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WALLACE BEIROZ IMBROSIO DA SILVA

UNDERSTANDING SPATIAL AND TEMPORAL SHIFTS IN TAXONOMIC AND FUNCTIONAL DIVERSITY: ASSESSING DUNG BEETLES IN A HUMAN-MODIFIED AMAZONIAN LANDSCAPE

Dual PhD Scheme
LAVRAS - MG
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Thesis submitted for the degree of Doctor of Philosophy as a Dual PhD with '*Ecologia Aplicada*' Postgraduate Program, Universidade Federal de Lavras, Brazil and Lancaster Environment Centre, Lancaster University, United Kingdom

PhD Júlio Louzada (Universidade Federal de Lavras)
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Ficha catalográfica elaborada pelo Sistema de Geração de Ficha Catalográfica da Biblioteca Universitária da UFLA, com dados informados pelo próprio autor

da Silva, Wallace Beiroz Imbrosio.

Understanding spatial and temporal shifts in taxonomic and functional diversity: Assessing dung beetles in a human-modified Amazonian landscape / Wallace Beiroz. – Lavras: UFLA, 2016.

132 p. : il.

Tese (Doutorado)–Universidade Federal de Lavras, 2016.
Orientador(a): Julio Louzada (UFLA) / Emma Sayer (Lancaster)
Bibliografia.

1. Scarabaeinae. 2. Functional Diversity. 3. Tropical Forest. I. Universidade Federal de Lavras. II. Título.

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I dedicate this thesis to my parents, Hélio Francisco and Lucy Imbrosio, whom gave me all the love where I was born and grew up.

Eu dedico esta tese aos meus pais, Hélio Francisco e Lucy Imbrosio, quem me deu todo o amor onde eu nasci e cresci.

Dedication

ACKNOWLEDGEMENTS / AGRADECIMENTOS

I am very grateful to my supervisors, **Emma Sayer, Eleanor Slade, Jos Barlow and Julio Louzada**, without their precious help I could not have done this thesis. Thank you for your patience, enthusiasm and for showing me that great researchers can also be great people!

Thank for the lovely, crazy, silly, friendly, weird, chaotic and warm '**Tropical Group**'! In special, **Natalie 'Cisne', Anne, Luke, Mari, Erika** and **Juliana**. Thank you for making my life much easier and happier in UK!

Thank you the people in the best office ever!!!! **Guy, James, Mounir, Deidre, Radim, Katherine**.

I am very thankful for **Tregidgo's** ('Tregedigdigdigo's') for one of the best Christmas ever and for looking after me during my stay in UK, specially my 'white bro' **Danny 'Lézo'**, for being such a terrific (or terrible) friend!

I also in debt with some amazing friends I have met in Lancaster (or even before). Specially, **Tom Walker, Sam Robinson**, **Maria 'Malakas'**, **Bobby**, **Hannah 'Maritaca'**, **Daniel Baxendale, Katherine Baxendale** and **Isobel**, thank you for all the serious and silly chats we had, for being such a lovely friend and always (I mean ALWAYS) being there for me!!

Thank you my lovely and graceful roomates. Thank you **Anni** (Dr. Úrsula) for being the most kind and cute person I ever met! Thank you **Kasia** ('Katarzina Milakovich') for taking care of me and being a great company in Lancaster!

I am also grateful for the lovely people I met in Oxford. Specially two great hosts, **Paul Manning** and **Olelokan**. Thank you guys for your friendship and kindness.

I also thank to my friends in Liverpool, **Olívia**, **Tom Bishop** and **Sofia**. You made my visits in Scouser's land very lovely and funny!

Quero agradecer também à outra família que me adotou, mas esta é de brasileiros, ao meus grandes amigos **Beto**, **Michelle** 'CatÚnda', **Daniel** e **Marina**. Agradeço também à outros amigos brasileiros que estavam 'turistando' na terra da Rainha, **Lígia**, **Lélis, Gabriel, Arlete, Caio, Pedro, Andrézão** e **Fábio.**

Agradeço muito ao meu pai **Hélio**, minha mãe **Lucy**, meu irmão **Helinho** e minha cunhada **Aline**. Obrigado por sempre me darem muito amor, apoio e ajuda; dando conselhos ou apenas ouvindo. Nunca vou esquecer a frase "vai fundo cara, olha onde suas decisões já te levaram".

Agradeço também ao **Ronaldo**, **Sílvia** e **Ramine**, por terem entrado na minha vida com dois pés direitos e também terem sempre me dado muito apoio e carinho.

Agradeço imensamente meu bem **Ananza**, por todos esses anos de companheirismo, diversão, amor e alegria. Muito obrigado por sempre “stand by me”, até nos meus maiores momentos de estresse. Te amo!

Aos meus amigos de Lavras, obrigado pelos anos de amizade e apoio. Especialmente **Rafael ‘Peixe’, Ruanny ‘Tatau’, Ivo, Yuri, Tonho, Ernesto, Lisi, Chaim, Carla, Danilo, Grazi, Poly, Nat, Guilherme, Gabi, Thalles.**

Tem duas pessoas de Lavras que quero agradecer separadamente por terem me ajudado bastante na tese. Muito obrigado **Julius** pela ajuda na identificação dos bichos e **Marina** por analisar as fotos do projeto, sem vocês eu não conseguiria. Claro, muito obrigado pela amizades de vocês, sem isso eu também não conseguiria.

Agradeço também à todos os **Rola-bosteiros** que me ajudaram a descontrair no laboratório, discutir as ideias, ou com um simples abraço. Especialmente **Cris ‘Bahia’, Toru, Lívia ‘Bagé’**.

Obrigado aos animais do extinto chiqueiro 1/CADA por todos os momentos de amizade e de descontração, muito obrigado. **Calorada, Tonho, André, Vini**.

Obrigado **Edvar, Irmão** e **Maria**, pela grande (essencial) ajuda no meu campo no Jari!

Obrigado ao **Programa de Pós-Graduação em Ecologia Aplicada da UFLA** pela oportunidade. Obrigado à **CAPES** pelas bolsas de doutorado no Brasil e sanduíche no exterior e ao **CNPq** por ter financiado o projeto que eu estive envolvido.

Thank you **Lancaster Univeristy** for the great opportunity to study abroad.

Obrigado à todos que de alguma forma ajudaram no processo desta tese, direta ou diretamente. Thank you the people that somehow was envolved on this Thesis and helped me to conclude it.

ABSTRACT

Tropical forests are under anthropogenic pressure, causing the replacement of native areas by modified habitats. These landscapes are composed of natural and modified components. Knowledge of community dynamics in these modified habitats is essential to ensure long-term conservation of species and ecosystem services. Many studies had evaluated the conservation value and impacts of anthropogenic modifications on biodiversity. However, the natural variation of communities in reference sites could obscure responses of biodiversity to disturbance. I evaluated the spatial and temporal shifts in dung beetle communities in undisturbed forest, and used these results to assess the influence of inter-annual variation on the evaluation of anthropogenic changes. Soil texture was the main factor affecting spatial variation in dung beetle communities, mainly due to different responses among beetles with distinct nesting behaviour. I found high variation in almost all community metrics after a severe dry season in the previous year, which also influenced the response of the community in modified habitats. Thus, future studies should consider inter-annual variation when studying the effect of anthropogenic change on dung beetle communities and use information about factors that could influence community metrics over time. In addition, many studies evaluate community responses to change from either taxonomic or functional perspectives, but little is known about the relationship between these components of biodiversity. I also addressed this by using conceptually similar taxonomic and functional metrics to evaluate the influence of anthropogenic changes on inter-annual variation in dung beetle communities and to compare taxonomic and functional metrics responses to modifications in forest structure. I did not find strong evidence for the influence of anthropogenic change on the inter-annual variation in the studied metrics. However, functional metrics varied less among years than taxonomic. Additionally, despite similar average effect sizes of functional and taxonomic metrics in response to forest modification, I found high variation among years for each metric and among metrics within each year. I therefore suggest that using taxonomic and functional metrics concomitantly could improve studies focusing on evaluating anthropogenic changes. Finally, I assessed the factors influencing taxonomic and functional diversity of dung beetles in plantations at the local and landscape scale. Understanding the factors modulating biodiversity in modified habitats has important applications, as these areas are likely to be the main component of tropical landscapes in the near future. I evidenced that dung beetle diversity increased with the extent of native forests surrounding the plantation, but there was no relationship between beetle diversity and yield. These findings could guide discussions with policy-makers and landowners in order to achieve sustainable management strategies. My results indicate that the restoration or retention of native areas in the landscape could facilitate species movement through plantations and those native areas could also work as ‘source’ habitats for colonisation of anthropogenic habitats by native forest species. In conclusion, this thesis demonstrates that using both taxonomic and functional diversity metrics to describe changes in dung beetle communities increases our understanding of biological community responses to change in modified areas.

Keywords: functional ecology, functional traits, Scarabaeinae, silviculture, temporal dynamic

RESUMO

As paisagens tropicais são compostas por componentes naturais e modificados devido a substituição de áreas nativas por agrícolas. O conhecimento de dinâmicas das comunidades nesses habitats é essencial para a conservação de espécies e serviços ecossistêmicos à longo prazo. Estudos tem avaliado os impactos dessas modificações e o seu valor de conservação. Porém, a variação natural das comunidades em áreas referência pode obscurecer as respostas da biodiversidade a distúrbios. Eu avaliei as alterações espaciais e temporais nas comunidades de rola-bosta em florestas sem distúrbio, e usei esses resultados para averiguar a influência da variação interanual na avaliação das mudanças antrópicas. A textura do solo foi o principal fator afetando a variação espacial das comunidades de rola-bosta, principalmente devido às diferentes respostas entre besouros com comportamento de nidificação distinto. Encontrei alta variação nas métricas das comunidades após uma estação seca severa no ano anterior, a qual também influenciou a resposta da comunidade nos habitats modificados. Portanto, estudos futuros deveriam considerar a variação interanual ao avaliar os efeitos das mudanças antrópicas na comunidade de besouros e usar informações sobre os fatores que podem influenciar as métricas da comunidade no tempo. Além disso, muitos estudos avaliam a resposta da comunidade às mudanças na perspectiva taxonômica e funcional, mas sabe-se pouco sobre a relação entre esses componentes da diversidade. Estudei essa relação utilizando métricas taxonômicas e funcionais conceitualmente similares para avaliar a influência das mudanças antrópicas na variação interanual da comunidade de rola-bosta e comparar as respostas das diversidade taxonômica e funcional às alterações na estrutura florestal. Não houve forte influência das mudanças antrópicas na variação interanual das métricas. Contudo, as métricas funcionais variaram menos entre os anos que os equivalentes taxonômicos. Apesar da alta similaridade das respostas entre as métricas taxonômicas e funcionais à modificação florestal, houve variação entre os anos para cada par de métricas e entre métricas dentro de cada ano. Portanto, sugiro que o uso de ambas as métricas poderia aprimorar bastante os estudos da avaliação de mudanças antrópicas. Por último, averiguei os fatores que influenciam a diversidade taxonômica e funcional da comunidade de rola-bostas nas plantações em escala local e de paisagem. Entender os fatores que modulam a biodiversidade em habitats modificados tem aplicações importantes, uma vez que essas áreas provavelmente serão o principal componente das paisagens tropicais em um futuro próximo. Eu achei fortes evidências que a diversidade de rola-bosta aumentou com a quantidade de florestas nativas no entorno das plantações, mas não houve relação entre a diversidade de besouros e produção. Portanto, esses resultados poderiam guiar discussões com políticos e donos de terra com o intuito de formular estratégias de manejo mais sustentáveis. Meus resultados indicam que a restauração ou manutenção de áreas nativas na paisagem podem facilitar o movimento de espécies pelas plantações e essas áreas nativas também podem funcionar como habitats "fonte" para a colonização de habitats antrópicos por espécies de floresta nativa. Concluindo, eu demonstrei que o uso de diversidade taxonômica e funcional melhora o entendimento das respostas de comunidades biológicas à conversão florestal.

Palavras-chave: dinâmica temporal, ecologia funcional, Scarabaeinae, silvicultura, traços funcionais

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Chapter 1

General introduction

1.1 LAND-USE CHANGE AND TROPICAL FORESTS

Scientists have described around 450,000 species of plants and 1.9 millions of animals to date, which has resulted in an estimated 5 to 11 million species in total worldwide (PIMM et al., 2014). Most species are concentrated in tropical zones and tropical humid forests are the most diverse habitats with two-thirds of world's terrestrial diversity (BROWN, 2014; GARDNER, 2000; GASTON, 2000). In addition, tropical rainforests contribute heavily to local, regional and global ecosystem processes and services. For example, tropical regions play an important role in regulating the climate via both biochemical and biophysical processes (ANDERSON-TEIXEIRA et al., 2012), mainly as consequence of their great capacity for carbon sequestration and storage (BERENGUER et al., 2014).

However, tropical forests have also suffered greatly from anthropogenic interference, which has caused high rates of forest degradation and land-use conversion (GIBSON et al., 2011; KIM; SEXTON; TOWNSHEND, 2015; NEWBOLD et al., 2015). Of the 4 billion hectares of forest in the world (31% of total land area), only one-third is still primary forest and 264 million hectares are planted forests, due to increased demand for timber (FAO, 2010). The area of modified habitat is still increasing, as human beings replace 'wild' landscapes with agricultural crops, pastures and plantations in order to take immediate profits (KAREIVA et al., 2007).

Thus, the conversion of native forest into agricultural lands has a great impact on tropical humid forests globally as it is linked to habitat loss, fragmentation, selective logging, climate change and other threats (ACHARD et al., 2014; HADDAD et al., 2015). Forestry plantations are currently the largest driver of deforestation in the subtropics (HANSEN et al., 2013), as well as in the moist tropical forests of Indonesia (ABOOD et al., 2015). It is widely thought that plantations are, generally less favourable than natural areas as a habitat for native forest species from a wide range of taxa (e.g. BREMER; FARLEY, 2010; PARITSIS; AIZEN, 2008), mainly due to changes in habitat space, resource availability, environmental conditions and forestry management practices, which all affect community dynamics.

Regarding to environmental conditions, one of the main negative aspects in forestry areas is the simplified canopy structure which has a large impact on biodiversity because it intercepts less solar radiation and alters environmental conditions, resulting in e.g. increased temperature and reduced humidity in the understorey (VON ARX; DOBBERTIN; REBETEZ, 2012). Thus, many sensitive species cannot tolerate strongly modified areas of forest because of their specific physiological requirements. For example, the conversion of Malaysian forests into oil palm plantations resulted in a 77% reduction in bird species and an 83% reduction in butterfly species compared to primary forest, or 73% and 79%, respectively, compared to secondary forest (KOH; WILCOVE, 2008). However, remnants of natural forest can contribute to the maintenance of biodiversity in anthropogenic landscapes by allowing the movement of species among patches, increasing the capacity of species to move from natural forests to modified habitats (e.g. increasing matrix permeability and spillover effects; (BLITZER et al., 2012; BRUDVIG et al., 2009).

Efforts to balance conservation and agricultural production have sparked a debate about whether we should intensify production in one part of the landscape to protect the remaining natural habitats (‘land-sparing’), or integrate production and conservation within the same area (‘land-sharing’; (GREEN, 2005; PHALAN et al., 2011). These options are mainly being explored for agricultural land, but the reality of tropical forestry is different, as there is a pressure to reduce deforestation, but increasing timber demand (CÔTÉ et al., 2010; FOLEY et al., 2005; LEYS; VANCLAY, 2010). Even that land-sparing sounds likely to be better for conservation, the national, regional or local need to increase income might favour the conversion of native forest into exotic plantations with higher profits. Thus, there is an urgent need for studies to address the question about the balance of land-use intensity and conservationist practices in tropical forests (GRISCOM; GOODMAN, 2015).

Most studies have evaluated impacts of land-use conversion using spatial approaches, in which different sites along temporal or environmental gradients are used to infer change (‘space-for-time’ design; (FRANÇA et al., 2016; KAPPES; SUNDERMANN; HAASE, 2010). However, tropical organisms are usually highly dynamic in time and human activities might influence these dynamics; for example, the turnover and extinction rates of forest-specialist bird species tend to be higher and the colonizing rate lower in fragmented habitats compared to intact forest (BLANDÓN et al., 2016). Besides the well-reported seasonal variation in natural habitats (e.g CLELAND et al., 2007; OLIVEIRA et al., 2011; VERNES et al., 2005), ecological communities can also show inter-annual variation in non-seasonal environments as a result of e.g. resource availability (DIDHAM; SPRINGATE, 2003). Thus, the lack of information about background rates and trajectories of community shifts in intact ecosystems complicates the assessment of anthropogenic impact (MAGURRAN et al., 2010).

Most scientists agree that the current rate of habitat change is causing the 'sixth mass extinction' (GARDNER, 2000). As threats have been evaluated for just a small number of species, it is highly conceivable that we are losing many species before we understand their role within a given ecosystem. Thus, studies focusing on the role of species diversity in ecosystem functioning are vital in this age of global environmental change.

1.2 FUNCTIONAL ASPECTS OF COMMUNITIES

Interest in the role of biodiversity in ecosystem functioning has increased markedly in the last decades (Figure 1.1). Many studies using the biodiversity-ecosystem functioning (BEF) approach have focussed on determining which species within a given community provide, assist or facilitate ecological processes in natural and modified habitats, to understand how diversity influences ecological functions and services (e.g. (DIAS et al., 2013; MANNING et al., 2016; SHEEHAN et al., 2008). Another approach involves investigating the role of environmental conditions as a factor influencing community assemblages via species' sensitivity to habitat conditions (e.g. CARREÑO-ROCABADO et al., 2012; COTTEE-JONES et al., 2015; PINHO et al., 2011). Regardless of the approach, these lines of research require information on the functional traits of species to identify links between diversity and ecosystem function.

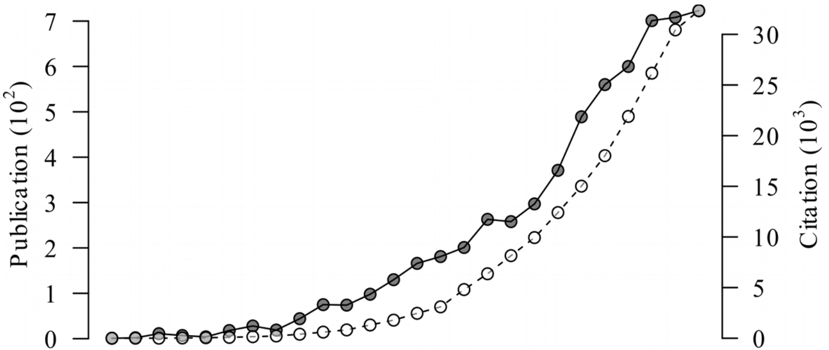

Figure 1.1: Number of published (grey dots) and cited (white dots) papers from 1990 to 2015 with both 'biodiversity' and 'ecosystem functioning' keywords in 'Environmental sciences ecology' research area. Data from Web of Science as search tool from all databases.

The term ‘Functional diversity’ arose in the 1990’s, but the most common definition defines functional diversity as a component of biodiversity that influences how an ecosystem operates or functions: ‘the range and value of those species and organismal traits that influence ecosystem functioning’ (TILMAN, 2001). Ecosystem functioning is mediated by ecosystem processes, which are in turn influenced by the biota composing the community (CHAPIN III et al., 2000). Thus, community assemblage affects ecosystem processes via the functional diversity of the biota and therefore underpins ecosystem function.

Species traits are any morphological, physiological or phenological characteristic measured at individual level, absent of references to environment or other organizational levels (MCGILL et al., 2006). Darwin's ‘On the Origin of Species’ was perhaps the first study to shed light on how species traits influence their performance and success in a habitat. More than a century later his ‘morphology, performance, fitness’ paradigm was included in scientific debate about ecological scales in time and space (ARNOLD, 1983). Since then, the trait-based approach has been widely used in ecological and evolutionary studies (VIOLLE et al., 2007).

The bedrock for functional diversity is the ‘functional trait’ - an attribute related to individual performance and fitness, which also significantly modulates an ecosystem process, and functional traits are often assigned to one of two broad categories: traits related to the response of organisms in the face of changing environmental conditions are defined as ‘response traits’, whereas those linked to the organism-mediated processes are ‘effect traits’ (MLAMBO, 2014; VIOLLE et al., 2007).

1.2.1 Response traits

Response traits are directly linked to the ecological performance of organisms in the face of biotic and abiotic interactions (performance filters), which can alter the distribution of organisms, consequently altering the frequency of traits within a community (WEBB et al., 2010). For example, a study with three plant species showed that foliar nitrogen decreases with altitude, which made the occurrence of the species with specific foliar nitrogen concentrations predictable at a given altitude (LAUGHLIN; LAUGHLIN, 2013). Here, foliar nitrogen concentration represents the response trait and altitude represents the performance filter for that trait. Performance filters can also vary in time and affect many different response traits over a wide range of time scales, for example seasonal temperature changes, human-induced global warming or ecological succession can all be considered performance filters (HELLMANN et al., 2008; KOCH et al., 2013; POUNDS et al., 2006).

Importantly, the performance filters can act in concert to determine community assemblage and the co-occurrence of species with similar traits (functional redundancy). The abiotic component of performance filter (habitat filtering) constrains species traits towards an optimum and hence selects for species with similar traits, whereas on the other hand, biotic interactions such as competition push species towards niche differentiation, consequently selecting species with dissimilar traits (MAIRE et al., 2012). Thus, the co-occurrence of species with similar traits (functional redundancy), community assemblage and composition are determined by the both components of performance filter acting on response traits.

1.2.2 Effect traits

Every organism contributes to ecosystem processes, but the nature and magnitude of contribution varies considerably (NAEEM et al., 1999). The role of organisms in ecological processes is mediated by their ‘effect traits’, which provide a measure of their influence on a given ecosystem process or property. For example, a study conducted in southern France showed that ecosystem-level net primary productivity can be predicted from species-level measurements of potential relative growth rates (VILE; SHIPLEY; GARNIER, 2006). Similarly, a study evaluating Bolivian, Brazilian and Costa Rican forests showed that the community weighted mean value (CWM) of specific leaf area was a good predictor of aboveground biomass (FINEGAN et al., 2015).

Trait-based approaches have given rise to two main hypothesis about how biodiversity influences on ecosystem processes: the (bio)mass ratio hypothesis and the functional (niche) complementarity hypothesis. Both hypotheses are generalizations for all taxa and ecosystem functions derived from a group of four hypotheses related to plant diversity and productivity (for details see PRADO-JUNIOR et al., 2016). The mass ratio hypothesis proposes that ecosystem processes are driven by the traits of dominant species, whereas the functional complementarity hypothesis predicts that more functionally diverse communities have higher niche differentiation, which increases resource-use efficiency (DE BELLO et al., 2010). However, the two hypotheses are not necessarily mutually exclusive. Despite of trait-based approach predicts ecosystem functioning better than taxonomic diversity in most cases, the mass-ratio (e.g. CWM) and functional complementarity hypothesis (e.g. Rao’s quadratic entropy) interchange as best predictors, and sometimes the best prediction is made by the combination of both hypothesis, showing the importance of functional identity of dominant species and diversity for the role of biodiversity in ecosystem processes (BÍLÁ et al., 2014; COHEN; RAINFORD; BLOSSEY, 2014; DIAS et al., 2013; GAGIC et al., 2015; ROSCHER et al., 2012).

In addition, the role of a species in a given habitat is not just a function of its traits but also depends on external factors; for example, a study in the Brazilian Amazon found that the linkage between dung beetle functional diversity and seed dispersal is dependent on soil texture (GRIFFITHS et al., 2015). Therefore, to assess how anthropogenic impacts affect ecosystem processes we first need to understand the changes in functional aspects of ecological communities (HOOPER et al., 2012).

1.2.3 Importance of functional diversity in human-modified habitats

Human beings depend on a variety of ecosystems services mediated by biodiversity (DE GROOT et al., 2010). People often alter habitats in order to increase service rates, which are underpinned by ecosystem processes via species effect traits (Figure 1.2). However, habitat modification tends to eliminate those species with response traits that make them sensitive to disturbance, while promoting the invasion and expansion of other species, which directly affects the frequency of the effect traits of interest (DÍAZ et al., 2007, 2013). This chain of events can ultimately feed back via species response traits to create undesirable effects on functional diversity and ecosystem processes and services (Figure 1.2).

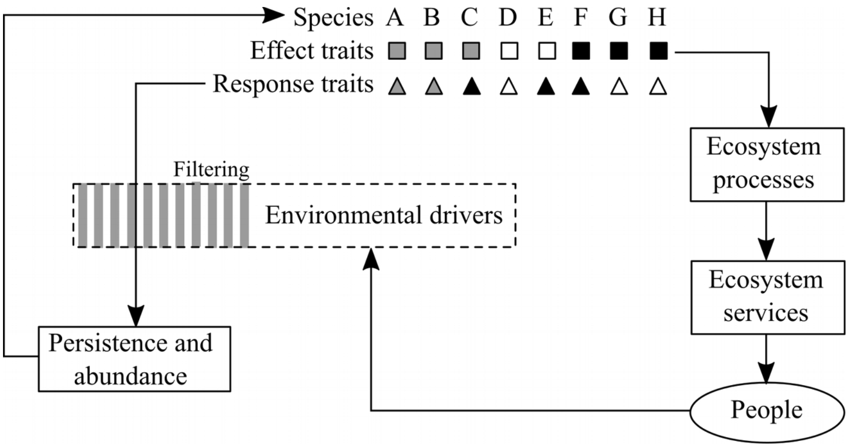

Figure 1.2: Relationship between species and ecosystem services. A hypothetical group of species (A to H) showing different effect traits (shaded squares) affect ecosystem processes, which deliver ecosystem services and benefit people. As people exploit the services, they alter the habitat to increase the provision of services and goods. Those changes can affect the way species interact with environmental filters via their response traits (shaded triangles) and drive changes in abundance and persistence of the original pool of species; consequently, the ecosystem processes and services will change over time. Modified from Díaz et al. (2013).

Few studies have attempted to establish the linkages between response and effect traits (LAVOREL; GARNIER, 2002; PAKEMAN, 2011). Despite these knowledge gaps, it is generally accepted that response traits are related to ecosystem resistance, as they determine whether communities can absorb disturbance without changing ecosystem functioning. Similarly, effect traits are related to the resilience of ecosystems, as they drive ecological processes and are determined by biodiversity. Consequently, both types of traits underpin ecosystem functioning (STERK et al., 2013) and the resistance and resilience conferred by the functional diversity of ecosystems is essential for sustainable production of natural resources and ecosystem services (ELMQVIST et al., 2003; GUNDERSON, 2000).

1.2.4 Functional diversity metrics

Many metrics have been developed to evaluate functional diversity, including approaches based on functional groups, single- or multiple traits, and with or without intraspecific variation (CHIU; CHAO, 2014; CIANCIARUSO; SILVA; BATALHA, 2009; DAMBORSKY et al., 2015; LALIBERTE; LEGENDRE, 2010; RICOTTA; MORETTI, 2011; VILLÉGER; MASON; MOUILLOT, 2008). Here I focus on three multidimensional metrics of functional diversity: functional richness (FRic), functional evenness (FEve) and Rao’s quadratic entropy (FDq):

1 - Functional richness: The FRic index is based on the volume of the convex hull surrounding all extreme trait values within a community; in other words, it is the volume occupied in a space in which each dimension is represented by a measured trait (Figure 1.3; VILLÉGER; MASON; MOUILLOT, 2008). FRic is a useful metric to determine assembly rules, as its value is based on the total range of traits, disregarding intermediate values and species abundance in the community (BHASKAR; DAWSON; BALVANERA, 2014; MOUCHET et al., 2010). However, results of analyses using FRic must be interpreted with caution because species losses are likely to remove extreme trait values and hence index values are highly correlated with species richness (Figure 1.3; VILLÉGER; MASON; MOUILLOT, 2008).

2 - Functional evenness: FEve represents the regularity of species distribution across the total functional niche space, weighted by species abundance. The index uses the minimum spanning tree among all species and weights each branch by species abundance (Figure 1.3; VILLÉGER; MASON; MOUILLOT, 2008). Accordingly, FEve decreases either when species abundance is less evenly distributed across the community, or when the variability in functional distances among species increases.

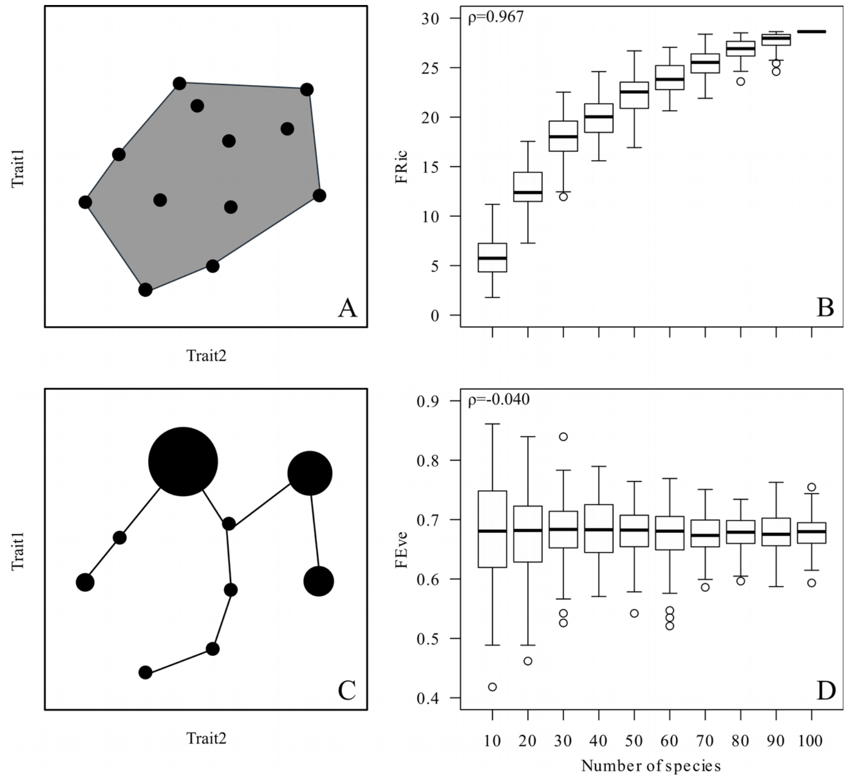

Figure 1.3: The functional indices FRic (A) and FEve (C) for a hypothetical community with two traits; black dots represent individual species and the size of the dots in C indicates number of individuals. Spearman’s correlations are given for the relationship between values of FRic (B) and FEve (D) and the number of species in hypothetical communities. Modified from Vílĺeger et al. (2008).

3 – Rao’s quadratic entropy: FDq was proposed as functional metric based on Rao’s quadratic entropy, considering ‘the relative abundances of species and a measure of the pairwise functional differences between species’ (BOTTA-DUKÁT, 2005). Thus, FDq calculates the mean dissimilarity of one species (or individual) to the whole community (RICOTTA et al., 2016), in other words, the probability to randomly sample two functional different individuals in the community. Then, high values of FDq indicate high species rarity and between-species functional differences (RICOTTA et al., 2016).

1.2.5 Taxonomic vs. functional diversity

Most hypothesis, theories and paradigms in community ecology were initially taxonomic-based, including the debate about biodiversity and ecosystem functioning (MCGILL et al., 2006). However, to identify general patterns relevant to community ecology, researchers proposed four main themes: traits, environmental gradients, the interaction milieu, and performance currencies (MCGILL et al., 2006). Taxonomic diversity considers all species as having similar influence on a given process, whereas functional diversity considers species' functional traits to forge a stronger connection between biodiversity and ecosystem processes (TILMAN, 2001). For example, a grassland study showed that the functional identity and functional divergence of species was a better predictor of multiple ecosystem processes (productivity and decomposition) than species diversity *per se*; indeed the predictive power of functional diversity was almost 80% (MOUILLOT et al., 2013).

Studies of species distributions might also benefit from a trait-based approach, as it could shed light on the basic questions of why organisms live where they do and how they will respond to environmental change, which would improve the predictive power of community responses (GREEN; BOHANNAN; WHITAKER, 2008; MOUILLOT et al., 2013). However, different biodiversity approaches may provide distinct information about community responses to change (e.g. when there is a decrease in functional diversity despite an increase in the number of species). Consequently, both approaches should be used as complementary tools to assess the effects of disturbance on communities and processes (VILLÉGER et al., 2010). The use of both approaches could help us to understand the mechanisms underlying change in a diverse and complex world and it may be particularly appropriate in studying communities that can serve as biological indicators of disturbance.

1.3 DUNG BEETLES

The Scarabaeinae subfamily is a monophyletic group subdivided into 12 tribes, many of which are considered polyphyletic (TARASOV; GÉNIER, 2015). There are more than 6,200 species of Scarabaeinae in 267 genera, which are distributed over all continents except Antarctica (TARASOV; GÉNIER, 2015). Despite their wide distribution, Scarabaeinae are particularly diverse in the tropics, with greater populations in forest and savannah environments, probably because their physiology is well-adapted to warmer regions, which historically reduces their distribution toward high latitudes (HANSKI; CAMBEFORT, 1991; HORTAL et al., 2011; NICHOLS et al., 2007; PHILIPS, 2011). In this context, dung beetles are an ideal model system, because: i) they have a wide distribution across different biomes, ii) they are sensitive to changes at different scales (NICHOLS et al., 2007); iii) have a relatively stable taxonomy (PHILIPS; PRETORIUS; SCHOLTZ, 2004); and iv) can be surveyed relatively cheaply compared to other taxa (GARDNER et al., 2008a).

1.3.1 The roles of dung beetles in ecological processes

Scarabaeinae are widely known as dung beetles thanks to their predominant dietary preference for animal faeces. Most species dig galleries in dung and the soil to feed or nest and this combination of diet and behaviour makes them agents of several ecological processes and functions (BRAGA et al., 2013; GIRALDO et al., 2011; SLADE et al., 2007), the most important of which are highlighted below.

The first important function provided by dung beetles is the incorporation of nutrients from vertebrate faeces into the ecosystem nutrient cycle by relocating faeces into the soil (NICHOLS et al., 2008; YAMADA et al., 2007; YOKOYAMA et al., 1991). Case studies demonstrate that the proportion of dung incorporated into the soil within 24 hours varies by ecosystem and the type of dung available. Only around 22% of the dung was relocated in Southeast Asian forests (KUDAVIDANAGE; SER; LEE, 2012); whereas 63-99% of cow dung was processed in forests of varying logging intensity in Malaysian Borneo (SLADE; MANN; LEWIS, 2011). In a study using human faeces in the Brazilian Amazon, 100% was processed within 24 hours in primary forest 60% in managed forest and 30% in introduced pastures, demonstrating the effect of disturbance on dung beetle function (BRAGA et al., 2012, 2013). During the processes of dung relocation and nest-digging, the beetles also promote changes in soil microbiota by increasing bioturbation, leading to significant impacts on plant productivity (SLADE et al., 2016a; YOSHITAKE; SOUTOME; KOIZUMI, 2014).

The second process is seed dispersal, a study comparing rodents and dung beetles as primary seed dispersers of acorns in southern Spain showed that although dung beetles dispersed fewer seeds than rodents, they were qualitatively more effective because they did not consume the seeds (rodents ate 95% of the dispersed seeds; PÉREZ-RAMOS et al., 2013). However, it is much more common the secondary seed dispersal from frugivorous and herbivorous vertebrates, which occurs when dung beetles exploit the faeces as a resource and disperse undigested seeds in the process (VANDER WALL; KUHN; BECK, 2005). As far as the dung beetles are concerned, the seeds in faeces represent a contaminant, but the intense competition for such an ephemeral resource obliges dung beetles to process faeces containing seeds and they are usually removed from the dung in transit or in the beetles' nesting gallery (ANDRESEN; FEER, 2005; NICHOLS et al., 2008). During transit, the horizontal distribution of removed seeds reduces seedling clustering, which also reduces seedling predation and competition (LAWSON; MANN; LEWIS, 2012). The vertical movement of the seeds (by burial) also affects plant fate: two studies conducted in Amazonian Forest found higher proportions of established seedlings from buried seed than from seeds left on the surface; however, establishment success declined with burial depth (ANDRESEN, 2001; FEER, 1999). The interaction between seed and dung beetles is complex, with several dung beetle morphological and behavioural traits, habitats conditions, and seed traits affecting the interaction (BRAGA et al., 2013; FEER, 1999; GRIFFITHS et al., 2015; SLADE et al., 2007).

The final important function provided by dung beetles is the reduction of greenhouse gas (GHG) emissions. Recent studies have shown the importance of dung beetles in reducing methane (CH_4) and carbon dioxide (CO_2) emissions from microbial activity in cattle dung (MENÉNDEZ; WEBB; ORWIN, 2016; SLADE et al., 2016b). The aeration of the dung by dung beetle activity reduces the emission of CH_4 because methanogens require anaerobic conditions, (CHADWICK et al., 2011; MØLLER; SOMMER; AHRING, 2004). The emission of carbon dioxide (CO_2) from dung increases initially probably due to the stimulation of microbial activity by dung aeration or even from respiration by the beetles themselves, however, the cumulative CO_2 emissions from dung are lower when dung beetles are present (SPERATTI; WHALEN, 2008; PENTTILÄ et al., 2013). Finally, the production of nitrous oxide (N_2O) depends on complex pedoclimatic interactions and microbial processes, which makes the emissions of this GHG hard to predict; however, some studies found that dung beetles might cause peaks in N_2O production by promoting denitrification (BOUWMAN; BOUMANS; BATJES, 2002; KAZUHIRA et al., 1991; LESSA et al., 2014).

1.3.2 Dung beetles as ecological indicators

Dung beetles are also often used as ecological indicators in studies of anthropogenic change and natural environmental variation (FILGUEIRAS et al., 2016; FILGUEIRAS; IANNUZZI; LEAL, 2011; GARDNER et al., 2008b). Despite their wide global distribution, high diversity and their abundance in both tropical and warm temperate ecosystems, they are also sensitive to changes at local and landscape scales (NICHOLS et al., 2007) because they are highly related to specific habitats (DAVIS et al., 2001; FILGUEIRAS et al., 2015) and form part of a specific intertrophic association (ANDRESEN; LAURANCE, 2007). They are particularly useful for ecological surveys because the required methods are cheaper than for many other taxa (GARDNER et al., 2008a) and they have a relatively stable taxonomy (PHILIPS; PRETORIUS; SCHOLTZ, 2004).

Thus, dung beetle responses can be easily evaluated from local to regional scales, where changes in soil texture or altitude can alter the species composition of dung beetle communities (DAVIS et al., 2001; HANSKI; CAMBEFORT, 1991). Changes in dung beetle communities can also be induced by anthropogenic pressures at different scales, for example a study in Mexico concluded that forest loss at both the patch and the landscape level were significant predictors of dung beetle community assemblage (SÁNCHEZ-DE-JESÚS et al., 2016). Some studies have reported that even more subtle changes in habitat can be detected in dung beetle community composition, for example when native grasses are replaced by exotic grass species, or under different low-intensity selective-logging regimes (ALMEIDA et al., 2011; BICKNELL et al., 2014).

As dung beetles are linked to upper trophic levels (mainly mammals) by their dung feeding behaviour, hunting pressure that causes selective changes in mammalian biomass, abundance and species composition has direct effects on dung beetle communities, which in turn may have consequences for ecosystem functioning (CULOT et al., 2013). A review paper highlighted that many studies across the globe indicate that changes in the composition and availability of dung resources, as a result of the decline or local extinction of medium and large bodied mammals, severely disrupts the diversity and abundance of dung beetles (NICHOLS et al., 2009). However, little is known about the processes and consequences of cascading effects in the faecal-detritus food web, as they are mediated by both species' traits and habitat type (NICHOLS et al., 2013a).

1.3.3 Dung beetles traits and functional diversity

Due to their role in various ecosystem processes, dung beetles have been largely used to evaluate the linkages between biodiversity and ecosystem functioning (LARSEN; WILLIAMS; KREMEN, 2005; MENÉNDEZ; WEBB; ORWIN, 2016; NICHOLS et al., 2008). The most common traits used to work with functional groups, functional diversity indices and other trait-based approaches are nesting behaviour (or food relocation strategy), activity period, dietary preference (or breadth), and body size (or biomass), which are used as both response and effect traits (for details on their use as response traits see (NICHOLS et al., 2013b); for effect traits see (GRIFFITHS et al., 2015; SLADE et al., 2007).

Dung beetles can be grouped into three categories according to their nesting behaviour: (1) rollers, which roll small balls of dung away from the dung pile; (2) tunnelers, which take a small portion of dung and bury it immediately beneath or around the dung pile; and (3) dwellers, which nest inside the dung pile (Figure 1.4; HALFFTER; MATTHEWS, 1966). Rollers and tunnelers are related to the main functions of seed dispersal and dung burial (PEYRAS et al., 2013). The activity of rollers is more affected by moisture in soils than tunnelers because they usually dig shallower nests and may therefore avoid open areas (ESCOBAR; CHACON DE ULLOA, 2000). As dwellers live inside or directly beneath the dung patch, their activity is mainly related to air humidity (DAVIS et al., 2010; HANSKI; CAMBEFORT, 1991; OSBERG; DOUBE; HANRAHAN, 1993).

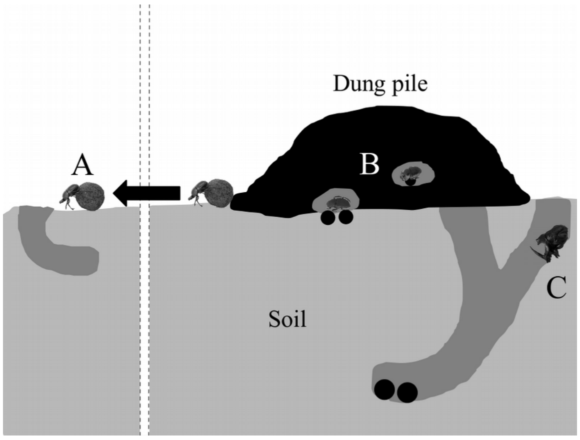

Figure 1.4: Dung beetle nesting behaviour. (A) Rollers or telecoprids, (B) dwellers or endocopids and (C) tunnelers or paracoprids. Modified from Halffter & Edmonds (1982).

Similar to many other tropical insects, dung beetle species have also developed diel segregation probably as a mechanism of competition avoidance (BOONROTPONG; SOTTHIBANDHU; SATASOOK, 2012; NIINO et al., 2014). Despite of the large variety of diel activity periods, dung beetles are commonly classed as diurnal or nocturnal species (FEER; PINCEBOURDE, 2005). The activity periods of dung beetles can play an important role in their response to disturbance. For example, a previous meta-analysis found that diurnal species were more sensitive to the conversion of intact forest to modified forest or non-forested areas than nocturnal species, probably because of the higher temperatures and lower moisture levels during the day in open or disturbed areas (KRELL-WESTERWALBESLOH; KRELL; LINSENMAIR, 2004; KRELL; KRELL WESTERWALBESLOH, 2003; LARSEN; LOPERA; FORSYTH, 2008; NICHOLS et al., 2013b).

There are many recorded dietary behaviours for dung beetles (HANSKI; CAMBEFORT, 1991; PUKER; CORREA; KORASAKI, 2014; SILVA et al., 2012), but the most common is coprophagy, followed by necrophagy (BOURG et al., 2016; HALFFTER; MATTHEWS, 1966). Species with either of the main dietary preferences play an important role in nutrient inputs and soil properties, but seed dispersal is strongly related to coprophagous beetles. Dietary preference can also influence the sensitivity of species to disturbance because specialist species have been reported as more sensitive to changes for many taxa (ANGERT et al., 2011; BOMMARCO et al., 2010; FERRER; NEGRO, 2004; NICHOLS et al., 2009). Specifically, dung beetles with a preference for carrion (necrophagous) are likely to have a higher nitrogen requirement, which reduces the viability of offspring and population growth in resource-poor habitats (HANSKI; CAMBEFORT, 1991).

The size or weight of dung beetles is commonly found in the literature and is usually measured at the community level to infer losses of functions by large beetles or by those sensitive to disturbance (NICHOLS et al., 2013b). However, some studies have used or discussed the use of body size as a functional trait. For example, a study in Borneo showed that excluding large beetles (10 cm^2 mesh) did not affect dung removal (SLADE et al., 2007), but the loss of large beetles might affect seed dispersal (ANDRESEN; ANDRESEN, 2003). This is important in the context of disturbance, as large species are often more prone to local extinction because they tend to have small populations, low fecundity and reproductive rates, a long lifespan, or because they require larger foraging areas (CARDILLO, 2005; LARSEN; LOPERA; FORSYTH, 2008).

In conclusion, there are a number of reliable effect and response traits that can be used to assess the role of dung beetle functional diversity in ecological processes. In Amazonian forest, researchers using these and additional morphological traits, showed that functional diversity is positively related to seed dispersal, whereby soil texture acted as an environmental filter for community assemblage (GRIFFITHS et al., 2015). Changes in the functional diversity of dung beetles are also expected in face of anthropogenic change, as it creates different environmental filters, which in turn select for different traits (BARRAGÁN et al., 2011; EDWARDS; LITCHMAN; KLAUSMEIER, 2013; WEBB et al., 2010). However, the functional diversity of dung beetle communities might not be as strongly affected by subtle and natural environmental changes, where documented shifts in species composition have not lead to changes in functional structure (e.g. Altitudinal gradient NUNES et al., 2016). Similarly, it is possible that disturbances such as low-intensity selective logging in tropical forests might not affect functional diversity (EDWARDS; LITCHMAN; KLAUSMEIER, 2013).

1.4 RESEARCH OBJECTIVES

The aim of this thesis was to explore and understand the effects of land-use change and temporal variation in both natural forest and human-modified land covers, as a background to sustainable landscape management. Thus, in this thesis I contribute research to fill the knowledge gap related to community dynamics in space and time

('Prestonian shortfall') and how response traits are related to those dynamics ('Hutchinsonian shortfall'; HORTAL et al., 2014) using dung beetles as a model system.

1.4.1 Chapter 2 – Dung beetle community dynamics in undisturbed tropical forests: implications for ecological evaluations of land-use change

My first research objective was to evaluate the spatial and temporal dynamics of dung beetle communities in a virtually undisturbed forest, to provide a baseline for ecological evaluations of anthropogenic disturbance. Research and monitoring programs concerned with disturbance or regeneration of habitats require reference areas to compare with disturbed sites. These are usually the closest natural (or original) areas but natural spatial and temporal dynamics can lead to misinterpretations of results if natural and human-induced shifts in community composition are confused. Thus, understanding the natural dynamics of dung beetle communities in reference habitats is essential for informing future studies and ensuring reliable interpretation of the results.

My specific research questions in Chapter 2 were: 1) Which factors are responsible for spatial variation in dung beetle communities? 2) Do dung beetle communities show inter-annual variation and if so, why? 3) Could natural temporal variation affect the evaluation of human-induced changes?

1.4.2 Chapter 3 – Spatial and temporal shifts in functional and taxonomic diversity in a human-modified tropical forest landscape

In my third chapter, I evaluated the response of taxonomic and functional metrics in two different modified habitats over five years. There is a increased interest in evaluating the biodiversity-ecosystem functioning (BEF) link in different habitats. To address this, researchers have explored the functional component of biodiversity using different functional metrics. Many studies show that functional and taxonomic metrics assess different ecological processes, and others have advocated combining both approaches in order to fully understand the mechanisms behind BEF interactions (BAISER; LOCKWOOD, 2011; GOSSELIN, 2012; VILLÉGER et al., 2010). However, few studies have compared changes in both taxonomic and functional metrics in response to the same disturbance or how they vary over years. This additional information will be valuable for monitoring programs, which intend to use both approaches to assess the impacts of change. Hence, in the second data chapter I evaluated the response of taxonomic and functional metrics in two different anthropogenic habitats over five years sampling.

The research questions I addressed in Chapter 3 were: 1) Does anthropogenic modification affect inter-annual variation in biological diversity? 2) Is the inter-annual variation of taxonomic and functional diversity similar? 3) Which approach shows higher sensitivity to human-induced changes?

1.4.3 Chapter 4 – Biodiversity in tropical plantations is influenced by surrounding native vegetation, but not productivity: A case study with dung beetles in Amazonia

In this chapter, I discussed the necessary conditions to improve biodiversity in *Eucalyptus* plantations and their implications for timber production. In the face of the constant agricultural advances that are turning tropical landscapes into a mosaic of anthropogenic and natural habitats, we must work towards aligning the production of resources for human use with biodiversity conservation to preserve ecosystem services and health. Thus, in this chapter I aimed to discuss about the conditions shaping biodiversity in *Eucalyptus* plantations and the relationship between biodiversity and timber production. Research on how to achieve the sustainable use of resources while preserving biodiversity will help policy makers and landowner to attenuate biodiversity loss with less reduction on goods production.

My research questions in Chapter 4 are: 1) Does plantations that most closely resemble native forests hold more biodiversity? 2) Is the amount of native forest surrounding plantations affecting biodiversity within *Eucalyptus* areas? 3) Does the intensity of timber production influence biodiversity?

1.5 THESIS STRUCTURE

Each of the data chapters has been written for publication: Chapter 2 has been accepted to *Journal of Insect Conservation and Diversity* and I intend to submit chapters 3 and 4 to *Ecography* and *Journal of Landscape Ecology*, respectively. Therefore, this thesis comprises a collection of stand-alone studies linked by the common theme of taxonomic and functional responses of dung beetle communities in different land covers and their use as a tool to evaluate anthropogenic changes in tropical forests. In Chapter 5, I summarize the key results from the individual chapters and highlight the remaining knowledge-gaps that need to be addressed in future studies.

Finally, the appendices contain other published papers, that are not directly related to this thesis but are a result of parallel research in which I have been involved.

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Chapter 2

Dung beetle community dynamics in undisturbed tropical forests: implications for ecological evaluations of land-use change

Publication status: Accepted in 'Journal of Insect Conservation and Diversity'

Format based on the guidelines of 'Journal of Insect Conservation and Diversity'

Dung beetle community dynamics in undisturbed tropical forests: implications for ecological evaluations of land-use change

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ABSTRACT

The impacts of human activities on tropical forests are widespread and increasing. Hence, a good knowledge-base about ecological processes in undisturbed tropical forest is crucial to provide a baseline for evaluating anthropogenic change. Our five year study focused on understanding the background spatial and inter-annual variation in dung beetle communities at 12 sites of undisturbed lowland tropical rainforest in the Brazilian Amazon. We then assessed how this variation may affect ecological evaluations of anthropogenic influence by comparing community metrics with comparable dung beetle data collected from 15 sites of *Eucalyptus* plantation in the same region. Of all measured environmental variables, soil texture best explained spatial variation in dung beetle communities in undisturbed forests. Furthermore, soil texture was important for community assembly as it was associated with dung beetle nesting behaviours. While the relative abundance of dung beetle functional groups was stable over time, there were important inter-annual temporal dynamics, with a five-fold variation in abundance and body mass, and with species richness ranging from 52-74. These temporal oscillations were probably caused by variation in dry season rainfall. This inter-annual variation influenced the comparison between undisturbed forests and plantations, which could lead to inconsistencies in evaluation of anthropogenic change. We therefore highlight the importance of understanding natural variation in studies evaluating the consequences of land-use change and other forest disturbances on forest biodiversity.

Keywords: Scarabaeinae, pristine forest, response traits, environmental condition, tropical forest, community assembly, drought

2.1 INTRODUCTION

The negative influence of human beings in natural habitats has reached an unprecedented level (Ceballos *et al.,* 2015; Lewis & Maslin, 2015). Tropical rainforests are threatened by the advance of monoculture and pasture, and the exploitation of timber and non-timber resources in the remaining forests. The effects of these changes on biodiversity have been evaluated in a variety of taxa and summarised in pan-tropical and global meta-analyses (Cullen *et al*., 2000; Koh & Wilcove, 2008; Gibson *et al*., 2011; Newbold *et al*., 2015; Panday *et al*., 2015).

Most studies have highlighted the negative impacts of large changes in vegetation structure. However, the natural spatio-temporal fluctuations of many populations from 'control' or 'undisturbed' areas might lead to misinterpretations of the real effects of anthropogenic changes (Magurran *et al.*, 2010). Conservation efforts could therefore benefit greatly from detailed information on spatio-temporal distribution ('Prestonian shortfall') of species and their sensitivity to habitat changes ('Hutchinsonian shortfall'; Hortal *et al*., 2015). Such information is especially important for organisms used as bioindicators of change, such as dung beetles (Cardoso *et al*., 2011; Davis *et al*., 2001).

Dung beetles are often used as focal organisms to evaluate anthropogenic impacts and habitat recovery from disturbance (e.g. Audino *et al*., 2014; Braga *et al*., 2013; Korasaki *et al*., 2013), with recent advances relating dung beetle sensitivity to disturbance to functional traits such as species body mass or size, nesting behaviour, diet preference, and activity period (Barragán *et al*., 2011; Nichols *et al*., 2013; Silva & Hernández, 2014). However, dung beetles also show high spatial variation due to their association with soil texture, which can cause changes in community composition over short distances (Hanski & Cambefort, 1991), even though some species show relatively high dispersal ability (Almeida *et al*., 2011; Gardner *et al*., 2008; Silva & Hernández, 2014, 2015). Furthermore, establishing baseline conditions is complicated by temporal change, as many dung beetle species show seasonality, and their abundances and distributions can vary inter-annually (Andrade *et al*., 2011).

To the best of our knowledge, there is no large-scale study that evaluates variation in dung beetle communities over multiple years in undisturbed tropical forests. We therefore assessed natural temporal and spatial variation in dung beetle communities over a five year period, focussing on undisturbed lowland tropical rainforest in the Brazilian Amazonia to explore the possible drivers and consequences of this variation.

We tested the following hypotheses: (1) dung beetle community parameters (abundance, richness, body mass, composition, structure and abundance of functional groups - activity period, nesting behaviour and diet preference) will display high local variation. We relate any observed changes to local variation in soil texture (Osberg *et al.*, 1993; Sowig, 1995), canopy openness (Andrade *et al.*, 2011), rainfall prior to the sampling period, and geographic distance between sites; (2) inter-annual variation will be low for the community parameters listed above, as the structure of undisturbed forest buffers against external changes in the climate and offers a stable environment; and (3) natural temporal variation will influence the dissimilarity between communities in undisturbed forests and a local prevalent anthropogenic habitat, *Eucalyptus* plantations.

2.2 MATERIAL AND METHODS

2.2.1 Study site

The study was conducted within a cellulose company area of 1.7 Mha situated in the Jari River basin on the border between the States of Pará and Amapá in north-eastern Brazilian Amazonia (00°27′00″ - 01°30′00″ S, 51°40′00″ - 53°20′00″ W). The climate is classified as tropical monsoon (Amw - Köppen classification), with an average annual rainfall of 2115 mm (Coutinho & Pires, 1997), a marked wet season from January to June, and a distinct dry season from September to November (Parry *et al.*, 2007). The mean annual temperature is 26.9 ± 0.6 °C, and is constant throughout the year, with monthly maxima and minima of 31.4 ± 1.1 °C and 22.5 ± 0.2 °C, respectively (Climate-Data.org, 2016).

The original continuous pristine forest was managed for Brazil nuts and subsistence livelihoods prior to 1967 (Coutinho & Pires, 1997). Since then, the area has been modified and is now a matrix of native forest with large patches of E*ucalyptus* plantations (c. 130,000 ha), disrupted by wide primary forest corridors (*c*. 200 m wide). There are a few human activities for subsistence within the native forest; mainly collection of Brazil nuts and other non-timber forest products, and some hunting (Parry *et al.*, 2009).

2.2.2 Dung beetle data

We sampled the dung beetle community during the wet season (from January to June) in each year from 2009 to 2013 at the same sampling points. We selected 12 sites of undisturbed forest, separated by 0.2 to 56 Km (average distance c. 27 km) to evaluate the shifts within this land cover, and 15 sites of *Eucalyptus* plantation, separated by 1.6 to 59.6 Km, to assess the influence of temporal variation on evaluation of human-induced impacts. In each site we installed five pitfall traps in a 600 m linear array, with traps aligned 150 m apart and 500 m from the forest/plantation edge. Pitfall traps consisted of plastic containers (19 cm diameter and 11 cm deep), which were part-filled with water, salt and detergent, and baited with 30 g of human and pig dung mixture, in the same proportion (Marsh *et al*., 2013). Each trap was protected from rain with a plastic lid suspended 20 cm above the surface. In every year, collections took place over a period of 48 hours at each sampling site.

Dung beetle specimens were transported in 90% alcohol from the field to the laboratory, then sorted, dried and stored in paper envelopes. Voucher specimens were deposited at Coleção de Referência de Escarabeíneos Neotropicais at the Universidade Federal de Lavras (CREN – UFLA) in Minas Gerais State, Brazil. We identified the dung beetles using a key to the genera and subgenera of the subfamily Scarabaeinae of the New World (Vaz-De-Mello *et al.*, 2011), a field guide for dung beetles of the Jari River basin (Louzada, J., *unpublished*), and the reference collection at CREN – UFLA.

We grouped the species into functional groups to describe groups of species that share the same traits, forming groupings based on nesting behaviour, diet preference and activity period. We inferred dung beetle nesting behaviour based on genus, grouped as (1) rollers, which roll portions of dung away from the dung pile in small balls; (2) tunnelers, which take a small portion of the dung and bury it directly below or around the dung pile; and (3) dwellers, which nest inside the dung (Halffter & Matthew, 1966).

To determine dung beetle diet preference (coprophagous or necrophagous) and activity period, we conducted two independent surveys in January-February 2012 and November-December 2013. We set up 14 traps, spaced 100m apart, in two paired transects. We alternated the baits between 30 g of the human-pig dung mixture and 30g of rotten bovine spleen (to represent carrion) to avoid having the same bait in adjacent traps. If more than 75% of individuals were sampled in dung or carrion bait we classified them as coprophagous or necrophagous, respectively; for those species with lower percentages we classified them as generalists. For species with less than five individuals we sought the advice of neotropical dung beetle specialist Dr. Fernando Z. Vaz-de-Mello. We assessed activity period (diurnal vs. nocturnal) by setting up five pitfall traps 100 m apart. All traps were baited with 30 g human-pig dung mixture. Traps were opened and baited at 7:00 and 19:00 and exposed for 11 hours during the day or night.

We considered total abundance as the sum of individuals of all species, and richness as the number of different species at each site. We oven-dried 15 individuals (or the maximum number available) of each species at 40 ºC for 48 h, and obtained the mean dry mass. For species with low numbers of specimens, we weighed individuals from collections held at CREN - UFLA. We obtained the total body mass by multiplying each species mean weight by their abundance and summing across sites. For community-level weighted mean (CWM) body mass we replaced the abundance of each species by their relative abundance. Extrapolated richness was obtained from individual-based extrapolation for the maximum number of individuals found (591 individuals; Colwell *et al.,* 2012). We determined community composition as the occurrence (presence or absence of species) and structure considering the abundance of species. We also plotted a species accumulation curve with 95% confidence intervals for each year using the *specaccum* function in the *vegan* package (Oksanen *et al*., 2014). All analyses were performed using R version 3.2.1 (R Core Team, 2014).

2.2.3 Environmental variables

We measured canopy openness at pitfall trap locations, using semi-hemispheric photography at 1.5 m above ground level. All pictures were analysed in GLA - Gap light analyser software (Frazer *et al*., 1999). As rainfall events may change community composition, due to temporal turnover in species within a season, we obtained the rainfall from three days before sampling from meteorological stations (Ramirez, 2014). To determine soil texture, we took soil cores at 0-10 cm depths in 2013 and measured the content (g/kg) of fine sand, coarse sand, silt and clay. For analysis, we selected fine sand content because it was not correlated with any other content ($r_s < 0.238$ and ≥ -0.392), and coarse sand content, as it was negatively correlated with silt and clay content ($r_s = -0.937$, $r_s = -0.916$, respectively). All environmental variables were standardized to a mean of zero and standard deviation of one before the analysis (Schielzeth, 2010).

2.2.4 Data analyses

2.2.4.1 Spatial variation of dung beetle communities

To assess the effects of environmental variables on the spatial variation of dung beetle communities we built models for each year with environmental metrics as explanatory variables. For total and functional group abundance (number of individuals with same trait), richness, and extrapolated richness we ran generalized linear models (GLM) using a negative binomial error distribution for total and functional group abundance, and quasi-Poisson for the richness metrics. We fitted total body mass and CWM body mass using linear models with Gaussian distribution. The significance of each environmental variable was determined by *z* tests for abundances and *t* tests for the other variables.

We built Bray-Curtis and Jaccard's dissimilarity matrices for community structure and composition, respectively, and for each year separately, using the function *vegdist*. We then compared each dissimilarity matrix with a matrix of geographic distances among sites, determined with Quantum GIS 2.4.0-Chugiak (Quantum GIS Development Team, 2015), using Mantel tests to evaluate the influence of spatial distribution on community structure and composition. To relate environmental variables to spatial variation in community structure and composition for each year, we used DistLM models with environmental variables as explanatory variables, using the function *adonis* with 999 permutations. All analyses were carried out using the R package *vegan* (Oksanen *et al*., 2014).

2.2.4.2 Inter-annual variation in dung beetle communities

To evaluate temporal variation in community metrics, we ran generalized linear mixed-effects models (GLMM) for both total and functional group abundance and richness, using a negative binomial and Poisson distribution, respectively. For total body mass, CWM body mass, and log-transformed extrapolated richness we ran linear mixed-effect models with a Gaussian distribution. We considered year as fixed and sampling site as random effects. Likelihood ratio Chi-square tests were used to compare each model against a null model to evaluate if year had an influence on community metrics. We also ran pairwise comparisons amongst years for all metrics, followed by a Holm-Bonferroni correction, using the *testInteractions* function in *phia* package (Rosario-Martinez, 2015; SAS Institute Inc., 1999). We explored if the temporal variation had any effects on functional group proportions by plotting the relative abundance of functional groups by year. We ran PERMANOVA analysis using the *adonis* function, to evaluate changes in community structure and composition over years. First, we used the respective Bray-Curtis and Jaccard matrices of dissimilarity as response variables and year as an explanatory variable. Then, we ran multiple pairwise comparisons among years, using Holm-Bonferroni corrected *p*-values.

2.2.4.3 Evaluating the effects of natural inter-annual variation in dung beetle communities on anthropogenic changes

To evaluate the effect of temporal shifts on dissimilarities between undisturbed forests and *Eucalyptus* plantations we standardized abundance, total richness, and total body mass (chosen as these metrics represent the most commonly used community metrics of dung beetle biodiversity) for both land cover classes in each year to have a mean of 0 and standard deviation of 1. Then, we plotted standardized means and their standard error for each metric to evaluate how they varied from the expected if there was no variation over years (zero-value) within land covers. We also calculated Hedge's *g*-value effect size between undisturbed forest and *Eucalyptus* plantation for the same metrics and years, using *mes* function in *compute.es* package, where zero values means no change, while positive and negative values represent a decrease and increase in means from undisturbed forest to *Eucalyptus* plantation, respectively (Del Re, 2013). The effect size was calculated in two ways: 1) comparing the value between undisturbed forest and *Eucalyptus* plantation in each year separately, and 2) using each year in undisturbed forest compared to the mean value of all five years in *Eucalyptus* plantation to isolate the effect of temporal variation in the undisturbed forests.

2.3 RESULTS

A total of 10,482 dung beetle individuals belonging to 90 species and morphospecies were sampled in undisturbed forest over the five years, wherein 48 species were identified to species level and 42 as morphospecies. We obtained data on diet and nesting behaviour for 70 species (78% of the total species collected across all years and 98% of all individuals; Table 2.S1), and data on activity period for 61 species (68% of species and 93% of individuals; Table 2.S1).

We sampled the highest number of individuals in 2009 (3,560), and the lowest in 2010 (623). Similarly, the highest number of species was collected in 2009 (74 spp.), and the lowest in 2010 (52 spp.). Species accumulation curves came very close to reaching their asymptote in all years, indicating that our sites provided a good representation of the overall dung beetle community in a given year (Figure 2.S2).

2.3.1 Spatial variation of dung beetle communities

Rain from 3-days before sampling and canopy openness had no influence on total abundance, richness, total body mass, or CWM body mass ($p > 0.05$ in all cases). Coarse sand showed a positive relationship with abundance and total body mass (Figure 2.1, Table 2.S3), whereas fine sand had a negative influence on abundance and richness (Figure 2.1, Table 2.S3), and positive effect on CWM body mass (Figure 2.1, Table 2.S3). Extrapolated richness was not related to any of the environmental variables ($p > 0.05$, Table 2.S3).

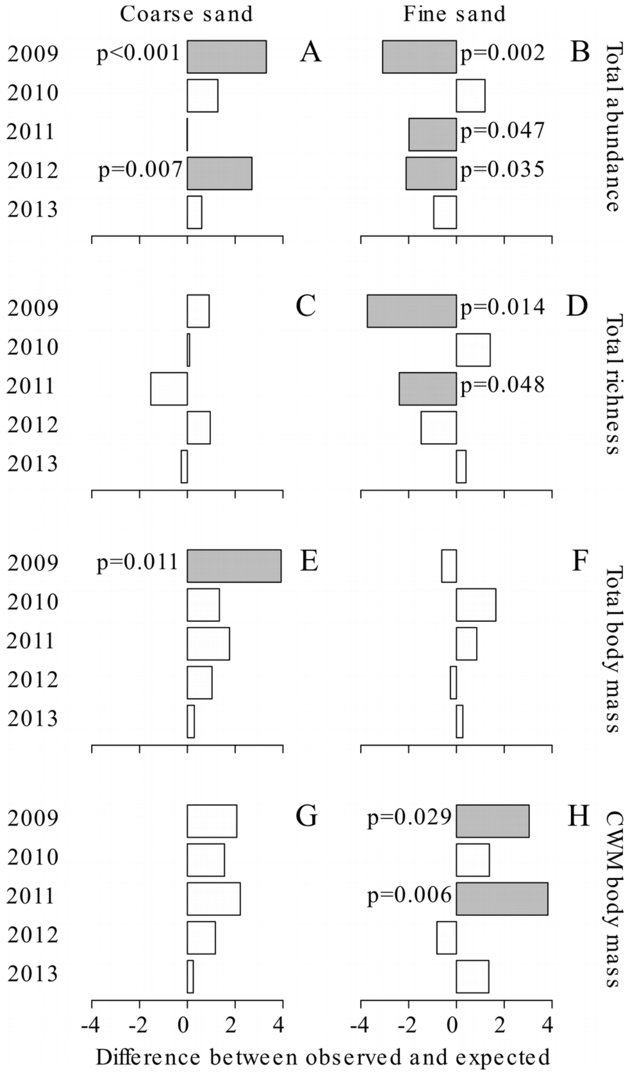

Figure 2.1: Difference between observed and expected of coarse sand content (left column) and fine sand content (right column) for abundance (z-values; A and B) and for richness (t-value; C and D), total biomass (t-value; E and F) and CWM biomass (t-value; G and H) obtained from the multiple regression model. Grey bars mean $p < 0.05$ and white $p > 0.05$.

For functional group abundance, fine sand content had a negative effect on all functional groups, except for necrophagous beetles, which were not affected (Figure 2.2). Coarse sand content had negative effects on necrophagous beetles in 2013, while the effects were positive on coprophagous and generalists species (Figure 2.2). There were also negative effects of canopy openness on coprophagous beetles, but positive effects on necrophagous species, while generalists were negatively related to canopy openness in 2009 and positively in 2011 (Figure 2.2). Coarse sand was also negatively related to rollers, but positively to tunnelers, while dwellers showed both positive and negative relationships (Figure 2.2). Canopy openness had no effect on dwellers, while rollers and tunnelers showed positive and negative responses, respectively (Figure 2.2). Both nocturnal and diurnal beetles were positively affected by coarse sand content (Figure 2.2). However, while diurnal beetles were negatively associated with canopy openness, nocturnal beetles were positively associated (Figure 2.2). Rain from 3-days before sampling was negatively related to necrophagous species ($z = -2.575$, $p = 0.010$), and positively with generalist species ($z = 2.257$, $p = 0.024$) only in 2009 and 2013, respectively.

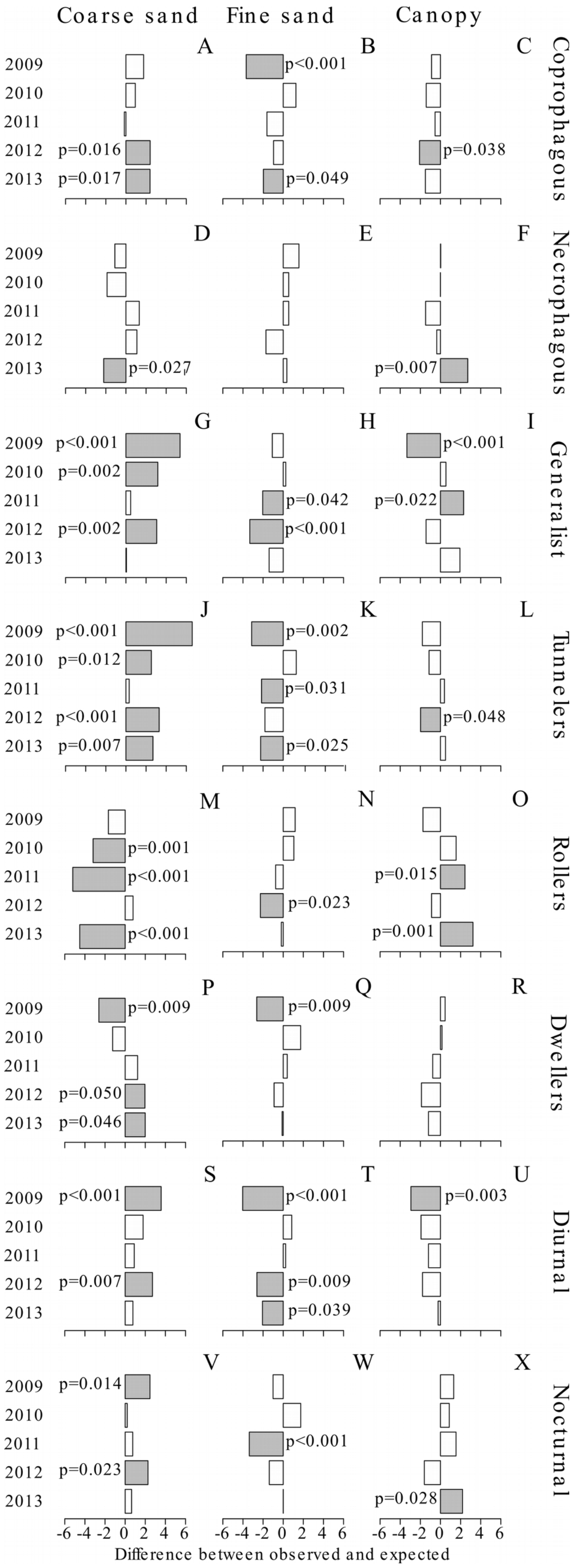

Figure 2.2: Difference between observed and expected (z-values) of coarse sand content (left column), fine sand content (middle column) and canopy openness (right column) for abundance of coprophagous (A-C), necrophagous (D-F), generalists (G-I), tunnelers (J-L), rollers (M-O), dwellers (P-R), diurnal (S-U) and nocturnal (V-X) obtained from the multiple regression model. Grey bars mean $p < 0.05$ and white $p > 0.05$.

Geographical distance significantly predicted overall spatial variation in community structure ($r_s = 0.267$, $p = 0.023$) and composition ($r_s = 0.256$, $p = 0.041$) only in 2009. On the other hand, both coarse and fine sand content influenced community composition and structure in almost every sampled year (Table 2.S4).

2.3.2 Inter-annual variation in dung beetle communities

All measured community metrics varied significantly among years (Figure 2.3, Table 2.S5). There was a marked decline in abundance, species richness and total body mass between 2009 and 2010 (Figure 2.3), but the values increased again during 2011 and 2012, so that the final measurements in 2013 were similar to the values in 2009 (Figure 2.3, Table 2.S5). We observed a severe dry season in 2009 (Figure 2.3). Extrapolated richness was significantly lower in 2010 compared to 2009 and 2013, and in 2012 compared to 2013 (Figure 2.3). CWM body mass was also higher in 2010 compared to 2011, 2012 and 2013, but similar to 2009 (Figure 2.3).

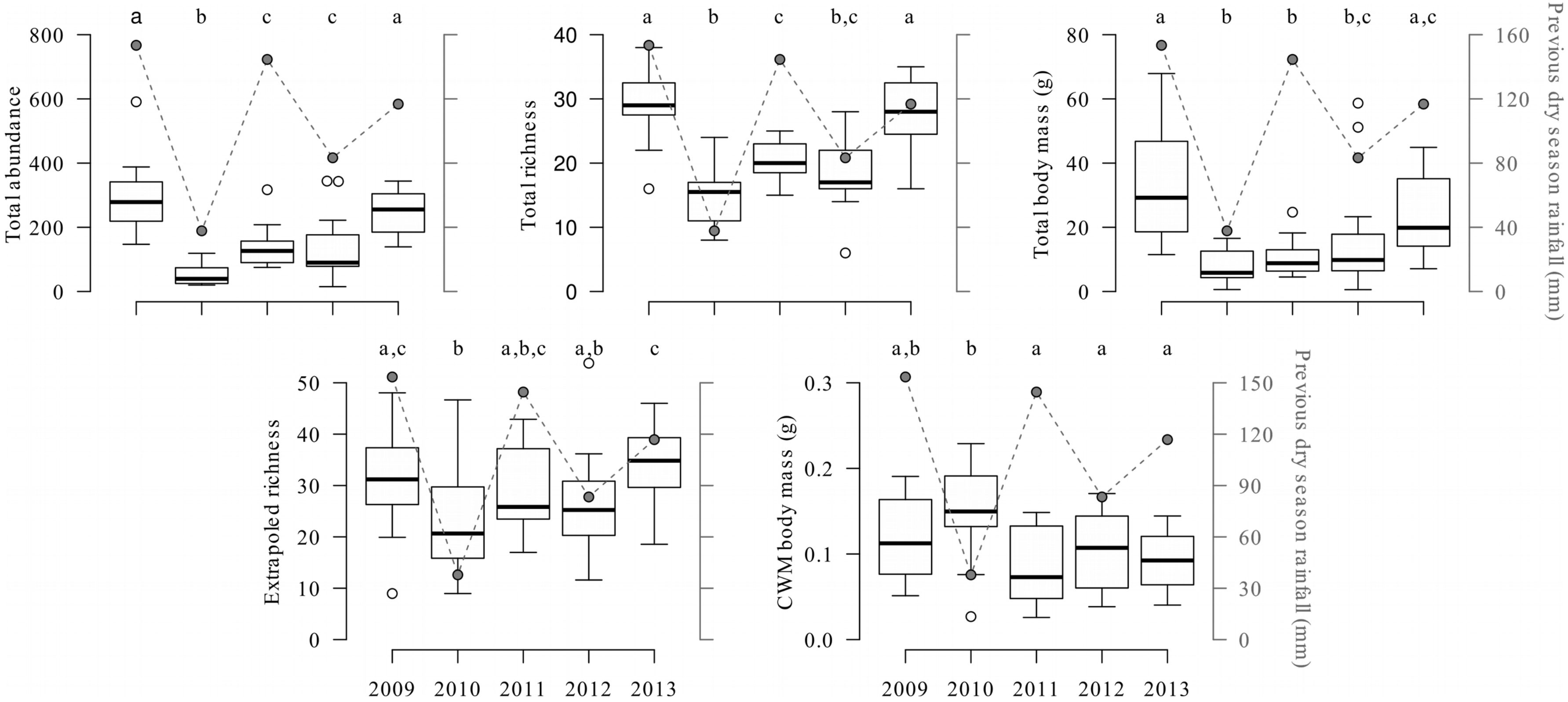

Figure 2.3: Community total abundance, total richness, total biomass, extrapoled richness and CWM biomass in sampled years with the previous year dry season rainfall (grey points and dashed line). Lower case letters represent similarity ($p < 0.05$) among sampled years for each metric.

Although there was significant variation in the absolute abundance of all functional groups across sampling years that matched inter-annual variation in overall community abundance (Figure 2.4, Table 2.S5), the relative abundance of functional groups was remarkably stable across years (Figure 2.S7).

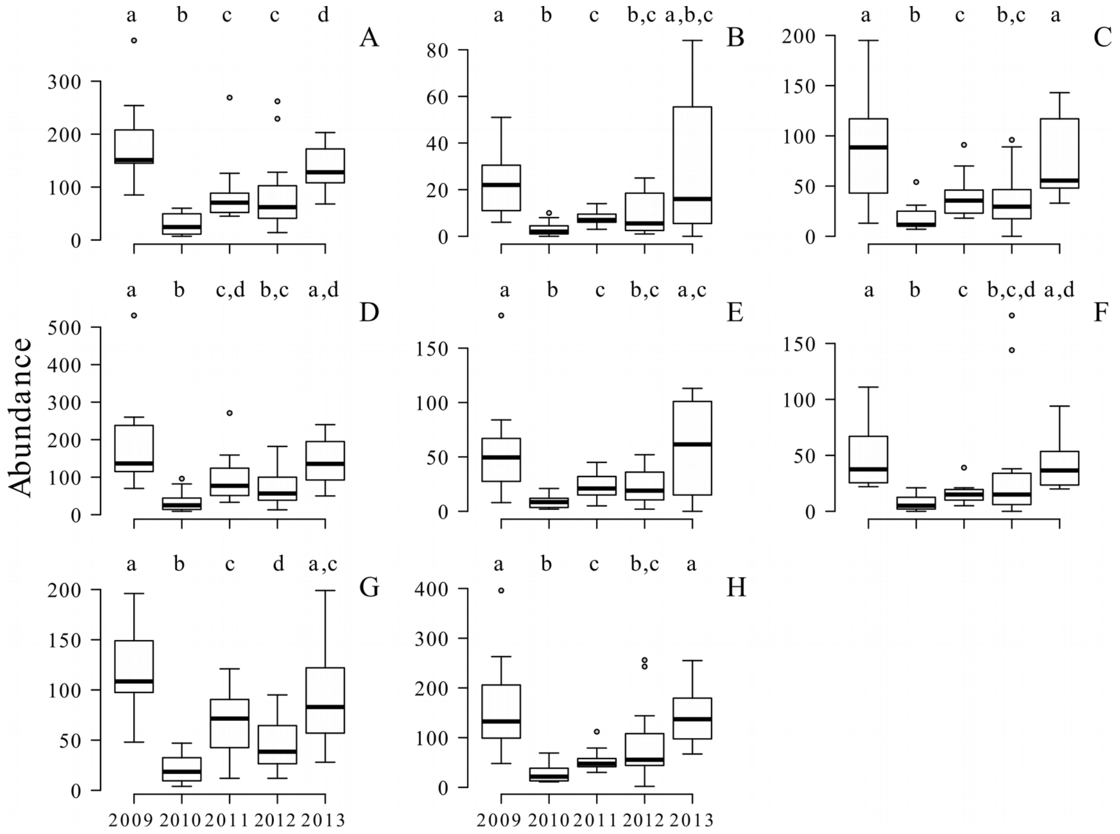

Figure 2.4: Abundance of coprophagous (A), necrophagous (B), generalist (C), tunnelers (D) rollers (E), dwellers (F), nocturnal (G), diurnal (H) in sampled years. Lower case letters represent similarity ($p < 0.05$) among sampled years for each trait.

There was strong evidence of variation in community structure and composition over years (Table 2.S5). Ordinations revealed similar community structure and composition in 2009 and 2013, which differed from 2010 and 2011 (Figure 2.5).

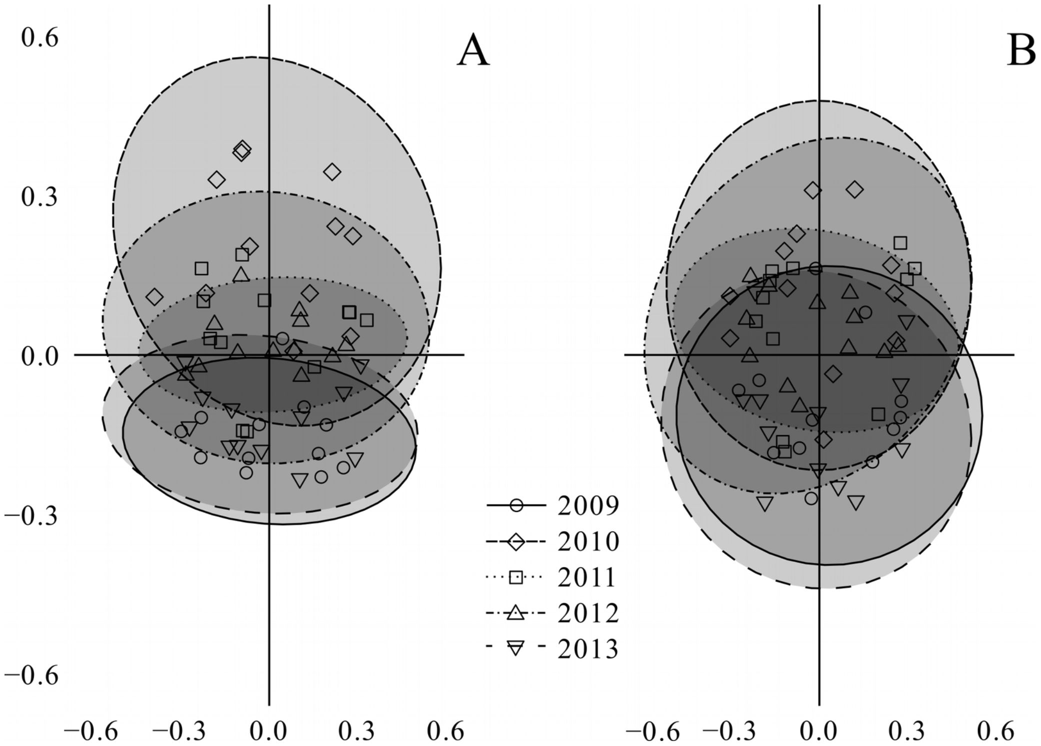

Figure 2.5: PCO plot for community structure (A) and composition (B) with 95% confidence interval (shaded area).

2.3.3 Evaluating the effects of natural variation in dung beetle communities on anthropogenic changes

Although both undisturbed forest and *Eucalyptus* plantation presented a similar pattern of inter-annual variation of dung beetle communities metrics within each land cover, undisturbed forest presented higher variation from the expected if there was no variation (zero-value for standardized metrics) in abundance, richness, and total body mass when compared to values in *Eucalyptus* plantations (Figure 2.6).

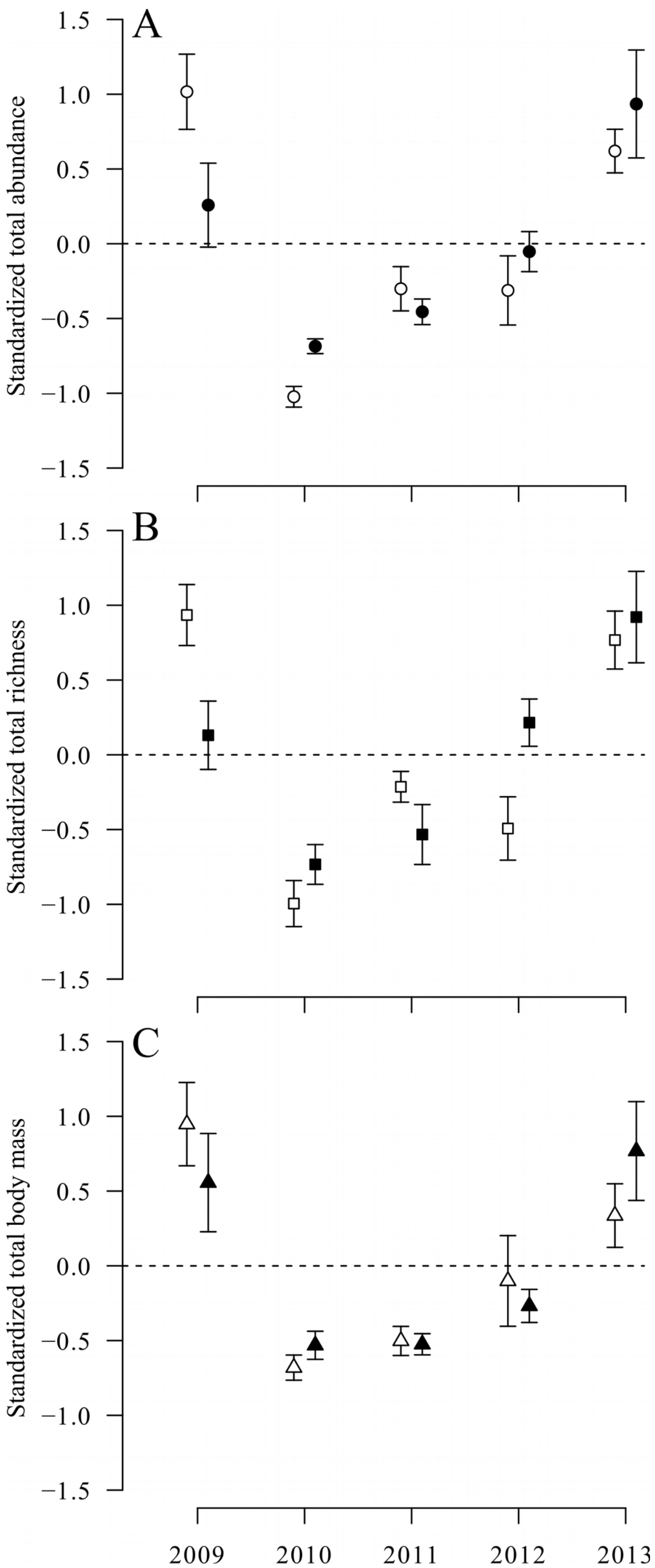

Figure 2.6: Mean and standard-error of standardized abundance (A), richness (B) and total biomass (C) in undisturbed forest (white symbols) and *Eucalyptus* plantation (black symbols) from 2009 to 2013. The symbols only represent the deviance of each mean from the expected value if there was no inter-annual variation (zero-value) within each land cover and not comparison between them.

We observed the negative effect of conversion of undisturbed forest to *Eucalyptus* plantation on abundance, richness, and total body mass (Figure 2.7A). For all metrics the effect size was higher in 2009 and 2011, followed by 2010; 2012 and 2013 were almost similar (Figure 2.7A). Specifically, for abundance, the last two years showed very little difference between undisturbed forest and *Eucalyptus* plantation (values of effect size close to zero; Figure 2.7A). When we isolated the variation of undisturbed forest there were much higher dissimilarities among years, with abundance and total body mass showing no effects of land-use (values close to zero), or even, showing a gain in abundance in 2010 (value lower than zero; Figure 2.7B).

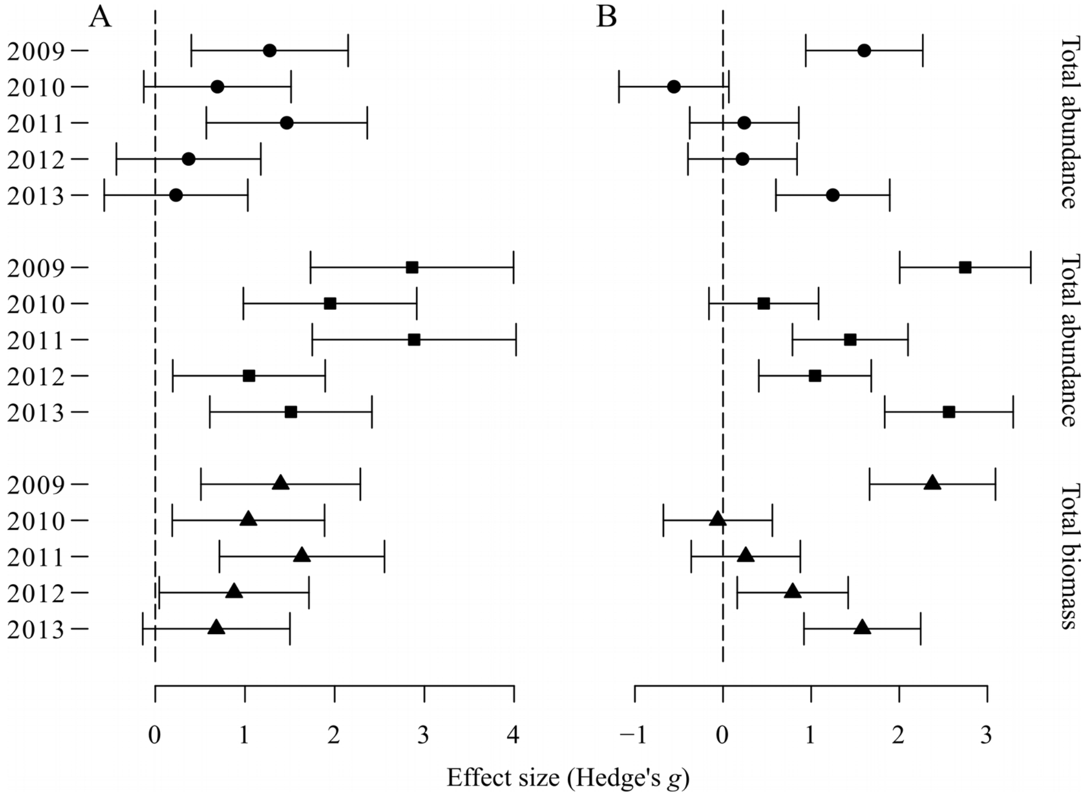

Figure 2.7: Hedge's *g*-value effect size with 95% confidence interval between undisturbed forest and *Eucalyptus* plantation considering the inter-annual variation of both land covers (A) and using the average value of *Eucalyptus* over the five years (B) for abundance (circles), richness (squares) and total biomass (triangles). Positive values indicate decrease in mean from undisturbed forest to *Eucalyptus* plantation (higher effect) and negative value increase, while zero-value indicates no effect (dashed line).

2.4 DISCUSSION

This five year study of dung beetle communities in Amazonian forests revealed support for two of our three hypotheses. First, we confirmed our expectation that dung beetle communities would vary in space, and this was driven predominantly by their responses to soil texture. Second, in contrast to our expectation, we found that all evaluated metrics of dung beetles community also differed markedly among years, although there was no evidence of shifts in functional group proportion. Finally, we show for the first time how inter-annual variation affects dung beetles in undisturbed forest, and that this can add noise to evaluations of human-induced changes on tropical biota. We discuss our results examining each hypothesis in turn.

2.4.1 Soil texture is the main environmental variable affecting spatial variation in dung beetle communities

Our results indicated a strong relationship between soil texture and spatial variation in dung beetle communities, which even overwhelmed any effect of geographic distance between sites. It is very likely that the role of soil acts via beetle nesting behaviour (Figure 2.1 and 2.2). For example, the negative effects of coarse sand on rollers could be associated with the lower retention of moisture in sandy soils, because they usually dig shallower nests than tunnelers (Davis *et al.*, 2010; Hanski & Cambefort, 1991; Osberg *et al.*, 1993). As dwellers live in or right under the dung patch, it is not surprising that their response was less related to soil properties (only in 2009 and weakly in 2012 and 2013). Moreover, any weak relationship could be potentially explained by the indirect effects of competition with rollers or tunnellers, although it is also a possibility that soil properties influence dung humidity and other characteristics directly.

Competition could also explain the lower abundance of beetles in areas with fine sand, as large dung beetles require looser soil to dig their nests giving them a competitive advantage over smaller species, and thus reducing the richness and abundance of the entire community (Carpaneto *et al.*, 2010; Doube, 1990; Hanski & Cambefort, 1991; Figure 2.1). This was supported by the positive effect of fine sand content on CWM body mass in 2009 and 2011 (Figure 2.1), which would be consistent with a loss of small individuals or increases in larger ones. The strong influence of soil texture on dung beetle communities suggests that this environmental attribute should be measured in further studies focussing on anthropogenic-induced changes on dung beetles. However, depending on the context, it will be important to recognise that other microhabitat conditions also may influence dung beetle sampling (Mehrabi *et al.*, 2014).

2.4.2 Inter-annual dynamics in dung beetle communities

Dung beetle communities showed highly non-random variation over time (Figure 2.3, 2.4 and 2.5). The variation of all metrics from 2009 to 2010 was most likely related to a severe dry season in 2009 (Figure 2.3). Even though most adults and immature dung beetles can shelter from desiccation below ground or inside dung pats during the dry season, a severe drought can expose the beetles to high temperatures and low humidity, which increases larval mortality and affects the size of the population in the next year (Hanski & Cambefort, 1991; Scholtz *et al*., 2009; Sowig, 1995; Vessby, 2001).

The low inter-annual variation in extrapolated richness shows that the severe dry season effects on species loss is related to the size of populations or frequency of capture in each site and not the richness *per se* (Figure 2.3). Additionally, dung beetle body mass is unlikely to be related to the decrease in species number, as we did not find high variation in CWM body mass (Figure 2.3), suggesting that the species were equally affected by drought, and that the slight elevation in CWM body mass was probably due the high numbers of small species (Table 2.S1).

It is expected that dung beetles in different functional groups will show different responses to changes in habitat, as discussed in previous studies (e.g. Barragán *et al*., 2011; Nichols *et al*., 2013). However, our study suggests that the changes in community metrics within undisturbed forest are not related to specific responses of functional groups, as there was no conspicuous inter-annual variation in the relative abundance of functional groups (Figure 2.4 and 2.S7) despite the change in community composition and structure (Figure 2.5 and Table 2.S5). This indicates a turnover or loss of species within each functional group, but not a loss of the community's functional groups structure. However, the results might be influenced by the coarse-scale to which we have assigned the functional groups, based on categorical traits; temporal changes may be influencing functional groups classified at a finer-scale, and further research is important to fully understand how functional groups shift in space and time (e.g. continuous traits, intra-specific variation).

The recovery of biodiversity after disturbance can be linked to the scale and intensity of the initial disturbance. So while previous studies have shown that dung beetle communities recover from severe disturbances such as habitat loss and fragmentation (Quintero & Roslin, 2005), or the restoration of degraded pasture (Audino *et al.* 2014) on decadal time scales, we showed a relatively quick recovery in just one to three years after severe dry seasons in forest unaffected by other forms of disturbance (Figure 2.3 and 2.4). However, although this resilience to climatic variation is positive, there are two important caveats to this conclusion. First, the expected reduction in wet season length and prolonged dry seasons with predicted climate change in Amazonian forests might disrupt the ability of communities to recover before the next disturbance event (Li *et al*., 2006; Malhi *et al*., 2008; Nimmo *et al*., 2015). Second, at the time of the study the native forest areas of our study site were protected from additional anthropogenic disturbances, such as logging, further fragmentation, or wildfires – the combination of which are known to reduce the biodiversity value of Amazonian forests (Barlow *et al*., 2016). Dung beetle communities could be far less resilient to climatic variation if affected by other forms of disturbance at the same time. The synergistic effects of climate change (e.g. extension and severity of dry season) and direct human-induced changes (e.g. habitat degradation, fragmentation) are known to affect trophic networks and ecosystem services in other taxa (Balvanera *et al*., 2006; Lewis *et al*., 2011; Silveira *et al.,* 2015), and could affect how dung beetles alter plant communities via their role in seedling establishment and soil properties (Lawson *et al*., 2012; Nichols *et al*., 2008; Pérez-Ramos *et al*., 2013; Slade *et al*., 2015).

2.4.3 Baseline variation could influence research on anthropogenic change

It is well known that anthropogenic modifications lead to negative impacts on tropical forest communities (Arellano *et al*., 2008; Korasaki *et al*., 2013; Louzada *et al*., 2010). However, we demonstrate that dung beetle abundance, richness and body mass also show inter-annual variation in both undisturbed forest and modified habitats (*Eucalyptus* plantation; Figure 2.6), which is often neglected, particularly in ‘space-for-time’ designs or short-term studies. Although both native forests and plantations showed similar trends in inter-annual variation, we observed some inconsistency in the effect sizes of the comparisons between these systems across different years. For example, effect sizes for abundance are close to zero in 2012 and 2013, but are much larger in other years (Figure 2.7A), showing that studies could report very different findings depending on the year in which they were carried out.

To isolate the effect of variation from the baseline condition (primary forest communities), we repeated the analysis keeping plantation communities constant. Under this scenario, the inter-annual variation of effect size significantly increased (Figure 2.7B), revealing the strong importance of variation in the baseline communities. Thus, the effects of baseline variation are likely to increase when comparing areas with temporal asynchrony, in other words, areas where the disturbance has changed the communities' responses to temporal shifts. These results demonstrate the importance of understanding natural variation within 'control areas', and disentangling these from anthropogenic-induced changes in communities.

This study shows that a failure to appreciate inter-annual variation could lead to a failure to detect the consequences of even severe forms of land-use change, such as the conversion of native forests to exotic tree plantations, which are well known to harbour different species composition and species-poor communities (Harvey *et al.*, 2006; Vieira *et al.*, 2008; Zurita *et al.*, 2006). The influence of inter-annual variation may be even greater on more subtle forms of anthropogenic change (e.g. restoration areas: Audino *et al.*, 2014; selective logging: Bicknell *et al.*, 2014; França *et al.,* 2016; and natural gradients: Nunes *et al.,* 2016). We are aware of all logistic issues related to longer-term assessments (e.g. funding, human resources), and that short-term projects usually give faster returns. However, by demonstrating the role of temporal variation, we highlight that rapid assessment studies need to be viewed with caution, and at the very least should place the survey conditions in a longer-term climatic context to highlight any abnormal conditions that could influence the findings (Chase, 2007; Slade *et al*., 2011; Trexler *et al*., 2005).

2.5 ACKNOWLEDGEMENT

We thank the Grupo Jari for logistic support, soil texture analyses, and rainfall data. Irmão, Edvar and Maria for their support in fieldwork. Marina Acero for preparing the vegetation variables. Julius Cerqueira and Amanda Arcanjo for helping with beetle identification. We thank the anonymous reviewers for their fruitful comments and suggestions to improve our manuscript. Conselho Nacional de Pesquisa e Desenvolvimento (CNPQ) and Fundação de Amparo à Pesquisa do estado de Minas Gerais (FAPEMIG) funded the project (Site Peld 23). JS was funded by a postdoc fellowship from FAPEMIG and WB a PhD scholarship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES; DS and BEX 3711-14-15).

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2.7 SUPPLEMENTARY MATERIAL

Table 2.S1: List of species and their respective functional groups. ‘Noc’ means nocturnal, ‘Diu’ means diurnal, ‘Cop’ means coprophagous, ‘Nec’ means, ‘Gen’ means generalist, ‘Tun’ means tunnelers, ‘Rol’ means rollers and ‘Dwe’ means dwellers. ‘body mass’ is the average species body mass.

Morphospecies	**Activity Period**	**Diet preference**	**Nesting Behaviour**	**Body mass (g)**
Ateuchus aff. *conexus*	Noc	Cop	Tun	0.0198
Ateuchus aff. *murrayi*	Diu	Cop	Tun	0.0065
Ateuchus irinus	-	Cop	Tun	0.0177
Ateuchus pauki	Diu	Gen	Tun	0.0134
Ateuchus sp. A	Noc	Cop	Tun	0.0073
Ateuchus sp. E	-	Cop	Tun	0.0080
Ateuchus sp. F	Diu	Cop	Tun	0.0010
Canthidium aff. *deyrollei*	Diu	Cop	Tun	0.0127
Canthidium aff. *lentum*	Noc	Cop	Tun	0.0095
Canthidium sp. A	Noc	Cop	Tun	0.0214
Canthidium sp. B	Diu	Cop	Tun	0.0278
Canthidium sp. D	Noc	Nec	Tun	0.0046
Canthidium sp. F	-	Cop	Tun	0.0055
Canthidium sp. H	Diu	Cop	Tun	0.0285
Canthidium sp. K	-	Cop	Tun	0.0037
Canthidium sp. L	-	Nec	Tun	0.0065
Canthon bicolor	Noc	Cop	Rol	0.0184
Canthon bimaculatus	Diu	Cop	Rol	0.0585
Canthon lituratus	Diu	Cop	Rol	0.0684
Canthon quadriguttatus	Diu	Nec	Rol	0.0094
Canthon scrutator	Diu	Nec	Rol	0.0091
Canthon simulans	Diu	Cop	Rol	0.0055
Canthon subhyalinus	Diu	Gen	Rol	0.0628
Canthon triangularis	Diu	Gen	Rol	0.0252
Coprophanaeus dardanus	Diu	Nec	Tun	0.2523
Coprophanaeus jasius	Diu	Nec	Tun	0.4884
Coprophanaeus lancifer	Diu	Nec	Tun	2.9072
Deltochilum aff. *peruanum*	Noc	Gen	Rol	0.0430
Deltochilum aff. *submetallicum*	Noc	Nec	Rol	0.2426
Deltochilum carinatum	Noc	Nec	Rol	0.0683
Deltochilum icarus	Noc	Gen	Rol	0.4736
Deltochilum orbiculare	Noc	Cop	Rol	0.4426
Deltochilum septemstriatum	Diu	Nec	Rol	0.0285
Deltochilum sp. A	-	Nec	Rol	0.0674
Deltochilum sp. B	-	Nec	Rol	0.0891
Dichotomius aff. *lucasi*	Noc	Gen	Tun	0.0407
Dichotomius apicalis	Noc	Cop	Tun	0.1297
Dichotomius boreus	Noc	Cop	Tun	0.6393
Dichotomius carinatus	Noc	Cop	Tun	0.4479
Dichotomius imitator	Noc	Cop	Tun	0.1167
Dichotomius latilobatus	Noc	Cop	Tun	0.2568
Dichotomius mamilatus	Noc	Gen	Tun	0.4531
Dichotomius robustus	Noc	Cop	Tun	0.1460

Cont. Table 2.S1

Dichotomius subaeneus	Noc	Cop	Tun	0.1215
Dichotomius worontzowi	Noc	Cop	Tun	0.0158
Eurysternus atrosericus	Diu	Cop	Dwe	0.0505
Eurysternus balachowskyi	Diu	Cop	Dwe	0.0290
Eurysternus caribaeus	Diu	Cop	Dwe	0.0645
Eurysternus cayennensis	Diu	Cop	Dwe	0.0220
Eurysternus foedus	Diu	Cop	Dwe	0.0714
Eurysternus hamaticollis	Noc	Cop	Dwe	0.1170
Eurysternus hypocrita	Diu	Cop	Dwe	0.1733
Eurysternus vastiorum	-	Cop	Dwe	0.0100
Eurysternus ventricosus	Diu	Cop	Dwe	0.0324
Ontherus carinifrons	Noc	Cop	Tun	0.0762
Ontherus sulcator	Noc	Cop	Tun	0.0528
Onthophagus aff. *bidentatus*	Diu	Cop	Tun	0.0072
Onthophagus aff. *clypeatus*	-	Cop	Tun	0.0111
Onthophagus aff. *haemathopus*	Diu	Cop	Tun	0.0075
Oxysternon durantoni	Diu	Cop	Tun	0.1891
Oxysternon festivum	Diu	Gen	Tun	0.3266
Oxysternon silenus	Diu	Gen	Tun	0.0790
Phanaeus cambeforti	Diu	Cop	Tun	0.1060
Phanaeus chalcomelas	Diu	Cop	Tun	0.0520
Sulcophanaeus faunus	Diu	Cop	Tun	1.9300
Sylvicanthon candezei	Diu	Cop	Rol	0.1705
Trichillum pauliani	Noc	Cop	Dwe	0.0205
Uroxys sp. A	Noc	Cop	Tun	0.0074
Uroxys sp. B	Noc	Cop	Tun	0.0011
Uroxys sp. C	Noc	Cop	Tun	0.0086

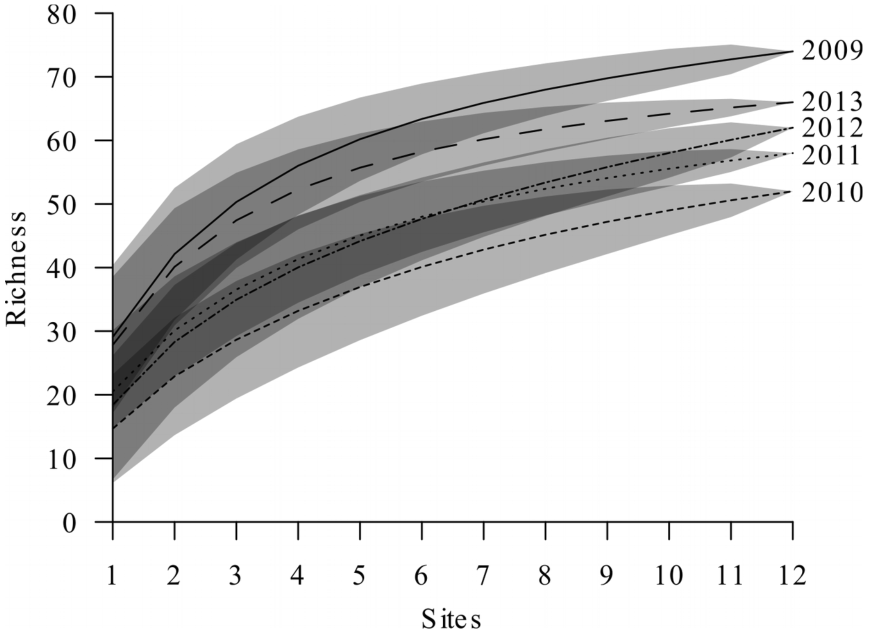

Figure 2.S2: Species accumulation curves of the estimated richness and its 95 % confidence interval (shaded areas).

Table 2.S3: Values of regression analysis for all response variables, with z or t-value depending on the response variable. ‘d.f.’ = degrees of freedom, ‘Canopy’ = Canopy openness, ‘Coarse’ = Coarse sand content, ‘Fine’ = Fine sand content and ‘Rainfall’ = Rainfall of three days before sampling.

Response variable	**Year**	**Explanatory variable**	**Slope**	**Standard error**	***z* or *t***	***p***	**d.f.**
Total abundance	2009	Canopy	-0.166	0.095	-1.743	0.081	12,5
		Coarse	0.251	0.076	3.304	<0.001*	12,5
		Fine	-0.219	0.071	-3.088	0.002*	12,5
		Rainfall	0.013	0.041	0.310	0.757	12,5
	2010	Canopy	-0.124	0.145	-0.851	0.395	12,5
		Coarse	0.317	0.248	1.276	0.202	12,5
		Fine	0.258	0.216	1.196	0.232	12,5
		Rainfall	0.622	0.486	1.279	0.201	12,5
	2011	Canopy	0.062	0.164	0.381	0.704	12,5
		Coarse	-0.002	0.132	-0.012	0.990	12,5
		Fine	-0.228	0.115	-1.984	0.047*	12,5
		Rainfall	-0.059	0.146	-0.408	0.684	12,5
	2012	Canopy	-0.518	0.277	-1.870	0.062	12,5
		Coarse	0.656	0.243	2.702	0.007*	12,5
		Fine	-0.352	0.167	-2.105	0.035*	12,5
		Rainfall	0.261	0.392	0.665	0.506	12,5
	2013	Canopy	0.107	0.101	1.066	0.287	12,5
		Coarse	0.052	0.086	0.601	0.548	12,5
		Fine	-0.070	0.074	-0.949	0.342	12,5
		Rainfall	0.184	0.221	0.832	0.405	12,5
Total richness	2009	Canopy	-0.075	0.055	-1.366	0.230	12,5
		Coarse	0.040	0.044	0.911	0.404	12,5
		Fine	-0.177	0.048	-3.728	0.014*	12,5
		Rainfall	0.003	0.023	0.142	0.893	12,5
	2010	Canopy	-0.045	0.107	-0.424	0.689	12,5
		Coarse	0.017	0.178	0.093	0.929	12,5
		Fine	0.201	0.142	1.414	0.216	12,5
		Rainfall	0.290	0.351	0.824	0.447	12,5
	2011	Canopy	0.002	0.050	0.031	0.976	12,5
		Coarse	-0.061	0.040	-1.529	0.170	12,5
		Fine	-0.089	0.037	-2.392	0.048*	12,5
		Rainfall	-0.012	0.045	-0.262	0.801	12,5
	2012	Canopy	-0.085	0.166	-0.510	0.626	12,5
		Coarse	0.138	0.144	0.957	0.371	12,5
		Fine	-0.179	0.121	-1.477	0.183	12,5
		Rainfall	0.219	0.209	1.049	0.329	12,5
	2013	Canopy	0.039	0.076	0.507	0.630	12,5
		Coarse	-0.017	0.067	-0.256	0.807	12,5
		Fine	0.022	0.055	0.399	0.704	12,5
		Rainfall	0.026	0.170	0.153	0.884	12,5

Cont. Table 2.S3

Total body mass	2009	Canopy	-1.163	4.909	-0.237	0.822	12,5
		Coarse	15.339	3.910	3.923	0.011*	12,5
		Fine	-2.181	3.553	-0.614	0.566	12,5
		Rainfall	0.798	2.109	0.378	0.721	12,5
	2010	Canopy	-0.934	1.516	-0.616	0.565	12,5
		Coarse	3.487	2.600	1.341	0.238	12,5
		Fine	3.735	2.264	1.650	0.160	12,5
		Rainfall	6.454	5.085	1.269	0.260	12,5
	2011	Canopy	0.856	2.298	0.373	0.720	12,5
		Coarse	3.273	1.856	1.764	0.121	12,5
		Fine	1.352	1.587	0.852	0.422	12,5
		Rainfall	-0.318	2.035	-0.156	0.880	12,5
	2012	Canopy	-3.826	8.952	-0.427	0.682	12,5
		Coarse	8.091	7.843	1.032	0.337	12,5
		Fine	-1.322	5.256	-0.252	0.809	12,5
		Rainfall	20.936	12.759	1.641	0.145	12,5
	2013	Canopy	6.531	6.023	1.084	0.320	12,5
		Coarse	1.487	5.126	0.290	0.781	12,5
		Fine	1.175	4.384	0.268	0.798	12,5
		Rainfall	10.505	13.159	0.798	0.455	12,5
Extrapolated richness	2009	Canopy	-0.264	0.122	-2.159	0.083	12,5
		Coarse	0.229	0.104	2.195	0.080	12,5
		Fine	-0.009	0.103	-0.084	0.937	12,5
		Rainfall	-0.108	0.054	-2.004	0.101	12,5
	2010	Canopy	-0.201	0.145	-1.388	0.224	12,5
		Coarse	0.211	0.230	0.915	0.402	12,5
		Fine	0.271	0.176	1.540	0.184	12,5
		Rainfall	0.007	0.460	0.014	0.989	12,5
	2011	Canopy	0.006	0.129	0.050	0.962	12,5
		Coarse	-0.078	0.103	-0.758	0.473	12,5
		Fine	-0.135	0.100	-1.351	0.219	12,5
		Rainfall	-0.111	0.130	-0.851	0.423	12,5
	2012	Canopy	0.223	0.159	1.409	0.202	12,5
		Coarse	-0.015	0.145	-0.103	0.921	12,5
		Fine	-0.225	0.124	-1.817	0.112	12,5
		Rainfall	-0.055	0.234	-0.235	0.821	12,5
	2013	Canopy	0.025	0.079	0.319	0.760	12,5
		Coarse	-0.045	0.067	-0.666	0.530	12,5
		Fine	-0.013	0.057	-0.236	0.822	12,5
		Rainfall	-0.170	0.178	-0.957	0.375	12,5

Cont. Table 2.S3

CWM body mass	2009	Canopy	0.019	0.011	1.733	0.144	12,5
		Coarse	0.018	0.009	2.069	0.093	12,5
		Fine	0.025	0.008	3.042	0.029*	12,5
		Rainfall	-0.003	0.005	-0.589	0.582	12,5
	2010	Canopy	-0.018	0.017	-1.075	0.331	12,5
		Coarse	0.044	0.028	1.553	0.181	12,5
		Fine	0.034	0.025	1.378	0.227	12,5
		Rainfall	0.045	0.056	0.812	0.454	12,5
	2011	Canopy	-0.003	0.011	-0.272	0.793	12,5
		Coarse	0.020	0.009	2.215	0.062	12,5
		Fine	0.029	0.008	3.827	0.006*	12,5
		Rainfall	0.010	0.010	1.019	0.342	12,5
	2012	Canopy	0.000	0.021	0.015	0.989	12,5
		Coarse	0.021	0.018	1.173	0.279	12,5
		Fine	-0.010	0.012	-0.817	0.441	12,5
		Rainfall	0.038	0.029	1.283	0.240	12,5
	2013	Canopy	0.011	0.014	0.761	0.476	12,5
		Coarse	0.003	0.012	0.247	0.813	12,5
		Fine	0.014	0.010	1.354	0.225	12,5
		Rainfall	0.017	0.031	0.559	0.596	12,5
Coprophagous	2009	Canopy	-0.092	0.104	-0.884	0.377	12,5
		Coarse	0.145	0.082	1.758	0.079*	12,5
		Fine	-0.286	0.078	-3.676	<0.001*	12,5
		Rainfall	0.077	0.044	1.731	0.083	12,5
	2010	Canopy	-0.263	0.185	-1.417	0.156	12,5
		Coarse	0.292	0.314	0.930	0.352	12,5
		Fine	0.345	0.273	1.265	0.206	12,5
		Rainfall	0.661	0.618	1.070	0.284	12,5
	2011	Canopy	-0.108	0.201	-0.535	0.593	12,5
		Coarse	-0.026	0.162	-0.160	0.873	12,5
		Fine	-0.229	0.141	-1.617	0.106	12,5
		Rainfall	-0.014	0.179	-0.080	0.936	12,5
	2012	Canopy	-0.651	0.313	-2.081	0.038*	12,5
		Coarse	0.659	0.274	2.407	0.016*	12,5
		Fine	-0.179	0.186	-0.960	0.337	12,5
		Rainfall	0.422	0.441	0.956	0.339	12,5
	2013	Canopy	-0.156	0.104	-1.498	0.134	12,5
		Coarse	0.210	0.088	2.396	0.017	12,5
		Fine	-0.153	0.077	-1.968	0.049*	12,5
		Rainfall	-0.027	0.226	-0.118	0.906	12,5

Cont. Table 2.S3

Necrophagous	2009	Canopy	0.006	0.232	0.027	0.978	12,5
		Coarse	-0.210	0.191	-1.101	0.271	12,5
		Fine	0.261	0.167	1.566	0.117	12,5
		Rainfall	-0.265	0.103	-2.575	0.010*	12,5
	2010	Canopy	0.000	0.212	-0.002	0.998	12,5
		Coarse	-0.688	0.366	-1.878	0.060	12,5
		Fine	0.137	0.251	0.547	0.584	12,5
		Rainfall	-0.453	0.726	-0.624	0.532	12,5
	2011	Canopy	-0.229	0.155	-1.478	0.139	12,5
		Coarse	0.161	0.121	1.326	0.185	12,5
		Fine	0.056	0.103	0.548	0.583	12,5
		Rainfall	-0.119	0.143	-0.833	0.405	12,5
	2012	Canopy	-0.150	0.404	-0.370	0.711	12,5
		Coarse	0.391	0.358	1.090	0.276	12,5
		Fine	-0.495	0.289	-1.714	0.087	12,5
		Rainfall	0.013	0.570	0.023	0.981	12,5
	2013	Canopy	0.755	0.278	2.713	0.007*	12,5
		Coarse	-0.535	0.242	-2.210	0.027*	12,5
		Fine	0.073	0.202	0.362	0.717	12,5
		Rainfall	0.085	0.621	0.137	0.891	12,5
Generalists	2009	Canopy	-0.566	0.170	-3.336	<0.001*	12,5
		Coarse	0.742	0.138	5.382	<0.001*	12,5
		Fine	-0.142	0.131	-1.085	0.278	12,5
		Rainfall	-0.128	0.073	-1.747	0.081	12,5
	2010	Canopy	0.052	0.096	0.547	0.585	12,5
		Coarse	0.536	0.169	3.168	0.002*	12,5
		Fine	0.040	0.156	0.255	0.799	12,5
		Rainfall	0.500	0.320	1.562	0.118	12,5
	2011	Canopy	0.360	0.157	2.300	0.022*	12,5
		Coarse	0.060	0.126	0.473	0.636	12,5
		Fine	-0.234	0.115	-2.039	0.042*	12,5
		Rainfall	-0.200	0.148	-1.351	0.177	12,5
	2012	Canopy	-0.456	0.319	-1.430	0.153	12,5
		Coarse	0.872	0.285	3.060	0.002*	12,5
		Fine	-0.829	0.250	-3.321	<0.001*	12,5
		Rainfall	-0.028	0.450	-0.062	0.950	12,5
	2013	Canopy	0.283	0.146	1.935	0.053	12,5
		Coarse	0.007	0.126	0.056	0.956	12,5
		Fine	-0.155	0.111	-1.397	0.162	12,5
		Rainfall	0.727	0.322	2.257	0.024*	12,5

Cont. Table 2.S3

Rollers	2009	Canopy	-0.396	0.228	-1.738	0.082	12,5
		Coarse	-0.306	0.184	-1.667	0.096	12,5
		Fine	0.197	0.166	1.188	0.235	12,5
		Rainfall	-0.177	0.099	-1.782	0.075	12,5
	2010	Canopy	0.195	0.125	1.557	0.120	12,5
		Coarse	-0.725	0.227	-3.188	0.001*	12,5
		Fine	0.167	0.158	1.059	0.290	12,5
		Rainfall	0.016	0.418	0.039	0.969	12,5
	2011	Canopy	0.303	0.124	2.436	0.015*	12,5
		Coarse	-0.562	0.108	-5.207	<0.001*	12,5
		Fine	-0.062	0.083	-0.750	0.453	12,5
		Rainfall	0.125	0.110	1.130	0.259	12,5
	2012	Canopy	-0.269	0.304	-0.883	0.377	12,5
		Coarse	0.210	0.266	0.789	0.430	12,5
		Fine	-0.461	0.203	-2.267	0.023*	12,5
		Rainfall	0.345	0.425	0.811	0.418	12,5
	2013	Canopy	0.636	0.197	3.232	0.001*	12,5
		Coarse	-0.773	0.171	-4.514	<0.001*	12,5
		Fine	-0.027	0.143	-0.188	0.851	12,5
		Rainfall	0.420	0.432	0.972	0.331	12,5
Tunnelers	2009	Canopy	-0.182	0.101	-1.798	0.072	12,5
		Coarse	0.531	0.081	6.589	<0.001*	12,5
		Fine	-0.241	0.077	-3.137	0.002*	12,5
		Rainfall	0.021	0.043	0.484	0.628	12,5
	2010	Canopy	-0.166	0.146	-1.134	0.257	12,5
		Coarse	0.632	0.250	2.525	0.012*	12,5
		Fine	0.283	0.218	1.298	0.194	12,5
		Rainfall	0.740	0.489	1.514	0.130	12,5
	2011	Canopy	0.092	0.235	0.392	0.695	12,5
		Coarse	0.061	0.189	0.323	0.747	12,5
		Fine	-0.357	0.166	-2.152	0.031*	12,5
		Rainfall	-0.056	0.209	-0.266	0.790	12,5
	2012	Canopy	-0.490	0.247	-1.980	0.048*	12,5
		Coarse	0.719	0.218	3.302	<0.001*	12,5
		Fine	-0.276	0.152	-1.813	0.070	12,5
		Rainfall	0.067	0.348	0.193	0.847	12,5
	2013	Canopy	0.060	0.119	0.501	0.616	12,5
		Coarse	0.274	0.102	2.686	0.007*	12,5
		Fine	-0.203	0.091	-2.242	0.025*	12,5
		Rainfall	0.276	0.263	1.047	0.295	12,5

Cont. Table 2.S3

Dwellers	2009	Canopy	0.076	0.164	0.462	0.644	12,5
		Coarse	-0.339	0.130	-2.611	0.009*	12,5
		Fine	-0.324	0.123	-2.628	0.009*	12,5
		Rainfall	0.109	0.070	1.548	0.122	12,5
	2010	Canopy	0.032	0.214	0.151	0.880	12,5
		Coarse	-0.450	0.361	-1.245	0.213	12,5
		Fine	0.502	0.290	1.731	0.084	12,5
		Rainfall	1.194	0.711	1.679	0.093	12,5
	2011	Canopy	-0.153	0.199	-0.769	0.442	12,5
		Coarse	0.198	0.160	1.237	0.216	12,5
		Fine	0.055	0.136	0.402	0.688	12,5
		Rainfall	-0.210	0.184	-1.142	0.254	12,5
	2012	Canopy	-1.159	0.613	-1.892	0.058	12,5
		Coarse	1.053	0.536	1.964	0.050*	12,5
		Fine	-0.335	0.369	-0.908	0.364	12,5
		Rainfall	0.707	0.861	0.821	0.412	12,5
	2013	Canopy	-0.193	0.163	-1.190	0.234	12,5
		Coarse	0.273	0.137	1.994	0.046*	12,5
		Fine	-0.013	0.119	-0.110	0.912	12,5
		Rainfall	0.179	0.351	0.512	0.609	12,5
Diurnal	2009	Canopy	-0.342	0.116	-2.938	0.003*	12,5
		Coarse	0.332	0.093	3.577	<0.001*	12,5
		Fine	-0.365	0.091	-4.027	<0.001*	12,5
		Rainfall	0.061	0.050	1.230	0.219	12,5
	2010	Canopy	-0.295	0.153	-1.933	0.053	12,5
		Coarse	0.459	0.258	1.783	0.075	12,5
		Fine	0.191	0.226	0.847	0.397	12,5
		Rainfall	0.599	0.507	1.181	0.238	12,5
	2011	Canopy	-0.175	0.147	-1.190	0.234	12,5
		Coarse	0.108	0.118	0.907	0.364	12,5
		Fine	0.024	0.101	0.240	0.810	12,5
		Rainfall	-0.086	0.131	-0.653	0.514	12,5
	2012	Canopy	-0.635	0.356	-1.783	0.075	12,5
		Coarse	0.849	0.313	2.716	0.007*	12,5
		Fine	-0.582	0.223	-2.614	0.009*	12,5
		Rainfall	0.251	0.504	0.498	0.619	12,5
	2013	Canopy	-0.029	0.124	-0.234	0.815	12,5
		Coarse	0.081	0.105	0.770	0.442	12,5
		Fine	-0.191	0.093	-2.060	0.039	12,5
		Rainfall	0.413	0.270	1.531	0.126	12,5

Cont. Table 2.S3

Nocturnal	2009	Canopy	0.126	0.095	1.317	0.188	12,5
		Coarse	0.187	0.076	2.468	0.014*	12,5
		Fine	-0.070	0.070	-1.011	0.312	12,5
		Rainfall	-0.029	0.041	-0.712	0.477	12,5
	2010	Canopy	0.123	0.141	0.873	0.383	12,5
		Coarse	0.050	0.244	0.207	0.836	12,5
		Fine	0.363	0.208	1.743	0.081	12,5
		Rainfall	0.751	0.473	1.587	0.113	12,5
	2011	Canopy	0.277	0.179	1.549	0.121	12,5
		Coarse	0.108	0.143	0.753	0.452	12,5
		Fine	-0.452	0.134	-3.370	<0.001*	12,5
		Rainfall	-0.133	0.163	-0.819	0.413	12,5
	2012	Canopy	-0.390	0.244	-1.601	0.109	12,5
		Coarse	0.485	0.214	2.269	0.023*	12,5
		Fine	-0.207	0.150	-1.383	0.167	12,5
		Rainfall	0.053	0.343	0.156	0.876	12,5
	2013	Canopy	0.309	0.141	2.197	0.028*	12,5
		Coarse	0.078	0.121	0.640	0.522	12,5
		Fine	0.000	0.103	0.004	0.997	12,5
		Rainfall	-0.087	0.316	-0.275	0.783	12,5

Table 2.S4: Environmental variables found to be significantly important for changes in community structure and composition in each year. Degrees of freedom is ‘1,9’ for each analysis.

		Structure			**Composition**		
		pseudo-*F*	R^2	***p***	**pseudo-*F***	R^2	***p***
2009	Coarse Sand	6.741	0.389	0.001*	5.730	0.340	0.001*
	Fine Sand	2.869	0.165	0.001*	3.492	0.207	0.001*
2010	Coarse Sand	3.286	0.309	0.003*	2.223	0.230	0.005*
2011	Coarse Sand	4.816	0.287	0.001*	5.370	0.311	0.001*
	Fine Sand	1.842	0.110	0.022*	1.379	0.080	0.180
	Rain	1.580	0.094	0.094	1.874	0.109	0.030*
2012	Coarse Sand	2.783	0.179	0.005*	3.291	0.195	0.006*
	Fine Sand	4.218	0.271	0.015*	4.989	0.296	0.019*
2013	Coarse Sand	5.547	0.380	0.003*	5.181	0.367	0.006*

Table 2.S5: Differences for community metrics in pairwise year comparisons. All p-values are corrected by Holm-bonferroni method. ‘E. Richness’ means extrapoled richness, ‘CWM body mass” means community weighted-level body mass and ‘*p-F*’ means *pseudo-F*.’

Years	**Abundance**		**Richness**		**Total body mass**		**Extrapolated Richness**		**CWM body mass**		**Structure**		**Composition**	
	X^2	*p*	X^2	*p*	X^2	*p*	X^2	*p*	X^2	*p*	*p-F*	*p*	*p-F*	*p*
Overall	97.670	<0.001	81.162	<0.001	43.526	<0.001	25.667	<0.001	30.307	<0.001	2.795	<0.001	1.826	<0.001
09-10	79.616	<0.001	54.888	<0.001	33.313	<0.001	12.240	<0.001	6.480	0.076	5.076	0.001	2.533	0.003
09-11	15.836	<0.001	17.667	<0.001	26.209	<0.001	0.828	0.677	5.727	0.100	3.118	0.006	1.711	0.042
09-12	16.660	0.765	28.278	<0.001	13.806	0.002	3.698	0.271	0.838	~1	2.403	0.017	1.854	0.031
09-13	0.763	<0.001	0.330	0.566	4.675	0.153	1.469	0.677	3.495	0.308	1.587	0.104	1.671	0.068
10-11	24.815	<0.001	11.515	0.003	0.425	0.514	6.758	0.065	24.389	<0.001	2.067	0.041	1.474	0.101
10-12	65.021	<0.001	5.084	0.072	4.228	0.158	2.528	0.447	11.977	0.004	1.155	0.307	0.643	0.874
10-13	65.021	0.879	47.357	<0.001	13.029	0.002	21.955	<0.001	19.493	<0.001	4.272	0.001	2.545	0.004
11-12	0.0230	0.006	1.339	0.495	1.971	0.361	1.031	0.677	2.184	0.558	1.116	0.311	1.386	0.115
11-13	9.568	0.005	13.261	0.001	8.745	0.019	4.490	0.205	0.274	~1	3.372	0.002	2.752	0.005
12-13	10.362	0.005	22.706	<0.001	2.413	0.361	9.773	0.014	0.911	~1	1.492	0.145	1.356	0.172

Table 2.S6: Differences for functional groups abundances in pairwise year comparisons. All p-values are corrected by Holm-bonferroni method. *F* means *pseudo-F*.

	Tunnelers		**Rollers**		**Dwelers**	
	X^2	p	X^2	p	X^2	p
Overall	42.718	<0.001*	38.365	<0.001*	29.371	<0.001*
2009-2010	58.747	<0.001*	42.934	<0.001*	30.436	<0.001*
2009-2011	9.043	0.011*	10.650	0.007*	10.684	0.008*
2009-2012	18.386	<0.001*	10.354	0.007*	0.445	~1.000
2009-2013	1.433	0.402	0.008	~1.000	0.183	~1.000
2010-2011	21.238	<0.001*	11.542	0.005*	5.314	0.085
2010-2012	11.190	0.005*	11.315	0.005*	23.703	<0.001*
2010-2013	42.050	<0.001*	42.163	<0.001*	26.020	<0.001*
2011-2012	1.636	0.402	0.000	~1.000	6.791	0.046*
2011-2013	3.319	0.205	9.828	0.007*	8.085	0.027*
2012-2013	9.874	0.008*	9.892	0.007*	0.057	~1.000

	Coprophagous		**Necrophagous**		**Generalists**	
	X^2	p	X^2	p	X^2	p
Overall	43.170	<0.001*	39.836	<0.001*	42.508	<0.001*
2009-2010	61.858	<0.001*	39.379	<0.001*	52.726	<0.001*
2009-2011	10.254	0.008*	10.807	0.006*	13.496	0.001*
2009-2012	9.988	0.008*	10.104	0.006*	18.796	<0.001*
2009-2013	1.615	0.408	0.040	~1.000	0.169	0.975
2010-2011	22.074	<0.001*	9.991	0.006*	13.545	0.001*
2010-2012	22.466	<0.001*	10.813	0.006*	8.832	0.009*
2010-2013	43.710	<0.001*	42.511	<0.001*	46.702	<0.001*
2011-2012	0.002	0.967	0.010	~1.000	0.482	0.975
2011-2013	3.735	0.213	11.653	0.005*	10.568	0.005*
2012-2013	3.575	0.213	11.742	0.005*	15.481	0.001*

	Nocturnal		**Diurnal**	
	X^2	p	X^2	p
Overall	51.124	<0.001*	44.964	<0.001*
2009-2010	78.099	<0.001*	53.916	<0.001*
2009-2011	9.387	0.009*	21.676	<0.001*
2009-2012	28.645	<0.001*	6.284	0.049*
2009-2013	2.148	0.221	0.161	0.688
2010-2011	33.756	<0.001*	7.467	0.031*
2010-2012	12.693	0.002*	22.841	<0.001*
2010-2013	55.198	<0.001*	48.200	<0.001*
2011-2012	5.362	0.062	4.411	0.103
2011-2013	2.546	0.221	18.155	<0.001*
2012-2013	15.314	0.001*	4.475	0.103

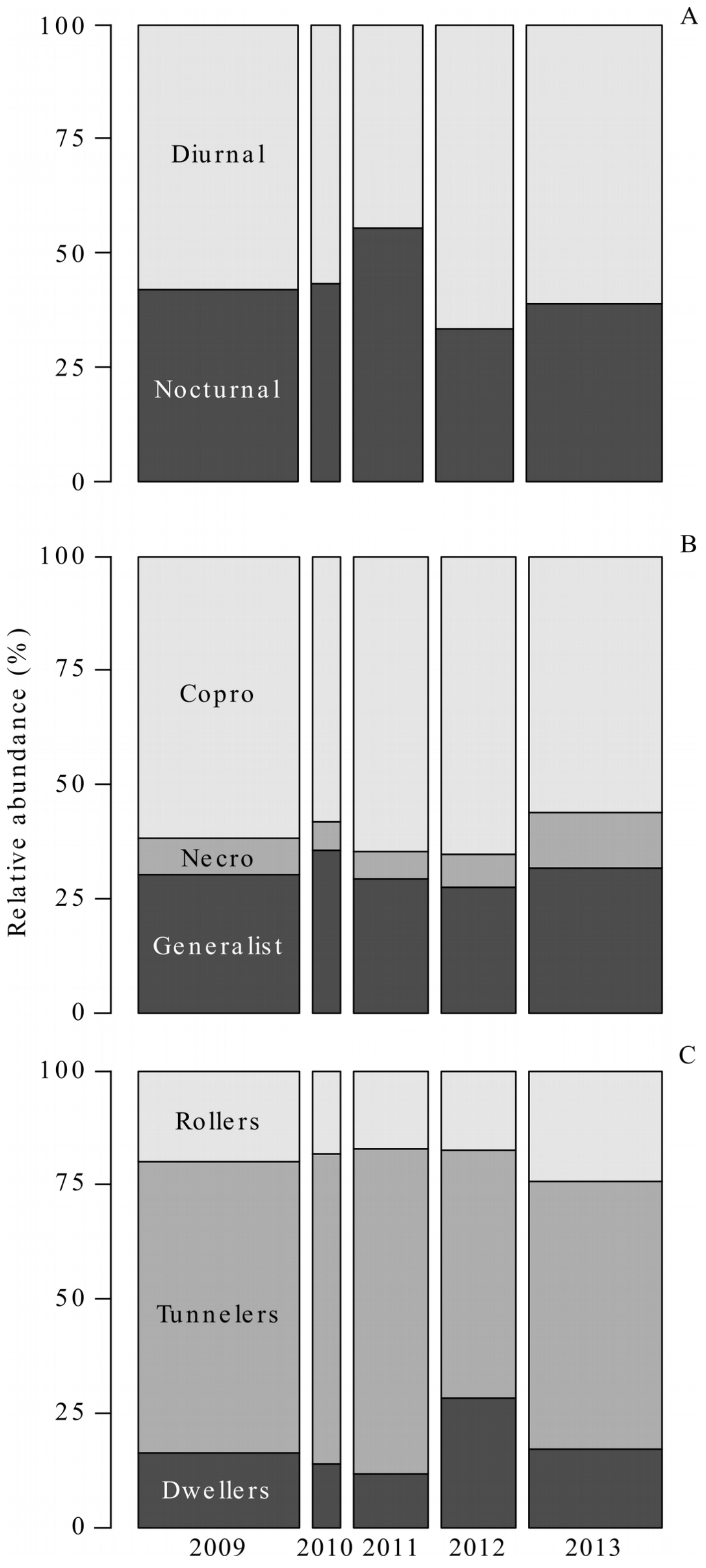

Figure 2.S7: Relative abundance of functional groups of activity period (A), diet preference (B) and nesting behaviour (C). Bars width represents the proportion of total abundance for each year. Copro = Coprophagous and Necro = Necrophagous.

Chapter 3

Spatial and temporal shifts in functional and taxonomic diversity in a human-modified tropical forest landscape

Publication status: In preparation to submit in Journal of Functional Ecology

Format based on the guidelines of 'Journal of Functional Ecology'

Spatial and temporal shifts in functional and taxonomic diversity in a human-modified tropical forest landscape

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ABSTRACT

Functional diversity metrics are becoming more common in ecological studies evaluating the conservation value of ecosystems. However, there is a lack of knowledge about how the information gained from taxonomic and functional approaches varies in time and in the face of human-induced changes. Here, we used a five-year dataset of dung beetles from undisturbed forest, primary forest corridors and *Eucalyptus* plantations to evaluate if the temporal dynamics of taxonomic and functional approaches are affected by forest modification. We also compared the sensitivity of conceptually similar diversity metrics to temporal variation and anthropogenic changes. We found that all metrics showed similar inter-annual variation across forest types, apart from species richness, which was more similar in forest corridors and *Eucalyptus* plantations than in undisturbed forests. However, the temporal variation was lower for most functional metrics than for taxonomic metrics, apart from functional evenness, which varied more over time than taxonomic evenness. In general, the temporal variation was higher in *Eucalyptus* plantations than in native forest sites for both approaches. Despite the overall similarity in the patterns of taxonomic and functional responses to human-induced changes, there was high variance of responses in each metric among years and incongruence between pairs of conceptually similar metrics in the same year. Thus, we highlight the importance of using taxonomic and functional diversity metrics in tandem to better understand biological responses to environmental and anthropogenic changes.

Keywords: Scarabaeinae, Functional ecology, Forest conversion, Land-use change, Temporal dynamics.

3.1 INTRODUCTION

The past decade has seen a rapid increase in the use of functional metrics to quantify biodiversity responses to anthropogenic change (e.g. Elmqvist et al. 2003; Bihn, Gebauer & Brandl 2010; Barragán et al. 2011), replacing or complementing the traditional taxonomic approach, which considers each species as a unit with an equal contribution to ecosystem functioning (Mouchet *et al.* 2010). The functional approach is particularly important in the tropics because of the rapid rate of land-use change and the importance of biodiversity in ecosystem functioning, promoting a prolific debate about the role of human-modified landscapes for ecosystem functioning and biodiversity conservation (Silver, Brown & Lugo 1996; Lambin, Geist & Lepers 2003; Gardner *et al.* 2008; Power 2010; Palm *et al.* 2014). Additionally, the exceptionally high biological diversity of tropical environments can make it very difficult to find empirical links between biota and ecosystem functioning, which increases researchers' reliance on proxies based on functional diversity metrics (Gaston 2000; Mouillot *et al.* 2013).

Many studies have estimated the conservation value of ecosystems using either taxonomic or functional diversity, and it is well established that human-induced changes affect both sets of metrics (Braga *et al.* 2013; Mouillot *et al.* 2013; Cottee-Jones *et al.* 2015; Bredemeier *et al.* 2015). Although these metrics can complement each other and provide very different insights into mechanisms driving community changes, they are rarely assessed together in the same study (but see Moretti et al. 2009; Villéger et al. 2010; Baiser & Lockwood 2011). It is therefore important to assess the sensitivity of functional and taxonomic approaches in assessing biodiversity change, and there are valid reasons to suggest that they will show very different responses. First, most functional metrics are not related to species diversity (Villéger, Mason & Mouillot 2008; Laliberte & Legendre 2010), and the loss of functionally specialised species can lead to a decrease in functional diversity, even if total species richness is greater due to increased abundance of generalist species (Villéger *et al.* 2010). Second, the similarity between taxonomic and functional approaches may depend on the intensity of disturbance; low-intensity disturbance could change species composition but functional redundancy in highly diverse communities would maintain the community’s functional structure, whereas high-intensity disturbances are likely to negatively affect both the taxonomic and functional components of biodiversity (Hidasi-Neto, Barlow & Cianciaruso 2012; Sterk *et al.* 2013; Edwards *et al.* 2014).

There is currently a lack of empirical evidence with which to assess the sensitivity of taxonomic and functional metrics to temporal dynamics, and to determine how natural variation interacts with human-induced modifications. It is important to resolve this knowledge gap for two reasons: First, tropical forest communities can be highly dynamic in time (Hanski and Cambefort 1991; Thesis Chapter 2) and the temporal variation of taxonomic or functional diversity might not show similar patterns. For example, we might expect fewer changes in functional compared to taxonomic diversity, as the traits of species within a community were selected by ecological filters (i.e. processes related to interactions among species as well as between species and the abiotic environment; Cornwell, Schwilk & Ackerly 2006; Webb et al. 2010; Swenson et al. 2012). Second, there is little evidence of how taxonomic and functional approaches vary across time in human modified systems; here, we would expect the two approaches to yield more similar results as the intensity of habitat modification increases, because functional diversity declines with increasing loss of sensitive species, making it more likely that the loss of a given species will also entail a loss of function in highly disturbed areas (Ricotta *et al.* 2016; Leitão *et al.* 2016).

We used a robust five-year study to investigate the spatial and temporal patterns of taxonomic and functional diversity of Amazonian dung beetle communities, contrasting the response of conceptually similar taxonomic and functional diversity metrics between undisturbed forest (used as a baseline for comparison) and two modified forest types - primary forest corridors, which comprise a reduction in forest extent with increased edge and isolation effects; and *Eucalyptus* plantations to represent the replacement of native vegetation by exotic trees. Dung beetles were chosen as a focal group for this study because they are sensitive to changes in vegetation structure (Gardner *et al.* 2008; Almeida *et al.* 2011; Korasaki *et al.* 2013), their response traits are well studied (Nichols *et al.* 2013) and they mediate important ecosystem functions, such as seed dispersal and incorporation of nutrient in soil (Slade *et al.* 2007, 2016; Nichols *et al.* 2008).

Specifically, we addressed three questions using empirical data to evaluate three potential scenarios for each:

1) Does anthropogenic modification affect inter-annual variation in biological diversity? Based on previous knowledge of inter-annual variation of dung beetle communities in undisturbed forest (Thesis Chapter 2), we contrasted the following scenarios: (A) the pattern of inter-annual variation of diversity metrics is mainly driven

by climate and will not be affected by forest type; (B) the extent of environmental changes in *Eucalyptus* plantations will reduce the temporal dynamics of dung beetle communities compared to native forest corridors and undisturbed forest; or (C) that forest modification will alter inter-annual variation, making it more similar between forest corridors and plantations compared to undisturbed forest (Figure 3.1A-C).

2) Is the inter-annual variation of taxonomic and functional diversity similar? Here we considered the following possible scenarios: (D) temporal variation in taxonomic and functional diversity will be similar at both high- and low levels of human-induced change; (E) taxonomic metrics will show lower temporal variation than functional metrics; or (F) the temporal variation of taxonomic metrics will be higher than functional metrics (Figure 3.1D-F).

3) Which approach shows higher sensitivity to human-induced changes? Here we assessed the following scenarios (G) both diversity approaches will show similar responses regardless of whether the disturbance either strongly alters the community or does not affect at all; (H) the taxonomic response will be lower if the disturbance causes a greater reduction in functional diversity; or (I) taxonomic metrics will be more affected by human-induced changes if species composition is more sensitive than functional metrics (Figure 3.1G-I).

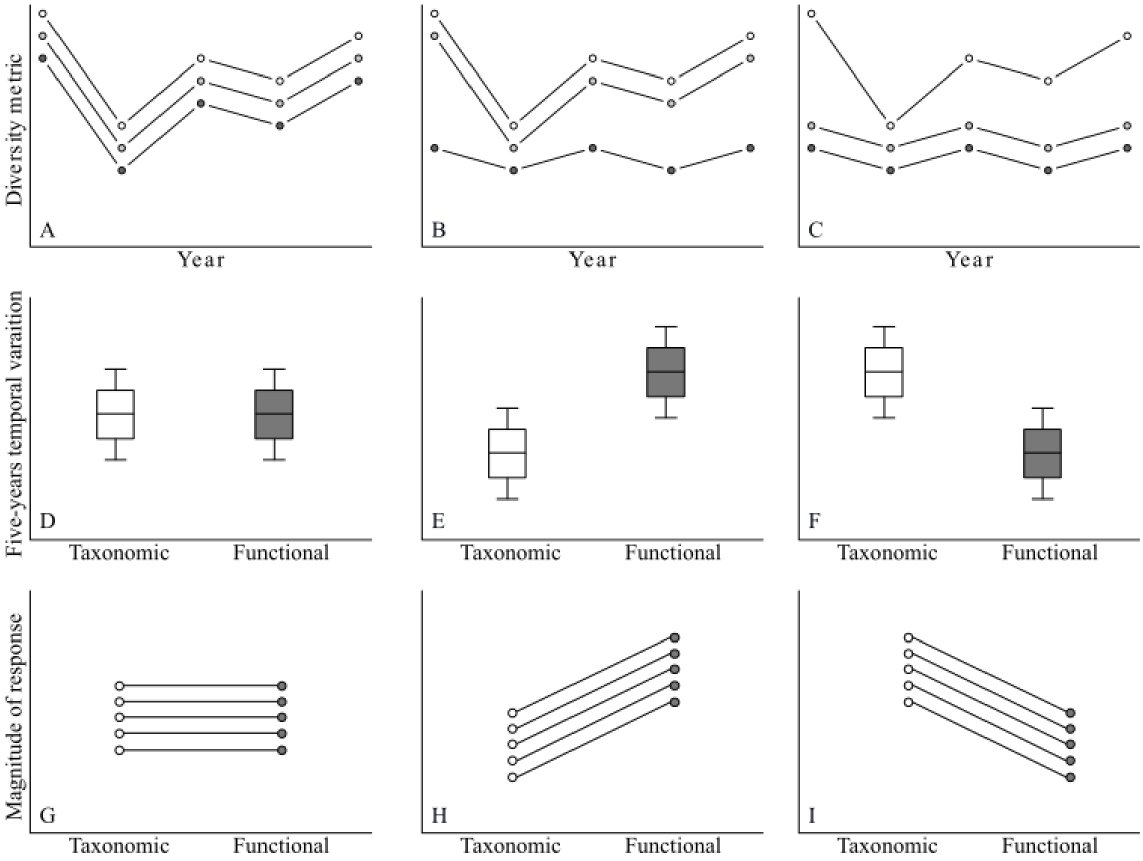

Figure 3.1: Three alternative scenarios relating to each of three research questions. For the effect of forest type on inter-annual variation of diversity metrics, undisturbed forest (white circles), primary forest corridor (light-grey circles) and *Eucalyptus* plantation (dark-grey circles) could show similar inter-annual variation (A); or only the strong ecological filter in *Eucalyptus* plantation could affect the inter-annual variation (B); or both changes are likely to modify the temporal dynamics (C). For inter-annual variation between taxonomic (white boxes) and functional metrics (grey boxes), taxonomic and functional metrics could show similar patterns (D); or taxonomic metrics could vary less than functional metrics (E); or the temporal variation of taxonomic metrics could be higher than functional metrics (F). Finally, the sensitivity of approaches (white and grey circles represent taxonomic and functional metrics, respectively) to habitat modification could be similar if the human-induced change strongly affects a community, or it barely does so (G); or the taxonomic response could be lower if anthropogenic change affects mainly functional structure (H); or taxonomic metrics could be more affected if the changes have low impact on functional structure (I). The lines in G, H and I connect different approaches in same year.

3.2 MATERIAL AND METHODS

3.2.1 Study site

We conducted the study in the Jari River basin, in the north-eastern Brazilian Amazonia (00°27′ - 01°30′ S, 51°40′ - 53°20′ W; Figure 3.2), an area of more than 1.5 Mha, which was partially converted from pristine forest to plantations of exotic trees about 50 years ago (Coutinho & Pires 1997). Currently the landscape has exotic tree plantations (450 km^2), and regenerating secondary forest (1,000 km^2) disrupted by large primary forest corridors (*c*. 200 m wide) and surrounded by *Terra Firme* primary forest (> 5,000 km^2; Figure 3.2; Coutinho & Pires 1997; Parry, Barlow & Peres 2007).

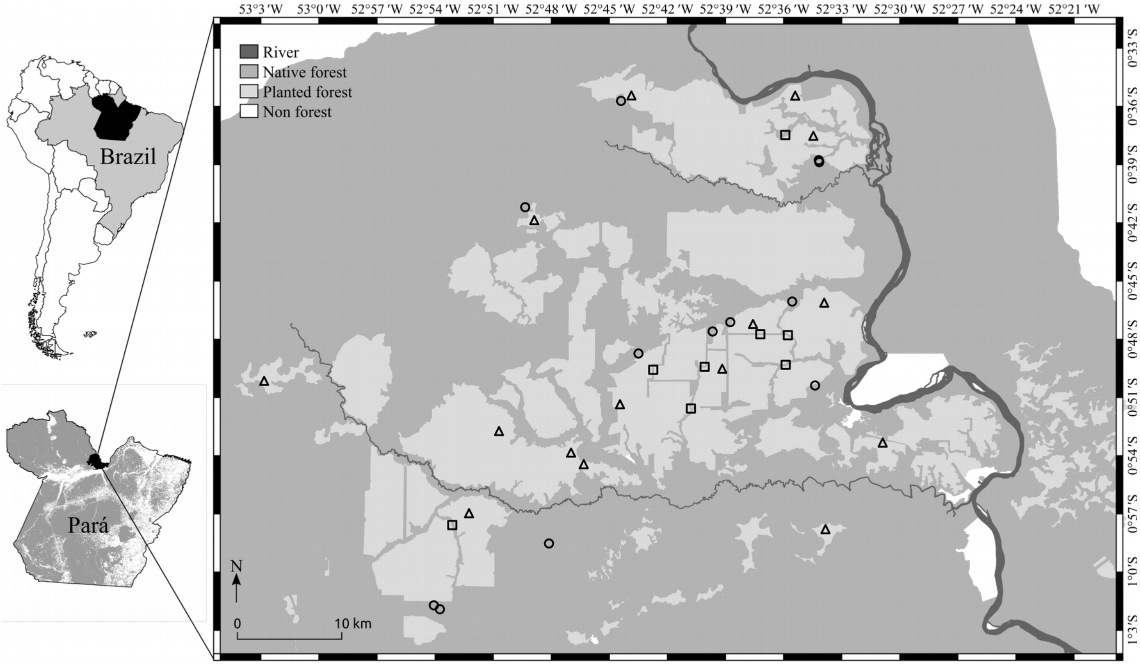

Figure 3.2: Location of sampling sites in undisturbed forest (circles), primary forest corridors (squares) and *Eucalyptus* plantations (triangles) within the Jari River basin in Pará State, Brazil.

The area has a marked wet season from January to June, and a distinct dry season from September to November, with a tropical monsoon climate (Amw – Köppen classification), and an average annual rainfall of 2115 mm (Coutinho & Pires 1997; Parry, Barlow & Peres 2007). The mean annual temperature is 26.7 ±0.6°C, monthly maxima and minima mean can reach 31.4 ±1.1°C and 22.5 ±0.2°C, respectively (Climate Data.org 2016).

We sampled in 12 undisturbed primary forest sites, eight primary forest corridors and 15 *Eucalyptus* plantations separated by 0.2 - 60 km (Figure 3.2). The undisturbed forest was used as a baseline, whereas primary forest corridors were considered a low-intensity modification, but still an unnatural arrangement of the vegetation at study site. *Eucalyptus* plantations represent a highly disturbed site, as the native forest has been completely replaced by exotic trees. Both modified forest types show different dung beetle species composition and community structure, with *Eucalyptus* presenting the greatest differences compared to undisturbed forest (Figure 3.S1, Barlow et al. 2010; Louzada et al. 2010).

3.2.2 Dung beetle sampling

We sampled dung beetles using pitfall traps baited with 30 g of human dung. The traps consisted of plastic containers (19 cm diameter and 11 cm deep), protected from rain with a plastic lid suspended 20 cm above the surface. Each trap was part-filled with water, salt and detergent. Five pitfall traps were placed 150 m apart along a transect, with at least 500 m distance to the nearest edge. Collections took place over a five-year period (2009 to 2013) during the wet season in each year (January to early June). Beetles were sampled in exactly the same locations each year, and for 48 hours per site in every year. Dung beetle specimens were transported from field to the laboratory in 90% alcohol, then sorted, dried and stored in paper envelopes. Beetles were identified using a key to the New World's Scarabaeinae genera and subgenera (Vaz-De-Mello *et al.* 2011), a field guide for dung beetles of the Jari River basin (Louzada et al. *in prep.*), and a reference collection held at the Universidade Federal de Lavras (CREN – UFLA; Coleção de Referência de Escarabeíneos Neotropicais), Minas Gerais State, Brazil. Identifications were made to species level and, where there was uncertainty, a morphospecies number was given. Voucher specimens were deposited at CREN – UFLA.

3.2.3 Trait assessment

We undertook two additional sample collections to assess dung beetle traits related to dietary preference and activity period. In January and February 2012, we collected specimens from previously selected sites with high species richness and abundance. In November and December 2013, we made additional collections of species for which there was little existing information about traits. The sampling sites were chosen based on data from a previous monitoring project and all were located within our study site. We set pitfall traps during the day (7:00-18:00 h) and night (19:00-6:00 h) to evaluate activity period, and determined beetles as diurnal or nocturnal. We used pitfall traps baited with either dung or carrion to assess dietary preference, which grouped dung beetles as necrophagous or coprophagous for those spcies with 70% of abundance in carcass or dung, respectivelly; or generalist those species with less than 70% individuals in any bait. We determined the beetles nesting behaviour as rollers, tunnelers or dwellers based on their genus (Thesis Chapter 2). We also recorded the body mass of each species using the mean dry weight of 15 individuals (or the maximum available; 1-15) sampled during the experiments or previously deposited at CREN – UFLA, using a precision balance (0.001 g).

3.2.4 Data analysis

All analyses were performed using R version 3.3.0 (R Core Team 2016). We used conceptually similar metrics of taxonomic and functional diversity and all metrics were calculated for individual sites and collection years. The taxonomic metrics were: 1) species richness, which is the number of different species at each site, 2) Pielou's evenness, which describes the dominance/evenness in communities based on species frequency and abundance, 3) Simpson's index of diversity (1-*D*), which is the probability of two individuals from a community belonging to the same species. The corresponding functional metrics were: 1) Functional richness (FRic), which is calculated as the functional space occupied by species in a given community; 2) Functional evenness (FEve) which evaluates the regularity of the trait distribution; 3) Rao's quadratic entropy (FDq) which is based on the probability of finding functionally similar species in a community by chance (Botta-Dukát 2005; Villéger *et al.* 2008). FRic and FEve were calculated based on species' dietary preference, activity period, nesting behaviour and body mass using the *dbFD* function in the *FD* package (Laliberté, Legendre & Shipley 2014), and FDq was calculated using the *mpd* function in the *picante* package (Kembel *et al.* 2010), using Gower's dissimilarity between species in the *gowdis* function from *FD* package.

To test the effects of inter-annual variation and anthropogenic modification on diversity approaches in dung beetle communities, we built generalized linear mixed models with Gaussian error distribution for all diversity metrics as response variables, except for species richness (count data), for which we used a Poisson error distribution (*lmer* and *glmer* functions in the *lme4* package; Bates et al. 2015). Our models included the categorical variables forest type and year of sampling, as well as their interactions as fixed effects, and sampling site as a random effect. We tested the significance of the fixed effects with type II Wald Chi-square tests, using the *Anova* function in the package *car* (Fox and Weisberg 2011). Finally, for those models with significant fixed effects, we ran Chi-square tests for multiple pairwise comparisons among forest types in each year and between consecutive years within each human-modified forest type using the *testInteractions* function in the *phia* package followed by Holm-Bonferroni correction of p-values (Rosario-Martinez 2015).

To assess the sensitivity of diversity metrics to inter-annual variation in each forest type, we calculated the inter-annual coefficient of variation (the ratio between the standard deviation and the mean for each taxonomic and functional metric) for each site. Then, we built linear models with the coefficient of variation for each group of metrics (richness, evenness and dispersion) as the response variable and the type of metric (taxonomic or functional) as the explanatory variable, respectively.

To evaluate the similarity in response magnitude between taxonomic and functional approaches, we calculated Hedge's *g* effect size for the comparisons of forest types for each taxonomic and functional metric individually in the *compute.es* package, which calculates the magnitude of changes in diversity metrics based on the mean of baseline (undisturbed forest) subtracted from the mean of modified forest type (Del Re 2013). Following, we multiplied the value to '-1' to positive (negative) *g*-value represents increase (decrease) in a given diversity metric of disturbed forest types compared to the baseline, and *g* of zero is expected when there is no response. We then used paired t-tests to compare the Hedge's *g*-values between the pairs of conceptually similar diversity metrics in each modified forest type; comparisons were made between species richness and FRic; Pielou's evenness and FEve; Simpson's diversity and FDq.

3.3 RESULTS

We collected 27,192 individual dung beetles from 102 species, of which 54 were identified at species level and 48 as morphospecies. We found 10,482 individuals of 90 species in undisturbed forest, 8,307 individuals of 82 species in corridors, and 8,403 individuals of 82 species in *Eucalyptus* plantations. Almost two thirds of all species (64) occurred in all forest types; undisturbed forest had seven exclusive species and shared 11 species with corridors and eight with *Eucalyptus* plantations, whereas corridors and *Eucalyptus* plantations had two and five exclusive species, respectively, and five species in common.

We obtained trait information for 75 species (74% of the total sampled), which represents 26,528 of the individuals captured (98%). In terms of nesting behaviour, most were classified as tunnelers (44 spp.; 59%), followed by rollers (20 spp.; 17%), and dwellers (11 spp.; 15%). The majority of species were classified as coprophagous (53 spp.; 71%), whereas necrophagous beetles and generalists represented 17% (13 spp.) and 12% (9 spp.), respectively. For activity period we sampled 66 species (65%) represented by 25,545 individuals (94%). Most species were classified as diurnal (38 spp.; 58%), compared to nocturnal (28 spp.; 42%).

3.3.1 Inter-annual variation and anthropogenic effects on taxonomic and functional diversity

Most of the functional and taxonomic metrics we assessed showed inter-annual variation (Figure 3.3, Table 3.S2), except for Simpson's diversity ($X^2_{4,175} = 7.260$, $p = 0.123$) and FDq ($X^2_{4,175} = 0.924$, $p = 0.924$). FRic was lower in 2009 and both Pielou's evenness and Feve were higher in the same year (Figure 3.3, Table 3.S4). Only species richness had distinct patterns of inter-annual variation among forest types, indicated by a significant interaction between forest type and year ($X^2_{8,175} = 33.833$ $p < 0.001$; Figure 3.3): there was a marked decrease in species richness in all forest types in 2009 but species richness showed a slight increase in forest corridors and *Eucalyptus* plantation in subsequent years, whereas there was no directional trend over time in undisturbed forest (Figure 3.3, Table 3.S3). Species richness in undisturbed forest was higher in 2011 and 2013 compared to 2010 and 2012, respectively, but did not change between 2011 and 2012 (Figure 3.3, Table 3.S3). In *Eucalyptus* plantations, species richness was higher in 2012 compared to 2011 and also in 2013 compared to 2012, but did not change between 2010 and 2011 (Figure 3.3, Table 3.S3). By contrast, FRic was lower in 2010 than in 2009 and 2011 for all forest types ($X^2_{4,175} = 40.398$, $p < 0.001$; Figure 3.3, Table 3.S4), whereas Pielou's evenness and FEve showed the highest values in 2010 ($X^2_{4,175} = 17.746$, $p = 0.001$; $X^2_{4,175} = 15.080$, $p = 0.005$, respectively).

Despite the inter-annual variation, we found consistent differences among forest for most of the metrics (Figure 3.3, Table 3.S2). Across all years, communities in *Eucalyptus* plantations had the lowest values of species richness, FRic, Pielou's evenness, Simpson's diversity and FDq ($X^2_{2,175} = 106.526$, $X^2_{2,175} = 47.061$, $X^2_{2,175} = 15.061$, $X^2_{2,175} = 49.412$, $X^2_{2,175} = 44.464$, respectively, $p < 0.001$ for all metrics; Figure 3.3); only FEve did not differ significantly among forest types ($X^2_{2,175} = 4.248$, $p = 0.120$; Figure 3.3) . We also found that the metrics describing dung beetle communities in corridors were similar to undisturbed forest in all metrics, apart from FRic, which was lower in corridors (Figure 3.3, Tables 3.S5 and 3.S6).

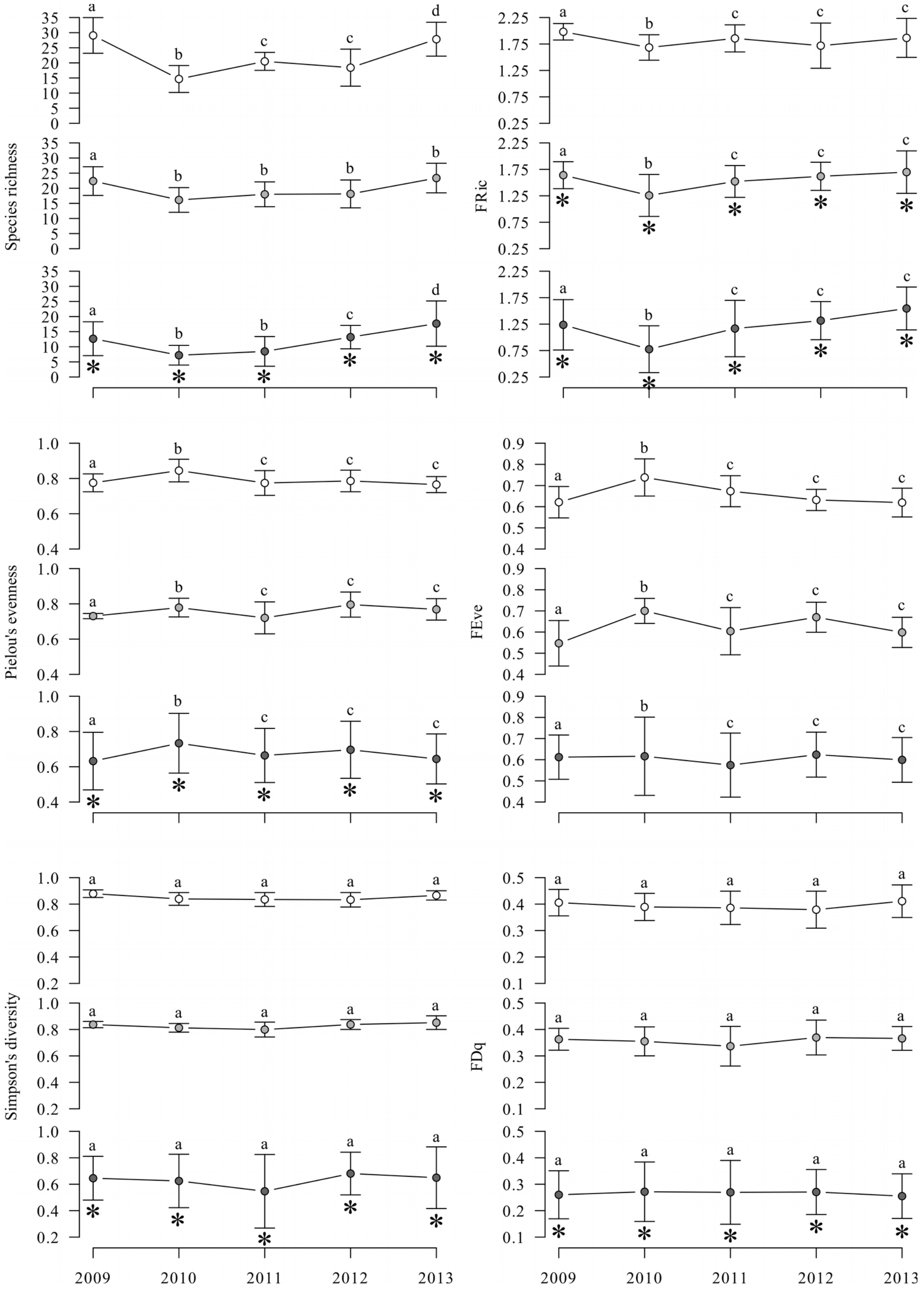

Figure 3.3: Mean (±SD) diversity metrics for dung beetle communities in undisturbed forest (baseline; white points), forest corridors (light-grey points), and *Eucalyptus* plantations (dark-grey points) over five years. Species richness, Functional richness (FRic), Pielou's evenness, Functional evenness (FEve), Simpson's diversity, and Rao's quadratic entropy (FDq). Significant differences ($p < 0.05$) between the human-modified and undisturbed forest in a given year are indicated by stars (*) below the deviation bars. Different letters represent significant dissimilarity between consecutive years within the same forest type.

3.3.2 Sensitivity of taxonomic and functional diversity metrics to inter-annual variation within forest types

There were substantial differences between taxonomic and functional diversity metrics when they were used to assess inter-annual variation in dung beetle communities within forest types (Figure 3.4). In undisturbed forests, species richness varied significantly more among years than FRic ($F_{1,24} = 21.239$, $p < 0.001$; Figure 3.4). Pielou's evenness varied less than FEve in both undisturbed forest ($F_{1,24} = 11.543$, $p = 0.003$) and native forest corridors ($F_{1,16} = 5.904$, $p = 0.029$; Figure 3.4). We also found higher variation in Simpson's diversity than FDq for undisturbed forest ($F_{1,24} = 11.125$, $p = 0.003$; Figure 3.4), but not in other forest types.

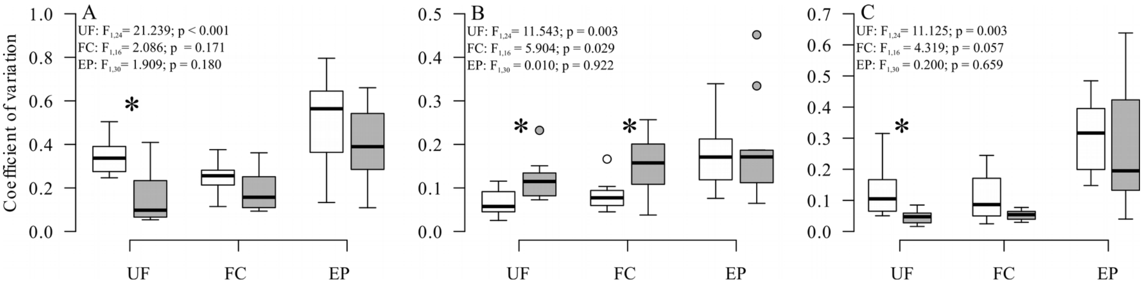

Figure 3.4: Coefficient of temporal variation in all forest types for pairs of conceptually similar taxonomic (white) and functional (grey) metrics. Species richness and Functional richness (A), Pielou's evenness and Functional evenness (B), and Simpson's diversity and Rao's quadratic entropy (C) of dung beetle communities in different forest types. Significant differences ($p < 0.05$) between taxonomic and functional diversity approaches are indicated by stars (*). 'UF' = undisturbed forest, 'FC' = primary forest corridor, and 'EP' = *Eucalyptus* plantation.

3.3.3 Magnitude of taxonomic and functional diversity responses to anthropogenic modification

The analysis of effect sizes (changes relative to undisturbed forest baseline) showed that all taxonomic and functional diversity metrics performed similarly when used to describe changes in beetle communities in forest corridors and *Eucalyptus* plantations ($p > 0.05$; Figure 3.5).

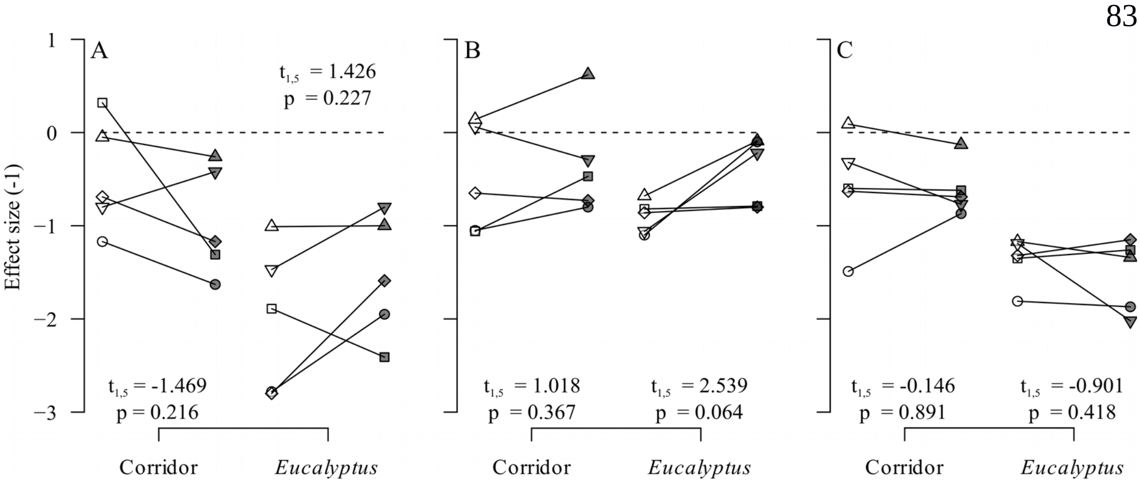

Figure 3.5: Hedge's *g*-value of effect size (times '-1') of taxonomic (white symbols) and functional diversity (grey symbols) for dung beetle species richness and functional richness (A), Pielou's evenness and functional evenness (B), and Simpson's diversity and Rao's quadratic entropy (C), using undisturbed forest sites as a baseline. Full lines connect the values for both approaches in the same year and dashed lines represent no change (zero-value of effect size). Circles, squares, diamonds, triangles and inverted triangles represent effect sizes from 2009 to 2013, respectively.

3.4 DISCUSSION

We evaluated taxonomic and functional diversity metrics as a tool to investigate changes in biodiversity over space and time in three different forest types. When we contrast our results with the initial possible scenarios, we show that all metrics showed similar levels of inter-annual variation across the three forest types, as predicted by scenario A (Figure 3.1A). We also found evidence of higher temporal variation in taxonomic compared to functional metrics, as predicted in scenario F (Figure 3.1F), whereas the sensitivity of taxonomic and functional diversity metrics to anthropogenic forest modification was similar, in line with scenario G (Figure 3.1G). We discuss these findings in the following sections.

3.4.1 Does anthropogenic modification affect inter-annual variation in biological diversity?

In general, we found that human modification of forests did not affect the inter-annual variation of either taxonomic or functional diversity (scenario A). One potential explanation for this result is that the core structure of the communities is shaped by internal filters (e.g. micro-environmental and density-dependent processes; (Violle *et al.* 2012) reducing the consequences of external pressures, such as the severe dry season from 2009 to 2010, which was the main driver of temporal variation in our case (see Thesis Chapter 2). Nonetheless, inter-annual variation of species richness was more similar between forest corridors and *Eucalyptus* plantations than between either modified forest type and undisturbed forest (scenario C). This response could occur if there was a systematic loss of climate-sensitive species with forest disturbance, which would make community dynamics in disturbed areas more sensitive to inter-annual climatic variation compared to undisturbed forest. Thus, this non-random loss does not substantially alter the temporal dynamic of other metrics, even though both forest modifications have already altered dung beetle communities through the loss of poorly adapted and vulnerable species (Mouillot *et al.* 2013; Leitão *et al.* 2016).

The drought from 2009 to 2010 likely had a negative effect on climate-sensitive species and the higher values of FEve in the native forest sites in 2010 were therefore not surprising. Functional and taxonomic evenness can increase following disturbance (Pakeman 2011; Luck, Carter & Smallbone 2013; Hitt & Chambers 2015), because the loss of sensitive specialists results in lower abundances of rare species with rarer combinations of traits (low FRic; Hitt & Chambers 2015). Consequently, the functional similarity of the remaining species and loss of rare species results in greater functional and taxonomic evenness (Pakeman 2011).

3.4.2 Is the inter-annual variation of taxonomic and functional diversity similar?

In general, we observed the pattern of greater temporal stability in functional metrics than taxonomic metrics in undisturbed forests and primary forest corridors, which partially supports scenario F (Figure 3.1F) and reinforces the idea that ecosystems can keep their functional structure in face of those external pressures that do not change the trait-environment relationship (Webb *et al.* 2010). However, we found that conceptually similar taxonomic and functional metrics can differ over time even when both approaches show low overall temporal variation (Flynn *et al.* 2009; Mason & De Bello 2013). For example, the higher variation in the functional evenness (FEve) compared to its taxonomic counterpart (Pielou's evenness) could be due to the loss of a few functionally unique species, which would increase the sensitivity of FEve without changing Pielou's index of taxonomic evenness (Pakeman 2011). As an overall conclusion, taxonomic and functional diversity show different degrees of temporal variation, and as two of the three taxonomic metrics showed greater temporal variation in our study we considered the taxonomic approach is more variable in time. Consequently, functional metrics could be used in long-term research concerned to evaluate changes in community assembly, whereas taxonomic approach could be more sensitive to smaller shifts in community.

Both functional and taxonomic approaches showed similar levels of inter-annual variation in *Eucalyptus* plantations (Figure 3.4), which supports our scenario D that temporal variation in functional and taxonomic metrics will be similar when disturbance is high. The plantations at our study site are constantly managed to intensify timber extraction (e.g. harvesting, fertilization, pest control) and the activities do not happen at all areas at the same time (*personal observation*). Hence, additional disturbances due to management activities likely explain the high between-year and between-site variance (see standard-deviations in Figure 3.1).

3.4.3 Which approach shows higher sensitivity to human-induced changes?

Our findings suggest that taxonomic and functional metrics are equally sensitive at detecting human-induced changes in forests (scenario G). This is at least partly explained by the strong correlation between the values of each pair of metrics (Figure 3.S7). However, although the pairs of metrics in the different forest types showed similar directional patterns of variation between years (Figure 3.3), the magnitude of the response varied among years for the same metric and also between conceptually similar metrics in each year (Figure 3.5). For example, although values of functional and species richness in *Eucalyptus* plantations were consistently lower than in undisturbed forest, the magnitude of the effect was greater for taxonomic compared to functional richness in three out of five years (Figure 3.5A). Thus, temporal variation on diversity components can affect the relationship between equivalent taxonomic and functional metrics under different levels of disturbance and the combination of both approaches will provide useful information to understand the effects of anthropogenic disturbance on community dynamics.

The marginally higher value of Hedge's *g* for FEve compared to Pielou’s evenness in *Eucalyptus* plantation must be interpreted with caution, as it can be partly attributed to the way in which FEve is calculated (Figure 3.5B). FEve does not consider the functional volume (‘convex hull’ in multidimensional trait space), and therefore communities dominated by few functional traits can have species equitably distributed in a reduced functional volume, which would give the same value of FEve as a community with a greater diversity of traits distributed in a larger functional volume (see Villéger et al. 2008 for further explanation and Appendix A in Laliberté &

Legendre 2010 for an example). In intensive land-use changes, such as the replacement of native forest by plantations, we would expect lower abundances of sensitive species and, consequently, a reduction of functional space and range in the community, as indicated by reduced functional richness in *Eucalyptus* plantations in our study (Larsen, Lopera & Forsyth 2008). Therefore, changes in FEve in functionally reduced communities may not be directly comparable to changes in undisturbed communities.

3.4.4 Final considerations

Our study demonstrates the importance of considering inter-annual variation in land-use studies, even in relatively aseasonal humid tropics. Although taxonomic and functional approaches are related to different mechanisms of community change, we found that conceptually similar taxonomic and functional diversity metrics show similar inter-annual variation among forest types. However, the magnitude and direction of community changes differed between the two approaches - both over time and in response to disturbance. Hence, studies of community dynamics using one approach to identify responses to anthropogenic change could differ markedly from a study using the other approach. Thus, we propose that the use of both taxonomic and functional metrics will provide a more complete picture of biological responses to disturbance, and this may be particularly important for evaluating the effects of anthropogenic change over the longer term (e.g. monitoring programs, creation of protected areas; (Mouchet *et al.* 2010; Villéger *et al.* 2010; Gagic *et al.* 2015).

3.5 ACKNOWLEDGEMENT

We thank *Jari Celulose, Papel e Embalagens S/A* for all logistic support, GIS, soil and rainfall data, Irmão, Edvar and Maria for all the support during the fieldwork. Conselho Nacional de Pesquisa e Desenvolvimento (CNPQ) and Fundação de Amparo à Pesquisa do estado de Minas Gerais (FAPEMIG) for funding the project (Site Peld 23). WB thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the PhD scholarship (and BEX 3711-14-15).

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SUPPLEMENTARY MATERIAL APPENDIX 1

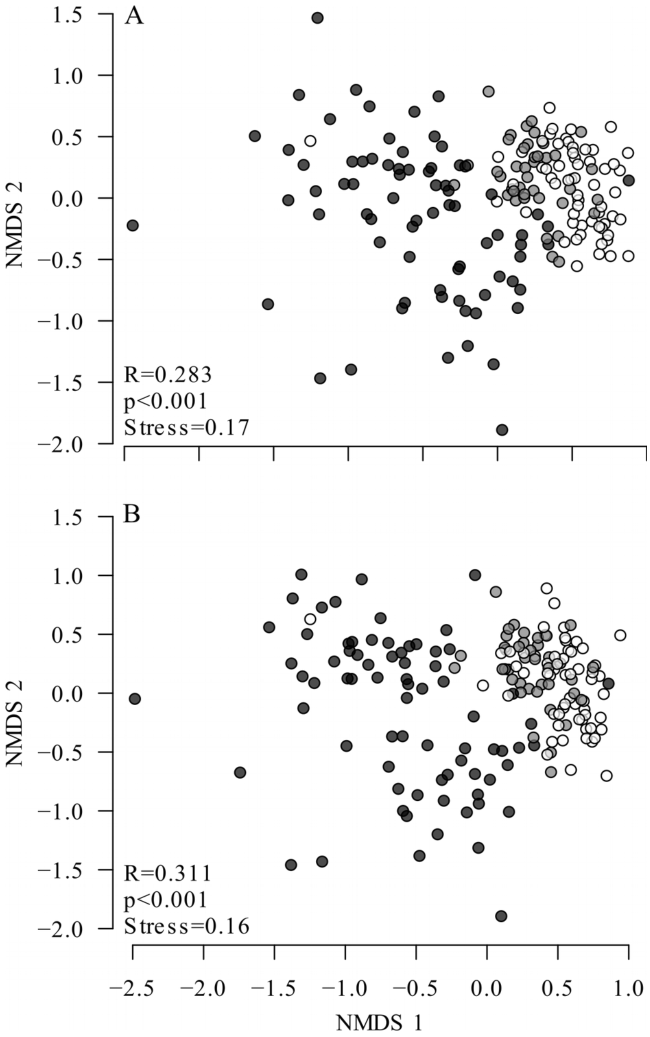

Figure 3.S1: NMDS plot to visualize community composition (A; based on presence-absence and Jaccard's dissimilarity) and structure (B; based on abundance and Bray-curtis' dissimilarity), showing undisturbed forest (white dots), primary forest corridors (light grey) and *Eucalyptus* plantations (dark grey) from 2009-2013. We found significant dissimilarity between undisturbed forest and corridors for composition ($R_{2,175} = 0.138$, $p < 0.001$) and structure ($R_{2,175} = 0.108$, $p < 0.001$); we also found differences comparing *Eucalyptus* plantation to undisturbed forest in both composition ($R_{2,175} = 0.445$, $p < 0.001$) and structure ($R_{2,175} = 0.475$, $p < 0.001$).

SUPPLEMENTARY MATERIAL APPENDIX 2

Table 3.S2: Statistical results of explanatory variables in global models to evaluate taxonomic and functional metrics of diversity changing over years, forest type and their interaction. ‘S’ = species richness, ‘FRic’ = Functional richness, ‘J’ = Pielou’s evenness, ‘FEve’ = Functional evenness, ‘S’ = Simpson’s diversity and ‘FDq’ = Rao’s quadratic entropy.

		Taxonomic metrics		**Functional metrics**		
Response variables	**Explanatory variables**	X^2	p	X^2	p	**df**
S and FRic	Year	147.711	<0.001*	40.398	<0.001*	4,175
	Forest type	106.526	<0.001*	47.061	<0.001*	2,175
	Interaction	33.833	<0.001*	14.736	0.064	8,175
J and FEve	Year	17.746	0.001*	15.080	0.005*	4,175
	Forest type	15.061	<0.001*	4.248	0.120	2,175
	Interaction	3.718	0.882	13.803	0.087	8,175
S and FDq	Year	7.260	0.123	0.904	0.924	4,175
	Forest type	49.418	<0.001*	44.464	<0.001*	2,175
	Interaction	4.250	0.834	2.652	0.954	8,175

SUPPLEMENTARY MATERIAL APPENDIX 3

Table 3.S3: Statistical results of pairwise comparison for species richness in each undisturbed forest (UF), primary forest corridor (FC) and *Eucalyptus* plantation (EP). Stars ('*') indicate significant values ($p<0.05$).

	UF		**FC**		**EP**	
Years	X^2	p	X^2	p	X^2	p
2009-2010	54.924	<0.001*	8.057	0.027*	22.010	<0.001*
2010-2011	11.522	0.006	0.824	0.861	1.535	0.861
2011-2012	1.339	0.861	0.003	0.953	15.284	0.001*
2012-2013	22.719	<0.001*	5.292	0.107	9.643	0.013*

SUPPLEMENTARY MATERIAL APPENDIX 4

Table 3.S4: Statistical results of pairwise comparison for Functional richness (FRic), Pielou's evenness and Functional evenness (FEve) between consecutive years. Stars ('*') indicate significant values ($p<0.05$).

	FRic		**Pielou's evenness**		**FEve**	
Years	X^2	p	X^2	p	X^2	p
2009-2010	21.125	<0.001*	10.228	0.006*	15.125	<0.001*
2010-2011	10.476	0.004*	9.510	0.006*	8.065	0.014*
2011-2012	0.228	0.633	3.749	0.106	1.084	0.298
2012-2013	3.495	0.123	1.751	0.186	2.154	0.284

SUPPLEMENTARY MATERIAL APPENDIX 5

Table 3.S5: Statistical results of comparisons between human-modified forest types and undisturbed forest for those metrics showing significant differences between forest types and similar inter-annual variation. All p-values were corrected by the Holm-Bonferroni method. 'FRic' = Functional richness, ' FDq' = Rao's quadratic entropy, 'FC' = primary forest corridor, 'EP' = *Eucalyptu* plantation, and 'UF' = undisturbed forest.

Metric	**Forest type comparison**	X^2	p	**df**
FRic	FC - UF	6.849	0.009*	1,100
	EP - UF	46.890	<0.001*	1,135
Pielou's evenness	FC - UF	0.687	0.407	1,100
	EP - UF	13.970	<0.001*	1,135
Simpson's diversity	FC - UF	0.315	0.575	1,100
	EP - UF	41.531	<0.001*	1,135
FDq	FC - UF	2.345	0.126	1,100
	EP - UF	41.610	<0.001*	1,135

SUPPLEMENTARY MATERIAL APPENDIX 6

Table 3.S6: Statistical results of comparisons between human-modified forest types and undisturbed forest for species richness All p-values were corrected by the Holm-Bonferroni method.

Metric	**Year**	**Forest type comparison**	X^2	***p***	**df**
Species richness	2009	FC - UF	6.094	0.068	1,20
		EP - UF	68.687	<0.001*	1,27
	2010	FC - UF	0.565	0.904	1,20
		EP - UF	30.127	<0.001*	1,27
	2011	FC - UF	1.213	0.812	1,20
		EP - UF	56.478	<0.001*	1,27
	2012	FC - UF	0.016	0.904	1,20
		EP - UF	9.736	0.011*	1,27
	2013	FC - UF	2.719	0.397	1,20
		EP - UF	23.845	<0.001*	1,27

SUPPLEMENTARY MATERIAL APPENDIX 7

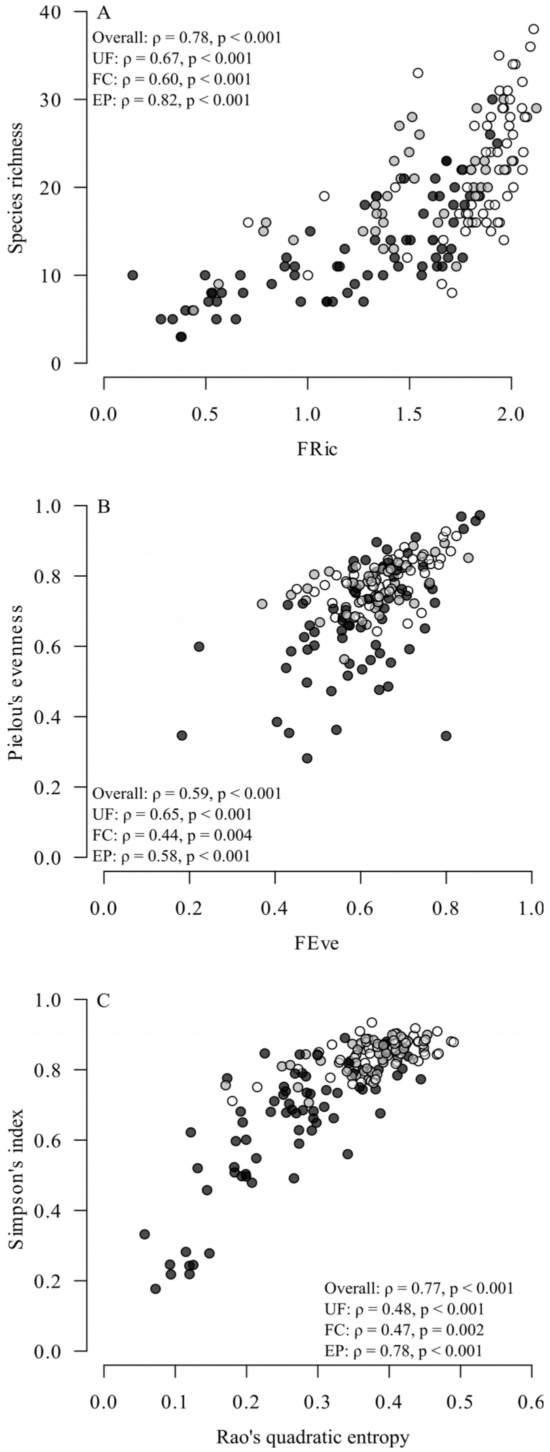

Figure 3.S7: Correlation between equivalent pairs of taxonomic and functional metrics: species richness and Functional richness (A), Pielou's evenness and Functional evenness (B), and Simpson's diversity and Rao's quadratic entropy (C). The correlations were made for all forest types together ('Overall') and also individually for undisturbed forest (UF; white dots), primary forest corridors (FC; light grey dots) and *Eucalyptus* plantation (EP; dark grey dots) separately. We used 1 degree of freedom from 60, 40, 75 and 175 sites for undisturbed forest, primary forest corridors, *Eucalyptus* plantation and the overall correlation, respectively.

Chapter 4

Biodiversity in tropical plantations is influenced by surrounding native vegetation, but not productivity: A case study with dung beetles in Amazonia

Publication status: In preparation to submit in 'Journal of Landscape Ecology'
Format based on the guidelines of 'Journal of Landscape Ecology''

Biodiversity in tropical plantations is influenced by surrounding native vegetation, but not productivity: A case study with dung beetles in Amazonia

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ABSTRACT

Planted forests will be a major component of tropical landscapes in the near future. To conserve biodiversity across modified tropical landscapes we must first understand what determines biodiversity in forest plantations. We used a study of dung beetle communities in *Eucalyptus* plantations to assess the influence of local and landscape factors on taxonomic and functional diversity and to determine whether biodiversity in plantations is related to timber production. Simpson's diversity, functional diversity, and functional uniqueness of dung beetle communities in *Eucalyptus* plantations were strongly and positively related to the amount of surrounding native forest. Functional similarity between planted and native forests also increased with the extent of natural forest cover. The total abundance of dung beetles in plantations was positively related to coarse sand content in the soil, but negatively related to canopy openness. Coarse sand content also explained a large proportion of the variation in dung beetle community composition and structure. whereas canopy openness only explained a small proportion of the variation in community composition. The number of species shared between *Eucalyptus* and native forests was negatively correlated with canopy openness but timber production did not explain the variation in any of the measured diversity parameters. These results highlight the importance of restoring or retaining native forest areas in modified landscapes to enhance biodiversity in plantations, and suggest that integrative management could improve biodiversity without negative influences on production. Future work should assess whether plantations are a viable habitat for dung beetle species and to what extent increased functional diversity enhances ecosystem functioning in tropical plantations.

Keywords: Scarabaeinae, silviculture, land-sharing, land-sparing, forestry, functional diversity

4.1 INTRODUCTION

Planted forests are rapidly expanding at a rate of around 5 million ha per year and tropical landscapes are particularly heavily affected by this expansion due to the growing demand for forest products (e.g. timber, cellulose, oils; (FAO 2010, Vijay et al. 2016). For example, the area of *Eucalyptus* plantations in Brazil was around 6 million ha in 2014, which is 100,000 ha more than in the previous year (IBGE 2014, Ibá 2015). The expansion of these silvicultural systems contributes to the worldwide loss of biodiversity and the decline of many ecosystem functions and services (Sala 2000, Green 2005, Newbold et al. 2014). To minimise these losses, it is important to assess how to maximise the biodiversity and functional value of the human-modified regions that are likely to cover most of the globe in the near future (Franklin and Lindenmayer 2009).

Despite the known negative impacts of some plantations, there is a growing interest in the value of forested production systems for maintaining biodiversity (Barlow et al. 2007). This is encouraged by the possibility of land-sharing, where biodiversity conservation can take place within production systems (Paul and Knoke 2015). A growing number of studies show how some faunal taxa can persist in tropical crops that emulate structural aspects of native forests and/or landscapes, including cocoa agroforestry (Schroth and Harvey 2007, Cassano et al. 2012), oil palm (Koh and Wilcove 2008, Gray et al. 2014, Dislich et al. *in press*), coffee plantations (Tadesse et al. 2014), and timber monocultures (Barlow et al. 2007). Importantly, such cited studies suggest that both local conditions, such as structural complexity or canopy cover, and landscape context, such as proximity to remnants of native forests, can enhance the biodiversity in plantations. Moreover, in some cases, native species from forest remnants can even improve ecosystem functioning within modified areas (Blitzer et al. 2012).

Despite advances in our understanding of biodiversity conservation in the tropics, efforts to make plantations more sustainable (e.g. certification by the Forest Stewardship Council) are undermined by a lack of knowledge about what determines biodiversity in forest plantations. In part, this lack of information has arisen because most studies assessing tropical biodiversity focus on the remaining patches of native vegetation instead of the production matrix (Carnus et al. 2006, Franklin and Lindenmayer 2009). Hence, although plantations are frequently established near or within areas of native forest, the relative importance of local conditions vs. the extent and proximity of nearby natural habitats is not always clear. Furthermore, most studies of biodiversity in tropical plantations to date have focused on species diversity, but we know very little about changes in functional diversity following forest modification. Finally, it is not clear whether there are trade-offs between creating the conditions required to maintain biodiversity and increasing plantation yield.

We aimed to assess the influence of local and landscape factors on biodiversity in *Eucalyptus* plantations set in a matrix of primary Amazonian forest in Brazil, using dung beetles as a focal organism. Dung beetles provide a useful indicator to assess the effects of habitat modification because many species show a high degree of habitat specificity and are sensitive to environmental modifications in tropical forests (Spector and Ayzama 2003, Larsen et al. 2006, Nichols et al. 2007, 2009). Dung beetles can also be examined from both taxonomic and functional perspectives, as they form distinct functional groups, which can be determined by measurable functional or behavioural traits (Barragán et al. 2011, Slade et al. 2011, Nichols et al. 2013). Our study compared dung beetle communities between *Eucalyptus* plantations and native forest sites, and determined the area of undisturbed forest habitat within a landscape around each plantation site to test the following hypotheses:

1) Plantations that have similar environmental conditions to native forests will also have comparable communities of dung beetles. Here, we used canopy openness as a key environmental variable, as more open canopies are associated with higher temperatures and lower levels of humidity in air and soil, which negatively affect many dung beetle species (Gardner et al. 2008, Larsen 2012, Hosaka et al. 2014).

2) Dung beetle communities in plantations depend on colonisation from source populations in native forests, and the communities in *Eucalyptus* plantations at our study site mainly represent a subset of native forest communities (Louzada et al. 2010). Accordingly, the diversity and structure of dung beetle communities in plantations will be related to the amount of native forest cover in the surrounding landscape. We expect that plantations with a high proportion of surrounding native forest cover will have a higher diversity of dung beetles and communities with a composition and structure similar to those in primary forest.

3) There will be a negative relationship between timber production and dung beetle diversity metrics, based on the premise that the intensification of production and the suppression of native vegetation will have negative impacts on biodiversity (Flohre et al. 2011).

4.2 MATERIAL AND METHODS

4.2.1 Study site

Our data was collected in the Jari River basin in the north-eastern Brazilian Amazon, on the border between Pará and Amapá States (00°27′00″ - 01°30′00″ S, 51°40′00″ - 53°20′00″ W). The area has a mean annual temperature of 26.9 ±0.6°C, with mean maxima and minima of 31.4 ±1.1°C and 22.5 ±0.2°C, respectively (Climate-Data.org 2016). It has a tropical monsoon climate, with a marked wet season from January to June, a distinct dry season from September to November, and an average annual rainfall of 2115 mm (Amw in Köppen climate classification; Coutinho and Pires 1997; Parry et al. 2007). The intensive replacement of native forest by exotic tree plantations started in 1967 and the area is now a continuous block of virtually undisturbed *terra firme* primary forest (> 5000 km^2) connected by primary forest corridors (c. 200 m wide) with large patches of exotic tree plantations, mainly *Eucalyptus* sp. (450 km^2; Figure 4.1; Coutinho and Pires 1997; Parry et al. 2007).

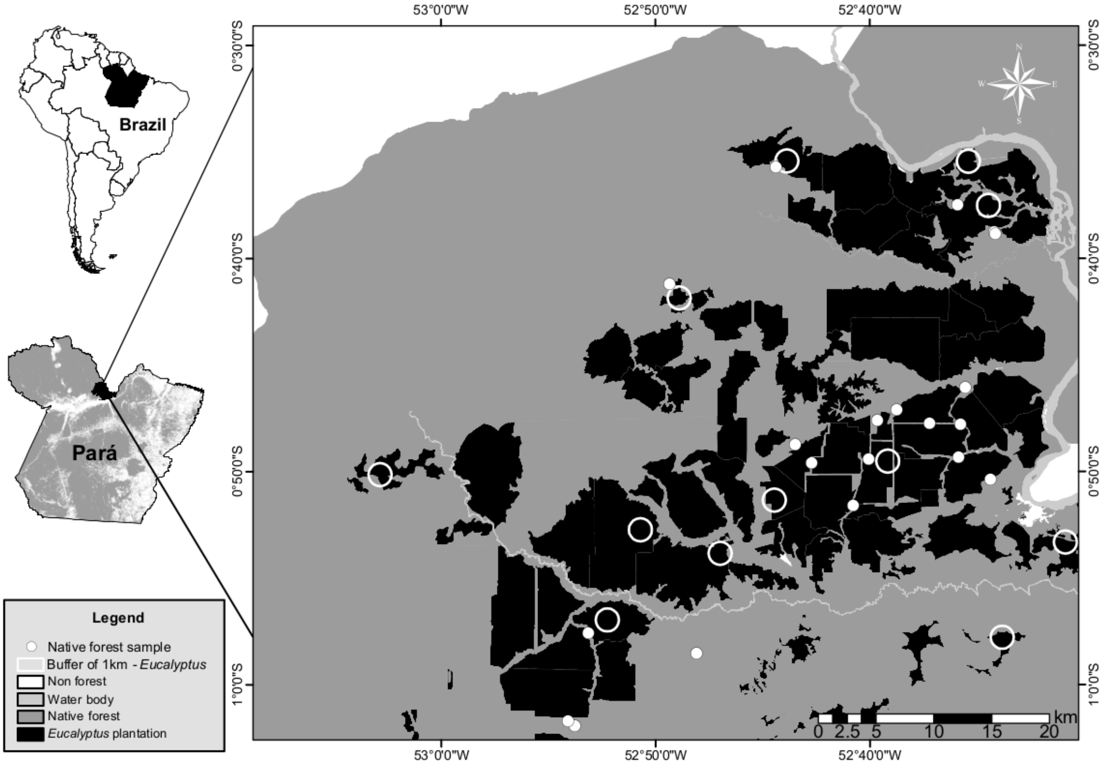

Figure 4.1: Location of sampling sites in and buffers around *Eucalyptus* plantation (white open circles) and reference sites in native forest (white dots) within the Jari River basin in Pará State, Brazil.

4.2.2 Dung beetle sampling

We sampled dung beetles during March and April 2009. The annual rainfall in 2009 was considered high for the region with 2081 mm during the wet season and 153 mm in the previous dry season (mean dry season rainfall from 2008 to 2013 was 113 mm). We sampled dung beetles in 12 *Eucalyptus* plantations, varying in age from 2–5 years (stands are harvested after 5–7 years). *Eucalyptus* sites were cleared, burned and bulldozed from the early 1970's to 1980's and all native vegetation colonizing the understorey is periodically cleared or suppressed by herbicidal treatment (Louzada et al. 2010). The distance between plantation sites and the nearest patch of native forest ranged from 0.2 to 1.6 km. We also sampled in eight primary forest corridors and 12 areas of undisturbed primary forest; we considered these collectively as sites of 'native forest', independently of their landscape configuration, as they could both facilitate colonisation into the plantations. Furthermore, although the community structure of dung beetles differs between forest corridors and undisturbed forest sites (Barlow et al. 2007), they are comparatively much more similar to undisturbed forest than plantations (Thesis Chapter 3).

At each site, we set up one transect of five pitfalls traps, located 150 m apart and at least 500 m from the edge. The traps consisted of plastic containers (19 cm diameter and 11 cm deep), which were part-filled with water, salt, and detergent, baited with 30 g of human dung, and protected from rain with a plastic lid suspended 20 cm above the surface. Sampling took place over a period of 48 hours at each sampling site. Dung beetle specimens were transported from the field in 90% alcohol, and then sorted and stored in paper envelopes in the laboratory. We identified the dung beetles using the New World Scarabaeinae key to genera and subgenera (Vaz-De-Mello et al. 2011), a field guide for dung beetles in the Jari River basin (Louzada et al. *in prep.*), and the reference collection 'Coleção de Referência de Escarabeíneos Neotropicais' at the Universidade Federal de Lavras (CREN – UFLA) in Minas Gerais State, Brazil. Identifications were made to species level where possible; where there was uncertainty beetles were identified to genus level, and assigned a morphospecies number. All specimens were deposited at CREN – UFLA.

We obtained information on dung beetle functional groups based with two independent surveys, in January and February 2012, and in November and December 2013 (see Thesis Chapter 2 for details). The beetles were grouped by activity period, dietary preference and nesting behaviour. To determine activity period (diurnal or nocturnal) we sampled beetles from 7:00 to 18:00 and from 19:00 to 6:00, respectively. To assess dietary preference (coprophagous, necrophagous, or generalists) we baited the pitfall traps with dung and carrion and assigned the species based on their occurrence in the different baits. Finally, beetles were classed as rollers (telecoprids), tunnelers (paracoprids), or dwellers (endocoprids), based on their genus. We obtained average species body mass using the mean dry mass of 15 individuals of each species oven-dried for 48 h in 40 ºC, for species with few sampled individuals we used additional specimens previously deposited at CREN – UFLA.

4.2.3 Explanatory variables

To estimate canopy openness we took semi-hemispheric photographs of forest canopy also in 2009 at 1.5-m above ground level at each pitfall trap location and analysed the images in gap light analyser (GLA) software to obtain the percentage openness (Frazer et al. 1999); canopy openness was not correlated to *Eucalyptus* tree age (r = 0.187, p = 0.560; Sup.1). We estimated the percentage of native forest cover within a 1-km buffer surrounding each sampling point in *Eucalyptus* plantations using GIS data provided by the landowner. The size of the buffer was determined based on previous studies of dung beetles movement (Silva and Hernández 2015) to give a realistic distance for recolonisation of disturbed areas within 1-2 years. Timber production was calculated from data provided by the landowner in tons of timber produced per hectare and corrected for the age of the trees at harvest (t ha^{-1} age^{-1}). Finally, we also determined the coarse sand content (g kg^{-1}) using soil samples collected from 0-10 cm depth at each site in 2013.

4.2.4 Data analysis

All analyses were conducted in R version 3.3.0 (R Core Team 2016) and in PRIMER version 6.0 using the PERMANOVA+ add-on (Clarke and Gorley 2006). All environmental variables were standardised to zero mean and unit standard deviation prior to analysis. We analysed data from *Eucalyptus* plantation plots using the native forest data as a reference, but we did not make direct comparisons between plantations and native forest sites.

To assess the composition and structure of dung beetle communities at each site, we calculated Jaccard's dissimilarity based on presence-absence data, and Bray-Curtis' dissimilarity based on number of individuals per species, using the *vegdist* function in the *vegan* package (Oksanen et al. 2016). Total dung beetle abundance and species richness were determined from the number of individuals and (morpho-) species at each *Eucalyptus* site. The total body mass of dung beetles at each site was determined by summing the abundance-weighted mean body mass of each species. We calculated the Simpson's diversity index (1-D) for each sampling site using the *diversity* function in the *vegan* package and the conceptually similar Rao's index (FDq) using the function *mpd* in the *picante* package (Kembel et al. 2010). FDq was calculated using beetle functional groups as categorical traits and the log-transformed data of mean species body mass as a continuous trait. These indices give a combined measure of taxonomic (Simpson's diversity) and functional (FDq) diversity and evenness. Finally, functional uniqueness (FUni) was calculated as the ratio between FDq and Simpson's diversity to assess the occurrence of unique species with a certain set of traits (Ricotta et al. 2016).

The taxonomic diversity shared between *Eucalyptus* plantations and native forests was evaluated using the proportion of species in *Eucalyptus* sites that were also found in native forest areas. We pooled all species from native sites, and calculated the number of shared species with each *Eucalyptus* plantation site using the *shared* function in the *rich* package (Rossi 2011). The shared functional diversity between *Eucalyptus* plantation and the native forest species pool was considered equal to functional β-diversity based on the partitioning of FDq using the *Rao* function (De Bello et al. 2010, Ricotta et al. 2011).

To evaluate the influence of environmental variables on biodiversity metrics, we built a distance-based linear model (DistLM) for dung beetle community composition and structure; we used generalised linear models (GLM) with a negative binomial error distribution for species abundance *(glm.nb* function of the MASS package; Venables and Ripley 2002), a quasi-Poisson distribution for species richness, and a Gaussian distribution for body mass, Simpson's diversity, FDq and Funi. All full models included canopy openness and forest cover as explanatory variables and coarse sand content as a covariate. We selected the best models for each response variable based on their AICc values using the *dredge* function in the *MuMIn* package (Bartoń 2016). As models for species richness were fitted using a quasi-Poisson error distribution, they were evaluated using quasi-AICc values (QAICc). We checked for collinearity among explanatory variables using the variance inflation factor (VIF), and we did not detect significant collinearity (VIF ≤ 2.16 in all cases).

To test if shared species and functional β-diversity between native and exotic forests were predicted by environmental variables we built a GLM with a quasi-binomial distribution for the proportion of species shared between *Eucalyptus* plantation and the native forest species pool, weighted by the total number of species in the *Eucalyptus* plantations. We used GLM with Gaussian distribution to test whether functional β-diversity was predicted by environmental variables. We used the same explanatory variables and model selection process as described above.

We evaluated the influence of timber production by adding it as the first explanatory variable in the best-fit model for each biodiversity metric with the other variables as co-variates and checked for model improvement using AICc values. For all final models, we calculated the percentage of explanatory power of each variable. For DistLM and GLMs with Gaussian error distribution, we used the r-squared (R^2) calculated from the sum of squares of each variable divided by the total sum of squares, and for GLMs with other error distributions, we used the *pseudo*-R^2 calculated from the deviance of each variable divided by the residual deviance of the null model.

4.3 RESULTS

We sampled 8,324 individuals of dung beetles from 89 species in the study area, 43 of which were labelled as morphospecies. In *Eucalyptus* plantations, we recorded 1,995 individuals of 50 species, and in native forests we sampled 6,329 individuals of 78 species. The number of shared species between *Eucalyptus* plantations and native forest plots ranged from 55% to 100%, with a mean of 86 ±13%. We obtained information to assign 8,218 individuals from 69 (morpho-) species to functional groups (99% of the total individuals and 78% of all morphospecies). When dung beetles were grouped by dietary preference, 72% were coprophagous (5,219 individuals of 50 species), 12% were necrophagous (467 individuals of 11 species) and 16% were generalists (2,532 individuals of 8 species). Regarding nesting behaviour, 58% were tunnelers (6,099 individuals of 40 species), 26% were rollers (1,056 individuals of 18 species) and 16% were dwellers (1,063 individuals of 11 species). We were able to assign activity period to 60 species, of which 55% (3,971 individuals of 33 species) were diurnal and the remaining 45% (3,913 individuals of 27 species) were nocturnal.

Although coarse sand content is not amenable to management practices, it explained a high proportion of the variation in dung beetle community composition (20.4%), community structure (34.0%) and abundance increased with coarse sand content (40.9%, Table 4.1, Figure 4.2). Canopy openness explained little of the variation in dung beetle community composition (14.3%) but abundance declined with increasing canopy openness (17%, Table 4.1; Figure 4.2), but there was no relationship between canopy openness and any other diversity metrics. None of the explanatory variables predicted variation in body mass or species richness (Table 4.1; Figure 4.2). However, the proportion of species shared between *Eucalyptus* plantations and native forest declined with increasing canopy openness (27.0%, Table 4.1, Figure 4.3). FDq, Simpson's diversity and FUni all increased with the proportion of forest cover surrounding the plantations; forest cover predicted 82.4% of the variation in FDq, 42.2% of the variation in Simpson's diversity, 28.7% of the variation in FUni, and 12.0% of the variation in community composition (Table 4.1, Figure 4.1 and 2). Surrounding native forest cover of around 20% was sufficient for Simpson's diversity and FDq values in plantations to approach the mean values for native forests, whereas FUni in plantations was similar to native forest values with a surrounding forest cover of *c.* 12% (Figure 4.3). Only functional β-diversity declined with forest cover (60.7% variation explained, Table 4.1, Figure 4.3) and none of the explanatory variables predicted variation in body mass or species richness (Table 4.1).

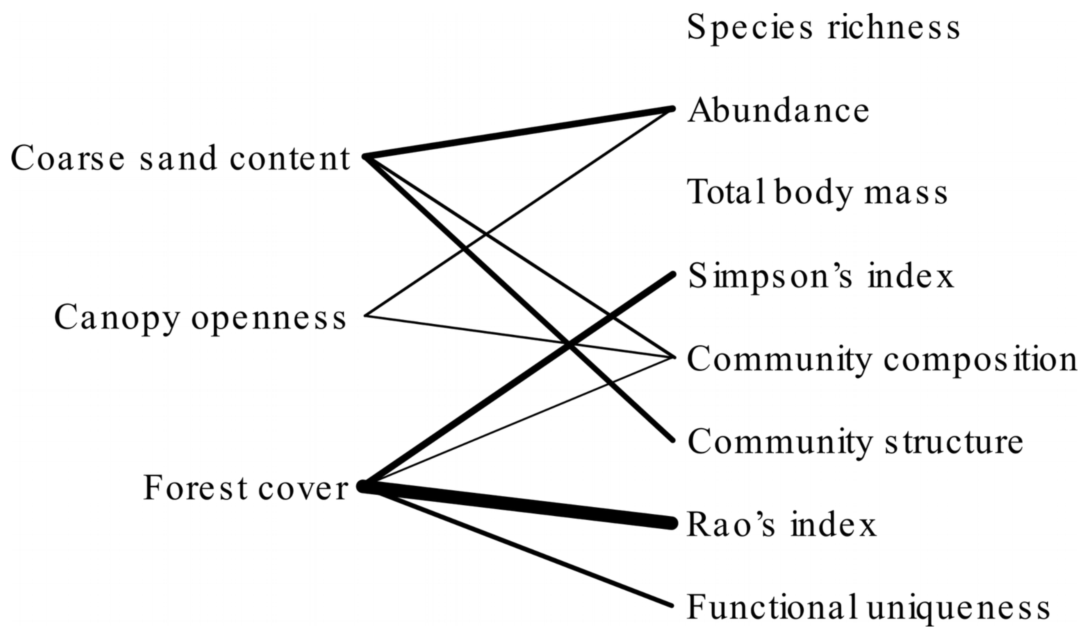

Figure 4.2. Explanatory variables (left) and response variables (right) of final models with ΔAICc ≤ 2; the line width is directly proportional to the variance explained by explanatory variables and the absence of connecting line indicates no explanation by measured variables.

Table 4.1: Best selected models based on AICc for each response variable with explanatory variables. 'CO' = Canopy openness, 'CS' = Coarse sand content, 'FC' = Forest cover and '*w*' = Akaike weight for each model. Bold font highlights the models with ΔAICc < 2. *Quasi-AICc for species richness.

Response variable	Model	AICc	ΔAICc	*w*	Cumulative *w*
Species richness*	**NULL**	**34.67**	**0.00**	**0.641**	**0.641**
	CO	38.08	3.41	0.116	0.757
	FC	38.27	3.60	0.106	0.863
	CS	38.33	3.66	0.103	0.966
Abundance	**CS**	**145.53**	**0.00**	**0.415**	**0.415**
	CO + CS	**146.04**	**0.51**	**0.321**	**0.736**
	NULL	148.50	2.97	0.094	0.830
	FC	148.77	3.24	0.082	0.912
Total body mass	**NULL**	**97.19**	**0.00**	**0.636**	**0.636**
	CS	100.68	3.49	0.111	0.747
	CO	100.69	3.50	0.110	0.857
	FC	100.70	3.51	0.110	0.967
Simpson's diversity index	**FC**	**-6.69**	**0.00**	**0.556**	**0.556**
	NULL	-3.76	2.92	0.129	0.685
	CO + FC	-3.20	3.49	0.097	0.782
	CS	-2.82	3.87	0.080	0.863
	CO	-2.34	4.34	0.063	0.926
Community composition	**CS**	**96.85**	**0.00**	**0.338**	**0.338**
	CO	**97.73**	**0.88**	**0.217**	**0.555**
	FC	**98.05**	**1.20**	**0.185**	**0.740**
	FC + CS	99.42	2.57	0.093	0.834
	CO + CS	99.55	2.70	0.088	0.921
Community structure	**CS**	**93.01**	**0.00**	**0.429**	**0.429**
	FC + CS	95.28	2.27	0.137	0.566
	CO	95.42	2.41	0.128	0.694
	CO + CS	95.53	2.53	0.121	0.816
	FC	95.73	2.73	0.110	0.925
Rao's quadratic entropy	**FC**	**-33.96**	**0.00**	**0.795**	**0.795**
	FC + CS	-30.22	3.74	0.122	0.917
Functional uniqueness	**FC**	**-18.86**	**0.00**	**0.391**	**0.391**
	NULL	-18.46	0.40	0.320	0.710
	CS	-16.05	2.81	0.096	0.806
	CO + FC	-15.48	3.38	0.072	0.878
	CO	-14.93	3.92	0.055	0.933
Species shared with native forest	**CO**	**39.70**	**0.00**	**0.433**	**0.433**
	NULL	**40.20**	**0.55**	**0.330**	**0.763**
	CO + CS	43.20	3.53	0.074	0.837
	FC	43.70	4.05	0.057	0.894
	CS	43.80	4.14	0.055	0.949
Functional β-diversity	**FC**	**62.60**	**0.00**	**0.515**	**0.515**
	FC + CS	**63.80**	**1.16**	**0.288**	**0.803**
	CS	66.00	3.33	0.097	0.900

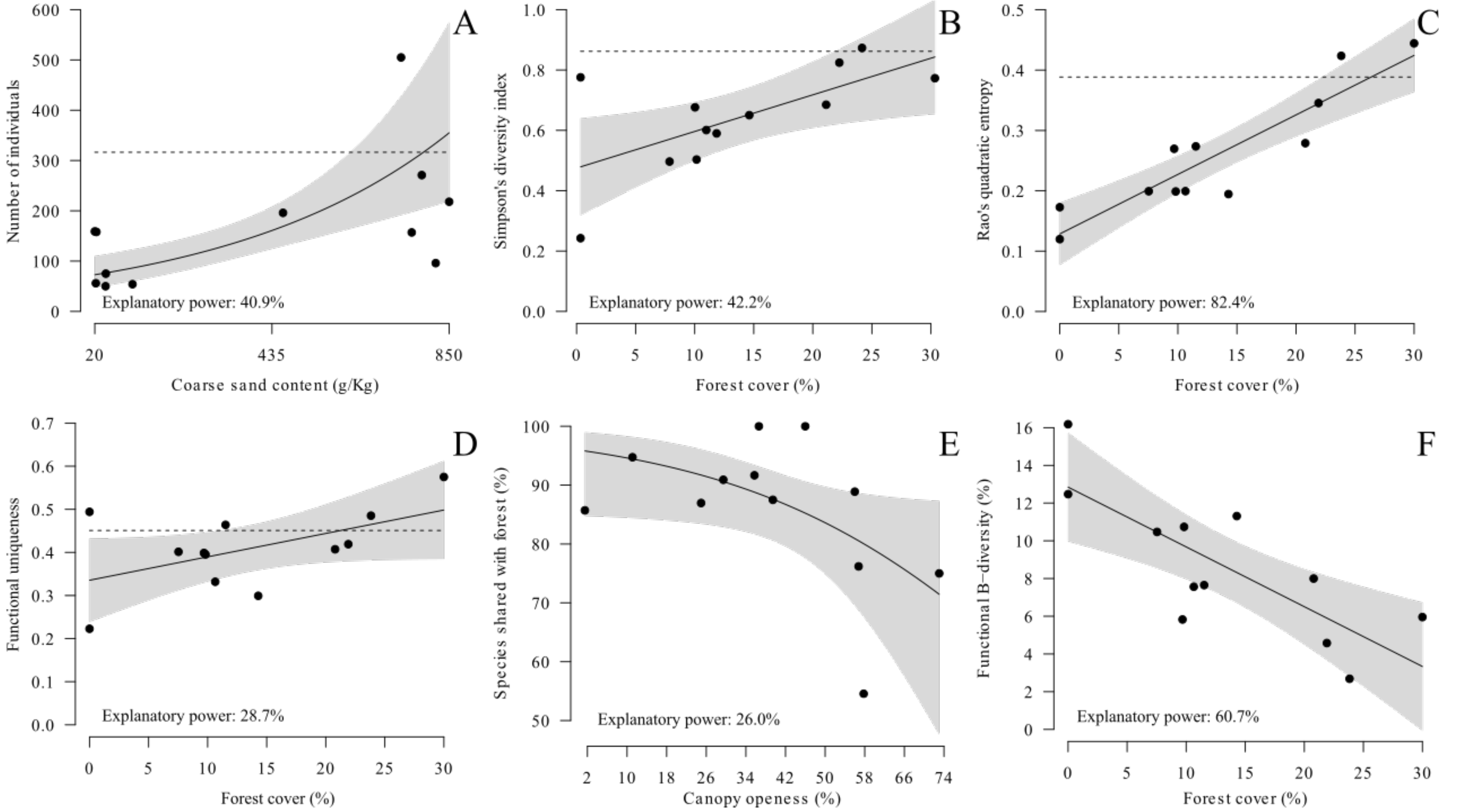

Figure 4.3: Factors explaining (A) dung beetle abundance, (B) Simpson’s diversity index, (C) Rao’s index, and (D) functional uniqueness in *Eucalyptus* plantation, as well as the (E) number of species shared between *Eucalyptus* plantation and native forest, and (F) functional β-diversity for dung beetles communities in *Eucalyptus* plantation in relation to native forest. The solid lines represent the predictive model, the shaded areas the confidence intervals and the dashed lines represent the average value of native forest areas.

We did not find clear effect of timber yield on dung beetle diversity; adding timber production to the models weakened the best-fit models for all response variables and inflated AICc and QAICc values (Figure 4.4).

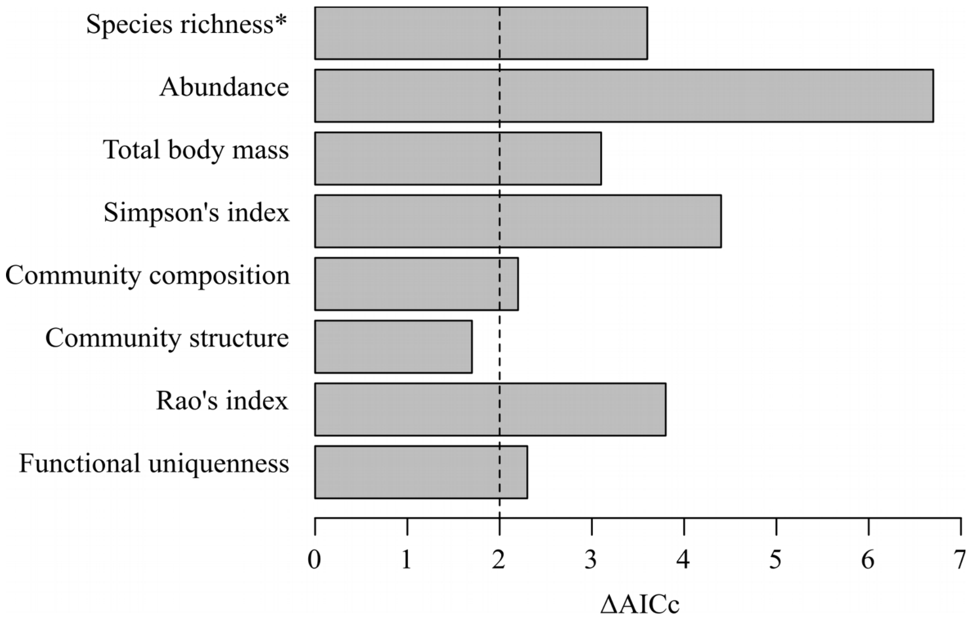

Figure 4.4: Variation in AICc (ΔAICc; grey bars) after adding timber production as an explanatory variable for the best-fit models. The dashed line shows the threshold of ΔAICc ≤ 2. * For species richness we calculated the quasi-AICc value.

4.4. DISCUSSION

We evaluated how local forest structure (canopy openness) and landscape context (extent of surrounding native forest) influence the taxonomic and functional diversity of dung beetles in *Eucalyptus* plantations. Our hypothesis relating canopy openness to dung beetle diversity was not strongly supported, as the negative influence of higher canopy openness on dung beetle abundance was weak and there was only a marginal influence on community composition. However, we found strong support for our hypothesis on the important role of landscape context, as the proportion of native forest cover surrounding *Eucalyptus* plantations was strongly and positively related to taxonomic and functional diversity, as well as the functional uniqueness of the dung beetle communities. Finally, our data did not support our hypothesis of a negative relationship between timber production and dung beetle diversity or composition.

4.4.1 Influence of local and landscape variables on dung beetle biodiversity in plantations

As expected, dung beetle species composition was related to differences in all measured environmental variables (coarse sand content, canopy openness and forest cover), but these relationships only explained a relatively small portion of the variation in community composition (Figure 4.2). Instead, dung beetle community structure and abundance was strongly related to coarse sand content in the soil. This matches results from undisturbed forest sites in the same region (Thesis Chapter 2; Figure 4.2 and 3), and could be related to nesting requirements because sand content is likely to influence the survival rate of the offspring of tunnelling dung beetles, which nest in a humid zone of sandy soils (Hanski and Cambefort 1991, Osberg et al. 1993, Davis et al. 2010). Although coarse sand content is not amenable to plantation management, it is nonetheless relevant in this context because soil texture and/or fertility could also be an important factor determining the suitability of an area for plantations and the extent of the required management (Zinn et al. 2002, Touré et al. 2013).

The lack of a strong relationship between canopy openness and dung beetle community metrics might be due to compensatory effects of native vegetation in the understorey, which could maintain a more favourable microclimate in the soil (Xiong et al. 2008, Wu et al. 2011). Nonetheless, plantations with a greater degree of canopy closure were associated with a higher probability of occurrence of native forest species (Figure 4.3), which may be due to increased abundance of diurnal beetle species in areas with lower desiccation risk (Larsen 2012, Nichols et al. 2013). As older plantations in our study did not necessarily have a more closed canopy, we suggest that management to increase canopy cover could enhance the conservation value of plantations for forest dung beetle species. However, this option must be carefully assessed to avoid loss of production due to competition among plantation trees.

Our results provide strong support for the important role played by landscape context, as the amount of native forest surrounding *Eucalyptus* plantations was associated with higher taxonomic and functional diversity as well as greater functional uniqueness of dung beetles in the plantations (Figure 4.3). There are two main mechanisms by which native forest extent could be important for increasing dung beetle biodiversity in plantations: First, there may be a spill-over effect, where the increase in forest cover reduces the distance between the sampled plantation areas and the nearest patch of native forest (Fahrig 2003). This increases the probability of collecting individuals from native forest that are foraging in *Eucalyptus* sites, as proposed in a previous study evaluating the influence of dung beetles from native riparian corridors on communities in oil palm tree plantation (Gray et al. 2014). Second, a greater proportion of primary forest cover close to plantations could improve the connectivity between native forest patches in landscape (Fahrig 2003), which would increase the movement of forest species through the plantation.

The mechanism underpinning the presence of forest species in plantations has important implications for their conservation value and needs further study. On the one hand, these findings could indicate that increased forest cover, rather than a matrix of open habitat, would improve species migration into or through plantations (Arellano et al. 2013), and facilitate the movement of forest species between native forest patches. On the other hand, plantations could function as ‘sink’ habitats for populations of native species; this would occur if mortality rates exceed birth rates and plantations are unable to sustain viable populations without repeated colonisation from native forests (Hansen and DeFries 2007). In this case, high levels of biodiversity within plantations could have negative connotations, as plantations would represent ecological traps for native forest species (Kokko and Sutherland 2001, Schlaepfer et al. 2002).

The extent of forest cover was related to greater functional similarity between native forest and exotic plantation (decreased functional β-diversity; Figure 4.3), as hypothesized. The number of potentially sensitive species with unique combinations of traits (represented by FUni; Figure 4.3) also increased with forest cover, resulting in greater functional diversity (FDq; Figure 4.3), as expected. Further studies are necessary to evaluate other properties of dung beetle communities (e.g. resistance and resilience to change), as well as the short- and long-term potential for plantations to sustain more diverse communities of dung beetles. However, our results indicate that dung beetle communities in plantations surrounded by a matrix of native forests can include rare and sensitive species and therefore have the potential to sustain their role in ecosystem functioning (Ricotta et al. 2016, Leitão et al. 2016). The inclusion of forest species in plantations could also increase or restore ecosystem processes affected by land-use change, by increasing functional diversity (Chacoff and Aizen 2006, Rand et al. 2006, Firbank et al. 2008, Blitzer et al. 2012).

4.4.2 Is there a trade-off between timber production and biodiversity conservation within plantations?

We did not find a relationship between timber production and any of the studied dung beetles community metrics (Figure 4.4). This suggests that plantations could potentially be managed to deliver both high yields and biodiversity conservation, therefore supporting the idea of ‘land-sharing’. However, much of the biodiversity within plantations was supported by the colonisation from the native forests, so our results also highlight the importance of 'land-sparing', as the native habitats are important for supporting source populations. Thus, we suggest that the dichotomy 'land-sharing/land-sparing' may not be the most fruitful debate, as wildlife-friendly habitats, favourable surrounding habitats, and large protected areas are not mutually exclusive (Kremen 2015).

4.4.3 Final considerations

Although plantations with just 20-30% of native forest cover in the surrounding buffer had a similar functional diversity to primary forest areas, the 1-km buffer considered in our study does not consider the fact that all sites were set within a much larger continuous area of native forest, which is likely to maintain diversity in forest patches (Martensen et al. 2012, Numa et al. 2012). It is therefore crucial that we maintain the extent of forest cover required by the current Brazilian forest code, which mandates the conservation of up to 80% of forest by landowners in the Legal Amazon region (Brasil 2012). We hope that our study will encourage the debate about how to enhance biodiversity and its intrinsic values in human-modified landscapes under different contexts, and provide information to improve land-use laws and create feasible management strategies.

Our findings suggest that the surrounding cover of native habitat is likely to improve taxonomic and functional diversity by facilitating the movement of forest species into plantation areas. However, further studies are required to understand the sustainability of dung beetle populations within plantations and to determine whether the functional diversity of dung beetle communities enhances ecosystem functioning.

4.5 ACKNOWLEDGEMENT

We thank *Grupo Jari*, especially Davi for logistic support, GIS , soil and rainfall and timber production data, Irmão, Edvar and Maria for support during the fieldwork. Conselho Nacional de Pesquisa e Desenvolvimento (CNPQ) and Fundação de Amparo à Pesquisa do estado de Minas Gerais (FAPEMIG) for funding the project (Site Peld 23). WB thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the PhD scholarship (and BEX 3711-14-15).

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4.7 SUPPLEMENTARY MATERIAL

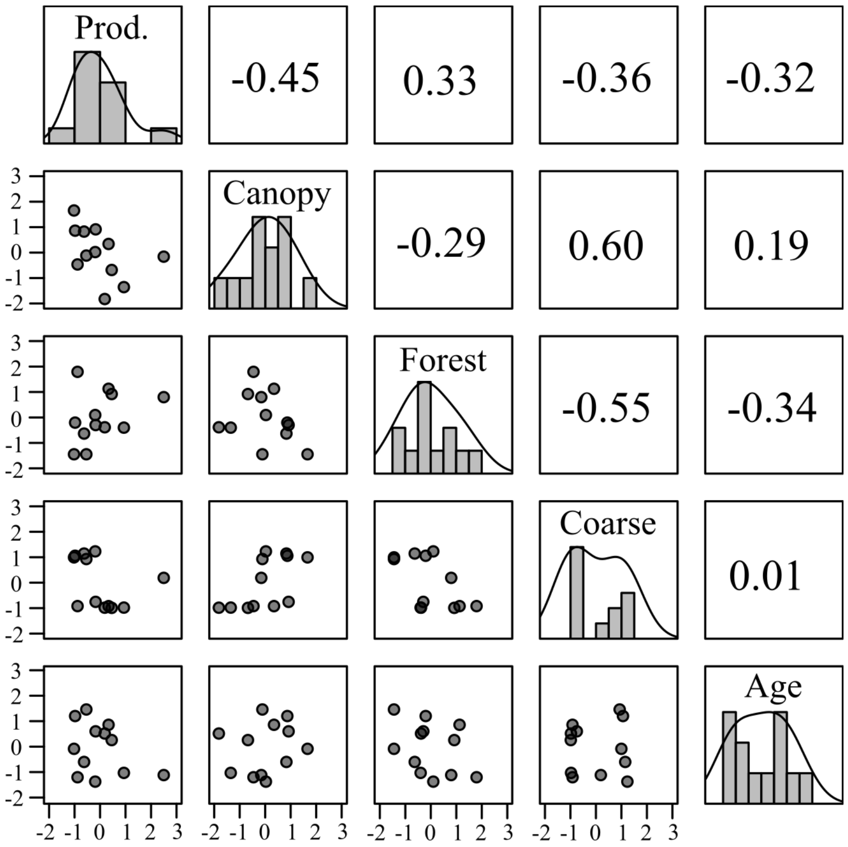

Figure 4.S1: Pearson correlations among standardized values of explanatory variables and age of *Eucalyptus* trees. 'Prod.' is timber production, 'Canopy' is canopy openness, 'Forest' is forest cover, 'Coarse' is coarse sand content and 'Age' is for trees' age.

Chapter 5

General discussion

In this thesis, I aimed to understand and explore the effects of human-induced changes and inter-annual variation on dung beetle communities in both natural and anthropogenic forest types in the tropics. I used detailed data on dung beetle communities in the Brazilian Amazon collected over a period of five years, combined with the development of a trait database, to calculate both taxonomic and functional indices to describe the beetle communities. Overall, I showed that using taxonomic and functional diversity together provides a more comprehensive assessment of biodiversity responses in human-modified systems, which can help to inform landscape management. Although the relationship between biodiversity and environmental variables are complex, the combined study of different components of diversity can help to avoid potentially misleading conclusions and greater clarification of results can be achieved using the different, but complementary, perspectives and interpretation of taxonomic and functional diversity (e.g. NUNES et al., 2016; VILLÉGER et al., 2010). Taxonomic diversity is evaluated at species-level, in other words, each species is considered as an ecological unit with similar influence on ecosystem processes, whereas functional diversity is a trait-based approach, which considers the role of each species in a given ecosystem process in relation to their traits, regardless of their taxonomic similarity (TILMAN, 2001). Thus, in using both approaches, I was able to gain insights into the links between the taxonomic and functional diversity of dung beetle communities and assess how each responds to natural environmental variation and human disturbance. In the following section, I highlight the key findings of each chapter and examine the management and research implications.

5.1 KEY FINDINGS AND THEIR SCIENTIFIC IMPACTS AND IMPLICATIONS

5.1.1 Chapter 2 – Dung beetle community dynamics in undisturbed tropical forests: implications for ecological evaluations of land-use change

The aim of this chapter was to evaluate both spatial and temporal variation of dung beetles communities in undisturbed forests to provide a ‘baseline’ for further studies, and to determine whether natural inter-annual variation could affect the interpretation of land-use changes. The key outcome from this chapter is that the inter-annual variation of ‘baseline’ can indeed affect the response intensity of the most commonly used metrics to evaluate dung beetle biodiversity (e.g. total abundance, species richness and total body mass or biomass); total abundance in particular varied strongly among years. I also showed that the inter-annual effects in disturbed habitats are related to the temporal dynamic of the 'baseline', by calculating the effect size for changes in dung beetle community metrics in *Eucalyptus* plantations in comparison to the values for undisturbed forest. This allowed me to isolate the inter-annual variation in dung beetle communities in an anthropogenic habitat, and the greater discrepancy of effect sizes among years for all metrics showed that human modification alters the temporal dynamic of communities and increases inter-annual variation.

Critically, I showed that anthropogenic effects on dung beetle communities could be underestimated due to the high inter-annual variation of baseline community metrics. Due to logistical and financial constraints, most studies of anthropogenic impacts on diversity do not evaluate the same site before and after disturbance, but instead use the 'space-for-time' approach (eg. KESSLER et al., 2009; REIDSMA et al., 2006), which potentially biases the effects of human-induced changes on biodiversity (FRANÇA et al., 2016; KAPPES; SUNDERMANN; HAASE, 2010). Here, I showed that a lack of information about the inter-annual variation in community metrics could strongly affect the interpretation of results from 'space-for-time' studies. As multi-year studies are not always affordable or viable, I suggest that researchers evaluating land-use change should explicitly consider environmental conditions that could affect the focal organism, such as climatic conditions, to correct statistical models or clarify their findings.

5.1.2 Chapter 3 – Spatial and temporal shifts in functional and taxonomic diversity in a human-modified tropical forest landscape

In this chapter, I evaluated the effects of anthropogenic changes on inter-annual variation in dung beetle communities using both taxonomic and functional diversity approaches. I assessed differences between the two approaches in detecting changes in the temporal stability and the response to human-induced modifications of dung beetle communities by comparing pairs of conceptually similar taxonomic and functional diversity metrics. The findings from this chapter suggested that anthropogenic modification does not change the temporal dynamics of either taxonomic or functional diversity metrics (with the exception of species richness), but that functional metrics are generally less variable in time than taxonomic metrics. Despite the overall similarity in approaches in detecting responses to anthropogenic change, the strength of the response often differed between equivalent taxonomic and functional metrics.

The main conclusion of the research presented in this chapter is that studies using only one approach to evaluate the impact of human activities on biodiversity might miss important consequences of change and draw incomplete or biased conclusions. Thus, I strongly suggest that the use of both metrics is required if studies are to fully identify the effects of spatial and temporal habitat changes on biodiversity.

5.1.3 Chapter 4 – Biodiversity in tropical plantations is affected by surrounding native vegetation, but not productivity: A case study with dung beetles in Amazonia

This last data chapter aimed to assess the local environmental conditions and landscape context shaping biodiversity in *Eucalyptus* monocultures, as well as the influence of silviculture yield on the taxonomic and functional diversity of dung beetle communities. I found that the amount of forest cover surrounding plantations was strongly linked to functional diversity and increased the number of native forest species in plantations. However, I did not observe the same patterns for other taxonomic metrics, which were mainly affected by soil texture. Additionally, I found no evidence of a relationship between dung beetle biodiversity and timber production in the studied plantations.

The outcomes of the study have important implications for the current scenario of intensive agricultural expansion, which is turning agricultural lands into a dominant component of tropical landscapes (VIJAY et al., 2016). As a result, there is a strong concern to increase the conservation value of anthropogenic areas in modified tropical landscapes (e.g. BARLOW et al., 2010; DE CASTRO; VAN DEN BERG, 2013; GRIES et al., 2012). I showed the importance of considering the landscape context (the amount of native forest cover) in sustaining the taxonomic and functional diversity of dung beetle communities in exotic plantations. I found strong evidence that native forest areas play an important role in facilitating species movement into and through modified habitats. Additionally, the lack of a relationship between the intensity of timber production and dung beetle biodiversity could indicate that ‘land-sharing’ is a viable management strategy. However, the native areas surrounding the plantations at my study site are mainly composed of primary forest corridors, which are likely to be dependent on larger areas of forest to sustain their populations (JORDÁN et al., 2003). This would suggest that sparing land for biodiversity conservation (‘land-sparing’) is also necessary. I therefore conclude that discussing land-sparing vs. land-sharing as a dichotomy is unhelpful, because wildlife-friendly plantations can be supported by large remnants of native habitat, and the two approaches are therefore not mutually exclusive (KREMEN, 2005). Consequently, based on my results, I suggest that areas of native forest should be retained or restored to improve the connectivity across the landscape and increase the permeability of agricultural areas for native forest species. My findings can therefore guide discussions with decision-makers to find solutions to more sustainable timber production.

5.2 PRIORITIES FOR FUTURE RESEARCH

5.2.1 The effects of inter-annual variation under different contexts

My results highlighted the importance of considering inter-annual variation of dung beetle communities in native (baseline) and modified habitats. Although I found strong evidence that baseline inter-annual variation affects the evaluation of human-induced changes, my findings were based in a landscape context of modified forest habitat within a matrix of native forest (Chapter 2). This gives rise to questions about the effects of temporal variation in dung beetle communities in other contexts. Many researchers have worked on other types of habitats modifications and land-use change (e.g. afforestation with forestry in savannah: EPRON et al., 2009, mining activities: NAVARRO et al., 2004, selective logging in forests: SLADE et al., 2007, replacement of native by exotic grasses: ALMEIDA et al., 2011) but little is known about the temporal dynamics of those land-use changes. This is important because my studies show that the response of a given community to anthropogenic change could differ in magnitude and direction depending on climatic or microclimatic conditions. Additionally, species from different habitats are more likely to be able to colonise modified areas with a heterogeneous or variegated landscape (RÖS; ESCOBAR; HALFFTER, 2012), which in turn could change the community structure and temporal dynamics within modified areas. Thus, futures studies should aim to improve our knowledge of the influence of temporal variation in evaluating the effects of land-use change on biodiversity; I have shown that this could be achieved by comparing the temporal dynamics of baseline data from natural habitats with communities in modified habitats in different contexts.

5.2.2 The consequences of consecutive disturbances on communities

In Chapters 2 and 3, I showed that dung beetle communities varied strongly in the year following a severe dry season. However, neither taxonomic diversity

(Simpson's diversity index) nor functional diversity (Rao's quadratic entropy) showed the same magnitude of variation among years in native forest areas. Future scenarios for Amazonian forests predict greater frequency and higher intensity of drought events (MALHI et al., 2008), which is concerning as this could cause the loss of important species related to many ecological processes (OLIVER et al., 2015a; STORK et al., 2009). Thus, I believe there is an urgent need for studies focusing on how the taxonomic and functional components of diversity respond to consecutive or long disturbance events.

My results showed that anthropogenic changes do not affect the inter-annual variation of diversity metrics (Chapter 3). However, I was unable to predict the scenario for periods longer than the five-year timeframe of my data. Consecutive waves of disturbance can reduce the resistance and/or resilience of communities to change (ISBELL et al., 2015; OLIVER et al., 2015b). If the diversity of a given community has low resistance to change, it is less likely to return to the original state after multiple consecutive or severe disturbances even if it has high resilience; similarly, if the resilience of the community is negatively affected, then species losses could be compounded by another wave of disturbance before the community can recover from the previous disturbance event. Finally, if both resistance and resilience are negatively affected, then the diversity of the community would decline at an elevated rate (STANDISH et al., 2014; WORM et al., 2006). I therefore suggest that future studies should focus on understanding the resistance and resilience of communities in both natural and modified habitats, as well as developing strategies to minimise species losses due to disturbance in anthropogenic landscapes.

5.2.3 Dung beetles in plantations and the spatial arrangement of landscape components

In Chapter 4, I showed that it is possible to maintain high biodiversity of dung beetle communities in *Eucalytpus* plantation through increased surrounding native forest cover. Despite this, it is unclear whether viable populations of forest species are able to persist in production systems over generations or whether the higher diversity was a result of transient foraging and/or tourist species. Population ecology studies focused on forest dung beetle species in plantations would provide valuable additional information to address the question of how the spatial arrangement of the landscape could maximise biodiversity conservation.

If forest species are able to colonise and persist in *Eucalyptus* plantations, policy-makers should encourage the landowners to increase the amount of surrounding native habitats in modified systems. This would increase the conservation of species at a landscape level, and reduce biodiversity loss in anthropogenic habitats. However, low quality habitats for forest species, such as plantations, could work as 'ecological traps' if they increase the permeability of disturbance-sensitive species without providing a suitable habitat for viable populations (BATTIN, 2004; SCHLAEPFER; RUNGE; SHERMAN, 2002). This could occur if, for example, the availability of resources in plantations is high but the microclimate is unfavourable for larval development and survival. In this case, plantations would attract individuals, which would increase the diversity of the dung beetle community, but habitat-quality would be too low to sustain viable populations (e.g. Allee effect: KOKKO; SUTHERLAND, 2001). In either case, 'land-sparing' may be necessary to conserve taxonomically and functionally diverse communities in human-modified habitats.

5.2.4 Linking response- and effect traits to evaluate the importance of biodiversity in modified landscapes

In the study described in Chapter 4, I found no relationship between timber production and dung beetle biodiversity, which could suggest that intense silviculture can be achieved while maintaining biodiversity in plantations. Alternatively, the lack of relationship could also indicate that the dung beetle functional traits included in my research were unable to fully capture the responses of specialist species to change. I developed the research in this thesis focusing on the response of broad dung beetle functional traits to natural or anthropogenic habitat changes, evaluating dietary preference, nesting behaviour, activity period, and body mass. However, other, more specific traits could provide valuable information about specific functional groups and their roles in ecosystem processes. For example, morphological measurements of dung beetles were used to address the link between dung beetle functional diversity and seed dispersal (GRIFFITHS et al., 2015). Consequently, the use of response and effect traits that are strongly related to a given ecological process could provide answers about how species are affected by environmental conditions and about their role in ecological functions and services (MLAMBO, 2014).

Communities are composed of groups of species with specific response traits, which partly determine their occurrence in a given habitat, and effect traits which are related to the role of organisms in ecosystem functions (STERK et al., 2013; VIOLLE et al., 2007). Further studies focused on identifying the links between response traits, effect traits, and function would greatly enhance our knowledge of the importance of biodiversity in ecosystem functioning and improve predictions about the consequences of species losses or gains under different scenarios and in different habitats. Knowledge of how the systematic loss of species is likely to affect ecosystem functions and services will also inform measures of biodiversity enhancement to restore ecosystem functioning in modified areas (DÍAZ et al., 2013).

5.3 CONCLUDING REMARKS

The research I present in this thesis is highly relevant to studies concerned with evaluating the conservation value of modified habitats and the impacts of human-induced changes on biodiversity. Firstly, I showed that local conditions can explain much of the spatial variation in dung beetle communities and must therefore be taken into account to predict community responses to change. I also demonstrated that temporal shifts in natural communities can result in different comparative responses of communities in anthropogenic habitats. Consequently, potential natural drivers of shifts in focal communities should be considered when assessing the effects of human-induced change. In addition, I showed that results can vary depending on whether taxonomic or functional diversity metrics are used to assess spatial and temporal responses to change, which could lead to the misinterpretation of results if either approach is used in isolation. I therefore highlighted that using both approaches concomitantly is preferable to understand changes in community diversity as a result of human activities. Finally, I applied the findings of these studies to assess how dung beetle biodiversity could be maintained in plantations. Specifically, I demonstrated that areas of native forest within human-modified landscapes play an important role in maintaining the taxonomic and functional diversity of dung beetle communities in *Eucalyptus* plantations.

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Appendices

Other outcomes

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Optimising Bait for Pitfall Trapping of Amazonian Dung Beetles (Coleoptera: Scarabaeinae)

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Abstract

The accurate sampling of communities is vital to any investigation of ecological processes and biodiversity. Dung beetles have emerged as a widely used focal taxon in environmental studies and can be sampled quickly and inexpensively using baited pitfalls. Although there is now a wealth of available data on dung beetle communities from around the world, there is a lack of standardisation between sampling protocols for accurately sampling dung beetle communities. In particular, bait choice is often led by the idiosyncrasies of the researcher, logistic problems and the dung sources available, which leads to difficulties for inter-study comparisons. In general, human dung is the preferred choice, however, it is often in short supply, which can severely limit sampling effort. By contrast, pigs may produce up to 20 times the volume. We tested the ability of human and pig dung to attract a primary forest dung beetle assemblage, as well as three mixes of the two baits in different proportions. Analyses focussed on the comparability of sampling with pig or human-pig dung mixes with studies that have sampled using human dung. There were no significant differences between richness and abundance sampled by each bait. The assemblages sampled were remarkably consistent across baits, and ordination analyses showed that the assemblages sampled by mixed dung baits were not significantly different from that captured by pure human dung, with the assemblages sampled by 10% and 90% pig mixes structurally most similar to assemblages sampled by human dung. We suggest that a 10:90 human:pig ratio, or similar, is an ideal compromise between sampling efficiency, inter-study comparability and the availability of large quantities of bait for sampling Amazonian dung beetles. Assessing the comparability of assemblage samples collected using different baits represents an important step to facilitating large-scale meta-analyses of dung beetle assemblages collected using non-standard methodology.

Citation: Marsh CJ, Louzada J, Beiroz W, Ewers RM (2013) Optimising Bait for Pitfall Trapping of Amazonian Dung Beetles (Coleoptera: Scarabaeinae). PLoS ONE 8(8): e73147. doi:10.1371/journal.pone.0073147

Editor: Andrew Wilby, University of Lancaster, United Kingdom

Received March 25, 2013; **Accepted** July 23, 2013; **Published** August 30, 2013

Funding: CJM was funded through a Natural Environment Research Council (NERC) studentship. JL was funded by by CNPq, FAPEMI and CAPES. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

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Introduction

Quantifying ecological processes and the effects of anthropogenic disturbance requires us to have an accurate and comparable representation of ecological assemblages. Inaccurate sampling may lead to spurious conclusions regarding the responses of species to anthropogenic processes and so it is essential that researchers implement standardised sampling protocols on appropriate indicator taxa.

Dung beetles are emerging as an increasingly popular focal taxon for ecological research [1–4]. They are cost-effective to survey [4], can be rapidly sampled using baited pitfall traps [5], and are sensitive to anthropogenic disturbances and habitat change [6]. They also fulfil several important functional roles including secondary seed dispersal, soil turbation, parasite suppression and nutrient cycling [7–9], and these functional roles can be easily manipulated in the field [10,11]. Furthermore, they may be separated into ecologically meaningful functional groups based upon diel activity, body size and one of three breeding strategies, rollers, tunnellers and dwellers [12,13], that determine rates of dung removal, seed dispersal and germination [8,14].

Dung beetles may be easily sampled using inexpensive baited pitfall traps [15]. However, the choice of bait has been largely driven by the idiosyncrasies of individual researchers rather than based upon empirical evidence and this can severely hinder the validity of inter-study comparisons [16]. By contrast, a large number of studies have investigated the resource preferences of dung beetle species [17–27]. Although some species are highly specialised, the majority of dung beetles have wide diet breadths and may be attracted to a variety of alternative baits, including dung, carrion and rotting

STRUCTURE AND COMPOSITION OF EDAPHIC ARTHROPOD COMMUNITY AND ITS USE AS BIOINDICATORS OF ENVIRONMENTAL DISTURBANCE

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(Received 2nd Dec 2013 ; accepted 22nd July 2014)

Abstract. We analyzed arthropod community structure and composition among different anthropogenic systems. The study was conducted in areas of secondary forest (control system), *Eucalyptus* plantation and pasture, where we sampled arthropods using pitfall traps. The systems did not differ in mean richness and mean abundance of arthropods, however, eucalyptus presented the highest total richness. The systems supported different arthropod communities in relation to structure and species composition. Pasture was the most simplified and different system in comparison to the others, probably because it is more open and presents low complexity. Our results demonstrate that different anthropogenic systems exhibit communities that reflect its characteristics, corroborating the evidence that human impacts are capable of changing community composition and structure. Our study serves to understand arthropod response in face of environmental disturbance, selecting indicator morphospecies and orders of arthropods for different anthropogenic systems and providing valid information for the development of conservation strategies.

Keywords*: Atlantic Forest, Eucalyptus, Habitat change, Pasture, Vegetation complexity*

Introduction

The introduction of different anthropogenic systems in natural ecosystems can reduce biodiversity and alter the functioning of these environments (Chapin et al., 2000; Sala et al., 2000). Biodiversity loss occurs by the simplification of complex and diversified ecosystems, since environments with high habitat heterogeneity present higher species diversity (Pianka, 1983). Therefore, the evaluation of biological communities is essential, due to the growing need to maintain ecological integrity of natural and anthropogenic systems (Basset et al., 2008).

In this context, soil arthropods have been widely used as bioindicator organisms in order to quantify and qualify the conditions of an environment (e.g. Dufrêne and Legendre 1997; Maleque et al., 2009; Almeida et al., 2011; Gerlach et al., 2013). Soil arthropods are considered good bioindicators because of their high diversity, easy and

Ecology, 96(6), 2015, pp. 1607–1619

Biodiversity and environmental context predict dung beetle-mediated seed dispersal in a tropical forest field experiment

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Abstract. Biodiversity–ecosystem functioning (BEF) literature is dominated by investigations conducted in temperate grassland ecosystems under homogenous environmental conditions. Consequently, studies concerned with the functional importance of higher trophic levels, or with the role of environmental conditions in shaping BEF relationships, are comparatively uncommon. To address this, we assessed dung beetle diversity-functioning relationships in situ, in a field experiment in the Brazilian Amazon. Dung beetles perform a number of ecological functions in habitats across the globe; in tropical forests they play a key role in the secondary dispersal of seeds. We therefore experimentally tested how the functional diversity of dung beetle communities affects seed dispersal and how BEF relationships varied with environmental context, by replicating the experiments under contrasting soil conditions. Relationships between dung beetle diversity and function were examined using diversity indices calculated using continuous morphological traits of the individuals involved in experiments, and functioning was measured as the dispersion of artificial seeds throughout the soil profile and the probability of burial. Ninety experimental plots were established across three distinct primary forest sites. We collected, identified, and measured almost 2000 beetles, and sieved around 11 Mg of soil to quantify the dispersion of 1800 seed mimics. There was a significant effect of dung beetle functional diversity on both seed dispersion and seed burial, although this depended on environmental context, with the strength or direction of responses differing across the contrasting soils. Regardless of soil type, functional richness, but not species richness, predicted seed dispersion. We therefore advocate the use of functional diversity indices over taxonomic approaches in dung beetle-focused BEF investigations. Furthermore, we highlight the difficulties in generalizing BEF relationships, even considering a single function within the same ecosystem.

Key words: animal-mediated functioning; BEF; context dependency; dung beetles; functional diversity; functional diversity indices; functional traits; secondary seed dispersal; soil.

INTRODUCTION

Species are disappearing from the planet at a faster rate than would be expected from the fossil record (MEA 2005, Barnosky et al. 2011), and this trend is likely to continue throughout the 21st century (Pereira et al. 2010). These high extinction rates are largely a result of human activities (Steadman 1995, Dirzo and Raven 2003), but aside from moral considerations, a key issue in ecology is, "Does it matter?" This question sparked the initial biodiversity–ecosystem functioning (BEF) studies (e.g., Naeem et al. 1994, Tilman and Downing 1994), and there is now a wealth of research demonstrating that biodiversity in producer systems matters for the maintenance of primary productivity, as well as the cycling of nutrients and water in soil (Cardinale et al. 2011, 2012, Hooper et al. 2012). This has important implications, because primary production and nutrient cycling underpin the provision of a number of goods and services to society (Cardinale et al. 2012). Disruption of these functions, therefore, has the potential to negatively impact human well-being (MEA 2005).

Despite progress made in our understanding of the role of diversity for ecosystem functioning (Hooper et al. 2005, Cardinale et al. 2012), three key areas remain underrepresented in the literature. First, there is a clear bias towards the role of diversity on resource capture (particularly biomass assimilation) in terrestrial plant communities (Balvanera et al. 2006, de Bello et al. 2010, Cardinale et al. 2011). Our knowledge of diversity effects in higher trophic levels is therefore patchy, being based on a limited number of investigations (e.g., Slade et al. 2007, Dangles et al. 2011, 2012, Braga et al. 2013, Nichols et al. 2013*b*). As higher trophic level organisms

Manuscript received 24 June 2014; revised 20 October 2014; accepted 4 November 2014. Corresponding Editor: M. D. Eubanks.

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