FILIPE MACHADO FRANÇA

ECOLOGICAL IMPACTS OF SELECTIVE LOGGING IN THE AMAZON: LESSONS FROM DUNG BEETLES

LAVRAS – MG
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Thesis submitted for the degree of Doctor of Philosophy as a Dual PhD with Applied Ecology Postgraduate Program, Federal University of Lavras, Brazil and Lancaster Environment Centre, Lancaster University, United Kingdom

Supervisors
Dr. Júlio Louzada
Dr. Jos Barlow

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APPROVED on 2nd of December, 2015

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2015

DECLARATION

I hereby declare that this work has been originally produced by myself for this thesis and it has not been submitted for the award of a higher degree to any other institution. Inputs from co-authors are acknowledged throughout.

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“Earth provides enough to satisfy every man's needs,

but not every man's greed.”

– Mahatma Gandhi

I dedicate this thesis to my mom Maria de Lourdes
for her unconditional love and constant support.

Dedico esse tese à minha mãe, Maria de Lourdes,
por todo amor incondicional e constante suporte.

DEDICATION

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RESUMO

O corte seletivo é um dos maiores agentes de degradação nas florestas tropicais, e o entendimento de seus impactos biológicos é essencial para elaborar estratégias de conservação associadas a produção madeireira. Igualmente importante é examinar se os desenhos experimentais mais usados são confiáveis para revelar os verdadeiros impactos das atividades antrópicas, e assim prover informações confiáveis para efetivar a conservação biológica. Essa tese objetiva tratar dessas lacunas de conhecimento através do uso do desenho experimental '*before-after-control-impact*' (BACI), que foi usado para quantificar os impactos do corte seletivo em besouros escarabeíneos e suas funções ecológicas. O primeiro capítulo de dados (Capítulo 2) compara até que ponto as abordagens BACI e '*space-for-time*' (SFT) geram diferentes conclusões sobre a relação entre o aumento da intensidade de corte seletivo e a riqueza e biomassa de besouros escarabeíneos. Esse capítulo mostra que SFT, o desenho amostral mais frequente na literatura, pode levar a subestimação dos impactos da degradação florestal na biodiversidade. O capítulo 3 investiga a ocorrência de pontos críticos de intensidade de corte seletivo influenciando os padrões de diversidade e funções ecológicas mediados pelos escarabeíneos; e como esses padrões são influenciados pela escala espacial que o corte seletivo é mensurado. Como resultado, foi encontrado que respostas biológicas ao corte seletivo podem ser não lineares e dependentes da escala. No capítulo 4 é explorado o papel que a estrutura florestal tem em mediar as respostas dos Scarabaeinae e seus processos ecológicos à realização do corte seletivo. Os resultados mostram que impactos da extração madeireira na estrutura florestal (abertura de dossel) não necessariamente explicam os efeitos negativos e desproporcionalmente mais fortes que esse distúrbio teve na riqueza e biomassa de besouros. Além disso, enquanto ressalta que o corte seletivo não influenciou outras duas variáveis ambientais (serapilheira e proporção de areia no solo) ou o consumo fecal e a bioturbação do solo realizados pelos escarabeíneos; esse capítulo mostra que as interações entre esses quatro componentes foram modificadas após a realização do corte seletivo. Finalmente, no capítulo 5, a quantidade de gordura corporal de três espécies de escarabeíneos foi avaliada para investigar, pela primeira vez na literatura, se o corte seletivo causa efeitos subletais em invertebrados tropicais. Esses resultados mostram que besouros coletados em áreas de floresta com corte seletivo tiveram maior proporção de gordura corporal do que besouros coletados em florestas não perturbadas; o que corrobora com os impactos negativos do corte seletivo observados na abundancia relativa de cada espécie. Dessa forma, essa tese discute sobre os desafios para conservação da biodiversidade em um mundo onde as taxas de degradação florestal aumentam a cada dia.

Palavras-chave: Florestas tropicais. Corte seletivo. Floresta Amazônica. Rola-bostas. Processos ecossistêmicos.

ABSTRACT

Selective logging is one of the main drivers of forest degradation in tropical forests, which makes the understanding of its biological consequences essential to inform conservation strategies associated to timber production in those forests. It is also important to examine whether the most frequently used study designs are likely to reveal the true impacts of human activities, thus provide reliable information to develop effective conservation strategies. This thesis aims to fill these knowledge gaps by using an experimental design known as before-after-control-impact (BACI) to quantify the impacts of selective logging on tropical dung beetles and their ecological functions. The first chapter (Chapter 2) compares to what extent space-for-time (SFT) and before-and-after approaches draw different conclusions regarding the relationship between selective logging intensity and dung beetle species richness and biomass. This chapter shows that SFT studies, the most frequently used approach, may underestimate the impacts of forest degradation on biodiversity. The Chapter 3 investigates the presence of thresholds in dung beetle responses to logging intensity, and whether those would be influenced by the spatial scale at which logging intensity is measured. The results from this chapter show that biological responses to selective logging can be non-linear and scale-dependent. The chapter 4 addresses the role of forest structure in mediating the responses of dung beetles and mediated faecal processes to selective logging occurrence. The results show that changes in the forest structure due to selective logging (here measured as canopy openness) not necessarily explain the negative and disproportionally stronger effects of this disturbance on dung beetle biomass and species richness. Therefore, while highlighting that selective logging did not influence two environmental variables (leaf litter and soil sand content) or dung beetle-mediated faecal consumption and soil bioturbation; this chapter shows that the linkages among these four components were modified after the selective logging. Finally, the last experimental chapter (Chapter 5) examines the amount of body fat of three dung beetle species to investigate for the first time in the literature whether selective logging could induce sublethal effects on tropical invertebrates. The results show that dung beetles sampled within selectively logged forests have a higher proportion of body fat than those from undisturbed forests, which matches with the negative impacts of selective logging on the relative abundance of each examined species. Overall, this thesis discuss about the challenges to conserve the biodiversity and ecosystem functioning in a world where forest degradation rates are increasing every day.

Keywords: Tropical forests. Selective logging. Amazon rainforest. Dung beetles. Ecosystem processes.

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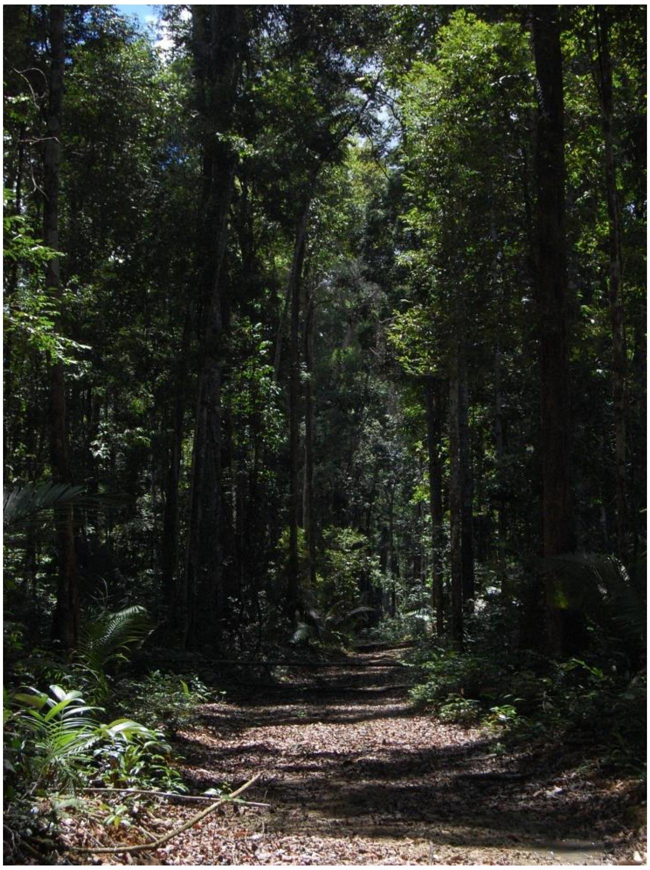
FIRST PART



Chapter 1: GENERAL INTRODUCTION

1.1 Tropical Forests

1.1.1. What about tropical forests?

Tropical forests are extremely diverse biomes, which house two-thirds of the known world terrestrial biodiversity (Gardner, 2010). These forests represent approximately 50% of total forest ecosystems on Earth (Pan et al., 2011) and cover around 1,240 Mha distributed across Southeast Asia, Africa and South America (Kim et al., 2015; Pan et al., 2011). Due to their great diversity, complexity and extension (Kim et al., 2015; Mayaux et al., 2005), tropical forests contribute disproportionately to local, regional and global ecosystem processes (Cardinale et al., 2012a; Foley et al., 2007). As examples, there are global climate regulation (Anderson-Teixeira et al., 2012), carbon sequestration and storage (Berenguer et al., 2015, 2014), disease control (Hahn et al., 2014), and biological diversity conservation (Foley et al., 2007). These forests also have an important economic role, providing timber and non-timber products to over 800 million people living in these ecosystems (Chomitz et al., 2007). Consequently, most tropical forests are now imperilled by the increased forest degradation and land-use conversion rates caused by anthropogenic activities (Gibson et al., 2011; Kim et al., 2015; Newbold et al., 2015).

1.1.2 Threats to tropical forests

Anthropogenic disturbances pose a major threat to the world’s forested environments (Newbold et al., 2015; Sala et al., 2000), and primary forests are rapidly disappearing due to land-use change and environmental degradation, which are widely recognized as the greatest drivers of biodiversity loss on Earth (Newbold et al., 2015; Pan et al., 2011). This is particularly so in the tropics, where most primary forests co-occur with the highest forest degradation rates (Kim et al., 2015; Lambin et al., 2003; Pan et al., 2011) and over 230 Mha of forests were lost between 2000 and 2012

(Hansen et al., 2013). This trend is expected to continue over the coming years (Newbold et al., 2015; Pereira et al., 2010) and, as a result, a growing number of attempts have focused on summarising the consequences of these disturbances through meta-analyses (Burivalova et al., 2014; Gibson et al., 2011; Newbold et al., 2015, 2012; Pfeifer et al., 2014). For example, a global meta-analysis clearly shows how land-use changes and associated pressures reduce the local terrestrial biodiversity (Newbold et al., 2015), while a pan-tropical meta-analysis provides some hope by highlighting the relatively high biodiversity value of selectively logged forests (Gibson et al., 2011). As a result, increased attention has also been given to policies and financial investments such as REDD+ (where REDD is Reducing Emissions from Deforestation and Forest Degradation; UNFCCC, 2008), which support the sustainable forestry management as a strategy to avoid the consequences of forest degradation in tropical forests (Panfil and Harvey, 2015).

1.1.3 Integrating tropical forest production and conservation

A central challenge for sustainability in tropical forests is how to preserve the forest biodiversity and ecosystem services while enhancing timber production. The insatiable global demand for timber products poses severe challenges to tropical forests outside protected areas (Asner et al., 2009; FAO, 2010), thus a key challenge arises for the future: How to integrate timber production to tropical forest conservation? This question is, so far, one of the most recognized and controversial trade-offs related to forest management (Duncker et al., 2012; Lafond et al., 2015) and has triggered debates over the need for REDD+ projects to more explicitly develop conservation efforts linked to anthropogenic activities in tropical forests (Panfil and Harvey, 2015). Yet, despite controversies over the synchronism between biodiversity conservation and the timber production in tropical forests (Zimmerman and Kormos, 2012), studies have suggested the sustainable forest management as a good alternative for the long-term maintenance of environmental, social and economic benefits derived from tropical forests (Gardner, 2010 and references therein). Consequently, sustainable forest management is among the most adopted REDD+ interventions to date (Salvini et al., 2014), and is enshrined as a key aim of international biodiversity targets for 2020 (Convention on Biological Diversity, 2014).

1.2 Selective logging in tropical forests

One example of sustainable forestry practice widely adopted in the tropics is the selective logging (Blaser et al., 2011; Salvini et al., 2014), which involves the extraction of particular high-cost commercial tree species with minimum trunk diameter (~40-60 cm), thus leaving a great number of non-commercial species with lower trunk diameter unlogged (Edwards et al., 2014c; Griscom and Cortez, 2013). Selective logging is considered the most widespread disturbance driver throughout tropical forests (Blaser et al., 2011; Edwards et al., 2014c; Koltunov et al., 2009; Putz et al., 2012) and contrasts with clear-cut methods frequently used in temperate and boreal regions. In the tropics, at least 28% of all forests were under industrial timber operations until 2009 (Laurance et al., 2009) and, due to its relevance to many local and national economies, tropical regions are now responsible for around one eighth of the global timber production (Blaser et al., 2011). As a consequence, over 400 Mha of tropical forests are now officially designated as timber concessions (Blaser et al., 2011) and, to date disturbed forests occupy larger extensions than primary ones in most of the tropics (Laurance *et al.*, 2014; Nelson and Chomitz, 2011). The Amazonian Basin is an exception, still retaining two-thirds of primary forests (Laurance *et al.*, 2014). However, this trend is rapidly changing due to the increased acceleration of deforestation in Latin America, which was the strongest among tropical regions from 1990 to 2010 (Kim et al., 2015).

1.2.1 Logging methods in tropical forests

In the tropics, most forests have been harvested by conventional logging techniques (CL) (FAO, 2010); whereas more recently the reduced-impact logging (RIL) system has been considered to reduce the deleterious environmental damages caused by selective logging (Bicknell et al., 2014b; Putz et al., 2008). The conventional logging practices are characterized by unsustainably high logging rates and poor road design and poor silvicultural practices (Laurance et al., 2009; Putz et al., 2012), which are known to increase the negative impacts on both forest structure and diversity (Martin et al., 2015; Putz et al., 2008). In addition, the common unsupervised tree fellers and lack of tangling liana cutting induces unnecessary damage to residual forest by bringing down the stand adjacent to felled trees (Sist et al., 2003). Consequently, even at low-harvest intensities, forests which are subject to CL lose much of their environmental importance due to increased impacts on soil and canopy cover (Asner et al., 2004a; Newbold et al., 2015; Pereira et al., 2002).

Contrastingly, RIL techniques aim to reduce the collateral damage from timber extraction by implementing a series of measures to minimize collateral impacts of selective logging (Pinard and Putz, 1996; Putz et al., 2008; West et al., 2014). Although the application of RIL methods is context-dependent and not uniform, it generally starts with a pre-harvesting plan, which inventories and maps all profitable trees (size, number, species and types) that can be cut (Putz and Pinard, 1993; Sist et al., 2003). This plan is designed to minimize ground disturbances caused by skid trails, roads and log yards (Figure 1.1), which are related to extensive impacts on tropical forests and biodiversity (Laurance et al., 2009; Yamada et al., 2014). Thus, tangling lianas are cut to improve work safety and to avoid damage to neighbouring trees during the tree felling, which is directional and bucking to alleviate collateral damage to other trees in the adjacent logging units or nearby protected areas. Lastly, silvicultural treatments and closing operations generally are applied to assure long-term prospects to increase the forest productivity recovery after the first cutting cycle (Putz and Pinard, 1993; Sist et al., 2003).

Whether RIL or CL is more profitable depends on the perspective from which benefits and costs are estimated (Putz et al., 2008). Overall, RIL methods can be more expensive, but costs and forest productivity of logged forests under RIL and CL are influenced by many factors, such as diversity and heterogeneity of the forest, labour compensation practices, marked timber, and also the spatial and temporal scales of the research (Medjibe and Putz, 2012; Putz et al., 2008). Nevertheless, when considering the long-term effects of both CL and RIL methods on logged forests from a broader perspective and including environmental and social impacts, RIL takes the lead as the best alternative (Bicknell et al., 2014b; Medjibe and Putz, 2012; Putz et al., 2008).

Additionally, growing evidence has shown the importance of other landscape strategies proposed to meet timber demands through more “biodiversity friendly” logging activities (Edwards et al., 2014a). As result, the debate about land-sparing versus land-sharing strategies, generally applied to agricultural production (Fischer et al., 2008; Phalan et al., 2011), has been applied to the logging context (Edwards et al., 2014a). This literature indicates that the shape of biodiversity-disturbance curves can bring insights into the best strategy for biodiversity conservation in modified environments (Phalan et al., 2011; von Wehrden et al., 2014). Overall, it has been suggested to spare lands for biodiversity conservation within production forests (Edwards et al., 2014a); or in the cases where concave biodiversity-yielding relationships are observed and the biodiversity is more sensitive to the initial presence of a disturbance (Phalan et al., 2011; von Wehrden et al., 2014). In contrast, land-sharing has been recommended as better strategy where the relationships between biodiversity-disturbance are concave and relatively large proportion of the biodiversity can be maintained across a low-disturbed landscape (Phalan et al., 2011; von Wehrden et al., 2014). From the perspective of maintaining higher biodiversity levels within logging concessions, it has been recently suggested that the conservation value of logged forests will be optimized if RIL methods are implemented under the land-sparing strategy (Edwards et al., 2014a).

Figure 1.1 Selective logging impact on tropical forest. (A) Secondary-level logging road; (B) Timber transport truck in a main logging road; (C) Physical evidence of timber removal resulting in (D) a forest canopy gap; (E) Forest gap caused by a log yard (timber already removed) and (F) wooden logs of *Dinizia excela* Ducke (Fabacea, Mimosoideae) timber species (*Angelim vermelho*) stored in a log yard. All photos were taken by F.F. in the Amazon forest, state of Pará, Brazil.

1.2.2 Ecological impacts of selective logging in tropical forests

The ecological impacts of selective logging depend very much on the harvesting intensity, logging methods and pre-logging regional forest aspects

(Bicknell et al., 2015, 2014a; Martin et al., 2015; Putz et al., 2012). Logging intensities can be calculated by different metrics (i.e. percentage of tree basal area removal and/or number of removed trees per hectare), but most studies measure the volume of timber extracted per hectare (m^3/ha), which ranges between 0.22 and 145.3 m^3 ha^{-1} in the tropics (Laufer et al., 2013; Zimmerman and Kormos, 2012). Although the RIL method can result in halved-damages to the residual stand when compared to CL practices (Sist et al., 1998), this method can fail in terms of sustainability in highly stocked forests, such as those in Southeast Asia (Medjibe and Putz, 2012). In such forests, logging intensities very often exceed 100 m^3/ha and damage to residual forests can exceed 50%, therefore threatening future yields, forest biodiversity and functioning (Medjibe and Putz, 2012; Sist et al., 1998). On the other hand, where forests have only a small proportion of tree species with high timber value, logging operations generally remove below 50 $m^3 ha^{-1}$ (Burivalova et al., 2014; Sist et al., 1998). Such low-intensity logging tends to be less damaging to forest structure, biodiversity and ecosystem functioning (Edwards et al., 2014c; Imai et al., 2012; Slade et al., 2011).

Regardless of the method, as logging intensity increases, so do the forest gaps caused by tree fall, log yards, skid trails and logging roads (Asner et al., 2004a; Laurance et al., 2009). These cause greater damage to residual stands (Gatti et al., 2015; Martin et al., 2015) and forest canopy (Asner et al., 2004a; Pereira et al., 2002), thus leading to changes in the microhabitat conditions due to understory desiccation caused by the higher exposition to sunlight (Yamada et al., 2014), heat and drying winds (Costa et al., 2015; Mazzei et al., 2010). For instance, higher canopy openness in selectively logged forests can influence tree seedling development (Duah-gyamfi et al., 2014), the amount and moisture of ground leaf litter (Chung *et al.*, 2000; but see: Burghouts *et al.*, 1992) and even the impacts of dry seasons, when compared to unlogged forests (Koltunov et al., 2009).

The response of animal communities to logging effects diverges among taxonomic groups and continental location (Burivalova et al., 2014), and can also depend on forest seasonality and characteristics (Davis and Sutton, 1998; Davis et al., 2001), logging methods (Edwards et al., 2012b), species traits and environmental tolerance (Burivalova et al., 2015; Schwitzer et al., 2011; Slade et al., 2011). Overall, studies have found both positive, neutral and negative consequences of selective logging on forest fauna populations and communities (Edwards et al., 2012b; Laufer et al., 2015; Schwitzer et al., 2011; Struebig et al., 2013; Wearn et al., 2013). In addition, although still under explored, studies have examined the sublethal stress-induced effects of selective logging on animal communities (i.e. Leshyk *et al.*, 2012; Lucas *et al.*, 2006; Mastromonaco *et al.*, 2014; Rimbach *et al.*, 2013; Suorsa *et al.*, 2003). This body of literature has shown that selective logging leads to increased stress-induced responses in vertebrates from logged forests; however, most studies were carried out in temperate regions (but see: Rimbach *et al.*, 2013) and, to date there are no assessments of sublethal effects caused by selective logging on tropical invertebrates.

1.2.3 Functional value of selectively logged tropical forests

The functional importance of selectively logged tropical forests is controversial. Studies have demonstrated that ecosystem processes have considerable resilience to logging operations (Mazzei et al., 2010; Newbold et al., 2015), whereas others suggest that it might take many decades for logged forests to fully recover (Osazuwa-Peters et al., 2015; Yamada et al., 2014). Indeed, selective logging has been suggested as a major driver of tropical forest degradation (Asner et al., 2009; Gatti et al., 2015; Zimmerman and Kormos, 2012), negatively affecting both carbon stocks (Berenguer et al., 2015, 2014) and ecosystem functioning (Edwards et al., 2014c; Foley et al., 2007; Gutiérrez-Granados and Dirzo, 2010; Schleuning et al., 2011; Slade et al., 2011). Nevertheless, selective logging is undoubtedly less environmentally severe than other forms of anthropogenic disturbances like fire, pastures and plantations (i.e. Barlow et al., 2006; Edwards et al., 2012;

Gibson et al., 2011; Scheffler, 2005). As such, logged forests and primary forests can retain similar biodiversity and ecosystem processes (Berry et al., 2010; Edwards et al., 2012a, 2012b; Ewers et al., 2015; Mazzei et al., 2010; Yamada et al., 2014), but this will depend on logging intensity (Burivalova et al., 2014) and absence of further logged-forest disturbances (Edwards et al., 2014c; Lee-Cruz et al., 2013; Luke et al., 2014).

Undoubtedly, when it comes to preserving tropical biodiversity, there is no better substitute than pristine forests (Gibson et al., 2011). However, the ecological value of logged forests should not be overlooked (Ewers et al., 2015), since these forests provide economic benefits through provision of timber and non-timber products, besides retaining tropical biodiversity and ecosystem processes (Berry et al., 2010; Edwards et al., 2012b; Ewers et al., 2015; Gardner et al., 2009; Gibson et al., 2011). In addition, most of the endemic and threatened species on Earth are found entirely outside the existing reserve network (Laurance *et al.*, 2014; Rodrigues *et al.*, 2004), which likely means that a great part of tropical biodiversity may be within the over 400 Mha of tropical forests officially designated as timber concessions (Blaser et al., 2011). Therefore, because protected areas alone may not be enough to conserve the exceptional biodiversity in tropical forests (Laurance et al., 2012), the forests selectively logged under sustainable forestry management appear as alternative refuges for the persistence of at least part of the forest-species in modified landscapes (Gardner, 2010 and references therein). Yet, the high ecological value of selectively logged forests (Gibson et al., 2011) justifies why conservation efforts should invest in both sustainable forest management (Zimmerman and Kormos, 2012) and protection of large extensions of logged forests to attenuate the threats to tropical biodiversity (Gibson et al., 2013; Reynolds et al., 2011).

1.3 Study taxa – Dung beetles

Dung beetles (Coleoptera: Scarabaeidae) are a dominant dung feeding group of insects globally distributed on every continent except Antarctica (ScarabNet, 2008). With just over 6,200 described species and 267 genera, dung beetles are one of the more morphologically diverse animal taxa (Tarasov and Génier, 2015). To date, the most commonly used dung beetle classification follows the precedent set by Balthasar (1963), which divides dung beetles into two distinct subfamilies with six tribes each, as follows: Coprinae with tribes Coprini, Dichotomomiini, Oniticellini, Onitini, Onthophagini and Phanaeini; and Scarabaeinae with tribes Canthonini, Eucranii, Eurysternini, Gymnopleurini, Scarabaeini and Sisyphini. Nevertheless, recent phylogenetic studies have called for further research integrating morphological, molecular and fossil date aspects to clarify the present dung beetle phylogeny (Mlambo et al., 2015; Tarasov and Génier, 2015).

Although a cosmopolitan group, Scarabaeinae beetles have their highest diversity in the tropical regions, where they are most abundant in savannah and forest environments (Hanski and Cambefort, 1991; Nichols et al., 2007; Philips, 2011). Their high abundance and diversity (Tarasov and Génier, 2015) coupled to their close association with specific vegetation and soil types (Hanski and Cambefort, 1991) make dung beetles an exceptional study model (Nichols and Gardner, 2011). Moreover, due to their high sensitivity to changes in environmental conditions (Bicknell et al., 2014a; Menéndez et al., 2014), inexpensive surveys and ability to predict responses of many other taxa (Edwards et al., 2014b; Gardner et al., 2008a), dung beetles are highly recommended as a cost-effective and responsive taxonomic group for biodiversity monitoring and inventory taking across the tropics (Gardner et al., 2008a; Nichols et al., 2007). As a consequence, a large body of literature has considered dung beetles in the evaluation of the impacts of anthropogenic activities in tropical forests (e.g. Audino *et al.*, 2014; Bicknell *et al.*, 2014;

Gardner *et al.*, 2008a; Nichols *et al.*, 2007). In addition, through dung manipulation for feeding and nesting purposes (Hanski and Cambefort, 1991), these detritivore beetles provide a number of ecological functions (reviewed in Nichols et al., 2008), as well as ecosystem services valued at $380 and £367 million for the cattle industry in the US and UK, respectively (Beynon et al., 2015; Losey and Vaughan, 2006).

1.3.1 Dung beetle breeding behaviour

Scarabaeinae dung beetles are among the most popular common Coleoptera subfamilies in the world, being among the most cited subfamily of beetles on Google Scholar (Tarasov and Génier, 2015). A large part of this is because of their consumption of faecal matter for feeding and nesting purposes, which allows them to thrive in most ecosystems and to crucially contribute to several key processes on Earth’s ecosystems (Nichols et al., 2008). Although dung beetles exhibit a range of feeding behaviours (i.e. feeding on rotting fruit and fungus, vertebrate carrion and dead invertebrates; Hanski and Cambefort, 1991; Larsen *et al.*, 2006), most species are coprophagous and feed primarily on the rich protein and microbial liquid content of animal excreta (Hanski and Cambefort, 1991; Tixier et al., 2015). As a result, these detritivore beetles are an essential component of the dung-based food webs in the “brown-world” (Nichols and Gardner, 2011; Wu et al., 2011).

Although there are some kleptoparasite species, which have lost the dung-collecting behaviour and become nest-parasites of other Scarabaeinae species, most dung beetles can be divided into three broad nesting/feeding strategies: the tunnelers (paracoprids), rollers (telecoprids) and dwellers (endocoprids) (Hanski and Cambefort, 1991). Briefly, tunneler species dig in close proximity to or below the dung pat and transport dung into these vertical tunnels for adult feeding or breeding (Figure 1.2A). The rollers make brood balls that are transported some horizontal distance away before burial beneath soil surface for feeding on or breeding in (Figure 1.2B). Lastly, the dweller species feed and breed within the dung mass itself, or in a pit immediately under dung pats (Figure 1.2C; Halffter and Edmonds, 1982a; Hanski and Cambefort, 1991). These varied patterns of dung consumption and relocation performed by dung beetles lead to a series of ecosystem functions, which are directly relevant to tropical forests (reviewed in Nichols *et al.*, 2008).

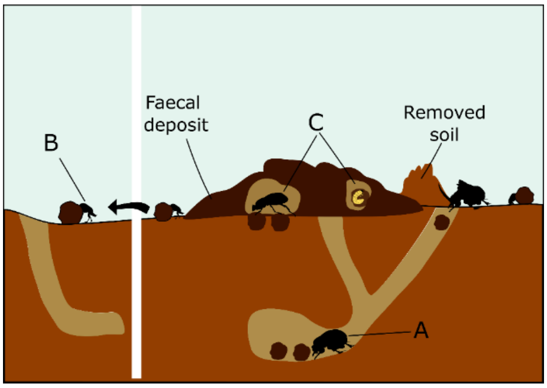


Figure 1.2 Dung beetle strategies: tunneler or paracoprid species (A); roller or telecoprid species (B); and dweller or endocoprid species (C). Modified from Halffter & Edmonds (1982).

1.3.2 Dung beetle-mediated ecosystem processes

1.3.2.1 Dung removal and consumption

Dung beetles are the most important taxa contributing to dung decomposition (Lee and Wall, 2006). Through their manipulation of the dung resources, these insects provide a range of key ecosystem processes that facilitate the transfer of energy and matter through dung-based detrital food webs (Nichols and Gardner, 2011). In tropical forests, dung beetles are attracted to dung within the first few minutes after deposition (F. França, *personal observation*), and removal can be very quick. In Southeast Asian forests around 22% of the dung was removed within 24 hours (Kudavidanage et al., 2012), whereas in Malaysian Borneo removal ranged from 63% in high intensity-logged forests to 99% in undisturbed and selectively logged forests

(780 g of cow dung; Slade *et al.*, 2011). In the Peruvian Andes around 50-100% of the dung was removed within three days (~100 g of pig dung, Horgan and Fuentes, 2005) and in the Brazilian Amazon the removal rates in 24 hours varied from 100% in primary forests to ~60% and 30% in managed forests and introduced pastures, respectively (70 g of human dung; Braga *et al.*, 2013, 2012). Furthermore, such differences in dung removal rates between forested and deforested habitats may be caused by the increased exposure of dung pats to sunlight and high temperatures in the opened habitats. This leads to crust formation on the surface of the dung and, consequently, a decrease of dung attractiveness to detritivores and reduced dung consumption and decomposition rates (Nadeau et al. 2015). On the other hand, in forested environments, dung pats may remain attractive longer, because their moisture and quality are retained under shade (Horgan et al. 2005).

1.3.2.2 Incidental ecosystem processes

While leading to increased dung beetle biomass production for predators (Young, 2015), the dung consumption also instigates incidental effects on edaphic properties with important implications for both green and brown worlds (Nichols et al., 2013b; Wu et al., 2011). Previous research has shown that dung beetle activity increases both dry matter yields and nitrogen content in vegetation (Bang et al., 2005), as well as leaf litter decomposition rates (Tixier et al., 2015). In addition, it has been noted that dung beetle activities decrease the volatilization of NH_3 and increase the mineralization and nitrification processes (Yokoyama et al., 1991), which may explain how dung beetles collaborate to the transfer of nitrogen from dung to soil (Yamada et al., 2007). However, these benefits may result not only from dung beetle activities, but also from the indirect effects they have on microorganisms responsible for the incorporation of nutrients into the soil (Slade et al., 2015). As well as promoting the recycling of nutrients, dung beetles promote the soil fertility through bioturbation, “the displacement and mixing of sediment particles" (Nichols et al., 2008). Through tunnelling activities and soil movement, dung beetles improve the soil aeration, water porosity and water absorption capacity, therefore improving soil conditions for root penetration (Miranda, 2006). Although Bang *et al.*, (2005) provide the only empirical evidence that soil bioturbation, as a consequence of tunnel building by tunneler dung beetle species, modifies soil physical properties; a previous study in Costa Rica has shown that soil water retention increased and soil bulk density declined under dung pats in seasonally dry pastures (Herrick and Lal, 1996). In addition, recent evidence has suggested that dung beetle-mediated soil bioturbation modifies the soil microbial diversity and functioning, therefore contributing as a mobile route between decomposition processes above and below ground (Slade et al., 2015).

Two other important dung beetle-mediated incidental ecosystem processes, are secondary seed dispersal and parasite suppression. Dung beetles very often influence the fate of dispersed seeds in tropical forests by relocating those, which are dispersed by mammal defecation (Andresen, 2002; Griffiths et al., 2015). In doing so, dung beetles transport seeds both horizontally (by roller species) and vertically (by tunnelers) from the deposition site (Nichols et al., 2008). This can benefit the survival of buried seeds by decreasing seed predation and pathogen mediated mortality (Estrada and Coates-Estrada, 2002), or by dispersing them to more favourable microclimates for germination and growth (Andresen and Levey, 2004) as well as reducing density dependent competition mortality (Lawson et al., 2012; Santos-Heredia and Andresen, 2014). Even though seeds are dung contaminants from a "dung beetle's perspective" (Nichols et al., 2008), by secondarily dispersing seeds the dung beetles can have far consequences on emergence and survival of seedlings (H. Griffiths J. Louzada, R. Bardgett, and J. Barlow, *unpublished manuscript*), therefore influencing plant communities and forest regeneration. In addition, a recent review has explored the diverse ways by which coprophagous beetles directly or indirectly contribute (or not) to parasite transmission (Nichols and Gómez, 2014). While showing that linkages between dung beetles and parasites may have divergent consequences on transmission intensity within specific transmission cycles and across transmission cycle types, they bring attention to the diverse mechanisms in which dung beetles can maintain, reduce or increase the mammal parasitic helminth contamination.

1.4 Study System – The Brazilian Amazon

Covering approximately 6.5 million km^2 and spanning nine countries in South America, the Amazon forest is the largest remaining tropical rainforest in the world. Housing ~25% of terrestrial species (Dirzo and Raven, 2003; Sala et al., 2000) and storing ~ 86 Pg of carbon (Berenguer et al., 2015, 2014; Pan et al., 2011), it clearly plays a vital role in the global, regional and local provision of ecosystem services (Leadley et al., 2014). Nevertheless, in recent years increased human activities have led to growing deforestation (Kim et al., 2015) and, consequently, less carbon storing (Berenguer et al., 2014) and potential modifications in river flow, higher forest fire frequency and large scale changes in rainfall (Leadley et al., 2014). Above all human activities, the selective logging is a major activity occurring in the Amazon, particularly so in the Brazil where the largest fraction of this ecosystem is retained (Foley et al., 2007). As result, over 50 Mha of Amazonian forests are under timber concessions (Macpherson et al., 2010) and between 1990 and 2010 the world’s largest acceleration of annual net forest area loss that occurred in Latin America was dominated by Brazil (Kim et al., 2015).

This present project was carried out within the 1.7 Mha *Jari Florestal* landholding, located in the state of Pará in the north-eastern Brazilian Amazonia (00°27′–01°30′ S, 51°40′–53°20′ W). The region comprises a mosaic of *Eucalyptus* plantations and regenerating secondary forests within ~1.5 Mha of primary forests subjected to very low levels of disturbance (Barlow et al., 2010; Parry et al., 2009a). These forests are characterized as evergreen dense tropical rainforest (Souza, 2009), often dominated by the timber species *Dinizia excela* Ducke (Fabacea, Mimosoideae) (Laufer et al., 2015), which corresponds to about 50% of exploited timber in some Amazonian regions (Barbosa, 1990). Within this large landscape about 544,000 ha of native forest is divided in “Annual Operating Planning” (POA) subsets, each one planned to be logged every year (since 2003) under a 30 year cutting cycle. Logging activities are planned following the FAO model code of forest harvesting (Dykstra and Heinrich, 1996) and during the pre-harvest inventory each POA is subdivided into 10 ha (250 x 400 m) units planned to be logged with a specific logging intensity (m^3 ha^{-1}). The experiments of this project were established in 34 planned logging units (Figure 1.3), where dung beetles and ecological functions were sampled before and after logging operations at the same sites and following the same methods.

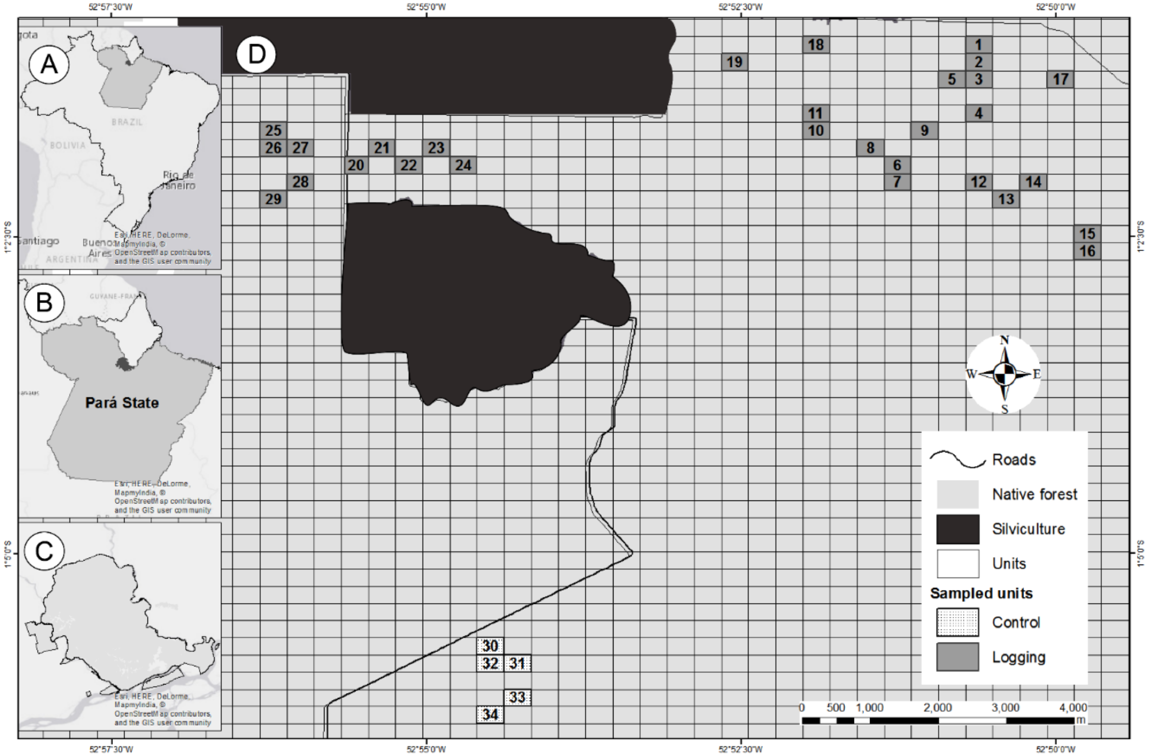


Figure 1.3 Map of study area. (A) Brazil; (B) state of *Pará*; (C) *Jari* landholding and (D) the experimental design in the *Jari* region where we sampled within 34 planned logging units. The units that we sampled and were selectively logged after the first dung beetle collection are highlighted in dark grey (1-29), whereas the five control units, which remained unlogged during the course of the study, are clear (30-34).

1.5 Research objectives

This thesis focuses on understanding the direct and indirect impacts of forest degradation on biodiversity and ecosystem processes. In particular, how selective logging influence tropical dung beetle diversity, physiology and the ecological process they govern. This was addressed in the following four topics:

- **Chapter 2:** ***What the eyes do not see, the forest does feel: Are we underestimating biodiversity loss in disturbed tropical forests?***

Understanding the rate and spatial distribution of biodiversity loss due to the human alteration of global environment requires realistic assessments. Most studies about the consequences of forest disturbances on biodiversity adopt the space-for-time substitution (SFT), but when researchers are able to sample prior to the disturbance event, a before-after-control-impact (BACI) design can be used. Yet, it is not clear to what extent a reliance on SFT studies could affect inference about impacts of human activities on biodiversity in terrestrial environments. Therefore, the first research objective was to compare the conclusions drawn by STF and BACI designs regarding the responses of dung beetle species richness and biomass to logging intensification.
Chapter 2 research questions: (1) Are we underestimating the biodiversity consequences of tropical forest degradation? (2) What are the pros and cons of SFT and BACI experimental designs?

- **Chapter 3:** ***Identifying thresholds in dung beetle responses to logging intensity to improve the sustainability of tropical forest management***

Selective logging is one of the most widespread economic activities in tropical forests. Despite progress made to understand logging consequences on tropical biodiversity and ecosystem processes, to date just few meta-analysis studies have explored logging intensities as a continuous, rather than a categorical metric, to identify thresholds of logging intensity above which multi-taxa biodiversity decreases. Yet, while studies have shown the scale-dependent responses of species richness in logged forests, our knowledge of logging impacts is also limited by uncertainty about the spatial-scale of management recommendations. Thus, the second aim of this research was to empirically examine whether dung beetle diversity and species composition, and associated ecological functions respond scale-dependently and non-linearly to increasing logging intensity.

***Chapter 3 research questions*:** (1) What are the effects of increasing the intensity of selective logging on dung beetles and ecological processes they govern? (2) What is the relationship between logging intensification and biological responses? (3) Are these relationships scale-dependent on the spatial range that the logging intensity is measured?

- **Chapter 4:** ***Assessing the influence of forest disturbance on 'brown world' ecosystem processes***

Despite evidence showing that forest degradation leads to direct and indirect impacts on biodiversity and ecosystem functioning, we have a limited understanding about how forest structure buffers and/or mediates these impacts along detritus-based food webs of the 'brown world'. Consequently, there is very little empirical evidence exploring the extent to which forest degradation modifies the influence of environmental factors on dung beetle mediated faecal pathways. The third research aim was therefore to address this by investigating how selective logging alters the relative importance of canopy openness, leaf litter weight and soil sand content on dung beetle-mediated consumption, production and incidental processes.

***Chapter 4 research questions*:** (1) Do logging impacts on forest structure mediate and/or buffer the negative consequences on dung beetle-mediated detritus-pathways? (2) Does selective logging alter the influence of environmental conditions on post-logging dung beetle-mediated brown processes? (3) Does selective logging generate cascade effects on dung beetle faecal consumption and soil bioturbation?

- **Chapter 5 –** ***Does selective logging stress tropical forest invertebrates? Using body fat stores to examine sublethal responses in dung beetles***

Most research on sublethal effects of forest degradation is focused on vertebrates in temperate regions. Consequently, we have a very limited understanding about how environmental disturbances could induce sublethal effects on invertebrates. Therefore, the final research aim of this thesis was to address this knowledge gap by investigating whether selective logging could stress-induce sublethal effects upon the body fat content of three dung beetle species, and how these sublethal responses link to population-scale patterns. *Chapter 5 research questions:* (1) Does selective logging cause stress-induced sublethal effects on dung beetles? (2) Do sublethal effects match with population-scale responses to selective logging?

1.6 Thesis Structure

Each of the experimental chapters of this thesis have been written for publication: Chapter 2 is under *peer-review* in *Journal of Applied Ecology*, and I intend to submit Chapters 3, 4 and 5 for review and publication (target journals are *Forest Ecology and Management*, *PLoS ONE*, and *Conservation Physiology*, respectively). The structure of this thesis is therefore made up of stand-alone chapters linked by a common theme of selective logging in tropical forests and the effects on dung beetle diversity, physiology and ecosystem processes they mediate. Chapter 6 provides a summary of the key findings resulting from each data chapter, considering their importance for science and conservation policies in tropical forests under timber production pressure, as well as highlighting future research needs. Lastly, I gathered all the references from each of the above chapters and placed them after the Chapter 6, therefore reducing the thesis length (as well as the unnecessary use of paper) and avoiding the repetition of references cited in more than one chapter. The appendices at the end of the thesis demonstrate publications that have resulted from research I was involved with in addition to my direct doctoral research.

Chapter 2: WHAT THE EYES DO NOT SEE, THE FOREST DOES FEEL: ARE WE UNDERESTIMATING BIODIVERSITY LOSS IN DISTURBED TROPICAL FORESTS?

Selectively logged forest in the Brazilian Amazon, state of Pará.

2.1 ABSTRACT

Human alteration of the global environment is leading to a pervasive loss of biodiversity. Most studies evaluating human impacts on biodiversity occur after the disturbance has taken place using spatially distinct sites to determine the undisturbed reference condition. This approach is known as a space-for-time substitution (SFT). However, SFT could be underestimating biodiversity loss if spatial controls fail to provide adequate inferences about pre-disturbance conditions. We compare the SFT substitution with a before-and-after (BA) approach by assessing dung beetles before and after a logging exploration in the Brazilian Amazon. We sampled 34 logging management units, of which 29 were selectively logged with different intensities after our first collection. We used dung beetles species richness, species composition and biomass as our biodiversity response metrics and the gradient of selective logging intensity as our explanatory metric. Only the BA approach consistently demonstrated the negative impacts of logging intensification on all dung beetle community metrics, and it doubled estimates of species loss when compared to SFT. Moreover, the BA approach explained more of the variance in the relationships, and reached the critical significance p-value with a smaller number of spatial replicates than SFT. Our results suggest that SFT substitution may greatly underestimate the consequences on local species diversity and community turnover. These results have important implications for researchers investigating human impacts on biodiversity. Incentivising BA approaches will require longer-term funding, more time spent to gather the data and stronger links between researchers and landowners. However, BA approaches are accompanied by many logistical constraints, making the continued use of SFT studies inevitable in many cases. Finally, we highlight that non-significant results and weak effects should be viewed with caution.

Keywords: Before-after-control-impact (BACI). Chronosequences. Dung beetles. Land-use change. Rain forest. Reduced-impact logging. Resampling. Selective logging.

2.2 Introduction

It is well known that human alteration of the global environment is leading to a pervasive loss of biodiversity (Cardinale et al., 2012b; Newbold et al., 2015). Habitat loss and degradation remain the main causes of biodiversity loss and species extinctions across the world (Krauss et al., 2010; Mantyka-pringle et al., 2012). This is particularly so in the tropics, which contain most of the world’s biodiversity and have some of the highest land-use change rates (Lambin et al., 2003; Romdal et al., 2013).

Understanding the rate and spatial distribution of biodiversity loss requires accurate assessments of the impacts of land-use change and land management (Gibson et al., 2011; Romdal et al., 2013). Much ecological research has been directed at this, and there are a growing number of attempts to summarise this in meta-analyses (Bicknell et al., 2014b; Burivalova et al., 2014; Gibson et al., 2011; Newbold et al., 2015, 2012; Pfeifer et al., 2014). For example, a global meta-analysis clearly shows how land-use changes and associated pressures reduce the local terrestrial biodiversity (Newbold et al., 2015), while a pan-tropical meta-analysis provides some hope by highlighting the relatively great biodiversity value from selectively logged forests (Gibson et al., 2011). Despite the obvious appeal of these global syntheses, any such meta-analyses will only ever be as reliable as the design of the many studies that supply the data. It is therefore timely and important to examine whether the most frequently used study designs are likely to reveal the true impacts of human activities, and provide information that can be used for developing effective conservation strategies.

One important problem researchers face when evaluating human impacts on biodiversity is that the main disturbance events have already taken place. As a result, studies are forced to use spatial reference sites in nearby regions where the human impact of interest has not yet occurred (e.g. Edwards *et al.* 2011, 2012b; a; Thomaz *et al.* 2012; Berenguer *et al.* 2014). This approach is known as a space-for-time (SFT) substitution and dominates the literature on land-use change. For example, we reviewed the available literature evaluating selective logging impacts on tropical invertebrates, and found that 49 out of 53 publications evaluating these effects were based on space-for-time approaches (see Appendix S2.1). A major issue with SFT approaches is to assume that average changes over space are representative of changes through time (Johnson and Miyanishi, 2008). In an ideal world, when researchers are able to sample prior to the disturbance event, they can use a before/after-control/impact design (BACI) (Smith, 2013) - abbreviated here to before-and-after (BA). Before-and-after designs have been conducted in several experimental landscape manipulations (Chai et al., 2012; Forkner et al., 2006; Kibler et al., 2011) and studies (e.g. see Table S1, Appendix A). While most researchers recognise the potential benefits of a BA design (Bicknell et al., 2015; Kibler et al., 2011), it is not clear to what extent a reliance on SFT studies could be affecting inference about human impacts on biodiversity in terrestrial environments.

We address this by using a planned commercial logging operation in the Brazilian Amazon to assess whether space-for-time assessments could result in an underestimation of biodiversity loss in tropical forests. We focus on selective logging as it is one of the most important economic activities in tropical forests (Guariguata et al., 2010; Wilson et al., 2010) and has been suggested as less environmentally damaging compared to other anthropogenic disturbances like fire, agriculture and fragmentation (e.g. Barlow *et al.* 2006; Gibson *et al.* 2011; Edwards *et al.* 2012a; b). We use dung beetle as a model system, since they are considered as a cost-effective and responsive taxonomic group for evaluating the biological impacts of forestry practices (Bicknell et al., 2014a; Edwards et al., 2012b, 2011; Gardner et al., 2008a; Scheffler, 2005; Slade et al., 2011).

In particular, we examine to what extent space-for-time and before-and-after approaches yield different conclusions regarding the relationship between selective logging intensity and changes in local dung beetle species richness, species composition and biomass. We focus on richness and composition as they have been frequently used in previous studies on a range of tropical taxa (Barlow et al., 2007; Bicknell et al., 2014b; Burivalova et al., 2014; Edwards et al., 2012b; Gibson et al., 2011; Imai et al., 2012; Socolar et al., 2015). We include biomass as this has been extensively used to assess the impacts of tropical forest disturbance on dung beetles (Nichols et al., 2013a; Scheffler, 2005; Slade et al., 2011). We compare SFT with BA by focusing on the difference in effect size (slope of regression) and proportion of explained variance (R^2). Finally, we use a resampling procedure to examine which approach can assess the effects of selective logging with the smallest number of sample units, given that before-and-after approaches require at least two visits to a study region.

2.3 Methods

2.3.1 Site description

Sampling was carried out in the *Jari Florestal* landholding, located at the State of *Pará* in the Northeastern Brazilian Amazon (0°27'S, 51°40'W; Chapter 1: Figure 1.3). The primary forests in the region are subject to low levels of disturbance from subsistence hunting and extraction of non-timber forest products (Parry, Barlow & Peres 2009). The climate is characterized by hot-humid (Köppen's classification), with annual average temperature and precipitation of 26 ºC and 2115 mm respectively (Coutinho and Pires, 1996). Reduced-impact commercial logging started in 2003, with plans to log approximately 544,000 ha of native forest over a 30 year cutting cycle. This management is certified by the Forest Stewardship Council (FSC) and is one of the largest certified logging concessions in the Amazon with average annual production of 30,000 m^3 of timber (FSC 2014). Logging activities are planned following FAO guidelines (Dykstra and Heinrich, 1996), which included a pre-harvest mapping and measuring of all commercially viable trees with DBH ≥ 45 cm. The harvesting and extraction of timber along skid trails generally take place during the dry season (August to November), and directional felling is used to minimise collateral damage to other trees. During the pre-harvest inventory the logging concession is subdivided into 10 ha (250 x 400 m) planning units. Commercially viable trees are mapped across all of these planning units, and this forms the basis for planning the logging operation in the following year.

2.3.2 Spatial design

We used the company's pre-harvest inventory and operational logging plan to select 34 sample units situated along a gradient of planned logging intensity (see Chapter 1: Figure 1.3). These included five control sites that would not be logged during the course of the study, and 29 logging units which were destined to be logged between July and September 2012 (Appendix S2.2). As logging impacts are related to logging intensity (Burivalova et al., 2014; Picard et al., 2012), we aimed to assess logging impact as a continuous (rather than categorical) effect. We therefore selected logging units along the gradient of planned logging intensities, which resulted in gradient from 0 - 7.9 trees ha^{-1} (or 0 - 50.31 m^3 ha^{-1}) of timber that was eventually extracted (see Table S2.2). The five unlogged control units included in this range were the same size as the logged units, and held dung beetle communities representative of undisturbed primary forests in our study region (see Appendix S2.3; Figure S2.2). They were located approximately 6.5 km from the closest logging operations to ensure sampling independence and to avoid any spillover effects from the logging operation (Block et al., 2001). As such, they are representative of the distance between logged and undisturbed reference sites in many logging studies using space-for-time approaches (Table S2.1).

We used the number of removed trees in each 10 ha sampled unit as our measure of logging intensity for all analyses, as *a priori* we assumed that the number of tree fall events and skidding trails would be the most important predictor of ecological impacts. Moreover, like others we found high co-linearity ($n=34$, $r = 0.91$, $p<0.001$) among number of trees and volume of removed timber by selective logging (c.f. Picard, Gourlet-Fleury & Forni 2012).

2.3.3 Temporal design

We carried out two dung beetle collections in all 34 sample units. The first collection gathered pre-logging data and occurred between June and July 2012, approximately 45 days before the logging operation began. The second collection took place in 2013, and gathered post-logging data approximately 10 months after logging activities ended. It also occurred in June and July, to minimize possible effects from seasonal variation. At all sites, dung beetles were sampled in exactly the same locations, and following the same methods, in both sample periods. Sampling locations were relocated based on marking tape, or by GPS when disturbance from logging activities meant this could not be found.

2.3.4 Sampling of dung beetles

In both collection periods, dung beetles were sampled in each unit using six pitfall traps spaced 100 meters apart in a 2x3 rectangular grid, so that traps were at least 75 meters from the edge of the logging unit (Appendix S2.1, Figure S2.3). This spacing of traps helped insure independence between them (Silva & Hernández 2015) as well as an even spatial coverage of each logging unit. Pitfall traps were plastic containers (19 cm diameter and 11 cm deep) buried with their opening at ground level, containing approximately 250 ml of a saline solution. A plastic lid was placed above the top as a rain cover. A small plastic cup containing approximately 35 g of pig dung mixed with human dung (4:1 pig to human ratio, Marsh *et al.* 2013) was attached by a wire above each pitfall. Data from the six pit fall traps in each unit were pooled to get an aggregate value and improve representation.

We restricted our sample window to 24 hours in each collection period, as short sample periods are known to be efficient at attracting a representative sample of the local beetle community (Braga et al., 2013; Nichols et al., 2013b). Moreover, longer sample periods would have increased the probability of attracting dung beetles from outside the sample units (Silva & Hernández 2015), and therefore from units with different logging intensities. Finally, evidence from data collected in the same region suggests a 24 hour sampling period as a good predictor of community metrics from longer sampling durations (see Appendix S2.3; Figure S2.5).

All dung beetles that fell in pitfall traps were dried and transported to the laboratory where they were identified to species, or morphospecies where this was not possible. We calculated the average biomass of each species from the dry weight of 15 individuals (when possible) using a Shimatzu AY220 balance with precision to 0.0001g. Voucher specimens were added to the Reference Collection of Neotropical Scarabaeinae in the Insect Ecology and Conservation Laboratory, Universidade Federal de Lavras, Brazil.

2.3.5 Data analyses

We ran all analyses and statistical models in the R Software version 3.2.0 (R Core Team, 2015). We used generalized linear models (GLMs) to obtain the slope, R^2 and p-value of the relationship between logging intensity and the dung beetle species richness, composition and biomass (Figure 2.1). All GLMs were submitted to residual inspection to evaluate the adequacy of error distribution (Crawley, 2002). We outline the two different sets of GLMs below.

Before and after (BA): The pre-logging dung beetle community metrics were used as a temporal control/baseline to examine post-logging effects under the BA approach. Thus, we used Δ species richness, Δ species composition and Δ biomass as dependent variables. Δ was based on the difference between total species richness and biomass from post-logging minus pre-logging collection within each sampled unit. The Δ species composition was measured as the pairwise beta-diversity (Socolar et al., 2015) based on the Bray-Curtis similarity index (1 – dissimilarity) among pre- and post-logging collections within each sample unit.

Space for time (SFT): We only considered the post-logging biological metrics and analysed the slope and R^2 using the actual values of species richness, species composition, and biomass. Species composition was estimated as the average Bray-Curtis similarity between each of the 29 logged units and the five control units. For control units, species composition was considered as the average similarity between each control plot and the other four control units. Species composition was calculated through the v*egdist* function (*vegan* package; Oksanen *et al.* 2015). Lastly, we tested whether our control sites represent typical undisturbed forest communities by comparing them with eleven primary forest sites sampled in the same year across the landscape (see Appendix S2.3).

To determine which sample design (BA or SFT) provided a more precise evaluation of the relationship between the number of removed trees and biological metrics, we used a resampling procedure based on 1000 bootstrap samples with replacement in the *boot.ci* function from *boot* package (Canty & Ripley 2015; Davison and Hinkley, 1997). This function was also used to estimate frequency distributions, median precision and 95% confidence intervals of regression slopes and R^2's from the SFT and BA linear models (Figure 2.2). To compare the sampling efficiency of the SFT and BA approaches, we checked the minimum sampling effort and number of spatial replicates needed to get a significant regression (at $p<0.05$). We ran the models 10000 times per sample size with a randomized input variable between five and 34 samples, without replacement, to generate the mean p-values (±SD) for each sample size (Figure 2.3).

As adjacent sites may be more similar and naturally hold more closely related biological communities (Kühn and Dormann, 2012; Soininen et al., 2007), we checked for spatial autocorrelation by performing Pearson-based Mantel tests (Legendre and Legendre, 1998) with 1000 permutations in the *mantel* function (*vegan* package; Oksanen *et al.* 2015). We repeated the

Mantel tests using both the pre- and post-logging dung beetle data, allowing us to examine whether spatial autocorrelation existed on both sets of analysis. We also repeated these including and removing the five control plots, to examine whether our controls were important in changing patterns. Finally, we plotted the residuals from the GLMs themselves on spatial maps of the sample sites, providing an intuitive visual assessment of the presence of spatial effects in the analysis (Baddeley et al., 2005; Kühn and Dormann, 2012) (see Appendix S2.4 for details of Mantel tests and residual plots).

2.4 Results

Across our 34 sample units, we recorded 4846 dung beetles (pre-logging: 3720; post-logging: 1126) from 53 species (pre-logging: 49; post-logging: 40). Irrespective of where or when we sampled, undisturbed forests (i.e. the control sites pre-logging, the control sites post-logging, and the logging units pre-logging) held statistically similar numbers of dung beetle species (Appendix S2.3, Figure S2.2).

2.4.1 Before-and-after (BA) and Space-for-time (SFT) approaches

Both BA and SFT approaches showed significant negative effects of increasing logging intensities on dung beetle species richness, although the BA approach was both more significant than SFT and explained more of the variance in the dung beetle richness (Figure 2.1A & D). The BA approach also had a higher proportion of variance explanation than SFT when considering species composition and biomass. Crucially, it was the only method to detect a significant effect of logging intensity at $p<0.05$ for these metrics (Figure 2.1B-C). The greater statistical power of the BA approach for detecting changes in the local species richness, species composition and biomass was clearly demonstrated using bootstrapping: BA had significantly higher R^2 values than SFT (Figure 2.2A-C), and the bootstrapped regression slopes for species richness, composition and biomass were significantly more negative for BA than SFT (Figure 2.2D-F).

Our analysis of sampling efficiency showed that the BA approach reaches the critical p-value (0.05) with fewer spatial replicates than SFT, and this occurred for species richness (>15 versus >23, respectively), species composition (>20 versus >35, respectively) and biomass (>24 versus >34, respectively) (Figure 2.3A-C). Results were somewhat different for species richness and biomass when we considered the sampling effort instead of the number of sample replicates, as the BA approach requires both pre- and post-logging collections. Under this scenario, the BA approach required approximately 35 and 50 sample units to reach the p-value line for species richness and biomass, respectively, while STF required over 25 and 35 sample units to reach the same critical p-value (Figure 2.3D & F). For species composition, the BA approach still required less sample units than SFT (Figure 2.3E).

The Mantel tests of distances among sampled units with corresponding dung beetle species richness and biomass showed a weak but significant degree of spatial autocorrelation in the pre-logging data (species richness $r = 0.18$, $p = 0.005$; biomass $r = 0.12$, $p = 0.035$). Importantly, this spatial autocorrelation disappeared in the post-logging collection (species richness $r = -0.41$, $p = 0.999$; biomass $r = -0.42$, $p = 0.999$), even when control units were excluded from analysis (see Appendix S2.4), and there was no discernible visual association between model residuals and geographical location (Appendix S2.4).

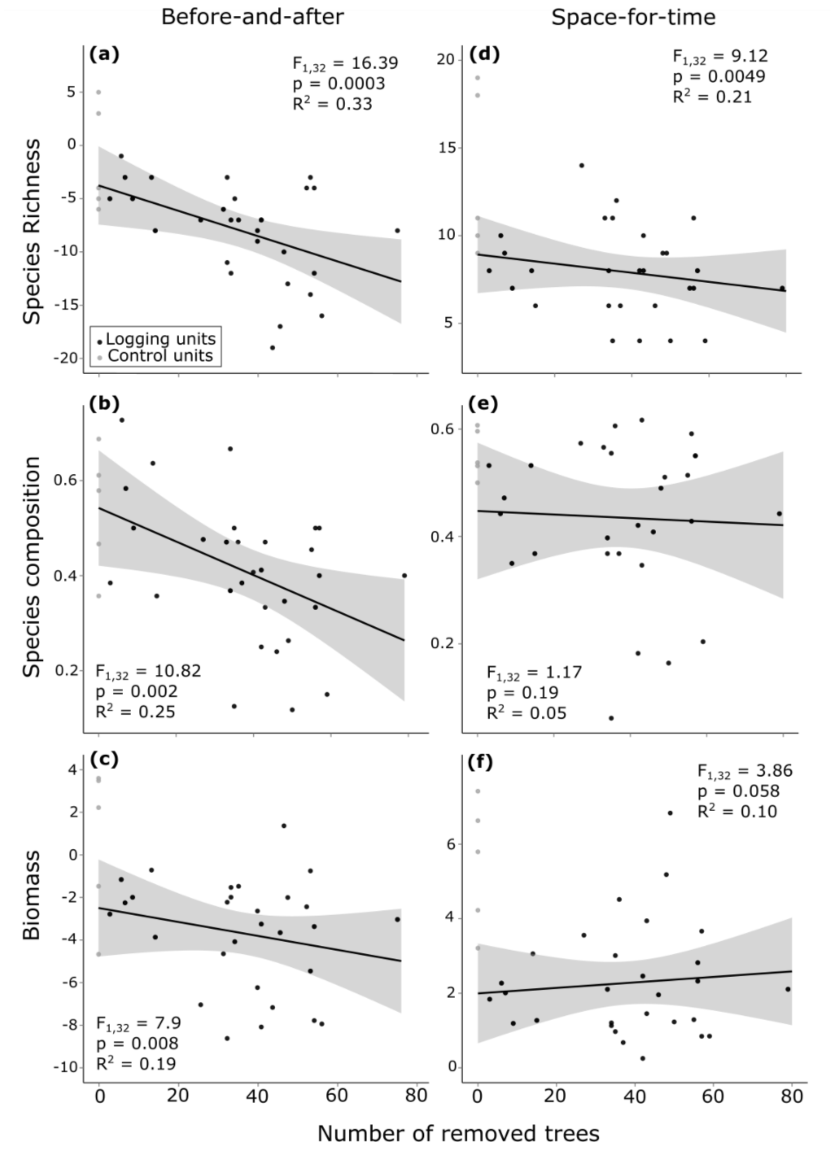


Figure 2.1 (A) Δ species richness; (B) Δ species composition; (C) Δ biomass; (D) post-logging species richness; (E) post-logging species composition and (F) post-logging biomass of dung beetles (n = 34) versus increased number of removed trees (n.10 ha^{-10}) in the Amazon forest, Brazil. Black dots represent the 29 logging units with different selective-logging intensities and the five grey dots represent the five unlogged control units. The lines result from fitting the data to the generalized linear models with respective family distribution.

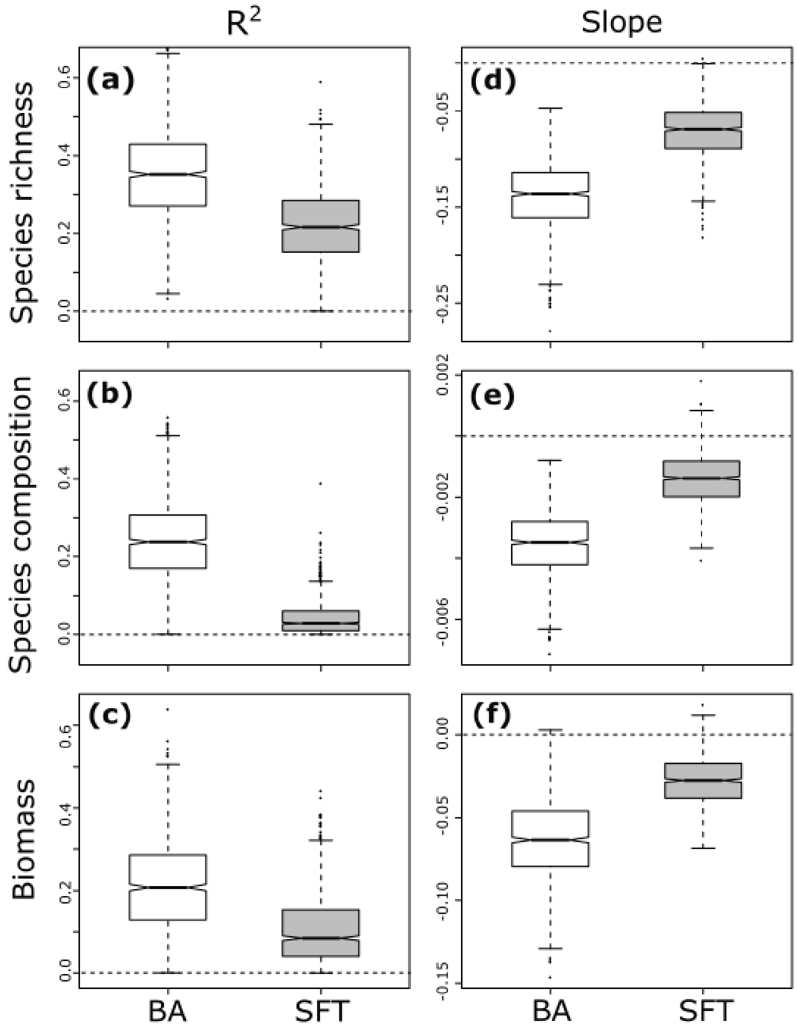


Figure 2.2 Accuracy comparison regarding the proportion of explanation (R2) and effect size (slope of fitted regression) from generalized linear models through the before-and-after (BA) and space-for-time (SFT) approaches. Proportion of explanation and effect size comparisons were made for dung beetle species richness (A & D), species composition (B & E) and biomass (C & F) facing the increased number of removed trees by selective logging on Amazon forest, Brazil. Bootstrapped confidence intervals (represented by vertical dashed lines) were created by resampling procedure based on 1000 bootstrap samples with replacement. On the boxplots, the notch area marks the 95% of confidence intervals for the medians (black horizontal lines). The grey and dashed horizontal line marks the zero line and outliers are shown in black dots.

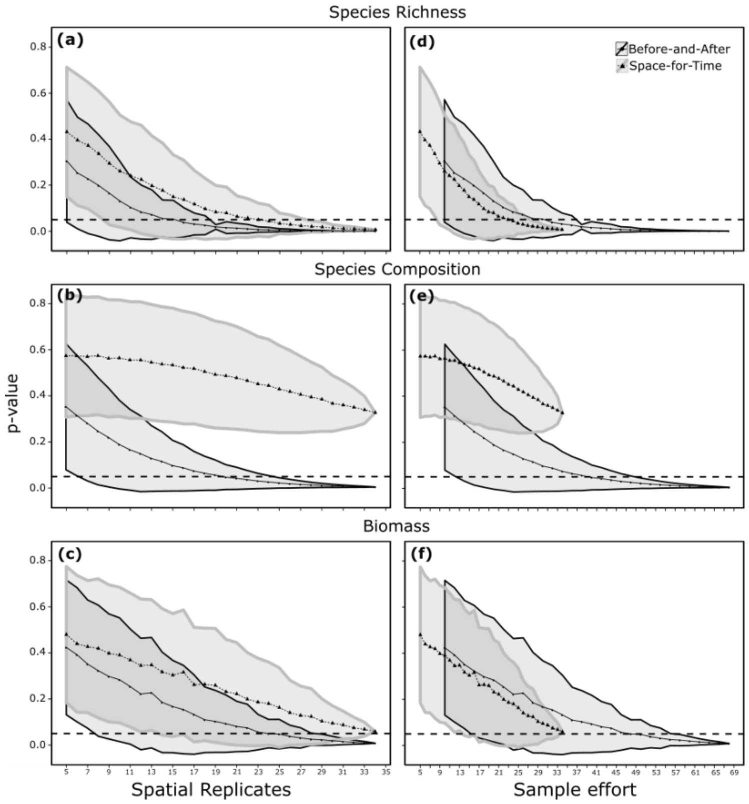


Figure 2.3 Minumum sampling effort and number of spatial replicates for BA and SFT approaches reach the critical 0.05 p-value (represented by the black horizontal dashed line). Bootstrapped p-values from GLMs with dung beetle species richness, species composition and biomass facing the increased number of removed trees in the Amazon forest, Brazil. On thex-axis, spatial replicates indicates how many sampled units each approach needs to achieve the siginificance level for (A) species richness, (B) species composition and (C) biomass, whereas sample effort indicates the number of replicates dubling the sampled units for before-and-after approach, since this approach needs to go twice in each spatial replicate, for species richness (C), species composition (D) and biomass (E). GLMs were run 10,000 times, without replacement and with a randomized input variable between 5 and 34 samples. For SFT inference we considered just the post-logging data, while for the BACI approach we ran the models with Δ species richness, Δ species composition and Δ biomass as dependent variables. The grey bounds represent the 95% confidence intervals.

2. 5 Discussion

Although both before-and-after and space-for-time approaches identified some disturbance effects on dung beetle communities, our comparison provide important evidence that BA approaches highlight more severe consequences of human disturbance on local (α) diversity (species richness) and β-diversity (compositional similarity; Socolar *et al.* 2015). In particular, BA approaches revealed more than double the number of species lost from the most disturbed plots, as well as significantly higher estimates of changes in dung beetle species composition and biomass. The significantly weaker effects revealed by the SFT approach are of great concern: SFT designs are the most commonly used method for assessing the biological consequences of selective logging on tropical invertebrates (Table S1), and underpin most assessments of biodiversity and ecosystem functioning losses caused by anthropogenic forest disturbances (e.g. Edwards *et al.* 2011, 2012b; a; Thomaz *et al.* 2012; Berenguer *et al.* 2014; Solar *et al.* 2015).

Although our comparison is restricted to a single taxa and a single disturbance event, the magnitude in the scale of effects revealed by BA and SFT approaches for dung beetle α and β diversity suggests that the potential issues of SFT could apply to other anthropogenic disturbances (such as wildfire, hunting or land-use intensification) and other taxa. Furthermore, the robustness of our conclusions was supported by the Mantel test results and spatial residual plots (Appendix S2.4) showing that these patterns were driven by logging intensity and not by any spatial autocorrelation in the data. However, our post-logging collection was conducted about one year after logging operations, when logged sites are in their most disturbed state (West et al., 2014). It would be important to evaluate how BA and SFT studies compare when examining longer-term recovery post-disturbance. Likewise, although providing evidence that BA approach better detect changes in species diversity and composition at local scales (Chai et al., 2012; Kappes et al., 2010), further work is needed to examine how study designs alter effect sizes based on gamma diversity, which often contribute to global or pan-tropical meta-analyses (e.g. Gibson *et al.* 2011; Newbold *et al.* 2015). With further investigation across sites and taxa it may be possible to develop a generalizable correction factor to be applied to biodiversity loss assessments relying on space-for-times designs (e.g. Cleary *et al.* 2009; Edwards *et al.* 2011, 2012b; a).

Despite the advantages of BA studies, there are good reasons why they have not been used with more frequency (Kibler et al., 2011). Even when disturbance events have not yet occurred, it is often impossible to accurately predict where and when they will happen. This makes it particularly hard to apply BA designs to wildfires, illegal logging or land-use change. Moreover, even where activities are planned 2-3 years in advance, as in the case of licenced and certified selective logging, it is necessary to have an effective communication between researchers, decision makers and practitioners (companies, planners, and resource managers) in order for BA studies to take place. The fact that most assessments of the biological impact of selective logging rely on SFT approaches (Appendix S2.1) shows the difficulty of developing these relationships within the time frame of research projects. Our results therefore support calls to close this ‘knowledge-doing’ gap that exists throughout conservation science (Boreux et al., 2009; Habel et al., 2013), and show how effective communication and partnerships between researchers and the private sector could be used to support effective conservation practice (Wu and Hobbs, 2002). These partnerships need to start long before research is undertaken, both to optimise the experimental design and integrate or overcome concerns from researchers and stakeholders.

We also highlight an important logistical constraint of BA, in that it needs double the sampling effort (Figure 2.3) compared to just once in the SFT approach. Achieving the pre- and post-disturbance samples inevitably increases both the time and costs required to collect data, but the additional time may be an equally important limiting factor: most research projects, including postgraduate studies, are a maximum of 3-5 years in duration, which limits the data collection phase of projects to just 1-2 years. It is clearly difficult for students and researchers to undertake BA studies in relatively short-term research projects or doctoral theses, which rarely allow time enough for two or more field seasons. This can be resolved by longer-term research partnerships that transcend individual studies.

Finally, if the biological baseline as a whole has been shifted by widespread disturbance, then before-and-after approaches themselves risk underestimating biodiversity loss. We were fortunate that *Jari* landholding has relatively undisturbed primary forests prior to logging operations (Parry, Barlow & Peres 2009). This allowed us to sample both pre- and post-logging, and verify the intactness of our pre-logging controls by comparing them with other sites in undisturbed primary forests (Appendix S2.3). However, where forests have been affected by widespread anthropogenic activities (e.g. fires or hunting), the biota present in the before survey will have been filtered by previous disturbances and will not contain the most disturbance-sensitive species. In these case, before-and-after comparisons risk underestimating biodiversity loss, and need to be interpreted accordingly (Baum and Myers, 2004; Gardner et al., 2009; Kibler et al., 2011).

2.6 Conclusions

Our study has broad implications for applied ecology and conservation science, as we show that the most frequently used experimental design may lead us to underestimate the consequences of land-use change and forest disturbances on local species diversity and their turnover. While before-and-after approaches are accompanied by many logistical constraints (e.g. they require a longer time and more sample effort), we believe they should be strongly encouraged in order to re-evaluate human impacts on biodiversity. Finally, although our main aim was to compare methodological approaches, our results also have some important implications for reduced-impact logging which is being planned in timber concessions across 400 Mha of tropical forest

(Blaser et al., 2011), as they demonstrate high rates of community turnover as well as sharp losses in species diversity and dung beetle biomass, particularly at high logging intensities (c.f. Burivalova, Şekercioğlu & Koh 2014). This emphasizes the need for careful planning and further research before forest management can be termed sustainable for biodiversity conservation.

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2.7 Supplementary Information

Appendix S2.1 Literature review

Using ISI Web of Knowledge (http://webofknowledge.com), we searched for publications on the impacts of selective logging on the tropical invertebrate biodiversity. We performed this search in December 2014 by using the terms “selective logging” AND “tropical forest” AND “invertebrate” AND “insects”. We did not specify where these terms should occur in the articles or the publication date of the articles. Web of Knowledge returned 31 publications, which were then examined and filtered to ensure we considered all studies reporting the impact of selective logging on tropical invertebrate fauna. We assessed the pertinence of each article according to its tittle and abstract: all field-based studies related to the impact of selective logging on biodiversity of invertebrate fauna were retained. Modeling studies and reviews were excluded. In total, 53 articles were considered for final assessment.

Table S2.1 List of studies examining the impacts of selective logging on tropical invertebrates. Table shows the authors and year of publication, the assessed taxa, published journal, evaluated experimental design (ED) and distance between control and logging units in kilometers (DC). [a]SFT = space-for-time; [b]BA = before-and-after approach; [c]NA = No information, [d]Adj = adjacent.

Study	**Taxa**	**Journal**	**ED**	**DC**
Aguilar-Amuchastegui & Henebry (2007)	Dung beetles	Forest Ecology and Management	SFT [a]	≤10
Akutsu, Khen & Toda (2007)	Different groups	Ecology Research	SFT	NA [c]
Andersen *et al.* (2009)	Ant	Forest Ecology and Management	SFT	≤2
Basset *et al.* (2001)	Herbivore insects	J. of Applied Ecology	BA [b]	≤2
Berry *et al.* (2010)	Ants	Biodiversity and Conservation	SFT	≤5
Bicknell *et al.* (2014)	Dung beetles	Ecological Indicators	SFT	≤2
Burghouts *et al.* (1992)	Litter invertebrates	Phil. Trans. Royal Soc. of London, Series B	SFT	NA
Cartar (2005)	Bumble bees	Biodiversity and Conservation	BA	≤5
Chung *et al.* (2000)	Beetles	Bulletin of Entomological Res.	SFT	80

Study	**Taxa**	**Journal**	**ED**	**DC**
Cleary (2003)	Butterflies	Oecologia	SFT	≤5
Cleary (2004)	Butterflies	J. of Economic Entomology	SFT	≤2
Cleary & Mooers (2006)	Butterflies	Diversity and Distributions	SFT	≤5
Cleary *et al.* (2005)	Butterflies	J. of Applied Entomology	SFT	NA
Cleary *et al.* (2009)	Butterflies	Basic and Applied Ecology	SFT	NA
Davis (2000)	Dung beetles	Environmental Entomology	SFT	>1
Davis *et al.* (2001)	Dung beetles	J. of Applied Ecology	SFT	>1
Davis & Sutton (1998)	Dung beetles	Diversity and Distributions	SFT	>1
Dumbrell & Hill (2005)	Butterflies	Biological Conservation	SFT	Adj [d]
Dumbrell *et al.* (2008)	Butterflies	J. of Applied Ecology	SFT	Adj
Edwards *et al.* (2010)	Dung beetles	Proc. Royal Soc. of London B Biol. Science	SFT	1-90
Edwards *et al.* (2012b)	Dung beetles and ants	Ecological Applications	SFT	1-90
Edwards *et al.* (2012a)	Understory invertebrates	J. of Insect Conservation	SFT	Adj
Edwards *et al.* (2014)	Dung beetles and ants	Global Change Biology	SFT	1-90
Eltz (2004)	Bees	J. of Tropical Ecology	SFT	>50
Eltz *et al.* (2002)	Bees	Oecologia	SFT	>50
Eltz *et al.* (2003)	Bees	Forest Ecology and Management	SFT	>50
Forkner *et al.* (2006)	Leaf-chewing herbivore insects	Conservation Biology	BA	NA
Ghazoul & Ghazoul (2002)	Butterflies	Biodiversity and Conservation	SFT	≤10
Gunawardene, Majer & Edirisinghe (2010)	Ant	Forest Ecology and Management	SFT	>1
Hamer *et al.* (2003)	Butterflies	J. of Applied Ecology	SFT	≤10
Hill (1999)	Butterflies	J. of Applied Ecology	SFT	Adj
Hill *et al.* (1995)	Butterflies	J. of Applied Ecology	SFT	>1
Hill *et al.* (2003)	Butterflies	J. of Applied Ecology	SFT	NA
Jones & Prasetyo (2002)	Termites	The Raffles Bulletin of Zoology	SFT	NA
Jones *et al.* (2003)	Termites	J. of Applied Ecology	SFT	<5
Kreutzweiser *et al* (2005)	Macroinvertebrates	J. North Am. Benth. Society	BA	<1
Lewis (2001)	Butterflies	Conservation Biology	SFT	Adj
Lima *et al.* (2000)	Termites	Forest Ecology and Management	SFT	Adj
Negrete-Yankelevich *et al.* (2007)	Soil macroinvertebrates	Applied Soil Ecology	SFT	≤2
Nummelin & Zilihona (2004)	Arthropod fauna	Forest Ecology and Management	SFT	NA
Oliver, Mac Nally & York (2000)	Arthropod fauna	Forest Ecology and Management	SFT	Adj
Scheffler(2005)	Dung beetles	J. of Tropical Ecology	SFT	Adj
Schleuning *et al.* (2011)	Bees, army-ants and decomposing leaf litter fauna	PLoS ONE	SFT	≤5

Study	Taxa	Journal	ED	DC
Schulz & Wagner (2002)	Ants	Oecologia	SFT	NA
Slade, Mann & Lewis (2011)	Dung beetles	Biological Conservation	SFT	≥5
Summerville & Crist (2002)	Butterflies	Ecological Applications	SFT	≤2
Vasconcellos *et al.* (2008)	Termites	Neotropical Entomology	SFT	NA
Vasconcelos, Vilhena & Caliri (2000)	Ants	J. of Applied Ecology	SFT	≤2
Wagner (2000)	Beetles	Biotropica	SFT	NA
Widodo *et al.* (2004)	Arboreal ants	Entomological Science	SFT	NA
Willott (1999)	Butterflies	Phil. Trans. Royal Soc. of London, Series B	SFT	4
Willott *et al.* (2000)	Butterflies	Conservation Biology	SFT	≤10
Wood & Gillman (1998)	Butterflies	Biodiversity and Conservation	SFT	≤5

Appendix S2.2 Information from the sample units

We accessed the company’s pre-harvest inventory before our first dung beetle collection (pre-logging), which provided an approximation of how many trees were eventually cut down and removed from each logging unit. Our 29 logging units were therefore representative of a long gradient of logging intensities.

Table S2.2 Details of sampled units. [a]NRT = Number of removed trees; [b]Vol = Volume of wood removed in the 10 ha sample units (m^3 ha^{-1}); [c]S-pre = Pre-logging sampling dates carried out in 2012; [d]S-post = Post-logging sampling dates carried out in 2013; Cutting dates = Dates when logging operation happened within the unit; [e]DI= Days interval between logging operation and post-logging collection; and *NL = No logging activities.

Unit	[a]NT	[b]Vol	[c]S-pre	[d]S-post		Cutting dates			[e]DI
1	27	88.19	09-jun	15-jun	18/08/12				300
2	43	231.76	09-jun	15-jun	14-23/08/12	19-21/09/12	28-29/01/13		304
3	57	301.07	09-jun	15-jun	14-23/08/12	21/09/12	29/01/13		304
4	48	117.76	09-jun	15-jun	15- 22/08/12	21/09/12			303
5	46	306.59	09-jun	15-jun	24 to 27/08/12	19-21/09/2012	06/10/12	28/01/13	294
6	36	189.25	13-jun	19-jun	29 & 30/08/12	06/09/12	21 &29/01/13		293
7	55	316.58	13-jun	19-jun	05 & 06/09/12	12/09/12	19/09/12		286
8	79	503.16	13-jun	19-jun	30/08/13	01-03/09/12	07-08/09/12	18/01/13	292
9	57	356.55	13-jun	19-jun	27 & 28/08/12	01 & 10/09/12			295

Unit	[a]NT	[b]Vol	[c]S-pre	[d]S-post		Cutting dates			[e]DI
10	33	89.519	16-jun	22-jun	02-04/09/12	07/09/12			292
11	43	115.45	16-jun	22-jun	06-08/09/12				257
12	56	277	16-jun	22-jun	29-31/08/12	21 & 27/09/12	30/01/13		296
13	42	132.69	16-jun	22-jun	29 & 31/08/12	04/09/12	22 & 28/09/12		296
14	37	107.11	16-jun	22-jun	16-18/08/12	29/08/12			309
15	35	188.47	20-jun	26-jun	22 & 23/08/12	20/12/12			307
16	50	175.65	20-jun	26-jun	21-23/08/12				308
17	34	204.07	20-jun	26-jun	02-06/08/12				327
18	56	231.72	20-jun	26-jun	25-28/07/12				335
19	59	327.05	20-jun	26-jun	26 -28/07/12	31/07-12	01-02/08/12	25/01/13	334
20	9	24.418	23-jun	03-07	25/07/12				342
21	6	14.528	23-jun	03-07	25 & 26/07/12				342
22	35	115.42	23-jun	03-07	25-27/07/12				342
23	49	142.56	23-jun	03-07	23-25/07/12	09/08/12			344
24	42	108.05	23-jun	03-07	10/08/12	23 & 24/09-12			326
25	14	30.15	26-jun	29-jun	20 & 21/07/12				343
26	3	7.27	26-jun	29-jun	02/08/12				330
27	34	128.14	26-jun	29-jun	21/07/12	23 & 24/07-12			342
28	7	15.07	26-jun	29-jun	23/07/12				330
29	15	38.84	26-jun	29-jun	24 & 25/07/12	08/08/12			339
30	0	0	29-jun	06-07	No logging				*NL
31	0	0	29-jun	06-07	No logging				*NL
32	0	0	29-jun	06-07	No logging				*NL
33	0	0	29-jun	06-07	No logging				*NL
34	0	0	29-jun	06-07	No logging				*NL

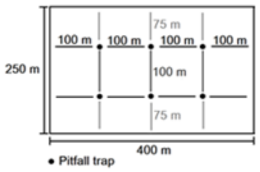

Figure S2.1 Experimental design within the sampled units. Pitfall traps were distributed in a 2x3 rectangular grid, spaced by 100 m apart each other and at least 75m from the sampled unit borders

Appendix S2.3 Supplementary experimental procedures

S2.3.1 Comparing our control units to primary forests in the study region

We examined if our five control units held levels of species richness that were typical of dung beetle fauna of primary forests across our study region, using data from other eleven primary forest sites sampled in 2010. We used generalized linear models using the *glm()* function on R (R Core Team, 2015) to compare the differences between average species richness, and *a posteriori* we used a contrast analysis to specify differences among levels.

Results showed no significant differences between dung beetle species richness among the eleven primary forests at our study region and pre and post-logging data from our five control units and pre-logging species richness from the 29 logging units. As expected from our main results, dung beetle species richness decreased after selective logging on the 29 logging units (Figure S2.2; $F_{4,75} = 22.88$; $p<0.001$).

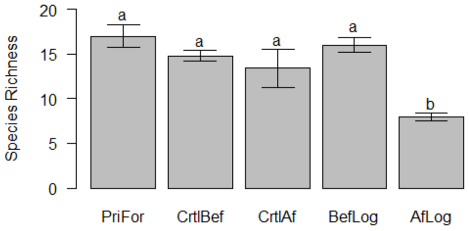

Figure S2.2 Dung beetle species richness from eleven primary forests at *Jari* Region (*PriFor*, n = 11), pre-logging control units (*CrtlBef*, n = 5), post-logging control sites (*CrtlAdf*, n=5), logging units pre-logging (*BefLog*, n = 29) and logging units post-logging (*AfLog*, n = 29).

S2.3.2 Sampling period comparisons

Baited pitfall traps are the most effective method to sample dung beetles (Flechtmann et al., 2009; Halffter and Favila, 1993; Larsen and Forsyth, 2005; Lobo et al., 1988; Marsh et al., 2013). We follow other researchers in opening our pitfalls traps during a 24 h period (Barraza et al., 2010; Braga et al., 2013; Estrada and Coates-Estrada, 2002; Medina and Kattan, 2002; Nichols et al., 2013b). This sampling period was specifically planned to avoid other known issues with bait traps, which is the risk of attracting individuals from far outside of our sampled units. This risk was recently confirmed by a study revealing the positive relation between time and distance moved by dung beetles (Silva and Hernández, 2015). However, we also show that a sampling period of 24 h is a good predictor of dung beetle communities sampled over longer periods of trap opening. We used data of dung beetle species richness from an experiment developed in 2010 at 11 primary forests from *Jari* region. Dung beetles were collected within each forest using five pitfall traps (one less than the number used in our study), baited with human dung and placed 50 m apart from each other. These pitfall traps were exposed to the dung beetle community during five days (120 h), whereas every 24 hours the dung beetles were collected and every 48 hours the baits were changed.

We used the *cor.test()* function from *stats* package on R (R Core Team, 2015) using the Pearson's coefficient to test the correlation between dung beetle species richness from 24 h sampling period with longer samples over 48 h and 120 h. In both comparisons, there was a strong positive correlation (Fig S2.3 - 48 h: Pearson's $\rho = 0.69$; $t = 2.88$; $p = 0.009$; and 120 h: Pearson's $\rho = 0.67$; $t = 2.73$; $p = 0.01$).

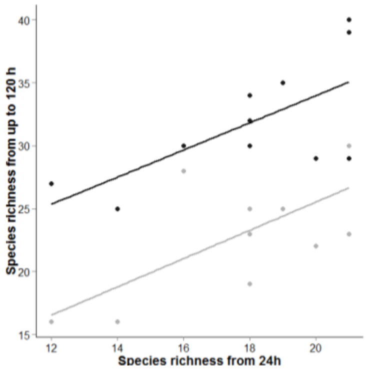

Figure S2.3 Correlations between dung beetle species richness from 24 h sampling period with longer sampling periods over 48 h (grey dots and line) and 120 h (black dots and line).

S2.3.3 Examining the pre-logging data

We examined the relationship between pre-logging dung beetle richness and biomass and the real number of trees removed after the pre-logging collection, as this provides us with an indication about any association between valuable timber stocks and dung beetle communities. In these models we excluded the five control units because they were not logged in the same year, so we have no information on planned or eventual tree removal.

There was a significant relationship between the number of trees eventually removed by selective logging and pre-logging dung beetle species richness and composition. However, we found no significant relationship among pre-logging dung beetle biomass and the number of trees that were eventually removed by selective logging (Figure S2.4).

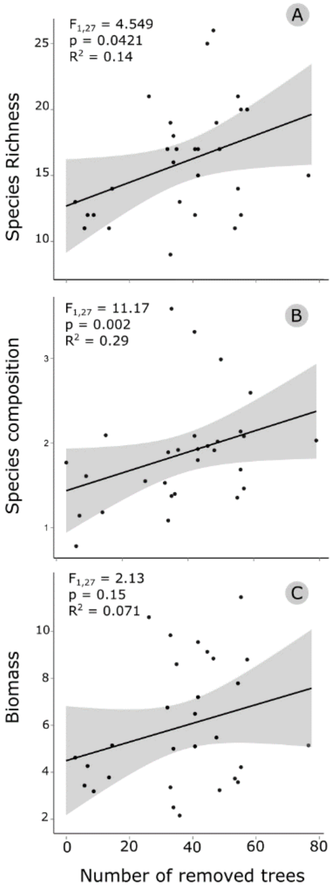

Figure S2.4 (A) Pre-logging dung species richness; (B) pre-logging species composition; and (C) pre-logging biomass of dung beetles (n=29) versus increased number of removed timber (n.10 ha^{-10}). The lines result from fitting the data to the generalized linear models with respective family distribution.

Appendix S2.4 Assessing spatial autocorrelation

S2.4.1 Mantel tests

We checked for spatial autocorrelation in our dataset by performing Pearson-based Mantel tests (Legendre and Legendre, 1998) with 1000 permutations in the ‘mantel()’ function from vegan package (Oksanen et al., 2015). We used the ‘Point Distance’ tool in ArcGIS Desktop 10.1 (ESRI, 2014) to calculate the straight line distance between the centroid of each sampled unit and the function ‘as.dist()’ from ‘stats’ package (R Core Team,

2015) to compute the distance matrices for geographical position and dung beetle species richness and biomass. Thereby, in order to verify whether the occurrence of spatial structuring changes after logging, Mantel tests were made separately for pre-logging and post-logging biological metrics. In addition, to check for the influence of control sites in the spatial autocorrelation tests, we excluded the five control sites from both pre and post-logging distance matrices of geographical and biological metrics and repeated the previous procedures. See the following Tables S2.3 to S2.5 for Mantel test results.

Table S2.3 Pearson-based Mantel results for dung beetle species richness.

	with control	*without control*
Pre-logging	r = 0.18; p = 0.005	r = 0.24, p = 0.02
Post-logging	r = - 0.41; p = 0.999	r = - 0.26, p = 0.99

Table S2.4 Pearson-based Mantel results for dung beetle biomass.

	with control	*without control*
Pre-logging	r = 0.12; p = 0.035	r = 0.16; p = 0.008
Post-logging	r = - 0.42; p = 0.999	r = - 0.21; p = 0.999

Table S2.5 Pearson-based Mantel results for dung beetle species composition.

	with control	*without control*
Pre-logging	r = 0.35; p = 0.01	r = 0.54 p = 0.001
Post-logging	r = 0.18; p = 0.01	r = 0.20; p = 0.01

S2.4.2 Spatial residual plots

We also used maps of residuals (spatial residual plots) to provide an effective diagnose of spatial trends influencing model results (Baddeley et al., 2005; Kühn and Dormann, 2012). Thus, we mapped the spatial distribution of residuals from each linear model, and used the function '*residuals.lm()*' from '*stats*' package (R Core Team, 2015) to obtain the residuals of each sampled unit from all fitted linear models. Then, the residuals of these models were plotted against its spatial location, wherein the magnitude of each point represents the absolute value of residuals for each sampled unit. The plots do not reveal any consistent influence of spatial location on model residuals.

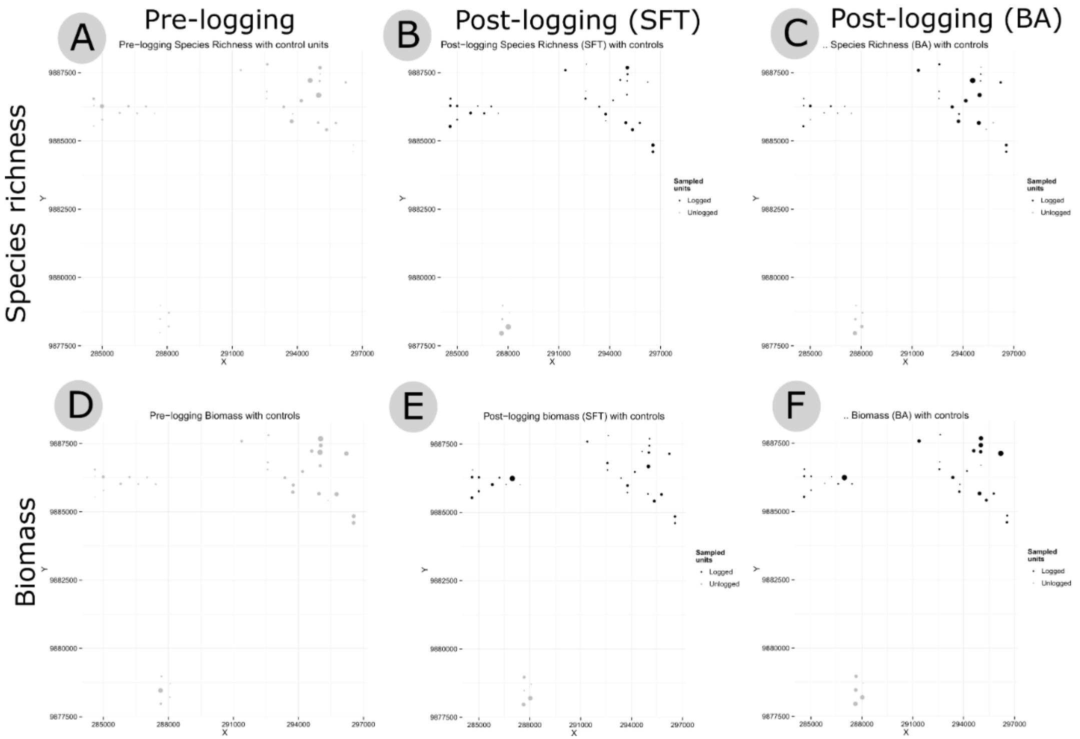

Figure S2.5 Map of residuals from linear models of dung beetle (A) pre-logging species richness; (B) post-logging species richness (SFT); (C) Δ species richness (BA); (D) pre-logging biomass; (E) post-logging biomass (SFT); and (F) Δ biomass (BA). Radii proportional to the absolute value of residuals. Logged sampling units are presented in black colour and pre-logging data or control units (unlogged) in grey.

Chapter 3: IDENTIFYING THRESHOLDS IN DUNG BEETLE RESPONSES TO LOGGING INTENSITY TO IMPROVE THE SUSTAINABILITY OF TROPICAL FOREST MANAGEMENT

3.1 ABSTRACT

Growing evidence suggests that the impacts of selective logging on both forest structure and biodiversity depend on logging intensities. Yet, few studies have explored logging intensities as a continuous metric to identify logging thresholds above which the biodiversity decreases. Similarly, our knowledge of logging impacts is limited by the uncertainty about the spatial scale of management recommendations. We used a before-and-after control-impact (BACI) design to assess the responses of dung beetle species richness, biomass, species composition and the ecological functions dung removal and soil bioturbation along a continuous gradient of logging intensities at two different spatial scales. We found concave-shaped relationships between the increased logging intensity and most of the dung beetle metrics. This demonstrates that biodiversity and ecosystem functioning processes may be lost even under low intensity disorders and highlights the importance of adopting land-sparing strategies within production forests. We also observed that most dung beetle metrics decreased steeply at low logging intensities until a threshold of selective logging around 18-20 m^3 ha-1 at local spatial scale (10 ha), and 17-27 m^3 ha-1, when measuring logging intensities at broader spatial scale (90 ha). Soil bioturbation was negatively affected by logging intensification; however, no evidence of logging impacts was found for dung removal rates. Our results reinforce that logging impacts on biodiversity depend on logging intensity; but measuring logging intensification at different spatial scales can improve our understanding of biological patterns within production forests. While empirically supporting that the biodiversity may not respond linearly to logging intensification, this study also promotes that logged forests can also retain ecosystem processes operating in primary forests.

Keywords: Logging thresholds. Reduced Impact Logging (RIL). Tropical forests. Logging intensity. Land-sparing. Reduced-impact logging. Selective logging.

3.2 Introduction

More than 403 million hectares of tropical forests have been officially designated for timber concessions (Blaser et al., 2011), where selective logging is one of the most widespread economic activities (Guariguata et al., 2010; Laporte et al., 2007; Pearce et al., 1999). Although it is undoubtedly less environmentally severe than other forms of forest disturbance or land-use change (i.e. Barlow *et al.*, 2006; Edwards *et al.*, 2012b; Gibson *et al.*, 2011), selective logging remains an important driver of degradation in tropical forests (Asner et al., 2009; Gatti et al., 2015), reducing carbon stocks (Berenguer et al., 2014) and negatively affecting both forest biodiversity (Asner, 2005; Burivalova et al., 2014) and ecosystem functioning (Edwards et al., 2014c; Foley et al., 2007; Schleuning et al., 2011; Slade et al., 2011). Improvements in the sustainability of forest management are fundamental for conservation in the tropics. For example, sustainable forest management is the most adopted REDD+ intervention in many tropical countries (Salvini et al., 2014) and is enshrined as a key aim of international biodiversity targets for 2020 (Convention on Biological Diversity, 2014).

Recent meta-analysis studies have demonstrated that logging impacts on forest structure and biodiversity are proportional to logging intensity (Burivalova et al., 2014; Martin et al., 2015). They also suggest non-linear biological responses, wherein there may be a logging intensity threshold above which multi-taxa animal species richness decreases (Burivalova et al., 2014). Defined as tipping points or zones at which sudden regime shifts occur from one ecological state to another (Bennett and Radford, 2003), ecological thresholds are likely if disturbance intensification (e.g. selective logging) induces nonlinear effects on community structure, composition and ecosystem functioning (Estavillo et al., 2013; Folke et al., 2004; Gardner et al., 2009; Huggett, 2005; Magnago et al., 2015; Thompson, 2011). Identifying these thresholds is therefore a major challenge for improving the sustainability of forest management (DeFries et al., 2004), and depending on the shape of the biodiversity response, could even help inform decisions about the land-sparing vs. land-sharing logging management debate (Edwards et al., 2014a). Yet, with the exception of a meta-analyses examining species richness (Burivalova et al., 2014), no empirical studies have used a robust before-and-after approach to assess the influence of logging thresholds on multiple metrics of ecological integrity, such as species composition, biomass and ecological functioning responses.

Our knowledge of the impacts of selective logging in tropical forests is also limited by uncertainty about the spatial scale at which management recommendations (i.e. limits on logging intensity) need to be implemented. For example, current legal requirements in Brazil impose limits to the volume of timber that can be removed from 10 ha logging units, but without any scientific evidence to support this decision. This is important, as a growing number of studies on different taxa demonstrate spatial scale-dependent responses of species richness to logging impacts (Dumbrell et al., 2008; Hamer and Hill, 2000; Hill and Hamer, 2004; Imai et al., 2012). There is also growing evidence that other biological metrics could respond to forest degradation at different spatial scales (Solar et al., 2015; but see Edwards et al., 2014a; Imai et al., 2012), but selective logging studies generally compare a range of sampling scales treating selective logging as a uniform land use with mean effect size (Burivalova et al., 2014). Yet, our understanding of how assessing logging intensities as a continuous (rather than categorical) effect at different spatial scales could influence the local responses of biodiversity and ecosystem functioning processes is limited.

In this paper, we address the above knowledge gaps using a before-and-after control-impact (BACI) experimental design to assess logging impacts on dung beetle species richness, biomass, species composition, and their associated ecological functions, in the eastern Brazilian Amazon. Dung beetles (Coleoptera: Scarabaeinae) are considered as good predictors of responses of many other taxa (Edwards et al., 2014b; Gardner et al., 2008a) and have been recommended as cost-effective and highly responsive indicators of changes caused by human disturbances in tropical forests

(Bicknell et al., 2014a; Davis, 2000; Davis et al., 2001; Edwards et al., 2012b, 2011; Gardner et al., 2008a). We focus on richness and composition as they have been frequently used in previous studies on a range of tropical taxa (e.g. Barlow *et al.*, 2007; Bicknell *et al.*, 2014b; Burivalova *et al.*, 2014; Edwards *et al.*, 2012b; Gibson *et al.*, 2011; Imai *et al.*, 2012; Socolar *et al.*, 2015). We include dung beetle biomass because it has been extensively used to assess the impacts of tropical forest disturbance on dung beetles (Nichols et al., 2013a; Scheffler, 2005; Slade et al., 2011). Furthermore, dung beetles provide insights into ecosystem functioning, such as secondary seed dispersal, dung burial and soil perturbation (Braga et al., 2013; Griffiths et al., 2015; Nichols et al., 2008; Slade et al., 2011).

We used this data to test three hypotheses about the impacts of selective logging on biodiversity and ecosystem functioning. (1) Dung beetle species richness, biomass, species composition and their associated ecological functions respond negatively to increased selective logging intensity (Burivalova et al., 2014; Martin et al., 2015). (2) The relationships with logging intensity are non-linear, with a convex shape. Ecosystems are likely to respond in a non-linear manner to land-use (DeFries et al., 2004; Peters et al., 2004); the shape of non-linear responses offer the opportunity to identify strategies with small losses in satisfying immediate human needs, but large gains in maintaining biodiversity and ecosystem function (Phalan et al., 2011; von Wehrden et al., 2014). Moreover, previous research comparing logged and unlogged forests has shown that dung beetle diversity and ecological functions can be maintained in low-intensity logged forests, whereas they reduce in high-intensity logged forests (Slade et al., 2011). (3) These relationships will also be spatially scale-dependent, with an important contribution of neighbourhood as well as local measures of logging intensity.

3.3 Methods

3.3.1 Study site

The study was conducted in the eastern Brazilian Amazon, within the private *Jari Florestal* landholding (0º53S, 52ºW; Chapter1: Figure 1.3) at the *Jari* River basin of north-eastern, state of Pará. The primary forests in this region are subject to low levels of disturbance such as light subsistence hunting and extraction of non-timber forest products (Barlow et al., 2010; Parry et al., 2009a). The predominant vegetation is an evergreen dense montane, submontane and lowland seasonally flooded rain forest (Souza, 2009). The climate is characterized as hot-humid (Köppen's classification), with annual rainfall and temperature of 2,115 mm and 26º, respectively (Ribeiro-Júnior et al., 2008; Souza, 2009).

The logging concession at *Jari* landholding is about 544,000 ha of native forest divided in "Annual Operating Planning" (POA) subsets, each one planned to be logged every year (since 2003) under a 30-year cutting cycle. This concession is one of the largest certified by the Forest Stewardship Council in the Amazon, with average annual production about 30,000 m^3 of timber (FSC, 2014). Reduced-impact logging (RIL) activities are planned following the FAO model code of forest harvesting (Dykstra and Heinrich, 1996), which include pre-harvest mapping and inventory, measurement and identification of all commercially viable trees with DBH ≥ 35cm and cut of tangling lianas before harvesting. During the pre-harvest inventory each POA is subdivided into 10 ha (250 x 400 m) units planned to be logged with a specific logging intensity (m^3 ha^{-1}). Then, logging and extraction of timber along skid trails take place during the dry season (August to November), and directional felling is used to minimise collateral damage to other trees in the adjacent logging units or protected areas nearby.

3.3.2 Experimental design

We used the company's pre-harvest inventory and operational logging plan to select 34 units (hereafter sample units). These included five control sites that would not be logged during the course of the study, and 29 logging units which were destined to be logged between July and September 2012. As logging impacts are related to logging intensity (Burivalova et al., 2014; Picard et al., 2012), we aimed to assess logging impact as a continuous (rather than categorical) effect. We therefore selected sample units along a gradient of planned logging intensities, which resulted in 0 - 50.3 m^3 ha^{-1} of timber (or 0 - 7.9 trees ha^{-1}) that was eventually extracted (Appendix S3.2). The five unlogged control units included in this range were the same size as the logged units, and held a dung beetle community representative of undisturbed primary forests in our study region (França et al., 2015, *in review*; Chapter 2). Control units were located approximately 6.5 km from the closest logged unit to insure sampling independence and to avoid any spillover effects from the logging operation (Block et al., 2001).

After logging operations, the planned harvest intensities within each sampled unit were fulfilled, resulting in an average timber removal of ~16.8 m^3 ha^{-1} across the POA, which is lower than RIL protocols based on the relationship between logging intensity and cut cycle ≤ 0.86 m^3 ha^{-1} $year^{-1}$ (IFT, 2014, CONAMA Resolution 406/2006). Therefore, differently from the previous chapter, we assumed the volume of removed timber per hectare (measured as the sum of the volume of timber logs extracted from each removed tree) in each 10 ha sampled unit as our measure of logging intensity and explanatory variable for all analyses, as this has been previously applied to assess logging intensity thresholds for biodiversity (Burivalova et al., 2014; Martin et al., 2015). Moreover, like others (Picard et al., 2012), we found high co-linearity among volume of timber (measured as the sum of the volume of timber logs extracted from each removed tree) and number of trees removed by selective logging (Figure S3.1; $n = 34$, $r = 0.91$, $p < 0.001$).

We sampled dung beetles and their ecological functions twice within each sampled units: the first collection gathered pre-logging data and occurred between June and July 2012, approximately 45 days before logging operation began. The second collection took place in 2013, and gathered post-logging data approximately 10 months after logging activities ended. It also occurred in June and July, to minimize possible effects from seasonal variation. In all sampled units, dung beetles and ecological functions were sampled in exactly the same locations and following the same methods in pre- and post-logging collections. Sampling locations were relocated based on marking tape, or by GPS when disturbance from logging activities meant this could not be found.

3.3.3 Dung beetle community functions

We evaluated the ecological functions of soil bioturbation and dung removal performed by the dung beetles (Nichols et al., 2008) following the protocol proposed by Braga et al. (2013), and setting up two arenas per sampled unit (Figure S3.2A). Each arena was a circular plot ~1 m in diameter and area of ~0.785 m^2, delimited by a nylon net fence (15 cm high) held by bamboo sticks. The nylon fence limited the horizontal movement of dung by the beetles to the contained area, allowing a more accurate quantification of the examined functions (Figure S3.3A). We also cleared the soil surface of any leaf litter and vegetation before placing each arena to facilitate the measurement of ecological functions (Braga et al., 2013, 2012). In the centre of each arena we placed a 200 g dung pile (4:1 pig to human ratio, Marsh et al., 2013), which was protected from the rain by a plastic lid and exposed in the field for 24 h. This exposure period was chosen based on known movements of dung beetles (Silva and Hernández, 2015) and to avoid the risk of beetles from outside the unit performing the ecological functions within the arena. After 24 h, the remaining dung (when present) was collected, taken to the laboratory and weighed to record the dung removal rates. We set up a parallel humidity control experiment (Figure S3.3B), excluding all insect groups from the dung, to account for water loss or gain in the calculation of dung removal rates (Appendix S3.3). Therefore, to quantify the ecological function of soil bioturbation as a consequence of tunnels building by the dung beetles, we collected the loose soil clearly found above the soil surface with spoons and spatulas, and weighed it after drying at 60 ºC for a week (Braga et al., 2013, 2012). Dung removal and soil bioturbation rates from the two arenas were pooled to get an aggregate value for each sample unit.

3.3.4 Sampling dung beetles

In both collection periods, dung beetles were sampled by using six pitfall traps spaced 100 meters apart in a 2x3 rectangular grid, so that traps were at least 75 meters from the edge of the unit (Figure S3.1). This spacing of traps helped insure independence between them (Silva & Hernández 2015), as well as an even spatial coverage of each sample unit. Pitfall traps were plastic containers (19 cm diameter and 11 cm deep) buried with their opening at ground level, containing ~250 ml of a saline solution. A plastic lid was placed above the top as a rain cover. A small plastic cup containing approximately 35 g of pig dung mixed with human dung (80:20 pig to human ratio following Marsh *et al.* 2013) was attached by a wire above each pitfall. All pitfalls were placed immediately after we withdrew the ecological function arenas, and data from the six pitfall traps in each unit were pooled to get an aggregate value and improve representation of dung beetle metrics within each sample unit.

We restricted our sample window to 24 hours in each collection period, as short sample periods are known to be efficient at attracting a representative sample of the local beetle community (Braga et al., 2013; Estrada and Coates-Estrada, 2002; Nichols et al., 2013b). Moreover, longer sample periods would have increased the probability of attracting dung beetles from outside the sample units (Silva & Hernández 2015), and therefore from units with different logging intensities. Finally, evidence from Chapter 2 suggests 24 hour sampling period as a good predictor of community metrics from longer sampling durations.

All trapped dung beetles were dried and transported to the laboratory where they were identified to species, or morphospecies where the former was not possible. We calculated the average biomass of each species from the dry weight of 15 individuals (when possible) using a *Shimatzu* AY220 balance (*Shimadzu Corporation, Kyoto, Japan*) with precision to 0.0001g. Voucher specimens were added to the Reference Collection of Neotropical Scarabaeinae in the Insect Ecology and Conservation Laboratory, Universidade Federal de Lavras, Brazil.

3.3.5 Statistical analyses

We ran all statistical analyses using the R Software version 3.2.0 (R Core Team, 2015). Sampled-based and individual-based rarefaction curves were calculated to examine the completeness of our dung beetle collection and compare the species richness patterns between pre- and post-logging. Curves and 95% confidence intervals (CI) were generated using the *specaccum* function in *vegan*, with 1000 permutations and rarefaction method. Therefore, as closer sites may naturally have more closely related biological communities (Soininen et al., 2007), we checked for spatial autocorrelation within dung beetle species richness, biomass and species composition data by performing Pearson-based Mantel tests (Legendre and Legendre, 1998) with 1000 permutations in the *mantel()* routine from the *vegan* package (Oksanen et al., 2015). We repeated the Mantel tests using both the pre- and post-logging dung beetle data, allowing us to examine whether spatial autocorrelation existed in both sets of analysis (see Appendix S3.3).

To examine the responses from biodiversity and its ecological functions along a gradient of logging intensification, we considered the pre-logging dung beetle community and function metrics as a baseline for post-logging collection data. Thus, we used Δ species richness, Δ biomass, Δ composition, Δ soil bioturbation and Δ dung removal as dependent variables. Except for the species composition, Δ was based on the differences between dependent variables from post-logging minus pre-logging collection within each sampled unit. For Δ composition, we used the *‘vegdist’* routine to calculate Bray-Curtis similarity index (1 – dissimilarity) among pre- and post-logging collections within each sampled unit.

To further investigate how dung beetle diversity and ecological functions respond to the increased logging intensity, we modified the function from Nagai (2011) to generate and compare linear and broken-stick regression models from the same dataset. Because models with lower Akaike’s information display lower information loss (Burnham et al., 2011), we used the Akaike’s criteria for small samples (AICc) to assess the model probability of being more suitable (Motulsky and Christopoulos, 2003). We considered the lowest AICc regression model as more accurate when the AICc difference between models was > 2. Moreover, we considered both linear and broken-stick regressions as plausible when AICc difference was ≤ 2. In cases where the broken-stick regressions had a lower AICc, the breakpoint was estimated. Finally, we used the functions *boot.ci* from *boot* package (Canty and Ripley, 2012) and *confint* in *stats* package (R Core Team, 2015) to generate the 95% confidence intervals (CI) from the regression lines and, when present, the breaking points.

We measured timber harvest intensity at two spatial scales. The volume of removed timber within the 10 ha sample unit was considered as the local scale. The broader scale was based on the average volume of removed timber in the sample unit and the eight neighbouring units (totalling 90 ha when all combined). Since volume of harvest at local and broader scales are collinear (Figure S3.1), we analyse both spatial scales separately. As before, we used the previous model-comparison function (Nagai, 2011) to evaluate the response from dependent variables over the gradient of logging intensity at broader scale, and compared the AICc weights from broader scale models with those obtained from local scale to determine at what spatial scale biodiversity and ecosystem services respond to logging intensity. Graphs were made with the *ggplot2* package (Wickham, 2009).

3.4 Results

3.4.1 Pre and post-logging comparisons

We recorded 4846 dung beetles in total (pre-logging: 3720; post-logging: 1126) from 53 species (pre-logging: 49; post-logging: 40) across 34 sampled units. Dung beetles sample-based rarefaction curves that communities were comprehensively collected and that selective logging operations resulted in a heavy loss of species (Figure 3.1). Reinforcing these results, we found negative effects of selective logging on the dung beetle abundance (Figure S3.4) and biomass (Figure S3.5) at logged sites. However, while soil bioturbation decreased in the post-logging collection at both control and logging units (Figure S3.6), no differences were found for dung removal rates (

Table *S3.6*).

Mantel tests of distance among sampled units with corresponding species composition showed a spatial autocorrelation influence on pre-logging data (r = 0.35; p = 0.001), which decreased after logging operations (r = 0.18; p = 0.01). The same patterns were found for pre-logging dung beetle species richness (r = 0.18; p = 0.005) and biomass (r = 0.12; p = 0.03). However, the spatial autocorrelation disappeared in the post logging collection for both metrics (species richness: r = -0.41; p = 0.999 and biomass: r = -0.42; p = 0.999) (Appendix S3.3).

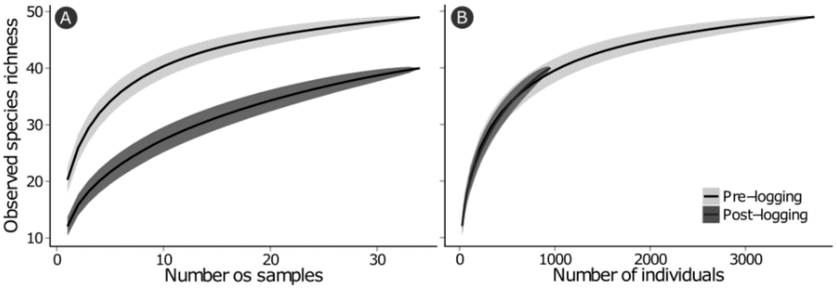

Figure 3.1 Dung beetle sample-based (A) and individual-based (B) rarefaction curves for pre-logging (light gray shaded) and post-logging (dark gray shaded) sampling periods collected within 34 logging management units in the Amazon forest, Brazil. The gray shading represents the 95% confidence intervals. Note that dung beetles were collected using pitfall traps and data from the six pitfall traps within each sampled unit were pooled for the analysis.

3.4.2 How do biodiversity and ecological functions respond to logging intensification?

Dung beetle species richness, biomass, composition and soil bioturbation were negatively affected by increasing logging intensity (Figure 3.2), whereas changes in dung removal were non-significant. In particular, dung beetle species richness, biomass and composition showed non-linear relationships with logging intensity at the local scale (Figure 3.2A-C). Surprisingly, the concave-shape of the non-linear relationships did not confirm our second hypothesis, as there was a rapid loss in dung beetle species richness (Figure 3.2A; 95% CI: 0-35 m^3 ha^{-1}) and changes in species composition (Figure 3.2C; 95% CI: 1-32 m^3 ha^{-1}) up to a logging intensity of around 18 m^3 ha^{-1}, after which there was no clear additional response to logging intensity. Biomass responded in a similar way, with the threshold at ~20.4 m^3 ha^{-1} (Figure 3.2C - 95% CI: 0-31 m^3 ha^{-1}). Both linear and broken-stick models were plausible predictors of change in soil bioturbation with logging intensity measured at the local scale (Figure 3.2D & H).

Broken-stick models also provided better predictions of the responses of dung beetle species richness and composition to broader scale assessments of logging intensity, with steep declines in both metrics up to logging thresholds of 27 (95% CI: 0-35 m^3 ha^{-1}) and 22 m^3 ha^{-1} (95% CI: 1-32 m^3 ha^{-1}), respectively (Figure 3.2 E&G). Both linear and broken-stick models were plausible predictors of dung beetle biomass and soil bioturbation, with the broken-stick model suggesting state-changes at logging thresholds around 17m^3 ha^{-1} for biomass (95% CI: 0-31 m^3 ha^{-1}) and 12 m^3 ha^{-1} for soil bioturbation (95% CI: 4-20 m^3 ha^{-1}).

3.4.3 Are we measuring the logging intensity at appropriate spatial scales to assess its impacts on biodiversity and ecological functions?

Measuring logging intensification at the local scale resulted in more accurate responses for dung beetle species richness ($AICc_{local}$: linear = 204.6, broken-stick = 199.8; $AICc_{broader}$: linear = 204.9, broken-stick = 202.2; Figure 3.3), whereas assessing logging intensities at the broader scale better fit the responses from dung beetle-mediated soil bioturbation ($AICc_{local}$: linear = 529.4, broken-stick = 534.5; $AICc_{broader}$: linear = 529.4, broken-stick = 531.43; Figure 3.3). Contrastingly, both local and broader spatial scales were accurate for dung beetle biomass ($AICc_{local}$: linear = 170.7, broken-stick = 168.6; $AICc_{broader}$: linear = 170.9, broken-stick = 169.8; Figure 3.3) and species composition ($AICc_{local}$: linear = 264.8, broken-stick = 259.6; $AICc_{broader}$: linear = 266.5, broken-stick = 258.6; Figure 3.3).

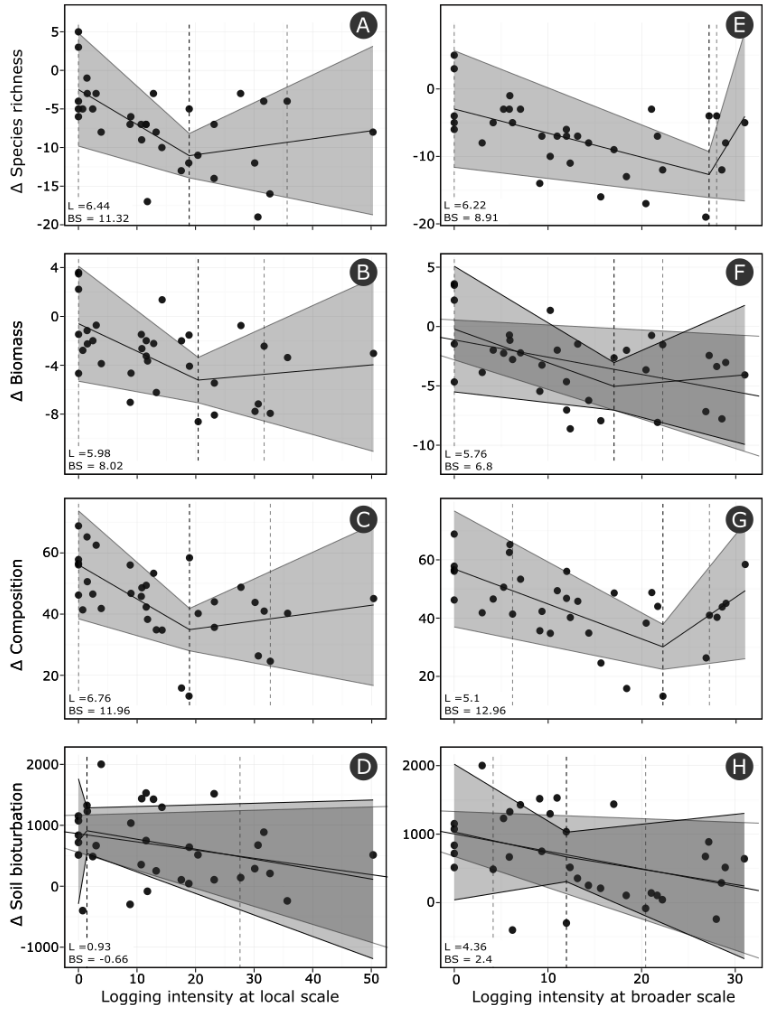

Figure 3.2 Responses of dung beetle (A-E) species richness, (B-F) biomass (g), (C-G) species composition and (D-H) soil bioturbation (g) to logging intensification (m^3 ha^{-1}) at two spatial scales. Local scale volume shows the logging intensity measured at the sampled unit (10 ha), while broader scale volume represents the logging intensity average within the sampled unit and its eight neighbour units (80 ha in total). The Δ calculation was based on the difference between post-logging results minus pre-logging data. The black dots represent the 34 sampled units with different logging intensities. The regression lines from linear and broken-stick regression models result from fitting the data to linear models and gray shading represents their 95% CI. Vertical dotted lines represent the threshold point (black line) and its 95% CI (grey lines). AICc differences among null minus linear (L) or broken-stick (BS) models are presented in each graph.

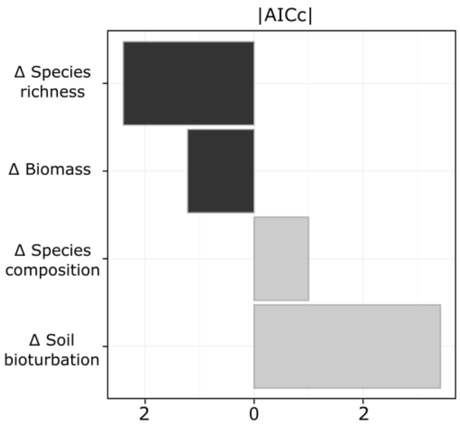

Figure 3.3 Akaike's differences from the best local and broader spatial scale regression models. Local scale volume represents the logging intensity measured at the sampled unit (10 ha), while broader scale volume represents the logging intensity average within the sampled unit and its eight neighbour units (90 ha in total). The Δ calculation was based on the difference between post-logging results minus pre-logging data. Logging intensification assessed at local scale (dark boxes) explained the responses from dung beetle species richness better, while assessing logging intensities at broader scale fitted the responses from soil bioturbation better. Changes in dung beetle biomass and specoes composition were well explained by assessing logging intensities at both spatial scales. The dung removal function is not shown since the null model was the best for this metric.

3.5 Discussion

The outcome of our research clearly demonstrates that biodiversity may not react linearly to selective logging intensification. Surprisingly, we found no convex-shaped associations between biological responses and logging intensity. Contrastingly, we found concave relationships with dung beetle diversity steeply decreasing at low intensities until a threshold of logging intensity around 18-20 m^3 ha^{-1} at local spatial scale, and 17-27 m^3 ha^{-1}, when measuring logging intensification at the broader scale. This result holds across most of the evaluated metrics in our study, underscoring the importance of considering non-linear responses from biodiversity and ecological functions to logging impacts (Peters et al., 2004). Thereby, as biodiversity and ecosystem functioning processes decrease at low logging intensities, our results give support to Edwards et al. (2014a) about the need for policy incentives encouraging land-sparing strategy as conservation priority within managed tropical forests. Furthermore, in agreement with Imai et al. (2012), we stress the importance of assessing the logging impacts at different spatial scales for improving the explanation of local biodiversity and ecosystem functioning responses to logging intensification. We discuss these results examining the implications for forest management practices and tropical forest conservation.

3.5.1 How do biodiversity and ecological functions respond to logging intensification?

To our knowledge, this is the first empirical study to quantify the responses of tropical invertebrates and associated ecological functions along a continuous gradient of logging intensity; thus providing support to previous meta-analysis about the non-linear response that biodiversity may have to logging intensification (Burivalova et al., 2014). In particular, we show dung beetle diversity metrics decreasing nonlinearly, thus changing their responses from decrease to a slight increase after crossing logging thresholds around 14-20 m^3 ha^{-1}. Dung beetles are very sensitive to changes in environmental conditions and even low-intensity human impacts (Bicknell et al., 2014a; Menéndez et al., 2014), therefore we believe this state change in species richness results from the loss of forest-interior species, which are adapted to close-canopy conditions (i.e. humidity and temperature; Klein, 1989) and decrease their diversity as logging intensity and its impacts on forest canopy increase (Davis et al., 2001; Hosaka et al., 2014). On the other hand, after crossing a logging threshold, as the forest structural changes driven by logging increase (e.g. harvest roads, skid trails and fallen trees gaps), so does the favouring of dung beetle species generally associated to environmental conditions from forest-gaps and -edges (Davis et al., 2001; Hill and Hamer, 2004; Willott et al., 2000). Moreover, given the absence of spatial autocorrelation we found for species richness and biomass in the post-logging operations, we are confident that those metrics are reliably driven by logging effects rather than natural spatial structuring (Kühn and Dormann, 2012; Ramage et al., 2013). However, our conclusions should be view with caution since we also found species turnover-by-distance relationships for pre- and post-logging dung beetle species composition.

Although soil bioturbation had both broken-stick and linear models as appropriate, both demonstrated the negative impacts of logging operations on this ecological function. We believe the decrease in soil bioturbation rates may result from the combined effects from shifts in dung beetle species richness, biomass and also due to the impacts of selective logging on soil characteristics (Ampoorter et al., 2012; Hartmann et al., 2014). The literature has shown dung beetle ecosystem functions being driven by both environmental context and dung beetle diversity (Nichols et al., 2008; Yoshihara and Sato, 2015), as well as the importance of larger-body dung beetles in performing the ecological functions they govern (Gregory et al., 2015). As result, we may expect that ecosystem process mediated by dung beetles, such as the transfer of microbe communities across the soil surface (Slade et al., 2015), soil aeration and fertility (Miranda, 2006; Yamada et al., 2007), water permeability and thus plant productivity (Bang et al., 2005) will be negatively affected within logged forests.

In addition, we believe that the range of selective logging intensities we assessed (0-50.31 m^3 ha^{-1}) may be relatively too low to influence the dung removal rates provided by dung beetles. Previous research comparing unlogged, low-intensity and high-intensity logged forests has found significantly lower dung removal rates only in the most impacted forests, where logging intensities were above 100 m^3 ha^{-1} (Slade et al., 2011). Furthermore, these findings give support that logged forests may retain at least part of the ecosystem functions and services from tropical primary forests (Edwards et al., 2014c); even when highly negative impacts are observed on the diversity of key invertebrates (Ewers et al., 2015). This likely functional redundancy may result from other taxa involved in the ecosystem processes, such as the influence of ants and termites on detrital consumption rates previously recorded in tropical forests (Dangles et al., 2012).

Alternatively, the increased competition for scarce resources (Horgan and Fuentes, 2005) is another good reason why dung removal might not respond to selective logging, nor to the changes in biodiversity (Nichols et al., 2013b). Selective logging is very likely to influence both dung availability and quality. The dung availability may decline as result of negative logging impacts on vertebrate populations and their food intake (Felton et al., 2010; Poulsen et al., 2011); whereas its quality may change due to higher exposition to sunlight and drying winds caused by increased canopy openness (Asner et al., 2004a, 2004b; Mazzei et al., 2010). As result, changes in dung quality and availability may lead to increased competition for the dung within the arenas (Horgan and Fuentes, 2005). However, because vertebrates in the study region appear not to be influenced by selective logging operations (Laufer et al., 2015), we suggest that changes in dung quality rather than in availability, would be a more likely explanation for the increased competition within dung beetle communities. Therefore, we suggest that future work should focus on understanding the role that dung quality has in mediating dung beetle competition for resources, and its consequences on dung beetle-mediated ecological functions.

3.5.2 Implications for forest management and conservation

The shape of the non-linear responses of biodiversity and their related functions provides important insights into the land-sharing vs. land-sparing debate (Law and Wilson, 2015). The literature has shown that when diversity-disturbance curves have a concave shape (Figure S3.7), overall diversity levels may be higher if high-intensity disturbed patches are mixed spatially within large undisturbed landscapes (Edwards et al., 2014a; Fischer et al., 2014; Phalan et al., 2011; von Wehrden et al., 2014). Therefore, the concave responses of dung beetle diversity to logging intensification we have found endorses that forest management practices implementing reduced impact logging activities coupled with the land-sparing strategy may increase the conservation value in logged forests (Edwards et al., 2014a).

3.5.3 Implications of increasing the spatial scale of logging intensity

We also highlight that logging studies in tropical forests should consider different spatial scales to improve the understanding of biodiversity and ecosystem functioning responses to logging intensification (Berry et al., 2008; Hamer and Hill, 2000; Hill and Hamer, 2004; Imai et al., 2012). Aside from dung beetle biomass and species composition, which had both local and broader scales of logging accurately assessing their patterns; our results show that assessing logging intensities at the local scale better explained the responses of dung beetle species richness, but measuring logging intensification at a broader scale better fit the logging impacts on soil bioturbation. As result, we strongly suggest that further environmental regulations on forest management adequacy should include different spatial scales of logging impacts (Hill and Hamer, 2004; Imai et al., 2012). Besides considering different spatial scales, this study also overcomes the issues of pseudoreplication and lack of pre-logging data (as baseline for post-disturbance data), which are suggested to be likely reasons for controversial patterns found by many logging studies evaluating the biodiversity responses to logging (Laufer et al., 2013; Ramage et al., 2013).

Our post-logging sampling was approximately 10 months after the logging activities and since the logging impacts may persist for years after the logging operations (Berry et al., 2008; Gatti et al., 2015; Osazuwa-Peters et al., 2015), we expect that the importance of broader spatial scales may increase with time post-logging. Our study area is a large forest concession (over 1.7 Mha), comprising a set of previously logged regions and large sections of low-disturbance primary forests, most of it planned to be selectively logged in the next years. We believe that such adjacent primary areas may also provide refuge for the biodiversity, from which the forest recovery would be improved by potential recolonization processes of biodiversity and, consequently, ecological processes (Edwards et al., 2014c; Willott et al., 2000).

3.6 Conclusions

The demand for logging concessions is increasing sharply in the coming century (Bicknell et al., 2015; Blaser et al., 2011; FAO, 2010) making critical the appropriate understanding of how the biodiversity and associated ecosystem processes will be affected by logging activities in tropical forests. At least for the specific goal of sustaining dung beetle species richness, biomass, species composition and soil bioturbation, our research shows these metrics markedly decreasing along a gradient of logging intensification. While giving support that primary forests are irreplaceable to maintaining the tropical biodiversity (Gibson et al., 2011), this study also supports that logged forests have a conservation value in retaining part of the ecosystem processes from primary forests, such as decomposition processes related to dung consumption (Edwards et al., 2014c; Ewers et al., 2015). Seeing that most metrics changed their response to logging intensity after a threshold at different spatial scales, we highlight that policy makers and researchers should consider the cross-scale impacts of timber exploration when establishing policy regulations and guidelines related to sustainable forest management. Finally, as our results show that biodiversity and ecosystem process may sharply decreases as logging intensity increases, we strongly support that policy incentives should be done to encourage the land-sparing strategy as a conservation priority within tropical production forests (Edwards et al., 2014a).

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3.7 Supplementary Information

Appendix S3.1 Supplementary figures

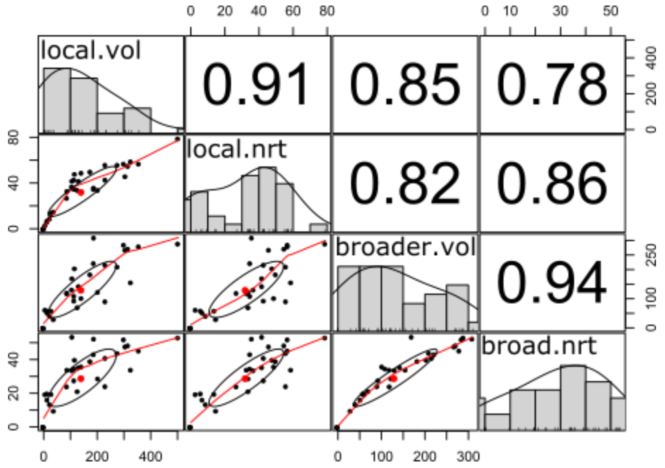

Figure S3.1 Association between local logging intensity (*local.vol*), local number of removed trees (*local.nrt*), broader scale logging intensity (*broader.vol*) and broader number of removed trees (*broad.nrt*): bivariate plots (lower panel), distributions (diagonal) and Pearson's ρ (upper panels).

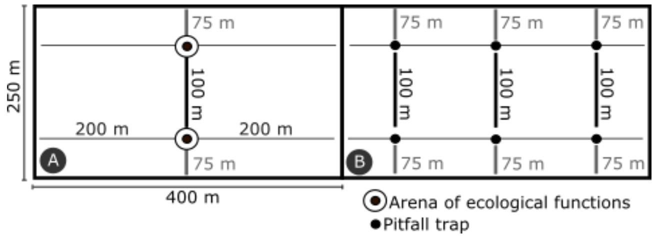

Figure S3.2 Experimental design within the sampled units. (A) Spatial design for arenas of ecological functions, which were placed in the central points of a 2x3 rectangular grid, spaced by 100 m apart each other and at least 75 m from the sampled unit borders. After ecological functions collection, we placed pitfall traps within the same sampled unit distributed in the 2x3 rectangular grid (B).

Figure S3.3 (A) Arena of ecological functions; and (B) Humidity control experiment (described below in the Appendix C).

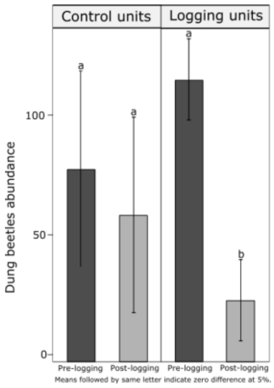

Figure S3.4 Dung beetle abundance among pre and post-logging data from control and logging units. Pre-logging data in dark gray and post-logging data in light gray. The post logging dung beetle abundance decreased just in logging units. See Table S3.2 for ANOVA results.

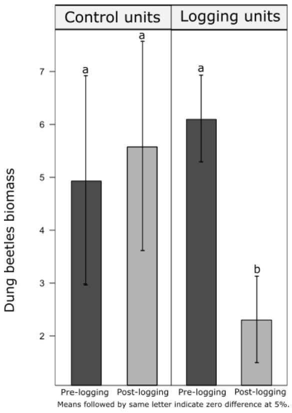

Figure S3.5 Dung beetle biomass among pre and post-logging data from control and logging units. Pre-logging data in dark gray and post-logging data in light gray. The post logging dung beetle biomass decreased just in logging units. See Table S3.3 for ANOVA results.

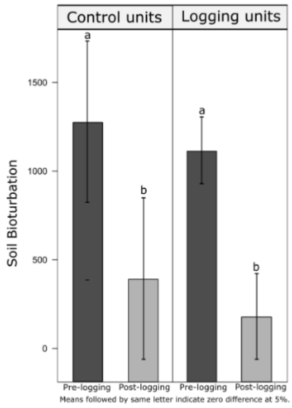

Figure S3.6 Soil bioturbation among pre and post-logging data from control and logging units. Pre-logging data in dark gray and post-logging data in light gray. The post-logging soil bioturbation was lower in both control and logging units. See Table S3.4 for ANOVA results.

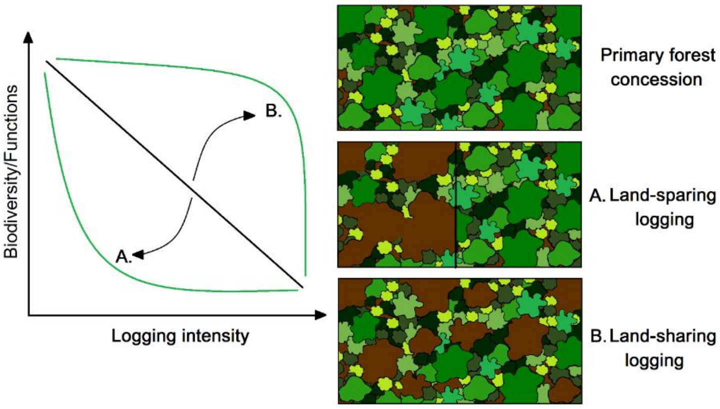

Figure S3.7 A primary forest concession can be either highly logged over a small area of the concession and sparing patches of forest (A. land-sparing) or through lower intensity of logging across the entire concession (B. land-sharing). Increasing the logging intensity the biodiversity decreases (Burivalova et al., 2014). This relation can be linear (black line) or nonlinear (green lines). Biodiversity/functions with concave logging intensity functions have the highest levels under a land-sparing strategy (A), whereas in the presence of logging the biodiversity/functioning drops. Biodiversity/functions with convex logging intensity functions have their highest levels under the lowest intensity of logging across the entire concession and drops when logging intensity increases (B. land-sharing). Modified from von Wehrden et al. (2014).

Appendix S3.2 Logging information from the sample units

Table S3.1 Details of sampled units and its biological and logging metrics. [a]NRT = number of removed trees within the 10 ha sampled unit; [b]LV = logging intensity (m^3 ha^{-1}) within the 10 ha sampled units; [c]BV = logging intensity average (m^3 ha^{-1}) in the sampled and its eight neighbour units (90 ha); [d]S-2012 = pre-logging sampling dates; [e]S-2013 = post-logging sampling dates; [f]ΔBiom = dung beetle biomass difference between pre- and post-logging collections within each 10 ha sampled unit; [g]ΔSp = dung beetle species richness difference between pre- and post-logging collections; [h]ΔDR = dung removal ratio between pre- and post-logging collections; and [i]ΔSB = soil bioturbation ratio between pre- and post-logging collections.

Unit	[a]NRT	[b]LV	[c]BV	[d]S-2012	[e]S-2013	[f]Δ Biom	[g]ΔSp	[h]ΔDR	[i]ΔSB
Par1	27	8.819	11.97	09/jun	15/jun	-7.04	-7	-41.71	298
Par2	43	23.176	21.66	09/jun	15/jun	-8.08	-7	16.18	-106
Par3	57	30.107	28.53	09/jun	15/jun	-7.78	-12	45.40	-288
Par4	48	11.776	20.43	09/jun	15/jun	-3.65	-17	-10.20	83.5
Par5	46	30.659	26.81	09/jun	15/jun	-7.17	-19	-63.47	-674
Par6	36	18.925	30.97	13/jun	19/jun	-4.08	-5	-101.58	-640.5
Par7	55	31.658	27.17	13/jun	19/jun	-2.44	-4	-194.49	-886.5
Par8	79	50.316	28.93	13/jun	19/jun	-3.03	-8	-14.78	-513.5
Par9	57	35.655	27.98	13/jun	19/jun	-3.37	-4	70.93	240.5
Par10	33	8.9519	11.96	16/jun	22/jun	-4.65	-6	-57.83	-1035
Par11	43	11.545	9.34	16/jun	22/jun	-3.25	-7	-48.08	-749
Par12	56	27.7	21.03	16/jun	22/jun	-0.75	-3	133.65	-141
Par13	42	13.269	14.32	16/jun	22/jun	-6.23	-8	-12.71	-251.5
Par14	37	10.711	13.15	16/jun	22/jun	-1.48	-7	-66.13	-354.5
Par15	35	18.847	22.22	20/jun	26/jun	-1.53	-12	-8.20	-43
Par16	50	17.565	18.36	20/jun	26/jun	-2.00	-13	-55.59	-105.5
Par17	34	20.407	12.36	20/jun	26/jun	-8.62	-11	-95.28	-515
Par18	56	23.172	9.12	20/jun	26/jun	-5.46	-14	-144.47	-1517
Par19	59	32.705	15.62	20/jun	26/jun	-7.94	-16	57.30	-209.5
Par20	9	2.4418	4.15	23/jun	03/jul	-1.99	-5	91.79	-486.5
Par21	6	1.4528	5.93	23/jun	03/jul	-1.16	-1	-102.05	-1326
Par22	35	11.542	10.97	23/jun	03/jul	-1.99	-7	-82.84	-1529
Par23	49	14.256	10.23	23/jun	03/jul	1.36	-10	-100.00	-1296
Par24	42	10.805	17.03	23/jun	03/jul	-2.64	-9	-117.31	-1437
Par25	14	3.015	5.88	26/jun	29/jun	-0.72	-3	63.39	-666.5
Par26	3	0.727	6.21	26/jun	29/jun	-2.78	-5	0.00	400
Par27	34	12.814	7.06	26/jun	29/jun	-2.22	-3	2.11	-1427.5
Par28	7	1.507	5.26	26/jun	29/jun	-2.25	-3	-69.45	-1230
Par29	15	3.884	2.98	26/jun	29/jun	-3.87	-8	0.00	-2001
Par30	0	0	0	29/jun	06/jul	2.22	-4	-48.59	-718.5
Par31	0	0	0	29/jun	06/jul	-1.47	-5	-88.53	-1152
Par32	0	0	0	29/jun	06/jul	-4.67	-6	11.38	-836.5
Par33	0	0	0	29/jun	06/jul	3.48	3	61.30	-1074
Par34	0	0	0	29/jun	06/jul	3.60	5	8.78	-513

Appendix S3.3 Supplementary experimental procedures

S3.3.1 Humidity control experiment

Aiming to avoid that changes in dung humidity interferes in the calculation of dung removal rates, we set a humidity control experiment (Figure S3) beside each arena of ecological functions. We weighted a 20.00 g control dung pile by using a *Shimatzu* AY220 balance (Shimadzu Corporation, Kyoto, Japan) with precision to 0.0001g. The dung used in this humidity control experiment was mixed together with the dung used in the arenas, thus having the same proportions of human and pig dung (4:1 pig to human ratio, Marsh et al., 2013). To exclude all insect groups we protected the control dung pile with a voile fabric, then, placed it in the field covered by a plastic lid to protect the experiment from the rain. We removed the dung from both humidity control and arenas jointly, and right afterward we used the same *Shimatzu* AY220 balance to assess the humidity loss or gain. Therefore, we considered any weight differences from control dung piles to account proportionally in the remaining dung from arenas (when present). Furthermore, to calculate the dung removal rates we used the following steps:

1. Weight the remaining dung from ecological arenas (WRDung).
2. Weight the control dung pile.
3. Assess the proportional weight difference from the humidity control experiment (ΔCtrW), by the equation

$$\Delta\mathrm{CtrW} = \frac{[(WCtrBef - WCtrAft) * 100]}{WCtrBef},$$

where *WCtrBef* is the control dung weight before (20.00 g in this study) and *WCtrAft* is the weight of the control dung after exposure in the field.

4. Apply the ΔCtrW to calculate the remaining dung weight accounting for humidity changes (RDH) by following the equation

$$RDH = \left(\left[\frac{WRDung}{100}\right] * \ \Delta\mathrm{CtrW}\right) + WRDung,$$

where WRDung is the weight of remaining dung from ecological arenas, and ΔCtrW is the proportional weight difference from the control dung pile (previously described)

5. Finally, to assess the dung removal rates, subtract the original dung weight (200 g in this study) of the RDH values for each arena, thus having the amount of dung removed accounting for influences from humidity loss or gain. See table S3.2 for pre- and post-logging ΔCtrW values.

Table S3.2 Proportional weight difference from the humidity control experiment (ΔCtrW). Values represent the average of difference between the two humidity control experiments for each sampled unit in the pre-logging ($\Delta CtrW_{pre}$) and post-logging ($\Delta CtrW_{post}$) collections.

Unit	$\Delta CtrW_{pre}$	$\Delta CtrW_{post}$
Par1	12.75	2.225
Par2	12.55	12.55
Par3	11.9	3.95
Par4	12.85	15.175
Par5	11.475	10.175
Par6	14.7	-2.775
Par7	15	-6.95
Par8	22.425	3.85
Par9	16.1	-1.375
Par10	30.3	-5.975
Par11	10.925	-8.775
Par12	11.925	-2.975
Par13	14.55	-5.725
Par14	15.05	0.425
Par15	8.45	0.75
Par16	9.1	3.35
Par17	7.55	1.65
Par18	8.4	3.775
Par19	7.625	8.45
Par20	16	16
Par21	8.45	-5.2
Par22	7.05	-1.8
Par23	2.75	-0.075
Par24	10.8	6.2
Par25	13.625	-4.65
Par26	30.525	-0.7
Par27	13.8	1.3
Par28	11.5	-5.825
Par29	31.55	5.725
Par30	3.675	-6.175
Par31	-1.5	-6.025
Par32	5.825	-4.95
Par33	6.7	-5.35
Par34	3.525	-3.275

S3.3.2 Mantel tests

We checked for spatial autocorrelation in our dataset by performing Pearson-based Mantel tests (Legendre and Legendre, 1998) with 1000 permutations in the '*mantel()*' function from *vegan* package (Oksanen et al., 2015). We used the '*Point Distance'* tool in ArcGIS Desktop 10.1 (ESRI, 2014) to calculate the straight line distance between the centroid of each sampled unit and the function '*as.dist()*' from '*stats*' package (R Core Team, 2015) to compute the distance matrices for geographical position and dung beetle species richness and biomass. Thereby, in order to verify whether the occurrence of spatial structuring changes after logging, Mantel tests were made separately for pre-logging and post-logging biological metrics.

S3.3.3 Pre- and post-logging differences in biological metrics

To evaluate whether the selective logging operations affect biodiversity and ecological functions, disregarding the logging intensities, we assessed the pre- and post-logging differences in dung beetle abundance, biomass and rates of dung removal and soil bioturbation. We used generalized linear models (GLMs) and ANOVA considering the dung beetle community and ecological functions from all 34 sampled units as response variables, responding to the interaction between the explanatory variables sampling period (pre- and post-logging) and treatment (control or logging unit). All models were submitted to residual inspection to evaluate the adequacy of error distribution (Crawley 2002).

We found a two-way interaction between sampling period (pre and post-logging) and treatment (control and logging units) for dung beetle abundance and biomass (See Appendix S3.1: Figure S3.4-3.6). No changes were observed within control units from pre-logging (both treatments) and post-logging collections. Thereby, there was no interaction between sampling period and treatment for soil bioturbation, which decreased at both control and logging units (see Table S3.3-3.6 and Appendix S3.1).

Table S3.3 ANOVA table for dung beetle abundance among pre and post-logging samples from control and logging units

Dung beetle abundance			
Variables	Df	F-value	Pr(>F)
Sampling-period	1	54.03	4.49e-10
Treatment	1	0.003	0.9562
Sampling-period:treatment	1	5.438	0.0229

Table S3.4 ANOVA table for dung beetle biomass among pre and post-logging samples from control and logging units

Dung beetle biomass			
Variables	Df	F-value	Pr(>F)
Sampling-period	1	34.175	1.86e-07
Treatment	1	1.931	0.1695
Sampling-period(pre-logging):treatment	1	8.58	0.0047

Table S3.5 ANOVA table for soil bioturbation provided by dung beetles among pre and post-logging samples from control and logging units

Soil Bioturbation			
Variables	Df	F-value	Pr(>F)
Sampling-period	1	30.92	5.61E-07
Treatment	1	0.07	0.793
Sampling-period:treatment	1	0.437	0.511

Table S3.6 ANOVA table for dung removal provided by dung beetles among pre and post-logging samples from control and logging units

Dung removal			
Variables	Df	F-value	Pr(>F)
Sampling-period	1	0.6065	0.4390
Treatment	1	1.3542	0.2489
Sampling-period:treatment	1	0.0014	0.9704

Chapter 4: ASSESSING THE INFLUENCE OF FOREST DISTURBANCE ON ‘BROWN WORLD’ ECOSYSTEM PROCESSES

4.1 ABSTRACT

Growing evidence suggests that human-disturbances shape ecological processes. Yet we still have a limited understanding of how forest disturbance changes the environmental influence in tropical ecosystem processes in the 'brown world'. We use a before-and-after control-impact (BACI) design to assess a 'brown chain' of dung beetle-mediated ecosystem processes – namely, production, consumption and incidental faecal detritus-pathways – within 34 logging management units, of which 29 were selectively logged after our first survey. As environmental predictors we recorded the canopy cover, leaf litter weight and soil sand content for each sample unit and survey. We show that changes in vegetation structure do not necessarily mediate the logging impacts on dung beetle diversity and biomass. In contrast, neither faecal removal and soil bioturbation rates, nor leaf litter or soil sand content, were influenced by selective logging; but the relationships between these environmental and biological components were. Our results suggest that logged forests can retain some important ecosystem processes, in particular faecal consumption processes, even when the dung beetle diversity is impoverished.

Keywords: Tropical forests. Detritus-pathways. Reduced-impact logging. Selective logging. Faecal detritus food webs. Dung beetles. Biomass production. Dung removal. Soil bioturbation. Leaf litter.

4.2 Introduction

Anthropogenic disturbances pose a major threat to the world’s forested environments (Sala et al., 2000). Pristine forests are rapidly disappearing due to land-use change and environmental disturbance, which are widely recognised as the greatest drivers of biodiversity loss (Kim et al., 2015; Newbold et al., 2015; Pan et al., 2011). This trend is expected to continue (Pereira et al., 2010; Sala et al., 2000), particularly so in the tropics where most of world’s biodiversity and pristine forests co-occur with the highest land-use change rates (Bang et al., 2005; Lambin et al., 2003; Pan et al., 2011).

There is growing evidence that biodiversity loss associated with the direct and indirect impacts of forest disturbance is likely to have important consequences for ecosystem functioning (Hooper et al., 2005; Laliberté and Tylianakis, 2012; Seidl et al., 2014). However, the majority of research has explored how human-induced impacts on forest structure can influence ecological functions provided by green-producers in temperate regions (Flower and Gonzalez-Meler, 2015; Gamfeldt et al., 2013; Seidl et al., 2014) and comparatively little is known about the importance of environmental conditions in buffering the impacts of forest degradation along tropical detritus-based food webs of the ‘brown world’ (Bicknell et al., 2015; Nichols et al., 2013a, 2013b; Wu et al., 2011). In particular, faecal detritus-processes are largely relevant for terrestrial environments and form essential linkages among both below - and above-ground pathways (Moore et al., 2004; Nichols et al., 2013b; Slade et al., 2015; Wu et al., 2011). Although these brown interactions do not necessarily involve direct trophic interactions, their decline or loss can instigate a cascade of ‘downstream’ impacts on ecosystem processes, with dramatic implications for both ‘green’ and ‘brown’ worlds (Nichols et al., 2013a, 2013b, 2009; Slade et al., 2015; Wu et al., 2011). As result, growing evidence support the cascade influence of human pressure on tropical forests affecting faecal-detritus pathways that are mediated by detritivores (Nichols et al., 2013a, 2013b, 2009; Slade et al., 2011).

Among the faecal detritivores of the brown world, Scarabaeinae dung beetles have been a focal group for ecological studies assessing the human impacts on tropical forests (Bicknell et al., 2014a; Braga et al., 2012; Edwards et al., 2014a; Korasaki et al., 2013; Nichols and Gardner, 2011; Nichols et al., 2007; Slade et al., 2011). Through dung manipulation for feeding and nesting purposes (Hanski and Cambefort, 1991), these detritivores play a vital role in the brown chain of faecal-detritus processes (i.e. consumption, production and incidental detritus-pathways; Figure 4.1) facilitating the transfer of energy and matter through dung-based food webs (Nichols and Gardner, 2011). Faecal consumption also leads to dung beetle biomass production (Young, 2015) and very important incidental detritus-pathways, i.e. soil bioturbation (Braga et al., 2013; Nichols et al., 2007), nutrient cycling (Yamada et al., 2007), microbial transport across the soil-surface (Slade et al., 2015), interference in helminth transmission to mammals (Gregory et al., 2015), and secondary seed dispersal (Griffiths et al., 2015; Lawson et al., 2012; Santos-Heredia and Andresen, 2014). Yet, despite progress made to comprehend the consequences of dung beetle faecal pathways in both green and brown worlds, and also how these can be impacted by human activities (Braga et al., 2013, 2012; Nichols et al., 2013b; Slade et al., 2011), there is little empirical evidence exploring the extent to which forest degradation alters the influence of environmental factors on dung beetle-mediated faecal pathways (but see Oliver et al., 2000). Thus, calls have been made for studies in real-world conditions exploring the role of environmental structure for ecosystem processes in disturbed forests (Dangles et al., 2012; Mehrabi et al., 2014; Nichols et al., 2013a).

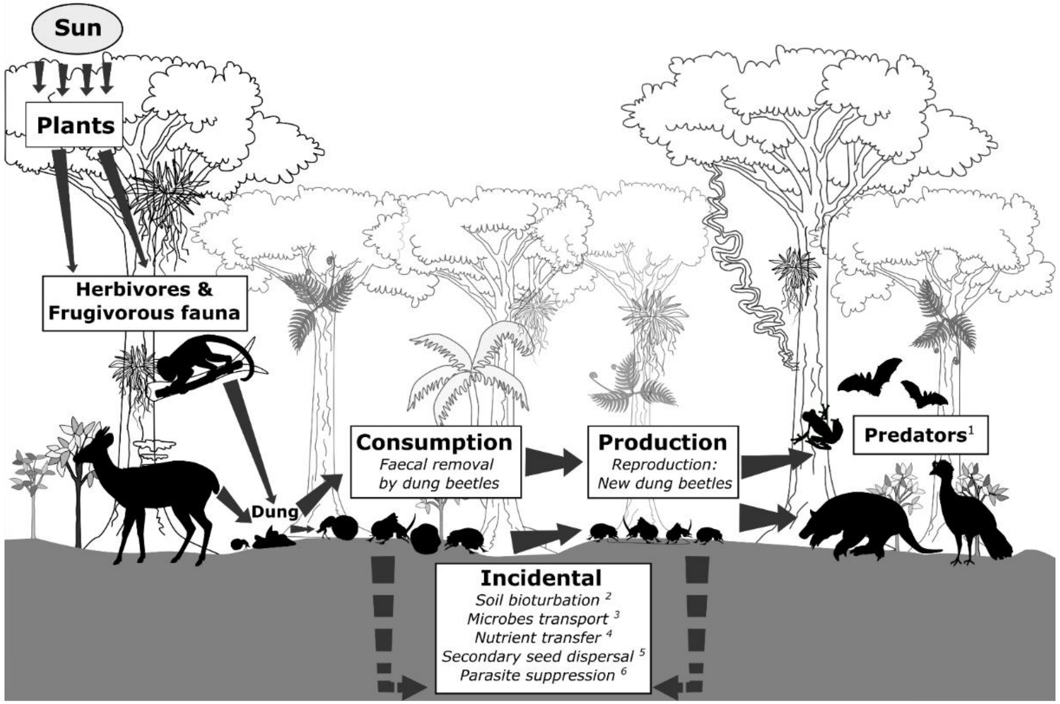

Figure 4.1 The dung beetle-mediate ‘brown chain’ of faecal detritus-pathways. The energy flow comes from the sun in the top left, being assimilated by primary producers, which are fed on by herbivores and frugivorous (here a Brown howler and *Mazama* sp. deer). These, through defecation allow the resource production for dung-based faecal-detritus food web. Dung beetles by faecal consumption and further secondary biomass production for beetle-predators ([1]Young, 2015) mediate the incidental detritus-pathways ([2]Nichols et al. 2007; [3]Slade et al. 2015; [4]Yomada et al. 2007; [5]Griffiths et al. 2015; [6]Gregory et al. 2015) which can affect both ‘brown’ and ‘green worlds’ (modified from Nichols &Gardner, 2011).

Here, we address the above knowledge gaps by using a BACI experimental design to investigate how selective logging in the eastern Amazon alters the influence of the forest structure on dung beetle-mediated faecal detritus-pathways. We focus on selective logging, as this is a major disturbance driver throughout forests (Asner, 2005; Asner et al., 2009; Gatti et al., 2015) with over 400 Mha of tropical forests planned as timber concessions (Blaser et al., 2011; FAO, 2010). Specifically we test three predictions, namely that forest disturbance caused by selective logging: (1) has negative consequences on forest structure, which will negatively affect the dung beetle-mediated detritus-pathways; as it has been shown that dung beetles are greatly influenced by differences in vegetation structure (Davis et al., 2001; Halffter and Favila, 1993; Halffter and Matthews, 1966); (2) alters the relative importance of environmental variables to faecal ecosystem processes mediated by dung beetles (Oliver et al., 2000); and (3) has disproportionately greater effects on dung beetle species and biomass, which will lead to cascade impacts on dung beetle faecal consumption and incidental detritus-pathways (Braga et al., 2013, 2012; Ewers et al., 2015; Slade et al., 2011).

4.3 Methods

4.3.1 Study area

The study was conducted within the 1.7 Mha *Jari Florestal* landholding, located in the state of *Pará*, north-eastern Brazilian Amazonia (0º53S, 52ºW; Chapter 1: Figure 1.3). This area comprises a mosaic of *Eucalyptus* plantations and regenerating secondary forests within expanses of largely primary forests subjected to low levels of disturbance (Barlow et al., 2010; Parry et al., 2009a). Forests in this region are characterized as evergreen dense tropical rainforest (Souza, 2009), often dominated by the timber species *Dinizia excela* Ducke (Fabacea, Mimosoideae) (Laufer et al., 2015), which corresponds for about 50% of exploited timber in some Amazonian regions

(Barbosa, 1990). The climate is characterized as hot-humid (Köppen's classification), with annual rainfall and temperature of 2,115 mm and 26º, respectively (Souza, 2009).

Reduced-impact commercial logging (RIL) started in 2003, with plans to log approximately 544,000 ha of native forests divided in "Annual Operating Planning" (POA) sections to be logged over a 30-year cutting cycle. This concession is one of the largest certified by the Forest Stewardship Council in the Amazon, with average annual production about 30,000 m^3 of timber (FSC, 2014). Logging activities are planned following the FAO model code of forest harvesting (Dykstra and Heinrich, 1996), which includes pre-harvest mapping, measurement and identification of all commercially viable trees with DBH ≥ 45cm. During the pre-harvest inventory each POA section is subdivided into 10 ha (250 x 400 m) logging management units planned to be logged with a specific logging intensity (m^3 ha^{-1}). Tangling lianas are cut before harvesting, which takes place during the dry season (August to November). Moreover, directional felling is used to minimise collateral damage to other trees in the adjacent logging units or protected areas nearby.

4.3.2 Experimental design

We used the company's pre-harvest operational logging project to select 34 management units planned to be logged (hereafter sample units). These included five control units that would not be logged during the course of the study, and 29 'logging' units which were destined to be logged along a gradient of planned logging intensities. The five unlogged control units were the same size as the logging units, and held a dung beetle community representative of undisturbed primary forests in our study region (Chapter 2; França et al., 2015, *in review*). Thus, they were located approximately 6.5 km from the closest logging units to insure sampling independence and to avoid any spillover effects from logging activities (Block et al., 2001). Logging operations started between July and September 2012, resulting in 0 - 50.3 m^3

ha^{-1} of timber (or 0 - 7.9 trees ha^{-1}) that was eventually extracted within our sample units, and an average timber removal of ~16.8 $m^3 ha^{-1}$ across the entire POA. This logging average is within the RIL upper limit of 25 $m^3 ha^{-1}$, which is based on the relationship between logging intensity and cut cycle ≤ 0.86 $m^3 ha^{-1} year^{-1}$ (IFT, 2014, CONAMA Resolution 406/2006).

We sampled dung beetles and their faecal detritus processes twice within each sample units: the first survey gathered pre-logging data and occurred between June and July 2012, approximately 45 days before logging operations began. The second survey took place in 2013, and gathered post-logging data approximately 10 months after logging activities ended. It also occurred in June and July, to minimize possible seasonal effects. All samples occurred in exactly the same locations and following the same methods in both surveys. Sampling locations were relocated based on marking tape, or by GPS when disturbance from logging activities meant this could not be found.

4.3.3 Consumption and incidental detritus-pathways surveys

We evaluated the consumption and incidental detritus-pathways by sampling dung beetle-mediated faecal removal and soil bioturbation rates, respectively (Table S4.1). The day before dung beetles were sampled, we followed the sampling protocol proposed by Braga et al. (2013), which consisted of establishing two circular, 1 m diameter mesocosm plots, spaced 100 m apart, and located at least 75 m from the edge of the sample units (Chapter 3, Figure S3.2). Each mesocosm arena was delimited by a nylon-mesh fence (~15 cm tall) held by bamboo sticks (Chapter 3; Figure S3.3A). To facilitate the evaluation of these processes, we cleared the soil surface of any leaf litter and vegetation before placing a single 200 g experimental faecal deposit (4:1 pig to human ratio following Marsh et al., 2013) at the centre of each mesocosm (Braga et al., 2013, 2012).

This mesocosm design allows dung beetles to freely enter the arena, and perform their feeding and nesting activities that result in further underground relocation of faecal resources, while limiting the horizontal dung removal of brood balls by roller species to the contained area (~0.785 m^2) (Braga et al., 2013, 2012). After 24-h exposure period to the dung beetle community, we weighed the remaining dung (when present) to record the faecal consumption rates. This period of exposition was the same as previous studies following this protocol (Braga et al., 2013, 2012; Nichols et al., 2013b) and was chosen based on known movements of dung beetles (Silva and Hernández, 2015) to avoid the risk of beetles from outside the unit performing the faecal detritus-pathways within the arena mesocosm. A parallel humidity control experiment was set beside each arena (Chapter 3; Figure S3.3B). Thereby, changes in humidity of each experimental faecal deposit were considered to calculate the faecal removal rates (Chapter 3; Appendix S3.3). To quantify the incidental detritus-pathway of soil bioturbation as consequence of excavations by dung beetles, we collected the loose soil clearly found above the soil surface and weighed it after drying it at 60 ºC for a week (Braga et al., 2013, 2012). We pooled the data of the detritus-pathway rates from the two arenas to get an aggregate value for each sample unit.

4.3.5 Dung beetle diversity and biomass surveys

We used the relative dung beetle species richness and biomass as a proxy of the production available for dung beetle predators (Young, 2015). Therefore, we refer to dung beetle species richness and biomass as quality and quantity production, respectively. Similarly, previous research has demonstrated both dung beetle richness and biomass as key predictors for faecal processes they perform (Braga et al., 2013, 2012; Nichols et al., 2013a, 2007; Slade et al., 2011, 2007).

We used six standardized baited pitfall traps (19 cm diameter and 11 cm deep) spaced 100 meters apart in a 2x3 rectangular grid within each sample unit (Chapter 3; Appendix S3.1). This trap spacing helped insure independence among them (Silva & Hernández 2015) as well as an even spatial coverage of each logging unit. Traps were buried with their opening at ground level, containing approximately 250 ml of a saline solution and a small bait-container with ~35 g of fresh dung (4:1 pig to human ratio, Marsh *et al.* 2013). We restricted our sample window to 24 hours in each collection period, as short sample periods are known to be efficient at attracting a representative sample of the local beetle community (Braga et al., 2013; Estrada and Coates-Estrada, 2002). Moreover, longer sample periods would have increased the probability of attracting dung beetles from outside of the sample units (Silva and Hernández, 2015), and therefore from units with different environmental conditions. In addition, evidence from data collected in the same region suggests 24-h sampling periods as good predictor of community metrics from longer sampling durations (Chapter 2; França et al., 2015, *in review*).

All trapped dung beetles were dried and transported to the laboratory where they were identified to species, or morphospecies where the former was not possible. We calculated the average biomass of each species from the dry weight of 15 individuals (when possible) using a *Shimatzu* AY220 balance accurate to within ±0.001g. Voucher specimens were added to the Reference Collection of Neotropical Scarabaeinae, Universidade Federal de Lavras, Brazil. Thus, the data from the six pitfall traps in each sample unit were pooled to get an aggregate value and improve representation.

4.3.5 Environmental drivers of ecosystem processes

To evaluate whether selective logging would lead to changes in forest structure and the relative importance of the environment to dung beetle-mediated faecal processes we assessed the canopy openness, leaf litter weight and soil texture at the same locations where the pitfall traps were placed at each of the pre- and post-logging surveys (Figure S3.2).

Canopy openness was quantified by taking hemispherical photographs with a Nikon FC-E8 fisheye lens attached to a Nikon D40 camera levelled ~1.20 meters from the ground. Photographs were taken when the sky was overcast or in early morning and late afternoon using optimum exposure for each site (Zhang et al., 2005). The Gap Light Analyser software (GLA version 2.0; Frazer et al., 1999) was used to estimate the 'canopy openness %' factor, which represents the ratio of the total amount of open space to the total area of the hemispherical photograph (Frazer et al., 1999). This approach has been widely used to account for the canopy openness (Gries et al., 2012; Medjibe et al., 2014; Niemczyk et al., 2015; Silveira et al., 2010). In addition, leaf litter was collected from the forest floor within a 25×25 cm square randomly placed ~1 m from each pitfall trap. We used a *Shimatzu* AY220 balance scale (*Shimadzu Corporation, Kyoto, Japan*) accurate to within ±0.001g to obtain the dry weight after oven drying it at 60 °C for 96-h. For analysis purpose and to get an aggregate value, canopy openness and leaf litter metrics were the average among the six samples taken within each of the sample units. Lastly, we also took a soil sample (0-10 cm depth) at the six trap locations, forming a composite soil sample to represent the soil texture (clay, silt and coarse sand fractions) within the sample units at each survey. Granulometric analysis was conducted in the soil laboratory of *Jari Celulose S.A.* In the same way as previous dung beetle-research, we also considered the soil sand content our soil texture measure (Gries et al., 2012; Griffiths et al., 2015).

4.3.6 Statistical analyses

All statistical analyses were performed within the R computing environment (R Core Team, 2015). To investigate selective logging effects on forest structure and dung beetle-mediated faecal processes we used generalized linear models (GLMs) with a logarithmic link function (Zuur et al., 2009) in the *glm()* routine (*stats* package, R Core Team, 2015). GLMs were tested by a two-way ANOVA including the factors 'survey' (2 levels: pre- and post-logging), 'treatment' (2 levels: control and logging sites) and the interaction between them, followed by post hoc pairwise t-test with non-pooled standard deviations. We also used GLMs with continuous data and tested by one-way ANOVA to investigate the effects of environmental variables on dung beetle-mediated production, faecal consumption and incidental soil bioturbation. As in previous studies, we also tested whether dung beetle richness and biomass (production pathways, Figure 4.1) would influence faecal removal and soil bioturbation; and whether faecal consumption would influence incidental detritus-pathways (Braga et al., 2013; Slade et al., 2011, 2007). A quasi-Poisson error structure was used for overdispersed count data; and quasi-binomial errors in the case of dung removal, canopy openness and soil texture, which were proportion data (Crawley, 2002). Spatial autocorrelation within our dataset was assessed by performing Pearson-based Mantel tests (Legendre and Legendre, 1998) with 1000 permutations (*mantel* routine, *vegan* package, Oksanen et al. 2015). Mantel tests were made separately for dung beetle species richness and biomass from each survey (Chapter 3; Appendix S3.3).

Hierarchical partitioning (HP) analysis (Chevan and Sutherland, 1991) was used to compare the relative and independent importance of our three environmental variables (canopy openness, litter weight, and soil structure) on the dung beetle-mediated quality and quantity production, faecal consumption and incidental faecal-pathways. Because we also sought to examine whether selective logging has disproportionately greater effects on dung beetle production than faecal consumption and incidental detritus-pathways, and whether these strong effects would lead to cascade consequences at the bottom of the brown chain, we checked for the importance of quality and quantity productions (dung beetle species richness and biomass), together with environmental metrics, on both faecal consumption and incidental detritus-pathways. As such, we examined the importance of detrital consumption for incidental soil bioturbation. We analysed each dependent variable separately at each survey to evaluate whether these faecal-detritus pathways are influenced by similar predictors after logging operations.

HP is a multi-regression technique in which all possible linear models are jointly considered to identify the most likely predictors, while minimizing the influence of multicollinearity and providing the independent contribution of each predictor (Chevan and Sutherland, 1991). Competing models were evaluated based on R^2 goodness of fit statistic, which allowed us to interpret the independent effects as proportion of explained variance. Significance ($\alpha = 0.05$) of independent effects of each predictor was calculated using a randomization test with 1000 iterations (Mac Nally, 2002; Walsh and Nally, 2013). The same error structure used for GLMs were applied for HP analysis. Gaussian distributions were tested using the Shapiro-Wilk normality test through the *shapiro.test()* function (*stats* package, Patrick Royston 1995). Hierarchical partitioning and further randomization-significance tests were executed using the *hier.part* package (Walsh and Nally, 2013).

4.4 Results

4.4.1 Between-surveys differences

Canopy openness was the only environmental condition that changed between pre- and post-logging surveys ($F_{1,66} = 166.4$, $p < 0.0001$), having higher values in logged sites than in control sites in the second survey (t-test, $p = 0.02$; Figure 4.2D). The leaf litter weight and sand proportion were not altered between surveys, although leaf litter came close to significance (*leaf litter:* $F_{1,66} = 3.37$, $p = 0.07$, *sand proportion:* $F_{1,66} = 1.5$, $p = 0.22$; Table S4.2). While post-hoc analysis supported these findings for sand proportion (t-test, $p \geq 0.22$), they also demonstrated significant differences in leaf litter weight between control and logged sites in the first survey (t-test, $p = 0.026$) and marginal differences between logging sites pre- and post-logging (t-test, $p = 0.057$).

Across our 34 sample units, we recorded 4,846 dung beetles (pre-logging: 3,720; post-logging: 1,126) in 53 species (Table S4.1 & S4.2). Irrespective of where or when we sampled, dung beetle species and biomass were higher in undisturbed forests (i.e. the control units pre- and post-logging, and the logging units pre-logging) (two-way ANOVA: treatment × site *species richness* $F_{1,64} = 10.8$, $p = 0.001$; *biomass* $F_{1,64} = 11.4$, $p = 0.001$; Figure 4.2A-B). Marginal differences were also found for faecal removal, with the second survey 28.26 g (±10.98 SE) lower than the faecal removal in the first survey ($F_{1,66} = 3.5$, $p = 0.06$), whereas soil bioturbation decreased after selective logging at both control and logging sites ($F_{1,66} = 35.2$, $p < 0.0001$; Fig 4.2C). Post-hoc analysis supported these findings for soil bioturbation (t-test, p-value ≤ 0.02) and faecal removal rates (t-test, p-value ≥ 0.06). A very weak spatial autocorrelation was found in the pre-logging data (*species richness* $r = 0.18$, $p = 0.005$; *biomass* $r = 0.12$, $p = 0.035$); however, after selective logging the differences between sites in species richness ($r = -0.41$, $p = 0.999$) and biomass ($r = -0.42$, $p = 0.999$) did not increase with the geographic distance, even when the control units were excluded from analysis (see Chapter 3; Appendix S3.3).

4.4.2 Relating forest strucutre and faecal-detritus pathways

Although dung beetle species richness and biomass decreased in the post-logging survey, these were not influenced by any environmental variable in both surveys (all $p>0.05$). On the other hand, faecal consumption rates increased with detritivore biomass in the pre-logging survey (Fig S4.1A), whereas they decreased with the increase of leaf litter weight in the post-logging survey (Fig S4.1B). Therefore, while soil bioturbation was positively influenced by leaf litter only before selective logging, this incidental process co-varied with sand proportion and faecal consumption in both surveys (Fig S4.2). These results were supported by HP analysis and randomization tests, which revealed a significant, independent and positive contribution of leaf litter weight and sand proportion to soil bioturbation in the first survey (Figure 4.3D). Additionally, leaf litter was the only significant predictor with explanatory power on the variation of faecal consumption after selective logging (Fig 4.3G) and soil bioturbation rates were positively influenced by faecal consumption, and again by soil texture in the post-logging survey (Fig 4.3H). Table S4.3 (Appendix S4.2) shows results of independent and joint effects of predictor variables for each faecal detritus-pathways performed by dung beetles.

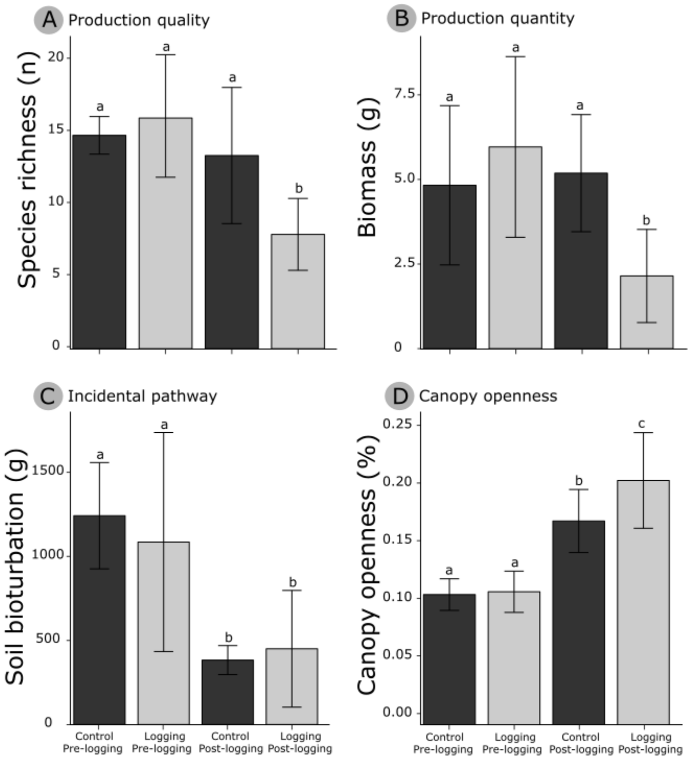

Figure 4.2 Differences between control (dark grey bars) and logging sites (light grey bars) in surveys performed before (left bars in the panels) and after selective-logging (right bars in the panels) for dung beetle species richness (A), biomass (B) and incidental soil bioturbation (C); and canopy openness (D). Means followed by the same letter indicate post hoc zero difference at 5%.

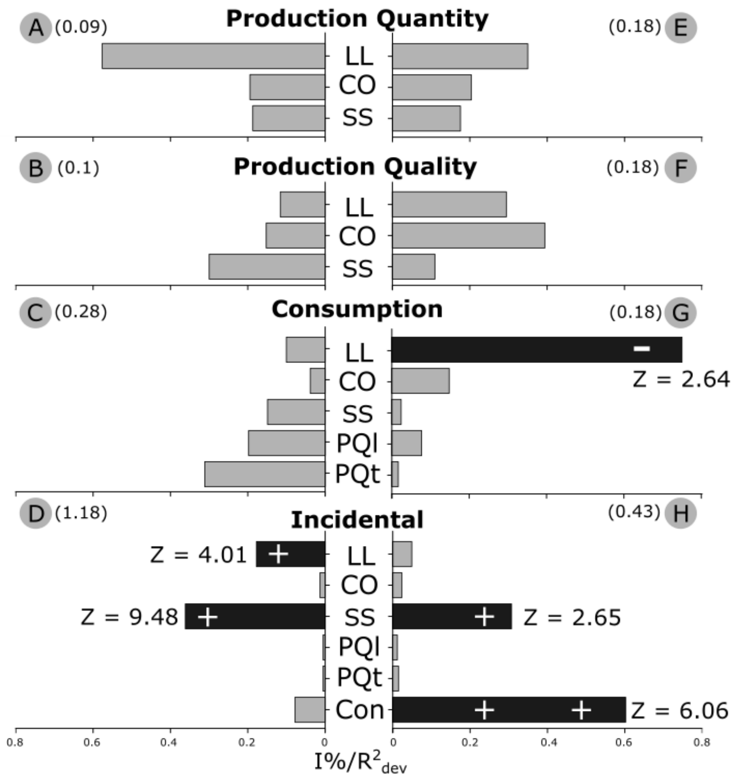

Figure 4.3 Distribution of the percentage of the independent effects of different predictors on dung beetle-mediated faecal detritus-pathways. Left panels show results from the pre-logging survey (A-D) and right panels from the post-logging survey (E-H). Black bars represent significant effects ($\alpha = 0.05$) as determined by randomization test. Z-scores for the generated distribution of randomized I's (I value = the independent contribution towards explained variance in a multivariate dataset) and an indication of statistical significance Z-scores are calculated as (observed – mean (randomizations)) /SD (randomizations), and statistical significance is based on the upper 0.95 confident limit ($Z \geq 1.65$). Pearson's (ρ) positive or negative relationships are shown by + or –, respectively. R^2_{dev} (displayed in parenthesis besides each capital letter) is the total deviance explained by a generalized linear model including all the predictors considered for each faecal-detritus pathway response. The x-axis shows the percentage of the independent effects (I%) divided by total explained variance of the complete model (R^2_{dev}). LL = leaf litter weight (g), CO = canopy openness (%), SS = Soil sandy (%), PQl = production quality (n), PQt = production quantity (g) and Con = detrital consumption.

4.5 Discussion

Our results demonstrate that although selective logging impacts the forest canopy (Asner et al., 2004a; Pereira et al., 2002), these changes are not necessarily major drivers of ecological processes associated with dung beetles within logged forests. Importantly, logging operations altered the influence that environmental variables have in explaining the dung beetle-mediated faecal consumption and incidental soil bioturbation. Moreover, we give support that forest degradation has disproportionally stronger impacts on dung beetle species richness and biomass (Braga et al., 2013, 2012; Nichols et al., 2013b; Slade et al., 2011), but ecosystem processes can still be maintained within production forests (Edwards et al., 2014c; Ewers et al., 2015).

Our results contrast markedly with the consensus reported by previous research (Chung et al., 2000; Davis et al., 2001; Halffter and Edmonds, 1982b; Hanski and Cambefort, 1991; Hosaka et al., 2014), which frequently suggest that dung beetle diversity following habitat degradation can be mainly explained by changes in forest structure and faecal availability (Gardner et al., 2008b). We found evidence that selective logging effects on dung beetle species richness and biomass occurred apart from our measures of canopy openness (Figure 4.3). As dung beetle communities are known to respond to logging intensity (Chapter 2 and 3), we presume that these results reflect the limitations of canopy openness as a measure of changes in forest structure. Hemispherical photos taken one year after disturbance inevitably capture both the state of the upper canopy and the regeneration in the understorey, with the latter often obscuring the former. The absence of environmental influence on dung beetle species richness and biomass within logged forests have been previously reported (Slade et al., 2011), which further outlines the difficulty of measuring appropriate environmental variables (Gardner et al., 2008b). Instead, it is possible that the low physiological tolerance that dung beetles have to temperature changes could explain this finding (A. Birkett, R. Bardgett, G. Blackburn and R. Menéndez, *unpublished manuscript*) since logging operations increase the number of forest gaps (Asner et al., 2004a), which leads to higher soil temperatures (Forrester et al., 2012).

Although primary forests are irreplaceable for tropical biodiversity conservation (Gibson et al., 2011), our study bring insights into the conservation value that logged forests have (Edwards et al., 2014c). In particular, we provide support to the idea that production forests can retain ecosystem processes operating in primary forests, even when the biodiversity of invertebrates is largely affected (Ewers et al., 2015). An explanation for this could lie on the influence that other detritivores have on faecal consumption in dung-based detritus food-webs (Slade et al., 2015; Wu et al., 2011), which has been already suggested for termites and ants (Dangles et al., 2012). Even though more empirical research is needed to better comprehend this 'functional redundancy' in faecal detritus-pathways, we highlight the role that logged forests can have in maintaining some of the faecal-detritus processes (Edwards et al., 2014c; Ewers et al., 2015).

Growing evidence has shown the role that environmental-dependency has on dung beetle diversity and associated faecal processes (Dangles et al., 2012; Griffiths et al., 2015; Hosaka et al., 2014; Nichols et al., 2013b). However, evidence that forest degradation can change the importance of environmental aspects to dung beetle-mediated processes are, to our knowledge, lacking in the literature. In particular, our results show that selective logging activities can alter the occurrence, direction and size of relationships between leaf litter, faecal consumption and incidental soil bioturbation (Figure 4.4). The positive influence that leaf litter has on soil chemistry and quality may explain its influence on soil bioturbation rates pre-logging (Nyeko, 2009; Uriarte et al., 2015); whereas, in the post-logging survey, leaf litter effects on roller dung beetles is a likely reason for its greater negative influence on faecal consumption. These roller species usually roll their brood balls away from the faecal deposit before burial beneath the soil (Halffter and Edmonds, 1982b; Hanski and Cambefort, 1991), a behaviour that may be hampered by the leaf litter (Nichols et al., 2013a). Lastly, it is very likely that the properties that sandy soils have (i.e. pore space and reduced cohesion) are potential explanations for its positive effects, at both surveys, on soil bioturbation rates (Griffiths et al., 2015; Marshall et al., 1996). However, regardless of the factors giving rise to it, these findings highlight the need for determining how forest degradation can influence the relationship between environmental aspects and ecosystem processes (Fayle et al., 2015). This could have implications in our understanding about long-term production forests recovery post-logging.

This work supports the prediction that forest degradation impacts are disproportionately stronger for dung species richness and biomass (Braga et al., 2013, 2012; Nichols et al., 2013b), as detritivore losses were not translated to effects on dung beetle-mediated faecal consumption and incidental soil bioturbation (Figure 4.3). This decoupled response has been previously found for dung beetle-mediated faecal removal and incidental secondary seed dispersal (Nichols et al., 2013b). However, it may be a result of a common sampling artefact. Overall, different amounts of dung are used to attract dung beetles to the pitfalls traps and to measure the faecal detritus-pathways (Braga et al., 2013, 2012; Nichols et al., 2013b). Such differences in dung amount (here 35 g and 200 g for pitfalls and arenas, respectively) may lead to a bias in the measurement of the faecal detritus-processes (Nichols et al., 2013b). Simple modifications in this methodology or sharper focus on this topic would allow us to overcome this issue, or even lead to the development of a correction factor to be applied when dung beetle diversity and mediated ecosystem processes assessments rely on this methodology.

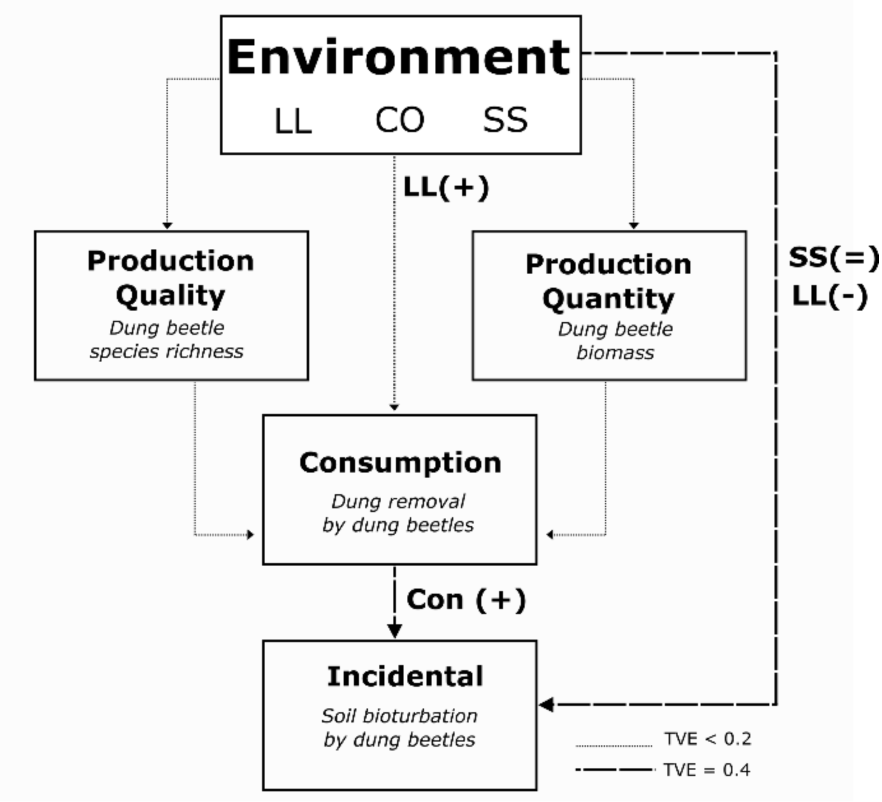

Figure 4.4 Flowchart illustrating how selective logging alters the relationships in-between dung beetle-mediated faecal-detritus pathways and those with the environmental predictors post-logging. The arrows indicate linkages between faecal-detritus pathways and significant predictors ($Z \geq 1.65$). Thicker dashed lines represent the total explained variance (TVE) = 0.4 and thinner dotted lines demonstrate TVE < 0.2. Signals (displayed in parenthesis besides capital letters) represent when a predictor was added (+), removed (–) or did not change (=) among pre- and post-logging surveys. LL = leaf litter weight (g), CO = canopy openness (%), SS = Sandy soil (%).

4.6 Conclusions

This investigation addressed the role of environmental aspects in mediating the logging impacts on dung beetle faecal-detritus pathways. The literature has frequently considered changes in vegetation structure and dung availability as the major drivers of these detritivores in disturbed environments (Davis, 2000; Davis et al., 2001; Gardner et al., 2008b). We found no evidence that canopy openness mediated dung beetle responses to logging, but we provide evidence that forest disturbances may change the occurrence, size and direction of relationships between environmental aspects and ecological processes. While the dung beetle patterns reported here highlight the irreplaceable role that pristine forests have to retain the tropical biodiversity (Gibson et al., 2011), we demonstrate that production forests nevertheless can retain ecosystem processes such as detrital consumption (Edwards et al., 2014c; Ewers et al., 2015)

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4.7 Supplementary Information

Appendix S4.1 Supplementary figures

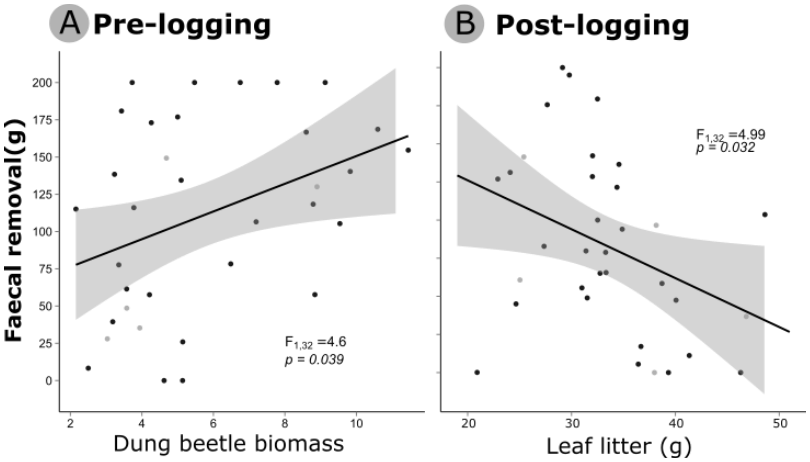

Figure S4.1 Pre-logging influence of dung beetle biomass (A), and post-logging influence of leaf litter on faecal removal rates (B).

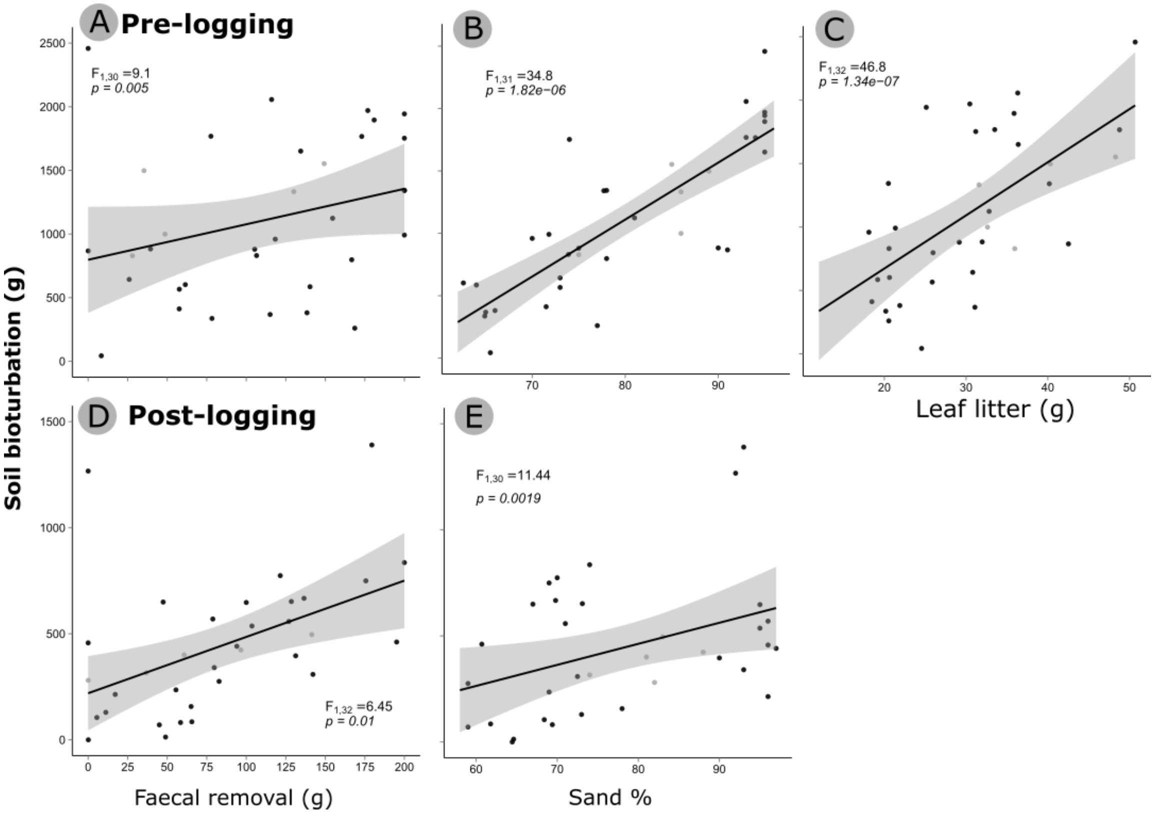

Figure S4.2 Pre- and post-logging influences of faecal removal (A&D), sand proportion (B&E) and leaf litter weight (C) on incidental soil bioturbation.

Appendix S4.2 Supplementary tables

Table S4.1 Dung beetle-mediated faecal pathways and environmental conditions sampled pre- and post-logging. [a]Treat = treatment (Log: logging units; Ctrl: control units), [b]PQl = production quality (n), [c]PQt = production quantity (g), [d]Con = detrital consumption, [e]Inc = incidental soil bioturbation, [f]LL = leaf litter biomass (g), [g]CO = canopy openness (%) and [h]SS = Soil sandy (%).

		Pre-logging survey							Post-logging survey						
Site	[a]treat	[b]PQl	[c]PQt	[d]Com	[e]Inc	[f]LL	[g]CO	[h]SS	PQl	PQt	Com	Inc	LL	CO	SS
Par1	Log	21	10.60	168.62	260	20.55	13.39	77	14	3.37	126.92	558	22.90	14.48	71
Par2	Log	17	9.54	105.32	880	29.16	10.72	75	10	1.41	121.50	774	34.38	20.00	70
Par3	Log	20	11.45	154.60	1123.5	32.82	12.53	81	8	3.46	200.00	835.5	29.13	20.10	74
Par4	Log	26	8.84	57.66	566	25.86	12.01	73	9	4.88	47.45	649.5	40.06	21.68	67
Par5	Log	25	9.13	200.00	1341	40.19	13.28	78	6	1.83	136.53	667	34.57	25.59	70
Par6	Log	17	8.60	166.69	797.5	25.96	11.23	78	12	4.26	65.11	157	32.75	23.79	78
Par7	Log	11	3.73	200.00	991.5	21.35	12.80	72	7	1.19	5.51	105	36.43	31.46	68
Par8	Log	15	5.14	25.95	643	30.81	11.01	73	7	1.94	11.17	129.5	41.34	32.85	73
Par9	Log	12	4.21	57.58	411.5	18.48	10.22	72	8	0.83	128.52	652	32.01	21.39	73
Par10	Log	17	6.75	200.00	1343.5	20.50	8.55	78	11	1.95	142.17	308.5	32.03	20.98	73
Par11	Log	15	7.20	106.51	830.5	20.57	10.10	74	8	3.61	58.43	81.5	38.71	17.28	69
Par12	Log	14	3.57	61.45	602	20.63	12.34	63	11	2.67	195.10	461	29.79	23.18	61
Par13	Log	12	6.49	78.29	336.5	20.18	11.40	65	4	0.23	65.58	85	33.33	22.25	62
Par14	Log	13	2.16	115.08	367.5	31.08	9.92	65	6	0.67	48.95	13	31.51	18.41	65
Par15	Log	16	2.50	8.31	43	24.56	9.11	66	4	0.90	0.10	0	20.91	25.92	64
Par16	Log	17	3.23	138.40	381	21.89	9.33	66	4	1.11	82.81	275.5	27.36	24.51	59

		Pre-logging survey							Post-logging survey						
Site	[a]treat	[b]PQl	[c]PQt	[d]Com	[e]Inc	[f]LL	[g]CO	[h]SS	PQl	PQt	Com	Inc	LL	CO	SS
Par17	Log	19	9.83	140.30	585.5	19.19	10.43	64	8	1.29	45.02	70.5	24.65	21.81	59
Par18	Log	21	7.78	200.00	1752.5	31.18	12.92	74	7	2.13	55.53	235.5	31.00	20.82	69
Par19	Log	20	8.79	118.33	959	18.11	9.80	70	4	0.89	175.64	749.5	27.67	17.14	69
Par20	Log	12	3.19	39.45	882.5	31.97	12.69	90	7	1.09	131.24	396	24.09	19.35	90
Par21	Log	11	3.43	180.88	1895.5	35.87	10.71	95	10	2.11	78.84	569.5	33.29	17.50	96
Par22	Log	18	5.00	176.87	1970	30.46	9.45	95	11	2.78	94.03	441	34.88	19.04	97
Par23	Log	19	5.47	200.00	1943.5	25.13	9.72	95	9	6.31	100.00	647.5	32.52	19.66	95
Par24	Log	17	5.10	134.42	1651	36.38	11.35	95	8	2.24	17.11	214	36.68	19.32	96
Par25	Log	11	3.78	116.02	2056.5	36.32	12.52	93	8	2.90	179.42	1390	32.50	22.48	93
Par26	Log	13	4.62	0.00	867	42.52	15.42	91	8	1.84	0.00	1267	39.33	22.64	92
Par27	Log	9	3.35	77.64	1768	33.51	14.35	93	6	1.08	79.75	340.5	31.39	17.72	93
Par28	Log	12	4.26	173.03	1766.5	48.77	15.04	94	9	1.97	103.59	536.5	48.62	17.23	95
Par29	Log	14	5.14	0.00	2458	50.69	12.03	95	6	1.32	0.00	457	46.29	15.80	96
Par30	Ctrl	14	3.58	48.59	999	32.63	10.76	86	10	5.37	0.00	280.5	37.99	17.99	82
Par31	Ctrl	16	4.69	149.26	1552.5	48.29	9.73	85	11	3.02	60.73	400.5	25.03	12.86	81
Par32	Ctrl	15	8.90	130.05	1332.5	31.59	12.12	86	9	3.94	141.43	496	25.41	19.26	83
Par33	Ctrl	16	3.94	35.29	1497.5	40.31	10.62	89	19	7.29	96.59	423.5	38.15	19.05	88
Par34	Ctrl	13	3.03	28.00	829	35.96	13.20	75	18	6.32	36.78	316	46.83	19.18	74

Table S4.2 Differences (mean ±SD) between environmental and faecal detritus pathways collected before and after selective logging at the same 34 management units.

	Pre-logging survey	**Post-logging survey**
Soil texture (%)	79.95±1.85	77.7±2.1
Canopy openness (%)	11.49±0.29	20.66±0.69
Leaf litter (g)	30.39±1.53	33.33±1.13
Production Quantity (g)	5.79±0.44	2.59±0.3
Production Quality (n)	15.8±0.67	8.74±0.58
Consumption (g)	111.54±10.98	83.28±9.94
Incidental (g)	1108.35±103.49	440. 67±54.43

Table S4.3 Results from hierarchical partitioning on pre and post-logging dung beetle-mediated faecal-detritus pathways from 34 sites surveyed.

Dependent	Predictor	I pre-log	J pre-log	Tot pre-log	I% pre-log	Z pre-log	ρ pre-log	I post-log	J post-log	Tot post-log	I% post-log	Z post-log	ρ post-log
Production Function Quantity	LL	0.055	0.005	0.06	60.1	0.58	-0.25	0.06	0.011	0.074	47.9	0.86	0.27
	CO	0.018	-0.015	0.003	20.3	-0.27	0.06	0.03	0.008	0.045	27.9	0.2	-0.21
	SS	0.018	0.014	0.032	19.5	-0.27	-0.18	0.03	0.028	0.06	24.1	0.08	0.24
Production Function Quality	LL	0.012	0.017	0.03	20.4	-0.43	-0.17	0.05	0.004	0.06	36.9	0.57	0.25
	CO	0.016	0.011	0.027	26.8	-0.36	-0.17	0.07	0.008	0.08	49.33	1.13	-0.29
	SS	0.031	0.017	0.049	52.7	0.07	-0.22	0.02	0.025	0.04	13.76	-0.28	0.21
Consumption Function	PQl	0.057	0.048	0.105	24.8	1.41	0.33	0.01	-0.005	0.008	7.5	-0.39	0.09
	PQt	0.09	0.05	0.14	39	0.74	0.38	0.003	-0.002	0.0002	1.6	-0.66	0.01
	LL	0.029	-0.005	0.023	12.5	0.08	-0.15	0.13	-0.001	0.134	73.7	**2.64**	-0.37
	CO	0.011	0.0017	0.012	4.8	-0.44	-0.11	0.02	0.009	0.036	14.6	-0.1	-0.19
	SS	0.043	-0.037	0.005	18.6	0.4	0.07	0.004	-0.002	0.002	2.4	-0.66	-0.05
Incidental Function	Con	0.092	-0.005	0.087	12.1	1.4	0.3	0.26	-0.028	0.235	59.6	**6.06***	0.48
	PQl	0.006	0.004	0.011	0.87	-0.58	-0.11	0.005	0.001	0.006	1.1	-0.61	0.08
	PQt	0.006	0.001	0.008	0.89	-0.59	-0.09	0.006	0.007	0.014	1.5	-0.58	0.12
	LL	0.211	0.176	0.388	20.7	**4.01***	0.62	0.021	-0.015	0.006	4.9	-0.22	0.08
	CO	0.015	0.009	0.025	2	-0.35	0.16	0.01	0.014	0.025	2.3	-0.54	-0.16
	SS	0.429	0.237	0.666	56.2	**9.48***	0.82	0.134	0.016	0.15	30.3	**2.65***	0.39

Shown are the independent (I), joint (J) and total effects of predictors on the response variables. I% represents the contribution of the I-values to the total explained variance in the response variables. The Z-scores shown are calculated as [observed mean (1000 randomizations)]/SD(1000 randomizations) and their statistical significance (*) based on the upper 95% confidence limit (Z = 1.65). The Pearson's coefficient (ρ) for each predictor variable was outside the HP, but it is included to indicate the nature of the predictor variables relationship against the response variable. LL = leaf litter biomass (g), CO = canopy openness (%), SS = Soil sandy (%), PQl = production quality (n), PQt = production quantity (g) and Con = detrital consumption (g).

Chapter 5: DOES SELECTIVE LOGGING STRESS TROPICAL FOREST INVERTEBRATES? USING FAT STORES TO EXAMINE SUBLETHAL RESPONSES IN DUNG BEETLES

5.1 ABSTRACT

Current research shows that forest degradation causes widespread declines in natural populations. There is a growing consensus that subletal effects manifested on individuals' physiology is a likely mechanism underlying the responses at population level. Yet, we have a very limited understanding about human-induced sublethal effects in tropical animals, particularly so with regard to invertebrates. We examined the body fat content in individuals of three dung beetle species (Coleoptera: Scarabaeinae) sampled through a before-after-control-impact design (BACI) to investigate whether selective logging would induce sublethal effects on tropical invertebrates. Therefore, we qualitatively compared the relative abundance and body fat content from each species to examine if sublethal and population level responses would match. Our findings demonstrate for the first time that selective logging can induce sublethal effects on tropical invertebrates. Furthermore, the sublethal and relative abundance responses were qualitatively similar; we thus support the measurement of body fat content as reliable biomarker to assess sublethal effects in insects. Understanding how environmental modification impacts natural wildlife has never been more pressing, therefore adopting physiological approaches can improve our ability to develop and evaluate conservation strategies.

Keywords: Sublethal effects. Conservation physiology. Tropical forests. Reduced-impact logging. Selective logging. Dung beetles. Early warning signal. Fat reserves. Lipid content.

5.2 Introduction

Understanding how natural populations respond to environmental modification has never been more pressing. Current research aiming to assess the negative impacts of anthropogenic activities relies chiefly on responses at the species and population levels (Burivalova et al., 2014; Newbold et al., 2015). More recently, there has been increased attention to evaluating the sublethal effects behind the faunal responses to environmental degradation (Coristine et al., 2014; Rimbach et al., 2013). This promises to provide important insights into the mechanisms which link faunal patterns to environmental modification, and may help devise effective conservation strategies (Coristine et al., 2014).

Most of environmental degradation impacts on natural populations start with sublethal effects on individuals (Dantzer et al., 2014; Martínez-Mota et al., 2007). Studies have shown that sublethal effects (e.g. fluctuating asymmetry, changes in body conditions and oxidative levels) are manifested in the physiology, morphology and behavior of individuals long before responses are expressed and observed at the population-scale (e.g. Beaulieu and Costantini, 2014; Cooke et al., 2013; Wagner et al., 2013). Therefore, these sublethal responses can act as 'early warning signals' to predict future population responses and identify conservation priorities (i.e. Beasley et al., 2013; Blanckenhorn, 2003; Dantzer et al., 2014; Hellou, 2011).

As the discipline of Conservation Physiology emerges, so does the need for reliable physiological biomarkers (Cooke et al., 2013; Coristine et al., 2014). Several biomarkers have been frequently used to quantify physiological stress (e.g. Beasley et al., 2013; Beaulieu and Costantini, 2014; Rimbach et al., 2013; Romero, 2004), and most of these focus on glucocorticoid levels (Dantzer et al., 2014; Dickens and Romero, 2013). However, other studies highlight the importance of downstream metrics (e.g. body fat content and mass changes) to properly assess the significance and impact of stress in free-living animals (Breuner et al., 2013; Dickens and

Romero, 2013). For example, the body fat content has been frequently measured as physiological biomarker to assess sublethal effects of many environmental stressors on vertebrates (Lucas et al., 2006; Suorsa et al., 2004, 2003) and insects (Desneux et al., 2007; Knapp and Knappová, 2013; Piiroinen et al., 2014; Reaney and Knell, 2015). Overall, studies have shown that organisms under stressful conditions exhibit increased fat storage (Gentle and Gosler, 2001; Piiroinen et al., 2014), which is suggested as a strategy to increase life span as result of improved energy consumption efficiency (Hansen et al., 2013) and increased starvation stress resistance (Arrese and Soulages, 2010). However, changes in the fat metabolism can have negative effects on organisms' physiological balance (Moghadam et al., 2015; Van Praet et al., 2014), which might reduce the individual fecundity and reproduction (Arrese and Soulages, 2010; Barry and Wilder, 2013; Hansen et al., 2013).

Despite progress made in our understanding of how forest degradation can induce sublethal effects on wildlife, two key areas remain underexplored in the literature. First, there is a clear bias towards temperate regions (i.e. Leshyk et al., 2012; Lucas et al., 2006; Mastromonaco et al., 2014; Suorsa et al., 2004, 2003; but see: Rimbach et al., 2013), yet biodiversity levels and deforestation rates in tropical forests are the highest in the world (Kim et al., 2015; Pan et al., 2011). Thus, our knowledge of forest degradation sublethal effects on the tropical fauna is very limited. Secondly, these studies have typically investigated how forest degradation influence vertebrates (Mastromonaco et al., 2014; Rimbach et al., 2013; Suorsa et al., 2004, 2003) and evidence of how such disturbances can induce sublethal effects on tropical invertebrates are, to our knowledge, lacking in the literature.

To fill this knowledge gap, the overarching aim of this study was to investigate the sublethal and population-scale impacts of selective logging on dung beetles (Coleoptera: Scarabaeinae). The selective logging is considered a major disturbance driver throughout tropical forests (Asner et al., 2009; Blaser et al., 2011) and has been reported to induce sublethal effects in vertebrates

(Lucas et al., 2006; Rimbach et al., 2013; Suorsa et al., 2004, 2003). We considered the fat content of three dung beetle species as a biomarker for logging sublethal effects, and their relative abundance as population-scale response to logging. We believe dung beetles are an appropriate focal insect group, given their extensive use to assess the selective logging impacts on biodiversity (Bicknell et al., 2014a; Davis et al., 2001; Edwards et al., 2014a, 2012b). Hence, we hypothesized that body fat content of dung beetles in selectively logged forests would increase as a sublethal response to new stressful environmental conditions. Furthermore, we also examine whether these stress-induced sublethal effects on the same species would match with their relative abundance responses to logging.

5.3 Methods

5.3.1 Study area and design

Beetles were sampled within the 1.7 Mha *Jari Florestal* landholding, located in the north-eastern Brazilian Amazonia (00°27′–01°30′ S, 51°40′–53°20′ W; Chapter1: Figure 1.3). The area comprises a mosaic of *Eucalyptus* plantations and regenerating secondary forests within ~1.5 Mha of primary forests subjected to very low levels of disturbance (Barlow et al., 2010; Parry et al., 2009a). Forests in this region are characterized as evergreen dense tropical rainforest (Souza, 2009), often dominated by the timber species *Dinizia excela* Ducke (Fabaceae, Mimosoideae) (Laufer et al., 2015), which corresponds to about 50% of exploited timber in some Amazonian regions (Barbosa, 1990).

Reduced-impact logging (RIL) started in 2003, with plans to log approximately 544,000 ha of native forest over a 30 year cutting cycle. This management produces ~30,000 m^3 of timber annually and is one of the largest Amazon logging concessions under the Forest Stewardship Council certification (FSC, 2014). Logging operations follow FAO guidelines (Dykstra and Heinrich, 1996) to minimize its impacts via a pre-harvest inventory, which maps, measures and identifies all commercially viable trees with DBH ≥ 45cm. Therefore, the skid trails and logging road network is minimized, tangling lianas are cut before harvesting and directional felling is used to reduce collateral damage to other trees. After logging operations in 2012, the timber removal average within the harvested area was about 16.8 m^3 ha^{-1}, which is within RIL protocols that set an upper limit from 25 m^3 ha^{-1} for the 30 years cutting cycle (IFT, 2014, CONAMA Resolution 406/2006).

We used a BACI experimental design to sample dung beetles at 34 independent sites of 10 ha (250 m x 400m) across this logging concession. Five of these sites were primary forest controls, which remained unlogged during the course of the study, and were about 6.5 Km from the closest logged sites. The other 29 sites were logged under a gradient of logging intensity from 0 - 50.31 m^3 ha^{-1} of extracted timber (or 0 - 7.9 trees ha^{-1}). Two dung beetle surveys were conducted at exactly the same locations and using the same methods at all 34 sites. The first survey (pre-logging) was conducted in June and July 2012, approximately 45 days before the logging operation began. The second survey (post-logging) took place in 2013, around 10 months after the logging activities ended. It also occurred in June and July, to minimize possible effects from seasonal variation. Sampling locations were relocated based on marking tape, or by GPS when disturbance from logging activities meant this could not be found.

5.3.2 Dung beetle collection

Dung beetles were collected with baited pitfall traps, which were plastic containers (19 cm diameter and 11 cm deep) buried in the ground with their opening at ground level, containing approximately 250 ml of a saline solution and a plastic lid as a rain cover. A small plastic cup containing approximately 35 g of pig dung mixed with human dung (80:20 pig to human ratio, Marsh *et al.* 2013) was attached by a wire above each pitfall. All dung beetles that fell in pitfall traps were dried and transported to the laboratory where they were identified to species level, or morphospecies level where this was not possible. Voucher specimens were added to the Reference Collection of Neotropical Scarabaeinae in the Insect Ecology and Conservation Laboratory, Universidade Federal de Lavras, Brazil.

5.3.3 Samples preparation and body fat extraction

To examine whether selective logging induces stress sublethal responses on invertebrates, we assessed the body fat content of the three dung beetle species *Oxysternon festivum* Linnaeus, 1767, *Dichotomius (Luederwaldtinia) lucasi* (Harold, 1869) and *Deltochilum (Deltohyboma)* aff. *submetallicum* (Castelnau, 1840). For analysis purpose, we selected these species based on the minimum abundance of 40 individuals within each treatment level (control and logging sites) for each survey event (pre and post-logging).

Before fat extraction, all examined individuals were oven-dried at 40 °C for 48 h and dry-weighed with a *Shimatzu* AY220 balance scale (*Shimadzu Corporation, Kyoto, Japan*) accurate to within ±0.0001g. Dried and weighed individuals were assigned an identification number and placed into a labelled extraction thimble (~30 mm width and 60 mm length) made from thick filter paper. In order to increase the measurement efficacy of fat storage of the smaller species, we placed two individuals of *D.* aff. *submetallicum* or *D. lucasi* (n = 156 and 160 individuals in total, respectively) into each extraction thimble. The average body fat content of two individuals of each species was then measured as an extraction sample. For the larger *O. festivum* species, we individually weighed 80 beetles before placing each one into an extraction thimble.

All extraction thimbles were loaded into the main chamber of the Soxhlet extractor apparatus (MA 487/6/250 *Marconi Equipamentos para Laboratórios, Piracicaba, Brazil*), which was fitted to a tared distillation flask containing five boiling glass regulators. Body fat content was extracted using

200 mL of *n*-hexane heated under reflux for 4 h (18-22 cycles/h) at 63-65 °C. We opted to use Soxhlet fat extraction as it has been suggested as a reference method for evaluation of other extraction methods (Tzompa-Sosa et al., 2014; Wang et al., 2010), and has been previously used to assess the body fat contents from dung beetles and other insects (Edwards et al., 1988; Hart and Tschinkel, 2012; Moya-Laraño et al., 2008; Tzompa-Sosa et al., 2014). After extraction, all thimbles were left in a walk-in fume cupboard (SP-Labor, model SP-150N, average duct velocity = $60m^3 min^{-1}$) for 24 h to eliminate the major excess of solvent. Subsequently, thimbles were oven-dried for another 48 h at 40 °C to assess the fat-free weight. Total fat content (g) was measured by subtracting the fat-free weight from the dry-weight for each beetle (or pair of beetles). In thimbles that contained two individuals, we considered the average weight difference as the measure of body fat content.

5.3.5 Statistical analyses

All analyses were performed in R (R Core Team, 2015). We used generalized linear models (GLMs) with a logarithmic link function (Zuur et al., 2009) in the *glm()* routine (*stats* package, R Core Team, 2015) to assess the effects of the explanatory variables ‘time’ (2 levels: pre- and post-logging) and ‘treatment’ (2 levels: control sites and logging sites) on the dependent variable body fat content. As data were overdispersed, we used quasi-Poisson likelihood models, which are recommended to deal with such data (Ver Hoef and Boveng, 2007). GLMs were analysed by performing a two-way ANOVA test, including the factors ‘time’, ‘treatment’ and the interaction between them, followed by post hoc pairwise t-test with non-pooled standard deviations.

We assessed two dependent variables: dung beetle biomass (dry-weight prior fat extraction) and body fat content (difference among dry and fat-free weight). Because we aimed to examine changes in the dung beetle body fat content, we opted to include the body mass values as an offset in the GLMs (Zuur et al., 2009). An offset includes a known term for the linear model without fitting its parameters. This approach has been recommended to handle ratios without missing the discrete nature of the response, or when collinearity may be expected (Bolker, 2012). Thus, we modelled the effects of explanatory variables on the ratio between the body fat content and body biomass, without being confounded by the biomass effect.

Finally, to examine whether sublethal changes are consistent with direct population-scale responses to selective logging, we also used quasi-Poisson GLMs to verify the responses of each species' relative abundance to the same explanatory variables and factors used for fat body content. In addition, we tested for significant differences in abundance by performing a two-way ANOVA test, followed by post hoc pairwise t-test with non-pooled standard deviations. Comparisons with changes in fat were made qualitatively.

5.4 Results

5.4.1 Sublethal effects of selective logging

On average, dung beetles had higher body fat content in the second survey, in both control and logged sites (Figure 5.1A-C). However the interaction between survey period and logging treatment was also significant for two species, which indicates the effect of logging treatment on fat levels (two-way ANOVA: *D.* aff. *submetallicum* time $F_{1,76} = 69.4$, $p < 0.001$ & treatment $F_{2,75} = 4.82$; $p = 0.03$; *D. lucasi* time $F_{1,78}= 164.2$, $p < 0.001$ & treatment $F_{2,77} = 14.4$; $p= 0.0002$; *O. festivum* treatment × time $F_{3,76}= 4.3$; $p= 0.03$; Figure 5.1A-C). Post-hoc analysis supported these findings for the species *D.* aff. *submetallicum* and *D. lucasi*, as the individuals had higher body fat content at logged sites compared with unlogged sites (t-test, p-value ≤ 0.02; Figure 1A-B). Nevertheless, no sublethal effect of logging was found on fat storage of *O. festivum* species (t-test, p-value = 0.95; Figure 5.1C)

5.4.2 Population-level effects of selective logging

Dung beetle relative abundances were negatively affected by the selective logging (Figure 1D-F; two-way ANOVA: *D.* aff. *submetallicum* time $F_{1,66} = 44.02$, $p < 0.001$ & treatment $F_{2,65} = 4.05$; $p = 0.04$; *D. lucasi* time $F_{1,66} = 7.31$, $p = 0.008$ & treatment $F_{2,65} = 29.6$; $p < 0.001$; *O. festivum* time $F_{1,66} = 80.6$; $p < 0.001$; Figure 5.1D-F).

Pairwise comparisons showed that more *D.* aff. *submetallicum* individuals were sampled at pre-logging control sites rather than in the post-logging sites, irrespective of where (t-test, control sites: $p = 0.02$; logged sites: $p < 0.001$; Figure 5.1D), thus, its abundance within the sites to be logged was higher than the number of individuals sampled after selective logging in the same sites (t-test, $p < 0.001$; Figure 5.1D). The abundance of *D. lucasi* was higher in control sites than logged sites in both surveys (t-test, $p < 0.001$; Figure 1E), decreasing at post-logging harvest sites (t-test, $p = 0.006$; Figure 5.1D). Although a trend of decreasing abundance of *O. festivum* in the second survey was found, pairwise comparisons showed significant differences just between its abundance at sites to be logged in the first survey and both post-logging control and disturbed sites (t-test, $p < 0.001$ for both; Figure 5.1F). More *O. festivum* individuals were sampled at pre-logging control sites than post-logging disturbed sites (t-test, $p = 0.03$). Lastly, these sublethal responses were qualitatively similar to the changes in dung beetle relative abundances.

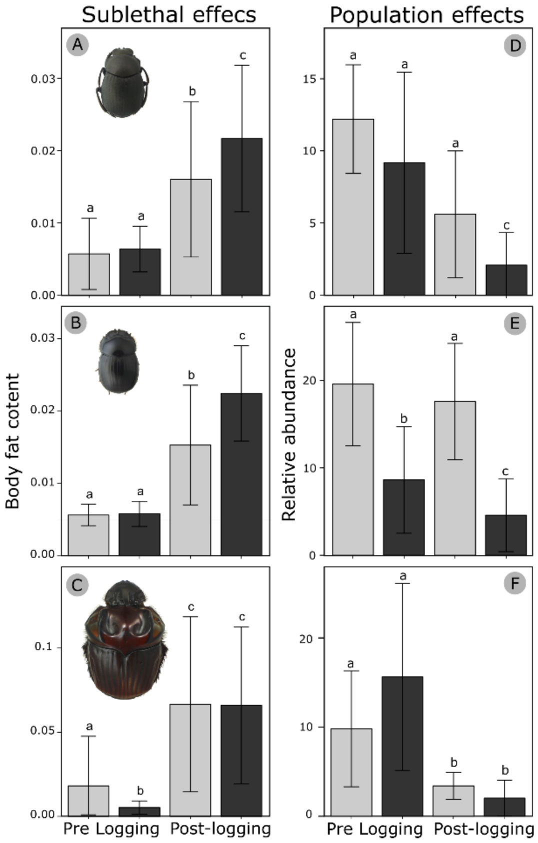

Figure 5.1 Sublethal and relative abundance effects of selective logging on the dung beetle species *Deltochilum* aff. *submetallicum* (A&D); *Dichotomius lucasi* (B&E); and *Oxysternon festivum* (C&F). On the left panels sublethal effects were measured on the fat body content (g) and right panels show dung beetle abundances of each species. Because we used a BACI experimental design, left bars from each panel show the pre-logging data and right bars represent post-logging. Data from control (n = 5) units are present in light grey bars and from logging units (n=29) are present in dark gray bars. Photographs are scaled to each other; the smallest species are (A) *Deltochilum* aff. *submetallicum* (length: 13.1 mm) and (B) *Dichotomius lucasi* (length: 11.5 mm); the largest species is (C) *Oxysternon festivum* (length: 20.6 mm). Means (± SEM) followed by the same lower-case letters indicate zero difference at 5% based on two-way ANOVA and pairwise comparisons. All t-test post hoc pairwise comparisons were performed with non-pooled standard variations comparisons between group levels. Two-way ANOVA showed significant interaction over time between control and logging sites in fat body content of *Oxysternon festivum* ($F_{3,76}$= 4.3; p= 0.03; panel C).

5.5 Discussion

Our results demonstrate that selective logging can generate sublethal responses in dung beetles, supporting the notion that forest disturbances can affect invertebrates' physiology. Moreover, these sublethal responses were qualitatively similar to the changes in dung beetles' relative abundance (Fig 5.1.A-C), which supports the measurement of body fat as a potential biomarker of insect stress.

5.5.1 Sublethal effects of selective logging

Most energy reserves of insects are accumulated in the body fat (Arrese and Soulages, 2010), which regulates physiological and behavioural responses to environmental and human-induced conditions (Arrese and Soulages, 2010; Edwards et al., 1988; Reaney and Knell, 2015). As many studies have shown the increased fattening of insects in response to other stress-induced conditions (Desneux et al., 2007; Moghadam et al., 2015; Piiroinen et al., 2014; Van Praet et al., 2014), we suggest that the increased body fat content in dung beetles from logged forests reinforces the use of this trait as a likely 'early warning' biomarker to be applied in the assessment of environmental quality of disturbed tropical forests.

A likely explanation for the observed fattening in dung beetles is the reduction in reproduction rates. Reproduction is a high cost process (Hansen et al., 2013) and fat content is considered the currency (Barry and Wilder, 2013). Although not always observed (Flatt et al., 2008; Wilder et al., 2015), the relationship between reduced reproduction and increased fat storage has been demonstrated for many insects (Hansen *et al.*, 2013; Moghadam *et al.*, 2015; Wilder *et al.*, 2015). Similarly, previous research has found a positive relationship between reduced fecundity, increased fattening and higher starvation stress resistance (Broughton et al., 2005). These findings indicate that under stressful conditions invertebrates may modify their fat metabolism as strategy to optimize energy allocation for surviving likely starvation periods (Hansen et al., 2013). However, a major concern is how increased body fat content will influence long-term patterns in dung beetle populations. Having plenty of fat does not necessarily result in high reproductive success when insects are deficient in other nutrients (e.g. protein and vitamin) needed for effective reproduction or for maintaining a healthy metabolic function (Barry and Wilder, 2013; Wilder et al., 2015). As organisms relocate part of energy reserves to repair or maintain their physiological integrity under stressful environments, less energy is left for individual growth and eventual reproduction (Van Praet et al., 2014). This could lead to further depopulation and may explain the qualitative connection between sublethal effects and the relative abundance we found for the three assessed dung beetle species.

Alternatively, the post-logging environmental conditions may also favour dung beetles that are pre-disposed to accumulating more fat. Piiroinen et al., (2014) have found that parental exposure to insecticide stress resulted in fatter individuals of the Colorado potato beetle (*L. decemlineata*) in subsequent generations, which then had a similar chance to survive overwintering period as did beetles descending from unexposed control beetles. In logged forests, it may be that only fatter larvae of dung beetles will survive logging impacts on the soil structure (Rist et al., 2012) and increased soil temperatures at forest gaps (Asner et al., 2004a; Forrester et al., 2012). Such below-ground environmental impacts could act as an ‘emergence-filter’ by selecting only the dung beetle larvae that accumulate the most fat (both as larvae and subsequently as adults). The decreased emergence of dung beetles as result of this filter may explain the lower abundance of beetles on logged sites; whereas the surviving larvae may explain the fatter dung beetles. While the larval environment has been shown to influence the fat content of adult beetles (Reaney and Knell, 2015), these mechanisms suggested here are speculative, but highlight an interesting avenue for further work.

5.5.2 Interannual variation and species-specific responses

Although we found that body fat content was higher in individuals of two species (*D.* aff. *submetallicum* and *D. lucasi*) sampled at disturbed sites, body fat content also increased, irrespectively of where, in the second survey for all species. This result was somewhat surprising, because dung beetle collections were carried out in the same months (June and July) in both years to minimize seasonal effects. Nevertheless, it may reflect the temporal variation of environments leading to changes in biomarkers related to reproduction and survival (i.e. fat content and body mass), as described for dung beetles (Edwards et al., 1988) and carabid beetles (Östman, 2005).

Studies have shown that different species may cope differently with forest fragmentation and selective logging (Leshyk et al., 2012; Lucas et al., 2006; Mastromonaco et al., 2014; Suorsa et al., 2004, 2003; Wasser et al., 1997). Thus, we highlight that probably not all species may have predictable and similar physiological responses to forest disturbances (as suggested by Rimbach *et al.*, 2013), even when consequences in relative abundance are negative for all of them. Moreover, it is very likely that these responses may also be sex-dependent (Zhang et al., 2010). However, the low sample sized in disturbed post-logging sites prevented us from separating dung beetles by gender and to make more inferences about reproduction aspects and sex-dependent responses. Another caveat of our study is that we assessed just one type of forest disturbance influencing just the fat storage from an insect group. We strongly suggest that further studies are needed to understand the following questions: (1) How do different forest disturbances induce sublethal effects on different invertebrates? (2) Do different invertebrate groups respond similarly to stress-induced impacts? and (3) How might sublethal effects influence ecological functions provided by invertebrates? Answering these questions may increase our ability to better understand the consequences of forest disturbances on tropical fauna, thus enabling us to improve conservation strategies (Coristine et al., 2014).

5.6 Conclusions

Understanding how impacts of environmental degradation on natural populations are driven by physiological mechanisms has never been more critical (Busch and Hayward, 2009). A first key finding of this study is that selective logging brings about sublethal effects indicative of stress in tropical forest invertebrates. Therefore, we are confident that body fat content is a reliable biomarker to assess stress in dung beetles because the relative abundance results we found and recommend its use as an 'early warning' biomarker to monitor insect communities associated with disturbed forests. Lastly, we reinforce the potential role of Conservation Physiology as a tool to improve the ecological value that logged forest already have (Edwards et al., 2014c).

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Chapter 6: GENERAL DISCUSSION

6. General Discussion

More than 20% of the word’s tropical forests have been selectively logged in recent decades (Blaser et al., 2011; FAO, 2010) and over 400 million hectares are now held as permanent timber production concessions (Blaser et al., 2011; Laurance and Edwards, 2014). The expansion of selective logging has been exacerbated by the growing global demand for tropical timber, particularly in Europe, US and emerging economies such as Brazil, China, India, Indonesia and Malaysia (Blaser et al., 2011; Dykstra and Heinrich, 1996; Wilson et al., 2010). Selective logging is now one of the most widespread economic activities in tropical nations (Guariguata et al., 2010; Laporte et al., 2007; Pearce et al., 1999) and tropical forest degradation is expected to increase in coming years (Newbold et al., 2015; Pereira et al., 2010).

The overarching aim of this thesis was to investigate how selective logging influences the tropical biodiversity, animal physiology and the ecological processes, using dung beetles as a model group (Figure 6.1). In addressing this aim, I first compare results from two experimental designs that are often used to measure the biological consequences of forest degradation (Chapter 2). I then assessed the shape and scale-dependency of the relationships between logging intensification and dung beetle diversity and mediated ecosystem functions (Chapter 3); I also explored the relative importance of environmental aspects underlying these relationships (Chapter 4). Finally, I evaluated the sublethal stress-induced impacts of selective logging on body fat of three dung beetle species (Chapter 5). Therefore, in this thesis I provide several advances to promote and evaluate the sustainable use of tropical forests, one of the key goals of an international plan to reduce the loss of biodiversity and ecosystem services by 2020 (Convention on Biological Diversity, 2014).

6.1 Key findings

The results presented in this thesis give support to previous research showing the consequences of selective logging on biodiversity and ecosystem processes (Asner, 2005; Berenguer et al., 2014; Edwards et al., 2014b, 2014c; Foley et al., 2007; Gutiérrez-Granados and Dirzo, 2010; Schleuning et al., 2011; Slade et al., 2011). However, by comparing the before-and-after (BA) and space-for-time (SFT) experimental designs, I also show that using SFT may lead us to underestimate the biological consequences of forest disturbances. Moreover, a weak but positive association between timber value for production and dung beetle diversity was found in the pre-logging assessments (Chapter 2). A previous pantropical meta-analysis has also outlined the thresholds of logging intensity for forest fauna by assessing logging as a continuous effect (Burivalova et al., 2014); this thesis has provided, for the first time, empirical support for this threshold, and importantly shows that it is concave rather than convex in shape (Chapter 3). This result demonstrates that biodiversity and ecosystem functioning processes may decrease as logging intensity increases, therefore giving support to the land-sparing strategy to maintain higher levels of biodiversity within production forests (Edwards et al., 2014a). Therefore, the scale-dependent patterns I found in Chapter 3 reinforce the need to consider different scales to improve our knowledge about logging impacts on biodiversity and ecological processes (Berry et al., 2008; Hamer and Hill, 2000; Hill and Hamer, 2004; Imai et al., 2012).

In Chapter 4, I show how changes in canopy openness do not necessarily result in declines in dung beetle species richness and biomass. Aside from not directly influencing the average rates of faecal consumption and soil bioturbation (neither leaf litter weight nor sand proportion in the soil), selective logging altered most linkages between these biological and environmental components (Chapter 4). Additionally, the absence of selective logging effects on dung removal rates (Chapter 3 and 4) adds weight to the suggestions that logged forests can retain ecological processes associated with primary forests (Edwards et al., 2014; Ewers et al., 2015). Finally, another key finding of this thesis is that logging operations have the potential to induce sublethal effects on dung beetles, which were qualitatively similar to the declines found in the relative abundance of the three examined species (Chapter 5). This work therefore provides the first empirical evidence that logging operations can induce physiological stress in tropical invertebrates.

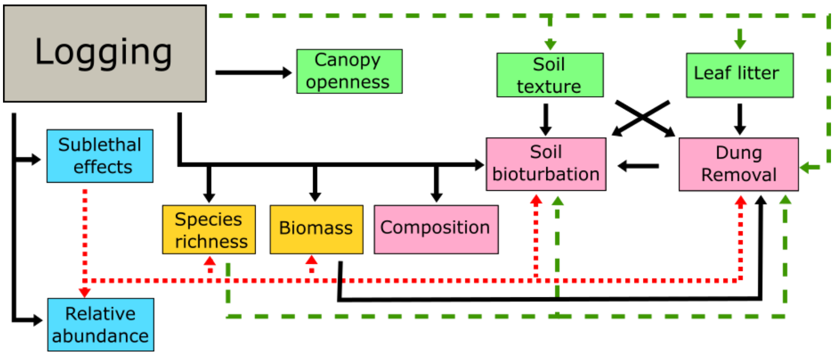

Figure 6.1 Summary of the ecological linkages associated with selective logging impacts on tropical dung beetles that are discussed in this thesis. The black straight lines are the linkages directly quantified and significantly presented. The green dashed lines signify linkages not found in this thesis, but are shown by previous research. The red dotted lines were not directly tested, but are believed to occur and may prove a particularly interesting avenue for further research. Coloured boxes indicate the chapter where the metrics are addressed (Chapter 2 orange, Chapter 3 orange and pink; Chapter 4 orange, pink and green; Chapter 5 blue).

6.2 Implications for forestry management and biological conservation

6.2.1 Space-for-time (SFT) and before-and-after (BA) comparisons

A key outcome of this thesis was that SFT assessments could result in undervaluation of forest disturbance impacts on biodiversity. In particular, this approach was too optimistic and suggested less severe consequences of selective logging on dung beetle diversity and biomass. This finding could have wide implications for conservation research, as the global assessments of biodiversity loss due to human impacts are mostly underpinned by SFT studies (Burivalova et al., 2014; Gibson et al., 2011; Newbold et al., 2015, 2012; Pfeifer et al., 2014) and therefore could be underestimating biodiversity loss.

Although it may be more realistic to examine the biological consequences of human activities through BA assessments, this is accompanied by many logistical issues (Kibler et al., 2011). Among them, I highlight the double sampling effort, which results in more time and money spent to gather the necessary data (Chapter 2, Figure 2.3), and also the impossibility to predict where and when some disturbances will happen (i.e. wildfires, secondary forests, illegal logging or land-use change). These two issues have implications regarding the need for effective communication between researchers and landowners in order for before-and-after studies to take place. Effective communication is a key solution to the 'knowledge-doing' gap that exists between conservation science and practice (Boreux et al., 2009; Habel et al., 2013; Wu and Hobbs, 2002). Regarding the unpredictability of disturbance events, in the section 'Priorities for future work' below I consider some suggestions to help resolve this issue.

6.2.2. How much logging is too much for holding biodiversity?

Using dung beetles in the Brazilian Amazon forest as a model study group, this thesis has shown that logging intensification leads to negative impacts on biodiversity and ecosystem functioning (Chapter 2 and 3). It is well established that logging impacts tropical forest biodiversity, and that ecosystem functioning depends on logging intensity (Burivalova et al., 2014; Gatti et al., 2015; Martin et al., 2015; Slade et al., 2011), but I am unaware of any empirical studies assessing logging impacts on tropical fauna as a continuous (rather than categorical) effect. Therefore, the findings from this thesis bring insights to the question previously highlighted in the introduction section: How to integrate timber production to tropical forest conservation? I outline below likely implications of this thesis regarding the sustainable forest management.

(i) Harvest intensity? According to this thesis, as soon as logging intensity increases, so do the impacts on biodiversity and ecological processes. Surprisingly, we found concave relationships with dung beetle species richness, biomass and composition decreasing at low intensities until a threshold of logging intensity around 18-20 m^3 ha^{-1} of timber (3-4 trees) at the local scale. Although close to the logging threshold previously suggested for amphibians (23 m^3 ha^{-1}), this is much lower than the value of 41 m^3 ha^{-1} indicated for tropical invertebrates (Burivalova et al., 2014). Consequently, I reinforce the need for more studies with other taxa that assess logging as a continuous variable to improve our understanding of how much timber can be removed without endangering tropical wildlife. This would greatly improve the development of better forestry management guidelines. Furthermore, logging intensity is not the only important aspect I found to influence biological patters, which raises the second question:

(*ii*) *Land-sparing vs. Land-sharing: which strategy?* This thesis also shows that dung beetle diversity and logging intensification relationships had a concave shape (Chapter 3). This suggests that land-sparing strategy may increase the conservation value of timber concessions (Edwards et al., 2014c), as overall levels of diversity will be greater if high-intensity disturbed patches are mixed spatially within large undisturbed landscapes (Fischer et al., 2014; Phalan et al., 2011; von Wehrden et al., 2014).

(iii) At what scale should harvest intensity be regulated? Results from Chapter 3 show that biodiversity can be negatively affected by logging intensification measured at different spatial scales. By measuring the logging intensities on a broader scale (90 ha) we observed changes in the biological responses of dung beetles at around 17-27 m^3 ha^{-1} of removed timber. These findings have methodological implications for further research, as it adds weight to the need of assessing logging impacts at different scales to improve our knowledge about its consequences on local biodiversity (Berry et al., 2008; Hamer and Hill, 2000; Hill and Hamer, 2004; Imai et al., 2012). Similarly, it brings insights into the need for policy frameworks regarding timber production to address the spatial scale of selective logging consequences.

6.2.3. What the eyes do not see the forest does feel –logging impacts on tropical forests

No evidence was found that logging impacts on canopy openness resulted in the negative effects of logging on dung beetle responses (Chapter 4). In contrast, selective logging does not directly affect the average rates of dung removal and soil bioturbation, in either the leaf litter or sand proportion of forest soil. However, when comparing the linkages among these environmental and functional components, I found that logging operations modified the occurrence, size and direction of leaf litter influence on dung removal and soil bioturbation. This may indicate that forest degradation can modify the environmental influence on ecological functions, which can further result in changes related to context dependency in biodiversity-ecosystem functioning relationships, as previously shown in the literature (Dangles et al., 2012; Griffiths et al., 2015; Lensing and Wise, 2006). Furthermore, if forest structure buffers the impacts of forest degradation on ecosystem processes, applying RIL techniques (described in Chapter 1) to minimize the logging collateral effects on soil and residual forest may maximize the ability of production forests to maintain ecosystem processes (Edwards et al., 2014c; Ewers et al., 2015).

6.2.4 Sublethal effects of selective logging

Although better explored for vertebrates in temperate regions (but see: Rimbach et al., 2013), evidence of logging-induced sublethal effects in tropical invertebrates are, to my knowledge, lacking in the literature. This thesis has contributed to this knowledge gap by reporting that dung beetle individuals from two species had higher body fat content in logged forests rather than those from unlogged forests (Chapter 5: Figure 5.1). Therefore, the patterns of relative abundance found for the examined species support the suggestion that sublethal effects caused by selective logging may be driving the dung beetle responses found in the Chapters 2, 3 and 4.

Examining the mechanisms behind this logging-induced sublethal responses was beyond the scope of this thesis; though based on other dung beetle studies, the role of environmental conditions such as soil type, canopy cover and leaf litter, in combination with microclimatic changes are likely to be important (Griffiths et al., 2015; Mehrabi et al., 2014; Menéndez et al., 2014). Additionally, given the logging impacts on canopy cover (Chapter 4) and the high temperatures within forest gaps (Forrester et al., 2012), a likely explanation for the logging stress-induced responses in dung beetles (Chapter 3) is the physiological tolerance these beetles have to temperature changes (A. Birkett, R. Bardgett, G. Blackburn and R. Menéndez, *unpublished manuscript*). However, at the moment this remains speculative: although canopy openness did not influence dung beetle richness and biomass in the forests of Jari, this may be due to the difficulty of measuring canopy damage and regeneration one year after logging. Logging intensity itself is a much better measure of changes in microclimate in logged forests.

6.4. Priorities for future work

In addition to contributing to our knowledge of the selective logging consequences on both forest biodiversity and ecosystem functioning, this thesis also highlights several key research priorities in which future work would further our comprehension of the impacts of human activities on tropical forests, and thus help to improve the sustainable use of natural resources. These research priorities are shown as following questions:

6.4.1 More timber, more biodiversity?

The first research priority is to better explore the biodiversity-productivity relationship I found for dung beetle species richness and composition with the number of trees to be removed by selective logging (Chapter 2: Figure S2.4 A-B). Previous research has shown that diversity-production relationships are true for plant species (e.g. Tilman et al., 2001; Vilà et al., 2013), but the understanding of these linkages between timber value and animal diversity is limited. Such relationships have been applied to the land-sparing and land-sharing debate in the agricultural context (Law and Wilson, 2015), which in this thesis was approached from a timber production perspective (Chapter 3). Finally, because production-biodiversity is also a trade-off suggested to segregate the timber production from the biodiversity conservation (Potts et al., 2013), a better understating would facilitate the targeted development of conservation strategies and polices regarding biodiversity maintenance within production forests.

6.4.2 How to improve space-for-time assessments?

In the cases where it is impossible to collect pre-disturbance data, researchers should conduct validation analyses to confirm the conclusions drawn from space-for-time designs. Alternatively, increasing the number of sample sites across large spatial scales could allow further studies to ‘kill two issues with one action’, by increasing the statistical power of space-for-time assessments (Chapter 2) and reducing the spatial scale issues (Chapter 3). However, increased sample sizes does not resolve the effect size issue demonstrated in this thesis. An alternative could be the development of a generalizable correction factor that would further improve the reliability of space-for-time conclusions, thus allowing generalizations to be made.

6.4.3 Selective logging as a continuous or categorical effect?

Although beyond the scope of this thesis, the results here also give support to the risk of drawing broader conclusions from categorical predictors (Caryl et al., 2014). Assessing logging as a continuous effect clearly demonstrated its negative impacts on soil bioturbation rates at both scales (Chapter 3: Fig 3.2D-H). However, when selective logging was treated as a categorical land-use with a mean effect size, weaker inferences were found regarding its impacts on soil bioturbation, even when applying a BA design (Chapter 4: Fig 4.2C). Additionally, the assessment of logging as a continuous effect also allowed a better investigation of logging thresholds for dung beetle biodiversity, that has important implications for predicting how biodiversity within managed forests can recover after logging operations (Scheffer et al., 2012; Thompson, 2011). Finally, while giving support to the stronger inference of continuous predictors (Burivalova et al., 2014; Caryl et al., 2014), this thesis also illuminates the debates surrounding continuous vs. categorical data (Pasta, 2009) as a key priority for further logging-impacts research.

6.4.4 Sublethal effects and context-dependency: one, another or both?

This thesis has provided some evidence that forest disturbances can have stress-induced sublethal effects on dung beetles. Similarly, it has demonstrated the role of some environmental aspects influencing dung beetle-mediated ecological functions. Through linking these findings (Figure 6.1), two interesting questions arise:

(a) ***Do human impacts on forest structure bring about important sublethal effects in tropical invertebrates?*** Although not directly tested in this thesis, I believe that the logging sublethal effects on dung beetle species (Chapter 5: Figure 5.1) are very likely to be related to the logging impacts on canopy openness (Chapter 4: Figure 4.2). However, further research is needed to provide firm evidence of these linkages and to respond this question (Figure 6.1).

(b) ***Do human-induced sublethal effects influence the invertebrates-mediated ecological functions?*** Similarly, it is important that the linkages between human-induced sublethal effects and the performance of ecological functions be considered. This would allow greater accuracy in predicting the ecological consequences of anthropogenic impacts on ecosystems, including both biodiversity and ecosystem processes.

6.4.5 What is the influence of other detritivores on the faecal detritus-pathways?

Despite being considered good predictors of responses of many other taxa (Edwards et al., 2014b; Gardner et al., 2008) and highly responsive indicators of changes in environmental conditions (Bicknell et al., 2014a; Gardner et al., 2008a), dung beetles are not the sole detritivores mediating the faecal detritus-pathways in the 'brown-world'. For example, ants, termites and earthworms are expected to have an additive influence on dung removal (Dangles et al., 2012; Nichols et al., 2007). Therefore, challenges for further researchers are the better understanding of the (a) linkages between dung beetles and other detritivores associated to faecal detritus pathways, and (b) responses from other detritivores to logging intensification. This would clearly elucidate patterns of faecal consumption, as well as validating whether these groups provided 'functional redundancy' in performing this process when dung beetles are affected by forest degradation (Newbold et al., 2015).

6.4.6 What is the conservation importance of selectively logged forests?

As this thesis demonstrates the negative impacts of logging operations on dung beetle diversity (Chapter 2 and 3), here I give support that primary forests are irreplaceable for maintaining tropical biodiversity (Gibson et al., 2011). Nevertheless, this work also provides insights into the role that logged forests can play in maintaining ecosystem processes related to detrital pathways. There is no evidence that selective logging operations influenced the dung removal rates in my experiments, regardless of logging being treated as a continuous (Chapter 2 and 3) or a categorical predictor (Chapter 4). While a likely explanation for this finding can be the influence of other detritivores of the 'brown world' performing the dung removal rates (Dangles et al., 2012; Wu et al., 2011), this outcome gives support that some ecosystem processes have considerable resilience to logging operations (Edwards et al., 2014c), even when biodiversity is lost (Ewers et al., 2015). Additionally, because much of the world's current tropical forests have been or will be selectively logged due to the growing global timber demand (Blaser et al., 2011; FAO, 2010), it is very likely that managers of production forests are controlling most of the worlds' diversity of life (FAO, 2010; Laurance et al., 2012). In this regard, production forests have been also suggested as complementary to primary forests in supporting tropical biota (Gibson et al., 2011), having a conservation value in providing an alternative refuge to forest-species within modified landscapes (Gardner, 2010).

6.5. Concluding remarks

This thesis has great implications for conservation science, as it shows that the most used experimental design may lead us to underestimate the consequences of anthropogenic disturbances on local biodiversity within tropical forests. Therefore, the results presented here also contribute to the understanding of the negative effects of selective logging on biodiversity and ecosystem processes by empirically demonstrating that dung beetle species richness, biomass, species composition and soil bioturbation decrease along a gradient of logging intensity. Because concave responses to logging intensification were observed for most biological metrics, this thesis also highlights that greater biodiversity levels may be maintained in tropical timber concessions that adopt the land sparing model (Edwards et al., 2014c). The scale on which logging intensification was measured may also influence the biological patterns within production forests; therefore, it is recommended that policy makers and researchers should consider the cross-scale impacts of timber exploration when establishing police regulations related to sustainable forest management.

It is becoming increasingly evident that the abiotic environment has a role in governing ecological processes (Griffiths et al., 2015; Lensing and Wise, 2006; Nichols et al., 2013b). Here, I show that selective logging can modify the linkages between the abiotic and biotic components of tropical forests, but whether this can influence biodiversity-ecosystem functioning relationships needs further research attention. Likewise, it is important to comprehend whether environmental variables can buffer the forest degradation impacts on biodiversity and ecological functions. Additionally, the negative impacts of selective logging on biodiversity may start with sublethal effects on individuals (Dantzer et al., 2014; Martínez-Mota et al., 2007). The assessment of physiological responses of organisms may allow us to improve our understanding of how forest degradation can reduce the likeliness of individual and species survival (Coristine et al., 2014). This is essential to examine whether conservation strategies are being effective in decreasing the negative effects of forest disturbances on natural populations (Coristine et al., 2014; Tracy et al., 2006; Wikelski and Cooke, 2006). Finally, assessing the logging impacts on different aspects of wildlife and ecosystem functioning processes can increase our comprehension of the biological patterns within logging concessions, and in so doing improves our ability to develop management guidelines to combine timber production and biodiversity conservation within tropical forests.

7. References

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8. Appendices – Other Outcomes

Appendix S8.1 Publication

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

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Appendix S8.2 | Publication

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RESEARCH ARTICLE

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New distributional data on *Oxysternon pteroderum* Nevison, 1892 (Scarabaeidae, Scarabaeinae, Phanaeini) and its possible implications in conservation

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Abstract

New distributional data are reported on the rare phanaeine dung beetle, *Oxysternon pteroderum* Nevison, 1892, based on five specimens recently collected between 1985 and 2010. Before the present study, *Oxysternun pteroderum* had been reported solely from the super-moist Atlantic coastal forests of southeastern Brazil. We now believe that the distribution of *O. pteroderum* follows the riparian areas of large rivers connected to the super-moist forest ecosystem.

Keywords

Atlantic Forest, Cerrado, Coleoptera, dung beetles

Resumo

Novos dados de distribuição da espécie *Oxysternon pteroderum* Nevison, 1892 baseado em cinco espécimes recentemente coletados entre 1985 e 2010. Antes do presente estudo, *Oxysternun pteroderum* tinha sido reportado apenas para Mata Atlântica de áreas costeiras do sudeste do Brasil. Agora, acreditamos que a distribuição de *O. pteroderum* segue áreas de florestas ripárias de grandes rios que são conectadas com este ecossistema.