFFTER & EDMONDS, 1982). They feed predominantly in feces, carcasses and decaying fruits (HALFFTER & MATTHEWS, 1966; HANSKI & CAMBEFORT, 1991). Because of their strong dependence on such resources, dung beetles communities often respond to variations in other organisms' populations, such as mammals (NICHOLS et al., 2009; CULOT et al., 2013). They play a key role in a number of ecological functions, such as nutrient cycling, secondary seed dispersal and parasite suppression (NICHOLS et al.; 2008) associated with their characteristic habit of making balls from food resources and burying them underground (HANSKI & CAMBEFORT, 1991). A recent study suggests that dung beetles also have a potential effect in reducing the emission of methane gas from cattle feces (PENTTILÄ et al., 2013; SLADE et al., 2016).

1.2.1 Responses to Tropical Forest Conversion and Degradation

Over the past 15 years, there has been increasing attention given to the impacts of tropical forest modification on dung beetles. These insects are highly sensitive to forest conversion to production systems, such as *Eucalyptus* plantations (GARDNER et al., 2007; BARLOW et al., 2007), cattle ranches (HORGAN, 2008) and agricultural systems in general (NICHOLS et al., 2007; QUINTERO, I.; HALFFTER et al., 2009; KORASAKI et al., 2013). Moreover, they respond to subtle changes in forest quality, such as those resultant from selective logging activities (SLADE et al., 2011; FRANÇA et al. in press), wildfires (ANDRADE et al., 2011; BARLOW et al., 2012) and hunting activities (NICHOLS et al., 2009). Overall, variations in dung beetle communities in response to tropical forest modification include reduction in species richness, changes in abundance distributions – with less and smaller species becoming hyper-abundant (NICHOLS et al., 2007), reduction in species turnover (SOLAR et al., 2015), loss of functional guilds and changes in the provision of ecosystem functions (NICHOLS et al., 2008, BRAGA et al., 2013). Despite a predominance of small-scale studies addressing this subject (NICHOLS et al., 2007), recent large-scale and highly replicated researches corroborates such general patterns of dung beetle response to forest modification (BRAGA et al., 2013; SOLAR et al., 2015; BARLOW et al., 2016).

1.2.2 Use as indicator of Environmental Changes

The use of dung beetles to indicate environmental changes and measure their potential impacts on biodiversity is a growing research field, mainly due to beetles' high diversity, widespread distribution, sensitivity to habitat modifications, and low costs of sampling (GARDNER et al., 2008; NICHOLS & GARDNER, 2011). For instance, dung beetles have recently been used in a multi-taxa assessment of the consequences of Amazonian forest degradation, and contributed to the identification of strong negative impacts of selective logging and wildfires in primary forests (BARLOW et al., 2016). Although the usefulness of these insects to indicate environmental changes is verified, some of the mechanisms underlying variations in dung beetle communities are not well known. For instance, it is still not clear which are the specific drivers (i.e. environmental, historical and spatial) of their diversity, and how these drivers influence dung beetles at local, landscape and regional scales. In part, this may be due to a lack of clear information about studies' scales, and a general absence of environmental measures, reducing the potential for extrapolating studies' results (NICHOLS et al. 2007).

1. 3 The Sustainable Amazon Network

This thesis was written as part of the Sustainable Amazon Network (RAS, http://www.redeamazoniasustentavel.org), a multidisciplinary research initiative focused on understanding the environmental and socio-economic trade-offs in the Brazilian Amazon (GARDNER et al., 2013). The RAS network collected ecological and socioeconomic data along broad gradients of human land use, allowing comparisons of environmental impacts and land-use sustainability at local, landscape and regional scales. An international and diverse group of research and non-research partners actively collaborates in the network. For this reason, the three papers to be submitted from this thesis will include other co-authors, mainly: my supervisor Dr Jos Barlow (Lancaster University), my co-supervisors Dr Julio Louzada (UFLA) and Dr Toby Gardner (Stockholm Environment Institute), and my research partners Dr Ricardo Solar (UFMG), Dr Rodrigo Braga (UFLA), Dr Erika Berenguer (Lancaster University) and Dr Joice Ferreira (EMBRAPA) for their significant contributions to RAS and, more specifically, to this thesis since my initial work during my MSc thesis, also conducted under RAS, since 2009.

1.4 Data sampling

Most of the data supporting this thesis was collected during field work conducted in 2010 and 2011. In each region, we sampled dung beetles in 18 catchments (landscapes scale) along the main land-use and cover classes (including. undisturbed and disturbed primary forests, secondary forests and introduced pastures). The number of transects (local scale) sampled per land-use and cover classes was proportional to their cover in each catchment (GARDNER et al., 2013). Dung beetle samples were conducted using pitfall traps baited with a mix of human:pig dung at 1:4 ratio.

The environmental predictors used in this thesis were measured following the same study design highlighted in Gardner et al., 2013. Methodological details of environmental measurements are provided by Berenguer et al., 2014 and Carvalho et al., 2016.

1.5 Thesis Aim and Structure

My main goal in this thesis is the quantification of dung beetle responses to anthropogenic changes in tropical forests. I address this topic in three data chapters that have been written for publication, constituting in stand-alone and multi-authored pieces of work focused on different aspects of a central theme. I intend to submit Chapter 2 and 3 for review and publication. Chapter 4 is currently under revision for *Basic and Applied Ecology* following receipt of initial reviewer comments.

Chapter 2 focuses on beetle responses to tropical forests disturbance. I use samples of dung beetles and measurements of eight environmental variables from 112 transects of undisturbed, logged and burnt forests and secondary forests regenerating on cleared land, to answer two main questions: (1) *How do dung beetle communities respond to a gradient of anthropogenic forest disturbance?* (2) *Which environmental variables related to forest disturbance best predict dung beetle species richness, abundance, composition and structure?*

Chapter 3 is focussed on assessing dung beetle assemblages in introduced pastures on deforested areas, a major human land use associated with deforestation across the tropics. In this chapter, I use data sampled in 261 introduced pastures and forests of two tropical human-modified regions to answer four questions: (1) *To what extent are dung beetle communities in pastures different from the surrounding forests communities?* (2) *What is the provenance of dung beetle species that are significant and consistent indicators of pastures?* (3) *To what extent is the richness, abundance, species composition and structure of dung beetle* *communities in pastures determined by local, landscape or spatial factors?* (4) *Are the patterns observed while answering all these questions consistent between two discrete study regions*?

Chapter 4 is based on information compiled from a literature review and a structured survey of the authors of 48 studies concerning dung beetle responses to anthropogenic changes in tropical landscapes. In this chapter, I ask two main questions regarding variables choice for dung beetle studies: (1) *To what extent are the response and explanatory variables deemed most appropriate by researchers actually being selected in published studies*? (2) *To what extent is the variable choice and study design processes clearly justified, and, if so, what kind of justification is presented in published work*? I address these questions separately for studies on forests and open agricultural lands because these systems are structurally divergent and host significantly different dung beetle communities determined by different factors (see Chapter 2 and Chapter 3).

I summarise the main findings from the three data chapters in Chapter 5 and discuss their importance for tropical biodiversity conservation and research. Finally, I present other outcomes from the data and ideas hereafter discussed - all of which I made significant contributions - including two multi-taxa published papers on biotic homogenisation (Appendix 1) and biodiversity loss (Appendix 2) from anthropogenic disturbances in tropical forests. I also present three published papers (Appendices 5) providing extra details on the sampling methods and variables used for analyses in Chapter 2 and Chapter 3.

CHAPTER 2

QUANTIFYING DUNG BEETLE COMMUNITY RESPONSES TO TROPICAL FOREST DISTURBANCE IN THE EASTERN AMAZON

ABSTRACT

Context: Tropical forests around the world are under continuous and increasing pressures from human activities. Although the biodiversity consequences of forests clearance are well studied, historically little attention has been given to the impacts of less evident human activities (e.g. selective logging) promoting forests degradation.

Objectives: We investigated the impact of anthropogenic forest disturbances on dung beetle communities in the Brazilian Amazon.

Methods: We used data on dung beetles and eight disturbance related environmental predictors sampled across 112 transects encompassing undisturbed primary forests, logged primary forests, logged and burnt primary forests and secondary forests regenerating from previous agricultural use. Dung beetles were sampled using baited pitfall traps.

Results: We sampled a total of 17,260 dung beetles from 83 species. Dung beetle communities were highly sensitive to human disturbances, with disturbed primary forests and secondary forests presenting reduced diversity and differences in composition and structure in comparison to undisturbed forests. Changes in dung beetle communities were mainly associated to variations in forests canopy openness and biomass.

Conclusions: Our study demonstrate that dung beetles are sensitive to anthropogenic disturbances in tropical forests, even at finer scales (i.e. within primary forests). Our findings highlight the need to incorporate the monitoring of tropical forest degradation to conservation initiatives aiming at protecting the Amazonian biodiversity. We suggest that, at least for dung beetles, it could be possible to assess forests quality by remotely measuring forests canopy openness and biomass.

Keywords: Degradation. Amazon. Biodiversity loss. Canopy. Aboveground biomass. Forest productivity. Dung beetles.

1 INTRODUCTION

The world’s remaining tropical forests are increasingly disturbed by human activities such as selective logging, wildfires, edge effects and extraction of non-timber products (e.g. bush meat). There is mounting evidence that the combined effect of these can be as harmful to biodiversity as deforestation when assessed across large spatial scales: a recent study carried out in the Brazilian Amazon showed that the number of species of dung beetles, birds and plants lost to disturbances such as fire and logging is comparable to the expected loss of species to deforestation across the study region (BARLOW et al., 2016). In providing the first robust comparison of the effects of deforestation and forest disturbances this study conclusively demonstrated that, to effectively protect biodiversity, conservation initiatives must move beyond simply preventing clearances and strive to prevent and reverse the effects of degradation. This is particularly important given that much of the world´s existing tropical forests are subject to anthropogenic disturbances (GARDNER et al., 2009).

However, forest disturbance is more difficult to measure than deforestation (e.g. PERES et al., 2006), and is neglected in many conservation programmes (PANFIL & HARVEY, 2016). Thus, many forms of disturbance such as selective logging may take a long time to be detected in satellite images, demanding meticulous investigation of images and field confirmation to be qualified and quantified (BERENGUER et al., 2014). Also, forest disturbance is not necessarily correlated with deforestation (ARAGAO & SHIMABUKURO, 2010; MORTON et al., 2013). For instance, within the same time frame it was registered a decrease of 22% of deforestation in the Brazilian Amazon and an increase of 213% of forest degradation (HAYASHI et al., 2010).

Despite recent advances on biodiversity consequences of forest degradation (BERENGUER et al., 2014; SOLAR et al., 2015; BARLOW et al., 2016), more studies are needed since previous assessments were mostly conducted at local scale (TABARELLI et al., 2012) or focused on one type of disturbance. As such, these studies may limit our understanding of disturbance across human-modified tropical forest landscapes, and preventing us to evaluate the effectiveness of current policy interventions, particularly for the conservation of biodiversity at larger scales.

Here, we examined the implications of anthropogenic disturbance by undertaking a multi-scale diversity assessment in 112 transects of variable forest quality (i.e. from undisturbed primary forests to secondary forests) of a large (ca. 20,000 km2) human-modified region of the Brazilian Amazon. This biome corresponds to a third of Earth’s tropical forests, hosts one quarter of the described terrestrial species (DIRZO & RAVEN, 2003) and is being threatened by agricultural expansion, cattle ranching activities, selective logging and building of dams (FEARNSIDE, 2015). Many of these activities leave the forests vulnerable to fires which are become increasingly prevalent in the severe dry seasons being faced by the Amazon (ARAGÃO et al., 2014) (e.g. EL NIÑO, see ALENCAR et al., 2015).

We used dung beetles as our focal study taxon because of their cost-effective responses to environmental changes (GARDNER et al., 2008) and high importance in nutrient cycling, soil aeration, soil fertilization and other ecological processes (NICHOLS et al., 2008). We address two specific questions: First, how do dung beetle communities respond to a gradient of anthropogenic forest disturbance? Second, which environmental variables related to forest disturbance best predict dung beetle species richness, abundance, composition and structure? Taken together, these analyses provide a quantitative understanding of the environmental drivers of dung beetle communities in one of the most species-rich areas of the planet, and can help provide a basis for predicting the biodiversity consequences across the human-modified forest landscapes of the future.

2 MATERIAL AND METHODS

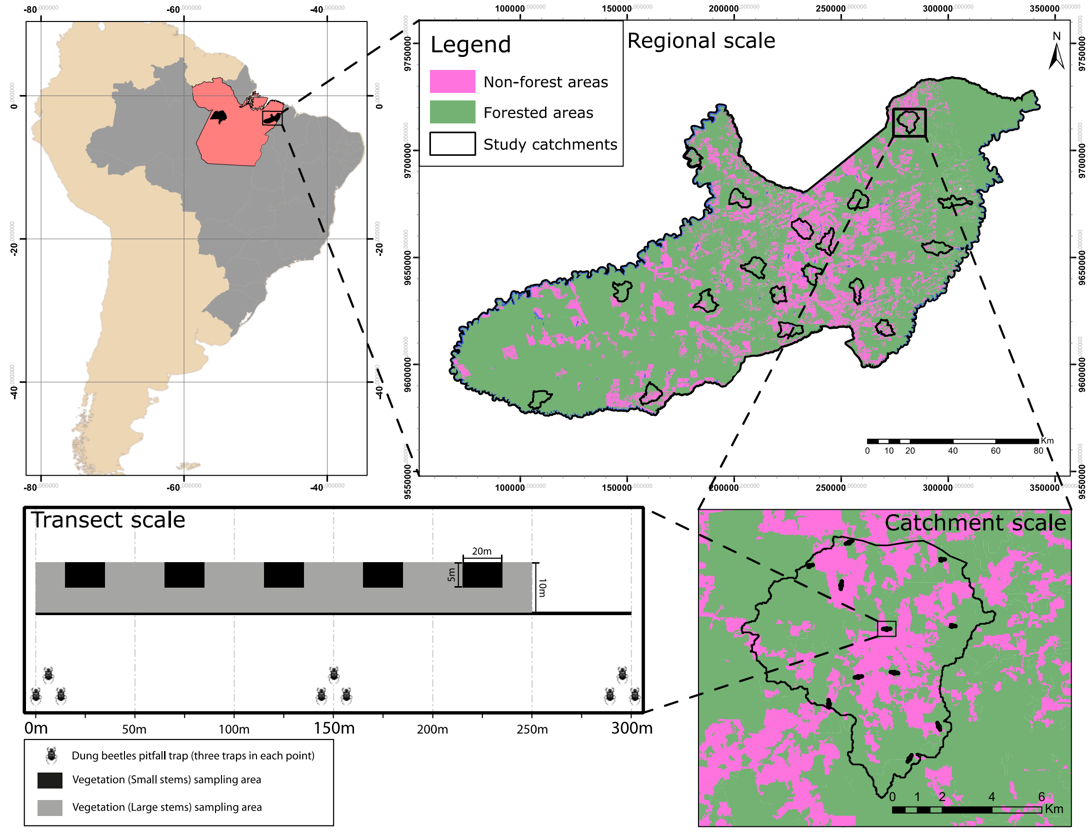
We conducted our study in the municipality of Paragominas. We sampled 112 forest transects, comprising the following gradient of forest degradation:

(a) Undisturbed primary forests (UPF, n = 9): well preserved primary forests with no detectable evidence of past anthropogenic disturbance.
(b) Logged primary forests (LPF, n = 44): primary forests subject to logging activities but with no detectable evidence of wildfire.
(c) Logged and burnt primary forests (LBPF, n = 42): primary forests subject to logging activities and fire events evidenced by scars on trees and/or by satellite images (Gardner *et al.* 2013).
(d) Secondary forests (N = 17): regenerating forests after complete clearance for agriculture.

2.1 Sampling Design

We used the *Soil and Water Assessment Tool* (SWAT) for ArcGIS to divide the studied region in 18 landscapes of *ca* 5000 hectares. We set 300 m long transects in forests within each landscape, at a maximum density of 1 transect / 400 hectares. The number of transects in each forest class was proportional to the overall area occupied by them within each catchment (Fig.1). Further details on the study sites are available in (GARDNER et al., 2013).

Figure 1 - Studied region of Paragominas (*ca.* 1.9 million ha) (Pará state, Brazil). Map of the sampling design for dung beetles and predictor variables in primary and secondary forests. We stratified our sampling in catchment and transect scales.



Source: Author

2.2 Sampling of Dung Beetles

We sampled dung beetles between April and June in 2010, using baited pitfall traps active in the field for 48 hours. This method is widely used in assessments of land use changes effects on dung beetles around the world. Each trap was made of plastic (diameter: 18 cm; height: 15 cm) and covered by a lid – to protect from the rain. We used 50 g of a mixture of 20:80 human:pig dung ratio as bait, which is ideal for dung beetle studies in the Amazon (MARSH et al., 2013). Each pitfall was filled with 250 ml of a saline solution (w/ detergent) in order to kill the insects and preserve their body parts while they were trapped. We sorted and identified all sampled dung beetles to the lowest taxonomic levels possible. A specialist in taxonomy of dung beetles, Dr Fernando Vaz de Mello, validated our identifications. Voucher specimens are deposited at the *Coleção de Escarabeíneos*

Neotropicais at the *Universidade Federal de Lavras* (BRA) and at the Zoological Collection of the *Universidade Federal do Mato Grosso* (BRA).

2.3 Sampling of Predictor Variables

We measured 08 environmental variables that represent a broad range of the changes that can take place after anthropogenic forest disturbance (Table 1). Data about forest structure (e.g. canopy openness, total aboveground biomass) was obtained from measurements made within transects (for more details, see BERENGUER et al., 2014). Deforestation curvature profile (DEFOR) was calculated in 500 m buffers by analysing time-series of satellite images (FERRAZ et al., 2009) (for more details, see GARDNER et al., 2013). Mean dry weight of duff samples (DUFF) and total aboveground biomass in leaf litter (AGBLT) were highly correlated with canopy openness (CANOPY) (Pearson $\rho = 0.62$) and total aboveground biomass (TOAGB) (Pearson $\rho = 0.97$) (Fig S1), respectively. The former variables were removed from the analyses (ZUUR et al., 2010) leaving six predictor variables (Table 1).

Table 1 - Selected environmental variables representing anthropogenic forest disturbance in primary and secondary forests of Paragominas (Pará, Brazil). For more details, see Gardner et al. (2013).

Variable	**Description**
PFCOV	Percentage of undisturbed primary forest in 1km buffer
DEFOR	Deforestation curvature profile in 500m buffer
CANOP	Mean canopy openness at the transect level
TOAGB	Total aboveground biomass at the transect level
AGBFW	Total aboveground biomass in fine wood debris at the transect level
UNDEN	Average density of understory stems (> 2 < 10 cm dbh) dead or alive, all life forms, at the transect level

Source: Author

2.4 Statistical Methods

We followed three steps to assess dung beetle communities’ responses to anthropogenic forest disturbance. First, we used generalised linear mixed models (GLMM; BOLKER et al., 2009) with forest classes (i.e. UPF, LPF, LBPF, SEF) as the explanatory variables, the 18 catchments as the random factor, and dung beetle species richness and abundance ($\log_{abundance}+1$) as response variables. We submitted the models to contrast analysis, combining statistically similar classes (CRAWLEY, 2013). Second, we compared richness from a rarefied curve (n = 9, the amount of transects in the least sampled forest class) with extrapolated sample-based curves (n = 44, the amount of transects in the most sampled forest class) because comparisons of regional diversity could be potentially biased by variations in the number of samples in each forest class. We acknowledge that extrapolation beyond three-times the sample size can be unreliable (COLWELL et al., 2012). We used presence/absence data (Hill numbers of order 0) and incidence data (Hill numbers of order 1) for extrapolations, in the attempt to reduce potential bias caused by rarely sampled species (CHAO et al., 2014). We considered non-overlapping confidence intervals as having accumulated different number of species. Finally, we used non-metric multidimensional scaling (NMDS) of individual transects to examine variation in dung beetle communities composition and structure, based on presence/absence (with Jaccard's dissimilarity index) or abundance (with Bray-Curtis dissimilarity index) data, respectively. NMDS was followed by analysis of similarity (ANOSIM) and a multivariate dispersion analysis (PERMDISP) to assess communities similarity and dispersion.

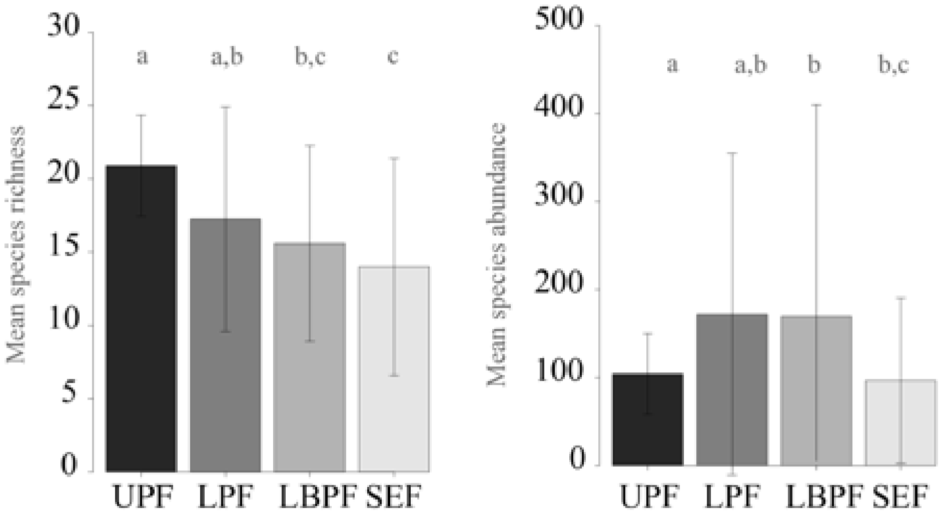
To identify the environmental variables affecting dung beetle species richness and abundance, and communities composition and structure, we used multi-model inference followed by model selection (BURNHAM et al., 2011). From derivations of a full model (with all explanatory variables), we averaged coefficients of all models within $\Delta AICc < 4$, capturing greater uncertainty in the final set of candidate variables (VIERLING et al., 2013). We calculated the relative importance of each explanatory variable on the multimodel inference (BURNHAM et al., 2011), indicating their contribution on the possible models. We used Poisson distribution whenever the response variable was species richness, and $\log_{abundance}+1$ for species abundance, correcting models for over-dispersion if required. For communities composition and structure (NMDS Axis 01) we used Gaussian distribution. We performed all analyses in the platform R (R Development Core Team 2016).

3 RESULTS

3.1 Dung Beetles Species Richness in Different LUCC

We recorded a total of 17,260 dung beetles from 83 species and 23 genera (Table S1). Species richness at the transect scale was significantly higher in UPF forests than in LBPF ($x^2 = 7.15$, $p = 0.03$) and SEF ($x^2 = 9.38$, $p = 0.01$), and higher in LPF than in SEF ($x^2 = 4.53$, $p = 0.09$) (Fig 2.2), but did not vary within the remaining forest classes. Species abundance was significantly higher in UPF and LPF forests than in SEF ($x^2_{undisturbed} = 7.06$, $p_{undisturbed} = 0.03$; $x^2_{logged} = 9.30$, $p_{logged} = 0.01$), but did not vary within the remaining forest classes (Fig 2).

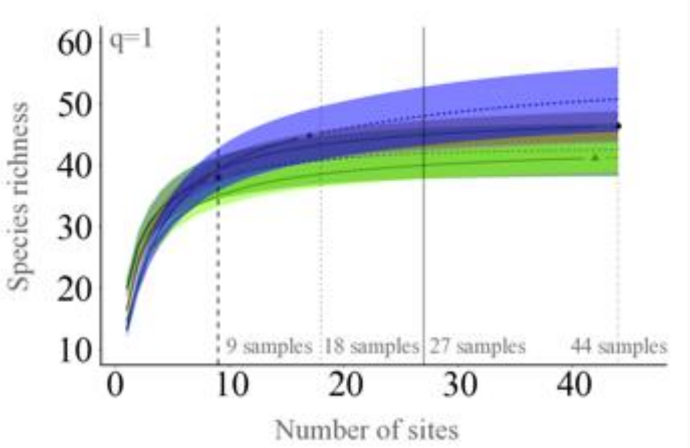
Figure 2 - Dung beetle mean species richness (left) and abundance (right) per forest classes, at the scale of individual transects, in Paragominas (Pará, Brazil). Forest classes grouped with the same letter are statistically similar (p>0.05). UPF – undisturbed primary forests; LPF – logged primary forests; LBPF – logged and burnt primary forests; SEF – secondary forests.



Source: Author

Extrapolated species accumulation curves did not reveal any differences in dung beetle species richness among forest classes at the landscape scale (Fig 3).

Figure 3 - Dung beetle species richness per forest classes, considering accumulation curves with extrapolated values per for classes for abundance data. Shaded polygons around each curve represent 95% confidence intervals. Curves represent estimated valued for undisturbed primary forests (squares), logged primary forests (circles), logged and burnt primary forests (triangles) and secondary forests (diamonds).



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3.2 Species Composition and Structure

ANOSIM and PERMDISP revealed that dung beetles differ regarding to community composition and structure across all the forest classes, and regarding community dispersion between UPF (lowest dispersion) and the remaining forest classes – which did not differ among themselves (Tables S2-S3). These differences can be visually assessed in the NMDS plots. Plots also reveal how the dung beetle communities' composition and structure varies along Axis 1 following gradients of aboveground biomass (i.e. decreasing from UPF to SEF) and canopy openness (i.e. increasing from UPF to SEF) (Fig 4).

Table 2 - Results of ANOSIM and PERMDISP testing for dung beetle community composition and dispersion among forest classes. Global R = 0.194.

GROUPS	**ANOSIM**		**PERMDISP**	
	R Statistic	**Significance**	**t**	**P(perm)**
Undisturbed - Logged	0.297	<0.01	30.28	<0.01
Undisturbed - LoggedBurnt	0.436	<0.01	3.13	<0.01
Undisturbed - Secondary	0.382	<0.01	51.67	<0.01
Logged - LoggedBurnt	0.092	<0.01	84.50	0.99
Logged - Secondary	0.266	<0.01	1.87	0.11
LoggedBurnt - Secondary	0.143	0.03	1.91	0.09

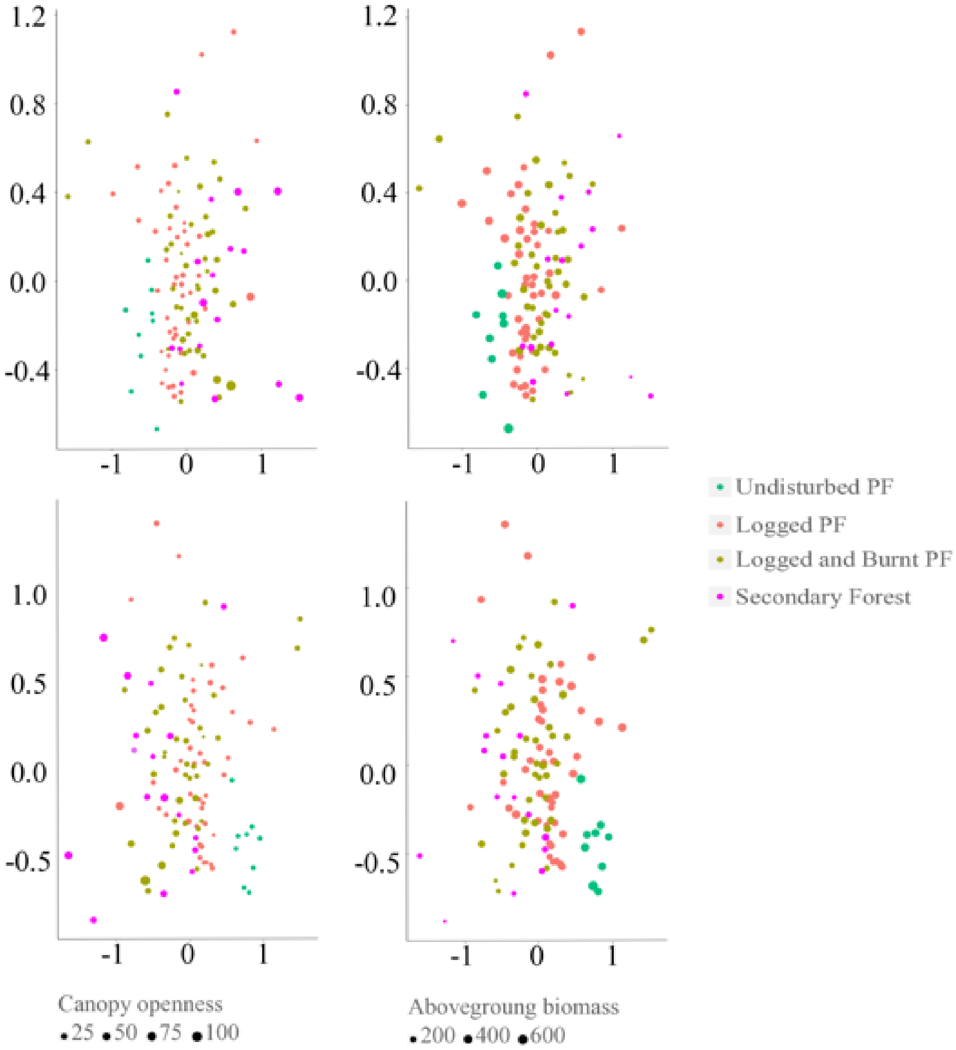
Source: Author

Table 3 - Results of ANOSIM and PERMDISP testing for dung beetle community structure and dispersion among forest classes. Global R = 0.194.

GROUPS	**ANOSIM**		**PERMDISP**	
	R Statistic	**Significance**	**t**	**P(perm)**
Undisturbed - Logged	0.381	<0.01	25.80	0.03
Undisturbed - LoggedBurnt	0.459	<0.01	39.57	<0.01
Undisturbed - Secondary	0.485	<0.01	58.44	<0.01
Logged - LoggedBurnt	0.091	<0.01	1.36	0.22
Logged - Secondary	0.315	<0.01	22.84	0.06
LoggedBurnt - Secondary	0.151	0.02	14.23	0.21

Source: Author

Figure 4 - NMDS plots of dung beetle communities' composition (top) and structure (bottom) per forest classes (point colors) according to canopy openness (left) and total aboveground biomass (right). Point sizes represent the values of predictors in each transect.

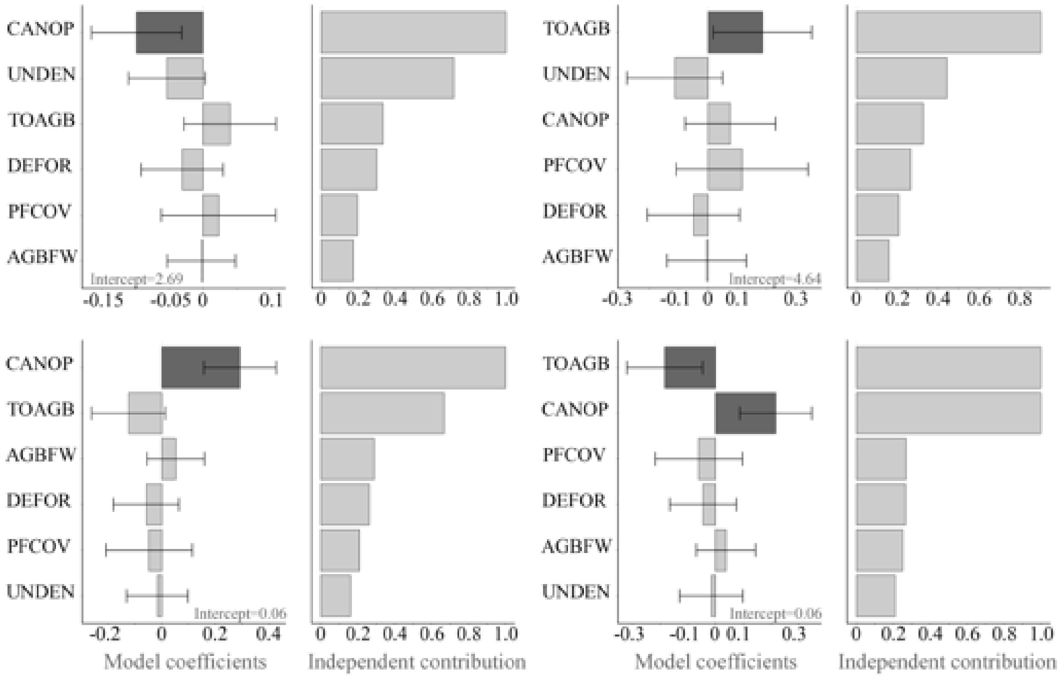


Source: Author

3.3 Environmental Predictors of Dung Beetle Diversity

Canopy openness explained variation in species richness (Best model R^2: 0.83; Relative variable importance: 0.99), composition (R^2: 0.49; 1.00) and structure (R^2: 0.49; 1.00) across all plots (Fig 5). Aboveground biomass explained variations in species abundance (R^2: 0.74; 0.90) and structure (R^2: 0.49; 1.00) (Fig 5). None of the four environmental variables remaining significantly explained differences in dung beetles across forest disturbance classes (i.e. the confidence intervals of the co-efficient all extend across zero). The complete set of models generated for all response variables is available in Supplementary material (Tables S2 – S5).

Figure 5 - Model averaging of candidate models within ΔAICc < 4 for transect scale dung beetle species richness and abundance (top) and communities' composition and structure (bottom). Averaged coefficients are shown on the left side, relative variables importance is shown on the right side. Predictor with significant effects on response variables are highlighted in dark grey. AGBFW – aboveground biomass; CANOP – canopy openness; DEFOR – deforestation curvature profile around transects; PFCOV – percentage of undisturbed primary forests around transects; TOAGB – total aboveground biomass; UNDEN – density of understory stems.



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4 DISCUSSION

Our assessment of dung beetle responses to anthropogenic disturbances in the Amazon examined samples from 112 transects across a continuum of forest disturbance encompassing undisturbed, logged, and logged and burned primary forests, as well as secondary forests recovering on land previously used for agriculture. We show that dung beetle communities are negatively affected by primary forest degradation and conversion, reflecting changes in canopy openness and total aboveground biomass. We discuss these results highlighting the impacts of different forms of forest disturbance on dung beetles and the potential implications of our findings for biodiversity conservation and research on this important invertebrate group in tropical forests.

4.1 Dung Beetle Responses to Anthropogenic Disturbances

Overall, dung beetle communities in primary forests disturbed by logging and/or burning and regenerating forests presented lower species richness per local (α-diversity) and greater variation in composition and structure than undisturbed forests. Although there was no variation in species richness at the landscape level (ß-diversity) among the different forest classes (Fig 3), this may be explained by sample design and the mechanisms that underpin ß-diversity. First, the legacy of land-use change in the region means that our undisturbed forest samples were inevitably restricted to a much smaller area than the disturbed forest samples. As such, the undisturbed sites likely captured a smaller portion of the gradient of naturally occurring ß-diversity than the disturbed sites, artificially reducing the overall estimate of gamma diversity. Second, the mechanisms that underpin ß-diversity in undisturbed forests highlight their higher diversity: previous analysis of these datasets revealed how ß-diversity in undisturbed primary forests was almost two times more determined by turnover of species among sites than in disturbed and regenerating forests, reflecting a trend towards biotic homogenisation in more disturbed forests (SOLAR et al., 2015).

Our results show that secondary forests contain different communities from those in undisturbed and disturbed primary forests (i.e. reduced dung beetle species richness and different community composition and structure). This reinforces evidence suggesting that regenerating forests provide fewer benefits for the conservation of tropical biodiversity than disturbed primary forests (e.g. GIBSON et al., 2011), and we show that this is applied even when the latter have been both logged and burned. Clearance of forest is often followed by the introduction of agricultural systems that can favour local colonisation by species from non-forest habitats (Chapter 03) and the exclusion of forest interior species. We acknowledge that regenerating forests play a critical role in conserving biodiversity in many tropical regions (LETCHER e CHAZDON, 2009) and their importance should not be neglected. However, our results also underscore the importance of maintaining primary forests where they remain, especially those little or not impacted by human activities (BICKNELL et al., 2014), due to their irreplaceable value for conserving tropical diversity.

4.2 Environmental Drivers of Change in Dung Beetle Communities

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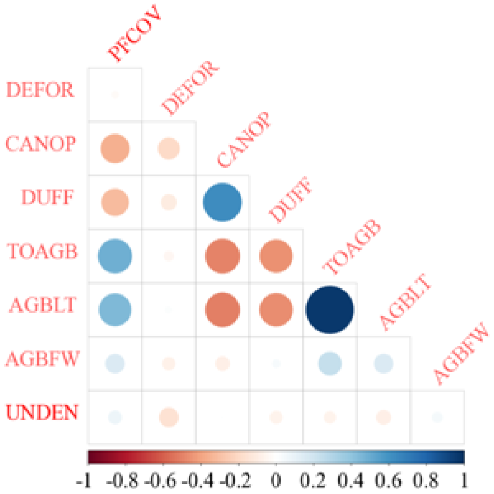
5 CONCLUSION

1. Canopy openness and total aboveground biomass seem adequate for predicting dung beetle diversity in disturbed forests. Because both predictors can be estimated using optical satellite imagery (e.g. canopy openness) and airborne LiDAR (forest biomass), monitoring their variation could help assist in understanding variation in forest condition, contributing towards the monitoring of policy effectiveness and the design of forest conservation strategies.
2. While supporting the irreplaceability of primary forests (GIBSON et al., 2011) for the conservation of tropical biodiversity.

SUPPLEMENTARY MATERIAL

Figure S 1 - Person correlations among the environmental variables measured in this study. AGBFW – aboveground biomass; CANOP – canopy openness; DEFOR – deforestation curvature profile around transects; PFCOV – percentage of undisturbed primary forests around transects; TOAGB – total aboveground biomass; UNDEN – density of understory stems; DUFF – mean dry weight of duff samples; AGBLT – aboveground biomass in leaf litter.



Source: Author

Table S 1 - List of dung beetle species collected in primary and secondary forests at Paragominas (Pará, Brazil) using baited pitfall traps. UPF – undisturbed primary forests; LPF – Logged primary forests; Logged and burnt primary forests; SEF – Secondary forests.

SPECIES	**REFERENCE**	**UPF**	**LPF**	**LBPF**	**SEF**
Anomiopus aff. *foveicollis*		0	1	0	0
Ateuchus sp.1		49	5	0	2
Ateuchus sp.2		3	11	0	1
Ateuchus sp.3		19	485	380	75
Ateuchus sp.4		3	0	0	0
Ateuchus sp.5		12	10	19	1
Bdelyrus sp.1		0	1	0	0
Canthidium aff. *lentum*		11	104	331	27
Canthidium funebre	Balthasar, 1939	2	1	0	0
Canthidium gerstaeckeri	Harold, 1867	13	45	104	8
Canthidium humerale	Germar, 1813	0	1	6	0
Canthidium semicupreum	Harold, 1868	5	25	13	1
Canthidium sp.1		15	14	32	26
Canthidium sp.10		5	1	0	1
Canthidium sp.11		0	0	1	0
Canthidium sp.12		0	0	0	0

To be continued …

Continuation …

Canthidium sp.2		0	7	24	3
Canthidium sp.3		1	0	0	0
Canthidium sp.4		46	99	7	15
Canthidium sp.5		13	566	508	107
Canthidium sp.6		2	20	0	0
Canthidium sp.7		1	1	0	0
Canthidium sp.8		1	0	0	0
Canthidium sp.9		24	0	0	0
Canthon aff. *sericatus*		0	1	1	1
Canthon aff. *simulans*		0	2	16	0
Canthon coeruleus		0	45	34	13
Canthon histrio	LePeletier and Serville, 1828	0	0	54	15
Canthon lituratus	Germar, 1813	0	0	90	22
Canthon proseni	Martinez, 1949	2	119	47	5
Canthon scrutator	Balthasar, 1939	0	0	35	11
Canthon sp.1		0	0	0	1
Canthonella sp.1		0	1	1	0
Coprophaneus dardanus	Macleay, 1819	6	0	3	3
Coprophaneus degallieri	Arnaud, 1997	9	6	2	0
Coprophaneus jasius	Olivier, 1789	5	1	0	2
Coprophaneus lancifer	Linnaeus, 1767	0	63	40	28
Cryptocanthon campbellorum	Howden, 1973	0	58	18	4
Deltochilum aff. *sextuberculatum*		3	18	69	7
Deltochilum carinatum	Westwood, 1837	0	4	1	0
Deltochilum enceladus	Kolbe, 1893	0	42	45	10
Deltochilum icarus	Olivier, 1789	3	10	23	3
Deltochilum orbiculare	Lansberge, 1874	0	99	47	9
*Deltochilum scheffleroru*m	* sp. nov.	0	5	0	0
Deltochilum sp.1		10	119	224	9
Diabroctis mimas	Linnaeus, 1758	0	5	61	35
Dichotomius aff. *globulus*		3	1540	527	299
Dichotomius aff. *lucasi*		26	16	28	20
Dichotomius boreus	Olivier, 1789	13	145	144	32
Dichotomius imitator	Felsche, 1901	0	4	6	1
Dichotomius inachus	Erichson, 1847	0	85	46	54
Dichotomius longiceps	Taschenberg, 1870	0	0	0	1
Dichotomius melzeri	Luederwaldt, 1922	1	36	106	13

To be continued …

Conclusion

Dichotomius telamon	Harold, 1869	1	23	40	12
Dichotomius worontzowi	Pereira, 1942	1	16	14	2
Digitontophagus gazella	Fabricius, 1787	0	7	1	0
Eurysternus atrosericus	Génier, 2009	0	9	1	1
Eurysternus caribaeus	Herbst, 1789	11	469	644	66
Eurysternus cavatus	Génier, 2009	9	88	84	5
Eurysternus foedus	Guérin-Méneville, 1844	5	45	27	5
Eurysternus hamaticollis	Balthasar, 1939	1	37	2	5
Eurysternus harlequin	Génier, 2009	0	1	0	0
Eurysternus howdeni	Génier, 2009	0	3	1	0
Eurysternus hypocrita	Balthasar, 1939	1	4	7	0
Eurysternus ventricosus	Gill, 1990	0	13	5	2
Eurysternus wittmerorum	Martinez, 1988	3	76	26	2
Eutrichillum sp.1		1	2	1	2
Hansreia affinis	Fabricius, 1801	16	152	5	17
Ontherus sulcator	Fabricius, 1775	1	12	294	107
Onthophagus aff. *hirculus*		0	259	119	65
Onthophagus onthochromus	Arrow, 1913	0	23	6	4
Ontophagus ophion	Erichson, 1847	26	365	269	25
Onthophagus rubrescens	Blanchard, 1843	153	1864	841	189
Oxysternon macleayi	Nevison, 1892	308	144	153	11
Oxysternon silenus	Castelnau, 1840	6	35	34	1
Phanaeus chalcomelas	Perty, 1830	41	8	5	1
Pseudocanthon aff. *xanthurus*		0	1	12	4
Sulcophanaeus faunus	Fabricius, 1775	1	2	1	4
Trichillum externepunctatum	Preudhomme de Borre, 1880	0	7	1	1
Trichillum pauliani	Balthasar, 1939	3	3	21	12
Trichillum sp.1		42	15	1427	226
Uroxys sp.1		1	16	10	3
Uroxys sp.2		0	11	0	0
Uroxys sp.3		0	6	3	2

Source: Author

Table S 2 - AICc-based model selection for transect dung beetle species richness among forest classes. Here are listed all possible variables in the models with ΔAICc < 4, followed by model R^2, degrees of freedom (df), model log-likelihood (logLik), AICc, ΔAICc, model weight (ω) and cumulative model weight. AGBFW – aboveground biomass; CANOP – canopy openness; DEFOR – deforestation curvature profile around transects; PFCOV – percentage of undisturbed primary forests around transects; TOAGB – total aboveground biomass; UNDEN – density of understory stems. In black, all models within ΔAICc < 4 and in grey all other models.

Intercept	**AGBFW**	**CANOP**	**DEFOR**	**PFCOV**	**TOAGB**	**UNDEN**	**R^2**	**df**	**logLik**	**AICc**	**ΔAICc**	**ω**	**Cumulative ω**
2.69	NA	-0.11	NA	NA	NA	-0.05	0.83	4	-337.8	684	0	0.13	0.13
2.69	NA	-0.09	NA	NA	0.04	-0.05	0.83	5	-337.11	684.8	0.81	0.09	0.22
2.69	NA	-0.11	-0.03	NA	NA	-0.05	0.83	5	-337.2	685	0.99	0.08	0.3
2.69	NA	-0.1	NA	NA	NA	NA	0.83	3	-339.54	685.3	1.32	0.07	0.37
2.69	NA	-0.1	NA	0.03	NA	-0.06	0.83	5	-337.56	685.7	1.7	0.06	0.43
2.69	NA	-0.08	NA	NA	0.04	NA	0.83	4	-338.78	685.9	1.95	0.05	0.48
2.69	NA	-0.09	-0.03	NA	0.04	-0.05	0.84	6	-336.63	686.1	2.08	0.05	0.53
2.69	0	-0.11	NA	NA	NA	-0.05	0.83	5	-337.8	686.2	2.19	0.04	0.57
2.69	NA	-0.1	-0.03	NA	NA	NA	0.83	4	-339.03	686.4	2.46	0.04	0.61
2.69	NA	-0.09	NA	0.02	0.04	-0.05	0.84	6	-336.99	686.8	2.8	0.03	0.64
2.69	-0.01	-0.09	NA	NA	0.04	-0.05	0.83	6	-337.08	687	2.99	0.03	0.67
2.69	NA	-0.11	-0.03	0.02	NA	-0.06	0.83	6	-337.14	687.1	3.11	0.03	0.7
2.69	0	-0.11	-0.03	NA	NA	-0.05	0.83	6	-337.19	687.2	3.21	0.03	0.73
2.69	NA	-0.08	-0.03	NA	0.04	NA	0.83	5	-338.38	687.3	3.36	0.02	0.75
2.69	NA	-0.1	NA	0.01	NA	NA	0.83	4	-339.49	687.3	3.38	0.02	0.77
2.69	0	-0.1	NA	NA	NA	NA	0.83	4	-339.53	687.4	3.45	0.02	0.79
2.69	0	-0.1	NA	0.03	NA	-0.06	0.83	6	-337.55	687.9	3.93	0.02	0.81

Source: Author

Table S 3 - AICc-based model selection for transect dung beetle species abundance among forest classes. Here are listed all possible variables in the models with ΔAICc < 4, followed by model R^2, degrees of freedom (df), model log-likelihood (logLik), AICc, ΔAICc, model weight (ω) and cumulative model weight. AGBFW – aboveground biomass; CANOP – canopy openness; DEFOR – deforestation curvature profile around transects; PFCOV – percentage of undisturbed primary forests around transects; TOAGB – total aboveground biomass; UNDEN – density of understory stems. In black, all models within ΔAICc < 4 and in grey all other models.

Intercept	**AGBFW**	**CANOP**	**DEFOR**	**PFCOV**	**TOAGB**	**UNDEN**	**R^2**	**df**	**logLik**	**AICc**	**ΔAICc**	**ω**	**Cumulative ω**
4.64	NA	NA	NA	NA	0.17	NA	0.74	4	-642.13	1292.6	0	0.1	0.1
4.64	NA	NA	NA	NA	0.19	-0.11	0.75	5	-641.15	1292.9	0.23	0.09	0.19
4.64	NA	0.08	NA	NA	0.21	NA	0.75	5	-641.58	1293.7	1.09	0.06	0.25
4.64	NA	NA	NA	0.12	0.17	-0.13	0.75	6	-640.57	1293.9	1.3	0.05	0.3
4.65	NA	NA	NA	0.09	0.16	NA	0.74	5	-641.78	1294.1	1.5	0.05	0.35
4.64	NA	NA	-0.06	NA	0.17	NA	0.74	5	-641.88	1294.3	1.68	0.04	0.39
4.64	NA	0.06	NA	NA	0.22	-0.1	0.75	6	-640.83	1294.5	1.83	0.04	0.43
4.63	NA	NA	-0.05	NA	0.19	-0.11	0.75	6	-640.92	1294.6	2.01	0.04	0.47
4.64	-0.01	NA	NA	NA	0.18	NA	0.74	5	-642.13	1294.8	2.19	0.03	0.5
4.64	NA	0.09	NA	0.11	0.2	NA	0.75	6	-641.07	1294.9	2.29	0.03	0.53
4.64	0	NA	NA	NA	0.19	-0.11	0.75	6	-641.15	1295.1	2.47	0.03	0.56
4.64	NA	0.08	NA	0.14	0.2	-0.12	0.75	7	-640.11	1295.3	2.66	0.03	0.59
4.64	NA	NA	NA	NA	NA	NA	0.73	3	-644.63	1295.5	2.84	0.02	0.61
4.64	NA	0.08	-0.05	NA	0.21	NA	0.75	6	-641.38	1295.6	2.92	0.02	0.63
4.65	NA	NA	NA	0.14	NA	NA	0.74	4	-643.73	1295.8	3.2	0.02	0.65
4.64	0	0.08	NA	NA	0.21	NA	0.75	6	-641.58	1296	3.32	0.02	0.67
4.64	NA	NA	-0.03	0.11	0.17	-0.13	0.75	7	-640.49	1296.1	3.43	0.02	0.69
4.64	NA	NA	-0.04	0.08	0.16	NA	0.74	6	-641.66	1296.1	3.47	0.02	0.71
4.64	NA	NA	NA	0.17	NA	-0.11	0.74	5	-642.79	1296.2	3.51	0.02	0.73
4.64	-0.01	NA	NA	0.12	0.17	-0.13	0.75	7	-640.56	1296.2	3.57	0.02	0.75
4.65	-0.01	NA	NA	0.09	0.16	NA	0.74	6	-641.77	1296.3	3.7	0.02	0.77
4.63	NA	0.06	-0.05	NA	0.21	-0.1	0.75	7	-640.64	1296.4	3.73	0.02	0.79
4.64	NA	NA	NA	NA	NA	-0.09	0.73	4	-644.02	1296.4	3.77	0.02	0.81
4.64	-0.01	NA	-0.06	NA	0.18	NA	0.74	6	-641.86	1296.5	3.88	0.01	0.82

Source: Author

Table S 4 - AICc-based model selection for transect dung beetle community composition among forest classes. Here are listed all possible variables in the models with ΔAICc < 4, followed by model R^2, degrees of freedom (df), model log-likelihood (logLik), AICc, ΔAICc, model weight (ω) and cumulative model weight. AGBFW – aboveground biomass; CANOP – canopy openness; DEFOR – deforestation curvature profile around transects; PFCOV – percentage of undisturbed primary forests around transects; TOAGB – total aboveground biomass; UNDEN – density of understory stems. In black, all models within ΔAICc < 4 and in grey all other models.

Intercept	**AGBFW**	**CANOP**	**DEFOR**	**PFCOV**	**TOAGB**	**UNDEN**	**R^2**	**df**	**logLik**	**AICc**	**ΔAICc**	**ω**	**Cumulative ω**
0.06	NA	0.28	NA	NA	-0.12	NA	0.49	5	-100.52	201.5	0	0.14	0.14
0.06	NA	0.33	NA	NA	NA	NA	0.48	4	-100.17	202.3	0.83	0.09	0.23
0.06	0.06	0.28	NA	NA	-0.13	NA	0.5	6	-101.99	202.7	1.15	0.08	0.31
0.05	NA	0.27	-0.06	NA	-0.13	NA	0.5	6	-101.93	202.7	1.22	0.08	0.39
0.06	NA	0.28	NA	-0.03	-0.12	NA	0.49	6	-102.05	203.6	2.05	0.05	0.44
0.06	NA	0.28	NA	NA	-0.12	-0.02	0.49	6	-102.42	203.7	2.17	0.05	0.49
0.06	NA	0.32	-0.05	NA	NA	NA	0.48	5	-101.74	203.9	2.38	0.04	0.53
0.06	0.04	0.33	NA	NA	NA	NA	0.48	5	-101.87	203.9	2.4	0.04	0.57
0.06	NA	0.32	NA	-0.05	NA	NA	0.48	5	-101.59	204.1	2.56	0.04	0.61
0.05	0.05	0.27	-0.05	NA	-0.14	NA	0.5	7	-103.5	204.1	2.63	0.04	0.65
0.06	NA	0.33	NA	NA	NA	-0.01	0.48	5	-102.07	204.5	2.97	0.03	0.68
0.05	NA	0.26	-0.07	-0.05	-0.12	NA	0.5	7	-103.32	204.5	3	0.03	0.71
0.05	0.06	0.28	NA	-0.04	-0.12	NA	0.5	7	-103.49	204.7	3.18	0.03	0.74
0.06	0.06	0.28	NA	NA	-0.13	-0.02	0.5	7	-103.87	204.8	3.32	0.03	0.77
0.05	NA	0.27	-0.06	NA	-0.13	-0.02	0.5	7	-103.8	204.9	3.38	0.03	0.8
0.06	NA	0.31	-0.06	-0.07	NA	NA	0.48	6	-102.97	205.3	3.78	0.02	0.82

Source: Author

Table S 5 - AICc-based model selection for transect dung beetle community structure among forest classes. Here are listed all possible variables in the models with ΔAICc < 4, followed by model R^2, degrees of freedom (df), model log-likelihood (logLik), AICc, ΔAICc, model weight (ω) and cumulative model weight. AGBFW – aboveground biomass; CANOP – canopy openness; DEFOR – deforestation curvature profile around transects; PFCOV – percentage of undisturbed primary forests around transects; TOAGB – total aboveground biomass; UNDEN – density of understory stems. In black, all models within ΔAICc < 4 and in grey all other models.

Intercept	**AGBFW**	**CANOP**	**DEFOR**	**PFCOV**	**TOAGB**	**UNDEN**	**R^2**	**df**	**logLik**	**AICc**	**ΔAICc**	**ω**	**Cumulative ω**
0.06	NA	0.22	NA	NA	-0.18	NA	0.49	5	-99.31	199	0	0.23	0.23
0.06	NA	0.22	NA	-0.06	-0.17	NA	0.49	6	-100.7	200.7	1.68	0.1	0.33
0.06	NA	0.22	-0.04	NA	-0.19	NA	0.49	6	-100.96	200.7	1.69	0.1	0.43
0.06	0.04	0.22	NA	NA	-0.19	NA	0.49	6	-101.08	200.8	1.74	0.1	0.53
0.06	NA	0.22	NA	NA	-0.18	-0.02	0.49	6	-101.22	201.2	2.16	0.08	0.61
0.05	NA	0.21	-0.06	-0.07	-0.18	NA	0.49	7	-102.17	202.1	3.03	0.05	0.66
0.06	0.04	0.22	NA	-0.06	-0.18	NA	0.49	7	-102.43	202.4	3.4	0.04	0.7
0.06	0.03	0.22	-0.04	NA	-0.19	NA	0.49	7	-102.77	202.6	3.58	0.04	0.74
0.06	NA	0.21	-0.04	NA	-0.19	-0.02	0.49	7	-102.84	202.9	3.85	0.03	0.77
0.06	0.04	0.22	NA	NA	-0.19	-0.02	0.49	7	-102.97	202.9	3.91	0.03	0.8
0.06	NA	0.21	NA	-0.05	-0.17	-0.01	0.49	7	-102.62	203	3.94	0.03	0.83

Source: Author

CHAPTER 3

THE RELATIVE IMPORTANCE OF MULTIPLE SCALE FACTORS FOR DUNG BEETLE COMMUNITIES IN AMAZONIAN INTRODUCED PASTURES

ABSTRACT

Context: Exotic pastures are a major threat to tropical forests, occupying most of the deforested areas. Despite the drastic environmental changes and biodiversity losses following forest clearance for pastures introduction, we have little understanding of determine the occurrence of the remaining species. Such information is important to help improving the conservation value of this land-use.

Objectives: We investigated how tropical forest conversion to pastures impact dung beetle communities.

Methods: We sampled dung beetles, and measured 10 local and three landscape environmental variables, as well as three spatial variables, across two different regions of the Brazilian Amazon. This study was conducted in 187 forest and 74 pasture transects. We used baited pitfall traps for the sampling of dung beetles.

Results: Dung beetle communities showed dramatic decreases in diversity as consequence of forest conversion to pastures. Pasture communities were predominantly dominated by a few hyper-abundant species typical from Brazilian open habitats, and appeared weakly influenced by pastures characteristics.

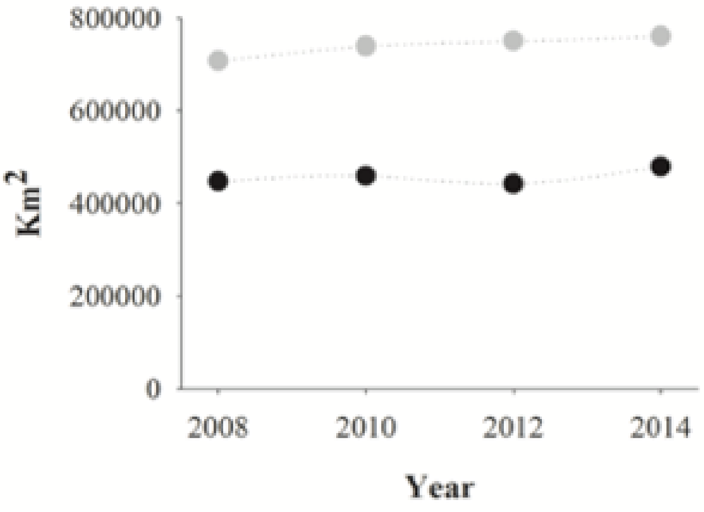
Conclusion: Our results show that the introduction of pastures in tropical forest landscapes drives significant reductions on dung beetle diversity, and generate communities largely dependent on Brazilian open habitats to serve as source of populations.

Keywords: Exotic pastures. Tropical grasslands. Dung beetles. Stochasticity. Neutral theory. Dispersion. Land sparing. Cerrado. Intra-Amazonian savannas.

1 INTRODUCTION

The rapid expansion of pasturelands is one of the greatest threats to tropical forest biodiversity (AIDE et al., 2013), and has been linked to the disruption of ecological processes (e.g. nutrient cycling), increase of greenhouse gases emissions and soil compaction (LATAWIEC et al., 2014), biotic homogenization (RODRIGUES et al., 2013; SOLAR et al. 2015; *but see* de CARVALHO et al., 2016) and the introduction of aggressive exotic grasses and large exotic mammals to tropical landscapes. In the Brazilian Amazon alone, introduced pastures cover more than 60 million hectares and occupy three out of five deforested hectares (Figure 1). Irrespective of whether the establishment of this system is driven by economic factors or for securing land ownership and for land speculation (FEARNSIDE, 2001; MERTENS, 2002), they continue to replace areas of native forest. Some authors argue that, even with the development of new techniques and strategies for land use intensification and land sparing (PHALAN et al., 2016), the introduction of pastures in the Amazon may continue due to the economic rebound effect (e.g. increase in demand for land due to increase in pastures profitability; *see* LAMBIN & MEYFROIDT, 2011).

Figure 1 - Deforested area in the Brazilian Amazon (grey dots) and the area covered by pastures (black dots) in the years of 2008, 2010, 2012 and 2014. Data obtained from the Terra Class project.



Source: ALMEIDA et al., 2016.

Despite their importance as a land-use system, few studies on tropical diversity are dedicated to understanding the importance of introduced pastures. Researchers often neglect this system, or only use data for comparative purposes, reinforcing introduced pastures low conservation value for forest biodiversity (e.g. KORASAKI et al., 2013; SOLAR et al., 2016). Yet given their extent, it is important to start identifying which species are favoured by major agro-ecosystems, especially introduced pastures, investigating how environmental characteristics and land use history explain species occurrence (reviewed by SWETNAM et al., 1999; LUNT & SPOONER, 2005). Understanding how these variables interact to drive the occurrence of species in pasturelands could act as a crucial starting point helping to improve management approaches that minimise the ecological impact of these systems, as well as reclaiming some of the conservation value that was lost following the initial clearing.

Here, we investigate the occurrence of dung beetle species in introduced pastures using a large-scale assessment of 261 independent sites – 74 introduced pastures and 187 forests transects – in two human-modified regions of the eastern Brazilian Amazon. Dung beetles are exceptionally diverse in the wet tropics (HANSKI & CAMBEFORT, 1991) and have been reported occupying introduced pastures in the Brazilian Amazon (SCHEFFLER, 2005; LOUZADA et al,. 2010; KORASAKI et al.; 2013). They are appropriate and cost-effective bioindicators (GARDNER et al., 2008), as they respond to both local and landscape level environmental changes (e.g. BARLOW et al., 2016) and have a very functional importance in nutrient cycling, soil aeration, soil fertilization and other ecological processes (NICHOLS & GARDNER, 2011). Their functional role is of particular importance in introduced pastures in the Brazilian Amazon, where livestock produce approximately 537 million tons/year of manure (calculation based on SANTOS & NOGUEIRA, 2012). To put this in context, it is almost 3 times the weight of the entire Brazilian production of grains expected for 2016 (CONAB, 2016).

In this study, we investigate the principal environmental factors driving dung beetle species occurrence in Amazonian introduced pastures. Specifically, we examined: (1) To what extent are dung beetle communities in pastures different from the surrounding forests communities? (2) What is the provenance (i.e. habitat, region of Brazil) of dung beetle species that are significant and consistent indicators of pastures? (3) To what extent is the richness, abundance, species composition and structure of dung beetle communities in pastures determined by local, landscape or spatial factors? and (4) if the patterns observed while answering all these questions were consistent between two discrete study regions, in order to evaluate their consistency and applicability to pastures from other tropical wet regions.

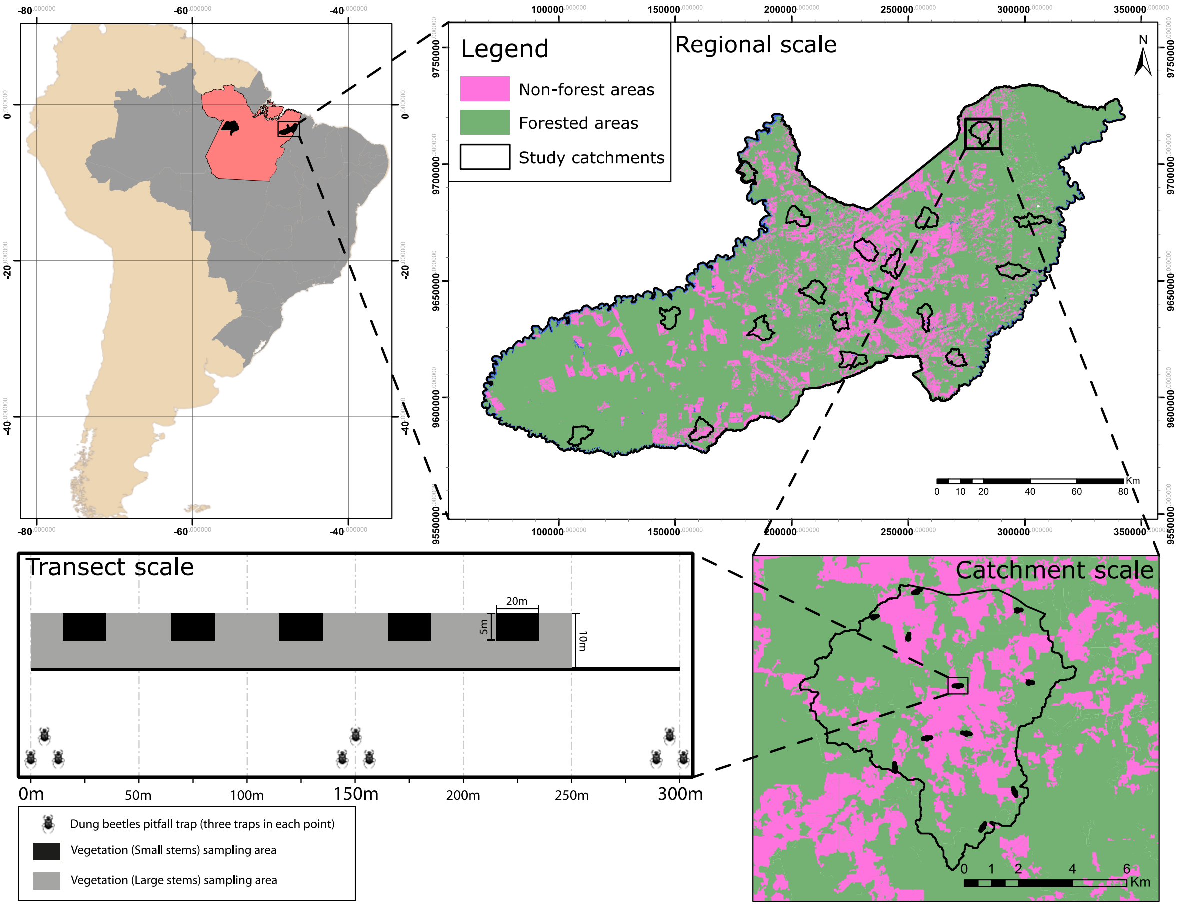
2 MATERIAL AND METHODS

2.1 Study Region

We studied two regions in the eastern Brazilian Amazon: Paragominas (‘PGM’; a single municipality of 1.9 million hectares) and Santarém (‘STM’; covering an area of *ca* 1 million hectares and composed by the municipalities of Santarém, Belterra and Mojuí dos Campos). Both regions are located in the state of Pará (Figure 2). Nevertheless, PGM and STM are situated more than 800 km distant from each other, have different biophysical characteristics and histories of human colonisation and use. For instance, PGM has experienced a recent and intensive colonisation, being founded in 1959 and becoming one of the world leaders of timber extraction in early 90s. STM have areas densely occupied for more than a century by small-scale farmers and other areas that remain largely inhabited – although this area is likely to be colonised and explored in the near future due to the paving of a highway.

The two studies regions also share some characteristics. The properties are predominantly smaller than 1000 hectares, despite the increase in mechanised farming since 2000s. Thus, differing from the other regions of the Brazilian Amazon arc of deforestation, such as in Mato Grosso state, where large farms were settled and are mainly focused on exportation of commodities (DeFRIES et al., 2013). Moreover, both PGM and STM experience an increase in initiatives for the establishment of practices toward sustainable development.

Figure 2 - Studied regions of Paragominas (*ca.* 1.9 million ha) and Santarém (*ca.* 1 million ha), in the state of Pará, eastern Brazilian Amazon. Map of the sampling design for dung beetles and predictor variables. We stratified our sampling in regional, catchment and transect scales.



Source: Author

2.2 Sampling Design

We used the *Soil and Water Assessment Tool* (SWAT) for ArcGIS to divide each studied region in 18 catchments (landscapes) of *ca* 5000 hectares, covering introduced pastures maintained through different management techniques, secondary forests and a gradient of primary forest cover (6-100%) and quality (i.e. undisturbed; logged; logged and burnt). We set 300 m long transects in pastures and forests within each landscape. Transects were distributed proportionally to pastures and forests coverage at each landscape, at a maximum density of 1 transect / 400 hectares. In total, we conducted our samples in a total of

49 / 25 pastures and 100 / 87 forest transects at PGM and STM, respectively (further details on the study sites are available in GARDNER et al., 2013).

2.3 Sampling of Dung Beetles

We sampled dung beetles using baited pitfall traps active in the field for 48 hours. This method is widely used in assessments of land use change effects on dung beetles around the world. Each trap was made of plastic (diameter: 18 cm; height: 15 cm) and covered by a lid – to protect from the rain. We baited pitfall traps with a 50 g of a mixture of human:pig dung, at a 1:4 ratio, following (MARSH et al., 2013). Each pitfall was filled with 250 ml of a saline solution (w/ detergent) in order to kill the insects and preserve their body parts during the field exposition. We sorted and identified all sampled dung beetles to the lowest taxonomic levels possible. A taxonomist of dung beetles, Dr Fernando Vaz de Mello, validated our identifications. Voucher specimens are deposited at the *Coleção de Escarabeíneos Neotropicais* at the Universidade Federal de Lavras (BRA) and at the Zoological Collection of Universidade Federal de Mato Grosso (BRA).

2.4 Sampling of Predictor Variables

We measured 10 local and three landscape environmental variables, and selected three spatial variables across each region. Local variables were mean elevation and slope per transect, and eight soil related variables (i.e. coarse sand, fine sand, silt, clay, P, K, Ca and pH). Soil data was obtained from measurements made within transects (further details on sampling techniques are available in BERENGUER et al., 2014; de CARVALHO et al., 2016). The landscape variables were the percentage of primary forest cover within buffers of 1 km and 10 km around transects, and the deforestation curvature profile (FERRAZ et al., 2009). Both variables were obtained from Gardner et al., 2013 and based on time series of satellite-images. From the total set of predictor variables, we removed those highly correlated with other variables (Pearson $\rho > 0.6$, for full lists of correlation tests see Figures S1-S2) and filtered the remaining variables based on the literature and our expertise, leaving seven predictors in the final models (Table 1). Spatial variables were calculated using principal coordinates of neighbour matrices (PCNM) analysis (BORCARD & LEGENDRE, 2002), derived from geographical coordinates. This analysis generates eigenfunctions describing spatial patterns among the sampling areas (DRAY et al., 2006), and resulted in a total of 17 positive eigenfunctions. To avoid overfitting, we selected some vectors based on their higher correlation (*P*<0.05) with our response variables. For PGM, we retained PCNM1, PCNM2 and PCNM3, and for STM, we retained PCNM1, PCNM7 and PCNM8.

Table 1- Predictor variables sampled in this study. Further details of sampling methodologies and techniques adopted are described in Gardner et al. (2013), Berenguer et al. (2014) and de Carvalho et al. (2016).

Variable	**Summary**
Coarse	Percentage of soil coarse sand at transect level
Slope	Mean slope at transect level
Elev	Mean elevation at transect level
For1k	Percentage of primary forest in 1km buffer
Defor	Deforestation curvature profile in 500 m buffer around transects
PCNM	Eigenfunctions describing spatial patterns among transects

Source: Author

2.5 Data Analysis

For answering our questions (1) and (2), we pooled dung beetle data from introduced pastures and forests samples. Question (3) was answered using data only from introduced pastures. We undertook all analyses in in the R statistical environment (R Development Core Team 2016). In order to assess the extent to which observed patterns were consistent between regions, we analysed data separately for PGM and STM.

First, we compared dung beetle species richness and abundance between introduced pastures and forests using linear mixed effects models (GLMM), with landscapes as the random variable, to account for dependence among transects within landscapes (BOLKER et al., 2009). We used Poisson distribution for species richness and log(abundance+1) for species abundance (correcting for over-dispersion using Negative Binomial).

Second, we examined the similarities between dung beetle communities' composition (presence-absence data) and structure (square root transformed and standardised abundance data) between introduced pastures and forests (nPGM = 149, nSTM = 112). We used non-metric multi-dimensional scaling (NMDS) ordination based on Bray-Curtis similarity indices and analysis of similarity (ANOSIM).

To identify species preferentially sampled in introduced pastures, we used a multinomial model for classification (CLAM, CHAZDON et al., 2011), using a specialization threshold (k) of 0.75 and a significance level of 0.05.

In order to assess the extent to which local, landscape and spatial factors determine dung beetles occurrence in Amazonian introduced pastures we performed a multi-model inference, with basis on a global (full) model, followed by model selection (BURNHAM et al., 2011). To do so, we used GLMM for dung beetle species richness, abundance, community composition and structure. Models for community composition and structure were built using the Axis 1 of NMDS ordinations as response variables. In this case, we used Gaussian distribution. The relative performance of each model was assessed with basis on AICc values. We selected models with AICc < 4 for model averaging, for capturing greater uncertainty in the final set of candidate variables (VIERLING et al., 2013). Finally, we calculated the relative importance of each predictor variable on the multi-model inference (BURNHAM et al., 2011), indicating their conditional contribution (i.e. a variable is only averaged across the models it appears) to all models averaged by their weight and AICc value.

3 RESULTS

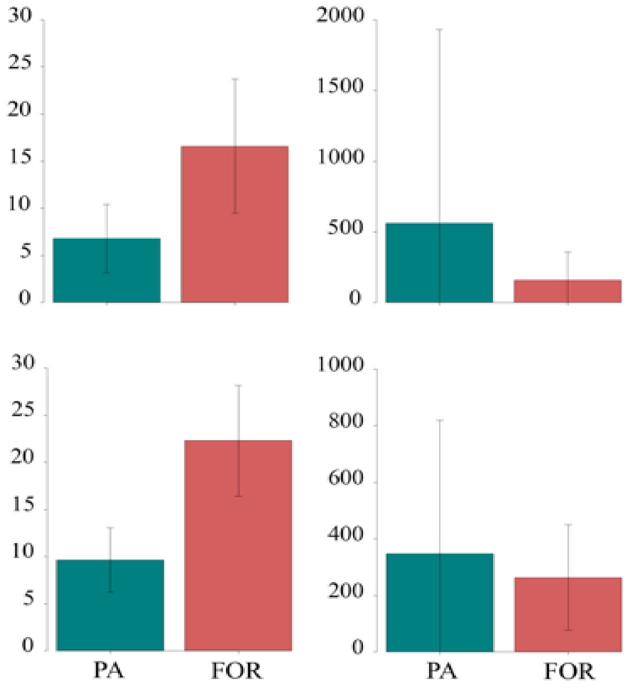
We sampled a total of 74,926 (PGM = 43,530; STM = 31,396) individuals and 149 (PGM = 84; STM = 96) species of dung beetles, from which 36,178 individuals (PGM = 27,503; STM = 8,675) and 48 species (PGM = 32; STM = 27) were sampled in introduced pastures (Table S 1 – S 2 for lists of species). The most abundant species in PGM pastures was *Trichillum* sp.1, with 19,563 individuals recorded. In STM, *Trichillum externepunctatum* was the most abundant species, accounting for 3,927 individuals.

3.1 Difference Between Dung Beetle Communities from Amazonian Introduced Pastures and Surrounding Forests

Introduced pastures and surrounding forests exhibited different dung beetle communities. Although most introduced pasture species were also found in forests in each study region (PGM = 97%; STM = 77%), simple observation of their abundances reveals that these species were highly predominant in only one land cover type (Table 2).

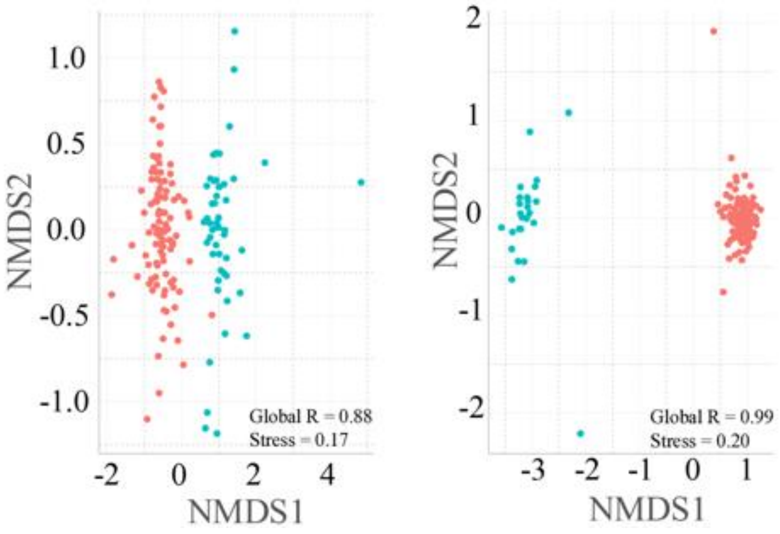
The differences between introduced pastures and forest dung beetle communities were further confirmed by the differences in mean species richness (PGM: $x^2 = 109.93$, $p < 0.001$; STM: $x^2 = 131.42$, $p < 0.001$) and abundance (PGM: $x^2 = 12.44$, $p < 0.001$) (Figure 3), and communities' composition and communities' structure ($p < 0.001$) (Figure 4). Introduced pastures and forests communities were similar only regarding species abundance at STM ($p = 0.45$).

Figure 3 - Mean dung beetle species richness and abundance in introduced pastures and forests from Paragominas (top) and Santarém (bottom) municipalities.



Source: Author

Figure 6 - Non-metric multidimensional scaling (NMDS) ordination of dung beetle community structure among forests (red circles) and introduced pastures (blue circles). NMDS was based on a matrix distance computed with Bray-Curtis similarity index for Paragominas (A) and Santarém (B) municipalities. Community composition is not presented since the observed similarity patterns were consistent between community composition and structure. Communities similarity is represented by the proximity among the symbols on the plots.



Source: Author

3.2 Amazonian Introduced Pasture Indicator Species

CLAM tests identified introduced pasture indicator species at both studied regions (PGM = 7 species; STM = 16 species). Six of the pasture indicator species were the same in PGM and STM: *Pseudocanthon* aff. *xanthurus*, *Canthon lituratus*, *Diabroctis mimas*, *Digitonthophagus gazella*, *Canthidium humerale* and *Canthon* aff. *simulans*. The indicator species alone accounted to more than 95% of the individuals sampled in both regions, and are typical species from Brazilian open habitats (Table 2).

Table 2 - List of dung beetles specialist in Amazonian introduced pastures according to the CLAM method for species classification. Species with more than 90% of occurrence in introduced pastures but not abundant enough to be classified by CLAM are highlighted in grey. The listed species account to more than 95% of the individuals sampled at both regions. Dung beetles were sampled at Paragominas and Santarém municipalities (Pará, Brazil) with baited pitfall traps (mix of human-pig faeces at 1:4 proportion). % - percentage of occurrence in introduced pastures; MEAN – mean abundance per introduced pasture transect; TOTAL – total abundance in introduced pastures; PGM – Paragominas; STM – Santarém.; DISTRIBUTION – General distribution of dung beetle species, across Brazil, according to a non-exhaustive survey of the literature and dung beetle experts; REFERENCES – Recent studies reinforcing dung beetle distribution.

SPECIES	**%**		**MEAN**		**TOTAL**		**DISTRIBUTION**	**REFERENCES**
	PGM	**STM**	**PGM**	**STM**	**PGM**	**STM**		
Pseudocanthon aff. *xanthurus*	99.61	100	68.06	48.04	3335	1201	Open areas	(Scheffler 2005, Louzada *et al.* 2007, França, Korasaki, *et al.* 2016)
Digitontophagus gazella	99.07	100	17.47	0.92	856	23	Open areas	(Matavelli & Louzada 2008, Silva *et al.* 2014)
Canthidium humerale	96.3	72.41	3.71	0.84	182	21	Caatinga and intra-Amazonian savannahs	(França *et al.* 2016, Campos *unpublished data*)
Canthon aff. *simulans*	94.97	100	6.94	0.64	340	16	Open areas, palm tree plantations and secondary forests	(Costa *et al.* 2013, Matavelli *et al.* 2013, Silva *et al.* 2014)
Diabroctis mimas	94.78	100	24.84	4.88	1217	122	Cerrado, pastures and tropical dry forests	(Almeida & Louzada 2009, Silva *et al.* 2014, Neves *et al.* 2010)
Canthon lituratus	88.33	100	13.9	12.16	681	304	Cerrado, Caatinga and pastures	(Almeida & Louzada 2009, Costa *et al.* 2009, Silva *et al.* 2014)
Trichillum sp.1	92.85	0	399.24	0	19563	0	-	-
Canthon aff. *octodentatus*	100	0	0.16	0	8	0	-	-
Canthon sp.1	92.31	0	0.24	0	12	0	-	-
Canthon obscuriellus	0	100	0	5.16	0	129	Cerrado and pastures	(Correa, Puker, Ferreira, *et al.* 2016)
Canthon aff. *acutus*	0	99.76	0	16.48	0	412	-	-
Trichillum externepunctatum	0	99.75	0	158.28	0	3957	Open areas	(Almeida & Louzada 2009, Costa *et al.* 2009, Silva *et al.* 2014)
Canthon aff. *heyrovskyi*	0	99.72	0	14.08	0	352	Cerrado and open areas	IUCN
Ontherus appendiculatus	0	99.35	0	12.32	0	308	Open areas	(Louzada & Carvalho & Silva 2009, Correa, Puker, Ferreira, *et al.* 2016)

To be continued …

Conclusion

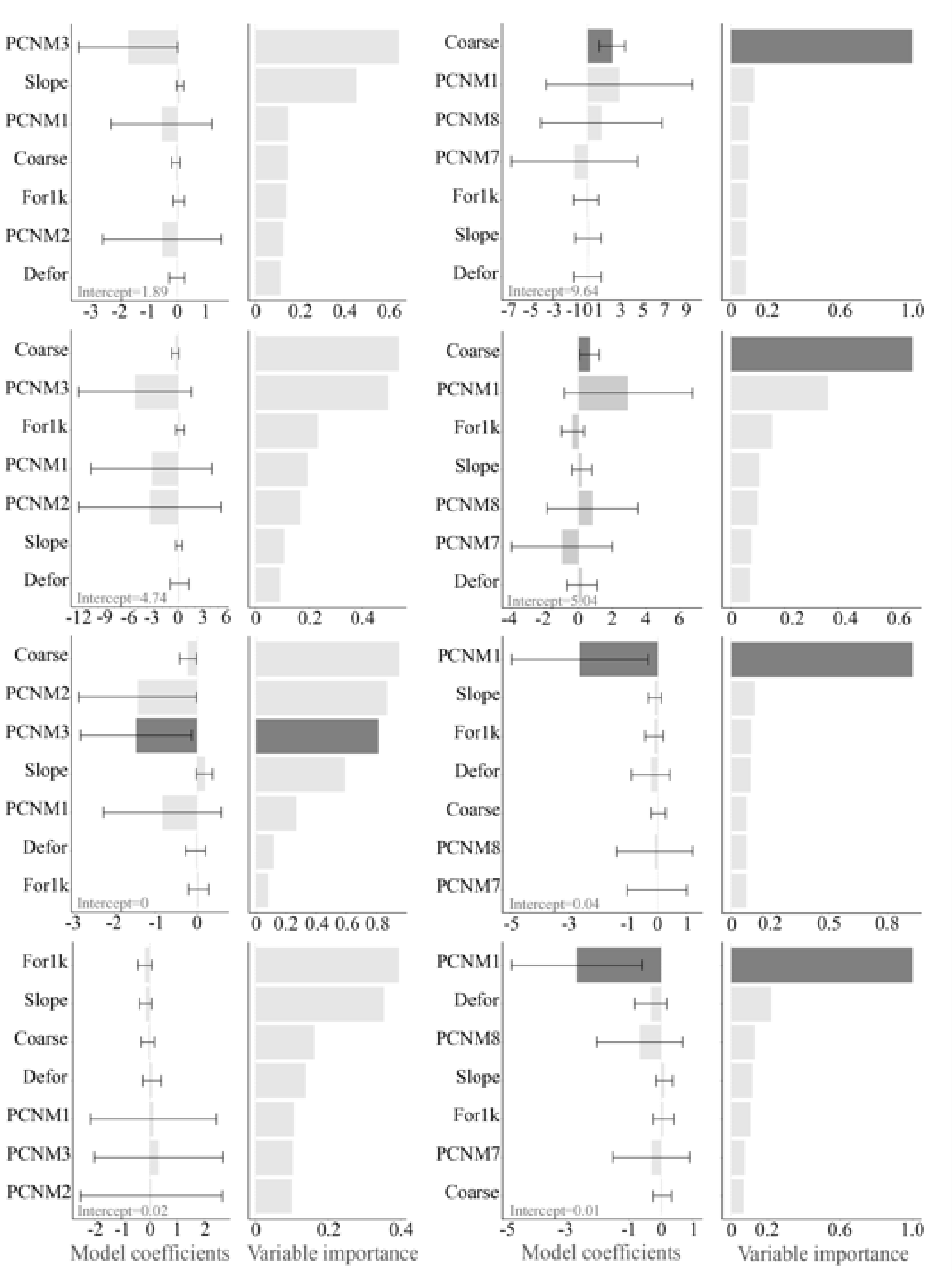
Dichotomius nisus	0	99.15	0	23.24	0	581	Open areas	(Koller *et al.* 2007, Audino *et al.* 2014, Correa, Puker, Ferreira, *et al.* 2016)
Canthon aff. *chalybaeus*	0	97.73	0	3.44	0	86	Caatinga, Cerrado and pastures	(Almeida & Louzada 2009, Costa *et al.* 2009, Silva *et al.* 2014)
Canthidium multipunctatum	0	96.59	0	3.4	0	85	Savannahs	(Spector & Ayzama 2003)
Onthophagus aff. *hirculus*	0	84.62	0	3.08	0	77	Caatinga, Cerrado and pastures	(Almeida & Louzada 2009, Costa *et al.* 2009, Silva *et al.* 2014)
Canthidium barbacenicum	0	82.65	0	28.4	0	710	Cerrado and tropical dry forests	(Almeida *et al.* 2011, Puker *et al.* 2013, Correa, Puker, Korasaki, *et al.* 2016, Novais *et al.* 2016)

Source: Author

3.3 Influence of Local, Landscape and Spatial Factors on Dung Beetle Communities in Amazonian Introduced Pastures

Spatial variables explained variation in community composition across both regions (PGM: variable importance = 0.9, best model R^2 = 0.32; STM: variable importance = 0.9, best model R^2 = 0.43) and community structure in STM (variable importance = 1.0, best model R^2 = 0.39) (Figure 5). Coarse sand explained variation in dung beetle species richness and abundance in STM (Richness: variable importance = 1.0, best model R^2 = 0.46; Abundance: variable importance = 0.7, best model R^2 = 0.2) (Figure 5). None of the remaining variables significantly explained differences in dung beetle species richness, abundance and structure in PGM (i.e. the confidence intervals of the coefficients included zero). The complete set of models generated for all response variables is available in Supplementary Material (Tables S 3 – S 10).

Figure 7 - Model averaging of candidate models within ΔAICc < 4 for dung beetle species richness, abundance, community composition and structure (from top to bottom) in Paragominas (left) and Santarém (right) municipalities. All averaged coefficients (±confidence intervals) are show on the left side, relative variables importance is shown on the right side. Slope – mean transect slope; Coarse – soil percentage of coarse sand; For1k – percentage of primary forest cover at 1km buffer around transects; Defor - deforestation curvature profile around transects; PCNM1 – spatial variation; PCNM2 – spatial variation; PCNM3 – spatial variation; PCNM7 – spatial variation; PCNM8 – spatial variation.



Source: Author

4 DISCUSSION

Our large-scale assessment of 261 pasture and forest sites in two independent Amazonian landscapes provide novel insights into the occurrence of dung beetles in introduced tropical pastures. We found that dung beetle communities from introduced pastures appear only weakly influenced by the surrounding forests, local, landscape and spatial factors, and that the communities were dominated by a few species that are typical of other Brazilian pastures and open habitats (e.g. the Cerrado and intra-Amazonian savannahs). We discuss these results assessing consequences for dung beetles of tropical forests conversion to pastures, highlighting the potential implications of our findings for the conservation of Amazonian biodiversity.

4.1 Dung Beetle Communities in the Amazonian Introduced Pastures

The high number of species (32 in PGM, 27 in STM, 48 in total) occurring in these introduced pastures is much higher than those reported in previous studies (12 species, KLEIN, 1989; 15 species, SCHEFFLER, 2005; 11 species, QUINTERO, I.; HALFFTER, 2009; 5 species, KORASAKI et al., 2013). Moreover, although introduced pastures had fewer species than forests in both studied regions, their total diversity exceeds that recorded in many other natural or human-modified habitats in the tropics, such as the intra-Amazonian savannas (15 species, LOUZADA et al., 2010), tropical dry forests (15 species, MEDINA & LOPES, 2014) Restinga (13 species, VIEIRA et al., 2008), Caatinga (13 species, LIBERAL et al., 2011) and agro-ecosystems (SHAHABUDDIN et al., 2005; NEITA & ESCOBAR, 2012).

There are two reasons that can help explain the high number of species relative to these other systems. The first may be a sampling artefact: our study had a much larger sample size (261 sites) and was spread out over very large (>1 Million hectare) regions, so our measure of gamma diversity in introduced pastures is likely to be both closer to the asymptote than other studies with small sample sizes (KLEIN, 1989; SCHEFFLER, 2005; QUINTERO, I.; HALFFTER et al., 2009) could also include a much larger contribution from beta diversity. Second, there may be a genuine biological explanation relating to dung beetle colonization opportunities in our study region. Most of the previous dung beetle studies in the Amazonian introduced pastures were conducted in areas surrounded by forest, which represents a nearly impermeable matrix for open-area dung beetles. This was supported by the communities they recorded, which were composed of a few forest dung beetles at very low abundances and very few (or none) species from open habitats (see KLEIN, 1989; SCHEFFLER, 2005). In contrast, the movement of species already adapted to the environmental conditions of the Brazilian pastures and open habitats would have been facilitated in our study regions, which present some of the highest levels of Amazonian deforestation and are located much closer to naturally open savanna enclaves (in the case of Santarem) or the Cerrado itself (in the case of Paragominas).

The dominance of a few species in Amazonian introduced pastures is characteristic of human modified habitats and introduced pastures elsewhere (NICHOLS et al., 2007; QUINTERO, I.; HALFFTER et al., 2009; ALMEIDA et al., 2011) and, in this case, may reflect the higher ability of a few species to feed in cattle dung and nest in the highly compacted pasture soils (HALFFTER et al., 1992). The long tail of rare species could be result of the presence of transient occasional species (FAGAN et al., 1999; ALMEIDA et al., 2011) from the surrounding forests, which are thought to influence biodiversity assessments in the human-modified tropics (BARLOW, GARDNER et al., 2010). Although it is unlikely that such species will be capable of colonising these systems, due to physiological limitations (VERDÚ et al., 2006; HALFFTER & EDMONDS, 1982), they may occasionally pass through to colonise new forest patches, or use resources in pastures during night times, when microclimatic conditions are less severe.

4.2 Drivers of Dung Beetle Communities in the Amazonian Introduced Pastures

We found that local, landscape and spatial factors do not determine dung beetle communities in Amazonian introduced pastures. Although local factors (i.e. coarse sand) and spatial variation influenced communities' attributes in some cases, the explanation power of our models was low, especially considering the number of predictor variables recorded and the high number of sample sites. Our results therefore suggest that neither pastures' environmental heterogeneity nor the locally-applied management practices are strong determinant of dung beetle communities in Amazonian introduced pastures.

To explain this surprising result, we suggest that drivers of dung beetle communities in Amazonian introduced pastures can be divided in three stages, based on the influence of different ecological filters. In the first stage, radical reductions in the pool of species capable of colonising pastures are imposed by environmental changes following the forest clearance.

Forest clearance acts as a deterministic ecological filter, producing biotic homogenization (SOLAR et al., 2015) and allowing only species that are capable to colonise the new environmental scenario to persist in pastures. The environmental changes resultant from forest clearance includes local decreases in air temperature, luminosity and soil compaction, as well as local decreases in air humidity (LAURANCE, 2004). Such changes may elevate forest dung beetles body temperature beyond their regulating capacity (VERDÚ et al., 2006), hamper their nesting behaviour (HALFFTER & EDMONDS, 1982; SOWIG, 1995) and promote resources desiccation (KLEIN 1989; LAURANCE et al., 2011), therefore negatively impacting their populations (NICHOLS et al., 2007). Forest clearance – often followed by fencing – may also promote local exclusion of many mammals, jeopardizing the provision of resources for several dung beetle species. As a result, most forest dung beetles are prevented from colonising introduced pastures (SILVA et al., 2014) creating marked and highly consistent differences between communities of forested and open land cover classes.

In the second stage of community structuring, a reduced pool of species composed predominantly by open habitat specialist species (e.g. Pseudocanthon xanthurus, Diabroctis mimas, Canthon lituratus, Canthidium humerale, Canthon aff. simulans, Digitonthophagus gazella) will be filtered by a combination of dispersal opportunities. Thus, the chance of colonisation of a introduced pasture is influenced by its distances from sources of species, as well as beetles' dispersal abilities (BENGTSSON, 2009). For instance, this could explain the notorious presence of Digitontophagus gazella in our samples. This African dung beetle was introduced in Brazil for the first time in 1989 to control horn fly (Haematobia irritans) populations and improve pastures' soil productivity. In the present study, it was the most abundant pasture indicator species, contrary to the low abundances previously documented for the Amazonian region (MATAVELLI & LOUZADA, 2008). Due to subsequent re-introduction events and for being good dispersers and competitors, D. gazella is rapidly colonising Brazilian pastures and open habitats.

In the third stage, when beetles finally reach the introduced pastures, their establishment will depend on complex arranges of factors related to pastures local conditions (e.g. soil texture) and management (e.g. intervals for alternating with crops; intensive versus extensive use). For instance, variations in coarse sand explained variations in dung beetle species richness (best model R2 = 0.46) and abundance (best model R2 = 0.2) in introduced pastures of one of our studied regions, but not in the other. While such difference might be in part reflecting two distinct categories of soil present in Santarém (i.e. soils with low or high percentage of soil) as opposed to those present in Paragominas introduced pastures (see

Figure S3), several lines of evidence demonstrate the importance of soil structure as a determinant of beetle activities: the percentage of soil sand has recently been reported as an important driver of seed burial rates by dung beetles (GRIFFITHS et al., 2015), increases in abundance and body weight of dung beetles and functional guilds were attributed to increases in coarse sand in Amazonian forests (BEIROZ et al., 2016 in prep.), while digging tunnels and nesting can be favoured by the soil looseness (HANSKI & CAMBEFORT, 1991) and reduced humidity in sandy soils (HALFFTER & EDMONDS, 1982).

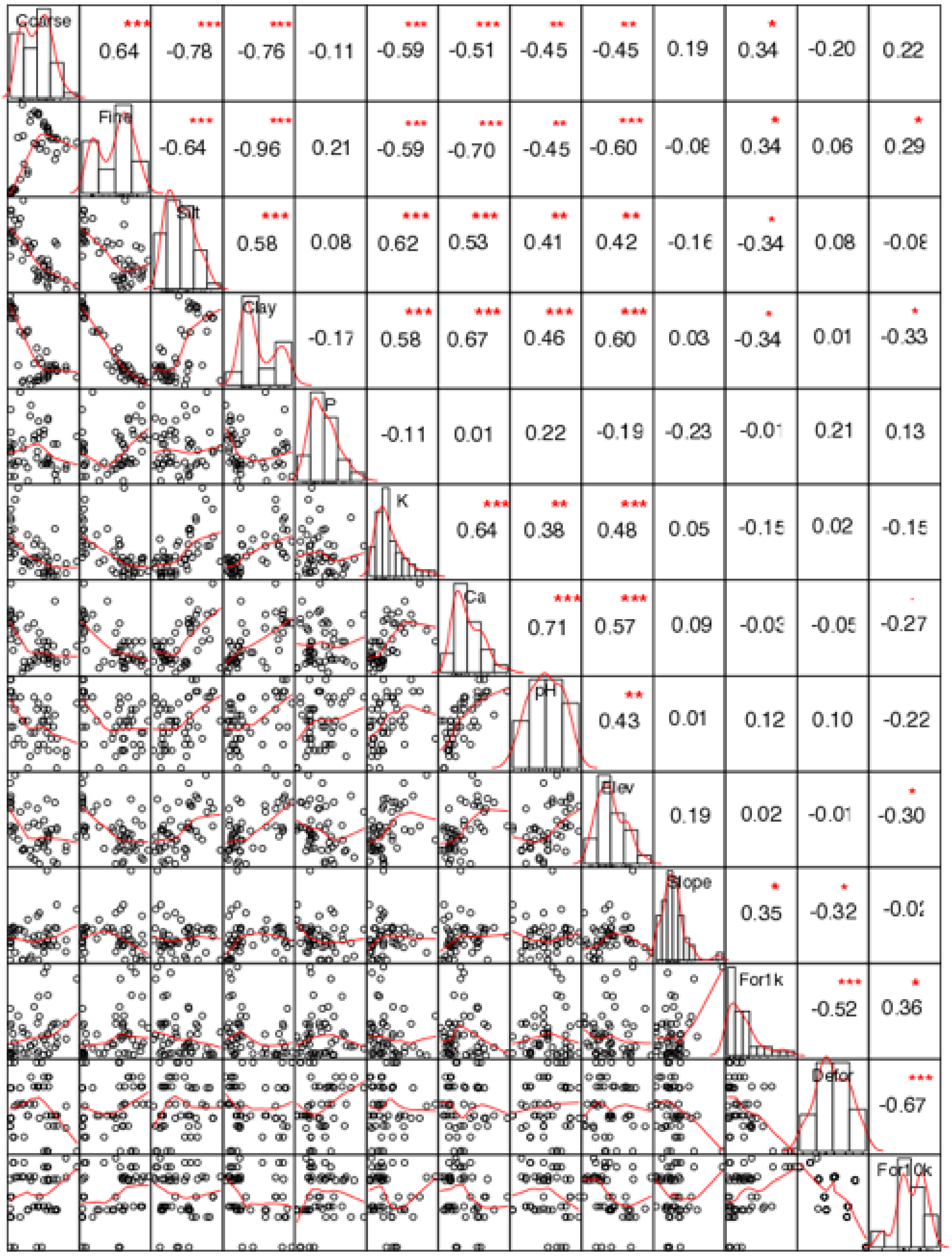
Finally, these filters are modified by important stochastic processes, such as alternations between pastures and crops (e.g. soya plantations), or severe climatic events such as the 2015-16 El Nino, which will drastically reduce populations' sizes and cause local extinctions, allowing the reorganisation of dung beetle communities from new starting points.

5 CONCLUSION

1. The Amazonian introduced pastures host dung beetle species poor and homogenized communities in comparison to the surrounding forests.
2. The Amazonian introduced pastures host uneven dung beetle communities dominated by dung beetle species from Brazilian pastures and open habitats, and with the presence of transient species.
3. Dung beetle diversity in the Amazonian introduced pastures is dependent on stochastic factors. Therefore, the maintenance of species sources is important to allow species to persist in this system. The conservation of natural open habitats that could serve as source, such as intra-Amazonian savannahs and the Cerrado and Caatinga biomes, may be determinant to guarantee diversity of these systems.

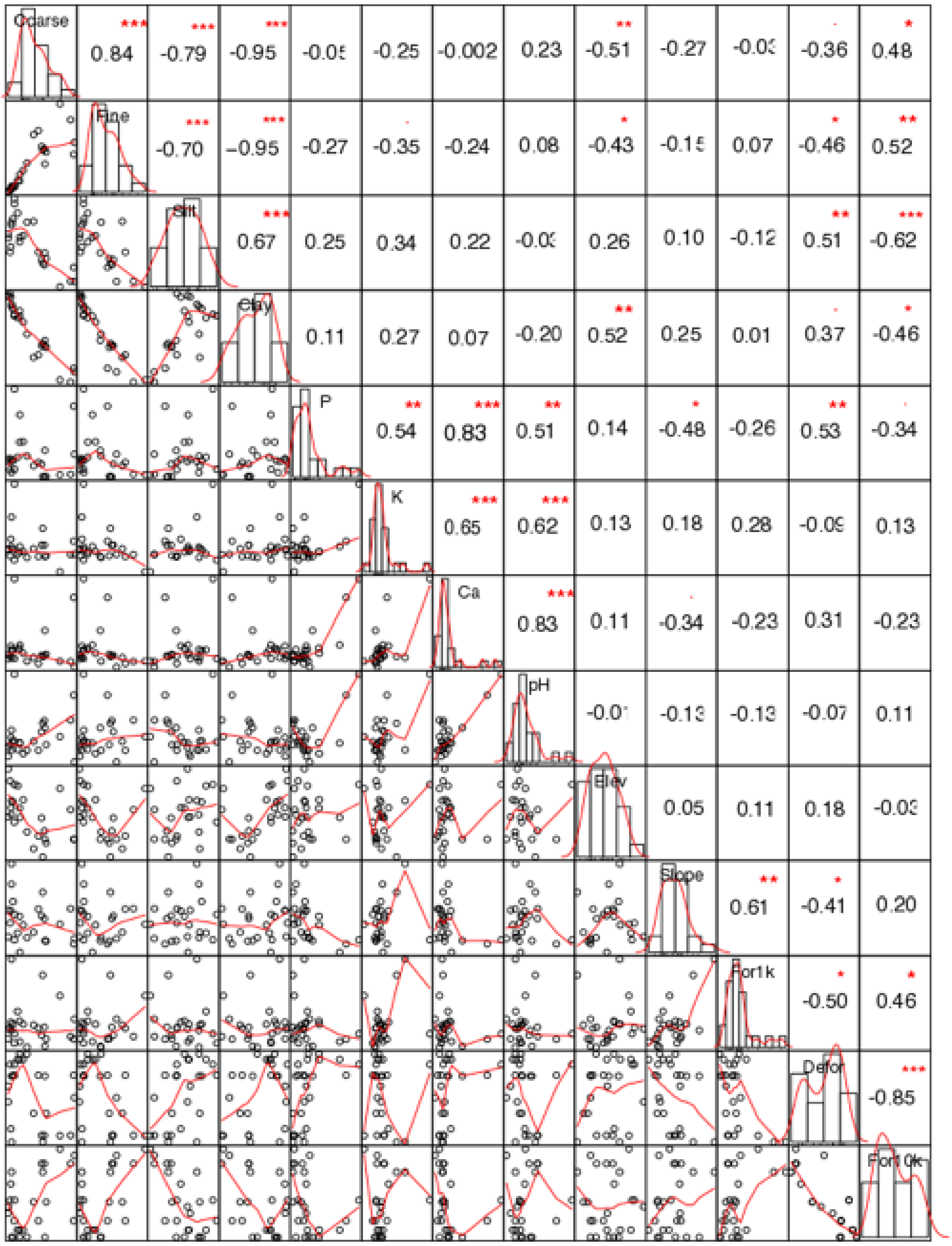
SUPPLEMENTARY MATERIAL

Figure S 1 - Association between environmental metrics measured in introduced pastures in Paragominas: bivariate plots (lower panels), distribution (diagonal) and Pearson’s ρ (upper pannels).



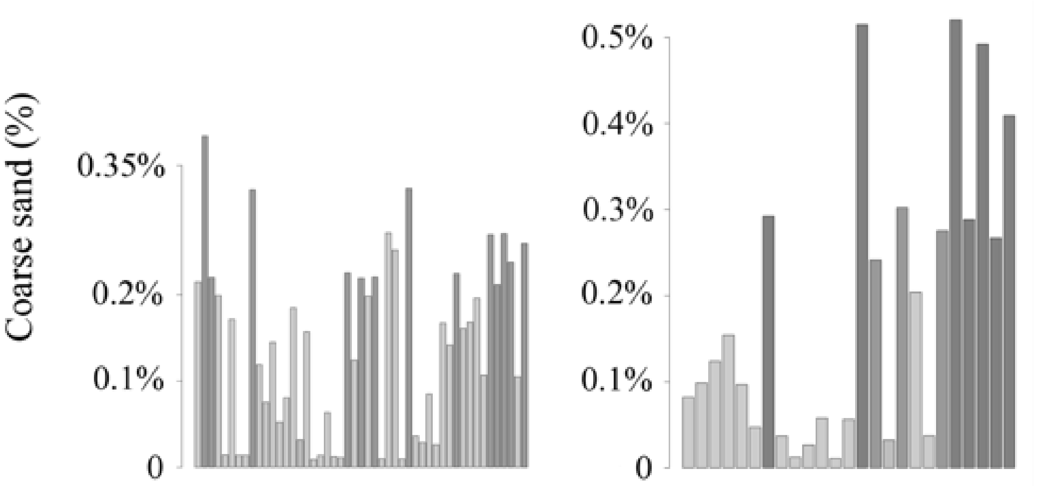
Source: Author

Figure S 2 - Association between environmental metrics measured in introduced pastures in Santarém: bivariate plots (lower panels), distribution (diagonal) and Pearson's ρ (upper pannels).



Source: Author

Figure S 3 - Percentage of soil coarse sand in transects of introduced in Paragominas (left) and Santarém (right).



Source: Author

Table S 1 - List of dung beetle species collected in Amazonian introduced pastures (PAS) and forests (FOR) at Paragominas (Pará, Brazil) using baited pitfall traps.

SPECIES	REFERENCE	PAS	FOR
Anomiopus aff. *foveicollis*		0	1
Ateuchus sp.1		0	63
Ateuchus sp.2		0	13
Ateuchus sp.3		0	914
Ateuchus sp.4		0	3
Ateuchus sp.5		0	41
Bdelyrus sp.1		0	1
Canthidium aff. *lentum*		26	446
Canthidium funebre	Balthasar, 1939	0	3
Canthidium gerstaeckeri	Harold, 1867	1	162
Canthidium humerale	Germar, 1813	182	7
Canthidium semicupreum	Harold, 1868	1	43
Canthidium sp.1		3	62
Canthidium sp.10		0	14
Canthidium sp.11		2	3
Canthidium sp.2		0	34
Canthidium sp.3		0	1
Canthidium sp.4		0	152
Canthidium sp.5		4	1096
Canthidium sp.6		0	20
Canthidium sp.7		0	2
Canthidium sp.8		0	1
Canthidium sp.9		0	24

To be continued …

Continuation …

Canthon aff. *octodentatus*		8	0
Canthon aff. *sericatus*		13	2
Canthon aff. *simulans*		340	18
Canthon coeruleus		6	87
Canthon histrio	LePeletier and Serville, 1828	113	54
Canthon lituratus	Germar, 1813	681	90
Canthon proseni	Martinez, 1949	0	172
Canthon scrutator	Balthasar, 1939	239	36
Canthon sp.1		12	1
Canthonella sp.1		0	2
Coprophaneus dardanus	Macleay, 1819	1	9
Coprophaneus degallieri	Arnaud, 1997	49	17
Coprophaneus jasius	Olivier, 1789	0	6
Coprophaneus lancifer	Linnaeus, 1767	0	107
Cryptocanthon campbellorum	Howden, 1973	0	78
Deltochilum aff. *sextuberculatum*	-	0	93
Deltochilum carinatum	Westwood, 1837	0	5
Deltochilum enceladus	Kolbe, 1893	0	95
Deltochilum icarus	Olivier, 1789	0	38
Deltochilum orbiculare	Lansberge, 1874	0	153
Deltochilum schefflerorum	* sp. nov.	0	5
Deltochilum sp.1		0	354
Diabroctis mimas	Linnaeus, 1758	1217	67
Dichotomius aff. *globulus*		4	2133
Dichotomius aff. *lucasi*		1	69
Dichotomius boreus	Olivier, 1789	0	318
Dichotomius imitator	Felsche, 1901	0	10
Dichotomius inachus	Erichson, 1847	1	174
Dichotomius longiceps	Taschenberg, 1870	0	2
Dichotomius melzeri	Luederwaldt, 1922	0	153
Dichotomius telamon	Harold, 1869	0	68
Dichotomius worontzowi	Pereira, 1942	0	32
Digitontophagus gazella	Fabricius, 1787	856	8
Eurysternus atrosericus	Génier, 2009	0	10
Eurysternus caribaeus	Herbst, 1789	1	1138
Eurysternus cavatus	Génier, 2009	0	175
Eurysternus foedus	Guérin-Méneville, 1844	0	81
Eurysternus hamaticollis	Balthasar, 1939	0	45
Eurysternus harlequin	Génier, 2009	0	1
Eurysternus howdeni	Génier, 2009	0	4
Eurysternus hypocrita	Balthasar, 1939	0	12

To be continued …

Conclusion

Eurysternus ventricosus	Gill, 1990	0	19
Eurysternus wittmerorum	Martinez, 1988	0	117
Eutrichillum sp.1		0	26
Hansreia affinis	Fabricius, 1801	0	187
Ontherus sulcator	Fabricius, 1775	287	318
Onthophagus aff. *hirculus*		486	392
Onthophagus onthochromus	Arrow, 1913	9	30
Ontophagus ophion	Erichson, 1847	11	651
Onthophagus rubrescens	Blanchard, 1843	48	2927
Oxysternon macleayi	Nevison, 1892	0	594
Oxysternon silenus	Castelnau, 1840	0	77
Phanaeus chalcomelas	Perty, 1830	0	54
Pseudocanthon aff. *xanthurus*		3335	13
Sulcophanaeus faunus	Fabricius, 1775	0	4
Trichillum externepunctatum	Preudhomme de Borre, 1880	1	8
Trichillum pauliani	Balthasar, 1939	0	27
Trichillum sp.1		19563	1507
Uroxys sp.1		0	28
Uroxys sp.2		2	11
Uroxys sp.3		0	9

Source: Author

Table S 2 - List of dung beetle species collected in Amazonian introduced pastures (PAS) and forests (FOR) at Santarém (Pará, Brazil) using baited pitfall traps.

SPECIES	REFERENCE	PAS	FOR
Anomiopus aff. *latistriatus*		0	1
Anomiopus aff. *pictus*		1	2
Anomiopus batesi	Waterhouse, 1891	0	1
Anomiopus brevipes	Waterhouse, 1891	0	3
Anomiopus parallelus	Harold, 1862	0	1
Ateuchus aff. *candezei*		0	340
Ateuchus aff. *murrayi*		0	1256
Ateuchus aff. *romani*		0	15
Ateuchus connexus	Harold, 1868	0	90
Ateuchus sp.1		0	92
Ateuchus sp.2		0	67
Bdelyrus paraensis	Cook, 1998	0	8
Canthidium aff. *deyrollei*		0	1511
Canthidium aff. *gerstaeckeri*		0	202
Canthidium aff. *lentum*		0	29
Canthidium barbacenicum	Preudhomme de Borre, 1886	710	149
Canthidium multipunctatum	Balthasar, 1939	85	3
Canthidium sp.1		2	406
Canthidium sp.2		53	80
Canthidium sp.3		0	19
Canthidium sp.4		0	143
Canthidium sp.7		1	9
Canthidium aff. *ardens*		225	695
Canthidium aff. *collare*		0	169
Canthidium aff. *funebre*		0	4
Canthidium sp.5		0	68
Canthidium sp.6		0	6
Canthidium sp.8		0	37
Canthidium humerale	Gemar, 1813	21	8
Canthon aff. *acutus*		412	1
Canthon aff. *angustatus*		0	78
Canthon aff. *chalybaeus*		86	2
Canthon aff. *heyrovskyi*		352	1
Canthon aff. *quadrimaculatus*		0	242
Canthon aff. *sericatus*		0	82
Canthon aff. *simulans*		16	0
Canthon fulgidus	Redtenbacher, 1867	0	3571
Canthon histrio	Lepelletier de Saint Fargeau e Audinet-Serville, 1828	3	263
Canthon lituratus	Germar, 1813	304	0

To be continued …

Continuation …

Canthon obscuriellus	Schmidt, 1922	129	0
Canthon proseni	Martinez, 1949	0	1153
Canthon semiopacus	Harold, 1868	0	14
Canthonella sp.1		0	1
Canthonella sp.2		0	1
Coprophanaeus degallieri	Arnaud, 1997	0	3
Coprophanaeus jasius	Olivier, 1789	0	10
Coprophanaeus lancifer	Linnaeus, 1767	0	118
Cryptocanthon peckorum	Howden, 1973	0	90
Deltochilum amazonicum	Bates, 1887	0	36
Deltochilum carinatum	Westwood, 1837	0	1
Deltochilum enceladus	Kolbe, 1893	0	111
Deltochilum orbiculare	Lansberge, 1874	0	70
Deltochilum sp.1		0	154
Deltochilum sp.2		0	818
Diabroctis mimas	Linnaeus, 1758	122	0
Dichotomius aff. *fortestriatus*		0	743
Dichotomius aff. *lucasi*		1	1309
Dichotomius boreus	Olivier, 1789	0	1
Dichotomius carinatus	Luederwaldt, 1925	0	166
Dichotomius imitator	Felsche, 1901	0	37
Dichotomius mamillatus	Felsche, 1901	0	4
Dichotomius melzeri	Luederwaldt, 1922	1	81
Dichotomius nisus	Olivier, 1789	581	5
Dichotomius robustus	Luederwaldt, 1935	0	12
Dichotomius worontzowi	Pereira, 1942	0	144
Digitonthophagus gazella	Fabricius, 1787	23	0
Eurysternus arnaudi	Génier, 2009	0	61
Eurysternus atrosericus	Génier, 2009	0	1694
Eurysternus balachowskyi	Halffter e Halffter, 1976	0	61
Eurysternus caribaeus	Herbst, 1789	1	2190
Eurysternus cayennensis	Castelnau, 1840	0	266
Eurysternus cyclops	Génier, 2009	0	7
Eurysternus hamaticollis	Balthasar, 1939	0	39
Eurysternus howdeni	Génier, 2009	0	1
Eurysternus hypocrita	Balthasar, 1939	0	18
Eurysternus plebejus	Harold, 1880	0	85
Eurysternus vastiorum	Martinez, 1988	0	10
Eurysternus wittmerorum	Martinez, 1988	0	1088
Eutrichillum sp.1		0	3
Ontherus appendiculatus	Mannerheim, 1829	308	2

To be continued …

Conclusion

Ontherus carinifrons	Luederwaldt, 1930	0	41
Onthophagus aff. *clypeatus*		0	1
Onthophagus aff. *hirculus*		77	14
Onthophagus aff. *onorei*		0	2
Onthophagus onthochromus	Arrow, 1913	0	1
Onthophagus sp.1		1	2167
Oxysternon macleayi	Nevinson, 1892	0	222
Oxysternon silenus	Castelnau, 1840	0	9
Phanaeus alvarengai	Arnaud, 1984	0	2
Pseudocanthon aff. *xanthurus*	1201	0	
Scybalocanthon sp.1		0	21
Sylvicanthon sp.1		0	84
Trichillum externepunctatum	Borre, 1880	3957	10
Uroxys sp.1		2	155
Uroxys sp.2		0	17
Uroxys sp.3		0	14

Source: Author

Table S 3 - AICc-based model selection for transect dung beetle species richness in introduced pastures at Paragominas (Brazil). Here are listed all possible variables in the models with ΔAICc < 4, followed by model R^2, degrees of freedom (df), model log-likelihood (logLik), AICc, ΔAICc, model weight (ω) and cumulative model weight. COARSE – percentage of soil coarse sand; FOREST – percentage of primary forest surrounding transects; DEFOR – deforestation curvature profile; PCNM1 – spatial variable, PCNM2 – spatial variable; PCNM3 – spatial variable; SLOPE – transects slope.

Intercept	**COARSE**	**FOREST**	**DEFOR**	**PCNM1**	**PCNM2**	**PCNM3**	**SLOPE**	**df**	**logLik**	**AICc**	**ΔAICc**	**ω**	**Cumulative ω**
1.88	NA	NA	NA	NA	NA	-1.79	NA	3	-117.32	241.2	0	0.08	0.08
1.89	NA	NA	NA	NA	NA	-1.67	0.09	4	-116.35	241.6	0.43	0.06	0.14
1.9	NA	NA	NA	NA	NA	NA	0.1	3	-118.01	242.6	1.38	0.04	0.18
1.9	NA	NA	NA	NA	NA	NA	NA	2	-119.18	242.6	1.43	0.04	0.22
1.87	NA	NA	NA	-0.61	NA	-1.85	NA	4	-117.08	243.1	1.89	0.03	0.25
1.88	-0.05	NA	NA	NA	NA	-1.83	NA	4	-117.1	243.1	1.93	0.03	0.28
1.89	-0.07	NA	NA	NA	NA	-1.71	0.09	5	-115.92	243.2	2.06	0.03	0.31
1.88	NA	0.04	NA	NA	NA	-1.66	NA	4	-117.21	243.3	2.15	0.03	0.34
1.87	NA	NA	NA	NA	-0.48	-1.8	NA	4	-117.21	243.3	2.15	0.03	0.37
1.88	NA	NA	NA	-0.65	NA	-1.74	0.09	5	-116.07	243.5	2.35	0.03	0.4
1.88	NA	NA	0	NA	NA	-1.79	NA	4	-117.32	243.6	2.38	0.02	0.42
1.88	NA	NA	NA	NA	-0.66	-1.68	0.09	5	-116.13	243.7	2.48	0.02	0.44
1.89	NA	0.1	NA	NA	NA	NA	NA	3	-118.63	243.8	2.61	0.02	0.46
1.89	NA	NA	0.02	NA	NA	-1.73	0.09	5	-116.34	244.1	2.89	0.02	0.48
1.89	NA	0	NA	NA	NA	-1.68	0.09	5	-116.35	244.1	2.92	0.02	0.5
1.9	-0.06	NA	NA	NA	NA	NA	0.1	4	-117.75	244.4	3.24	0.02	0.52
1.89	NA	NA	-0.08	NA	NA	NA	NA	3	-118.99	244.5	3.34	0.02	0.54
1.89	NA	NA	NA	NA	-0.6	NA	0.1	4	-117.87	244.6	3.47	0.01	0.55
1.9	NA	0.05	NA	NA	NA	NA	0.08	4	-117.87	244.7	3.48	0.01	0.56
1.9	-0.03	NA	NA	NA	NA	NA	NA	3	-119.09	244.7	3.53	0.01	0.57
1.9	NA	NA	-0.06	NA	NA	NA	0.09	4	-117.92	244.7	3.57	0.01	0.58
1.89	NA	NA	NA	NA	-0.42	NA	NA	3	-119.11	244.8	3.57	0.01	0.59
1.9	NA	NA	NA	-0.4	NA	NA	0.1	4	-117.93	244.8	3.58	0.01	0.6
1.89	NA	NA	NA	-0.33	NA	NA	NA	3	-119.12	244.8	3.6	0.01	0.61
1.87	NA	0.06	NA	-0.73	NA	-1.7	NA	5	-116.89	245.2	3.99	0.01	0.62

Source: Author

Table S 4 - AICc-based model selection for transect dung beetle species richness in introduced pastures at Santarém (Brazil). Here are listed all possible variables in the models with ΔAICc < 4, followed by model R^2, degrees of freedom (df), model log-likelihood (logLik), AICc, ΔAICc, model weight (ω) and cumulative model weight. COARSE – percentage of soil coarse sand; FOREST – percentage of primary forest surrounding transects; DEFOR – deforestation curvature profile; PCNM1 – spatial variable, PCNM2 – spatial variable; PCNM3 – spatial variable; SLOPE – transects slope.

Intercept	**COARSE**	**FOREST**	**DEFOR**	**SLOPE**	**PCNM1**	**PCNM7**	**PCNM8**	**df**	**logLik**	**AICc**	**ΔAICc**	**ω**	**Cumulative ω**
9.64	2.29	NA	NA	NA	NA	NA	NA	4	-57.33	125.6	0	0.29	0.29
9.64	1.96	NA	NA	NA	2.88	NA	NA	5	-54.87	128	2.38	0.09	0.38
9.64	2.28	NA	NA	NA	NA	NA	1.28	5	-55.34	128.5	2.94	0.07	0.45
9.64	2.21	NA	NA	NA	NA	-1.17	NA	5	-55.32	128.6	2.97	0.07	0.52
9.64	2.28	-0.1	NA	NA	NA	NA	NA	5	-57.03	128.8	3.15	0.06	0.58
9.64	2.3	NA	NA	0.07	NA	NA	NA	5	-57	128.8	3.19	0.06	0.64
9.64	2.28	NA	0.02	NA	NA	NA	NA	5	-56.96	128.8	3.24	0.06	0.7

Source: Author

Table S 5 - AICc-based model selection for transect dung beetle species abundance in introduced pastures at Paragominas (Brazil). Here are listed all possible variables in the models with ΔAICc < 4, followed by model R^2, degrees of freedom (df), model log-likelihood (logLik), AICc, ΔAICc, model weight (ω) and cumulative model weight. COARSE – percentage of soil coarse sand; FOREST – percentage of primary forest surrounding transects; DEFOR – deforestation curvature profile; PCNM1 – spatial variable, PCNM2 – spatial variable; PCNM3 – spatial variable; SLOPE – transects slope.

Intercept	**COARSE**	**FOREST**	**DEFOR**	**PCNM1**	**PCNM2**	**PCNM3**	**SLOPE**	**df**	**logLik**	**AICc**	**ΔAICc**	**ω**	**Cumulative ω**
4.75	-0.37	NA	NA	NA	NA	-5.34	NA	5	-83.66	182.2	0	0.06	0.06
4.78	-0.36	NA	NA	NA	NA	NA	NA	4	-87.04	182.3	0.14	0.06	0.12
4.79	NA	NA	NA	NA	NA	NA	NA	3	-87.72	182.6	0.43	0.05	0.17
4.76	NA	NA	NA	NA	NA	-5.33	NA	4	-84.41	182.7	0.52	0.05	0.22
4.77	-0.38	0.27	NA	NA	NA	NA	NA	5	-86.96	183.8	1.6	0.03	0.25
4.68	-0.34	NA	NA	-2.98	NA	-5.46	NA	6	-81.13	184	1.8	0.03	0.28
4.68	NA	NA	NA	-3.74	NA	-5.44	NA	5	-81.7	184	1.83	0.03	0.31
4.72	NA	NA	NA	-3.36	NA	NA	NA	4	-85.09	184.1	1.94	0.02	0.33
4.66	-0.35	NA	NA	NA	-3.6	-5.68	NA	6	-80.96	184.2	2.02	0.02	0.35
4.74	-0.38	0.2	NA	NA	NA	-4.95	NA	6	-83.8	184.3	2.07	0.02	0.37
4.73	-0.34	NA	NA	-2.56	NA	NA	NA	5	-84.58	184.3	2.1	0.02	0.39
4.78	NA	0.23	NA	NA	NA	NA	NA	4	-87.78	184.3	2.11	0.02	0.41
4.79	-0.4	NA	NA	NA	NA	NA	0.13	5	-87.52	184.3	2.11	0.02	0.43
4.76	-0.4	NA	NA	NA	NA	-5.24	0.12	6	-84.19	184.3	2.12	0.02	0.45
4.71	-0.34	NA	NA	NA	-2.95	NA	NA	5	-84.44	184.4	2.22	0.02	0.47
4.66	NA	NA	NA	NA	-4.16	-5.77	NA	5	-81.58	184.5	2.3	0.02	0.49
4.71	NA	NA	NA	NA	-3.38	NA	NA	4	-85.03	184.5	2.32	0.02	0.51
4.78	-0.35	NA	0.27	NA	NA	-5.91	NA	6	-83.21	184.7	2.46	0.02	0.53
4.76	NA	0.17	NA	NA	NA	-5.02	NA	5	-84.64	184.9	2.66	0.02	0.55
4.8	NA	NA	NA	NA	NA	NA	0.06	4	-88.41	184.9	2.69	0.02	0.57
4.78	-0.35	NA	0	NA	NA	NA	NA	5	-86.73	184.9	2.71	0.02	0.59

To be continued …

Conclusion

4.8	NA	NA	0.34	NA	NA	-6.03	NA	5	-83.85	185	2.76	0.02	0.61
4.8	NA	NA	0.06	NA	NA	NA	NA	4	-87.36	185.1	2.89	0.02	0.63
4.77	NA	NA	NA	NA	NA	-5.27	0.05	5	-85.13	185.1	2.9	0.01	0.64
4.7	-0.35	0.29	NA	-3.1	NA	NA	NA	6	-84.38	185.7	3.48	0.01	0.65
4.69	NA	0.26	NA	-3.88	NA	NA	NA	5	-85.02	185.7	3.53	0.01	0.66
4.58	NA	NA	NA	-3.83	-4.3	-5.87	NA	6	-78.85	185.9	3.68	0.01	0.67
4.67	-0.36	0.23	NA	-3.33	NA	-5.03	NA	7	-81.17	186.1	3.87	0.01	0.68
4.63	NA	NA	NA	-3.43	-3.57	NA	NA	5	-82.37	186.1	3.9	0.01	0.69
4.59	-0.32	NA	NA	-3.08	-3.8	-5.82	NA	7	-78.39	186.1	3.91	0.01	0.7
4.71	-0.36	0.26	NA	NA	-2.55	NA	NA	6	-84.4	186.1	3.92	0.01	0.71
4.67	NA	0.2	NA	-4.08	NA	-5.07	NA	6	-81.83	186.2	3.98	0.01	0.72

Source: Author

Table S 6 - AICc-based model selection for transect dung beetle species abundance in introduced pastures at Santarém (Brazil). Here are listed all possible variables in the models with ΔAICc < 4, followed by model R^2, degrees of freedom (df), model log-likelihood (logLik), AICc, ΔAICc, model weight (ω) and cumulative model weight. COARSE – percentage of soil coarse sand; FOREST – percentage of primary forest surrounding transects; DEFOR – deforestation curvature profile; PCNM1 – spatial variable, PCNM2 – spatial variable; PCNM3 – spatial variable; SLOPE – transects slope.

Intercept	**COARSE**	**FOREST**	**DEFOR**	**SLOPE**	**PCNM1**	**PCNM7**	**PCNM8**	**df**	**logLik**	**AICc**	**ΔAICc**	**ω**	**Cumulative ω**
5.04	0.68	NA	NA	NA	NA	NA	NA	4	-41.47	91.1	0	0.15	0.15
5.04	NA	NA	NA	NA	2.81	NA	NA	4	-40.81	93.1	2.01	0.06	0.21
5.04	NA	-0.49	NA	NA	3.83	NA	NA	5	-39.76	93.3	2.16	0.05	0.26
5.04	0.52	NA	NA	NA	1.4	NA	NA	5	-39.71	93.4	2.24	0.05	0.31
5.04	0.74	NA	NA	0.21	NA	NA	NA	5	-41.55	93.6	2.48	0.04	0.35
5.04	0.68	NA	NA	NA	NA	NA	0.84	5	-40.09	93.8	2.68	0.04	0.39
5.04	0.67	-0.13	NA	NA	NA	NA	NA	5	-41.77	94	2.89	0.04	0.43
5.04	0.64	NA	NA	NA	NA	-0.55	NA	5	-40.16	94.1	2.97	0.03	0.46
5.04	0.68	NA	0	NA	NA	NA	NA	5	-41.81	94.3	3.16	0.03	0.49
5.04	NA	NA	NA	NA	NA	NA	NA	3	-44.13	94.7	3.58	0.03	0.52
5.04	NA	NA	NA	NA	2.81	-1.57	NA	5	-38.9	94.7	3.6	0.03	0.55
5.04	NA	NA	0.51	NA	4.78	NA	NA	5	-40.02	94.7	3.62	0.03	0.58

Source: Author

Table S 7 - AICc-based model selection for transect dung beetle community composition in introduced pastures at Paragominas (Brazil). Here are listed all possible variables in the models with ΔAICc < 4, followed by model R^2, degrees of freedom (df), model log-likelihood (logLik), AICc, ΔAICc, model weight (ω) and cumulative model weight. COARSE – percentage of soil coarse sand; FOREST – percentage of primary forest surrounding transects; DEFOR – deforestation curvature profile; PCNM1 – spatial variable, PCNM2 – spatial variable; PCNM3 – spatial variable; SLOPE – transects slope.

Intercept	**COARSE**	**FOREST**	**DEFOR**	**PCNM1**	**PCNM2**	**PCNM3**	**SLOPE**	**df**	**logLik**	**AICc**	**ΔAICc**	**ω**	**Cumulative ω**
0	NA	NA	NA	-1.14	-1.39	-1.59	NA	6	-46.55	107.1	0	0.19	0.19
0.01	NA	NA	NA	NA	-1.37	-1.58	NA	5	-48.48	108.4	1.25	0.1	0.29
0.02	NA	NA	NA	-1.11	NA	-1.59	NA	5	-48.91	109.2	2.11	0.07	0.36
0	-0.2	NA	NA	NA	-1.12	-1.55	NA	6	-47.76	109.5	2.41	0.06	0.42
0	-0.16	NA	NA	-0.75	-1.17	-1.56	NA	7	-46.63	110	2.88	0.05	0.47
0.03	NA	NA	NA	NA	NA	-1.55	NA	4	-50.58	110.1	2.96	0.04	0.51
0	NA	NA	NA	-1.12	-1.73	-1.5	0.15	7	-46.78	110.3	3.18	0.04	0.55
0.02	NA	NA	NA	-1.09	-1.35	NA	NA	5	-49.51	110.4	3.31	0.04	0.59
0.01	-0.22	NA	NA	NA	NA	-1.56	NA	5	-49.61	110.6	3.51	0.03	0.62
0.03	NA	NA	NA	NA	-1.32	NA	NA	4	-51.1	111.1	3.99	0.03	0.65

Source: Author

Table S 8 - AICc-based model selection for transect dung beetle community composition in introduced pastures at Santarém (Brazil). Here are listed all possible variables in the models with ΔAICc < 4, followed by model R^2, degrees of freedom (df), model log-likelihood (logLik), AICc, ΔAICc, model weight (ω) and cumulative model weight. COARSE – percentage of soil coarse sand; FOREST – percentage of primary forest surrounding transects; DEFOR – deforestation curvature profile; PCNM1 – spatial variable, PCNM2 – spatial variable; PCNM3 – spatial variable; SLOPE – transects slope.

Intercept	**COARSE**	**FOREST**	**DEFOR**	**SLOPE**	**PCNM1**	**PCNM7**	**PCNM8**	**df**	**logLik**	**AICc**	**ΔAICc**	**ω**	**Cumulative ω**
0.04	NA	NA	NA	NA	-2.6	NA	NA	4	-21.51	53.5	0	0.21	0.21
0.04	NA	NA	NA	-0.1	-2.59	NA	NA	5	-22.37	55.7	2.23	0.07	0.28
0.05	NA	-0.13	NA	NA	-2.34	NA	NA	5	-22.14	56	2.53	0.06	0.34
0.03	NA	NA	-0.24	NA	-3.36	NA	NA	5	-21.47	56.1	2.59	0.06	0.4
0.04	0.02	NA	NA	NA	-2.66	NA	NA	5	-22.7	56.6	3.09	0.05	0.45
0.04	NA	NA	NA	NA	-2.59	NA	-0.1	5	-21.06	56.6	3.09	0.05	0.5
0.04	NA	NA	NA	NA	-2.59	-0.01	NA	5	-21.32	56.6	3.1	0.05	0.55
0	NA	NA	NA	NA	NA	NA	NA	3	-25.3	56.8	3.31	0.04	0.59

Source: Author

Table S 9 - AICc-based model selection for transect dung beetle community structure in introduced pastures at Paragominas (Brazil). Here are listed all possible variables in the models with ΔAICc < 4, followed by model R^2, degrees of freedom (df), model log-likelihood (logLik), AICc, ΔAICc, model weight (ω) and cumulative model weight. COARSE – percentage of soil coarse sand; FOREST – percentage of primary forest surrounding transects; DEFOR – deforestation curvature profile; PCNM1 – spatial variable, PCNM2 – spatial variable; PCNM3 – spatial variable; SLOPE – transects slope.

Intercept	**COARSE**	**FOREST**	**DEFOR**	**PCNM1**	**PCNM2**	**PCNM3**	**SLOPE**	**df**	**logLik**	**AICc**	**ΔAICc**	**ω**	**Cumulative ω**
0.02	NA	NA	NA	NA	NA	NA	NA	3	-55.21	117	0	0.07	0.07
0.03	NA	NA	NA	NA	NA	0.51	NA	4	-54.08	117.1	0.11	0.07	0.14
0.02	NA	NA	NA	NA	-0.01	NA	NA	4	-54.09	117.1	0.12	0.07	0.21
0.03	NA	NA	NA	NA	-0.02	0.53	NA	5	-52.91	117.2	0.25	0.06	0.27
0.02	NA	NA	NA	-0.02	NA	NA	NA	4	-54.2	117.3	0.36	0.06	0.33
0.02	NA	NA	NA	-0.02	-0.04	NA	NA	5	-53.02	117.4	0.49	0.06	0.39
0.03	NA	NA	NA	0.01	NA	0.53	NA	5	-53.03	117.5	0.5	0.06	0.45
0.03	NA	NA	NA	0.01	-0.04	0.55	NA	6	-51.8	117.6	0.64	0.05	0.5
0.02	NA	-0.19	NA	NA	NA	NA	NA	4	-55.15	119.2	2.24	0.02	0.52
0.02	NA	-0.2	NA	NA	-0.16	NA	NA	5	-54.05	119.5	2.54	0.02	0.54
0.03	NA	-0.21	NA	0.4	NA	NA	NA	5	-54.08	119.6	2.61	0.02	0.56
0.03	NA	-0.19	NA	NA	NA	0.06	NA	5	-54.12	119.6	2.67	0.02	0.58
0.02	NA	NA	NA	NA	NA	NA	-0.17	4	-55.37	119.7	2.7	0.02	0.6
0.02	NA	NA	NA	NA	0.37	NA	-0.17	5	-54.14	119.7	2.73	0.02	0.62
0.03	NA	-0.21	NA	0.39	-0.19	NA	NA	6	-52.94	119.9	2.92	0.02	0.64
0.02	NA	NA	NA	NA	NA	0.4	-0.17	5	-54.25	119.9	2.93	0.02	0.66
0.03	NA	-0.19	NA	NA	-0.19	0.08	NA	6	-52.96	119.9	2.97	0.02	0.68
0.03	NA	NA	NA	NA	0.36	0.43	-0.17	6	-52.98	120	3	0.02	0.7
0.03	NA	-0.2	NA	0.4	NA	0.08	NA	6	-53.01	120	3.07	0.02	0.72
0.02	NA	NA	NA	-0.02	NA	NA	-0.17	5	-54.32	120	3.09	0.02	0.74
0.02	NA	NA	NA	-0.01	0.34	NA	-0.18	6	-53.06	120.1	3.16	0.02	0.76

To be continued …

Conclusion

0.02	NA	NA	NA	0	NA	0.42	-0.17	6	-53.15	120.3	3.35	0.01	0.77
0.04	NA	-0.2	NA	0.4	-0.22	0.1	NA	7	-51.8	120.3	3.38	0.01	0.78
0.03	NA	NA	NA	0.02	0.33	0.44	-0.18	7	-51.84	120.4	3.45	0.01	0.79
0.04	NA	NA	0.14	NA	0.39	NA	NA	5	-54.6	120.6	3.64	0.01	0.8
0.03	NA	NA	0.12	NA	NA	NA	NA	4	-55.85	120.6	3.64	0.01	0.81
0.03	NA	NA	0.11	NA	NA	0.22	NA	5	-54.72	120.8	3.87	0.01	0.82
0.04	NA	NA	0.12	NA	0.32	0.22	NA	6	-53.43	120.9	3.9	0.01	0.83

Source: Author

Table S 10 - AICc-based model selection for transect dung beetle community structure in introduced pastures at Santarém (Brazil). Here are listed all possible variables in the models with ΔAICc < 4, followed by model R^2, degrees of freedom (df), model log-likelihood (logLik), AICc, ΔAICc, model weight (ω) and cumulative model weight. COARSE – percentage of soil coarse sand; FOREST – percentage of primary forest surrounding transects; DEFOR – deforestation curvature profile; PCNM1 – spatial variable, PCNM2 – spatial variable; PCNM3 – spatial variable; SLOPE – transects slope.

Intercept	**COARSE**	**FOREST**	**DEFOR**	**SLOPE**	**PCNM1**	**PCNM7**	**PCNM8**	**df**	**logLik**	**AICc**	**ΔAICc**	**ω**	**Cumulative ω**
0.02	NA	NA	NA	NA	-2.39	NA	NA	4	-22.2	53.9	0	0.21	0.21
0	NA	NA	-0.32	NA	-3.47	NA	NA	5	-21.84	55.1	1.24	0.11	0.32
0.01	NA	NA	NA	NA	-2.39	NA	-0.67	5	-21.23	55.7	1.82	0.08	0.4
0.02	NA	NA	NA	0.11	-2.42	NA	NA	5	-22.98	56.1	2.21	0.07	0.47
0.01	NA	0.08	NA	NA	-2.56	NA	NA	5	-23.01	56.8	2.9	0.05	0.52
0.02	NA	NA	NA	NA	-2.42	-0.21	NA	5	-21.79	56.9	2.97	0.05	0.57
0.02	0.04	NA	NA	NA	-2.5	NA	NA	5	-23.21	56.9	3.07	0.04	0.61
0	NA	NA	-0.38	NA	-3.73	-0.47	NA	6	-21.15	57.8	3.92	0.03	0.64

Source: Author

CHAPTER 4

DO WE SELECT THE BEST METRICS FOR ASSESSING LAND USE EFFECTS ON BIODIVERSITY

ABSTRACT

Biased and subjective choices in the variable selection processes used in ecological studies commonly lead researchers to reach misleading conclusions regarding patterns of biodiversity response to disturbances. Nevertheless, little attention has been given to these processes in the majority of studies published to date. Here, we assess the extent to which variables commonly employed in ecological studies correspond to those deemed to be most important by researchers of the same studies. Specifically, we examined both biodiversity (response) and environmental (explanatory) metrics from a comprehensive literature review and compared their use with their relative importance, according to a survey with the studies' authors. We used the literature concerning land use change effects on dung beetles as our study case. Our results highlight marked disparities between researchers opinion and their choice of variables in published papers. We suggest that these disparities are due to the high costs of sampling and processing some variables, as well as to logistical constraints and researchers own bias. If current practices and these discrepancies persist then our understanding of the biodiversity consequences of land-use change will remain compromised, while further undermining our confidence in the results of ecological studies.

Keywords: Agricultural expansion. Conversion. Dung beetles. Inference. Research scope. Variables selection.

1 INTRODUCTION

Over the last few hundred years humans have significantly altered the surface and functioning of the biosphere, heralding what is now widely recognised as the start of the Anthropocene (ELLIS, 2015). Agricultural systems such as croplands and pastures already encompass more than one third of the Earth´s land surface (ASNER et al., 2004; RAMANKUTTY & FOLEY, 1999) and continue to expand to meet burgeoning human needs. This unprecedented modification of natural landscapes includes habitat loss and fragmentation, land-use intensification, and habitat degradation. The ecological impacts of these changes include biodiversity loss and species extinctions, turnover in species composition, and a loss of the critical ecosystem services provided by biodiversity (MILLENNIUM ECOSYSTEM ASSESSMENT, 2005; SUKHDEV et al., 2014). These events are particularly important in the tropics, which hold both the highest levels of biodiversity and the highest rates of land-use change (HANSEN et al., 2013).

Despite recent advances in our understanding of environmental change and biodiversity responses to human disturbance, there are widespread uncertainties about the quality and reliability of information produced by ecological studies, which can be strongly influenced by (among other things) variable selection processes, inadequate sampling methods and biases in data analysis and interpretation (GUISAN & ZIMMERMANN, 2000; MAC NALLY, 2005; VAUGHAN & ORMEROD, 2003). In particular, studies may fail to find significant effects if they focus on inappropriate response metrics (BARLOW et al., 2007; SU et al., 2004), while interpretation of results can be confounded if researchers fail to capture the components of environmental variability that have the strongest influence on the biodiversity of interest. In both cases, such studies could easily reach misleading conclusions about the distribution and dynamics of biodiversity in human-modified landscapes, which in turn may have important consequences for policies and management recommendations aiming to safeguard the availability of ecosystem services and biodiversity.

Here we are interested in investigating researcher’s choices of environmental explanatory and biodiversity response variables using dung beetle research papers and researchers as our study system. Dung beetles have been increasingly used to assess and monitor environmental changes in tropical forest ecosystems (BICKNELL et al., 2014; FAVILA & HALFFTER, 1997; GARDNER et al., 2008; HALFFTER & FAVILA, 1993; LEE et al., 2009) and have been considered good ecological disturbance indicators (BARLOW; LOUZADA et al., 2010; NICHOLS & GARDNER, 2011). Their sensitivity to alterations in habitat structure, (micro) climate and natural environmental gradients is well documented in the literature through studies conducted worldwide (MENÉNDEZ et al., 2014; NICHOLS et al., 2007) and across habitats under several different management regimes (BEIROZ et al., 2014; HARVEY et al., 2006; KORASAKI et al., 2013; NEITA & ESCOBAR, 2012; SPECTOR & AYZAMA, 2003; VIEIRA et al., 2008). Dung beetles also play important ecological roles (NICHOLS et al., 2008), present different morphological and behavioural traits and a relatively stable taxonomy (PHILIPS et al., 2004). We restric our analysis to the forested regions of the tropics, because (1) they have suffered some of the most severe land-use changes in recent decades (HANSEN et al., 2013), (2) they are the richest reservoirs of the world's terrestrial biodiversity and hold the highest diversity of dung beetles (NICHOLS & GARDNER, 2011), and (3) they are where the majority of dung beetle studies have been conducted (NICHOLS & GARDNER, 2011).

We examined the choices researchers make by assessing the degree of correspondence between theory and practice in studies of the effects of land-use change on dung beetle communities in the tropics. To do so, we compiled information from a literature review and a structured survey of the authors of 48 different studies. This allowed us to compare the response and explanatory variables considered by researchers as most appropriate for understanding dung beetles' responses to land-use change with those variables actually selected and used by the same researchers in their published work. Variable selection processes were assessed separately for forested habitats and open agricultural lands because these systems are structurally divergent, host significantly different dung beetle communities and therefore should be driven by different environmental predictor variables. We also assessed justifications given for selecting certain variables and study design choices by researchers. We used this information to address the following questions: (1) To what extent are the response and explanatory variables deemed most appropriate by researchers actually being selected in published studies? (2) To what extent is the variable selection and study design processes clearly justified, and, if so, what kind of justification is presented in published work? We use our results to discuss some of the systemic problems in drawing ecological inferences from biodiversity and land-use change studies.

2 MATERIAL AND METHODS

We compiled information through a two-stage process. First, we undertook a literature review to identify the variables commonly selected in published studies, and to assess studies' justification level. Second, we surveyed the authors of the reviewed studies to identify the relative importance of variables according to researchers' opinions. Because dung beetle communities exhibit marked differences between forested habitats (e.g. primary and secondary forests, Eucalyptus sp. plantations and shaded coffee) and open agricultural lands (e.g. soya plantations and pasturelands) and are unlikely to present similar responses to a single factor (NICHOLS et al., 2007), the information was analysed separately for both land-use types.

2.1 Literature Search and Papers Selection Criteria

We searched ISI Web of Knowledge and Science Direct (accessed on 15 November 2013) using the following keywords: ((‘Tropical Forest’ OR ‘Rainforest’ OR ‘Deciduous Forest’ OR ‘Dry Forest’) AND (‘Dung Beetles’ OR ‘Scarab*’)). The search returned a total of 815 studies. From this total, we retained the papers addressing variations in dung beetle communities' attributes (e.g. richness, abundance, composition and biomass) between two or more land-uses. Therefore, we excluded those focused on single species, on a single land-use (e.g. forest fragments of different sizes) or not focused on dung beetle communities' responses to land-use change (e.g. NUMMELIN, 1998). We also excluded studies not conducted on tropical forests.

In order to avoid pseudo replication and maintain independence between studies, where two or more papers were based on the same dataset, we considered only the study published in the journal with the highest impact factor. We assume these studies represented the main findings of the work, and higher impact journals should also help ensure careful peer review and greater scientific influence. Finally, we disregarded papers on functional ecology (i.e. studies focused on seed dispersal and burial, flight activity, feeding behaviour) because the response variables usually are generally attributed to the functional groups (e.g. richness and abundance of traits of group x, y and z) rather to the entire community. Following all the criteria above, we selected 48 papers for analysis (Table S 1).

2.2 Variables Identification and Grouping

Each paper was carefully revised for the identification and categorization of the response and explanatory variables presented. For each habitat type, variables were grouped into different categories to reflect their main use. For example, ‘total species richness’ and ‘average species richness’ were grouped into the category ‘Species richness’, while ‘basal area of large trees’ and ‘canopy cover’ were grouped into ‘Forest structure’. Explanatory variables were grouped in a way that there were different categories according to their use for providing indirect measurements of resources availability (e.g. mammal abundance and biomass) or for describing environmental conditions at local (e.g. forest structure and local disturbance history), landscape (e.g. amount of forest in the surrounding landscape) or temporal (e.g. temporal pattern of forest loss in the surrounding landscape) scales. In total, we evaluated seven different categories of explanatory variables for open agricultural lands and eleven categories for forested habitats, due to a higher diversity of variables selected in these habitats. For response variables, we used seven categories for both habitat types. The full list of categories is presented in the Table S 1.

2.3 Study Design Choices

We reviewed the papers to identify information about study design choices that can affect the reliability of ecological data collected. The evaluated choices were related to information about study area, sampling effort and sampling methods (Appendix A, Supplementary material).

2.4 Assessment of Studies Justification Level

We reviewed the 48 published papers to identify any justifications for variable and study design choices, providing a conservative measure of the description of the reasons underpinning these choices. Justifications were quantified based on presence-absence, and were considered as present when authors provided at least a justification for at least one of the variables or study design choices, irrespective of how detailed it was. Therefore, there was no distinction between studies that justified all the response and explanatory variables choices and studies where only one or few of the response and explanatory variables choices were justified. Justifications were categorised as follows: (1) available literature – when authors provided references to support their choices, (2) methodological constraints – when authors use the lack of logistical/financial resources, inadequacy of methods or impossibility of performing a specific choice as justification, and (3) researcher experience – when authors justify their choices based on previous research experience.

2.5 Survey of Dung Beetle Researchers

The authors of the 48 focal studies were emailed a short survey containing a list of response and explanatory variables. Presented variables were selected based on their use in studies of the effects of land-use change on dung beetles and/or for being expected by experts to exert influence on dung beetle communities in modified habitats. Respondents were asked to rank the variables according to their relative importance. Variables were ranked separately for forested and open agricultural lands, and the ranks ranged from one (least important) to seven or 11 (most important), depending on the number of variables considered in each land use (seven in open lands, 11 in forests). For our purposes, we calculated the mean of rank values attributed to each variable by respondents. Two specific questions were asked: (1) “In your opinion, what are the response variables that are likely to most adequately capture the effects of land-use change on dung beetle communities?” And (2) “In your opinion, what are the explanatory variables that most adequately describe variability in habitat quality (due to land-use change) for dung beetles?” Respondents were allowed to add and rank additional variables that may have been missed from the list. In order to avoid possible bias, variables were randomised in the lists and presented in a different order for each respondent. The full survey is available in the Appendix B (Supplementary material).

3 RESULTS

3.1 Variable Selection in Publication

The 48 studies selected for review encompassed 21 different countries, with the highest number in Brazil and Mexico (11 and 10 studies, respectively) (Fig 1). In total, we reviewed 48 studies that presented data sampled on forested habitats. The highest ranked response variables selected in these studies were: ‘Species richness’ (included in 94% of papers), ‘Community composition and/or community structure’ (70%), ‘Evenness and/or dominance’ (32%), ‘Biomass’ (30%) and ‘Diversity’ (30%), ‘Species-level abundance’ (10%) and ‘Body size’ (9%) (Fig 2). The explanatory variables selected in studies in forested habitats were: ‘Forest structure’ (19%), ‘Landscape connectivity’ (9%) and ‘Patch size’ (9%), ‘Topography’ (6%), ‘Leaf litter’ (4%) and ‘Understory structure’ (4%), ‘Local disturbance history’ (2%) and ‘Mammal abundance and biomass’ (2%) and ‘Mammal diversity’ (2%). No paper presented variables related to either ‘Landscape history’ or ‘Soil’, that featured in the author survey of variable importance for being expected to exert influence on dung beetle communities in modified habitats.

Figure 1 - Studies occurrence by country. From light grey (no study) to dark grey (11 studies), colours correspond to the amount of studies about the effects of land-use change on dung beetles communities in tropical forests that were reviewed in this study.

Source: Author

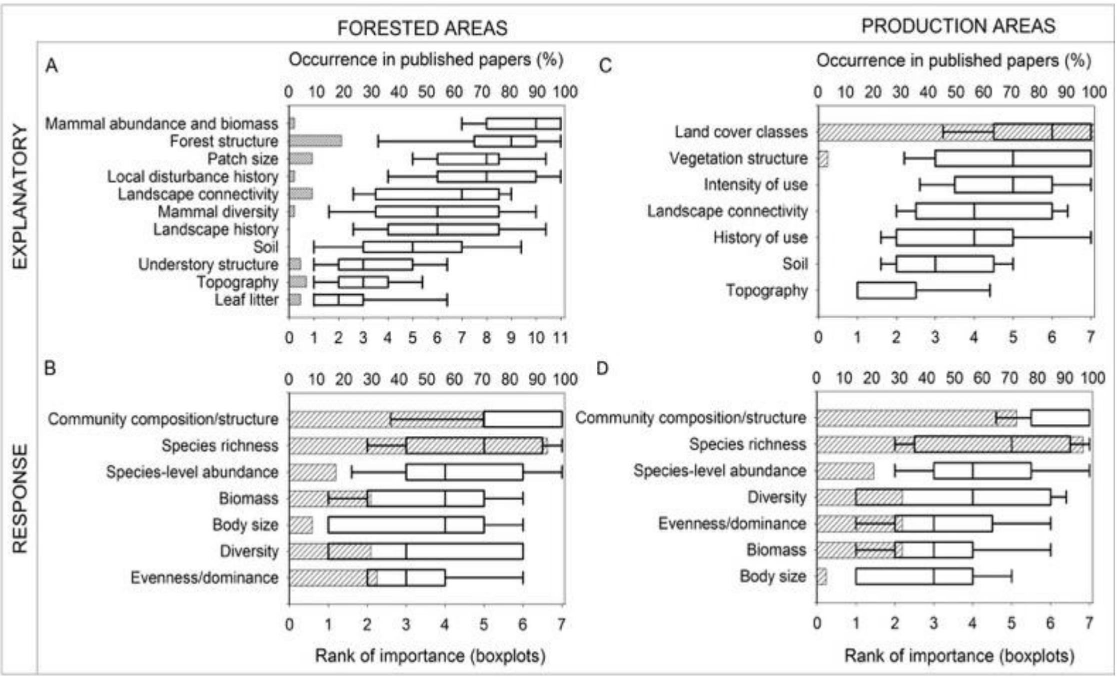
In total, we reviewed 29 studies that presented data sampled on open agricultural lands. The response variables selected in studies were: ‘Species richness’ (97%), ‘Community composition and/or community structure’ (72%), ‘Biomass’ (31%) and ‘Diversity’ (31%) and ‘Evenness and/or dominance’ (31%), ‘Species-level abundance’ (21%) and ‘Body size’ (3%). The explanatory variables selected in studies in open agricultural lands were: ‘Land cover class’ (100%) and ‘Vegetation structure’ (3%). No paper presented variables related to any of ‘History of use’, ‘Intensity of use’, ‘Landscape connectivity’, ‘Topography’ or ‘Soil’ (Fig 2).

One fifth of the studies reviewed did not present any justification at all for either the variables or study design choices used. Only 28 percent of studies presented some justification for at least one of the response variables, and only 10 percent in the case of explanatory variables. A total of 72 percent of studies presented some justification for at least one of the study design choices. When presented, justifications were mainly based on available literature (64%), followed by researcher experience (22%) and methodological constraints (10%).

3.2 Variable Importance Assessed by Authors

More than half (25/48) of the authors we approached responded to our survey. The highest ranked response variables in terms of their importance for studies in both habitat types were ‘Community composition and/or community structure’, followed by ‘Species richness’. ‘Evenness and/or dominance’ received the lowest rank (Fig 2). The highest ranked explanatory variables for studies in forested habitats were ‘Mammal abundance and biomass’, ‘Forest structure’, ‘Local disturbance history’, ‘Patch size’ and ‘Landscape connectivity’; for studies in open agricultural lands, highest ranked variables were: ‘Land cover class’, ‘Intensity of use’ and ‘Vegetation structure’. According to respondents, ‘Leaf litter’ and ‘Topography’ are the least important explanatory variables (Fig 2).

Figure 2 - The relative importance of response and explanatory variables according to both dung beetle researchers' opinions and the occurrence of the same variables in the literature published by the same authors regarding the effects of land-use change on dung beetle in tropical forests. The rank of importance attributed to the explanatory (A, B) and response (C, D) variables relating patterns of dung beetle diversity to environmental change (boxplots), and the percentage of studies that actually selected each of the recommended variables for use (bar-plots) are represented for both forested habitats (A, C) and open agricultural lands (B, D).



Source: Author

4 DISCUSSION

To our knowledge, this is the first study to compare response and explanatory variables importance according to experts' opinions with the use of these same variables in studies about land-use consequences for biodiversity in the tropics. We used data from the tropical forest dung beetles literature as our test case and found that researchers overwhelmingly do not select the explanatory variables that they themselves deem to be most important for answering the questions they are trying to address, although they do commonly select what are perceived to be the most important response variables. We also show that published studies commonly lack any justification regarding the variable selections and study design choices made by the authors. These findings undermine our ability to explain the patterns of biological communities responses to land use change that are reported in many dung beetles studies, and, assuming that there is no a priori reason why dung beetle studies should be systematically different to the treatment of other taxa, on biodiversity studies of land use change in general. The shortcomings we have identified reveal some important concerns about the adequacy of the design, implementation and publication of ecological studies about the consequences of land-use change to biodiversity.

4.1 Why are Researchers Failing to Include in Their Studies the Most Important Explanatory Variables?

We identified three main reasons for this. First, obtaining information about some variables and/or processing these data in the appropriate way may be too expensive and/or too time consuming for projects' budgets and schedules. Despite the fact that dung beetles surveys are usually quick and cheap to conduct, measuring some of the explanatory variables deemed to be important can require either a relatively high investment of resources (e.g. acquiring remote sensing data to asses patch size, local disturbance history, landscape connectivity and intensity of use) or long periods of time for data processing, for example due to the difficulties in assessing specialists necessary to the study (e.g. plant species identification, GARDNER et al., 2008). As such, unless researchers have access to sufficient resources and time, they end up having to choose between using inadequate measures (e.g. using gross measurements or categories, poor quality image or less field expeditions) or disregarding important variables.

Second, the use of land cover classes as the primary explanatory variable of interest offers an appealing "quick fix" to a study of land-use change effects. Making simple comparisons of species diversity between major land-use types allows comparison with the vast majority of published works, and allows researchers to use categorical variables as proxies for the whole suite of changes that may be too numerous to measure. Furthermore, it is much easier to find significant statistical differences between categories of land-use that are markedly different, than to understand what is happening within any given land-use in response to changes in more fine-scale predictor variables. In keeping with this, the majority of the studies we examined did not explicitly attempt to understand the processes that may be linked to finer-scale patterns of environmental heterogeneity, but were largely concerned with understanding broad patterns.

Finally, potential mismatches between the spatial scale of a given study and the spatial scales that describe much of the heterogeneity in explanatory variables may limit the variables that are selected. In particular, it could be challenging to link small-scale variation in the occupancy and abundance of dung beetles to the distribution and activity patterns of mammal communities that play out at much larger spatial scales (NICHOLS et al., 2009).

As a result of the combined effect of these three reasons, researchers opted to use only land cover classes to explain observed variability in biodiversity patterns in 80 percent of the studies reviewed. This dependence on land cover classes as the main explanatory factor means that we are lacking important information about variables that are very likely to exert a strong influence on dung beetles communities – a limitation that is also common to other taxa (e.g. amphibians and reptiles, GARDNER; BARLOW & PERES, 2007).

Neglecting such variables could lead researchers to risk drawing misleading or spurious conclusions about species environment relationships, even when using meaningful response variables. For instance, changes in dung beetles diversity as a consequence of changes in mammal populations (e.g. due to overhunting) – and hence the availability and composition of dung resources – may have been erroneously attributed to a direct effect of habitat fragmentation (NICHOLS et al., 2009). Declines in mammal populations could also help explain the low levels of dung beetle species diversity in relatively un-fragmented areas of forest. Moreover, it could help explain observations of similar dung beetles communities between different land-uses (e.g. ESTRADA & COATES-ESTRADA, 2002). In spite of the potential confounding influence of changes to mammal populations in disturbed and non-disturbed habitats on dung beetle communities, we found only two papers where authors attempted to sample differences in the diversity of both groups of organisms (i.e. BARLOW et al., 2010; ESTRADA & COATES-ESTRADA, 2002) – both of which were suggestive of a strong link between mammals and dung beetles.

The worrying implications of the inconsistencies we have observed between the stated importance of different variables and their occurrence in the literature are further exacerbated by the general lack of any form of justification for study design choices and variable selections in published papers. Almost all researchers failed to provide a biological or methodological explanation for their selection of response and explanatory variables, and provided justification for only a few of their study design choices. This lack of explicit justification prevents readers from understanding whether the choices made by researchers were based on biological and/or statistical understanding, projects constraints or simply based on arbitrary decisions (JACKSON & FAHRIG, 2015).

5 CONCLUSIONS

While exposing some of the problems and difficulties of performing reliable assessments of land-use effects on biodiversity we reinforce the importance of careful study design and variable selection, and the need for constructive spaces to exchange ideas on methods and approaches between researchers. We believe that the number and reliability of inferences from studies on land-use change could be improved if researchers follow a few basic recommendations for good practice. Perhaps most obviously, researchers should assess what they consider to be the most important variables based on their personal experience, theory and familiarity with other work on the subject (see Fig 2). Wherever possible, researchers should also use and test the relative importance of these variables in their own research, or provide a careful explanation of why certain variables were included and others were excluded. Shared protocols would be useful to standardise research, and make it easier for newcomers to sample key variables of interest.

ACKNOWLEDGEMENTS

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SUPPLEMENTARY MATERIAL

Table S 1 - Summary of the response and explanatory variables used in the 48 studies surveyed regarding the effects of land-use change on dung beetle communities in tropical forests. Variables presence or absence in each paper is indicated by "1" or "0" respectively. When it is not applicable (e.g. the presence in studies performed only in forested habitats of a variable recommended for studies on agricultural lands), columns were filled with "-". * PART I of IV

Reference	**Categories of response variables**						
	Body size	**Biomass**	**Composition / structure**	**Diversity**	**Evenness / dominance**	**Species-level abundance**	**Species richness**
Aguilar-Amuchastegui e Henebry 2007	0	0	1	1	1	0	1
Andresen 2008	0	0	1	1	1	0	1
Arellano *et al*. 2005	0	1	1	0	0	0	1
Arellano *et al*. 2008	0	0	1	1	1	0	1
Arellano *et al*. 2013	0	0	1	0	1	0	1
Avendano-Mendonza *et al*. 2005	0	0	1	0	0	0	1
Barlow *et al*. 2010	0	0	1	0	0	1	1
Barlow *et al*. 2012	0	0	1	0	0	0	1
Barraza *et al*. 2010	0	0	1	0	0	0	1
Botes *et al*. 2006	0	0	1	0	0	0	1
Braga *et al*. 2013	0	1	0	0	0	0	1
Davis & Philips 2009	0	0	1	0	0	0	1
Davis *et al*. 1999	0	0	0	1	0	0	1
Davis *et al*. 2001	0	0	1	0	1	0	1
De Andrade *et al*. 2011	0	0	1	0	1	0	1
Edwards *et al*. 2012	0	0	1	0	1	0	1
Estrada e Coates-Estrada 2002	0	0	0	1	1	1	1
Halfter & Arellano 2002	0	1	0	1	1	0	1
Harvey *et al*. 2006	0	0	1	0	0	0	1
Harvey *et al*. 2006	0	0	1	0	0	0	1
Hayes *et al*. 2009	0	0	0	1	0	0	1
Hill 1996	0	0	0	0	0	1	1
Horgan 2005	0	1	1	0	0	0	1
Horgan 2008	0	1	0	0	0	0	1

To be continued …

Conclusion							
Horgan 2009	0	1	1	0	0	0	1
Janzen 1983	0	0	0	0	0	1	0
Larsen 2012	0	0	0	0	0	1	0
Lee *et al*. 2009	1	1	0	0	0	0	1
Liberal *et al*. 2011	0	0	1	1	1	0	1
Navarrete & Halffter 2008	0	0	1	0	0	0	1
Neita & Escobar 2012	0	1	1	0	1	0	1
Neves *et al*. 2010	0	0	1	0	0	0	1
Nielsen 2007	0	1	1	0	1	0	1
Nyeko 2009	0	0	1	0	0	0	1
Oldekop *et al*. 2012	0	0	0	0	0	0	1
Pineda *et al*. 2005	0	0	0	1	1	0	1
Quintero & Roslin 2005	1	0	1	1	0	0	1
Ros *et al*. 2012	0	0	0	1	0	0	1
Scheffler 2005	1	1	1	1	0	0	1
Schulze *et al*. 2004	0	0	1	0	0	0	0
Shahabuddin 2010	0	0	1	0	0	1	1
Shahabuddin *et al*. 2010	0	1	1	0	0	0	1
Silva *et al*. 2010	0	0	1	1	0	1	1
Slade *et al*. 2011	1	1	0	0	0	0	1
Spector & Ayzama 2003	0	1	1	0	0	0	1
Verdu *et al*. 2007	0	0	1	1	1	0	1
Vieira *et al*. 2008	0	0	1	0	0	0	1
Vulinec 2002	0	1	1	0	0	1	1

Source: Author

* PART II of IV

Reference	Categories of explanatory variables						
	Soil	**Topography**	**Forest structure**	**Landscape connectivity**	**Landscape history**	**Local disturb. history**	**Leaf litter**
Aguilar-Amuchastegui e Henebry 2007	0	1	1	1	0	1	0
Andresen 2008	0	0	0	0	0	0	0
Arellano *et al*. 2005	0	0	0	0	0	0	0
Arellano *et al*. 2008	0	0	0	0	0	0	0
Arellano *et al*. 2013	0	0	1	0	0	0	0
Avendano-Mendonza *et al*. 2005	0	0	0	0	0	0	0
Barlow *et al*. 2010	0	0	1	1	0	0	0
Barlow *et al*. 2012	0	0	0	0	0	0	0
Barraza *et al*. 2010	0	0	0	0	0	0	0
Botes *et al*. 2006	0	0	0	0	0	0	0
Braga *et al*. 2013	0	0	0	0	0	0	0
Davis & Philips 2009	0	0	0	0	0	0	0
Davis *et al*. 1999	0	1	0	0	0	0	0
Davis *et al*. 2001	0	0	0	0	0	0	0
De Andrade *et al*. 2011	0	0	1	0	0	0	1
Edwards *et al*. 2012	0	0	0	0	0	0	0
Estrada & Coates-Estrada 2002	0	0	0	0	0	0	0
Halffter & Arellano 2002	0	0	0	0	0	0	0
Harvey *et al*. 2006	0	0	0	0	0	0	0
Harvey *et al*. 2006	0	0	0	0	0	0	0
Hayes *et al*. 2009	0	0	1	0	0	0	0
Hill 1996	0	0	0	0	0	0	0
Horgan 2005	0	0	0	0	0	0	0
Horgan 2008	0	0	0	0	0	0	0
Horgan 2009	0	0	0	0	0	0	0
Janzen 1983	0	0	0	0	0	0	0
Larsen 2012	0	1	0	0	0	0	0
Lee *et al*. 2009	0	0	0	0	0	0	0
Liberal *et al*. 2011	0	0	0	0	0	0	0
Navarrete & Halffter 2008	0	0	1	0	0	0	0

To be continued …

Conclusion							
Neita & Escobar 2012	0	0	0	0	0	0	0
Neves *et al*. 2010	0	0	0	0	0	0	0
Nielsen 2007	0	0	0	0	0	0	0
Nyeko 2009	0	0	1	0	0	0	1
Oldekop *et al*. 2012	0	0	1	1	0	0	0
Pineda *et al*. 2005	0	0	0	0	0	0	0
Quintero & Roslin 2005	0	0	0	0	0	0	0
Ros *et al*. 2012	0	0	0	1	0	0	0
Scheffler 2005	0	0	0	0	0	0	0
Schulze *et al*. 2004	0	0	0	0	0	0	0
Shahabuddin 2010	0	0	0	0	0	0	0
Shahabuddin *et al*. 2010	0	0	0	0	0	0	0
Silva *et al*. 2010	0	0	0	0	0	0	0
Slade *et al*. 2011	0	0	1	0	0	0	0
Spector & Ayzama 2003	0	0	0	0	0	0	0
Verdu *et al*. 2007	0	0	0	0	0	0	0
Vieira *et al*. 2008	0	0	0	0	0	0	0
Vulinec 2002	0	0	0	0	0	0	0

Source: Author

* PART III of IV

Reference	Categories of explanatory variables						
	Mammal abund. / biomass	**Mammal diversity**	**Patch size**	**Understory structure**	**History of use**	**Intensity of use**	**Land cover class**
Aguilar-Amuchastegui e Henebry 2007	0	0	0	0	-	-	-
Andresen 2008	0	0	0	0	0	0	1
Arellano *et al*. 2005	0	0	0	0	0	0	1
Arellano *et al*. 2008	0	0	0	0	0	0	1
Arellano *et al*. 2013	0	0	0	0	0	0	1
Avendano-Mendonza *et al*. 2005	0	0	0	0	0	0	1
Barlow *et al*. 2010	0	0	0	0	-	-	-
Barlow *et al*. 2012	0	0	0	0	-	-	-
Barraza *et al*. 2010	0	0	0	0	0	0	1
Botes *et al*. 2006	0	0	0	0	-	-	-
Braga *et al*. 2013	0	0	0	0	0	0	1
Davis & Philips 2009	0	0	0	0	0	0	1
Davis *et al*. 1999	0	0	0	0	0	0	1
Davis *et al*. 2001	0	0	0	0	-	-	-
De Andrade *et al*. 2011	0	0	0	1	-	-	-
Edwards *et al*. 2012	0	0	0	0	-	-	-
Estrada & Coates-Estrada 2002	1	1	0	0	0	0	1
Halffter & Arellano 2002	0	0	0	0	0	0	1
Harvey *et al*. 2006	0	0	0	0	0	0	1
Harvey *et al*. 2006	0	0	0	0	0	0	1
Hayes *et al*. 2009	0	0	0	0	-	-	-
Hill 1996	0	0	1	0	0	0	1
Horgan 2005	0	0	0	0	-	-	-
Horgan 2008	0	0	0	0	0	0	1
Horgan 2009	0	0	0	0	-	-	-
Janzen 1983	0	0	0	0	0	0	1
Larsen 2012	0	0	0	0	-	-	-
Lee *et al*. 2009	0	0	0	0	-	-	-
Liberal *et al*. 2011	0	0	0	0	0	0	1
Navarrete e Halffter 2008	0	0	0	0	0	0	1

To be continued …

Conclusion							
Neita e Escobar 2012	0	0	0	0	-	-	-
Neves *et al*. 2010	0	0	0	0	0	0	1
Nielsen 2007	0	0	0	0	0	0	1
Nyeko 2009	0	0	1	0	-	-	-
Oldekop *et al*. 2012	0	0	0	0	-	-	-
Pineda *et al*. 2005	0	0	0	0	-	-	-
Quintero & Roslin 2005	0	0	1	0	-	-	-
Ros *et al*. 2012	0	0	0	0	-	-	-
Scheffler 2005	0	0	0	0	0	0	1
Schulze *et al*. 2004	0	0	0	0	0	0	1
Shahabuddin 2010	0	0	0	0	0	0	1
Shahabuddin *et al*. 2010	0	0	0	0	0	0	1
Silva *et al*. 2010	0	0	0	0	0	0	1
Slade *et al*. 2011	0	0	0	1	-	-	-
Spector & Ayzama 2003	0	0	1	0	0	0	1
Verdu *et al*. 2007	0	0	0	0	0	0	1
Vieira *et al*. 2008	0	0	0	0	0	0	1
Vulinec 2002	0	0	0	0	0	0	1

Source: Author

* PART IV of IV

Reference	Category of explanatory variables	
	Landscape connectivity	Vegetation structure
Aguilar-Amuchastegui e Henebry 2007	-	-
Andresen 2008	0	0
Arellano *et al*. 2005	0	0
Arellano *et al*. 2008	0	0
Arellano *et al*. 2013	0	1
Avendano-Mendonza *et al*. 2005	0	0
Barlow *et al*. 2010	-	-
Barlow *et al*. 2012	-	-
Barraza *et al*. 2010	0	0
Botes *et al*. 2006	-	-
Braga *et al*. 2013	0	0
Davis & Philips 2009	0	0
Davis *et al*. 1999	0	0
Davis *et al*. 2001	-	-
De Andrade *et al*. 2011	-	-
Edwards *et al*. 2012	-	-
Estrada & Coates-Estrada 2002	0	0
Halffter & Arellano 2002	0	0
Harvey *et al*. 2006	0	0
Harvey *et al*. 2006	0	0
Hayes *et al*. 2009	-	-
Hill 1996	0	0
Horgan 2005	-	-
Horgan 2008	0	0
Horgan 2009	-	-
Janzen 1983	0	0
Larsen 2012	-	-
Lee *et al*. 2009	-	-
Liberal *et al*. 2011	0	0
Navarrete & Halffter 2008	0	0
Neita & Escobar 2012	-	-

To be continued …

Conclusion		
Neves *et al*. 2010	0	0
Nielsen 2007	0	0
Nyeko 2009	-	-
Oldekop *et al*. 2012	-	-
Pineda *et al*. 2005	-	-
Quintero & Roslin 2005	-	-
Ros *et al*. 2012	-	-
Scheffler 2005	0	0
Schulze *et al*. 2004	0	0
Shahabuddin 2010	0	0
Shahabuddin *et al*. 2010	0	0
Silva *et al*. 2010	0	0
Slade *et al*. 2011	-	-
Spector & Ayzama 2003	0	0
Verdu *et al*. 2007	0	0
Vieira *et al*. 2008	0	0
Vulinec 2002	0	0

Source: Author

APPENDIX

APPENDIX A - Studies information assessment

We summarize below the categories of study design choices selected for assessing to what extent studies about the effects of land use change on dung beetle communities in tropical forests are informative.

1 Information about study area
    1.1 Natural vegetation type
    1.2 Main soil type
    1.3 Geographical coordinates
    1.4 Climate zone
    1.5 Altitude
    1.6 Quality of the reference habitat
    1.7 Estimative of size of the study area
    1.8 Distance between treatments

2 Information about sampling effort
    2.1 Distance among sites
    2.2 Number of treatments (replicates)
    2.3 Number of replicates within treatments
    2.4 Number of sampling events

3 Information about sampling methods
    3.1 Trap spacing
    3.2 Sampling technique
    3.3 Bait type

APPENDIX B – Survey of dung beetle researchers

The survey was sent to the authors of the revised papers. We divided the survey in three sections (A, B and C) with six questions each, as listed below. In order to avoid possible bias questions' alternatives were shuffled and presented in a different order for each respondent.

Section A

The following SIX (1-6) questions are related to the selections of explanatory and response variables in studies assessing the effects of land cover change on dung beetle communities in FORESTED HABITATS. Please answer the questions according to your opinion and experience in this research area.

Question 1

What EXPLANATORY VARIABLES best describe habitat QUALITY for forest dwelling dung beetles? (Rank the variables below in order of importance, with 1 being the most important).

a) Mammal diversity
b) Landscape connectivity (e.g. amount of forest in the surrounding landscape, distance to the nearest source population)
c) Landscape history (e.g. temporal pattern of forest lost in surrounding landscape)
d) Forest structure (e.g. basal area of large trees, canopy cover)
e) Soil (e.g. nutrient status, structure and humidity)
f) Leaf litter (e.g. leaf litter depth)
g) Mammal abundance and biomass
h) Topography (i.e. altitude and slope)
i) Patch size (e.g. patch area, distance to the edge)
j) Local disturbance history (e.g. logging and fire history)
k. Understory structure (e.g. density of small stems)

Question 2

IF you consider that the previous list is missing and important variable, please IDENTIFY THE VARIABLE and attribute a RANK number to the variable in the box below.

Question 3

Please, describe in the box below WHY you have ranked the variables in that order.

Question 4

What RESPONSE VARIABLES best reflect the EFFECTS of land cover change on forest dwelling dung beetles? (Rank the variables below in order of importance, with 1 being the most important).

a) Community composition and/or structure (e.g. community similarity based on Jaccard, Bray-Curtis or other indices)
b) Biomass (e.g. total biomass, average biomass)
c) Body size (e.g. average body length)
d) Species-level abundance
e) Diversity (e.g. Shannon or Simpsons' indices)
f) Evenness and/or dominance (e.g. Pielou's evenness)

Question 5

IF you consider that the previous list is missing and important variable, please IDENTIFY THE VARIABLE and attribute a RANK number to the variable in the box below.

Question 6

Please, describe in the box below WHY you have ranked the variables in that order.

Section B

The following SIX (7-12) questions are related to the selection of adequate explanatory and response variables for studies addressing the effects of land cover change on dung beetle communities in OPEN AGRICULTURAL LANDS (e.g. pastures, mechanised agriculture). Please answer the questions according to your knowledge and experience in this research area.

Question 7

What EXPLANATORY VARIABLES best describe habitat QUALITY for all dung beetles? (Rank the variables below in order of importance, with 1 being the most important).

a) Land cover class (e.g. agriculture, pasture)
b) Vegetation structure (e.g. density of shrubs or weeds)
c) Landscape connectivity and proximity to natural features (e.g. distance to the nearest source population)
d) History of use (e.g. time since deforestation or clear cut, previous uses)
e) Soil (e.g. nutrient status, structure and humidity)
f) Intensity of use (e.g. if mechanised agriculture or received chemical inputs)
g) Topography (i.e. altitude and slope)

Question 8

IF you consider that the previous list is missing and important variable, please IDENTIFY THE VARIABLE and attribute a RANK number to the variable in the box below.

Question 9

Please, describe in the box below WHY you have ranked the variables in that order.

Question 10

What RESPONSE variables best reflect the EFFECTS of land cover changes on all dung beetles? (Rank the variables below in order of importance, with 1 being the most important).

a) Biomass (e.g. total biomass, average biomass)
b) Body size (e.g. average body length)
c) Community composition and/or structure (e.g. community similarity based on Jaccard, Bray-Curtis or other indices)
d) Species richness (e.g. total species richness, average species richness)
e) Species-level abundance
f) Evenness and/or dominance (e.g. Pielou’s evenness)
g) Diversity (e.g. Shannon or Simpsons’ indices)

Question 11

IF you consider that the previous list is missing and important variable, please IDENTIFY THE VARIABLE and attribute a RANK number to the variable in the box below.

Question 12
Please, describe in the box below WHY you have ranked the variables in that order.

Section C

Almost there!!! We would love if you answer the following questions about your scientific career. This information would help us to interpret the results of the survey.

Question 13
Where did you get your PhD? (Please write down at least the NAME AND COUNTRY of the university. IF you do NOT have a PhD degree, please write 'NONE' in the box below)

Question 14
When did you get your PhD?
a) 2011-2013
b) 2006-2010
c) 2001-2005
d) 1996-2000
e) 1991-1995
f) 1985-1990
g) I do not have a PhD
h) Other (please specify)

Question 15
What is your current position?
a) Professor/Lecturer
b) Researcher
c) PhD student
d) Other (please specify)

Question 16

How many dung beetles related papers have you published in the last two years?

a) None

b) 1

c) 2

d) 3

e) 4

f) 5

g) 6

h) 7

i) 8

j) 9

k) ≥ 10

Question 17

What is your current university?

Question 18

Can I contact your for further enquiries? (Please, type your preferred email in the box below if you agree to be contacted later – if necessary)

a) No

b) Yes

CHAPTER 5

GENERAL DISCUSSION

The broad aim of this thesis was to provide a better understanding of how anthropogenic impacts influence biodiversity in tropical forest regions. Using dung beetles as a focal taxon I assessed changes in in species community attributes (e.g. species richness, species abundance, composition, structure) along a gradient of tropical forest degradation and in areas where forest has been converted to pastures. To do so, I sampled dung beetles in 272 forests and introduced pastures across two regions that together make up approximately 3 million ha. I employed a wide range of environmental, historical and spatial variables to help identify possible mechanisms by which anthropogenic impacts influence biodiversity. In addition, I conducted a thorough review of the dung beetle literature on this topic and surveyed the authors of published studies to better understand the choices made in designing field sampling and data analysis, thus helping to identify key gaps and limitations in current research practices and contribute to the improvement of future biodiversity assessments. Below, I summarise the main findings from each chapter.

1 KEY FINDINGS

1.1 Quantifying Dung Beetle Community Responses to Tropical Forest Disturbances in the Eastern Amazon (Chapter 2)

Research questions: (1) How do dung beetle communities respond to a gradient of anthropogenic forest disturbance? (2) Which environmental variables related to forest disturbance best predict dung beetle species richness, abundance, composition and structure?

A major finding in Chapter 2 was the negative impacts, across multiple scales, on dung beetle communities of disturbances affecting tropical forest canopy and biomass, at multiple scales. Decreasing canopy openness and forest biomass was associated with an impoverishment of dung beetle communities. Reductions in species richness were followed by changes in composition and structure, due to a loss of several forest-interior species (BARLOW et al., 2016). Biotic homogenisation (SOLAR et al., 2016) raises concern about the fate of biodiversity in human-modified landscapes and in the remaining areas of degraded forest that exist in these landscapes. The strong relationship found between dung beetles assemblage diversity and structure and canopy openness and forest biomass highlights the potential to predict a forests' conservation value using both optical satellite imagery and airbone LiDAR techniques. Such approaches would make it easier to monitor impacts of anthropogenic changes in tropical forests and to identify priority areas for conservation. These results also demonstrated that conserving the least disturbed primary forest remnants is still an effective and crucial strategy for maintaining tropical diversity (BICKNELL et al., 2014), due to the comparatively lower conservation value of disturbed or secondary forests. These findings provide useful insights that could help assist the development of strategies for monitoring and reducing the biodiversity impacts of human activities in tropical forests.

1.2 The Relative Importance of Multiple Scale Factors for Dung Beetle Communities in Amazonian Introduced Pastures (Chapter 3)

Research questions: (1) To what extent are dung beetle communities in pastures different from the surrounding forest communities? (2) What is the provenance of dung beetle species that are significant and consistent indicators of pastures? (3) To what extent is the richness, abundance, species composition and structure of dung beetle communities in pastures determined by local, landscape or spatial factors? (4) Are the observed patterns of dung beetle diversity consistent between two discrete study regions?

In Chapter 3, I provide the first large-scale assessment of dung beetle diversity in exotic pastures on cleared tropical forest land. A key finding of this chapter was the importance of natural open habitats – savannahs, grasslands and other open formations - in providing source populations for dung beetle assemblages in pastures. I observed that dung beetle communities in introduced Amazonian pastures are radically different and simplified in comparison with those from the surrounding forests. A few species typical from Brazilian open habitats accounted for more than 95% of pastures communities at both studied regions. These are: *Pseudocanthon* aff. *xanthurus*, *Digitonthophagus gazella*, *Canthidium humerale*, *Canthon* aff. *simulans*, *Diabroctis mimas*, *Canthon lituratus*, *Trichilum* sp.1, *Canthon* aff. *octodentatus*, *Canthon* sp.1, *Canthon obscuriellus*, *Canthon aff.* acutus, *Trichillum externepunctatum*, *Canthon* aff. *heyrovskyi*, *Ontherus appendiculatus*, *Dichotomius nisus*, *Canthon* aff. *chalybaeus*, *Canthidium multipunctatum*, *Onthophagus* aff. *hirculus* and *Canthidium barbacenicum*. Neither local environmental nor historical factors appeared to exert significant influence on dung beetle communities. These results demonstrate that, even when surrounded by extensive and megadiverse forests, tropical introduced pastures rely on the conservation of natural open habitats (e.g. the Cerrado, intra-Amazonian savannahs and the Caatinga) for being colonised. Moreover, the results of Chapter 3 challenge researchers and stakeholders to move beyond closed biome-based conservation strategies, but rather, integrate initiatives that promote ecosystems functioning by recognising their interdependence.

1.3 Do We Select the Best Metrics for Assessing Land Use Effects on Biodiversity? (Chapter 4)

Research questions: (1) To what extent are the response and explanatory variables deemed most appropriate by researchers actually being selected in published studies? (2) To what extent is the variable selection and study design processes clearly justified, and, if so, what kind of justification is presented in published work?

In Chapter 4, I examined researcher choices of variables in the assessment of dung beetle responses to anthropogenic disturbances in the tropics, looking for discrepancies in the importance assigned to variables used to describe both forest and non-forest habitat and the variables actually used in published studies. I demonstrate that the explanatory variables deemed as most important by researchers are in fact little used in their own studies, although the commonly selected response variables seem appropriate for such assessments. These findings suggest that information is being lost due to an inadequacy of the predictors selected, resulting in incomplete conclusions about dung beetle responses to human disturbance. Alternatively, researchers may reach misleading conclusions based on spurious relationships between the response and explanatory variables selected, undermining current knowledge about dung beetle communities-environment relationships. In conclusion, the study presents a comprehensive assessment of current attempts to understand the consequences of human activities on tropical forest dung beetle biota, and offers a list of variables to be considered in future studies, ranked by their relative importance according experts.

2 Implication of Research Findings for the Management of Human-Modified Amazonian Landscapes

The Amazon is a megadiverse tropical forest covering almost 7 million km^2 across nine South American countries (BARTHEM et al., 2004). This forest has great and undeniable ecological and socio-economic importance at local, regional and global scales (TRIVEDI et al., 2009). Increasing human pressures, however, are threatening the Amazonian biodiversity and compromising the provision of several ecosystem services (GARDNER et al., 2009). The worrying implications of human impacts on Amazonian forests have fuelled a wide-ranging debate debate the most fective strategies for reducing its historically high levels of deforestation, largely determined by the expansion of agricultural activities (GEIST & LAMBIN, 2002). In this scenario, Brazil has played a prominent role, since it hosts most of the Amazonian territory (FOLEY et al., 2007) and exerts international influence on conservation initiatives (FERREIRA et al., 2014). At the same time, it is responsible for most of the deforestation and degradation happening in the Amazon, for instance, with over 60 million ha converted to pastures (ALMEIDA et al., 2016) and 50 million ha of forests under timber concession (MACPHERSON et al., 2010).

The findings in this thesis could help to improve current assessments and strategies for monitoring and reducing the biodiversity impacts of human activities in tropical forest regions. The most significant conclusion of this thesis is the need to integrate ongoing efforts to combat deforestation with initiatives to prevent forest disturbance and the suppression of habitats that could serve as population sources for the already modified landscapes. This general conclusion is based on the following specific findings:

- i) Anthropogenic disturbances in tropical forests (e.g. selective logging and wildfires) promote reductions in forest canopy openness and biomass, leading to an impoverishment of dung beetle communities at local and landscape scales (Chapter 2). This highlights the value of remote sensing assessments of forest canopy openness and biomass in monitoring and management programs, to evaluate patterns of conservation value in remaining forests and provide more accurate measures of human impacts on biodiversity.
- ii) In comparison to undisturbed primary forests, disturbed primary forests and secondary forests regenerating after agricultural use have low conservation value for tropical forest dung beetles (Chapter 2). The maintenance of least disturbed primary forests should be a priority in programs focused on the conservation of tropical forest biodiversity.
- iii) Forest conversion to pastures result in the loss almost all forest dung beetle species (Chapter 3).
- iv) The colonisation of introduced pastures by dung beetles appears to be dependent on pastures proximity to natural open habitats and species dispersal abilities. A well-defined group of species that dominates pasture communities is composed by dung beetles typical from Brazilian open habitats, such as the Cerrado, intra-Amazonian savannahs and Brazilian native grasslands (Chapter 3).

3 Implications for Future Research

This thesis offers scientific advances that could increase the quality and reliability of information produced by ecological assessments of human impacts on biodiversity. In Chapter 5, I identified potentially important variables that have been little or not used in dung beetle studies to describe forest and non-forest habitats. In Chapter 3 and Chapter 4, I assessed the influence of some of these variables on dung beetle communities in human-modified landscapes of the Brazilian Amazon. Taken together, the findings of the three data chapters provide valuable guidance for the design of future research programs, especially the selection of key environmental variables in species-environment models. Based on these findings, I suggest that future works focused on dung beetle responses to human modification of tropical forests include at least:

- i) Measures of mammal abundance and biomass: because most dung beetles depend on mammals for obtaining their feeding, breeding and nesting resources (Halffter e Edmonds 1982, Hanski e Cambefort 1991), their occurrence in tropical forests will likely vary according to mammal abundance and biomass (Nichols *et al.* 2009, Culot *et al.* 2013). However, these measures are almost absent from dung beetle studies of forests degradation. Although I have not used data on mammals for this thesis, according to the surveyed dung beetle researchers these are among the most important measures that should be included in forest assessments (Chapter 5).
- ii) Measures of forest structure: while its known that dung beetles are sensitive to changes in forest structure (Nichols *et al.* 2007, Audino *et al.* 2014) few studies have measured forest structural variables to help explain changes in dung beetle communities in response to anthropogenic disturbances in tropical forests. In Chapter 3, I show that two variables describing forest structure (i.e. forest canopy openness and biomass) were strong related to variations in dung beetle species richness, abundance, composition and structure.

Importantly, the conclusions of Chapter 4 suggest that future work should separately address dung beetle communities from forest and non-forest habitats. Both habitat types are radically different in terms of physical and environmental conditions (LAURANCE, 2004), reflected in contrasting dung beetle communities. In Chapter 4, I show that forest dung beetles do not to colonise pastures that have replaced tropical forests, and are weakly influenced by pastures environmental characteristics. In fact, this system is dominated by species already adapted to the environmental conditions of open habitats, and are therefore unlikely to respond to environmental changes in the same way as forest beetles.

Finally, irrespective of the focus given to future works, researchers should dedicate extra attention to the justification of their selection of variables, clarifying whether their choices were based on biological and/or statistical reasons, projects constraints or arbitrary decisions (JACKSON & FAHRIG, 2015). The provision of this kind of information will certainly improve the reliability of ecological studies, facilitate the identification of appropriate predictors and provides a guide for future studies.

4 CONCLUSION

In summary, the results presented in this thesis indicate that anthropogenic disturbances highlight the significant impoverishment of dung beetle communities in tropical forests, exclusion of the forest dung beetle species from cleared areas, and a strong dependence of natural open habitats to serve as source populations for such areas. I provide evidence that forest canopy openness and biomass are important predictors of forest quality for dung beetles, and that dung beetle communities in pastures in previously forested areas are highly dependent on stochastic dispersal. Finally, I identify discrepancies between variable importance and their use in studies on dung beetle responses to anthropogenic disturbances in tropical forest regions, highlighting the need for measures of mammal populations and forest structure in future works.

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APPENDIX

OTHER OUTCOMES

Appendice 1

Solar, R.R.C.; Barlow, J.; Ferreira, J.; Berenguer, E.; Lees, A.C.; Thomson, J.R.; Louzada, J.; Maués, M.; Moura, N.G.; **Oliveira, V.H.F.;** Chaul, J.C.M.; Schoereder, J.H.; Vieira, I.C.G.; Mac Nally, R.; Gardner, T.A. How pervasive is biotic homogenization in human-modified tropical forest landscapes? *Ecology Letters* (Print), 18(10):1108–1118, 2015.

Abstract

Land-cover change and ecosystem degradation may lead to biotic homogenization, yet our understanding of this phenomenon over large spatial scales and different biotic groups remains weak. We used a multi-taxa dataset from 335 sites and 36 heterogeneous landscapes in the Brazilian Amazon to examine the potential for landscape-scale processes to modulate the cumulative effects of local disturbances. Biotic homogenization was high in production areas but much less in disturbed and regenerating forests, where high levels of among-site and among-landscape β-diversity appeared to attenuate species loss at larger scales. We found consistently high levels of β-diversity among landscapes for all land cover classes, providing support for landscape-scale divergence in species composition. Our findings support concerns that β-diversity has been underestimated as a driver of biodiversity change and underscore the importance of maintaining a distributed network of reserves, including remaining areas of undisturbed primary forest, but also disturbed and regenerating forests, to conserve regional biota.

Appendice 2

Barlow, J.; Lennox, G.D.; Ferreira, J.; Berenguer, E.; Lees, A.C.; Macnally, R.; Thomson, J.R.; Ferraz, S.F.B.; Louzada, J.; **Oliveira, V.H.F.;** Parry, L.; Solar, R.R.C.; Vieira, I.C.G.; Aragão, L.E.O.C.; Begotti, R.A ; Braga, R.F.; Cardoso, T.M.; Oliveira Jr, R.C.; Souza Jr, C.M.; Moura, N.G.; Nunes, S.S.; Siqueira, J.V.; Pardini, R.; Silveira, J.M.; Vaz-De-Mello, F.Z.; Veiga, R.C.S.; Venturieri, A.; Gardner, T.A. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* (London), v. 535, p. 144-147, 2016.

Abstract

Concerted political attention has focused on reducing deforestation1–3, and this remains the cornerstone of most biodiversity conservation strategies4–6. However, maintaining forest cover may not reduce anthropogenic forest disturbances, which are rarely considered in conservation programmes6. These disturbances occur both within forests, including selective logging and wildfires7,8, and at the landscape level, through edge, area and isolation effects9. Until now, the combined effect of anthropogenic disturbance on the conservation value of remnant primary forests has remained unknown, making it impossible to assess the relativeimportance of forest disturbance and forest loss. Here we address these knowledge gaps using a large data set of plants, birds and dung beetles (1,538, 460 and 156 species, respectively) sampled in 36 catchments in the Brazilian state of Pará. Catchments retaining more than 69–80% forest cover lost more conservation value from disturbance than from forest loss. For example, a 20% loss of primary forest, the maximum level of deforestation allowed on Amazonian properties under Brazil's Forest Code5, resulted in a 39–54% loss of conservation value: 96–171% more than expected without considering disturbance effects. We extrapolated the disturbancemediated loss of conservation value throughout Pará, which covers 25% of the Brazilian Amazon. Although disturbed forests retained considerable conservation value compared with deforested areas, the toll of disturbance outside Pará's strictly protected areas is equivalent to the loss of 9.2 – 13.9 milion ha of primary forest. Even this lowest estimate is greater than the area deforested across the entire Brazilian Amazon between 2006 and 2015 (ref. 10). Species distribution models showed that both landscape and within-forest disturbances contributed to biodiversity loss, with the greatest negative effects on species of high conservation and functional value. These results demonstrate an urgent need for policy interventions that go beyond the maintenance of forest cover to safeguard the hyper-diversity of tropical forest ecosystems.

Appendice 3

Gardner, T.A.; Ferreira, J., Barlow, J.; Lees, A.C.; Parry, L.; Vieira, I.C.l.G.; Berenguer, E.; Abramovay, R.; Aleixo, A.; Andretti, C.; Aragão, L.E.O.C.; Araújo, I., de Ávila, W.S.; Bardgett, R.D.; Batistella, M.; Begotti, R.A.; Beldini, T.; de Blas, D.E.; Braga, R.F.; Braga, D.L.; de Brito, J.G.; de Camargo, P.B.; dos Santos, F.C.; de Oliveira, V.C.; Cordeiro, A.C.N.; Cardoso, T.M.; de Carvalho, D.R.; Castelani, S.A.; Chaul, J.C.M.; Cerri, C.E.; Costa, F.A.; da

Costa, C.D.F.; Coudel, E.; Coutinho, A.C.; Cunha, D.; D'Antona, A.; Dezincourt, J.; Dias-Silva, K.; Durigan, M.; Esquerdo, J.C.D.M.; Feres, J.; Ferraz, S.F.B.; Ferreira, A.E.M.; Fiorini, A.C.; da Silva, L.V.F.; Frazão, F.S.; Garrett, R.; Gomes, A.S.; Gonçalves, K.S.; Guerrero, J.B.; Hamada, N.; Hughes, R.M.; Igliori, D.C.; Jesus, E.C.; Juen, L.; Junior, M.; Junior, J.M.B.O.; Junior, R.C.O.; Junior, C.S.; Kaufmann, P.; Korasaki,V.; Leal, C.G. Leitão, R.; Lima, N.; Almeida, M.F.L.; Lourival, R.; Louzada, J.; Mac Nally, R.; Marchand, S.; Maués, M.M.; Moreira, F.M.S.; Morsello, C.; Moura, N.; Nessimian, J.; Nunes, S. **Oliveira,V.H.F.** et al. A social and ecological assessment of tropical land uses at multiple scales: the Sustainable Amazon Network. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368, 2013.

Abstract

Science has a critical role to play in guiding more sustainable development trajectories. Here, we present the Sustainable Amazon Network (Rede Amazônia Sustentável, RAS): a multidisciplinary research initiative involving more than 30 partner organizations working to assess both social and ecological dimensions of land-use sustainability in eastern Brazilian Amazonia. The research approach adopted by RAS offers three advantages for addressing land-use sustainability problems: (i) the collection of synchronized and co-located ecological and socioeconomic data across broad gradients of past and present human use; (ii) a nested sampling design to aid comparison of ecological and socioeconomic conditions associated with different land uses across local, landscape and regional scales; and (iii) a strong engagement with a wide variety of actors and non-research institutions. Here, we elaborate on these key features, and identify the ways in which RAS can help in highlighting those problems in most urgent need of attention, and in guiding improvements in land-use sustainability in Amazonia and elsewhere in the tropics. We also discuss some of the practical lessons, limitations and realities faced during the development of the RAS initiative so far.

Appendice 4

Berenguer, E.; Ferreira, J.; Gardner, T.A.; Aragão, L.E.O.C.; De Camargo, P.B.; Cerri, C.E.; Durigan, M.; De Oliveira, R.C.; Vieira, I.C.G.; Barlow, J. A large-scale field assessment of carbon stocks in human-modified tropical forests. *Global Change Biology*, v. 20 (12), p. 3713-3726, 2014.

Abstract

Tropical rainforests store enormous amounts of carbon, the protection of which represents a vital component of efforts to mitigate global climate change. Currently, tropical forest conservation, science, policies, and climate mitigation actions focus predominantly on reducing carbon emissions from deforestation alone. However, every year vast areas of the humid tropics are disturbed by selective logging, understory fires, and habitat fragmentation. There is an urgent need to understand the effect of such disturbances on carbon stocks, and how stocks in disturbed forests com- pare to those found in undisturbed primary forests as well as in regenerating secondary forests. Here, we present the results of the largest field study to date on the impacts of human disturbances on above and belowground carbon stocks in tropical forests. Live vegetation, the largest carbon pool, was extremely sensitive to disturbance: forests that experienced both selective logging and understory fires stored, on average, 40% less aboveground carbon than undis- turbed forests and were structurally similar to secondary forests. Edge effects also played an important role in explaining variability in aboveground carbon stocks of disturbed forests. Results indicate a potential rapid recovery of the dead wood and litter carbon pools, while soil stocks (0–30 cm) appeared to be resistant to the effects of logging and fire. Carbon loss and subsequent emissions due to human disturbances remain largely unaccounted for in green- house gas inventories, but by comparing our estimates of depleted carbon stocks in disturbed forests with Brazilian government assessments of the total forest area annually disturbed in the Amazon, we show that these emissions could represent up to 40% of the carbon loss from deforestation in the region. We conclude that conservation pro- grams aiming to ensure the long-term permanence of forest carbon stocks, such as REDD+, will remain limited in their success unless they effectively avoid degradation as well as deforestation.

Appendice 5

Carvalho, T.S.; Jesus, E.C.; Barlow, J.; Gardner, T.A.; Soares, I.C.; Tiedje, J.M.; Moreira, F. M.S. Land use intensification in the humid tropics increased both alpha and beta diversity of soil bacteria. Ecology, v. 97 (20), p. 2760-2771, 2016.

Abstract

Anthropogenic pressures on tropical forests are rapidly intensifying, but our understanding of their implications for biological diversity is still very limited, especially with regard to soil biota, and in particular soil bacterial communities. Here we evaluated bacterial community composition and diversity across a gradient of land use intensity in the eastern Amazon from undisturbed primary forest, through primary forests varyingly disturbed by fire, regenerating secondary forest, pasture, and mechanized agriculture. Soil bacteria were assessed by paired-end Illumina sequencing of 16S rRNA gene fragments (V4 region). The resulting sequences were clustered into operational taxonomic units (OTU) at a 97% similarity threshold. Land use intensification increased the observed bacterial diversity (both OTU richness and community heterogeneity across space) and this effect was strongly associated with changes in soil pH. Moreover, land use intensification and subsequent changes in soil fertility, especially pH, altered the bacterial community composition, with pastures and areas of mechanized agri- culture displaying the most contrasting communities in relation to undisturbed primary forest. Together, these results indicate that tropical forest conversion impacts soil bacteria not through loss of diversity, as previously thought, but mainly by imposing marked shifts on bacterial community composition, with unknown yet potentially important implications for ecological functions and services performed by these communities.