Dung beetle - mammal interactions in tropical forests

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A thesis submitted for the degree of

Doctor of Philosophy

Michaelmas 2018

Acknowledgements

Acknowledgements

I would like to express heartfelt thanks to Eleanor Slade and Owen Lewis for their supervision and guidance over the last four years. Thank you to the CERO group for dicussions which have improved the science of my work. I am especially grateful to Chris Terry for patiently sharing his skills in data analysis with me. Thank you to MERG and Mike Bonsall. I am sincerely grateful to Adriana de Almeida and Maria Eduarda Malva for supporting me during my field work. Big thanks to my housemate Callum Munday whose calm approach to his DPhil has been a positive influence on my own. Finally thank you to my mother and father for their continued support and encouragement.

Abstract

Dung beetles are functionally-important insects which feed on the faeces of mammals. They are widely studied as biodiversity indicators, and as a model taxon for investigating relationships between biodiversity and ecosystem functioning. In this thesis I explore dung beetle - mammal associations in tropical forests, aiming to place dung beetle resource use in the context of the mammal species on which they rely. In a systematic review of the literature (Chapter 1) I find a growing literature on dung beetle ecology in the context of ecosystem functioning and habitat and land use change; this growth has not been matched by a corresponding increase in research into the associations of dung beetles with mammals. I summarise the methods and findings from previous dung beetle - mammal association studies, finding that the few field studies of dung beetles that include mammal data document a large impact of mammal species presence and species composition on dung beetle species richness and abundance. This highlights a research gap in our understanding of how dung beetles and mammals are associated.

In a mesocosm choice experiment (Chapter 2), I find that five dung beetle species from the Atlantic Forest of Brazil vary in their preference towards dung types, but there was no evidence of intraspecific variation in dung choice. In Chapter 3 I assess the magnitude of interactions between dung beetles and dung used either for dung removal (brood ball formation or feeding) or general attraction (liquid feeding or breeding). I show that the trapping method and the type of dung used affect the suite of beetles captured, with the potential to influence the outcome of experiments linking functions to interactions. In Chapter 4 I construct the first quantitative mammal- dung beetle networks and use them to model mammal species extinction scenarios, exploring the consequences for dung beetle populations. I find dung beetle feeding and breeding networks do not differ significantly in structure and show high nestedness and low levels of trophic specialization. Simulations suggest that mammal extinction scenarios based on mammal body mass and mammal dung volume will impact dung beetle populations to a greater extent than random scenarios of mammal loss.

Finally (Chapter 5), I use a joint species distribution modelling approach to investigate the role of mammal species composition, abiotic factors and forest structure in determining dung beetle species distributions, using data from Malaysian

Borneo. I find that the mammal feeding group biomass explained over half of the variation in dung beetle species occurrence. I show that all 43 dung beetle species are significantly less likely to be observed where carnivore biomass and air temperature are high. Dung beetle species show idiosyncratic responses to the other explanatory variables, and these responses were poorly explained by species traits. Pairwise dung beetle - mammal co-occurrence patterns reveal a higher proportion of positive associations in oil palm compared to old growth and logged forest.

Overall, results from this thesis suggest that although dung beetles exhibit generalist intraspecific and interspecific feeding and breeding behaviour, mammal species composition and abundance is a key factor influencing their distribution. Further work is needed to identify the strength and extent of interactions among different dung beetle species and mammal trophic groups to gain an improved understanding of how environmental change will directly and indirectly affect dung beetle species and the ecosystem functions they provide.

Format of Chapters

This thesis is presented as an integrated thesis, with each of five papers presented as separate journal articles which they have been, or intend to be to submitted to academic journals. The supplementary material for each chapter are presented in Appendices A-E. The journals are:

Chapter 1: *Proceedings of the Royal Society of London B: Biological Sciences* (Review) - In review

Chapter 2: *Ecological Entomology* (Short communication)- In press

Chapter 3: *Biotropica* (Insights) - In prep

Chapter 4: *Ecosphere* (Article) - In press

Chapter 5: *Journal of Animal Ecology* (Article) - In prep

An additional journal article published during this thesis which I co-authored is included in Appendix F.

Funding

This thesis was made possible by fuding from the Natural Environment Research Council, grant number: NE/L02612/1.

Contents

Appendices

Introduction

Contents

The world is biodiverse (Willig *et al.* 2003; Mittelbach *et al.* 2007). This is most apparent in tropical ecosystems, where for example over 300 species of tree can be found in the same hectare (Wills *et al.* 1997; Kraft *et al.* 2015), but is also true of temperate regions, where more than 78 species of chironomid midges have been found to inhabit small streams in Southern England (Ruse 1995). The cause and maintenance of such high numbers of species inhabiting the same spatial area is still poorly understood (Gravel *et al.* 2011).

The mechanisms assembling and maintaining ecological communities are thought to fall along a spectrum from niche to neutral based processes (Gravel *et al.* 2006; Leibold & McPeek 2006; Matthews & Whittaker 2014). Neutral processes, which are now largely considered to have influence at the biogeographical scale, consider processes such as speciation, extinction and dispersal that can have stochastic effects on shaping species communities, and are not explored in detail in this thesis (Bell 2001; Chave 2004). Niche theory identifies ecological selection as the drivers of community assembly (see Figure 1). Species distributions are determined by the ways in which a species interacts with the environment and uses resources, in addition to the biotic associations between species which influence their distributions (e.g. herbivory, predation, competition etc.) (Chesson 2000; Barabás *et al.* 2018). As such, a species' niche is a combination of multiple dimensions of the ways in which it interacts with, and is affected by, the environment (Leibold *et al.* 2004). Within the niche theory framework, there are several dimensions with which niche structuring can be understood: namely, resource use, predation, time and space (Chesson 2000). Stable coexistence requires ecological differences among species in their niche dimensions which are large enough to limit the negative interspecific effects on population growth to a level below intraspecific density dependence (Siepielski & McPeek 2010). Two species inhabiting the same area that have the same niche cannot coexist, as one species will outcompete the other (Gause 1934).

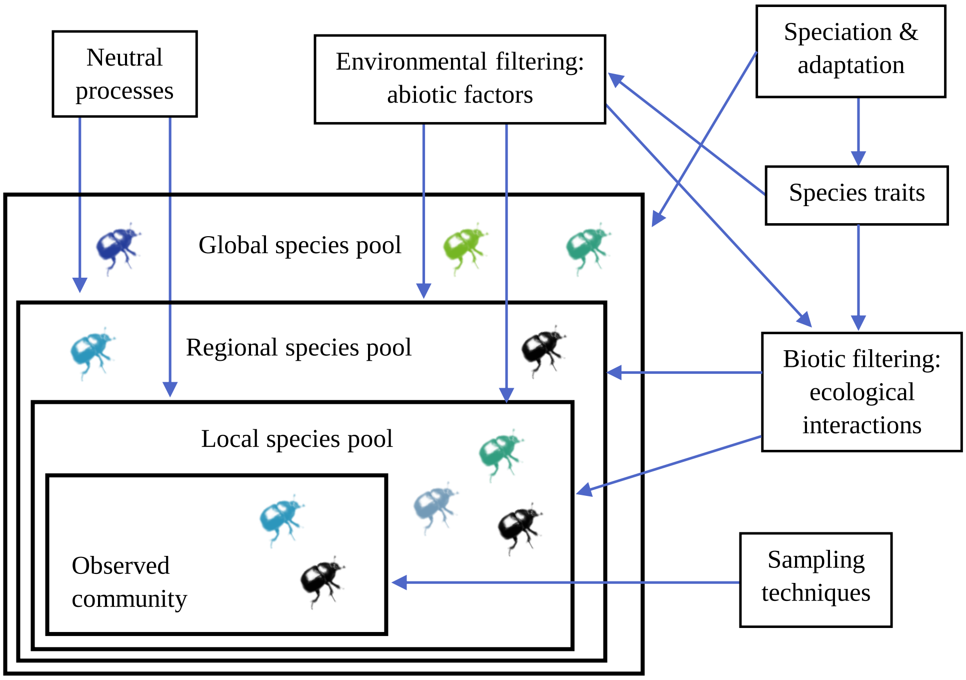

Figure 1: The assembly processes influencing (dung beetle) species communities at different spatial scales. Environmental conditions drive local adaptation and speciation at regional spatial scales, and act to filter species based on their niche at local scales. Biotic interactions among species affect local community composition. Our understanding of each of these processes is based on how the local community is sampled to give the observed community in an area. Adapted from Ovaskainen *et al.* (2017).

There are many instances of related species that coexist by diversifying into a range of ecological niches e.g. Darwin's finches on the Galápagos (Grant & Grant 2006) and Anolis lizards in the Caribbean (Bolnick *et al.* 2007). However, there are also many examples of highly speciose groups of ecologically similar species that coexist, such as generalist insect herbivores (Kaplan & Denno 2007), Hawaiian

Location		**Species richness**	**Study**
South America	Brazil, Amazon forest	53	Marsh et al. (2013)
	Brazil, Atlantic forest	39	Hernández & Vaz de Mello (2009)
	Guyana, tropical forest	34	Bicknell et al. (2014)
Central America	Costa Rica, tropical wet forest	50	Escobar et al. (2008)
	Mexico, tropical rainforest	44	Navarrete & Halffter (2008)
Africa	Côte d'Ivore, savannah	64	Kunz & Krell (2011)
	South Africa, mixed woodland	64	Van Rensburg et al. (1999)
	Madagascar, wet forest	30	Viljanen et al. (2010b)
Asia	Sabah, Malaysian Borneo, lowland tropical forest	86	Davis et al. (2001a)

Table 1: Examples of local dung beetle species richness in tropical regions

Drosophila (Boake 2005), and African Lake Cichlids (Turner *et al.* 2001; Ready *et al.* 2006). In these instances, the lack of obvious niche differentiation challenges our understanding of how species coexist (Chesson 2000; Siepielski *et al.* 2010). In this thesis I explore one such group of species which show high diversity but apparently lack niche differentiation. My aim is to unravel some of the factors that may contribute to their coexistence, focusing in particular on their trophic niches.

Why are there so many beetles?

When asked, *"What can be made of the mind of the creator from the works of his creation?"* the evolutionary biologist J.B.S Haldane responded, *"An inordinate fondness for beetles"* (Hutchinson 1959; Farrell 1998). As the most speciose order of all animals and plants, Coleoptera represent over 380,000 species, ∼ 25% of all known species on earth (Slipinski *et al.* 2011; Mckenna *et al.* 2015). This order is particularly relevant for addressing questions about community assembly and species coexistence, as despite much progress in the study of ecology, the reasons behind the huge species richness within beetle taxa remains elusive.

Ecosystem function	**Example**
Dung removal/ decomposition	Slade *et al.* (2007)
Seed dispersal	Vulinec, Lambert & Mellow (2006)
Carbon/ methane fluxes	Penttilä *et al.* 2013
Parasite suppression	Horgan (2005)
Soil bioturbation	Bang *et al.* (2005)
Nutrient cycling	Hanafy & El-Sayed (2012)
Plant nutrient content	Santos-Heredia *et al.* (2016)
Plant productivity	Slade *et al.* (2017)
Microbial diversity	Slade *et al.* (2016)

Table 2: Examples of dung beetle ecosystem functions and corresponding studies

Dung beetles exemplify this trend, as despite consisting of over 6000 species found on every continent except Antarctica (Hanski & Cambefort 1991; Scholtz & Grebennikov 2016), and being particularly speciose in tropical systems (Table 1), we still have little understanding of the causes of their high species richness. Many co-occurring dung beetle species show little differentiation in the ways that they interact with the environment. For example, many species show similar responses to environmental change (Nichols *et al.* 2007) and are thought to be generalist dung feeders (Hanski & Cambefort 1991; Frank *et al.* 2018).

The true dung beetles make up the subfamily Scarabaeinae (Coleoptera: Scarabaeidae), that feed and breed predominantly in mammal dung (Scholtz *et al.* 2009). It is thought that they originated with dinosaurs (Tarasov & Génier 2015; Gunter *et al.* 2016) and subsequently spread with the evolution of major mammalian taxa (Arillo & Ortuño 2008; Sole & Scholtz 2010; Sole *et al.* 2011). Globally, dung beetles are distributed according to climatic suitability and mammal species diversity (Davis & Scholtz 2001; Viljanen *et al.* 2010a). Dung beetles are also frequently used as a model study group in evolutionary- and ecological- developmental biology (Simmons & Ridsdill-Smith 2011). As a result this research has revealed their use of the Milky Way (Dacke *et al.* 2013; Smolka *et al.* 2016) and polarised light for orientation (el Jundi *et al.* 2014), as well an improved understanding of sexual selection (Rowland & Emlen 2009), developmental plasticity (Shafiei *et al.* 2001), and their sophisticated parental care (Beckers *et al.* 2015; Schwab *et al.* 2016; Snell-Rood *et al.* 2016).

The relevance of dung beetle ecology in a changing world

The effects of anthropogenic disturbance on dung beetle species has a corresponding impact on the ecosystem functions and services provided by dung beetles (Larsen *et al.* 2005; Braga *et al.* 2013), including regulating soil nutrient cycles and plant growth (Nichols *et al.* 2008) (Table 2). Therefore, an incomplete understanding of the processes that structure their distribution limits the efficacy of measures to reduce the impact of environmental change on dung beetles and their associated functions.

Conservation management often relies on a compromise between ecological research and funding constraints. Bioindicator species have been championed as a way to provide high resolution data on focal taxa that give a reliable indication of the ecological integrity of the area. Arthropods are popular study groups, as large amounts of data can be collected and stored (Uehara-Prado *et al.* 2009). Dung beetles are a frequently used bioindicators as they can be sampled quickly and cheaply, and taxonomic developments means identification is becoming easier. Together with the growing body of evidence of dung beetle response to environmental change (see Table 3), they are an ideal indicator group which are also suggested as surrogates for difficult-to-survey groups such as mammals (Gardner *et al.* 2008; Nichols & Gardner 2011).

Dimension of niche partitioning in dung beetles

Dung beetle species' distributions are strongly influenced by environmental conditions, showing high species turnover between habitat types (e.g. Kunz & Krell 2011; Gray *et al.* 2014) and declines in species richness with increasing habitat degradation (see Nichols *et al.* 2007 for review). This suggests environmental conditions are an important factor influencing many dung beetle species' niches (Soberón 2007), and many of these responses to habitat conditions have been related to dung beetle species traits such as body size and functional group (Nichols *et al.* 2013).

There are some obvious ways in which dung beetle species differentiate dung use, such as nesting strategy (Figure 2) (Doube 1990) and activity period (diurnal,

Assessment	**Example**
Deforestation/ fragmentation	South Africa, Savannah (McGeoch et al. 2002)
	Borneo, tropical rainforest (Davis et al. 2001)
	Brazil, tropical forest fragments (Leal et al. 2012)
Riparian forest widths	Southern Brazil, tropical forest (Viegas et al. 2014) Malaysian Borneo, tropical forest (Gray et al. 2014)
Restoration success	Southern Brazil, tropical forest (Audino et al. 2014)
	Australia, rain forest (Derhé et al. 2016)
Logging impact	Costa Rica, tropical forest (Aguilar-Amuchastegui & Henebry 2007)
	Guyana, tropical forest (Bicknell et al. 2014)
	North East Brazil, tropical forest (França et al. 2018)
	Malaysian Borneo, tropical forest (Slade et al. 2011)
Pasture condition	Southeast Brazil, Cerrado (Almeida et al. 2011)
Crop management	Southern Brazil, tropical forest (Campos & Hernández 2015a, b)

Table 3: Examples of studies of dung beetles as bioindicator species in the tropics

nocturnal or crepuscular) (Caveney *et al.* 1995). Competition for dung in tropical regions is intense (Horgan & Fuentes 2005; Vernes *et al.* 2005), and dung is often removed quickly and completely in tropical forests (Slade *et al.* 2011). Brood ball rolling as a dung relocation strategy is only found in tropical dung beetle species, and is thought to have evolved as a strategy to bypass competition at the dung mound (Simmons & Ridsdill-Smith 2011). Moreover, some species show behavioural plasticity in their nesting strategy when in particularly fierce competition for dung (Kon *et al.* 2004; Zidek & Pokorny 2010; Raine *et al.* 2018), and can use behavioural strategies to bypass dung searching to gain access to dung (Jacobs *et al.* 2008). The males of many dung beetle species possess large horns for mate contest but also acquisition and possession of dung (Edwards & Aschenborn 1988) (see Figure 3).

Dung beetles and dung

Despite the differentiation between dung beetles in the timing and methods of interacting with dung, there are still large numbers of coexisting species that are remarkably similar, such as the abundant small-bodied, diurnal tunnelling Onthophagus species in Malaysian Borneo (Slade *et al.* 2011). As resource

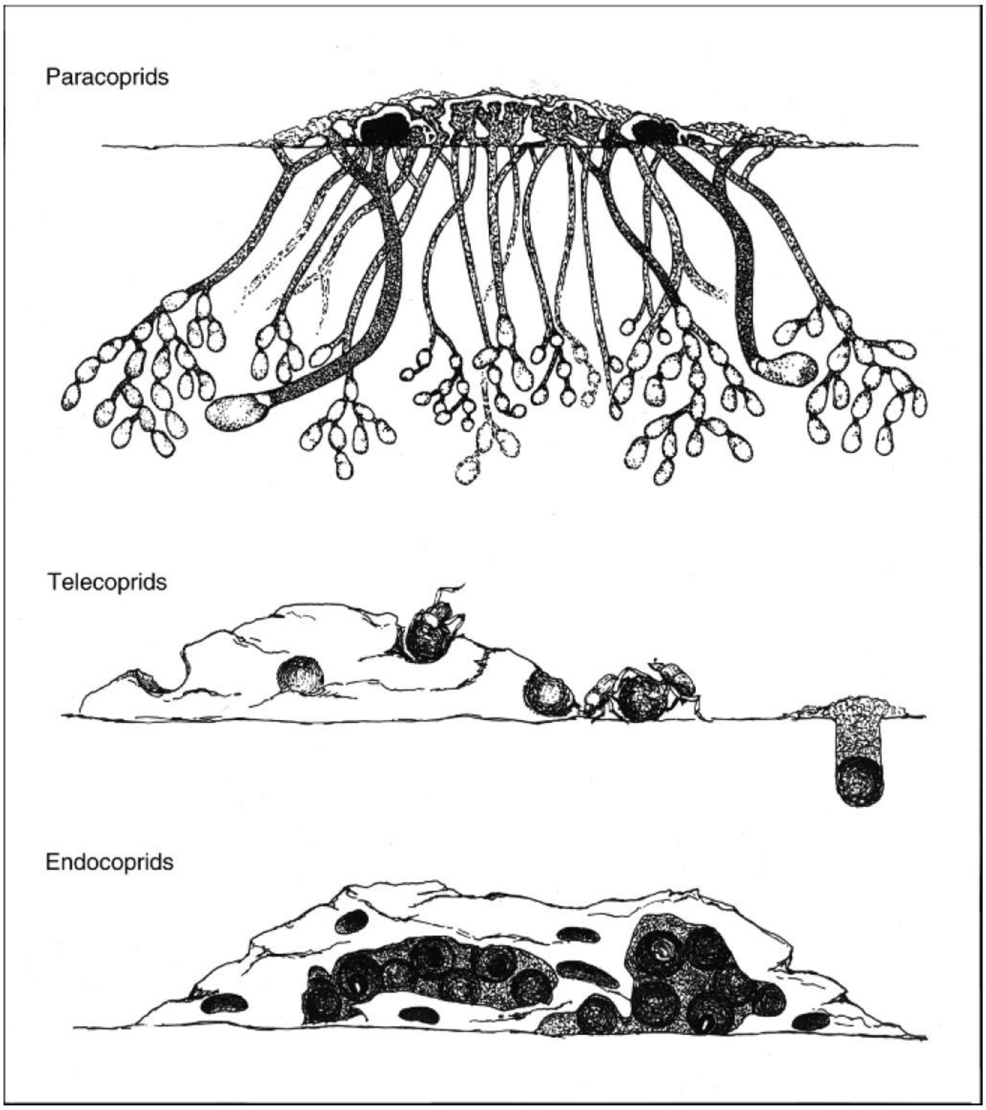

Figure 2: Nesting behaviours of scarabaeine dung beetles can be classified into three broad types. (a) Tunnelling or paracoprid species dig tunnels beneath the dung pad and pack fragments of dung they bring from the surface into the blind ends of tunnels before laying a single egg into the brood chamber. A brood mass provides all the resources for the development to adulthood of a single offspring. (b) Rolling or telecoprid species build a dung ball and roll it away from the pad before burying it in the soil. The dung ball can be used as food for the adults or fashioned into one or more brood balls. (c) Dwelling or endocoprid species build broods within the dung pad itself (reproduced from Boremissza, 1976).

availability affects growth, survival and reproduction, the evidence points to dung as a limiting factor to dung beetles in tropical regions (Thomson *et al.* 1996). But this would suggest there are further ways in which dung beetles show differentiation

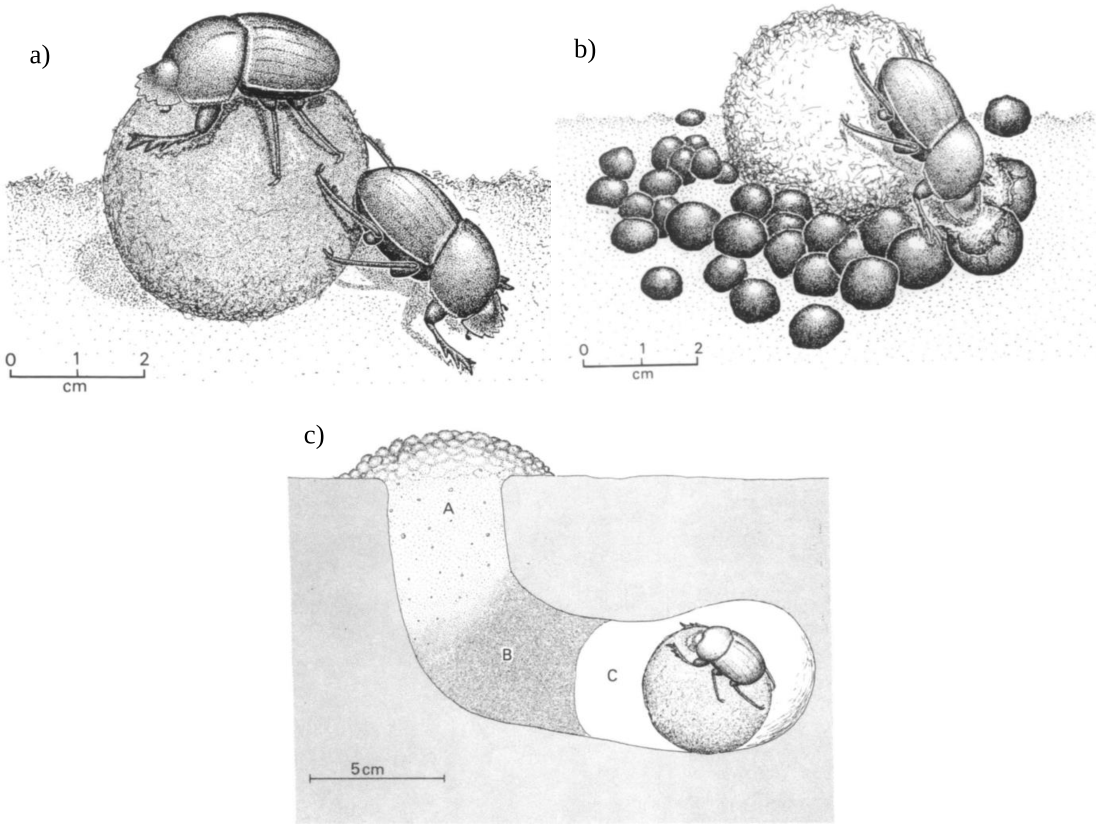

Figure 3: *Kheper nigroaeneus* behaviour and ecology. a) A pair of beetles rolling a brood ball. The male rolls the ball backwards while the female sits on the ball, b) A beetle constructing a food ball from pelleted impala dung, c) A brood chamber containing a female with a brood ball. The male departs after packing the chamber entrance firmly closed with soil A= loose soil, B= hard packed soil, C= chamber. Taken from Edwards & Aschenborn (1988).

between species in their dung use that are currently not known. Sympatric species that appear morphologically similar and are closely related often show differences in their interaction with the environment when studied in detail. Examples include variability in nutritional requirements in grasshoppers (Behmer & Joern 2008), variation across local environmental gradients in damselflies (Siepielski *et al.* 2011), trophic niche differentiation in soil microarthropods (Schneider *et al.* 2004).

Outline of thesis

In this thesis I consider dung beetle resource use in the context of the mammal dung they exploit, and by studying networks of interactions rather than individual associations as is the norm in most dung beetle studies (Frank *et al.* 2018; Godoy *et al.* 2018). In turn, these interaction networks can be used to understand how how species extinctions have impacts on other positions in the network. By incorporating information surrounding mammal species involved in the dung - dung beetle association, we are also able to make more robust assessments of the ways in which dung beetles interact with the environment, which is largely neglected in studies of dung beetle species distributions that only consider abiotic factors.

This thesis investigates whether there is variation among dung beetle species in their use of mammalian dung with reference to tropical dung beetle species found in Brazil (Chapters 2-4) and Malaysian Borneo (Chapter 5). It will assess untested assumptions about the way dung beetles use resources and interact with the environment.

Specifically, this thesis will address the aims:

1. To review how dung beetle resource use has been researched to date,

2. To identify whether the methods used to sample dung beetle populations are an accurate representation of resource use in natural systems,

3. To identify whether dung beetles show variation among individuals, species, or life cycle stages (feeding or breeding) in their resource use,

4. To determine the importance of environmental conditions and mammal species composition for the distribution of dung beetle species.

5. To assess how dung beetle species respond to environmental change, and how dung beetle - mammal associations are affected.

I use methods at a range of scales to understand the dung beetle - mammal associations and the ecological processes that contribute toward community assembly within dung beetle communities. Chapter 1 reviews the work that has been published and provides direction for future work on the study of dung beetle diet preference and the association between dung beetles and mammals. Chapter 2 explores the potential role of intraspecific variation in dietary choice in dung beetles as an explanation for their generalist feeding behaviour using mesocosm experiments. Chapter 3 tests the effectiveness of commonly used sampling methods in capturing the local community of dung beetles using field experiments. In Chapter 4 we use a network approach to understand how dung beetle species interact with resources and how this differs between species and life cycle stages. Chapter 5 uses species occurrence data across a tropical forest landscape in Malaysian Borneo to understand the factors influencing dung beetle species distribution. The thesis concludes with insights drawn from these five data chapters and considers the mechanisms that could be promoting and maintaining such high species diversity in dung beetles.

1

Dung beetle - mammal associations: methods, research trends, and future directions

E. H Raine & E.M Slade, in review, *Proceedings of the Royal Society of London B: Biological Sciences*

Contents

Author contributions

EHR carried out the literature review and wrote the manuscript. EMS contributed ideas and gave feedback on the manuscript at multiple stages.

Abstract

Dung beetles are increasingly used as a study taxon - both as bioindicators of environmental change, and as a model system for exploring ecosystem functioning. The advantages of this focal taxon approach are many; dung beetles are abundant in a wide range of terrestrial ecosystems, speciose, straightforward to sample, respond to environmental gradients, and can be easily manipulated to explore species-functioning relationships. However, there remain large gaps in our understanding of the relationship between dung beetles and the mammals they rely on for dung. Here we review the literature, showing that despite an increase in the study of dung beetles linked to ecosystem functioning and to habitat and land use change, there has been no increase in research into their associations with mammals. We summarise the methods and findings from dung beetle - mammal association studies to date, revealing that although empirical field studies of dung beetles rarely include mammal data, those that do indicate mammal species presence and composition has a large impact on dung beetle species richness and abundance. We then review the methods used to carry out diet preference and ecosystem functioning studies, finding that despite the assumption that dung beetles are generalist feeders, there are few quantitative studies that directly address this. Together this suggests that conclusions about the effects of habitat change on dung beetles are based on incomplete knowledge. We provide recommendations for future work to identify the importance of considering mammal data for dung beetle distributions, composition, and their contributions to ecosystem functioning; a critical step if dung beetles are to be used as a reliable bioindicator taxon.

Introduction

Indicator species are used as a more efficient way to assess ecosystem integrity than sampling a large number of taxa (Carignan & Villard 2002). However, for a focal taxa to be used to assess a community or habitat type, environmental condition, or the effects of environmental change, robust quantitative data and a detailed understanding of its ecology are needed (Dufrene & Legendre 1997). Dung beetles are an ideal indicator taxon in many ways due to their sensitivity to habitat change (Davis et al. 2001; Spector 2006; Gollan *et al.* 2013) in combination with broad geographical distributions and ease of collection (Didham *et al.* 1998; Nichols & Gardner 2011; Oliveira *et al.* 2017). As such they have been increasingly used as bioindicators to inform conservation management decisions (Davis & Scholtz 2004; Gollan *et al.* 2011; Audino *et al.* 2014; Filgueiras *et al.* 2015). However, the effect of mammal species compositional change on dung beetles and their associated ecosystem functions has been little explored, resulting in a lack of understanding of the association between dung beetles and their resource use (Figure 1.1).

By feeding and breeding in dung and other detritus (Hanski & Cambefort 1991) dung beetles contribute to the ecosystem functions of dung removal (Ortega-Martínez, Moreno & Escobar 2016), seed dispersal (Andresen & Feer 2005; Nichols *et al.* 2008; Culot, Huynen & Heymann 2015), nutrient cycling (Menéndez, Webb & Orwin 2016; Nervo *et al.* 2017), and reduction of greenhouse gas emissions (Slade *et al.* 2017; Piccini *et al.* 2017). For this review, we consider coprophagic dung beetles (Coleoptera: Scarabaeoidea) in the families Geotrupidae and Scarabaeinae that feed primarily on dung, and so are expected to have clear associations to mammals. Dung beetles can be classified into clearly defined functional groups that can be easily manipulated for ecosystem functioning experiments (Stokstad 2004), and as a result are increasingly used for understanding trait - functioning associations (Slade *et al.* 2007; Larsen, Lopera & Forsyth 2008; Kunz & Krell 2011). Moreover, they show niche differentiation in resource use; for example, in the age (Holter 1982) and type of dung utilised (Filgueiras *et al.* 2009), daily activity period (Feer & Pincebourde 2005), and dung manipulation and nesting strategy (Macagno, Moczek

& Pizzo 2016). However, while studies of dung beetles have provided a large body of information on species' distributions and responses to land use change, they rarely shed light on the biotic interactions between dung beetles and mammals.

Dung beetles are generally assumed to display generalist feeding and breeding strategies (Hanski & Cambefort 1991; Frank *et al.* 2018), and as a group are able to utilise a wide range of resources, such as dung from native or exotic mammal species (Whipple & Hoback 2012; Stavert *et al.* 2014b). Mammalian dung varies in nutrient and fibre content between species (Holter & Scholtz 2007) but also seasonally based on diet (Edwards 1991). The quality and quantity of the dung provisioned to larvae has been shown to affect development, number and size of offspring, and result in resource allocation trade-offs in adult beetles (Moczek 1998; Arellano *et al.* 2015; Schwab, Casasa & Moczek 2017). Therefore, dung is used in different ways by adults and larvae (Holter & Scholtz 2007), and selection of dung for breeding may differ to that used for feeding, although the consequences of this for ecosystem functioning has been little explored (Arellano 2016; Goh & Hashim 2018). In addition, variation in the digestive system and gut microbia in dung beetles may play a role in determining feeding preferences (Estes *et al.* 2013; Shukla *et al.* 2016; Franzini *et al.* 2016), and while dung volatiles are thought to be key to determining the attractiveness of dung to dung beetles (Whipple & Hoback 2012; Frank *et al.* 2017b), how they relate to dung beetle resource use is still not well understood (Holter & Scholtz 2007; Holter 2016).

Mammals are also often used as an indicator or flagship taxon (Walpole & Leader-Williams 2002; Morrison *et al.* 2007), and there has been extensive research concerning mammal species responses to disturbance (Cardillo *et al.* 2006; Canale *et al.* 2012; Effiom *et al.* 2013), and species' associations to habitat types (e.g. Yackulic, Sanderson & Uriarte 2011). However, in contrast to dung beetles, mammals are notably harder to survey, requiring more time, effort, and at greater cost (Gardner *et al.* 2008). Yet, despite their close ecological association, and despite being two of the best studied vertebrate and invertebrate taxa individually, dung beetles and mammals are rarely studied in combination (Nichols *et al.* 2009).

We conducted a systematic review of studies documenting the associations between dung beetles and mammals to address the following questions: 1) What have been the research trends in the study of dung beetle ecology? 2) What methodological approaches are used to study dung beetle - mammal associations, and dung beetle - dung associations? 3) Is diet preference and association with mammals accounted for in the methods of studies of dung beetle ecosystem functioning? We then highlight the knowledge gaps and give recommendations for how dung beetle - mammal interactions can be incorporated into future work on dung beetle ecology.

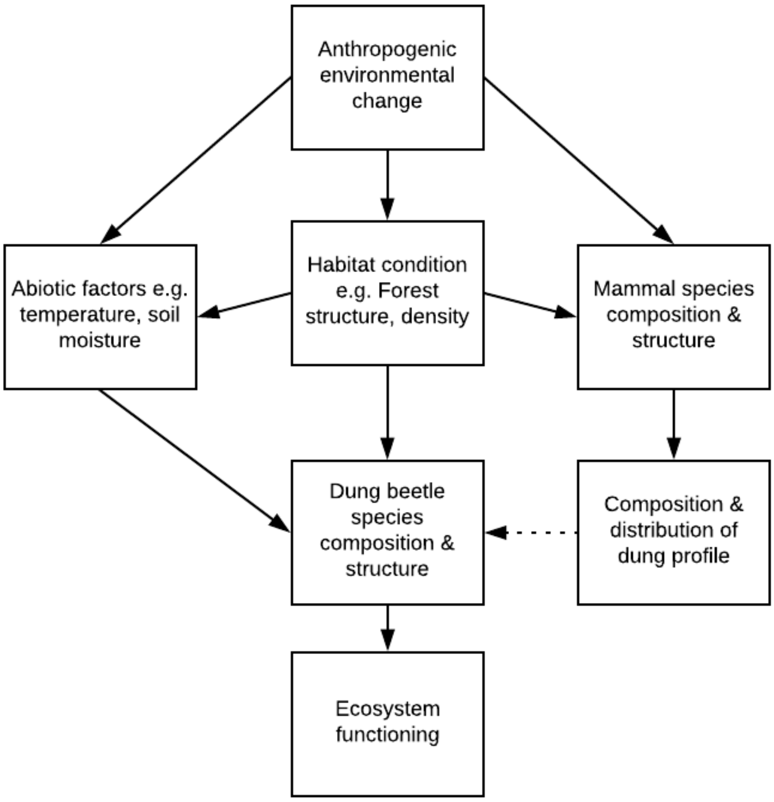

Figure 1.1: Conceptual diagram of the processes by which environmental change can affect coprophagous dung beetle composition and ecosystem functioning. Although the effects of habitat structure and abiotic factors on dung beetles have been explored (solid lines), the association between dung availability, mammal composition, and dung beetle species occurrence is still poorly understood(dashed line).

Methods

We carried out a review of the literature to identify trends in the study of dung beetle ecology over the last 27 years (1991 - 2017) using Web of Science (February, 2018). All searches used the keyword topic ("dung beetle" OR scarabaeinae OR geotrupidae). We identified literature considering dung beetle - mammal associations using the search term (mammal* OR preference* OR diet*). The papers were then reviewed to identify the approach to classifying the dung beetle - mammal associations and interaction networks (Figure 1.1). We distinguished between studies that tested interactions directly through dung beetle dietary preference experiments using different dung types (Figure 1.1 a-d), and those that used mammal and dung beetle co-occurrence data to indirectly infer associations between the two (Figure 1.1 e-f). Further papers that were not detected from the key word search were identified by following publications cited in these articles to provide an in-depth review of the literature. For diet preference studies, only those that used at least two dung types were included.

We systematically reviewed the approach taken to classifying the dung beetle - mammal associations in the dung beetle - mammal co-occurrence studies. We recorded three aspects of the studies: 1) How the mammal composition was classified; 2) how the analysis of the association between dung beetles and mammals was carried out; 3) the direction of the effect of the mammal communities on the dung beetle population metrics.

We then reviewed the diet preference literature to identify the support for dung beetles being generalist feeders, identifying location, study design, and approach to data analysis. We recorded the dung types and dung volumes used, as well as the experimental design employed in each of the studies. Studies concerning dung beetle ecosystem functioning were assessed for the extent to which they considered feeding variation among dung beetle species. For these studies we recorded location, the number of dung types used, dung volumes, and ecosystem function.

To compare the numbers of dung beetle-mammal association studies with other studies of dung beetle ecology, two additional searches were undertaken. This used the keyword search topic: (habitat* OR environment*) for dung beetle - habitat associations, and: (ecosystem* service* OR ecosystem* function*) for ecosystem function studies. We included studies that measured a form of ecosystem function performed by the dung beetle population, but excluded studies exploring the effects of pesticide and insecticide application on ecosystem functions as this verged into studies of agricultural management which was beyond the scope of this review. This literature search was not exhaustive, as papers that did not refer specifically to these search terms were not further identified. Rather, the search was used to provide a minimum indicator of the amount of ecological survey work documenting the study of dung beetles in two popular areas compared to the dung beetle - mammal association search explained above.

Results

Trends in dung beetle ecological research

The literature review yielded a total of 319 papers. Studies of dung beetle - mammal associations accounted for 57 papers, 57 papers focused on dung beetle - ecosystem functioning, and 205 studies consisted of empirical field studies of dung beetle - habitat associations (see Appendix A2). Forty- one of the dung beetle - mammal association studies addressed direct interactions and dung beetle dietary preference, and 16 considered the indirect effect of mammal presence on dung beetle populations or community composition. These two categories were found to be mutually exclusive and were therefore explored separately. There has been an increase in publications on ecosystem functions and habitat associations using dung beetles since 1991. In contrast, studies of dung beetle - mammal associations, both diet preference and species co-occurrence studies, have remained low throughout this period (Figure 1.3), with studies largely focused in Europe and South America, and with relatively few studies in Asia, Australasia, Africa, and North America (Figure 1.4).

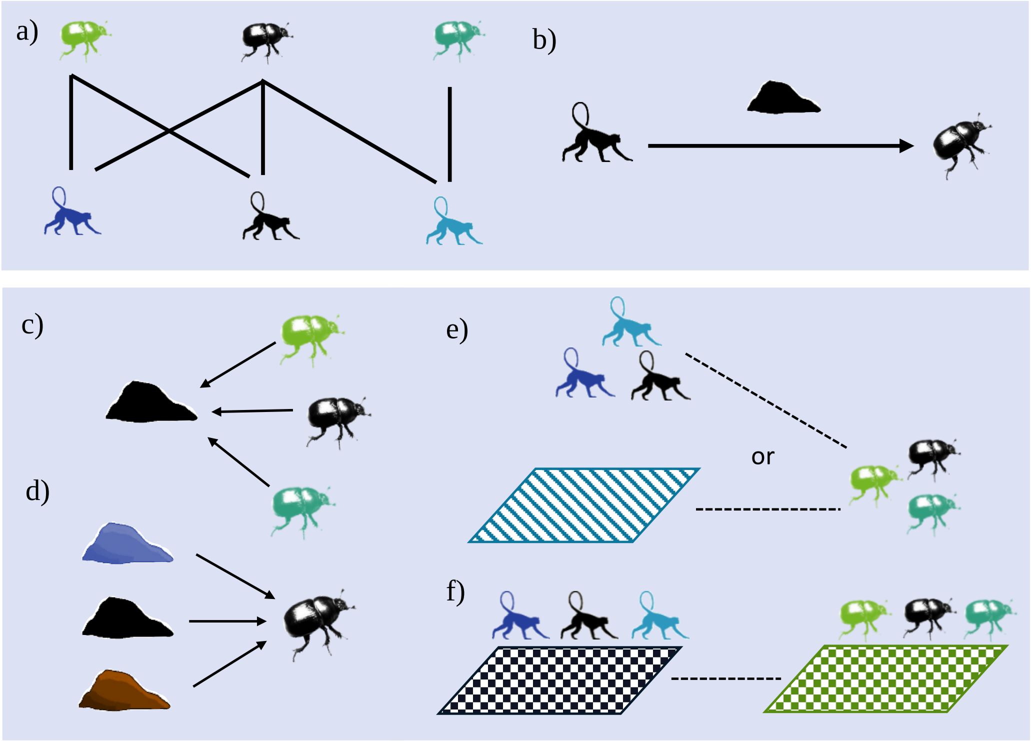

Figure 1.2: The different approaches to studying dung beetle - mammal associations. Solid lines represent interactions directly identified and dotted lines represent inferred interactions. a) Dung beetle - mammal interaction network consisting of species-species interactions, which is estimated through b) species level mammal - dung - dung beetle associations. There are several approaches to classifying this interaction: c) Directly identifying the dung beetle species composition attracted to a dung type (which does not identify dung beetle feeding preference); d) Identifying dung beetle species resource use breadth by identifying attraction to multiple dung types; e) Inferring population level associations between dung beetles and mammals either via pooled mammal composition data or via a proxy for mammal composition such environmental condition; f) Inferring species level interactions between dung beetles and mammals via associations between species that co-occur.

Dung beetle - mammal association studies

Co-occurrence data & indirect interactions

There were fifteen studies that assessed dung beetle - mammal associations through population level co-occurrence (Figure 1.2 e) (summarised in Table A2). One study used co-occurrence data to estimate species level interactions between dung beetles and mammals based on checkerboard scores (Nichols *et al.* 2016) (Figure 1.2 f). The studies used a range of approaches to identify mammal composition, with nine using proxies or a subset of mammal species in their analysis, and the other six using quantitative estimates. Five of the 15 studies reviewed included information on small mammals in their estimates of mammal species composition. Sixty percent of papers considered environmental variables in their analysis in addition to assessing the effect of mammal compositional change on dung beetle populations. Only one study trapped dung beetles with a range of different dung types (Tshikae, Davis & Scholtz 2013b).

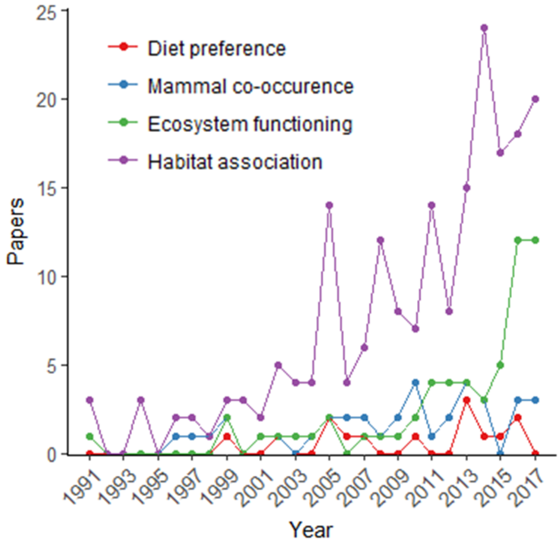

Figure 1.3: Journal articles published on dung beetle ecology from 1991 - 2017.

We identified the effect a decline in mammal abundance or richness had on the dung beetle population in each of the studies. All studies showed at least one positive association between dung beetle species richness and abundance and the mammal metric chosen, indicating that a reduction in the mammal community had a negative effect on the dung beetle community. Dung beetle community composition was significantly different between areas of varying mammal composition for all but one study.

Diet preference & direct interactions

Of the 41 diet preference studies, 85% were field experiments and 15% lab experiments (Appendix A1). The most commonly used study design for field surveys included two dung types (Figure 1.5a) and distance between traps varied from 1m

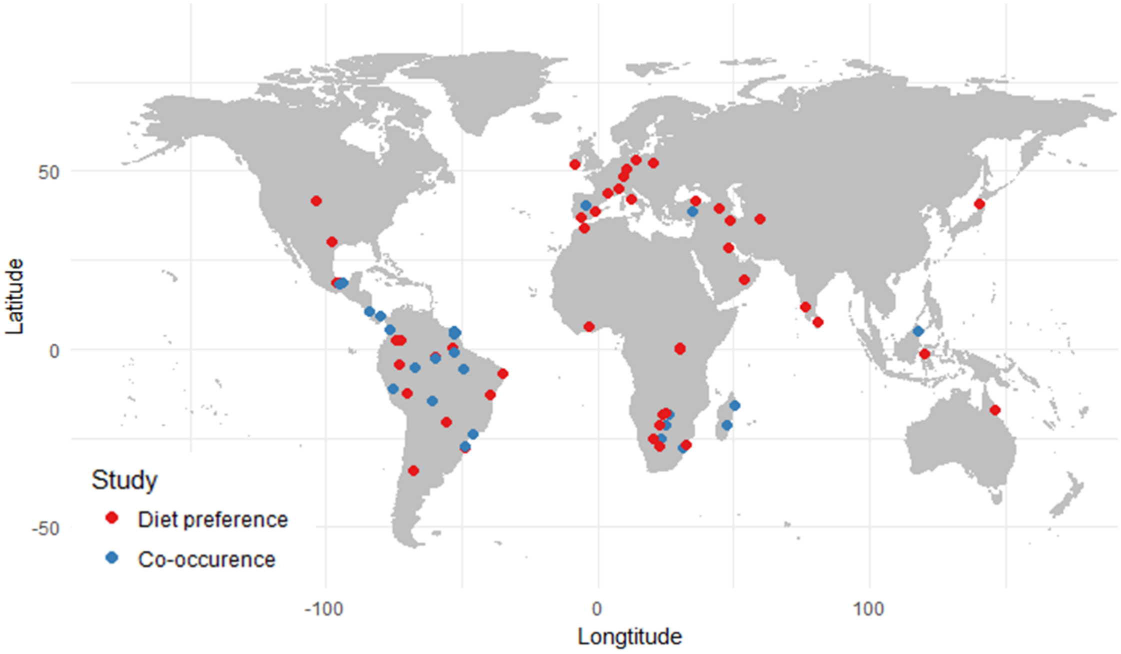

Figure 1.4: Study locations for papers addressing dung beetle - mammal association studies, separated into mammal co-occurrence and diet preference studies (1991 - 2017). Where the study carried out sampling at disparate locations, multiple points are included.

to 100m (mode= 50m). The trapping methods varied, with studies either using pitfall traps, directly collecting dung beetles from dung, or using burial intercept traps (Arellano 2016; Goh & Hashim 2018). Cattle dung was the most commonly used dung type, followed by pig, and human dung (Figure 1.5a). Sixty percent of the field studies were designed to identify dietary breadth in dung beetles: 13 studies assessed feeding preference for only two dung types, and six studies assessed the attractiveness of several different bait types. Lab experiments of diet preference tested the attractiveness of two to 22 dung types. All but one lab study (Dormont *et al.* 2007) assessed diet preference for just one dung beetle species. Across the 57 papers that studied ecosystem functioning, the majority used only one dung type, with cattle dung the most frequently used bait (Figure 1.5b, Table A3). The dung volume used in ecosystem functioning studies varied greatly and larger volumes were used than in dietary preference studies (Figure 1.5c).

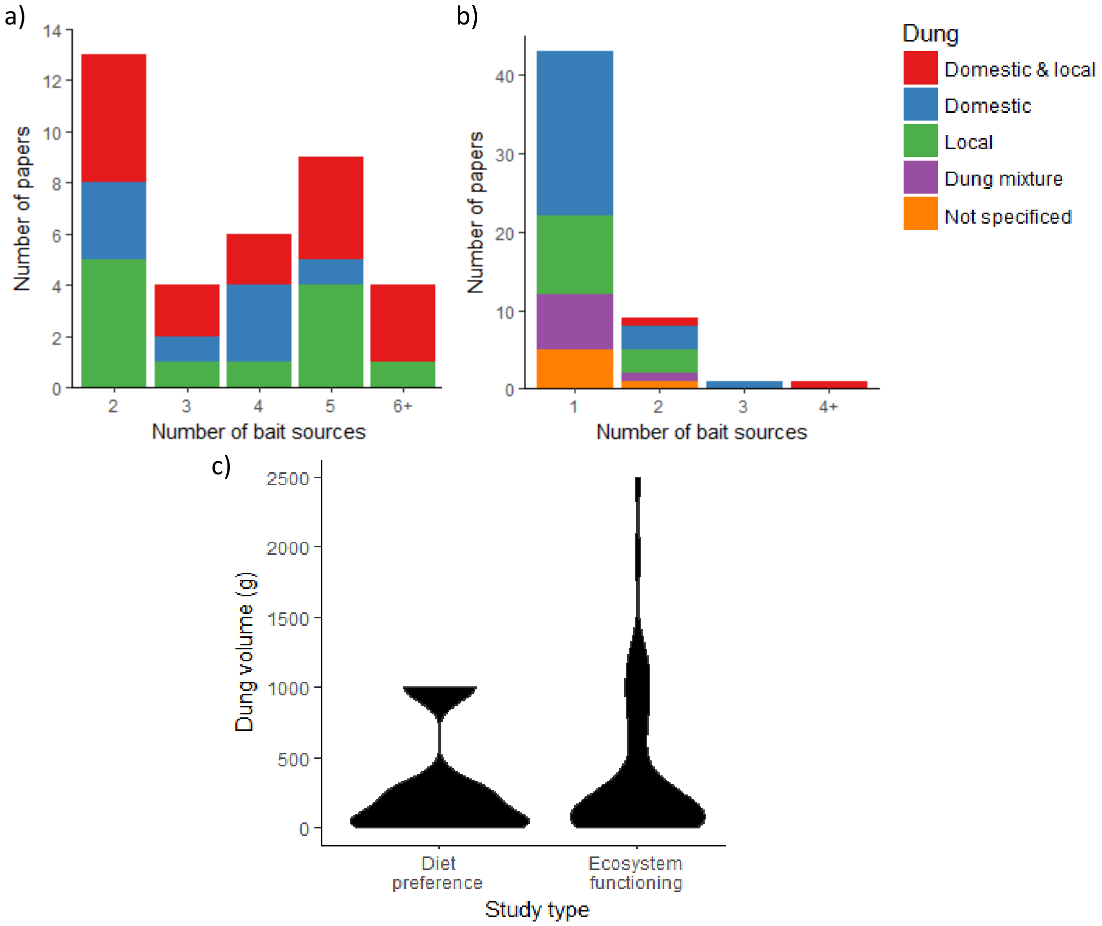

Figure 1.5: Number of bait sources and dung types used in studies of: a) diet preference; b) ecosystem functioning; Local dung: dung of mammals that naturally occur in the local area, Domestic dung: dung of cattle, sheep, pigs, goats, Dung mixture: combination of several dung types to bait one trap. c) Dung volumes used in diet preference and ecosystem functioning studies.

Discussion

There has been a rapid increase in the study of coprophagous dung beetles over the last 27 years, yet despite their reliance on mammal dung (Nichols *et al.* 2009), the understanding of dung beetle - mammal associations is still limited. Improved data availability of dung beetle associations with the environment and their functional contributions to ecosystems has not been mirrored by an advancement of the mechanistic understanding of how dung beetles use dung for feeding and breeding. This lack of research is apparent across both tropical and temperate regions.

Dung beetle - mammal associations

We found that studies on the effects of mammals on dung beetle community composition, species richness, and abundance have largely been neglected, despite calls to increase the inclusion of mammal data in dung beetle studies (Nichols *et al.* 2009). Fewer than half of the studies reviewed conducted a direct assessment of the association between dung beetles and mammals (Figure 1.1 c, d), whilst the rest inferred an association through other factors - e.g. using a difference in habitat condition as a proxy for mammal richness (Tshikae *et al.* 2013b), or using the presence of one mammal species as a proxy for the mammal community (Koike *et al.* 2014) (Figure 1.1 e). Several studies identified the importance of large bodied mammals in dung beetle species composition (Viljanen *et al.* 2010a; Koike *et al.* 2014), yet only a third of studies accounted for small bodied mammals in their assessment of faunal composition.

Overall studies reported consistent trends towards co-declines in dung beetles and mammals (Kanda *et al.* 2005; Escobar, Lobo & Halffter 2006; Andresen & Laurance 2007; Culot *et al.* 2013). This suggest that changes in mammal species composition, such as those occurring as a result of habitat disturbance, are likely to have significant impacts on dung beetle communities, and associated ecosystem functioning (Nichols *et al.* 2009). To understand the responses of dung beetles to disturbance it is necessary to incorporate both biotic and abiotic conditions. Thus, the lack of studies including mammals in analyses of dung beetle responses to disturbance and habitat change neglects an important factor influencing their distribution.

Dung beetle diet preference & direct interactions

It is commonly assumed that dung beetles show broad dietary widths (Hanski & Cambefort 1991; Simmons & Ridsdill-Smith 2011), and a recent meta-analysis suggests generalist feeding preferences in dung beetles across a latitudinal gradient (Frank *et al.* 2018). However, the experimental methods used in the majority of the studies reviewed here cannot provide conclusive evidence to support this. Many studies compared the attractiveness of just two dung types (Galante &

Cartagena 1999; Shahabuddin *et al.* 2010; Puker *et al.* 2013), or assessed dung beetle species composition attracted to a single dung type (Figure 1.2 c), rather than individual dung beetle species feeding breadth (Figure 1.1 d) (Martín-Piera & Lobo 1996; Plewińska 2007; Carpaneto, Mazziotta & Ieradi 2010; Tshikae, Davis & Scholtz 2013a).

Several studies show that dung beetle species can vary in their attraction to the dung of different mammal trophic groups (Filgueiras, Iannuzzi & Leal 2011; Bogoni & Hernández 2014), and particular mammal species (Santos-Heredia, Andresen & Zárate 2010; Noriega 2012; Enari, Koike & Sakamaki 2013). Equally experimental choice trials have shown variation in dung beetle species resource use. Although more time consuming, feeding and breeding choice experiments in the field ex situ have enabled mechanistic questions surrounding attractiveness of dung to dung beetles to be addressed, such as identifying the association between dung type used for brood provisioning and adult body size (Edwards 1991; Arellano *et al.* 2015).

In the past 20 years the study of biodiversity-ecosystem functioning relationships has grown markedly and dung beetles are increasingly used as a focal taxon for such studies (Noriega *et al.* 2018). Research has moved from investigatory studies of species - functioning relationships (Loreau 2001) to manipulative experiments which identify interactions between functional groups in the provision of ecosystem functions (Gagic *et al.* 2015), and for which dung beetles are particularly valuable (Slade *et al.* 2007). In this review, 60% of ecosystem functioning studies used only one dung type, and over 50% of the time this was domesticated animal dung. As a consequence, variation in choice between feeding and breeding - two functionally very different interactions - is still unknown. Although livestock dung is important for dung beetle populations globally, especially in agro-ecosystems, it can provide a limited snapshot of the extent of ecosystem functions provided by dung beetles, especially those not performed by domestic animals, such as seed dispersal (Culot *et al.* 2011, 2015; Santos-Heredia, Andresen & Stevenson 2011).

Our review also highlights the variation in experimental design amongst resource use studies, which means comparison of results is challenging. The composition of dung beetles captured in traps is affected by dung volume (Peck & Howden 1984; Finn & Giller 2000; Errouissi *et al.* 2004), and trap spacing (Dormont, Epinat & Lumaret 2004; Dormont *et al.* 2010), and trapping methods to detect the difference between feeding and breeding in dung beetles have only recently been developed (Arellano 2016; Goh & Hashim 2018). Moreover, the effective sampling area for different trapping methods, and how dung attractiveness to dung beetle species varies across different habitats is not well understood (Larsen & Forsyth 2005; Silva & Hernández 2015).

Avenues for future work

The importance of natural history

Further manipulative experiments are needed to gain a mechanistic understanding of dung beetle species distributions; for example, how larval feeding requirements impact dung choice for breeding in adult beetles. Establishing species-level interactions is crucial to answering questions about whole interaction networks and the impacts of environmental change at larger scales (Cardoso *et al.* 2011; Schilthuizen *et al.* 2015), but relies on an understanding of the natural history, which is currently lacking for many dung beetle species.

Thinking quantitatively about interactions

Dung beetle feeding and breeding represent functionally different interactions which can, and should, be explored separately. Although specialism in coprophagous dung beetles may be uncommon (Frank *et al.* 2018), preference towards one dung type over another may not be, especially at different life cycle stages. This can only be explored using a range of dung types in realistic volumes. These different interactions may have consequences for estimates of ecosystem functioning and network structure, but this can only be understood by using a quantitative approach to estimate interaction frequencies. Such networks can then be used to understand the consequences of disturbance on the structure and function of these networks (e.g. Nichols *et al.* 2016).

Considering mammals in dung beetle studies

Disentangling the effects of mammal species presence, abundance, and richness on dung beetle species composition from abiotic factors is still a challenge which can only be addressed by accounting for both in population level assessments. A next step is to link population level trends of mammal species richness and composition to dung beetles at the level of species and traits (Nichols *et al.* 2013), which would further verify the use of dung beetles species or functional groups as bioindicator taxa.

Modelling interactions from co-occurrence data

Identifying ecological interactions from community patterns in species occurrence from spatial data is commonplace (Götzenberger *et al.* 2012), where non-random species occurrence patterns are used to infer interspecific interactions (Gotelli & McCabe 2002; Ulrich & Gotelli 2013). Advances in the use of joint species distribution modelling has enabled species co-occurrence analysis to account for environmental filtering and also identify species interactions (Warton *et al.* 2015a; Zurell, Pollock & Thuiller 2018; D'Amen *et al.* 2018). Applying this framework to the study of mammal- dung beetle associations using spatial data of co-occurrence has the potential to reveal commensalistic interactions between the two trophic levels, and also identify the effect of ecological processes, such as dispersal, as well as abiotic factors on dung beetle species distributions (Kohli, Terry & Rowe 2018; D'Amen *et al.* 2018).

Utilising new molecular methods to understand direct interactions

A developing area is understanding the contribution of the microbiome to resource selection, and how it can vary with environmental conditions (Carrier & Reitzel 2017). The dung beetle maternal gut microbiome is transmitted to larval dung beetles through the brood ball (Estes *et al.* 2013; Shukla *et al.* 2016), and can promote larval development (Byrne, Watkins & Bouwer 2013; Schwab *et al.* 2016). Identifying differentiation in gut microbiota between dung beetle species with different diets

(Franzini *et al.* 2016) and unravelling the role of bacterial symbiosis in nutrient acquisition in dung beetles may shed light on the processes driving resource selection.

Advances in DNA barcoding mean it is now possible to identify vertebrate genetic material from invertebrates that feed on them (Calvignac-Spencer *et al.* 2013; Ji *et al.* 2013). DNA in dung beetle gut contents has been used to successfully identify the mammal species source in a pilot study (Gómez & Kolokotronis 2017), and the same method used to identify dung beetle diets at different life cycle stages (Kerley *et al.* 2018). Although the methods are not quite developed yet, in principle, vertebrate species composition of an area could be identified from analysing dung beetle gut contents and may be an important addition to camera trap studies, particularly in detecting rare or cryptic species. These methods would enable quantitative interaction networks between dung beetles and mammals to be build and could also be used to explore feeding variation and feeding plasticity. What makes these new molecular methods so attractive is that they have the potential to side step the issues affecting ecological sampling (e.g. the size and dung type of the bait used in the trap) and allow identification of species interactions under natural conditions.

Synthesis

There has been a stagnation in the amount of research conducted on basic dung beetle ecology and natural history, particularly with regards to their feeding preferences. Although there has been an increase in dung beetle research related to their response to disturbance and their importance for ecosystem functioning, further work is now needed to put this into context with regard to their resource use and interactions with mammals. The use of dung beetles as bioindicators is currently constrained by the lack of understanding of the associations between dung beetles and mammals; a necessary pre-requisite if data are to be scaled up to give a broader understanding of the extent of functioning provided by dung beetles within whole ecosystems. We highlight several new avenues for research and note that recent advances in molecular and modelling techniques, and the first attempts to construct quantitative interaction networks are beginning to address these issues.

2

Interspecific and intraspecific variation in diet preference in five Atlantic Forest dung beetle species

E.H. Raine, S.B. Mikich, O.T. Lewis & E.M. Slade, in press

Ecological Entomology

Contents

Author contributions

EHR designed the experiment and carried out data collection, with logistical support from SBM. EHR carried out data analysis and wrote the manuscript with multiple rounds of feedback from EMS, SBM and OTL.

Abstract

Dung beetles are commonly assumed to be generalist feeders, but there has been limited work in identifying whether there is interspecific variation in feeding preference. Equally, there has been no work exploring whether generalist feeding behaviour in a species is a result of within species specialisation. Here we identify individual and species level feeding preferences of five dung beetle species towards human, jaguar and pig dung using a choice experiment. We found that species showed variation in their preference towards the dung types, but there was no evidence that within a species individual beetles varied in their dung choice. These findings were similar to results from field experiments which are more typically used to assess feeding preferences in dung beetles. The results suggest individual specialism in feeding may not be common in dung beetles, however there is variation in feeding preferences among species which is often overlooked and can have implications for the ecosystem functions they provide. We suggest that choice arenas can be used to assess feeding preferences in dung beetle species that are not abundant enough to reliably estimate dietary choice from field studies.

Introduction

Resource use can vary at the level of the species (interspecific variation) or the level of the individual (intraspecific variation) (Bolnick *et al.* 2003; Violle *et al.* 2012). For example, within species variation, is common in insects such as bees and butterflies (Gibson & Hunter 2010). Intraspecific variation in diet is based on functional trade-offs that prevent an individual from exploiting all available resources (Araújo *et al.* 2010; Araújo, Bolnick & Layman 2011). Identifying niche variation in feeding is of particular relevance for taxa where resource use relates to ecosystem functions, such as dung beetles that contribute towards dung removal and secondary seed dispersal (Nichols *et al.* 2008).

The majority of dung beetle species are thought to be generalists, able to utilise a wide range of dung from naturally co-occurring vertebrates (Frank *et al.* 2018), as well as non-native species (Whipple & Hoback 2012; Stavert *et al.* 2014a). Although species can vary in their preference towards certain dung types (Bogoni & Hernández 2014), interspecific feeding variation is often overlooked in studies of dung beetle ecology. Equally, there has been no research investigating whether apparently generalist resource use in dung beetles could be a result of individual specialist feeding and inter-individual variation.

Bacterial symbionts present in the gut are thought to play a role in nutrient acquisition in dung beetles (Holter 2016), and have been found to vary in composition between dung beetle species with different diets (Franzini *et al.* 2016; Shukla *et al.* 2016). Variation in gut microbiota between individuals may affect the ability to digest nutrients in the dung that would be otherwise unavailable and could result in inter-individual diet selection in dung beetles.(Schwab, Casasa & Moczek 2017). We investigated within and between species variation in diet preference for five dung beetle species using a choice experiment and three dung types representative of the omnivore and carnivore feeding guilds. This was compared to field experiments to identify whether the preference of individuals is equivalent to that detected at the population level - the standard method for assessing dietary specialism in dung beetles.

Species	**No. individuals**	**Diet preference**
Dichotomius mormon	33	Generalist (Falqueto, Vaz-de-Mello & Schoereder 2005)
Dichotomius sericeus	14	Necrophage (Silva & Hernández 2007) Coprophage (Bogoni & Hernández 2014)
Coprophanaeus dardanus	15	Necrophage (Feer & Pincebourde 2005)
Coprophanaeus saphirinus	12	Coprophage (Bogoni & Hernández 2014) Necrophage (Silva *et al.* 2012) Generalist (Silva & Di Mare 2012)
Phanaeus splendidulus	19	Coprophage (Silva & Di Mare 2012; Bogoni & Hernández 2014) Generalist (Silva et al. 2012)

Table 2.1: Dung beetle species, number of individuals trialled, and diet preference as indicated from the literature.

Methods

The study was conducted in an area of continuous lowland tropical forest in the Atlantic forest, Paraná state, Brazil at each of three sites separated by 500m-1km (Figure B1) (25'27'11"S, 48'52'57"W). Jaguar dung was provided by Curitiba Zoo, and pig dung collected from nearby farms. Both of these dung types and human feces were frozen upon collection to ensure they remained fresh, and to kill any beetles or beetle predators.

Collection of dung beetles

Five large-bodied tunnelling species, chosen due to their abundance in the area, were used in the experiment (Table 2.1). Beetles were collected along the three transects in February 2016 using live pitfall traps baited with 50g of human dung. Dung beetles were kept in cool ventilated containers with damp soil. Beetles were exposed to normal daylight hours and deprived of food for five days before trials.

Choice experiment

The diet preference arena was a 43cm x 30cm tray with a mesh top, lined with 4cm of fresh compact soil and used to assess choice of omnivore (human, pig) and carnivore (jaguar) dung. 30g of fresh dung of each type was added to the arena separated 20cm apart in an equilateral triangle. Ninety-three beetles were tested in total (Table 2.1). Each trial consisted of a beetle placed in the centre of the triangle (Figure 2.1a). Diet choice was recorded for those that showed movement within five minutes. Choice was determined by the observation of feeding for 30 seconds. If no feeding occurred after ten minutes, despite movement, the trial ended. Each beetle individual was tested five times with a minimum of one hour between trials. The tray was rotated between trials.

Field data

Sampling was carried out monthly (December 2015 - March 2016) using traps placed at 200m intervals along the transects. Pitfall traps consisted of a 1L cup buried flush with the soil surface and half filled with water, with a small amount of detergent and salt. The traps were baited with natural volumes of human (∼90g), pig (∼210g), or jaguar dung (∼74g). Natural dung volumes were used to attract a realistic dung beetle community that would feed on a dung pat. Dung beetles were identified by a taxonomist (F. Vaz-de-Mello) and voucher specimens were deposited at the Universidade Federal de Mato Grosso (UFMT) and Embrapa Florestas, Paraná.

Statistical analysis

We tested whether there was variation both between and within species in preference for the three dung types using a linear mixed effect model (LME). We excluded trials where no feeding took place. For each individual beetle, the proportion of times each dung type was chosen was logit-transformed to meet model assumptions and used as the response variable (Warton & Hui 2011). Interactions between species and dung type were included as an explanatory variable to identify whether feeding preference varied by species for each dung type, and a random effect for beetle individual was included to assess how much variation in choice can be attributed to the beetle individual. We also tested whether there were differences amongst species in the proportion of times an individual was observed to feed using a generalised linear mixed effect model (GLMM) with a binomial error distribution. Species and trial number were included as explanatory terms, and the beetle individual as a random effect.

Dung beetle species diet preference was compared to the results from population level assessments of feeding preference from the field. We calculated the total proportion of trials per species that a dung type was chosen, and the total proportion of individuals captured from the field experiment per species. This was then compared using Spearman's coefficient. Models were fit using the lme4 package (Bates *et al.* 2015) and confidence intervals calculated with emmeans (Lenth 2018) for R 3.4.3 (R Core Team 2017).

Results and discussion

The mammalian dung type chosen varied significantly depending on the dung beetle species ($F_{8,264} = 2.25$, p=0.025). There was no evidence of strong preference toward a dung type by any of the five species, but jaguar dung was chosen less regularly than expected at random for two species, *D. mormon* and *D. sericeus* (Figure 2.1b). However, beetle individual explained very little of the variation in choice (SD=0, 95 % CI 0 - 0.13).

Dung beetle species differed in the proportion of times they chose to feed versus not feed (χ^2=28.28, df=4, p <0.001), which was also significantly different across the trials (χ^2=29.40, df=4, p <0.001), with all species choosing dung less frequently as the trials progressed. Four species preferentially chose to feed on the dung, whilst C. dardanus, showed no preference. There was also large variation amongst beetle individuals in whether they chose dung (SD = 1.6, 95% CI= 0.95 - 2.07). The field experiment identified 432 individuals of the five species attracted to the three dung types (Table B1) and the proportion that each dung type was chosen by each species did not differ between the lab and field experiment (t=1.58, df=13, p=0.14).

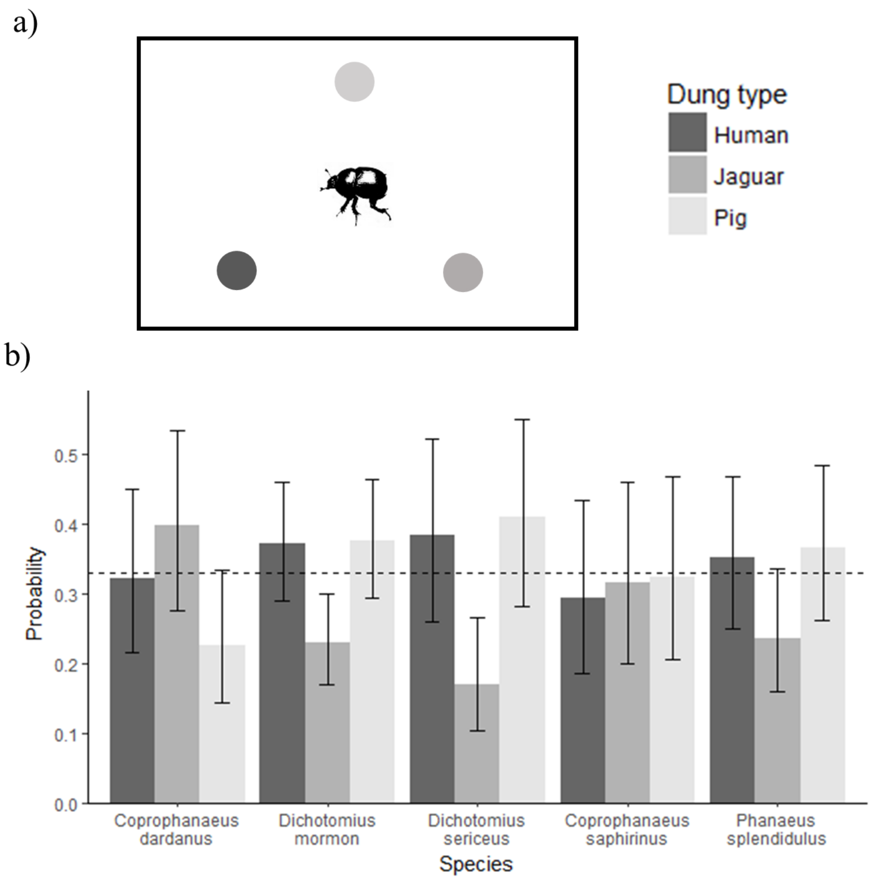

Figure 2.1: a) Choice arena design b) Model estimates and 95% confidence intervals for the probability of each dung type being chosen. Dashed line for reference, representing no preference between dung types.

Individual beetles within a species accounted for little variation in dung choice, which suggests that, within species, beetles do not vary in the type of dung they then chose to feed on. *Coprophanaeus dardanus* was the only dung beetle species that did not show a preference toward feeding on dung. This could be accounted for by its necrophagous feeding habits (Table 2.1), but that it did feed sometimes shows that when resource deprived it may still utilise dung.

Jaguar dung was the least preferred dung type by two species in the choice experiment, and field studies have also found carnivore dung to be the least attractive (Bogoni & Hernández 2014; Hewavithana *et al.* 2016). Adult dung beetles require liquid to filter feed high nutrient particles from dung, and the low moisture content of carnivore dung could explain the avoidance by some species (Al-Houty & Al-Musalam 1997; Frank *et al.* 2017a). Pathogenic bacteria in carnivore dung may also deter dung beetles from feeding (Mansourian *et al.* 2016).

Previous work has shown feeding preferences vary among dung beetles species (Dormont *et al.* 2007; Santos-Heredia *et al.* 2010; Filgueiras *et al.* 2011). Similarly, these results suggest that there is variation in preference towards types of dung by dung beetle species from the Atlantic Forest. This has implications for identifying the robustness of dung beetles to environmental change, and by extension the ecosystem functions that they provide.

The comparison of findings between the field and the choice experiment suggest that the estimates of dietary choice made across individual beetles are similar to those from population level assessments, which are frequently used to classify dung beetle diet preference. Should this assessment hold true for other species, feeding trials could be used as a valid way to assess dietary preference for rarer dung beetle species. This provides a new potential for assessing dietary specialism in dung beetles, as the extent to which these specialisms are a relic of undersampling is unknown (Larsen, Lopera & Forsyth 2006).

3

Linking dung beetle mediated functions to interactions in tropical forests: sampling design matters

E.H.Raine, S.B. Mikich, O.T. Lewis & E.M Slade, in prep. *Biotropica*

Contents

Author contributions

EHR, EMS, OTL and SBM designed the experiment. EHR carried out data collection with support from SBM. EHR carried out data analysis and wrote the manuscript with multiple rounds of feedback from EMS, SBM and OTL.

Abstract

Interactions between dung beetles and vertebrate dung are intimately linked to a suite of ecosystem functions in tropical forests. We show that the trapping method and the type of dung used affect the suite of beetles captured, with the potential to influence the outcome of experiments linking functions to interactions.

Introduction

Not all species interactions are equal in terms of their contribution to the functioning of an ecosystem. Often it is assumed that observational data on frequencies of interactions measured using standard methods can provide an accurate and meaningful estimate of functional interactions (Balvanera *et al.* 2006). But, distinguishing functionally important species interactions and quantifying their strength is needed to be informative about ecosystem functioning. For example, in plant-pollinator networks this can be done by distinguishing pollination from visitation (King, Ballantyne & Willmer 2013), and measuring the frequency of these interactions (Chacoff, Resasco & Vázquez 2018).

Understanding the functional consequences of interactions is particularly relevant in tropical systems, where anthropogenic pressure is causing changes in the structure and function of many ecosystems (Morris 2010). Dung beetles are widely used as biological indicators, and for the study of ecosystem functions in tropical forests (Santos-Heredia *et al.* 2010; Nichols & Gardner 2011). The majority of dung beetles use dung for both feeding as adults, and for breeding (i.e., as the resource for larval development), with the formation and burial of brood balls contributing to ecosystem functions such as nutrient cycling, bioturbation, and seed dispersal (Nichols *et al.* 2008). Dung beetles relocate dung by rolling brood balls and burying them (rollers) or by burying directly beneath the dung pad (tunnellers) (Hanski & Cambefort 1991). In addition to dung beetle body size (Nervo *et al.* 2014), the nesting strategy of dung beetles has been shown to influence the rate of dung removal (Slade *et al.* 2007). Dung beetle species assemblages could therefore have an impact on the ecosystem functions provided. There has been no work identifying whether dung beetles discriminate between dung use for feeding or breeding and, as a result, the magnitude of interactions between dung beetles and dung have rarely been quantified (but see Slade *et al.* 2016).

Although dung beetles are commonly assumed to be generalist feeders (Hanski & Cambefort 1991; Frank *et al.* 2018), species can show preference towards dung of certain mammal species or trophic guilds (Santos-Heredia *et al.* 2010; Bogoni

& Hernández 2014). But few studies have specifically tested the attractiveness of dung from mammal species native to the area of study (but see Enari, Koike & Sakamaki 2013; Frank *et al.* 2017b), and standardised bait sizes are often used irrespective of the mammal dung (e.g. Marsh *et al.* 2013; Bogoni & Hernández 2014). Several factors influence dung choice by dung beetles. Dung volume affects the body size of dung beetles attracted, as well as the total abundance of individuals (Peck & Howden 1984; Finn & Giller 2000). Dung beetles also vary in their method of feeding on dung between the larval and adult stage, and may show life-stage specific preferences (Holter & Scholtz 2007). In addition, dung quality can influence the size of brood balls and subsequently adult body size (Gittings & Giller 1998; Arellano *et al.* 2015; but see Frank *et al.* 2017), and so may also influence whether an individual chooses to feed on or breed in the dung.

We explored whether the type of mammal dung and the volume of it used in a trap influences the assemblage of dung beetles attracted to it. In addition, we compared dung beetle species and traits from burial interception traps, which are thought to give a more realistic picture of the dung beetle assemblages actually using (rather than just attracted to) the dung, especially for nesting (see Arellano 2016; Goh & Hashim 2018), with data from pitfall traps, which represent attraction for both feeding and nesting, and which are frequently used as a proxy for dung exploitation (Larsen & Forsyth 2005). We asked (i) Does the type of dung and volume used affect the assemblage of beetles attracted to a trap? and (ii) Are dung beetles differentially attracted to dung for feeding versus breeding? We compared each dung and trap type in terms of two assemblage-level metrics, total dung beetle abundance and biomass, and two functional categorisations, based on nesting strategy and per-beetle biomass.

Methods

Field experiment

Dung from native Atlantic Forest mammals from a local zoo was used for trap baits in a naturally occurring range of sizes for each mammal species. Lesser Grison

(*Galictis cuja*), Jaguar (*Panthera onca*), Ocelot (*Leopardus pardalis*), Crab-eating raccoon (*Procyon cancrivorus*), and Black Capuchin (*Sapajus nigritus*) as well as human and pig dung were individually collected, weighed, and frozen until use (see Table C1 for mammal species dung volumes). These dung types were used where available for both trap types once per month from December 2015 - February 2016 and only for pitfall traps in March 2016.

Dung beetles were collected at three sites of lowland tropical forest separated by 500m - 1km within a continuous area of Atlantic Forest in Paraná, Brazil (25’27’11"S, 48’52’57"W). Two transects 200m apart were established in each site, one for burial intercept traps and one for pitfall traps, with eight traps set 200m apart along each transect. Pitfall traps consisted of 1 litre cups buried flush with the ground, half filled with water, detergent and salt, with a rain cover. Individually collected dung baits were suspended in muslin and traps left for 48 hours before collection. Burial intercept traps consisted of an agricultural bag 35cm in diameter and buried 75cm deep and refilled with soil, leaving a 3cm lip at the soil surface. Dung was placed on top of the soil and left for 24hrs before the soil was sieved and dung beetles collected. Dung beetles from both traps types were stored in 70% alcohol and frozen until identification at Universidade Federal de Mato Grosso (UFMT) by an expert taxonomist (F. Vaz-de-Mello). Dry biomass of each species was calculated by weighing up to 30 individuals using scales accurate to 0.001g.

Statistical analysis

We first calculated sampling completeness of the dung beetle species attracted to each mammal dung and trap type. We then ran linear mixed effect models with per-beetle biomass and total dung beetle biomass log transformed as response variables, with trap type and dung type as explanatory variables. A random effect of dung volume nested within dung type in each model was fitted to take into account the effect of using naturally varying dung volumes. A generalised linear mixed effect model was fitted with dung beetle abundance as the response, with a quasipoisson error structure to account for over-dispersion. To assess variation in the ratio of rolling to tunnelling dung beetles in different dung types, we also ran a generalised linear mixed effect model. This analysis was only carried out for the pitfall traps, as dung beetles are not reliably captured in burial intercept traps (Arellano 2016). The number of rolling and tunnelling beetles in each sample was specified as a binomial response variable, with dung type as an explanatory variable. A random effect of dung volume nested within dung type was again included to account for variation in dung volume.

We tested the significance of the terms included in each of the models compared to a model with the term removed using Chi-Squared tests for generalised linear models and F tests for linear models, reporting p-values. A permutational analysis of variance (PERMANOVA) was used to identify whether there were differences in the dung beetle assemblage composition among trap and dung types, and non-metric multidimensional scaling (NMDS) was used to produce ordination plots of the dung beetle communities. Statistical analyses were carried out using the packages *iNEXT* (Hsieh, Ma & Chao 2016), *lme4* (Bates *et al.* 2013) and *vegan* (Oksanen *et al.* 2017) in R 3.4.3 (R Core Team 2017).

Results and discussion

From a total of 203 traps using the seven dung types, we collected 2295 beetles of 26 species (Table C3). Sampling completeness was >80% for each dung type in each trap type, apart from two instances where very few dung beetle individuals were collected (Table C3). Dung beetle abundance, total biomass and per-beetle biomass all differed significantly among trap types and dung types (all $p<0.05$, Figure 3.1, see Table C2 for test statistics), and in all cases were higher in pitfall traps than burial intercept traps. Only two burial intercept traps caught rolling dung beetles, and within the pitfall traps the proportion of rolling dung beetles collected varied with dung type ($p=0.055$, Table C2). For both dung beetle abundance and biomass, human and pig dung were the most attractive, and grison dung the least attractive; this also corresponds to increasing attractivity with dung size (Figure 3.1 a,b, Fig C1). For the measures of dung beetle functional composition, pig dung attracted a low proportion of rolling dung beetles compared to other dung types. Ocelot, raccoon, jaguar, and human dung attracted dung beetles with the largest average body sizes (Figure 3.1 c,d).

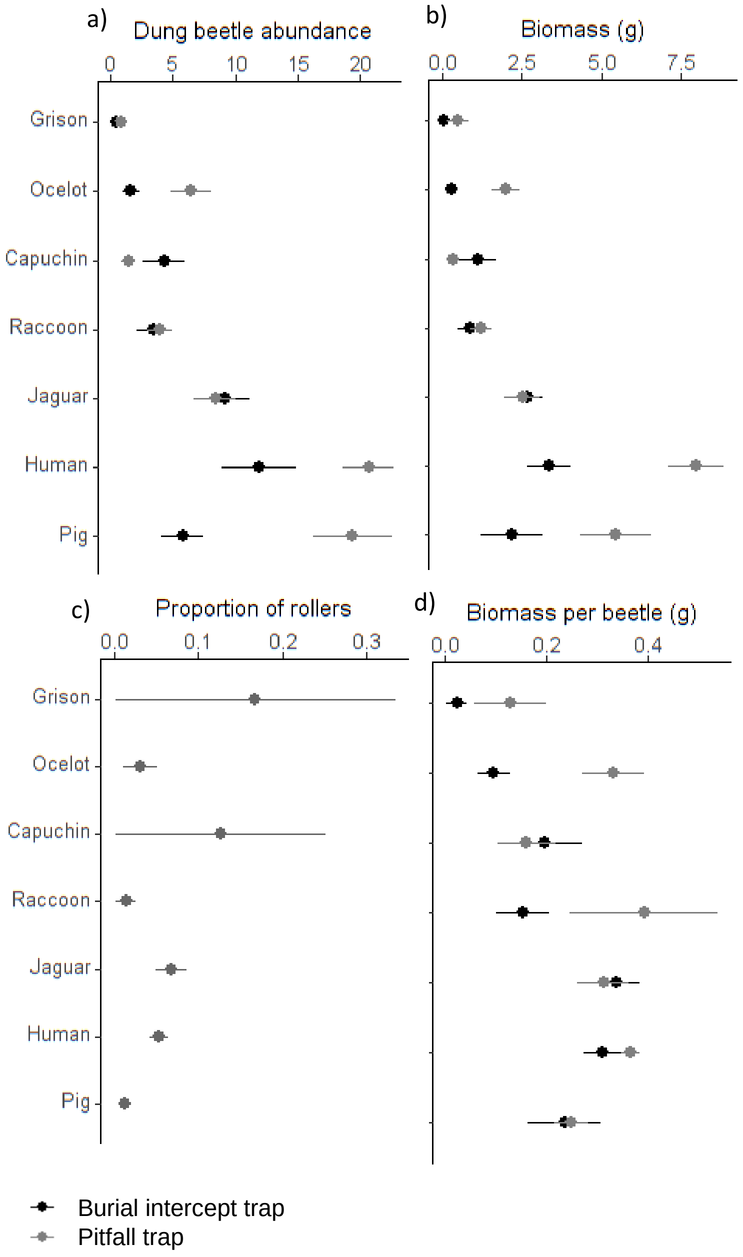

Figure 3.1: Mean ±SE for trap and dung types for a) total dung beetle abundance, b) total dung beetle biomass (g), c) the proportion of rolling beetles (pitfall traps only) and d) biomass per beetle (g). Dung types ordered by volume from smallest (grison) to largest (pig).

The dung beetle species assemblage differed significantly between trap types

($F_{1,150}$ =7.14, p=0.002) and amongst dung types ($F_{6,150}$=2.6152, p=0.002), yet these factors explained only 5.1% and 12% of the variation in community composition, respectively. Dung beetle assemblages recorded using the burial intercept and pitfall traps were overlapping (Figure 3.2a), with the assemblages trapped in pitfalls nested within those trapped using the intercept traps. Assemblages attracted to the dung of Atlantic Forest mammals overlapped with those collected in human dung, with only grison dung having substantially different assemblages (Figure 3.2b).

The dung beetle assemblage composition captured within burial intercept traps were nested within those captured in pitfall traps. This indicates a subset of the dung beetle assemblage attracted to pitfall traps utilises dung in burial intercept traps either for brood provisioning or feeding. This could be explained by a difference in choice of dung by dung beetles depending on its use (Holter 2016). As the dung remains exposed, pitfall traps continue to be attractive for the complete sampling period, whereas burial intercept traps which mimic the natural temporal distribution of dung are attractive for shorter periods as dung is buried. The difference in the total abundance and biomass of dung beetles collected between the two trap types suggests that pitfall traps may give an overestimate if used to approximate the extent of ecosystem functions provided by dung beetles. However, burial intercept traps do not reliably capture rolling dung beetles (Arellano 2016; Goh & Hashim 2018), so alternative methods are needed to estimate how dung removal varies amongst dung beetle guilds in systems where rolling beetles make up a larger proportion of the dung beetle population.

We also found differentiation in the attractiveness of the seven dung types. This could be attributed to dung quality (Bogoni & Hernández 2014) but also consistency, water content, and volume (Frank *et al.* 2017a). Human dung is often used as a convenient proxy for other mammal dung when surveying dung beetle communities (e.g. Larsen & Forsyth 2005), and here we found it was the most attractive in terms of the amount of dung beetles collected. The lower dung beetle abundance and biomass collected in many of the native dung types indicates that human dung baits may overestimate the magnitude of dung beetle - dung

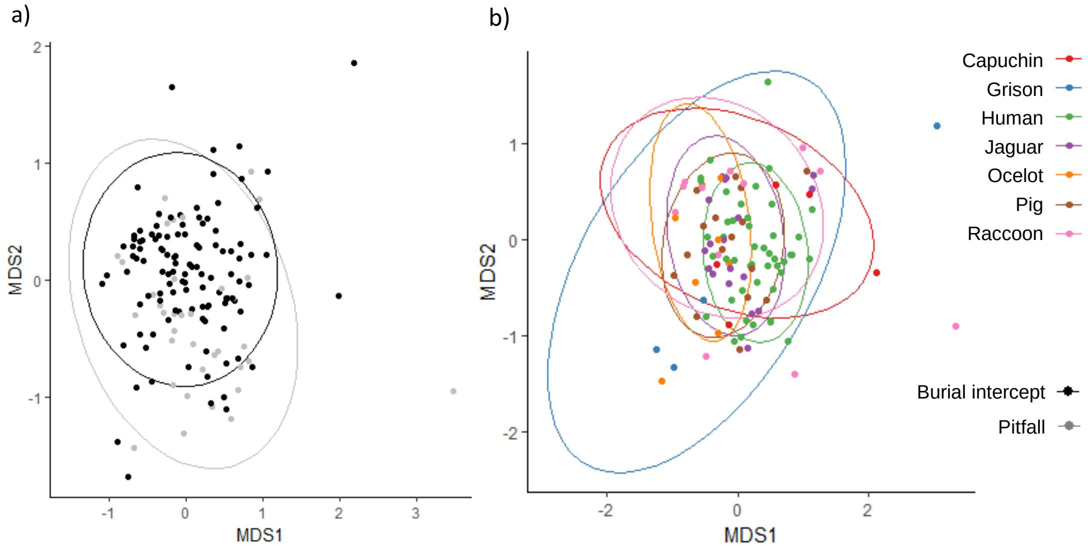

Figure 3.2: Non - Multidimensional Scaling representing dung beetle species assemblage a) attracted to each dung type (across both trap types) and b) attracted to the two trap types (across all dung types), ellipses represent 95% confidence intervals.

interactions. This suggests the number of dung beetles associated with naturally-occurring mammal dung types is smaller than might be expected from human dung baits and highlights the importance of using the dung of naturally occurring mammal species in realistic dung sizes to quantify functional interactions between dung beetles and mammals (Frank *et al.* 2018).

Dung beetle body size (Horgan 2001; Nervo *et al.* 2014) and functional group richness (Slade *et al.* 2007; Manning *et al.* 2016) affect the amount of dung removed. Here we found that dung beetles captured in burial intercept traps were smaller-bodied than those in pitfall traps, and that body size differed significantly among dung types. This suggests a difference in olfaction between dung beetle species could be driving this pattern, although there is no evidence to suggest olfaction capacity is associated to body size in dung beetles. Within the pitfall traps, there was also variation in the attractiveness of dung types to rolling and tunnelling dung beetles. This suggests that the common practice of using a single dung type (e.g. Slade & Roslin 2016; Nervo *et al.* 2017), deployed only within pitfall traps, to explore functioning - species traits associations may result in an unrealistic composition of dung beetles assigned to each functional group. This may subsequently affect estimates of ecosystem functioning, if standardised dung bait is used as a proxy. Such differences between attractiveness of dung types among species could be compounded in studies of multifunctionality provided by dung beetles when other ecosystem services such as seed dispersal and nutrient cycling are also considered (Slade *et al.* 2017).

Moving from documenting biodiversity to recording ecosystem functions will require methods to infer functioning that are robust, representative and meaningful. In conclusion we suggest that trapping method and dung type used as bait should be considered when designing experiments to identify mammal-dung beetle interactions, and when conducting experiments that link dung beetle species to ecosystem functioning.

4

Extinctions of interactions: Quantifying a dung beetle - mammal network

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in press *Ecosphere*

Contents

Author contributions

EMS and SBM conceived the idea for the study. The study was designed by EMS, SBM, HER, OTL, FM and PR. EHR carried out data collection with support from SBM, PR and FM. EHR and FM identified specimens. EHR analysed data and wrote the manuscript with feedback from EMS, OTL, SBM and PR.

Abstract

Loss of large-bodied mammals across the globe through hunting, habitat degradation and fragmentation is one of the most significant anthropogenic impacts on the environment. Cascading effects of these extinctions through ecosystems have been little studied, although correlative studies have revealed co-extinctions in closely linked groups, with implications for ecosystem structure and function. Despite playing important roles in seed dispersal and hence seedling recruitment, mammals have been largely neglected in network studies. Similarly, the role of secondary seed dispersers, such as ants and dung beetles, has been largely unexplored. Dung beetles rely on mammal feces for feeding and breeding and provide a suite of important ecosystem functions and services. While dung beetle community responses to environmental change have been widely investigated, studies quantifying the network of associations between dung beetle and mammal species are lacking. By developing the first quantitative mammal- dung beetle networks, we address several important knowledge gaps, contributing to understanding of how interactions in networks involving mammals and secondary insect seed dispersers are structured. We use the resulting quantitative interaction networks to model mammal species extinction scenarios to further explore the consequences for dung beetle populations, and the extent to which networks change the magnitude of interactions through resource switching. Dung beetle feeding and breeding networks did not differ significantly in structure, and showed high nestedness and low levels of trophic specialization. Simulations suggested that mammal extinction scenarios based on mammal body mass and mammal dung volume will impact dung beetle populations to a greater

extent than random scenarios of mammal loss. Thus, despite their generalist feeding preferences, realistic mammal extinction scenarios have the potential to negatively impact the dung beetle community, which may have consequences for ecosystem functioning.

Introduction

Habitat loss, defaunation, climate change and other large-scale anthropogenic disturbances continue to drive species extinctions across the globe, with particularly rapid biodiversity loss in tropical forests (Canale *et al.* 2012). While the majority of research has focused on species as the unit of biodiversity loss, an overlooked component is the extinction of ecological interactions (Valiente-Banuet *et al.* 2015). These extinctions are important as they often accompany or precede the loss of species, and may have direct effects at the ecosystem level (Koh *et al.* 2004). Loss of large-bodied mammals across the globe, through hunting, habitat degradation and fragmentation is one of the most significant anthropogenic impacts on the environment (Peres & Palacios 2007; Wright *et al.* 2007). Cascading effects of these extinctions through ecosystems have been little studied, although correlative studies have revealed co-extinctions in closely linked groups, with implications for ecosystem structure and function (Colwell, Dunn & Harris 2012; Kurten 2013; Nichols *et al.* 2016).

One approach to understanding direct and indirect interactions in multi-species communities is to construct and analyze quantitative trophic networks, which document both the incidence and frequency of interactions among species (Tylianakis *et al.* 2010). Quantitative interaction networks have proved valuable in identifying shifts in food web architecture in response to anthropogenic environmental change (e.g. Tylianakis *et al.* 2007), and have provided a tool for predicting indirect interactions within communities (e.g. Morris *et al.* 2014). They have also been used as the basis for simulating species extinctions and the resulting trophic reorganization, using the quantitative information embedded within the networks to predict rewiring and reallocation of feeding interactions, and concurrent changes in network properties associated with community stability and robustness (e.g. Ramos-Jiliberto *et al.* 2012, Evans *et al.* 2013).

Quantitative interaction networks have been employed widely to document plant-herbivore and plant-pollinator interactions (e.g. Kaiser-Bunbury *et al.* 2010, Novotny *et al.* 2010). However, most such studies of plant-animal interaction networks have been phyto-centric i.e. compiling data from focal plant species in the form of e.g. visitation frequencies of pollinators or attack rates by herbivores or predators (King *et al.* 2013), rather than zoo-centric i.e. sampling animal activity, such as the analysis of fecal samples (Jordano *et al.* 2007), or pollen samples from the body of pollinators (Bosch *et al.* 2009). Of those interaction networks that do include vertebrates, most focus on birds as frugivores dispersing seeds, and only a few include bats (Mello *et al.* 2011) and fewer still, other mammals (Donatti *et al.* 2011). Thus, despite their important roles in seed dispersal and hence seedling recruitment, mammals have been largely neglected in network studies (Vidal, Pires & Guimarães 2013). To date there have been few such studies of networks of commensal species (Sayago *et al.* 2013; Nichols *et al.* 2016) and the role of secondary seed dispersers, such as ants and dung beetles, remains largely unexplored.

Dung beetles use mammal dung as a food and nesting resource, meaning that dung availability is directly related to dung beetle reproduction and survival (Hanski & Cambefort 1991; Moczek & Emlen 2000; Shafiei *et al.* 2001). Dung beetles play an important role in dung removal and associated ecosystem functions such as secondary seed dispersal and nutrient availability, factors which may ultimately influence plant dynamics and diversity (Spector 2006; Slade *et al.* 2007; Santos-Heredia *et al.* 2016). Mammal abundance and the abundance and species richness of dung beetles have been found to covary (Andresen & Laurance 2007; Viljanen *et al.* 2010a; Culot *et al.* 2013; Nichols *et al.* 2016) yet beyond estimating interactions from co-occurrence data (Nichols *et al.* 2016) there are no dung beetle - mammal association networks and there is a lack of data demonstrating this association directly through trapping with native mammal dung (Nichols *et al.* 2009). Studies of the direct interactions between dung beetles and the mammal dung they feed on are therefore needed to understand the effects of mammal species extinctions on dung beetle community structure, and the cascading effects on ecosystem functioning (Larsen *et al.* 2008; Slade *et al.* 2011; Nervo *et al.* 2017).

Despite numerous studies addressing dietary preference in dung beetles, few have used methods that enable the interactions between dung beetles and mammalian dung sources to be quantified reliably. Most sampling of dung beetle communities use standardized human or pig dung baited pitfall traps (Marsh *et al.* 2013), a method that may not accurately represent species' use of different resources (Amézquita & Favila 2010). Furthermore, dung size influences the abundance and size of dung beetles attracted (Peck & Howden 1984). Several recent studies have used wild animal dung at standardized sizes to attempt to ascertain dung beetle feeding preferences and have suggested that defaunation has strong effects on dung beetles (Martín-Piera & Lobo 1996; Culot *et al.* 2011; Enari *et al.* 2013; Bogoni & Hernández 2014). However, no previous work has used wild animal dung at the realistic sizes necessary to enable the incidence and frequency of interactions between individual dung beetle and mammal species to be calculated and to construct whole interaction networks. In addition, the dung type used for breeding influences brood mass and adult beetle size (Arellano *et al.* 2015), and dung beetle selectivity could vary between dung used for feeding or breeding.

Here, using mammal and dung beetle data collected from the Atlantic Forest of Brazil, we present the first fully-quantified interaction networks for a coprophagous dung beetle community and associated mammalian dung resources. We compare a feeding interaction network derived from pitfall trapping data with a functional interaction network that can more accurately represent the breeding interactions between dung beetles and mammal dung. Finally, we present the effects of simulating mammal species extinctions from the interaction network on dung beetle populations and communities under a variety of extinction scenarios.

Methods

Study area

Fieldwork took place between 6th November 2015 and 13th April 2016 within a large remnant of Atlantic Forest in the Serra do Mar mountain range, in South East Brazil (25'27'11"S, 48'52'57"W). The Atlantic rainforest supports high levels of endemic flora and fauna, but only 12% of the original forested area now remains (Ribeiro *et al.* 2009; Tabarelli *et al.* 2010). There are records of local extinctions of medium and large-bodied mammal species from the area, resulting in impoverished mammal assemblages in many remaining fragments (Canale *et al.* 2012). The Serra do Mar mountain range is recognized as a center of species endemism and is the second largest area of continuous Atlantic forest remaining with an extent of 41,000km^2 (Ribeiro *et al.* 2009). The study was conducted in three sampling sites separated by 0.5-1km within continuous lowland tropical forest, with an altitude of 40-100m. Sites were predominantly primary forest but with signs of hunting or heart-of-palm (*Euterpe edulis*) harvesting.

Data collection

Dung beetle sampling

Dung samples from seven mammal species native to the Atlantic forest were obtained from the Municipal Zoo of Curitiba and the natural mass of each dung sample recorded before use (Table 4.1). All dung was stored at -18°C until used to keep it fresh, and to kill any beetles or beetle predators. Dung beetles use olfactory cues to locate dung (Dormont *et al.* 2004, 2010), and the odor profile of dung is a crucial aspect of its attractiveness. Pitfall trapping with unrealistic dung sizes is likely to provide odor cues that differ substantially from those generated by the spatiotemporally ephemeral distribution of dung in a tropical forest (Filgueiras *et al.* 2009; Whipple & Hoback 2012; Enari *et al.* 2013; Silva & Bogoni 2014). Therefore, we used mammal dung of realistic sizes in our sampling. To distinguish between the functional use of dung we deployed two types of trap, to identify dung beetle visitation (pitfall trap) and dung removal (bag trap).

Pitfall traps attract coprophagous dung beetles that would both feed and breed on a dung source. We buried 700ml plastic cups (10cm top diameter, 7cm bottom diameter, 15.5cm depth) flush with the ground, half filled with a water, salt and detergent solution. The dung bait was suspended over the cup, protected with a rain cover, and left for 48 hours before collection. Bag traps (Arellano 2016; Goh & Hashim 2018), designed to capture dung beetles exploiting the dung to form brood balls or balls buried for feeding, were made from large agricultural plastic

Species	**Common name**	**Mean dung mass (g) ± SE**	**Mammal status**	**Trophic guild**
Myrmecophaga tridactyla	Giant ant eater (Linnaeus, 1758)	23-28*	Critical	Insectivore
Sapajus nigritus	Black capuchin (Linnaeus, 1758)	37.2 ± 5.3	Not at risk	Frugivore
Cerdocyon thous	Crab-eating fox (Linnaeus, 1766)	32.5 ± 14.5	Not at risk	Carnivore
Panthera onca	Jaguar (Linnaeus, 1758)	73.6 ± 5.4	Critical	Carnivore
Leopardus pardalis	Ocelot (Linnaeus,1758)	33.0 ± 3.3	Vulnerable	Carnivore
Galictis cuja	Lesser Grison (Molina, 1782)	11.9 ± 1.0	Not at risk	Carnivore
Procyon cancrivorus	Crab-eating racoon (Cuvier, 1798)	46.1 ± 2.9	Not at risk	Omnivore

Table 4.1: Atlantic forest mammal species, mean dung mass, mammal status for Paraná state (Mikich & Bérnils 2004), and trophic guild feeding group for the dung used in this study. * only two dung samples obtained.

bags with drainage holes in the bottom, buried in the ground and back-filled with approximately 70L of soil (0.45m x 0.45m). Bags were buried flush with the soil surface; mammal dung was placed on top of the soil inside the bag and left for 24 hours. Upon collection the bags were sealed, and dung beetles collected by sifting through the soil onto a white sheet. Bag traps can capture a realistic abundance and biomass of dung beetles attracted to a dung type as dung burial limits the period that the dung is attractive to beetles. This method does not reliably capture dung beetles that roll away dung balls from a dung pad for burial (rollers), but these make up a small proportion the dung beetle fauna in the Atlantic forest (Filgueiras *et al.* 2011), which mainly consists of tunneling dung beetles (that bury dung directly beneath the dung pad). Dung of all seven mammal species was used for pitfall trapping, and six dung types were used in the bag traps due to insufficient quantities of giant anteater dung (Table D1).

In each of the three sites, two 1400 m line transects were established spaced at least 150m apart and starting at least 100m from the forest edge. One transect was used for pitfall traps and the other for bag traps. Each line transect had eight sampling points spaced 200m apart, to limit interference between traps (Figure D1). Both types of traps were set once per month, on three occasions for the bag traps and four occasions for the pitfall traps. Dung from the native mammal species in naturally occurring volumes (Table 4.1) were randomly allocated to sampling positions along each transect. All traps were set in the morning between 0900 - 1100. Dung beetles from both trap types were kept in 70% ethanol in a freezer until they were identified by a dung beetle taxonomist (F. Vaz-de-Mello) and using genus-specific keys (Vaz-de-Mello & Edmonds 2011). Voucher specimens were deposited at the Universidade Federal de Mato Grosso (UFMT) and Embrapa Florestas, Paraná. Dung beetle dry biomass was quantified by weighing up to 30 individuals per species (depending on the abundance of the species) with a microbalance accurate to 0.001g.

Mammal sampling

Mammal sampling coincided with dung beetle sampling. For each site, line transect surveys were carried out twice per week between 0900 and 1500 from 17th November 2015 to 4th March 2016. Line transect surveys consisted of following two 1400m trails within each of the three sites, with observations of footprints recorded and photographed, fecal samples collected and identified, and visual sightings recorded. Motion detection cameras (LTL Acorn 5210 & 6210) were set at each site covering 141 camera-trap nights from 24th November 2015 - 13th April 2016. Eight cameras were used in a grid configuration spread across both dung beetle trapping transects, with cameras spaced approximately 200m apart and rotated among the sites to enable high density sampling in each site for three weeks (24th Nov 2015 - 2nd Feb 2016). Following this, three cameras were placed in each site for 11 more weeks (3rd Feb 2016 - 13th April 2016) Following standard protocols, cameras were placed within sites in areas where animals were likely to pass (Kays & Kranstauber 2009; O'Connell, Nichols & Karanth 2010).

Data analysis

As the three sites were not spatially independent in terms of mammals or dung beetles, data were pooled to produce two matrices, the first (from the bag trap data) representing dung beetles using dung as a resource for their offspring ('breeding') and the second representing dung beetle - mammal interactions based on attraction to pitfall traps ('feeding'). The total number of camera sightings, sign and visual sightings per species were used to calculate the relative abundance of each mammal species. Due to the mis-match between the detection of animals and the dung used (jaguar dung was used in trapping; puma but not jaguar was recorded in the field), the categories 'large felid' and 'small felid' were used in place of species as nodes in the interaction network, indicative of the mammal trophic guild (Bogoni & Hernández 2014).

To test sampling completeness, coverage-based rarefaction (Chao & Jost 2012) was applied to the network using the *iNEXT* package (Gotelli & Chao 2013). Both dung beetle species and mammal dung types were tested to assess the sampling completeness in terms of diet breadth of dung beetle species, and the range of dung beetles detected on each dung type. An interaction accumulation curve was plotted to identify completeness of feeding interactions.

To test whether the dung beetle - dung networks differed in structure from a random network with similar structural properties, linkage density (L/S), specialism (H2') (Blüthgen, Menzel & Blüthgen 2006), and nestedness were compared between the observed network and 10,000 random networks. Linkage density (L/S), specialism (H2') (Blüthgen *et al.* 2006), and nestedness were compared between the bag network and the resampled pitfall network using a one-sample t-test (Tylianakis *et al.* 2010). Nestedness values range from 0-100 where 0 is perfectly nested, and H2' values range from 0 (no specialization) to 1 (perfect specialization). Linkage density is the mean number of links per species (Dormann *et al.* 2009). Random networks were simulated using the bipartite package (Dormann, Gruber & Frund 2008), constraining the total species abundance and links, and compared to the empirically-observed networks using a one-sample t-test (Dormann *et al.* 2009).

To identify whether there were differences in structure between the feeding and breeding network, whilst controlling for sampling intensity, subset of beetles were selected at random 1000 times from the pitfall network to create networks of the same size as the bag network. To test whether there were differences in the dung beetle community attracted to each trap type, a permutational multivariate analysis of variance (MANOVA) was calculated, and visualized using nonmetric multidimensional scaling (NMDS).

Quantifying dung beetle - mammal interaction networks

The feeding and breeding dung beetle - mammal dung networks created were based on the relative volume of dung available in the ecosystem. This was estimated based on the abundance of each mammal species recorded that also had dung available to use for dung beetle trapping. Dung volume (g) produced per mammal species per day (d_j) was estimated based on the mammal species body mass (m_j) (Blueweiss *et al.* 1978; Emmons & Feer 1997) and raw proportional occupancy (a_j), following Nichols *et al.* (2016):

$$d_j = (0.85 m_j^{-0.37}) m_j a_j \tag{4.1}$$

The interaction frequency between dung beetle species i and mammal species j was based on dung beetle numbers recorded, defined for each trap type as:

$$I_{ij} = \frac{d_j}{p_j} B_{ij} \tag{4.2}$$

where pj is the total volume of dung of mammal species j in one trap type (bag or pitfall), and B_{ij} represents the number of beetles captured through trapping of dung beetle species i on dung from mammal species j in one trap type. The relative abundance of a dung beetle species is therefore the sum of the interactions it is a part of:

$$b_i = \sum_{j=1}^{n} \frac{d_j}{p_j} B_{ij} \tag{4.3}$$

Mammal species extinction scenario simulations

To explore the effect of mammal species extinctions on the dung beetle community, the feeding and breeding networks were combined to create one network using the methods described above to represent the total interactions (both feeding and breeding) of dung beetles with each dung type. We estimated the average biomass of dung beetles reproducing within a realistic mass of dung of each mammal species using a linear model fitted between the transformed log biomass of dung beetles and log dung mass from the bag trap network. This was incorporated into the interaction frequency equation (I_{ij}, see above) for the mammal species extinction scenarios.

We simulated network responses to four alternative mammal extinction scenarios. Scenarios were selected to reflect extinction risk on the basis of (i) rarity, where the least abundant mammal species goes extinct first (Cardillo *et al.* 2006), based on relative mammal abundance from this study; (ii) local status of extinction-proneness from the Paraná Red Book (Mikich & Bérnils 2004), where the most endangered mammal species goes extinct first; (iii) body size, with the largest mammal species going extinct first, which has been used as an indicator of extinction risk (Cardillo *et al.* 2006); (iv) dung volume, where mammal species extinction was based on total volume of dung produced per day by the mammal species d_j, (mammal species with the largest dung volume removed first) (Table D1).

Based on the generalist interactions of many dung beetles with mammal dung (Hanski & Cambefort 1991), the simulations incorporated the potential for dung beetle individuals to change their feeding interactions to alternative resources following mammal extinctions. Where jr represents the mammal species that are removed from the network, the dung beetle individuals feeding on this dung type (I_{ijr}) were reallocated to other remaining dung types available ($_{ij}$), in proportion to that species' use of each dung type as recorded from the combined bag and pitfall traps. Thus, the reallocation of dung beetles to the mammal species remaining in the network is represented as:

$$R_{ij} = I_{ik} \frac{B_{ij}}{\sum_{j=1}^{n} B_{ij} - B_{ijr}}. \tag{4.4}$$

where B_{ijr} represents the dung beetles feeding on the dung of the mammal species that have been removed (k). Dung beetle individuals (drawn from all species feeding on a dung source) were then removed at random until the biomass (s) of dung beetles feeding on a dung type (B_{sij}) was equal to that predicted to be supported by that dung source (based on the bag trap data; see above): $Rs_{ij} = Bs_{ij}$. Each extinction scenario ran for 1000 iterations to attain the range of dung beetle populations that would persist given the stochastic element during dung beetle individual reallocation. The scenarios assume a direct association between dung beetle biomass and volume of dung used and incorporates competition into the network by restricting the total biomass of dung beetles that can be supported on a dung source. Our method of feeding reallocation assumes that dung beetle individuals are capable of switching their feeding source to other dung types used by the same species, and that this occurs without any fitness cost to the dung beetle individual.

Each mammal loss scenario (1000 iterations) was compared with a null model (1000 iterations) with a random order of mammal species extinction. For simplicity, we assumed that mammal species extinctions would not result in any compensatory response from other mammal species. For each simulated network we calculated dung beetle species richness, dung beetle abundance, total dung beetle biomass, and average biomass per beetle individual. These metrics were compared between the realistic scenarios and random null scenarios of mammal species extinction using confidence intervals. Code for extinction scenarios is available in the Supplementary Material. All data analyses were carried out in R (R Core Team 2017), and interaction networks visualized using Food Web Designer (Sint & Traugott 2016).

Results

Dung beetle and mammal data

In total, 435 dung beetles of 15 species were collected using 69 dung baited pitfall traps and 44 dung baited bag traps (Table D2). The majority of dung beetle species captured were coprophagous or generalist in their feeding preferences according to the existing literature (Table D3). Rolling dung beetles made up only 6.8% of individuals. Mammal surveys identified 17 mammal species through 151 camera records, 40 animal signs, and five visual sightings (Table D4).

Trophic networks

The networks for breeding (Figure 4.1a) and feeding (Figure 4.1b) interactions of Atlantic forest mammals and dung beetles incorporated half of the mammal species identified at the site through the mammal census. All mammal dung types had high sample completeness (76-100%), indicating that the data are robust in terms of the number of dung beetle species attracted to each bait type (Figure D1). Equally, dung beetle species had high sample completeness (>90%), with the exception of Canthidium punctatostriatum (73%), indicating that diet breadth detected for dung beetle species was also robust. The interaction accumulation curve showed that sample size, as expected, is an important influence on the number of interactions detected for each dung beetle species (Figure D2). There were no specialist dung beetles interacting with a single dung type, other than those with very low abundances (two or fewer individuals).

The feeding interaction network included 15 dung beetle species and 7 mammal species, and the breeding interaction network included 11 dung beetle species and 6 mammal species. Connectance (the realized proportion of possible links, from 0 - 1) was 0.49 for both networks. For the feeding network, nestedness, specialism and linkage density did not differ significantly from the null expectation under random association ($p>0.05$). In contrast, in the breeding interaction network both linkage density ($p=0.19$) and H2’ ($p=0.011$), but not nestedness ($p>0.05$), were

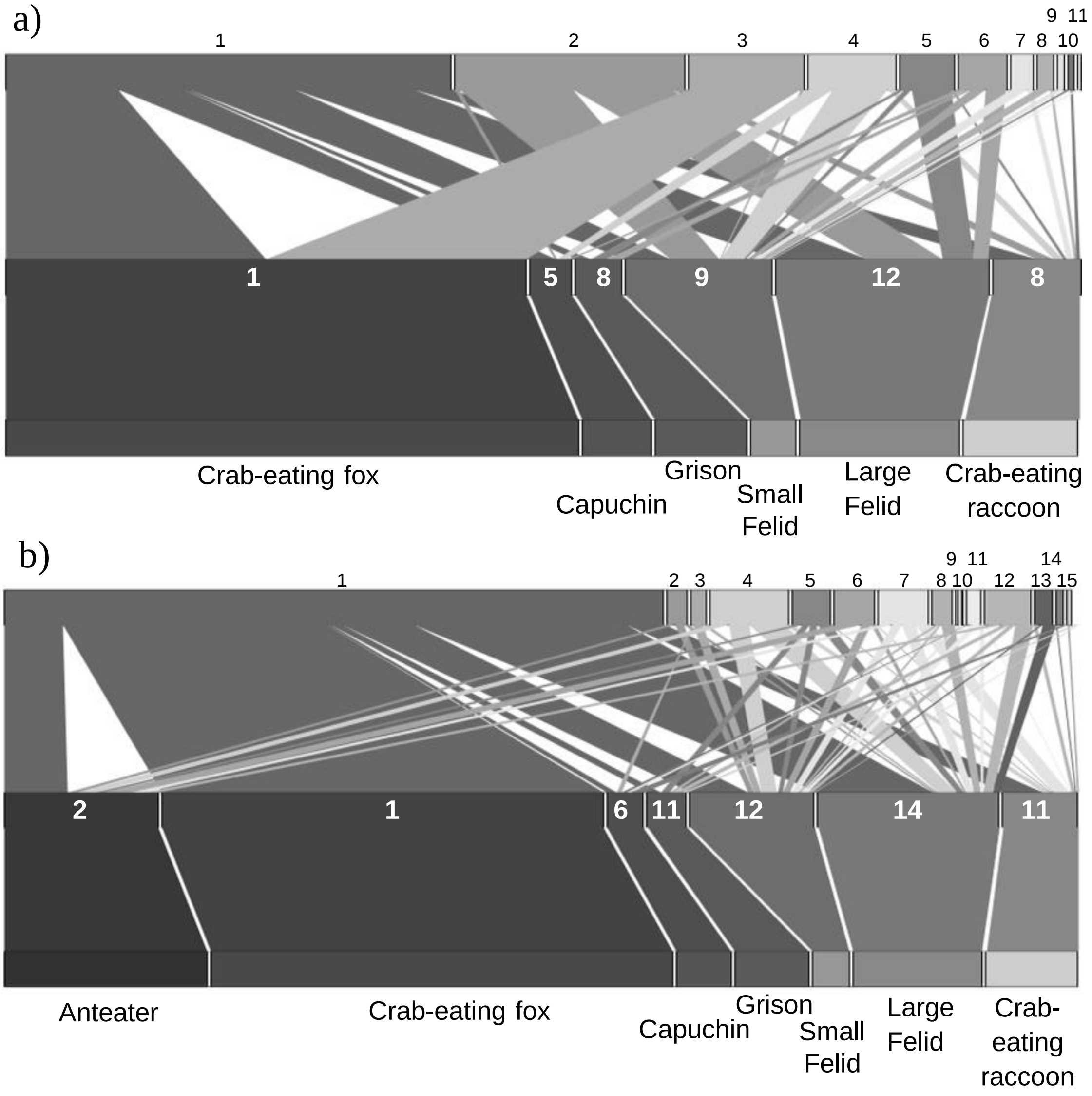

Figure 4.1: a) Dung beetle breeding interaction network b) Dung beetle feeding interaction network. Networks depict the dung beetle - dung - mammal interactions based on relative mammal abundance. Bottom level: relative mammal species abundance; mid level: dung volume produced per day per mammal species, numbers represent number of samples of each dung type; top level: proportional abundance of dung beetle species. Connecting bars represent the proportional frequency with which each dung beetle species utilizes the dung. 1) *Dichotomius sericeus*, 2) *Phanaeus splendidulus*, 3) *Deltochilum furcatum*, 4) *Dichotomius mormon*, 5) *Canthidium sp. 1*, 6) *Onthophagus catharinensis*, 7) *Dichotomius quadrinodosus*, 8) *Coprophanaeus dardanus*, 9) *Deltochilum aff. irroratum*, 10) *Canthidium punctatostriatum*, 11) *Coprophanaeus saphirinus*, 12) *Coprophanaeus bellicosus*, 13) *Deltochilum morbillosum*, 14) *Dichotomius fissus*, 15) *Canthon smaragdulus*.

significantly different from the null model expectation (Table S5). The metrics for the feeding network subsampled to the same number of beetles as the breeding network revealed significant differences in nestedness (p=0.002), H2' (p=0.001) and linkage density (p=0.001), all of which were larger in the feeding network.

Dung beetle biomass increased significantly with dung volume ($F_{1,47}$=14.43, R^2=0.22, p=0.00042), and the fitted regression was used to calculate maximum biomass of dung beetles attracted to each dung type in the equation for Iij (see Methods). There was a small, but significant, effect of the trap type - dung bait interaction on dung beetle species composition ($F_{16,161}$ =1.85, R^2=0.16, p=0.001): the dung beetle species composition captured in bag traps overlapped but was distinct from the composition found in pitfall traps (Figure D3). We therefore pooled the bag and pitfall trap data for simulations of mammal species extinction scenarios.

Extinction scenarios

The effects of mammal extinctions differed among scenarios and for each measure of the dung beetle community (Figure 4.2). The mammal extinction scenarios based on local mammal status, dung volume, and body mass all showed higher predicted losses of dung beetle abundance, biomass, and species richness than to the random extinction scenarios. The extinction scenario based on local mammal status showed a greater range of predicted effects on dung beetle abundance, biomass, and species richness from the third species extinction onwards. This can be accounted for by the "low risk" status of four mammal species, which were removed at random following removal of the higher-risk species (see Table 4.1).

Extinction due to mammal rarity, as based on the mammal survey data collected in this study, resulted in declines in dung beetle abundance, biomass, and species richness that were within the confidence intervals of the random extinction scenarios. However, extinction scenarios based on mammal body mass and dung volume resulted in dung beetle average biomass that fell below the 95% quantile of the random mammal species, whereas the extinction scenarios based on mammal rarity and local mammal status resulted in average dung beetle biomass within the confidence intervals found in the random extinction scenarios.

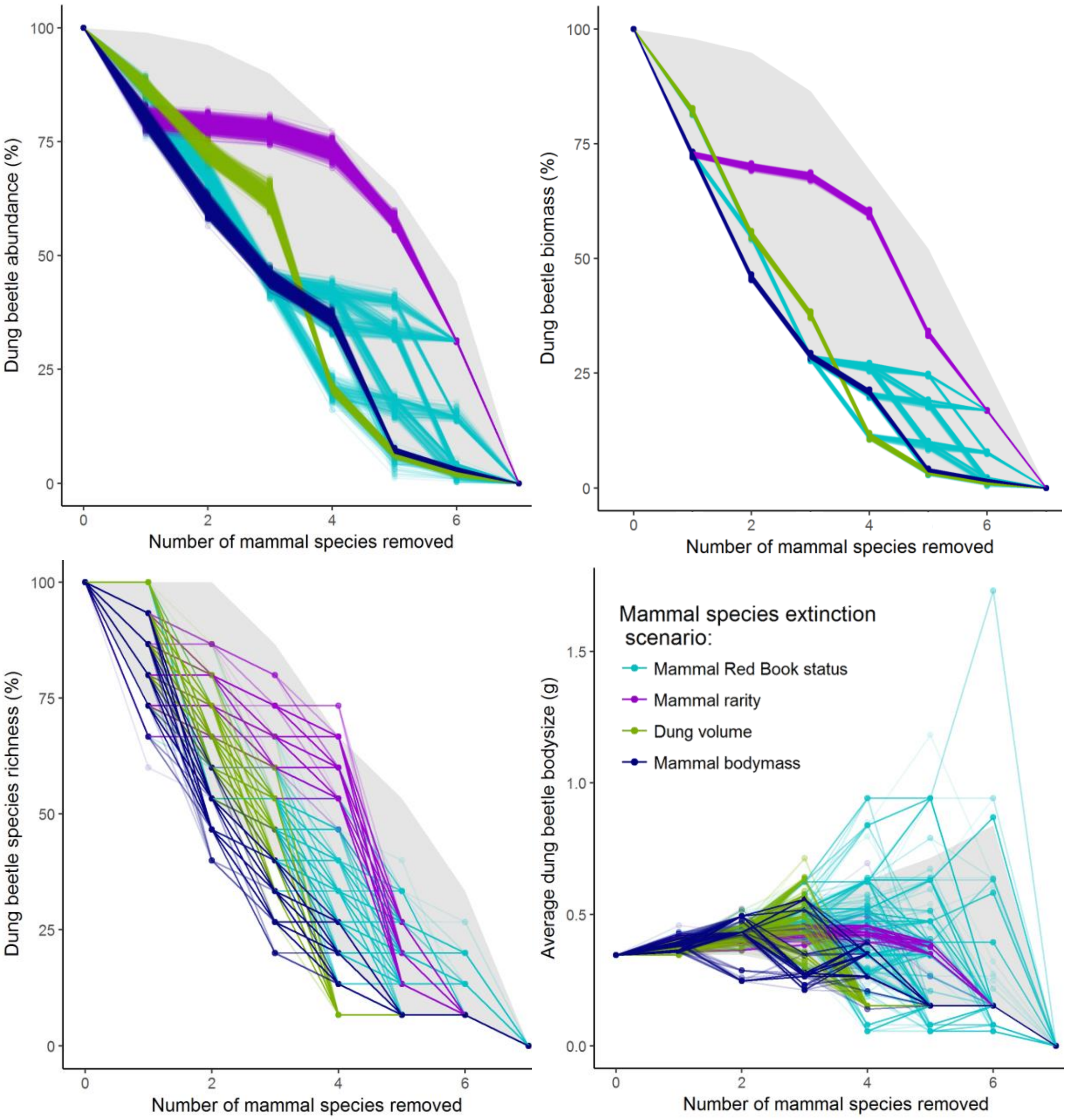

Figure 4.2: Mammal species extinction scenarios (1000 iterations per scenario) plotted against dung beetle population metrics of abundance, biomass, species richness (as a percentage of the intact community), and average dung beetle body size (g). Gray areas represent the 95% quantiles produced from the 1000 random mammal species extinction scenarios. See Methods for explanation of extinction scenarios.

Discussion

Structure and specialization of dung beetle-mammal networks

We present the first documented dung beetle - mammal networks that quantify dung beetle interactions based on mammal dung types. By using a range of dung sources of native mammal species of the Atlantic Forest tested at realistic sizes, the interaction networks display the realistic magnitude of interactions between dung beetles and mammals, in addition to separating the functional interactions of dung beetles into feeding and breeding networks. Moreover, quantifying the strength of interactions between mammals and dung beetles allows specialization within this network to be measured more robustly on a community-wide basis, rather than on a species-by-species basis (Ings *et al.* 2009). Both the feeding and breeding interaction network were characterized by high nestedness, consistent with other commensalist interaction networks e.g. for epiphytes and their host trees (Burns & Zotz 2010; Piazzon, Larrinaga & Santamaría 2011; Sayago *et al.* 2013). A highly-nested dung beetle - mammal dung network is likely to be formed by a set of common dung beetle species interacting with many dung types, and where rarer species feed on a subset of these dung types.

Realistic dung sizes were used in both the feeding and breeding networks to check for species specialization that might have been undetected in previous studies, which often use non-native dung types (e.g. human, pig) and/or unrealistic dung sizes (Enari, Koike & Sakamaki 2011; Whipple & Hoback 2012). The bag traps enabled the quantification of a breeding interaction network (for tunneling species) that represents the patterns of dung beetle species interactions within the process of dung removal. Both networks showed community-wide generalism. While some rare dung beetle species were found to feed on only one dung type, this may be a consequence of small sample sizes for these species. The structure of the feeding and breeding networks is therefore consistent with the ecological theory that the majority of dung beetle species will show generalist feeding behaviour in order to utilise patchily distributed and ephemeral dung resources (Hanski & Cambefort 1991). Although specialist feeders do exist (Larsen *et al.* 2006), none were reliably identified in this study. It is possible that the defaunated state of the forest has already resulted in selective local extinction of any trophic specialist dung beetle species.

Differences in dung preference for breeding and feeding could be driven by increased resource selectivity for the formation of brood balls where dung quality is of high importance (Shafiei *et al.* 2001; Moczek & Nijhout 2004; Arellano *et al.* 2015). This is relevant for the construction of interaction networks: by burying dung, rather than just feeding on the liquid component, the breeding networks represent the ecosystem function contributions of dung beetles to a greater extent than feeding networks. This is analogous to pollination networks, which can identify ecosystem functioning in plant-pollinator systems more reliably than visitation networks (King *et al.* 2013; Popic, Wardle & Davila 2013), and help predict functional consequences of species extinctions (Anderson *et al.* 2011). However, the feeding network had higher specialization and lower connectance than the breeding network, when comparing networks of equal size. Comparison of the fully-sampled feeding network revealed very similar structure to the breeding network, with the same specialization and connectance. The dung beetle community of the breeding network overlapped with the feeding network which suggests that more dung beetle species choose to feed than breed on any dung type. This suggests that standardized pitfall trapping approaches to gathering data on dung beetle species dung preferences can also reliably identify the functional interactions of dung beetles. However, using bag traps can reveal realistic numbers of dung beetles breeding in a dung source, unlike pitfall traps (Arellano 2016), and so may be useful when linking dung beetle communities to ecosystem functioning measures. In both networks, the number of interactions documented between resources and dung beetle species increased with sample size (i.e. the number of individuals of a species that were recorded), again indicating a highly generalist feeding ability.

Consequences of mammal species extinctions for dung beetles

Mammal extinction scenarios based on total dung volume available in the system, the local extinction status of the mammal species, and mammal body mass resulted in patterns of secondary extinctions in dung beetles where abundance, species richness, and total biomass declined more rapidly than the majority of random extinction scenarios. This suggests that the extinction of mammals will have severe impacts on dung beetles in this system, despite the model accounting for their trophic flexibility (Hanski & Cambefort 1991). For two of the scenarios, dung volume and mammal body mass, mammal extinction resulted in greater declines in individual dung beetle biomass than the random extinction scenarios. As the total biomass of dung beetles is closely related to dung removal (Nichols *et al.* 2016), these extinction scenarios indicate the potential for the loss of the associated ecosystem functions provided by dung beetles, such as declines in seed dispersal (Culot *et al.* 2015), seed burial (Lugon *et al.* 2017), and seed germination (Lawson, Mann & Lewis 2012) at rates higher than predicted for random extinction scenarios. As mammal body size is closely correlated with dung size (Blueweiss *et al.* 1978), the extinction scenario based on mammal body size represents the community-level effect on the dung beetle population of loss of dung source by size. Both the abundance and size of dung beetles decrease with decreasing bait sizes (Peck & Howden 1984; Andresen 2002b), trends that were also found in our analysis. A reduction in the average body size of beetles would reduce the amount of dung buried per beetle and could further reduce the potential for complementarity in dung removal between dung beetle functional guilds (Slade *et al.* 2007).

The mammal extinction scenario based on rarity as detected in this study did not result in losses in dung beetle populations that differed from those observed under a scenario of random mammal species extinction. This suggests that the dung of less common species may not represent a critical contribution to maintaining dung beetle populations. The defaunated ecosystem in the study area lacked key Atlantic forest mammal species such as the South Ameican tapir (Tapirus terrestris) and white lipped peccary (*Sus pecari*), and primate species were apparently rare, a common scenario in many degraded neotropical forests (Redford 1992; Wilkie *et al.* 2011; Galetti, Bovendorp & Guevara 2015). This suggests that the dung profile within the study sites may have already shifted away from large moist defecations to smaller pellets (Nichols *et al.* 2009), and a loss of many large herbivores and frugivores. Thus, functional interactions may have already been lost from the observed networks (Harvey *et al.* 2017), and dung beetle species may have already changed their feeding preferences to other dung sources, whilst specialist dung beetle species may have already been lost.

Assumptions and uncertianties

The dung used for this study came from animals fed diets which may not be realistic for wild animals, which could have impacted the attractiveness of dung to dung beetles (Edwards 1991; Bogoni & Hernández 2014). However, the generally broad dietary preference detected in this study suggests minor changes in consistency, odor or nutritional quality of dung would not have had great effects on the dung beetle composition detected. The networks represented here consider dung beetles attracted to fecal material. We note that carrion, fungi, and rotting fruit are also important food sources for some dung beetle species (Hill 1996; Halffter & Halffter 2009). In addition, the displayed interaction network is a case study and not a systematic analysis of the dung beetle - mammal interaction network in the Atlantic Forest, and repeated sampling would be needed to elucidate the variation in network structure over time or environmental gradients (Tylianakis & Morris 2017).

The species extinction scenarios displayed here represent a static system without the potential for mammal species populations to vary in response to the modified community structure. The loss of large-bodied mammal species could result in population increases in smaller mammal species and a subsequent compensation in dung availability (Wright 2003; Nichols *et al.* 2009). This prevent declines in dung beetle populations by buffering dung beetles against the loss of mammal species, although the extent to which changes in dung composition effects reproductive success is still unknown (Holter 2016). We have also assumed that resource use switching in feeding or breeding resources will not have fitness consequences in the dung beetle species. However, the effects of feeding on less suitable dung sources could manifest through reduced body size in future generations, or reduced fecundity (Gittings & Giller 1998; Moczek 1998; Arellano *et al.* 2015).

Conclusions

By developing the first quantitative mammal - dung beetle networks, we have addressed several important knowledge gaps. In particular, we contribute to the understanding of how interactions in networks involving mammals and secondary insect seed dispersers are structured and may respond to extinctions of interactions. Crucially, the dung beetle - mammal networks presented here demonstrate the utility of including quantitative information on species specific interactions, which can enable the exploration of alternative functional interactions under differing realistic extinction scenarios. There was no evidence of higher selectivity in the breeding network compared to the feeding network, and both networks showed a similar structure to other commensalist systems that have been previously quantified. However, despite this low trophic specialism, simulations of mammal extinction scenarios suggest that dung beetle populations will be strongly negatively impacted by mammal extinctions, with the potential for cascading consequences for ecosystem functioning.

5

Mammals drive the distributions of dung beetle species in tropical rainforests

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Journal of Animal Ecology

Contents

Author contributions

EMS, MS and OW conceived the idea for the study. EMS collected dung beetle data, OW and ND collected mammal data. OW and ND carried out mammal occupancy analyses. EHR developed the statistical approach and carried out the data analysis and wrote the manuscript, with feedback from EMS, MS, OW and ND.

Abstract

The effects of environmental change on mammal species communities can result in large scale alterations to ecosystem structure by impacting upon dependent species such as dung beetles. Although the majority of dung beetle species rely on mammal dung for feeding and breeding, high resolution mammal data is rarely included in analyses of dung beetle species distributions. As a result, the mechanisms behind dung beetle distributions are poorly understood. Here we apply a joint species distribution modelling approach to understand the importance and role of mammal species composition, abiotic factors and forest structure in determining dung beetle species distribution in Malaysian Borneo. We also reveal patterns of co-occurrence between dung beetle and mammal species across a land use gradient.

We found that mammal feeding group biomass explained >50% of the variation in dung beetle species occurrence. Across all dung beetle species assessed, there was a negative association with increasing carnivore biomass and air temperature. Dung beetle species showed idiosyncratic responses to the other explanatory variables, including soil moisture and temperature, canopy density, as well as frugivore, herbivore, omnivore and insectivore biomass. Traits did not explain dung beetle species response to covariates. Most species exhibited declines in occupancy along the land use gradient, from old growth to logged forest to oil palm plantation, but some species of nocturnal and diurnal tunnellers increased in occurrence. These results indicate that traits are not always a reliable indicator of responses to environmental change, and suggest that a combination of environmental conditions, including mammal biomass, rather than forest structure itself, drives dung beetle species distributions. Dung beetle - mammal co-occurrence patterns revealed a higher proportion of positive associations for all mammal species in oil palm compared to old growth and logged forest. These results may be due to either the lower availability of suitable habitat in oil palm, or the increased importance of biotic associations driving distribution patterns in dung beetles in degraded landscapes. We present an improved understanding of the ways in which dung beetle distributions are influenced by both habitat conditions and mammal community composition.

Introduction

Anthropogenic habitat degradation and deforestation has resulted in major declines in biodiversity globally (Pereira, Navarro & Martins 2012). The direct effects of habitat change on species can have cascading effects through an ecosystem, triggering further biodiversity loss, and associated declines in ecosystem functions (Estes et al. 2011; Jorge *et al.* 2013). To minimise and prevent the effects of future environmental change, understanding how species respond to habitat modification and the knock-on effects on other species within an ecosystem is needed. These issues are particularly pertinent in tropical forests where human pressures are causing high rates of deforestation and modification in areas that possess some of the highest species richness globally (Kurten 2013).

Changes in mammal community structure and abundance can have large knock-on effects on dependent taxa, and therefore also on the functioning of ecosystems (Morris 2010; Estes *et al.* 2011; Valiente-Banuet *et al.* 2015). The consequences of defaunation can be large for associated arthropod species such as predaceous ants and beetles (Letourneau & Dyer 1998), and especially so for functionally important taxa such as insect herbivores (Spiller & Schoener 1994; McIntosh & Townsend 1996; Pace *et al.* 1999), and dung beetles (Nichols *et al.* 2009).

Most dung beetles (Coleoptera: Scarabaeinae) utilise mammal dung for feeding and breeding (Hanski & Cambefort 1991; Frank *et al.* 2017a), and by burying dung beneath the surface of the soil they contribute to a range of ecosystem functions (Nichols *et al.* 2008; Slade *et al.* 2017). Dung beetle species richness and abundance is thought to be negatively affected by habitat change in tropical ecosystems (see Nichols *et al.* 2007 for review), and there are associated declines in the ecosystem functions performed by dung beetles (Slade, Mann & Lewis 2011). Their reliance on dung suggests that mammal species composition is an important component in determining dung beetle species occurrence and distribution in space (Nichols *et al.* 2009). Dung beetles and mammals have been shown to spatially covary (Culot *et al.* 2013; Nichols *et al.* 2016; Bogoni *et al.* 2016b), but there are no analyses that model both environmental data and high resolution mammal data together. Dung beetle community change is therefore commonly attributed to habitat filtering, overlooking the potential importance of mammal species composition in determining beetle distribution (Nichols *et al.* 2009). Incorporating estimates of mammal composition will therefore improve our understanding of the effects of habitat and abiotic factors on dung beetle distribution. By extension, this will improve the capacity to assess the effects of different kinds of habitat change on dung beetle populations.

Directly identifying dung beetle - dung interactions through experimentation is restricting as it can only be used to identify interactions for small numbers of species at local scales (Bogoni & Hernández 2014; Frank *et al.* 2017b). Inferring ecological interactions based on non-random co-occurrences of species using spatially explicit data has become a commonly used method (Gotelli & McCabe 2002; Ulrich & J. Gotelli 2007; Ovaskainen, Hottola & Shtonen 2010; Götzenberger *et al.* 2012; Wisz *et al.* 2013). Commensalistic interactions, such as dung feeding by dung beetles can be identified this way (Sander, Wootton & Allesina 2017; Freilich *et al.* 2018), although there are few examples in the literature (Morales-Castilla, Matias & Gravel 2015 but see Sayago *et al.* 2013; Nichols *et al.* 2016).

By grouping species with similar characteristics, functional traits can be useful to infer mechanistic causes of species-specific responses to environmental change (Kohli, Terry & Rowe 2018). Dung beetles are clearly separated into functional guilds based on their nesting strategy, activity period, and body size (Gardner *et al.* 2007; Filgueiras, Iannuzzi & Leal 2011), and show trait-dependent responses to land use change (Larsen, Lopera & Forsyth 2008; Nichols *et al.* 2013; Gómez-Cifuentes *et al.* 2017). Species traits could serve a useful framework for understanding dung beetle responses to environmental change.

Here we apply a joint species distribution modelling approach to understand the importance of mammals influencing the distribution of dung beetle species. We used data on dung beetle and mammal distributions, forest structure and abiotic factors to address four main questions: 1) How does dung beetle species composition change over a land use gradient? 2) How important are mammal feeding guild biomass, forest composition and abiotic factors in determining dung beetle species distribution? 3) Do species traits serve as a useful framework for assessing dung beetle responses to the environment and mammal composition? 4) How do dung beetle species and mammal feeding guilds co-occur, and how do these associations change across a land use gradient?

Methods

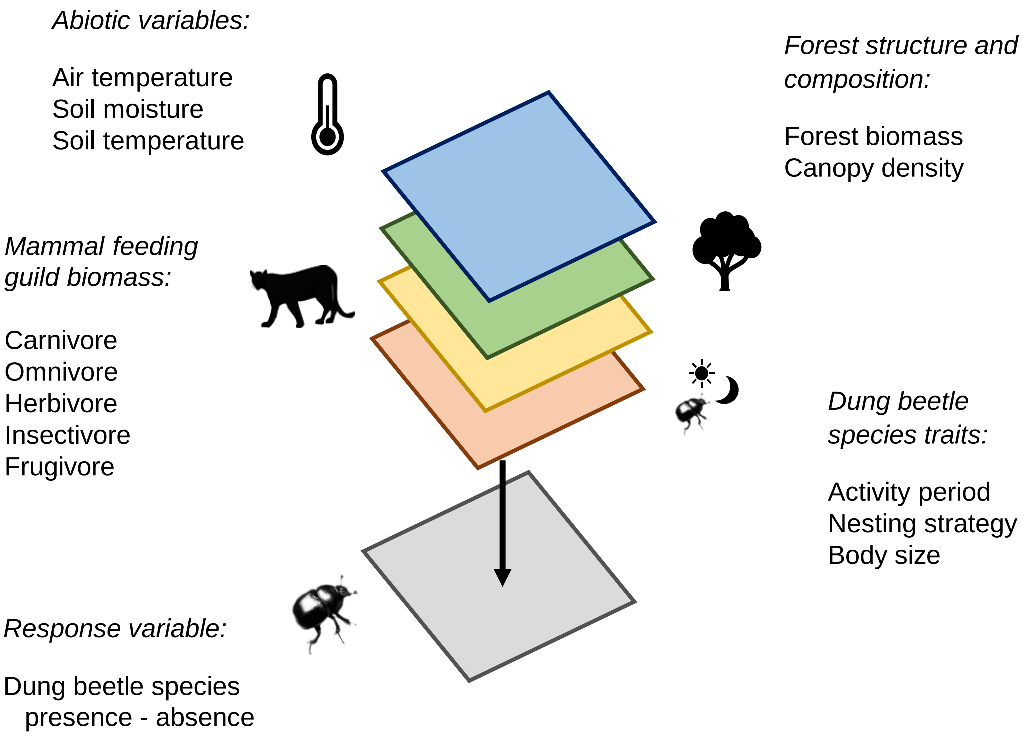

Figure 5.1: Model schematic: abiotic factors, forest composition, mammal feeding guild biomass, and dung beetle functional traits were included as explanatory variables in the joint species distribution model to predict dung beetle species occurrence. Model fitted using spatially co-occurring data sets for each explanatory variable across 120 points.

Study site

Data were collected within the Stability of Altered Forest Ecosystems project (SAFE; www.safeproject.net), Sabah (Malaysian Borneo; N'4.58 E'117, Figures E1&2). This area comprises undisturbed and repeatedly-logged lowland dipterocarp rainforest, and oil palm plantations in which palms were planted between 1998

	Habitat	2011	2012	2013	2014	2015	2016	Total
Dung beetles	**Old growth**	22				6		**28**
	Logged forest	56				34		**90**
	Oil palm	14				22		**36**
Mammals	**Old growth**	18	31	44	19			**112**
	Logged forest	144	162	11	72	3	24	**416**
	Oil palm			37	62			**99**

Table 5.1: Number of sampling points for dung beetle and mammals. Dung beetle sampling points represent one human dung baited pitfall trap, with sampling carried out in two years (2011 and 2015). Each mammal sampling point represent multiple (n=1-3) of passive infrared camera trap within 85m of a dung baited pitfall trap.

and 2011 (see Ewers, Didham & Fahrig 2011 for further details). As data were collected where mammal and dung beetle surveys coincided, sampling was unequal in each land use type and block.

Dung beetle data

Dung beetle sampling was carried out at over the SAFE design which are 178m apart, organised into blocks 560m apart (Figure E1). Data were collected from 154 points across 12 blocks in the study area (3 old growth, 3 oil palm, 6 logged forest) (Table 5.1). Dung beetles were collected using pitfall traps, with 25g of human dung bait suspended over a 250ml cup buried flush with the soil surface, and half filled with a water, detergent, and salt mixture. Traps were protected with a rain cover and left for 48 hours before collection. Trapping took place in two sampling periods, in Jan-Feb of both 2011 and 2015 (Table 5.1). Specimens were stored in 90% alcohol and identified using (Boucomont 1914; Balthasar 1963; Ochi, Kon & Kikuta 1996), and reference collections from the Oxford University Museum of Natural History. Voucher collections are deposited at the Forest Research Centre in Sandakan, Sabah and the Borneensis collections at Universiti Malaysia Sabah. Dung beetle species traits of breeding guild, activity period (diurnal/nocturnal), and body mass were compiled for each species (Slade *et al.* 2011) (Table E1). Species with <5 occurrences were excluded from further analysis.

Mammal data

Mammals were sampled using passive infrared camera traps (Reconyx HC500). From 2011 -2014 camera trapping methods followed Wearn *et al.* (2013), with cameras placed randomly inside 46 plots, clustered into 11 blocks across the SAFE land use gradient (mean effort per camera location = 49 trap nights). From 2014 - 2016 camera trapping methods followed Deere *et al.* (2018) with cameras separated by a mean distance of 1.4 km across the SAFE landscape (mean effort per camera location = 42 trap nights).

Mammal species relative abundance was estimated using a hierarchical multi-species occupancy model using the modelling approach described in Wearn *et al.* (2017). This uses replicated sampling in space and time to correct for imperfect detection (see Appendix of Wearn 2017 for further details). The model was used to produce an estimate of 'realized' local abundance (i.e. conditional on the data) for each sampling point, which is the number of individuals estimated to be using it. Note that this relative abundance measure accounts for detectability differences across space, according to land-use and microhabitat, but it is not equivalent to density. In particular, it is likely sensitive to the home-range size of species, since species with larger home-ranges will use a larger number of sampling points (Efford & Dawson 2012).

Mammal local abundance estimates were extracted for camera trap locations within 85m of the dung beetle pitfall traps. This distance is considered biologically realistic for dung beetle movement (Silva & Hernández 2015), and would therefore be indicative of dung beetle feeding activity on mammal dung within this area. This gave a total of 627 camera trap locations that were used for subsequent analysis with associated dung beetle data (Table 5.1).

Using the mammal relative abundance estimates, we calculated a proxy for dung availability. We converted local abundance into local biomass for each mammal species using species specific body weights (Jones *et al.* 2009; Wearn *et al.* 2017). Then we summed across species in each mammal feeding guild (carnivore, herbivore, omnivore, frugivore and insectivore) to give a mammal feeding guild biomass (Table E2). Mammal data were grouped so there were no more than two years between collection of mammal and dung beetle data (Table 5.1).

Environmental covariates

Environment variables were chosen that have previously been identified as affecting dung beetle species presence and distribution, including temperature (Verdú, Arellano & Numa 2006; Arellano *et al.* 2017), soil moisture (Barkhouse & Ridsdill-Smith 1986; Sowig 1995; De Farias *et al.* 2015) and soil temperature (Navarrete & Halffter 2008). Abiotic variables were collected at each dung beetle pitfall trap in 2011-12 (Hardwick *et al.* 2015). Forest structure and composition affects dung beetle species presence and abundance (e.g. França *et al.* 2017), so forest biomass and canopy density were extracted from LiDAR data collected in September/October 2014 at a resolution of 100m. Forest biomass was calculated from models of canopy height using methods from Jucker *et al.* (2017) in tonnes per ha. Canopy density, calculated using Moran's I (Tiefelsdorf & Boots 1995), represents the degree of aggregation in canopy heights in space, with values close to zero representing strong clumping of forest such as large gaps or forest edges.

Hierarchial joint species distribution modelling

In order to identify dung beetle species' responses to environmental variables, we analysed dung beetle species distribution using a hierarchical joint species distribution model (Ovaskainen *et al.* 2017) which allows modelling the distribution of multiple species at once (Ulrich & Gotelli 2013; D'Amen *et al.* 2018). This approach accounts for environmental covariates and random variation in species occurrence over space for multiple species (Warton, Wright & Wang 2012; Bush *et al.* 2017; Ovaskainen *et al.* 2017). The approach has greater predictive power than a collection of single species distribution models and allows greater inference for rare species (Ovaskainen & Soininen 2011).

We converted the dung beetle species abundance to presence-absence data and modelled it using a Bernoulli distribution and probit link function. Explanatory variables included: air temperature, soil temperature, soil moisture, canopy density, total forest biomass, and the biomass of the five mammal feeding guild groups. All variables were centred and scaled by one standard deviation. To assess the extent of correlation between the explanatory variables included in the model, variance inflation factors were calculated for each pair of variables using the *fmsb* package in R (Nakazawa & Nakazawa 2018). The functional traits of dung relocation strategy and activity period were included as categorical variables, and the log transformed body mass of each dung beetle species were also added as explanatory variables. Block and year were included as random factors to account for spatial autocorrelation based on the hierarchical structure of the SAFE project sampling design, and temporal autocorrelation in the data.

The model was fit using the *HMSC* package (Blanchet 2017) for R version 3.4 (R Core Team 2017) using the default prior distributions for the community level parameters as described in the supporting information of Ovaskainen *et al.* 2017. We ran the model for 50,000 iterations with 40,200 discarded. The robustness of the model was tested by comparing the estimates of species-specific parameters between the full model and with each explanatory term removed one at a time.

Variation partitioning

We used Tjur's R^2, which calculates the predictive power of a model, to partition the amount of variation explained by the model based on environmental covariates, mammal biomass, dung beetle species traits, and the random factors to explain dung beetle species distribution (Tjur 2009; supplementary material of Ovaskainen *et al.* 2017).

Species richness & composition across land use types

The parameterised model was used to predict the mean dung beetle species richness using the average environmental conditions in each of the three land use types. The mean species richness was then the model prediction of the number of species expected, which was the sum of the species-specific occurrence probabilities for the average environmental conditions in old growth, logged forest and oil palm. We calculated the similarity of dung beetle assemblages in the oil palm and logged forest compared to the old growth forest by calculating the correlation between the model predicted log transformed species-specific occurrence probabilities in each land use type (Ovaskainen & Soininen 2011). To identify whether dung beetle species that share functional traits show common responses to land use change, we calculated the change in species occurrence probability between land use types.

Species- and trait- environment relationships

The model estimates regression coefficients for each dung beetle species' response to each explanatory variable. This is also grouped at the level of the species trait, to estimate the amount of variation in dung beetle species response to each of the environmental variables that can be accounted for by traits. To visualise the multidimensional species-specific regression coefficients, a principal component analysis (PCA) was fit to identify whether dung beetle species with shared traits showed similar responses across all environmental variables.

Mammal - dung beetle species co-occurence

To investigate associations between dung beetle and mammal species within each land use type, we used models to calculate the probability that each pair of species would co-occur less or more often than expected based on their observed frequency (Veech 2013). Species pairwise associations can identify species aggregation (representative of a positive biotic interaction or also shared environmental requirements) and segregation (indicative of negative biotic interactions or different environmental niches) (Peres-Neto *et al.* 2001; Ulrich & J. Gotelli 2007; Ulrich & Gotelli 2013).

As dung beetles are considered as generalist feeders, but often show preference towards certain food sources, it is possible to consider positive associations between dung beetle and mammal species as indicative of shared habitat preference which could also result in a feeding interaction, irrespective of the mechanism behind their co-occurrence. Data for the 62 mammal species detected by the camera traps were included in the analysis. Mean incidence probabilities for the mammal species, and presence- absence data from the dung beetle species were used to classify interactions as significantly positive or negative separately for the species found in each of the three land use types. Analyses were carried out using the co-occur (Griffith, Veech & Marsh 2016) package for R.

Results

We recorded 7693 dung beetle individuals of 61 species across the sampling plots. This corresponded to 43 dung beetle species with five or more occurrences that were included in the model. Mammal trophic guild biomass, abiotic variables, and forest structure varied across the land use types (Table E3), but there were no strong correlations between the explanatory variables as variance inflation factors were low for all pairs of explanatory variables. Re-running the model with each variable removed had minor effects on the estimation of parameters, and as such the full model was deemed robust.

Overall the joint species distribution model explained dung beetle species distribution a third better than random (Tjurs $R^2 = 0.33$). The biomass of the five mammal feeding groups combined was the most important explanatory variable, which accounted for 53% of the explained variation in dung beetle species distribution, followed by forest structure (19.3%) and abiotic factors (14.3%) (Figure 5.2). Recent studies have called for repeated sampling of dung beetles to account for temporal variation in species distribution estimates (Jiménez-Valverde, Lobo & Hortal 2008; Beiroz *et al.* 2017), however we found low variability between sampling years (4.2%). The random factors of block accounted for the remaining 9.3% of variation explained by the model.

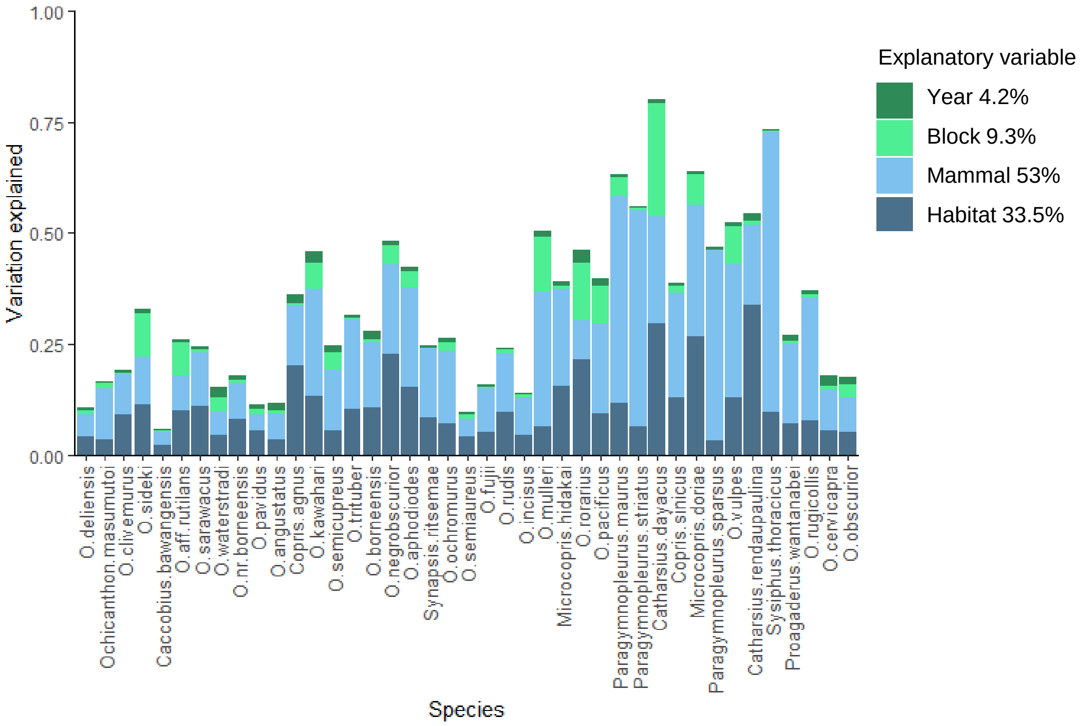

Figure 5.2: Variation in occurrence explained by the joint species distribution model for each dung beetle species. Colour indicates partitioning between four main explanatory variables, percentages represent average amount of variation explained by the model across all species. Species are ordered from low to high abundance.

Land use change

Predictions based on the environmental variables of each land use type showed a decrease in dung beetle species richness across the land use gradient from old growth forest to logged forest to oil palm (Figure 5.3 a), with logged forest showing an assemblage that contained less than half the taxa from old growth forest, and oil palm plantations supporting a markedly different assemblage from old growth forest (Figure 5.3 b). All three species trait groups showed declines in occurrence probability from old growth into logged forest and oil palm. Diurnal rolling species all declined in occurrence in degraded lands, whereas some nocturnal and diurnal tunnelling species showed significant increases in occurrence probability in logged forest and oil palm (Figure 5.4).

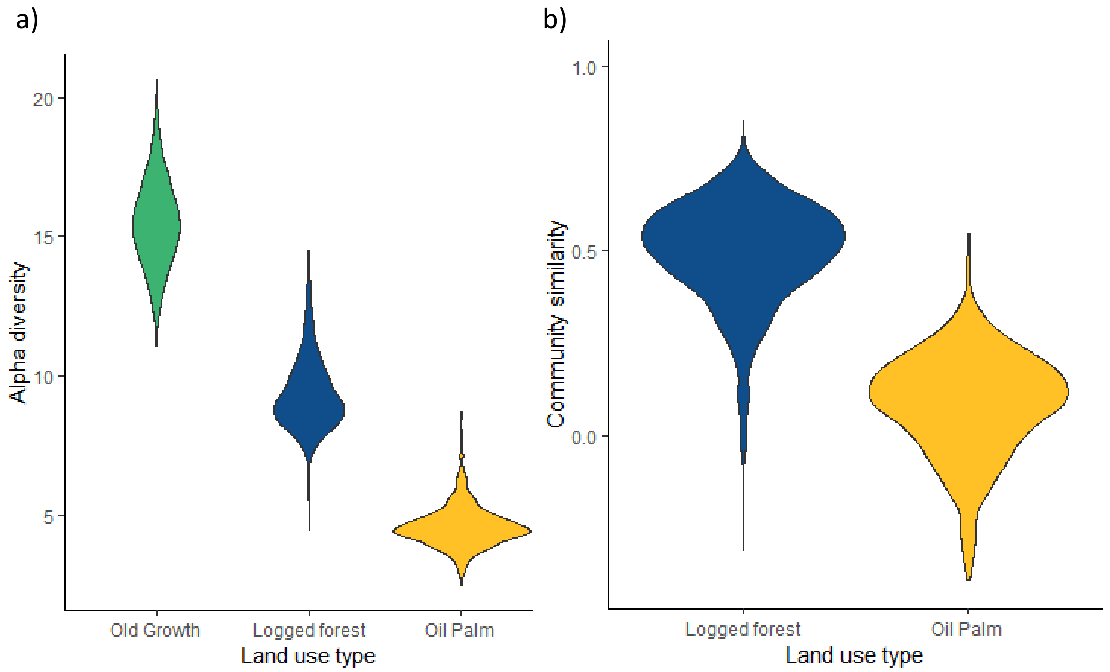

Figure 5.3: a) Dung beetle species richness in each of three land use types in the SAFE landscape. Species richness per land use type calculated from model estimate of the mean number of species per point. Data generated through model predictions of dung beetle species occurrence in the environmental conditions in each of the points, b) Dung beetle species composition similarity with reference to average old growth forest dung beetle species composition, based on predictions of mean species richness from (a).

Dung beetle species-specific responses

Across all dung beetle species there was a negative association between dung beetle occurrence and carnivore biomass, and also a negative association between beetle occurrence and increasing air temperature (Figure 5.5). Several dung beetle species showed significant positive associations toward frugivore biomass and forest biomass, although the trend across all species was not significant. Individual dung beetle species showed positive associations to increasing forest biomass, and soil temperature, and several were significantly negatively associated to increasing forest biomass, soil moisture, soil temperature, and air temperature (Figure 5.5). Model parameters for regression coefficients with species-specific identities are presented in the supplementary material (Figure E4).

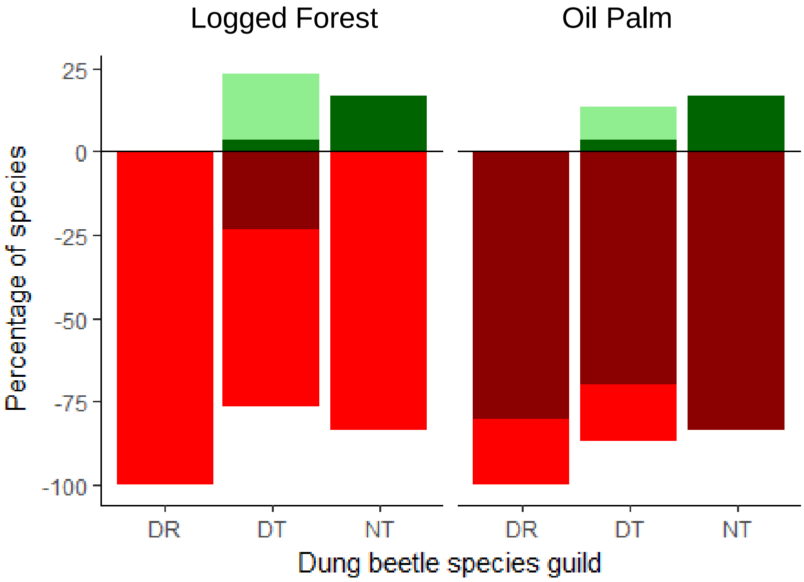

Figure 5.4: Model predictions for dung beetle species change in occurrence from old growth to logged forest, and oil palm plantation. Dark green represents a significant increase, pale green represents a non-significant increase, red represents a non-significant decrease, and dark red represents a significant decrease (all at the 95% confidence level, calculated from posterior distributions). DR= diurnal roller, DT = diurnal tunneller, NT = nocturnal tunneller.

Dung beetle trait level responses

Of the variation in dung beetle species response to the explanatory variables, only 9.6% could be attributed to shared species traits. Dung beetle species with shared traits showed large variation in their response to the explanatory variables, none of which were significant (Figure E3). For diurnal rolling dung beetles, there was a non-significant positive association between and frugivore dung, and non-significant negative associations with herbivore dung and carnivore dung. Nocturnal tunnellers showed a negative association with temperature and forest biomass. There were also no significant associations between dung beetle species body size and the explanatory variables. Visualising the mean dung beetle species specific regression coefficients as axes of a principal component analysis showed that beetle species did show similar responses when considered across all environmental variables, but this was not strongly conserved within each trait group (Figure 5.6).

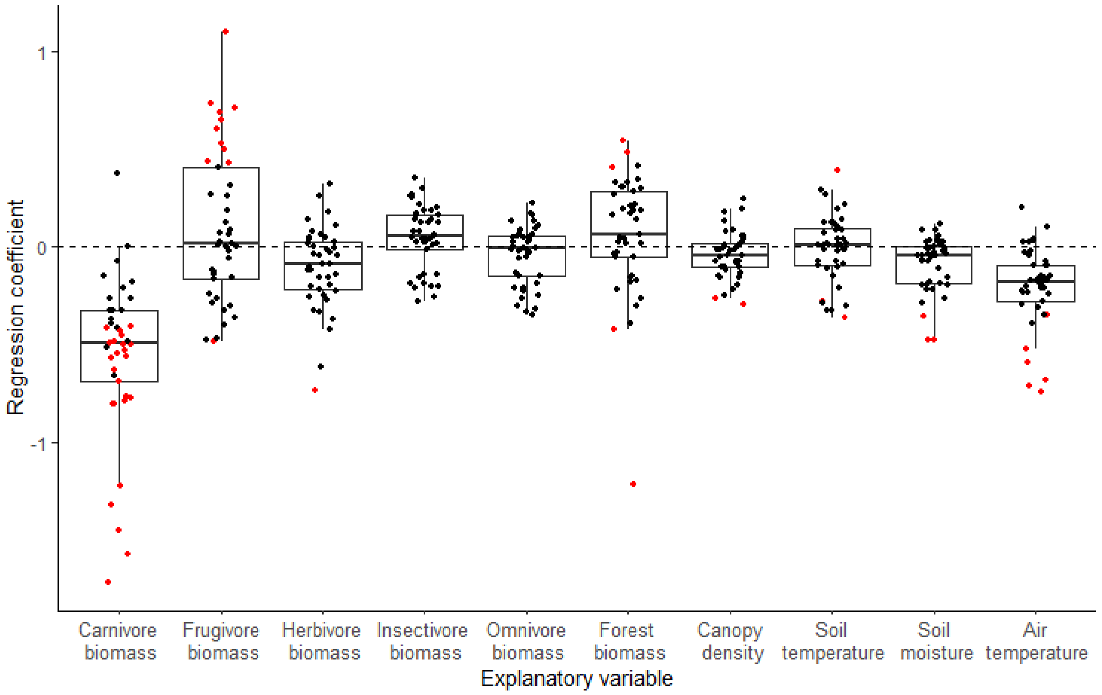

Figure 5.5: Mean parameter estimates for each explanatory variable per dung beetle species. Red: statistically significant at the 95% level, black: non-significant at the 95% level, calculated from posterior distributions. Box plots represents median and quantiles of response across all dung beetle species.

Dung beetle - mammal co-occurence

The total number of significantly associated species pairs was highest in logged forest and lowest in old growth (Figure 5.7 & Figures E5-E7). Of the non-random associations, positive associations were more common, and made up 13% of species pairs in old growth, 4.3% in logged forest and 40% in oil palm. There were few significant positive associations between dung beetle species and carnivorous mammal species in both old growth (n=1) and logged forest (n=2), but the association was far more common in oil palm (n=11). There were the most positive associations to frugivorous mammal species in both oil palm (n=15) and logged forest (n=17), and the most negative species pairs were between dung beetles and omnivorous mammal species in logged forest (n=29).

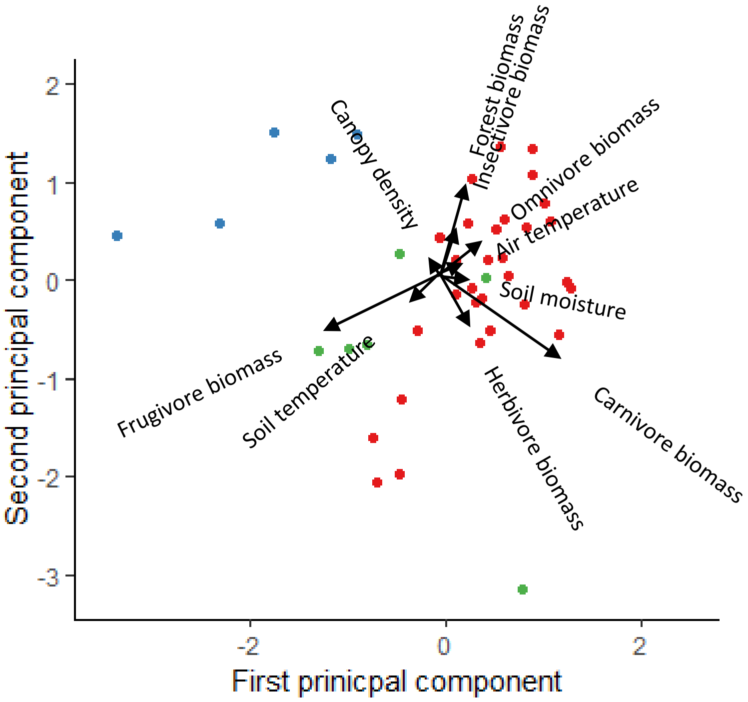

Figure 5.6: Ordination plot showing each dung beetle species as points along the first two axes of a principal component analysis, based on dung beetle species specific responses to environmental variables. Coloured by dung beetle trait: red= diurnal tunneller, blue = diurnal roller, green = nocturnal tunneller

Discussion

We found that including high resolution mammal data into models of dung beetle responses to land use change enabled the identification of the relative importance of habitat versus mammal trophic group biomass on dung beetle species distributions. We were also able to identify dung beetle species- and trait- level responses to these explanatory variables, providing insight into mechanistic explanations of dung beetle species distributions across a tropical land use gradient. We then identified how dung beetle species co-occur with mammal trophic feeding groups and how these associations change across the gradient.

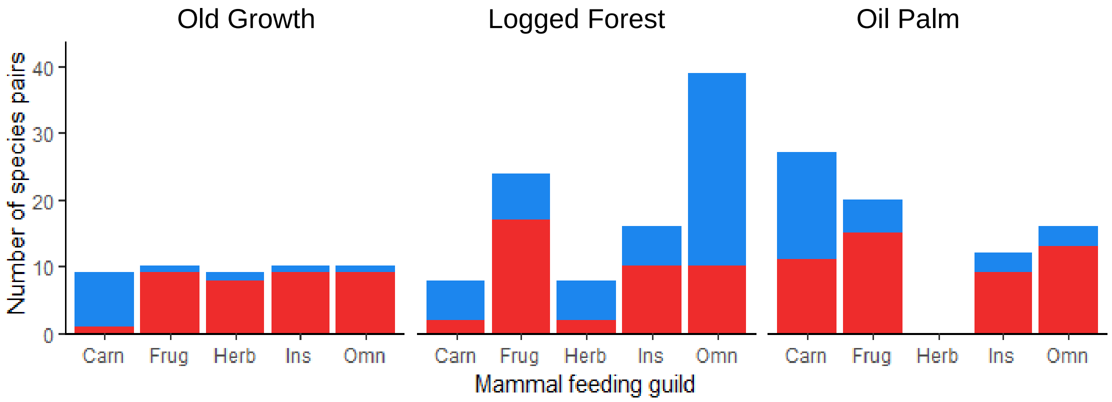

Figure 5.7: Number of observed species pairs between mammal and dung beetle species for each land use type. Red = significnat positive association, blue: significant negative assocation.

How important are mammal feeding guild biomass, abiotic factors and forest composition in influencing dung beetle species distribution?

Mammal biomass explained over half of the variation in dung beetle species distribution in the model. This suggests that the presence and type of mammalian dung available to dung beetles has a strong influence on their distributions. Many of the associations between dung beetle species and individual mammal trophic guilds were non-significant, which supports research that indicates generalist feeding for dung beetles (e.g. Frank *et al.* 2018). We identified a far larger role of mammal species composition in determining dung beetle species distribution than previous studies (Bogoni *et al.* 2016), which could be contributed to the use of composition and relative abundance measure for mammal distributions rather than species richness or a proxy such as defaunation for mammal presence.

Many dung beetle species were negatively associated with areas supporting relatively high carnivore biomass. Carnivore dung attracts fewer dung beetle species and individuals than other dung types (Bogoni & Hernández 2014), potentially due to its low fluid content (Holter 2016) or odour profile (Mansourian *et al.* 2016; Frank *et al.* 2017a). Several dung beetle species were positively associated with frugivore biomass, suggesting this represents an important feeding source for many

Scarabaeinae in South-East Asian, as well as in neotropical forests (see Andresen 2002; Jacobs *et al.* 2008; Culot *et al.* 2011). It is not possible to identify whether this trend is in fact caused by a confounding co-variate. For example the biomass of the other mammal feeding guilds may be negatively associated with carnivore biomass. The parameters estimated by the model were robust to removal of carnivore biomass which suggests this trend is not the case. However, identifying the role of alternative mammal feeding groups and habitat composition on dung beetle species distribution requires manipulative experiments to separate out these effects.

Across all dung beetle species, increasing air temperature was negatively associated with distribution. Thermoregulation is thought to be a key factor driving dung beetle species distributions (Lobo 2008; Verdú, Alba-Tercedor & Jiménez-Manrique 2012), and this finding provides support for this mechanistic explanation, however not all species were negatively associated with soil temperature and the covariate was not significant overall. Dung beetle species richness and abundance has previously been found to be highest in undisturbed forest (Nichols *et al.* 2007), and here we found an overall positive association with forest biomass, but across all species there was no strong negative association with the aggregation of the canopy. This suggests that a combination of environmental conditions, including mammal species relative abundance and biomass, rather than forest structure itself drives dung beetle species distributions.

In order to estimate dung beetle species response to the explanatory factors included in the model, we assume that species-environment associations are constant over the extent of their distribution and that there is no intraspecific variation in a species response to the environment. Yet, intra-specific variation in traits across land uses has been shown in dung beetles (Raine *et al.* 2018), which could manifest in variation in response to environmental conditions. In addition, confounding interactions between explanatory variables could affect the associations identified, so interpretation of effects should be made with caution.

How does dung beetle species composition change over a land use gradient?

The majority of dung beetle species declined in occurrence probability along the land use gradient, from old growth to logged forest and oil palm plantation. Previous work has found similar trends in dung beetle composition as land use intensifies in Malaysian Borneo (Edwards *et al.* 2011; Slade *et al.* 2011; Gray *et al.* 2014). However, this trend was not uniform across each of the dung beetle functional groups. Nocturnal tunnellers and some species of diurnal tunnellers showed significant increases in occupancy across the land use gradient. Previous work has suggested that larger dung beetles are negatively associated with temperature due to reduced thermal tolerance (Verdú *et al.* 2006), and that rolling dung beetles are absent from oil palm probably due to high soil temperature (Gray *et al.* 2014). However, in this study there were no strong environmental-trait associations, suggesting that changes in the composition of dung beetle communities is driven by a combination of environmental variables, rather than strong responses to a single characteristic of degraded habitat.

Do species traits determine dung beetle species' responses to the environment and mammal composition?

A trait-based approach can be used to reveal more informative species groups for responses to environmental change than single species alone, by grouping taxa that show similar responses to the environment and providing a mechanistic explanation for ecological trends (Legendre, Galzin & Harmelin-Vivien 1997; Brown *et al.* 2014; Oldén *et al.* 2014). However, in this system beetle traits explained less than 10% of the variation in their response to environmental variables, and there were no significant associations between any explanatory variable and any of the dung beetle species traits. These results suggest that traits are not always a reliable indicator of responses to individual environmental variables. This may be due to the idiosyncratic response of individual species to habitat change, or that we are missing some important traits, such as those associated with thermal tolerance (Verdú *et al.* 2012) or dispersal (Raine et al, 2018).

Dung beetle - mammal co-occurence

As the majority of dung beetles are considered to be indiscriminate feeders (Frank *et al.* 2018), it is possible to infer that co-occurrence between mammals and dung beetles is representative of a feeding interaction, irrespective of whether their aggregated distributions are a result of shared environmental conditions or directly a consequence of a biotic interaction. In this instance negative interactions can be interpreted as contrasting environmental niches between dung beetle and mammal species.

Here we found that the proportion of positive dung beetle - mammal co-occurrences were highest in oil palm, despite the total possible interactions being lowest in the land use type. There were also far more positive associations with carnivorous mammals in oil palm, relative to old growth and logged forest. This suggests that habitat conditions in oil palm plantations are conducive to mammal and dung beetle species co-occurrence, potentially as a result of the lower availability of suitable habitat. Alternatively, the role of biotic interactions may be a stronger determinant of species distributions in more degraded landscapes, resulting in the greater proportion of positive co-occurrences (Wearn *et al.* 2018). Across the mammal feeding groups, there were the most positive associations between dung beetles and frugivorous mammals in logged forest and oil palm. This suggests high habitat suitability for dung beetles in areas where frugivorous mammals are found and the potential role of frugivorous mammal dung as a key food source for dung beetles.

The impact of biotic associations on species distributions is still debated (Gotelli & Ulrich 2010; Wisz *et al.* 2013), yet there is more support for positive non-trophic interactions such as commensalistic interactions being represented as aggregations in space (Peres-Neto *et al.* 2001; Ulrich & J. Gotelli 2007; Ulrich & Gotelli 2013). More evidence is needed, through experimental work to demonstrate a commensalistic interaction between dung beetle and mammal species.

Applications

Dung beetles are frequently used as a performance indicator for forest condition due to their graded response to environmental change, combined with their abundance, and being time and cost efficient to survey (Gardner *et al.* 2008; Nichols & Gardner 2011). We present an improved understanding of the ways in which dung beetle species distributions are influenced by both habitat conditions and the mammal species composition of an area (Davis *et al.* 2001; McGeoch *et al.* 2002; Uehara-Prado *et al.* 2009). Mammals are not often considered as drivers of dung beetle species distributions, despite being acknowledged as important (e.g. Nichols *et al.* (2009)), and we suggest caution in extending the use of dung beetles as indicators of forest condition without full consideration of the influence of mammal species composition on their occurrence and distribution.

Species co-occurrence data can be used in situations to infer interactions where directly quantifying an interaction would require prohibitive time and resources (Abrego *et al.* 2017; Tikhonov *et al.* 2017). Such a modelling approach could potentially be used to inferring associations between dung beetles and mammals to contribute towards extending understanding of species - ecosystem functioning interactions performed by dung beetles (Slade *et al.* 2011), and the functional consequences for defaunation in associated fauna (Donoso *et al.* 2017).

General Discussion and Outlook

Contents

The intention of this work was to extend studies of dung beetle communities that consider dung beetles in isolation from their resources, and to link dung beetles to mammal species in tropical systems. I first reviewed past research that has investigated dung beetle resource use, and the approaches used to assess interactions between dung beetles and mammals. I then used experimental methods to explore dung use. I used mesocosm experiments to identify intraspecific variation and field studies to detect variation in dung use among species and between life cycle stages. Finally, I used landscape-level data on dung beetle species occurrence to examine the importance of different niche dimensions influencing regional patterns in dung beetle species' distributions. My findings are explored below with reference to the five general themes set out in the Introduction and summarised in Figure 1.

Summary of chapters

1. How is dung beelte resource use researched?

The systematic review in Chapter 1 assessed research on dietary preferences in dung beetles, finding that most such research has assumed that dung beetles are indiscriminate feeders. Standardised experimental designs and failure to use naturally occurring dung types has led to an inaccurate assessment of dung use in real ecosystems (e.g. Enari, Koike & Sakamaki 2013). Most studies make the assumption that dung choice occurs based purely on discrimination of odour profiles and does not consider the distribution of dung within an ecosystem and the variation in detectability that might occur amongst dung types. The few studies that have focused on identifying dung beetle – mammal interactions found a strong impact of mammals on the dung beetle community, despite indirectly assessing the association through low quality mammal data (Culot et al. 2013; Bogoni *et al.* 2016). This indicated a gap in the literature surrounding our understanding of the associations between dung beetles and mammals which I addressed in the subsequent chapters.

A recent meta-analysis of dung beetle resource use (Frank *et al.* 2018), which I co-authored (Appendix F), indicates that dung beetles are generalist feeders. I contributed data from the Atlantic forest to this paper (Chapter 3). My review

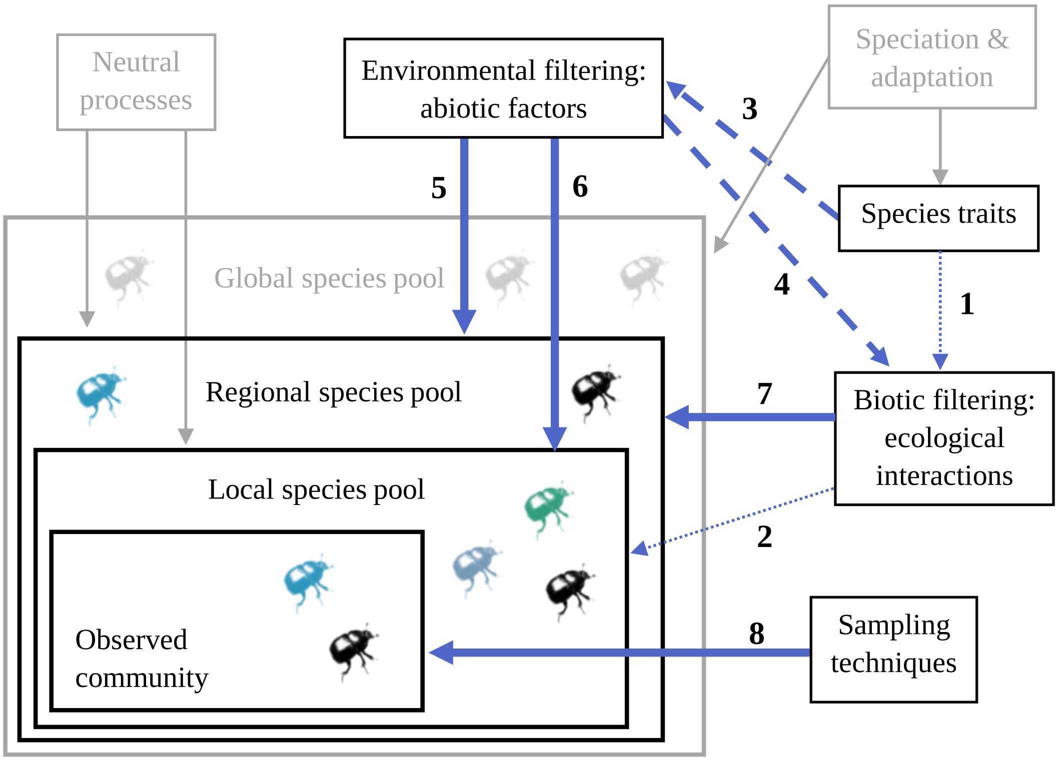

Figure 6.1 The relative importance of environmental and biotic factors found to influence dung beetle species niche. Grey areas are not explored within this thesis. Dotted arrows: low importance. **1**: Dung beetle species traits were found to have little importance in determining mammal – dung beetle interactions (Ch5). **2**: Dung beetles showed no specialisation on different dung types, suggesting that biotic filtering due to mammal presence will have little consequence for the local dung beetle species community (Ch 2,3,4). Dashed arrows: medium importance. **3**: Dung beetle species traits explained dung beetle species response to environmental factors to some extent (Ch5). **4**: Dung beetle – mammal interactions changed over a land use gradient (Ch5). Thick arrows: important. **5&6**: Environmental filtering was an important factor determining dung beetle species distributions across the regional landscape and locally. Dung beetle species showed similar responses to environmental change. (Ch5). **7**: Mammal species community had a large impact on determining dung beetle species distribution at regional spatial scales (Ch5). **8**: Sampling techniques have greatly influenced our measures of dung beetle species community composition and dung feeding behaviour (Ch1, 3).

considers many of the same papers, and highlighted inconsistencies in data collection methods. The conclusions from Frank *et al.* (2018) may therefore in part reflect data collection methods rather than dung beetle resource use. Despite this, it is unlikely that specialisation in dung beetles would have gone undetected across such a wide range of studies, even with incomparable sampling methods.

2. Do the methods used to sample dung beetles give an accurate representation of resource use in natural systems?

I wished to assess the attractiveness of naturally occurring dung types and volumes to dung beetles. Chapter 4 revealed differences in the dung beetle community composition in traps designed to capture beetles performing dung removal activity versus traps to identify overall dung attractivity (i.e. liquid feeding or dung removal). There were also differences in the dung beetle assemblages captured amongst dung types. This suggests that many previous studies that use standardised dung types and volumes are not accurately documenting the frequency of dung beetle – dung interactions. For example, using human dung in pitfall traps, or cattle dung for dung removal measurements, may not accurately represent frequencies of dung removal, or truly represent the dung beetle species community assemblage in an area. This is relevant within the context of estimating ecosystem functioning provided by dung beetles, particularly as the field moves from exploratory analysis of species – functioning associations (e.g. Slade *et al.* 2007) to quantifying interactions. With the current popularity of valuing ecosystem services and natural capital approaches to conservation, obtaining realistic functioning measurements will be key to quantifying the ecosystem services performed by dung beetles (Noriega *et al.* 2018).

The quantitative networks in Chapter 4 were based on the relative mammal abundance in the ecosystem to estimate the interactions with dung beetles that could be feasible with the amount of dung in the system. Expanding upon the interaction networks to quantify ecosystem functioning provided by dung beetles would be an interesting extension of the quantitative network, and could give rates of dung removal in tropical forest systems which could be used to assess the effects of environmental change on ecosystem processes.

3. Do dung beetles show variation between individuals, species or life cycle stages in their resource use?

All of the amino acids and nutrients required by dung beetles are in theory available in dung, meaning microbial symbionts in the gut might not be needed to perform additional compound synthesis (Byrne *et al.* 2013; Holter 2016). However, there are contradictory results on the role of microbiota in the diet of dung beetles (Byrne *et al.* 2013; Schwab *et al.* 2016; Shukla *et al.* 2016). We hypothesised that variation in gut microbiota could have an impact on individual feeding behaviour within species (Bolnick *et al.* 2002), and conducted a preliminary test of diet preference in Chapter 2 which assessed individual variation in dietary preference for dung beetles. Should gut microbiota play an important part in diet determination, maternal feeding behaviour and dung brood mass type could affect the diet choices of individuals. This could result in individual beetles showing specialist diets that vary across individuals within a species. There was no evidence that, within a species, individual beetles varied in dung choice. This suggests that individual dung beetles show the generalist dung feeding behaviour, rejecting our alternative hypothesis. However, there was evidence of interspecific variation in dung preference in Chapter 2, largely between coprophagous and necrophagous dung beetle species. This highlights that dietary choice varies to some extent among species and can be detected in mesocosm-style experiments.

Further research into intraspecific variation in dietary preference using rearing experiments that manipulate the dung type used in brood masses would be an extension of the work presented in Chapter 2. This could identify the association between feeding and breeding behaviour in adults and the composition of their gut microbiota, how this is transmitted from mother to offspring, and how this then relates to offspring feeding habits. Assays to identify the range of microbiota in the dung beetle gut and their influence on feeding and compound synthesis would support conclusions on the role of microbiota in diet. However, at the present time tropical dung beetle life cycle stages and natural history are poorly understood, limiting the capacity to carry out rearing experiments in the systems in which I was working.

The quantitative dung beetle – mammal interaction networks in Chapter 4 included separate feeding and breeding interaction networks. These also illustrated the generalist feeding behaviour in tropical forest dung beetles. There were differences in the structure of the interaction networks based on dung use either for dung removal (brood ball formation or feeding balls) versus overall attraction (pitfall traps). The network approach used here enables an understanding of dung beetle – dung interactions which are often considered independently and not as whole networks. Quantitative networks are massively time and labour consuming to construct. While my intention was to increase the number of sampling replicates in a second field season, but this was ultimately not achievable within the time available. Thus, while Chapter 4 has provided a step forward in providing the first quantitative interaction network between dung beetles and the mammal dung they consume, future work should aim to replicate these networks and to expand this work to look at how dung beetle- mammal interactions change across environmental and land use gradients.

The experimental design used in Chapters 3 and 4 was driven by the aim to identify dung beetle resource use under realistic dung sizes, with the intention of identifying the role of olfaction in dung finding, and to quantify the realistic frequencies of interactions among tropical forest dung beetles and mammals. These are aspects that are not addressed in the majority of papers (Chapter 1). Although the method taken thus provided biological realism in the creation of a dung beetle – dung interaction network, it meant it was not possible to identify individual species dietary breadths with confidence due to the low numbers of dung beetles attracted to most dung types. The variation in dung beetle density over multiple spatial scales (Horgan 2006) and with microhabitat conditions (Mehrabi *et al.* 2014) also suggest larger sample sizes would be required to draw conclusions about dietary preference in dung beetles.

4. What is the importance of environmental conditions and mammal species in determining dung beetle species distributions?

I took an alternative approach to understanding dung beetle species resource use in Chapter 5, by analysing landscape level occurrence data to consider how abiotic and biotic factors affect dung beetle species distributions. I demonstrated that mammal feeding guild biomass exerted a large influence on dung beetle species distributions (>50%), far more than previous studies have found (Tshikae *et al.* 2013a; Bogoni *et al.* 2016). By using higher quality mammal species abundance data than previous studies (e.g. Andresen & Laurance 2007; Culot *et al.* 2013; Nichols *et al.* 2016), this work gives a more robust assessment of the role of mammals in determining dung beetle species distributions.

In full this work indicates that anthropogenic change on dung beetle species distributions cannot be estimated based solely on abiotic factors without including the influence of mammal species distribution. Although we identified that dung beetles are generalist feeders, we did find that the mammal species composition is an important determining factor for dung beetle species distributions. This suggests further work is needed to identify the strength and extent of interactions among different dung beetle species and mammal trophic groups. Dung beetles are used regularly as indicators of forest composition (McGeoch *et al.* 2002), quality and restoration success (Audino *et al.* 2014b). Mammal species abundance and composition may not be directly or linearly associated with such measures of habitat change, and could easily confound the use of dung beetles as a bioindicator group.

5. How do dung beetle species respond to environmental change, and how are dung beetle – mammal associations affected?

In Chapter 5 I found that dung beetle response to land use change was not determined solely by their traits. This is contradictory to previous work that found dung beetle species show trait-dependent responses to land use change across tropical regions (Nichols *et al.* 2013). The large data sets available to use in my work meant there was power to identify species level responses to biotic and abiotic factors in the joint species distribution model across the land use gradient in Malaysian Borneo. This approach enabled me to identify associations between dung beetle traits and explanatory variables as well as species specific responses, which are often assessed using lower power modelling approaches (e.g. Nichols *et al.* 2013). It was also possible to include data on rarer dung beetle species in Chapter 5 (Ovaskainen *et al.*

2017) which may often be excluded in studies of species distribution, but trait data for these species is particularly important for identifying trait- environment associations.

The quantitative dung beetle – dung interaction network produced in Chapter 4 was used to simulate the effects of mammal species extinction. It showed that despite the generalist feeding preferences of dung beetles, realistic scenarios of mammal species loss had larger negative effects on dung beetle populations than random scenarios of mammal species loss. We also identified dung beetle – mammal species co-occurrence across a land use gradient (Ch6). Changes in patterns of co-occurrence between dung beetles and mammals did not necessarily correspond with species' responses to land use change which suggests some of the dung beetle species distribution could be affected by dung availability and composition.

Field experiments directly identifying interactions are only useful for small numbers of species at local scales, as well as being intensive and time consuming. One possible extension of Chapter 5 would be to dung beetle – mammal associations in terms of species-specific associations rather than grouping at the level of the mammal trophic group. This could be used to create species interaction networks, as in Nichols *et al.* (2016). However, the main assumption here is the inference that two species co-occurring together are interacting. There has been much work addressing this assumption which is based around the role of biotic interactions shaping species distributions in space, which has remained contentious despite continued debate (Gotelli 2000; Gotelli & McCabe 2002; Ulrich & Gotelli 2007; Connor, Collins & Simberloff 2013). One avenue of work we hope to pursue is to use data that identifies direct dung beetle – dung feeding interactions from Malaysian Borneo together with dung beetle and mammal species distribution data to identify whether known interactions between dung beetles and mammals are reflected in species distribution patterns. This is a way to test the efficacy of species co-occurrence models in predicting dung beetle – mammal associations.

Recent advances in joint species distribution modelling enable the approximation of biotic associations between species. This assumes that all environmental variation in species distribution is accounted for by the model, so any residual variation in species distribution is contributed to biotic associations (Pollock *et al.* 2014; Warton *et al.* 2015b; Ovaskainen *et al.* 2017). Yet, tests of the use of residual correlations as an indicator of species interactions misidentify the number and type of interaction (e.g. competitive rather than mutualistic) in simulated data sets (Zurell *et al.* 2018) and different methods of fitting joint species distribution models produce different results (Barner *et al.* 2018; Zhang *et al.* 2018). However, commensal interactions are predicted with the greatest accuracy (Zurell *et al.* 2018), and could maybe be used in the case of dung beetle – mammal interactions, as mammal species are likely to be unlinked to the population demographics of dung beetles (Anderson 2017).

In the joint species distribution model used in Chapter 5, a latent variable is used to represent missing environmental covariates or biotic interactions between species (Warton *et al.* 2015a). But we hypothesised that there are unknown functional traits that are structuring dung beetle species distributions which confounded the use of this latent variable as an estimation of biotic associations between dung beetle species. However, for demonstrative purposes these residual correlation matrices can be used to identify different kinds of interactions between dung beetle species. Biological explanations for associations between dung beetle species such as competition (Finn & Gittings 2003; Vernes *et al.* 2005; Sullivan *et al.* 2017) and facilitation (Slade *et al.* 2007) could be explored using this approach. But methods to account for interaction asymmetry in these situations have yet to be developed. An interesting avenue for future work would be using alternative trapping methods (sensu Chapter 34) across environmental gradients. A joint species distribution model as in Chapter 5 could then be used to examine the residual correlation matrices as true biotic associations and could provide a potential way to understand how interspecific interactions in dung beetles vary between different modes of resource use (feeding or dung burial).

Broader implications

The work presented in this thesis addresses how dung beetles are associated to mammal species, and how these networks of interactions are affected by environmental change. This work can be applied to understand broader questions species coexistence and diversity in dung beetles by considering the implications the results have on understanding dung beetle niche partitioning. As a hypothesis driving this work, I identified dung as a limiting factor for tropical dung beetles. However the work presented in this thesis suggests that dung beetles do not show strong differentiation in their resource use, and rather that the majority of dung beetles are generalist feeders (Frank *et al.* 2018). As found in this work and elsewhere (Nichols *et al.* 2007), in general dung beetles show a strong and conserved response to environmental conditions. Therefore, dung beetle species appear to be ecologically very similar in the known axes of their niche. Should there be no differentiation in their dung use, alternative processes must explain how dung beetle species coexist. Two ways in which coexistence in dung beetles can be promoted, neutral community dynamics and aggregated models of coexistence, are explored below.

Neutral community dynamics

A neutral approach to community assembly regards species as ecologically equivalent (Chave 2004). The work presented here suggests that dung beetle species are ecologically very similar in terms of their dung use, and species show similar responses to abiotic factors. In ecologically equivalent species, the population dynamics of a species will depend on the total abundance of all species and not on its specific abundance (Siepielski & McPeek 2010). Tropical dung beetle species could be effectively equivalent in terms of their response to the environment, and be governed by neutral processes (Bell 2001; Chave 2004; Siepielski *et al.* 2010).

A neutral approach is probably unlikely. Although it was not strongly supported in our findings in Chapter 5, previous work has found dung beetle species traits have an impact on their response to the environment in terms of effects on species dynamics (e.g. body size and forest biomass, nesting strategy and association with soil composition) (Purves & Turnbull 2010; Nichols *et al.* 2013; Nunes *et al.* 2016a), which violates a key assumption in neutral theory that species identity does not affect species' response to the environment (Siepielski & McPeek 2010). Identifying neutral processes in dung beetle species requires testing invasibility of the community, by experimentally manipulating species densities to see if each species can increase when rare without affecting the growth rates of other species (Siepielski & McPeek 2010; Siepielski *et al.* 2010).

Aggregated models of species coexistence

Another approach to explain species coexistence is based around the effect that environmental heterogeneity can have on species distributions (Hanski 1981), and were developed based on the observed patterns of aggregation of insect communities on patchy resources, such as carrion flies (Woodcock 2002) and ants (Andersen 2008). Under this approach coexistence is facilitated by spatial variation disrupting direct competition between two species using the same ecological niche (Amarasekare 2003, 2010). This occurs by the concentration of intraspecific aggregation relative to interspecific aggregation which reduces population growth of the aggregated species. As a result a competitively inferior species is then able to utilise resource patches that would otherwise be unavailable to them (Figure 3) (Hartley & Shorrocks 2002). In this model, patterns of aggregation within a species are understood as a result of life history traits which are not directly associated to resource use and vary between species (Ruokolainen & Hanski 2016). The ephemeral nature of dung and dung beetle dispersal between patches present a feasible way in which this model could explain species coexistence (Figures 2 & 3).

Mate searching can be a driving factor for changing patterns of species abundance under an aggregation model of coexistence (M'Gonigle *et al.* 2012; Ruokolainen & Hanski 2016). Ruokolainen and Hanski (2016) modelled coexistence of two ecologically identical species where mate searching and ephemeral resource patches resulted in continued dispersal due to reproductive interference and transient food sources. As species were 'identical', reproductive interference between species caused continual dispersal between the patchy resources. The spatially aggregated distributions of the two species disrupted the amount of correlation between the two species in the way they respond to the environment, reducing competition (Figure 3). This model was based on the biology of dung beetles and other detritivores. Reproductive interference is ecologically realistic in this case, as many closely related dung beetles species show large differentiation in sexual characteristics of genital morphology (e.g. Nunes *et al.* 2016) and secondary sexual traits such as male horn shape (e.g. Maldaner *et al.* 2018) often in the absence of any other morphological differences.

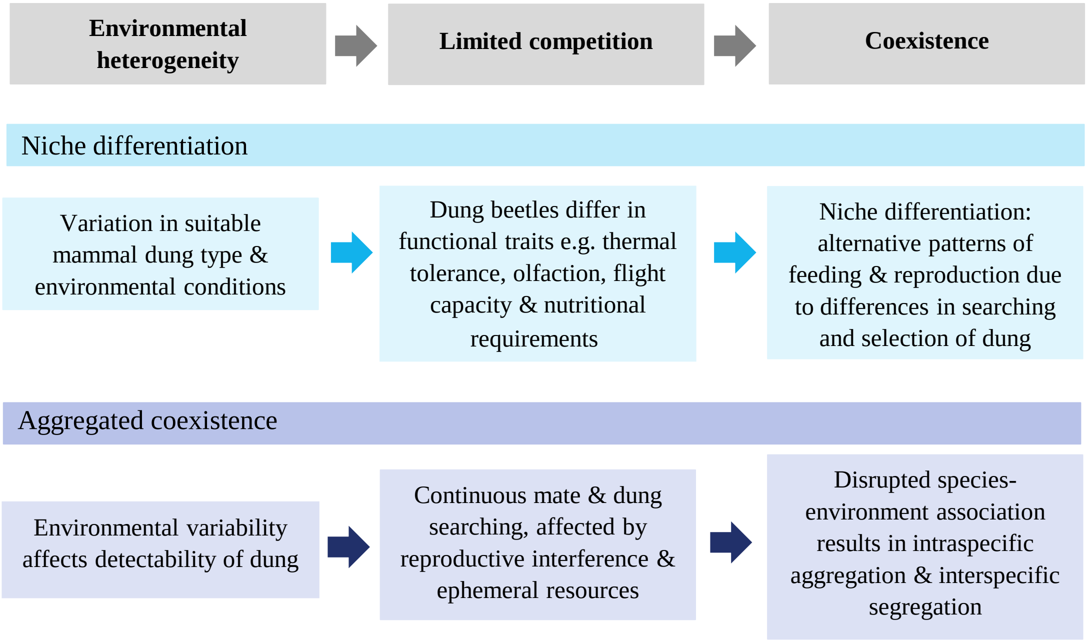

Figure 6.2 Different approaches to explaining species coexistence in dung beetle species.

Empirical work on spatial patterns in temperate and tropical dung beetles suggests intraspecific aggregation is strong and interspecific aggregation is weak in many communities, which does not rule out the potential for aggregation to promote coexistence, but could also be contributed to resource partitioning among species (Giller & Doube 1994; Hutton & Giller 2004; Horgan 2006). Aggregated distribution patterns could also account for some of the observed distributions of dung beetle species that are currently unexplained (Mehrabi *et al.* 2014). One way

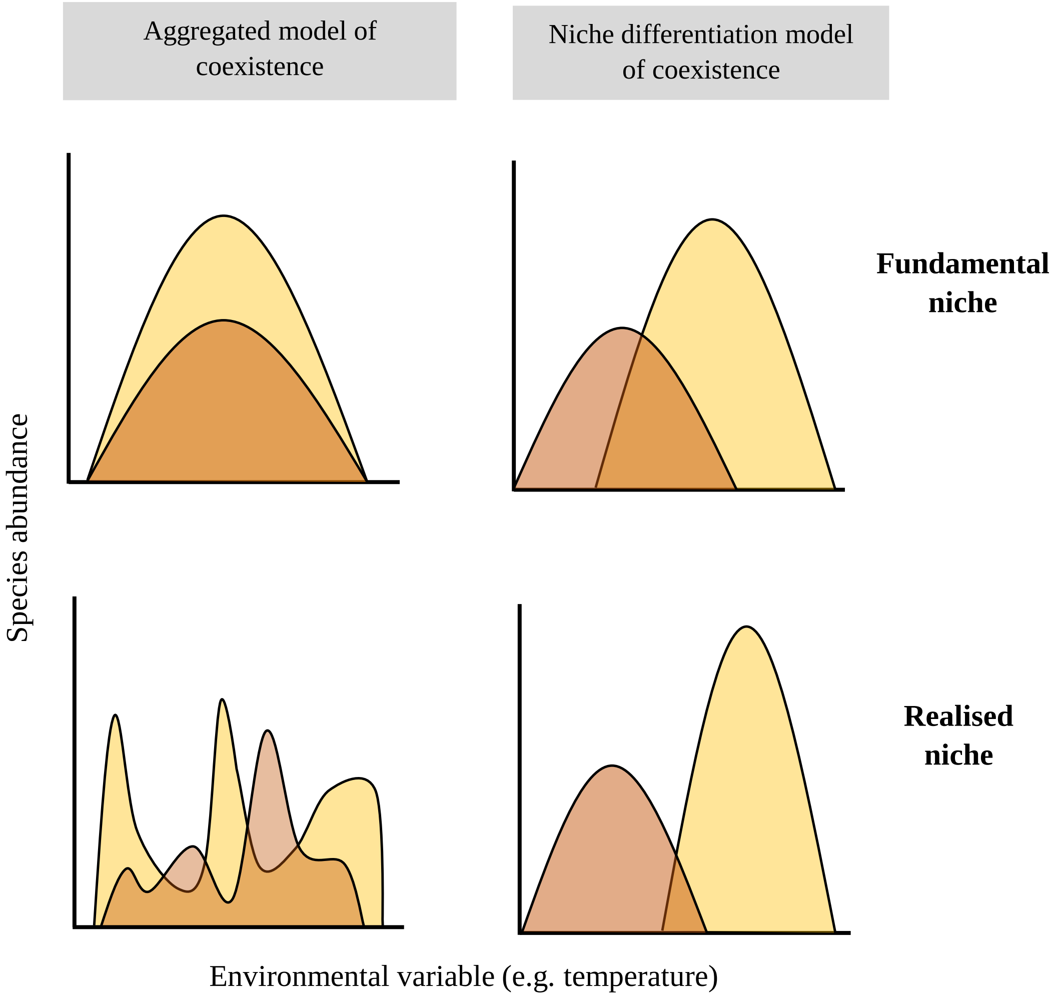

Figure 6.3 Diagram of density of two species inhabiting the same spatial area under two different models of species co-occurrence. In the aggregated species coexistence model, species are ecologically equivalent. Coexistence can be facilitated by the effects of mate searching and continued dispersal between ephemeral, patchy resources, which disrupts environmental – species abundance associations. In a niche differentiation model, species co-occur through responding differently to the environment or resources. Competition between species in the overlapping areas drives species distribution and resource use.

in which variation in dispersal between species could lead to aggregation includes pheromones, which are widely used in dung beetle mating behaviour (e.g. Edwards & Aschenborn 1988; Cook 1990; Sato & Hiramatsu 1993) and can assist mate finding and influence aggregation in dung beetles (Manning & Ford 2016). Other potential causes of aggregation in dung beetles are poorly understood but can be influenced by dung size, time of deposition, beetle flight capability, dung quality, spatial distribution and the amount of dung in the area (Hutton & Giller 2004). An aggregation model poses a markedly different approach to explaining dung beetle species coexistence to the niche partitioning hypothesis proposed in this thesis (Figure 2 & 3) but may well provide a more convincing explanation for trends in dung beetle species distribution and variation in species density.

Extensions of the work

Rather than being ecologically equivalent, dung beetles may well show niche differentiation in ways other than resource use as I explored in this thesis. Another aspect of dung beetle ecology that has not been considered could promote species coexistence. Five understudied areas are briefly considered below that present alternative perspectives in how niche differentiation in dung beetles could be explored.

Biotic factors

The ecological niche is multifaceted, and it may well be that this work and other ecological research into dung beetle species populations has not addressed an important aspect that affects niche partitioning in dung beetle species (Laughlin & Messier 2015). For example, competition with other dung-using insects is poorly understood (see Table 1). In this thesis we have only considered biotic associations between dung beetles and mammals, but interactions with other species, for example competition with flies and predator-prey interactions with staphylinid beetles (Skidmore 1991) could influence the dung beetle realised niche. The vast majority of dung beetle research does not even acknowledge the potential role of such biotic factors, so their importance in dung beetle ecology is unknown.

Table 5.2: Some dimensions of niche partitioning in coprophagic dung beetles that could be further explored to understand dung beetle species richness and coexistence in tropical regions.

	Trait	Understanding
Spatial		
Dispersal ability	Flight capacity, agility, dung searching behaviour (Lobo 2008; da Silva & Hernández 2015).	Poor
Temporal		
Seasonal segregation	Seasonality more pronounced in temperate than tropical regions (Hanski 1980; Errouissi, Labidi & Nouira 2009; Agoglitta et al. 2012, Vernes et al. 2005; Hernández & Vaz de Mello 2009).	Somewhat in temperate systems
Daily segregation	Diurnal, crepuscular and nocturnal activity patterns, thought to be related to mammal activity periods (Caveney, Scholtz & Mcintyre 1995; McIntyre & Caveney 1998).	Somewhat in temperate systems
Dung age	Differential patterns of succession in egg laying based on dung age (Holter 1982; Gittings & Giller 1998).	Somewhat in temperate systems
Resource use		
Environmental conditions	Species show strong response to habitat change (e.g. Howden & Nealis 1975; Slade et al. 2011), and also between habitat types/across environmental gradients (Verdú, Numa & Hernández-Cuba 2011; Kunz & Krell 2011).	Reasonable
Feeding & breeding dung use	Thought to be generalist (Frank et al. 2018, Chapters 1-5)	Poor
Intra-guild competition	Competition for access to dung e.g. dung feeding flies (Skidmore 1991).	Poor
Different parts of the dung pad	Variation in dung colonisation in temperate systems (Gittings & Giller 1998; Finn & Giller 2000).	Somewhat in temperate systems
Natural enemies		
Predation	409 species of birds, mammals, amphibians, reptiles and other invertebrates are recorded to predate dung beetles, the impact on dung beetle species distribution is unknown (Young 2015).	Negligible
Mites (phoresy)	Mites found on Scarabaeinae species, the impact on dung beetle species distributions are unknown (Bajerlein & Błoszyk 2004; Mašán & Halliday 2009).	Negligible

The nutritional niche

Variation in nutritional physiology can facilitate long term coexistence for generalist herbivores with overlapping diets (Behmer & Joern 2008). It is possible that certain amino acids might not be available in concentrations required by dung beetles, therefore suggesting a role for microbiota in digestion (Estes *et al.* 2013; Schwab *et al.* 2016). Gut microbiota influence dung beetle dietary specialisations (Shukla *et al.* 2016) and there is variation in the particle size dung beetles can ingest based on their functional group and body size (Holter & Scholtz 2007). An extension of Chapter 2 could consider the potential for variation in requirements of nutrient components between dung beetle species (Douglas 2009; Feldhaar 2011).

Testing such a theory in dung beetle species would require identifying species-specific requirements of the range of nutrients acquired through dung feeding. Comparing requirements among dung beetle species to measure performance optima of development times and growth rates (Raubenheimer & Simpson 2004). This could identify otherwise cryptic behavioural resource partitioning and unique nutritional niches in dung beetle species. The dung beetle life cycle provides several opportunities to classify fitness optima in breeding (e.g. development time, brood number and size, larval growth rates) and feeding (e.g. flight capacity) (Arellano *et al.* 2015; Schwab & Moczek 2016; Schwab *et al.* 2016). A more detailed understanding of the nutritional dimensions and variation within and between species would be required, should nutritional variation be a driving factor in dung beetle species attraction. Work to date classifies the proportion of alternative nutritional compounds available in the dung of different mammal trophic groups (Bogoni & Hernández 2014), and has identified a small amount of within-species variation in nutritional content in dung (Frank *et al.* 2017a), but how much this varies in wild mammal communities, between habitat types or seasons is not known (Holter 2016). It is not known whether variation in dung composition relates to variation in dung beetle attraction and how this influences population level patterns of dung use.

If nutrient requirements or aggregated models of species coexistence explain dung beetle species co-occurrence, then differences in the resource use niche are likely to be very small. The effects of random variation from field studies of dung beetle dietary preference could make detecting this difficult. DNA metabarcoding of leech blood meals has enabled identification of mammal species communities (Drinkwater in press). These methods are still in development in dung beetles (Kerley *et al.* 2018), but provide a potential alternative approach to identifying dietary widths.

Natural history and tropical dung beetles

The life cycles of many tropical species are particularly poorly understood. Detailed descriptions of species' feeding and breeding habits would reveal life history information far beyond our current understanding of the majority of tropical species. For example, Kheper nigroaeneus (Boheman), a large rolling species from southern Africa can live for several years by overwintering below ground, and females provide parental care to larvae for the twelve weeks of their development. This life history information was identified from hundreds of hours of field observations (Edwards & Aschenborn 1988). Detailed studies in the 1970s and 1980s revealed much about nesting behaviour (Klemperer 1981), flight capacities (Bartholomew & Heinrich 1978) and larval development (Kingston & Coe 1977). Now such work tends not to be prioritised by funding agencies or prominent journals, when in fact it is a vital underpinning for any ecological research. An improved understanding of natural history would advance capacity to carry out rearing experiments and identify fitness optima (extension of Chapter 2) as well as provide more knowledge about aspects of dung beetle ecology that are not well understood (e.g. foraging behaviour).

Abiotic factors

Work presented in this thesis uses niche models based on spatial occurrence of species across environmental conditions; these methods are descriptive and correlative rather than providing a causal understanding of what is driving population dynamics (Kearney *et al.* 2010). A mechanistic approach to modelling the niche instead consider species functional traits and the ways in which they interact with the environment to affect species fitness (McGill *et al.* 2006; Violle *et al.* 2007; Kearney *et al.* 2010). The behavioural, physiological and morphological traits of individuals indirectly affect fitness of an organism through their effects on growth, reproduction and survival (Violle *et al.* 2007). A mechanistic niche model approach could be used to explore dung beetle species niches to reveal more about why species distributions are structured the way they are.

Thermal tolerance influences geographical distribution of insects globally (Addo-Bediako *et al.* 2000; Kearney *et al.* 2010). Thermoregulatory traits in dung beetles are known to enable niche differentiation across altitudes (Gaston & Chown 1999; Verdú *et al.* 2007b) and prevent ambient temperature from limiting activity period and habitat usage (Verdú *et al.* 2007b). Large bodied dung beetles are able to regulate body temperature, and the capacity for endothermy influences the outcome of competition for dung (Bartholomew & Heinrich 1978) but constrains flight agility and increases risks of predation during flight muscle warm up (Lobo 2008). Thermal tolerance has wide ranging impacts on searching behaviour, activity period, habitat associations, competitive interactions and predation risk in dung beetles. It could be explored in more detail to then relate to fitness in dung beetles. Other biophysical processes such as desiccation tolerance (Chown *et al.* 1995), digestive morphology (Holter & Scholtz 2013), olfaction (Dormont *et al.* 2007), and eye morphology (McIntyre & Caveney 1998) could be explored to understand the association between traits and the environment in dung beetles and contribute to explaining the patterns of species' distribution across environmental gradients as found in Chapter 5.

Temperate versus tropical dung beetles

This thesis focuses on understanding dung beetle – mammal interactions and dung use in tropical systems, where competition in tropical beetles is thought to be at the adult stage in access to dung for breeding (Horgan and Fuertes 2005). In temperature systems the higher proportion of dwelling species mean beetles compete at the larval stage to gain space within the dung pad (Finn & Gittings 2003). Dung does not appear to be as much of a limiting factor for dung beetles in temperate systems (Holter 1982), and seasonal segregation plays a larger role in differentiating between species in temperate than tropical systems (Hanski 1980; Giller 1997). The relative importance of the processes influencing dung beetle community assembly identified in this work (Figure 1) could vary in temperate regions, and in turn the processes maintaining dung beetle species diversity in temperate systems could be substantially different. Comparison of temperate and tropical dung beetle systems could help to reveal ways in which species coexist in tropical regions by highlighting the similarities and differences in species' ecology.

Conclusion

This thesis explored dung beetle resource use within the context of the mammal species they rely on for dung. The findings in combination suggest a limited role of niche differentiation in terms of dung use between dung beetle species. Although it suggests that there is little intraspecific variation in feeding choice, it suggests some degree of niche differentiation in terms of dung preference at the level of the species (Chapters 2&3) and highlights the importance of mammal abundance and composition in determining dung beetle species distribution (Chapter 5), which has previously been overlooked (Chapter 1). It also presents the potential for variation in dung use between feeding and breeding interactions (Chapter 3&4) which have not been previously addressed in the literature. A key area is identifying variation in the magnitude of functional interactions taking place (Chapters 3&4) which is a necessary step for developing understanding of the extent of dung removal in natural systems. Overall, results from this thesis suggest that although dung beetles exhibit generalist intraspecific and interspecific feeding and breeding behaviour, mammal species composition and abundance is a key factor influencing their distribution. Further work is needed to identify the strength and extent of interactions among different dung beetle species and mammal trophic groups to gain an improved understanding of how environmental change will directly and indirectly affect dung beetle species and the ecosystem functions they provide.

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Appendices

A
Supplementary Material for Chapter 1

Contents

1: Diet preference studies

Diet preference study methodology

Table A.1: Dung beetle diet preference studies where at least two dung types were used to capture dung beetles in an area. Additional factors: factors included in the analysis in addition to variation in dung type, method/trap spacing: lab-based studies recorded as 'lab', field studies record the spacing between traps. Dung volume: 'NS': not stated in the study, 'realistic': collected from dung mounds found in the wild, dung volume not stated. Analysis focus: 'Dung beetle': analysis of specialism of individual species, consideration of variation between dung types. Reporting of percentages feeding on each dung type. Quantitative assessment/reporting of dung beetle abundance on each dung type. 'Mammal': analysis of dung beetle population metrics (e.g. species number, beetle abundance, biomass, comparison of community composition).

Paper	**Ecosystem**	**Location**	**Additional factors**	**Methods/ trap spacing**	**Dung volume**	**No bait sources**	**Mammal dung used as bait**
Al-Houty & Al-Musalam 1997	-	Kuwait		lab	Realistic	5	Horse, sheep, camel, Arabian fox, dog
Ameziquita & Favila 2010	Tropical rain forest and cloud forest	Mexico	Fragment size, dung removal	50m linear	200g	2	Spider monkey, cow
Barbero et al. 1999	Mosaic of wooded and open patches	Italy		Blocks: traps>3 m apart	300g	4	Cow, wild boar, horse, sheep
Bogoni & Hernandez 2014	Atlantic forest	Brazil		Blocks 25m apart	10g	4	Puma, Crab-eating fox, black-horned capuchin, tapir
Carpento et al. 2010	Savanna, open grasslands	Uganda	Soil type	Realistic	Realistic	3	Hippo, buffalo, warthog
Carpento et al. 2005	Small deciduous woodlands, grasslands and ponds.	Italy		Realistic	∼5L	4	Sheep, dog, cow, horse
Correa & Puker 2016	Cerrado	Brazil	Habitat	Blocks 50m apart traps 10m apart within blocks	50ml	4	Cow, human, pig
Davis et al. 2010	Open grassland	South Africa		Blocks with traps 50m apart within block	250g	4	Elephant, cow, sheep, pig
Dormont et al. 2004	Mediterranean climate: Pasture vegetation and herbaceous pasture	France		Blocks 10m apart, with traps 1m apart within block & lab	300g	2	Horse, cow
Dormont et al. 2007	Mediterranean climate: Pasture vegetation and herbaceous pasture	France		Blocks 10m apart, with traps 1m apart within block & lab	300g	4	Horse, cow, sheep, red deer
Enari et al. 2013	Cool temperate forest, beech and oak	Japan		10m linear	15g	5	Macaque, Asiatic black bear, Japanese serow, Temminck and cow
Enari et al. 2016	Cool temperate forest, beech and oak	Japan		50m linear	Realistic		Macaque, Japanese serow, Japanese hare

Paper	**Ecosystem**	**Location**	**Additional factors**	**Methods/ trap spacing**	**Dung volume**	**No bait sources**	**Mammal dung used as bait**
Estrada et al. 1993	Lowland evergreen tropical rainforest	Mexico		Blocks 20m apart, traps 5m apart within block	5g	2	Howler monkey, coati
Frank et al. 2017	Forest, grassland	Germany	Land use	10m linear	35g	6	Cow, horse, deer, sheep, fox, wild boar
Frank et al. 2017	Forest, grassland	Germany		Field	35g	12	Wolf, lynx, fox, brown bear, wild boar, cow, horse, sheep, deer, elephant, elk and wisent
Filgueiras et al. 2009	Brazilian Atlantic rainforest fragment	Brazil		Traps 2m apart blocks 15m apart	NS	3	Human, jaguar, waterbuck
Finn & Giller 2002	Cattle pasture, wildlife park	Ireland		5m	1000g	3	Cow, horse, sheep
Galante & Cartagena 1999	Mediterranean forest	Spain		Realistic	1000g	2	Rabbit, cow
Gharaklhoo et al. 2009	Iran	Iran	Natural history	Realistic	Realistic	2	Yellow ground squirrel, Asian Minor Ground Squirrel
Gittings & Giller 1998	Grazed pastures	Ireland		Grid with traps 5m apart	1l	6	Cow, giraffe, zebra, guanaco, ostrich, red lechwe
Hewavithana et al. 2016	Tropical monsoon forest	Sri Lanka	Habitat	50m linear	200ml	5	leopard, cervid, elephant, bear, buffalo
Jones et al. 2012	-	New Zealand	Native/ exotic diet sources	lab	4-6g	18	Cow, sheep, pig, brushtail possum, dog, kakapo, kereu, kiwi, emu, caterpillar, wetapunga, phasmid, tuatura.

Paper	**Ecosystem**	**Location**	**Additional factors**	**Methods/ trap spacing**	**Dung volume**	**No bait sources**	**Mammal dung used as bait**
Larsen et al. 2006	Forest of varying disturbance	Peru	Extreme specialists	50m linear	NS	28	Human, cow, horse, tayra, puma, lizard, bird, howler monkey and snail.
Marsh et al. 2013	Primary rainforest, secondary forest and plantations	Brazil	Optimum bait	100m linear	20g	2	Human, pig and mix
Martin-Piera & Lobo 1996	Mediterranean forest	Spain		Grid ∼10m apart	1000g, 250g	8	Cow, deer, horse, fox, lynx, human, badger and wild boar
Medina & Lopes 2014	Seasonally dry tropical forest	Brazil		Blocks 2m apart 25m between	NS	4	Human and cow
Mroczynski et al. 2014	Grazed meadow	Poland		Grid 30cm apart	Realistic	2	Cow and horse
Noriega 2012	Mixture lowland wet tropical forest	Colombia		Realistic	realistic	2	Wooly monkey and howler monkey
Plewinska 2007	Mixed coniferous forest	Poland		10m, linear	21g	5	Bank vole, horse, cow, rodent
Puker et al. 2013	Riparian strips, tropical forest	Brazil	Habitat	Blocks 100m apart, traps 20m apart	40g	2	Human, capybara
Santos-Heredia et al. 2010	Moist forest fragments, agricultural land	Colombia		50m linear	30g	2	Spider monkey, howler monkey
Shahabudin et al. 2010	Rainforest, agroforestry	Indonesia	Habitat disturbance	10m linear	26g	2	Cow, anoa (small buffalo)
Siddall 2004	Evergreen forest	Uganda		Blocks, traps 10m apart and 200m between blocks		2	Primate, elephant

Paper	**Ecosystem**	**Location**	**Additional factors**	**Methods/ trap spacing**	**Dung volume**	**No bait sources**	**Mammal dung used as bait**
Tshikae et al. 2008	Woodland	Botswana	Dung source	50m linear	250g	5	Pig, cow, sheep, elephant
Tshikae et al. 2013	Desert	Botswana	Aridity gradient, dung source	50m linear	250g	5	Pig, cow, sheet, elephant
Vernes et al. 2005	Eucalyptus woodland, allocasuarina forest	Australia		100m linear	Realistic	5	Northern Brown Bandicoot, Northern Bettong, Giant white tailed rat, norther quoll, long nosed bandicoot
Vinod & Sabu 2007	Moist forests	India		100m linear	$1000cm^3$	2	Gaur, Asian Elephant
Whipple & Holback 2012	Pasture	US	Native/exotic diet sources	100m linear	113g	15	American bison, Shiras moose, cougar, pig, human, chimp, Bengal tiger, Africa lion, zebra, waterbuck and carrion.
Wurmitzer et al. 2017	Lowland monte desert and meadow	Argentina, Austria	Real/ synthetic odours Habitat	20m, linear	15-30g	5, 3	Argentina: Horse, buffalo, capybara, patagonian mara, guanaco. Austria: horse, donkey and cow.
Edwards 1991	Hot summer-rainfall regions South Africa	South Africa	Dung water content	Lab	-	3	Zebra, wildebeest, impala
Errousi et al. 2004	Bioclimatic gradient of pasture land	France, Morocco	Bait size	10m linear	30g, 750g	3	Cow, goat, sheep
Stavert et al. 2014	Waitakere Ranges	New Zealand	Native/ exotic diet sources	Lab	3-5g	22	Tuatara, short tailed bat, Kakapo, Brown kiwi, Australasian gannet, Brown teal, Weka, Cow, Pig, Dog, Common brushtail possum, sheep, horse, Wetapunga, green looper caterpillar, stick insect.

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3. Mammal association studies

Dung beetle - mammal association study methodology

Table A.2: Studies that explore dung beetle - mammal associations through co-occurrence of dung beetle and mammal data. Explanation of Methods classifications: Mammal species abundance/density (Raw abundance/density calculated from the total survey time carried out in each area and the number of sightings); Mammal species richness (presence/absence from mammal survey data); Qualitative index (categorical classifications of large mammal presence/density); Human disturbance (hunting or human disturbance as a proxy for mammal defaunation); Focal species (study of one or several species known a priori to contribute a significant proportion to the dung profile); Grazing intensity (as an estimate for mammal/dung density); Literature (deriving mammal species composition and density from IUCN lists or aerial surveys). Direction of effect of mammals on dung beetles: if a decline in mammal abundance or richness led to a decline in dung beetle abundance or another metric, this is signified by '-'. If the dung beetle community composition varied significantly among areas with different mammal species composition, this is signified by '$\neq$'. Non-significant differences are signified by '='. Empty cells represent no data, or no analysis carried out.

Author	Methods			Direction of effect of mammal decline on dung beetles			
	Location	Mammal data classification	Additional explanatory variables	Species richness	Abundance	Community composition	Additional findings
Bogoni et al. 2016	Brazil	Mammal abundance Mammal spp. richness	Habitat structure	-			40% of dung beetle species composition attributed to mammal species composition
Pryke et al. 2016	South Africa	Grazing intensity	Fragment size			≠	Quantity of dung explained 60% of variance in species richness
Feer & Boissier 2015	French Guiana	Qualitative index Hunting proxy			=	≠	Beetle size varied between sites and with hunting pressure
Koike et al. 2014	Japan	Focal sp.	Understory cover	-		≠	
Culot et al. 2013	Brazil	Mammal abundance Mammal spp. richness		-	+		+ Small bodied beetles - Large bodied beetles
Nichols et al. 2013	Brazil	Mammal abundance Hunting		=		≠	
Tshikae 2013	Botswana	Literature	Spatial distance, aridity, vegetation, soil	Large mammal composition was the third strongest factor influencing regional patterns of dung beetle species assemblages.			
Barlow et al. 2010	Brazil	Qualitative index	Forest structure, landscape context	=	-	=	
Viljanen 2010	Madagascar, C&S America, Africa, SE Asia	Literature		-			
Andresen & Laurance 2007	Panama	Mammal abundance Mammal spp. richness Hunting	Dry season days	-	-	≠	+ Proportion of nocturnal beetles
Lobo 2006	Spain	Focal sp. Grazing intensity		-	-		
Kanda et al. 2005	Japan	Focal sp.		-	-		
Feer & Hingrat 2005	French Guiana	Focal sp. Mammal spp. richness		-		≠	
Verdu 2002	Iberian Peninsula	Grazing	Bioclimatic factors				Rate of dung beetle endemism affected by faunal composition
Estrada 1999	Mexico	Focal sp.	Season, forest type		-		

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4: Ecosystem functioning studies

Ecosystem functioning study methodology

Table A.3: Ecosystem services studied on dung beetle diet preference papers. Ecosystem services classified into eight categories: Dung removal: studies that measured the amount of dung removed from a system by dung beetles; GHG: greenhouse gasses released from dung (methane, carbon dioxide, nitrogen gasses); Plant growth: plant shoot nitrogen content, plant growth; seed removal: removal of seeds from dung; seed dispersal: horizontal and vertical burial of seeds, seed clustering, seedling recruitment; soil properties: soil characteristics such as bioturbation, nutrient quality; nutrient cycling: soil nitrogen, phosphorous, micro/macro nutrient content, biotic: microbial activity and fly presence.

Paper	ES no.	Ecosystem services	Dung type	Size (g)	Dung no.
Braga et al. 2017	1	Seed dispersal	Human + pig combined	200	1
Frank et al. 2017	1	Dung removal	Cattle, horse, sheep, deer, fox, wild boar	220, 34, 50, 32, 14.5, 47	6
Lugon et al. 2017	1	Seed dispersal	Tapir, muriqui	Unclear	2
França et al. 2017	2	Dung removal, soil bioturbation	Human + pig combined	200	1
Slade et al. 2017	5	Dung removal, plant productivity, GHG, nutrient cycling, microbial activity	Dung (species undetermined)	Unclear	1
Batilani-Filho & Hernandez 2017	1	Dung removal	Pig, dog	50	2
Piccini et al. 2017	1	GHG	Cattle	300	1
Nervo et al. 2017	3	Dung removal, Nitrogen content of soil and dung, Plant productivity	Cattle	Unclear	1
Milotic et al. 2017	2	Dung removal, seed dispersal	Cattle, horse, sheep	200, 300	3
Farias & Hernández 2017	3	Organic matter, macro and micronutrients, soil pH	Rotting meat, dung (Species undetermined)		1
Ortega-Martínez, Moreno & Escobar 2016	1	Dung removal	Sheep, cattle	200	2
Derhé et al. 2016	3	Seed dispersal, dung removal, soil bioturbation	Wallaby	50	1
Slade & Roslin 2016	2	Dung removal, plant productivity	Cattle	940	1
Kenyon et al. 2016	1	Dung removal	Kangaroo + wallaby combined	50	2
Johnson et al. 2016	3	Soil water retention, plant productivity, plant nitrogen	Cattle	800	1
Ardali, Tahmasebi & Bonte 2016	1	Seed dispersal	Sheep	Unclear	1
Santos-Heredia et al. 2016	2	Plant nitrogen, Plant phosphorous	Howler monkey	25	1
Menéndez, Webb & Orwin 2016	2	Dung removal, Dung soil carbon cycling	Sheep	200	1
Griffiths et al. 2016	3	Seed dispersal, Seedling emergence, seedling recruitment	Human + pig combined	100	1

Paper	**ES no.**	**Ecosystem services**	**Dung type**	**Size (g)**	**Dung no.**
Manning et al. 2016	2	Dung removal, seed dispersal	Cattle	550	1
Slade et al. 2016	1	Microbial communities	Cattle	1200	1
Slade et al. 2016a	1	GHG	Cattle	1200	1
Tixier, Bloor & Lumaret 2015	2	Dung removal, leaf litter removal, decomposition	Dung (species undetermined)	Unclear	1
Yoshihara & Sato 2015	2	Nutrient cycling, plant productivity	Cattle	100	1
Iwasa, Moki & Takahashi 2015	1	GHG	Cattle	1000	1
Griffiths et al. 2015	1	Seed dispersal	Human + pig combined	100	1
Enari & Sakamaki-Enari 2014	1	Seed dispersal	Macaque	Natural	1
Santos-Heredia & Andresen 2014	2	Seed dispersal, seed movement	Howler monkey	50	1
Nervo et al. 2014	1	Dung removal	Dung (species undetermined)	Unclear	1
Feer et al. 2013	1	Seed dispersal	Howler monkey	80	1
Braga et al. 2013	3	Dung removal, seed removal, soil bioturbation	Human + pig combined	70	1
Penttilä et al. 2013	1	GHG	Cattle	1200	1
Gollan et al. 2013	1	Dung removal	Pig	10	1
Dangles, Carpio & Woodward 2012	1	Dung removal	Human, carrion	40	2
Lawson, Mann & Lewis 2012	2	Seedling clustering, seed recruitment	Horse	280	1
Braga et al. 2012	2	Dung removal, Fly abundance	Human + pig combined	70	1
Kudavidanage, Qie & Lee 2012	1	Dung removal	Dung (species undetermined)	75	1
Kunz & Krell 2011	1	Seed dispersal	Olive baboon	30	1

Paper	ES no.	Ecosystem services	Dung type	Size (g)	Dung no.
Dangles, Carpio & Woodward 2012	1	Dung removal	Human, carrion	40	2
Lawson, Mann & Lewis 2012	2	Seedling clustering, seed recruitment	Horse	280	1
Braga et al. 2012	2	Dung removal, Fly abundance	Human + pig combined	70	1
Kudavidanage, Qie & Lee 2012	1	Dung removal	Dung (species undetermined)	75	1
Kunz & Krell 2011	1	Seed dispersal	Olive baboon	30	1
Culot et al. 2011	1	Seed dispersal	Tamarin	Natural	1
Giraldo & Escobar 2011	4	Dung removal, soil removal, fly activity, seed removal	Cattle + pig combined	70	1
Slade, Mann & Lewis 2011	2	Dung removal, seed burial	Cattle	780	1
Santos-Heredia, Andresen & Stevenson 2011	1	Seed dispersal	Howler monkey, spider monkey	10	2
Brown et al. 2010	1	Soil hydrological properties	Cattle + pig	2500	1
Amézquita & Favila 2010	1	Dung removal	Cattle, spider monkey	200	2
Santos-Heredia, Andresen & Zárate 2010	2	Seed movement, seed survival	Howler monkey, spider monkey	30g	2
Lee et al. 2009	1	Dung removal	Cattle	50	1
Rosenlew & Roslin 2008	1	Dung removal	Cattle	1920	1
Slade et al. 2007	2	Dung removal, seed dispersal	Cattle	620	1
Bang et al. 2005	3	Plant productivity, Soil nitrogen content, soil bioturbation	Cattle	1000,500	1
Horgan 2005	2	Dung removal, fly activity & Pig	100	1	
Bustamante- Sánchez, Grez & Simonetti 2004	1	Dung removal	Cattle	100	1
Chapman, Chapman & Vulinec 2003	1	Seed dispersal	Cattle	25	1
Vulinec 2002	1	Seed dispersal	Dung (species undetermined)	Unclear	1
Andresen 2001	1	Seed dispersal	Howler monkey	25	1
Feer 1999	1	Seed dispersal	Howler monkey	30	1
Kazuhira, Hideaki & Hirofumi 1991	1	Nitrogen gas loss	Cattle	100	1
Estrada & Coates-estrada 1991	1	Seed dispersal	Howler monkey	20	1

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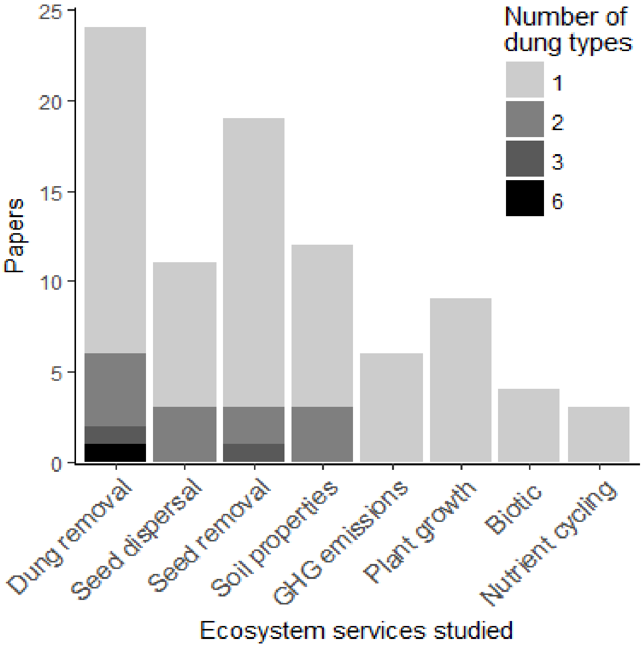


Figure A.1: Studies of ecosystem services and number of dung types used. Dung removal: studies that measured the amount of dung removed from a system by dung beetles; GHG: greenhouse gasses released from dung (methane, carbon dioxide, nitrogen gasses); Plant growth: plant shoot nitrogen content, plant growth; seed removal: removal of seeds from dung; seed dispersal: horizontal and vertical burial of seeds, seed clustering, seedling recruitment; soil properties: soil characteristics such as bioturbation, nutrient quality; nutrient cycling: soil nitrogen, phosphorous, micro/macro nutrient content, biotic: microbial activity and fly presence.

B

Supplementary Material for Chapter 2

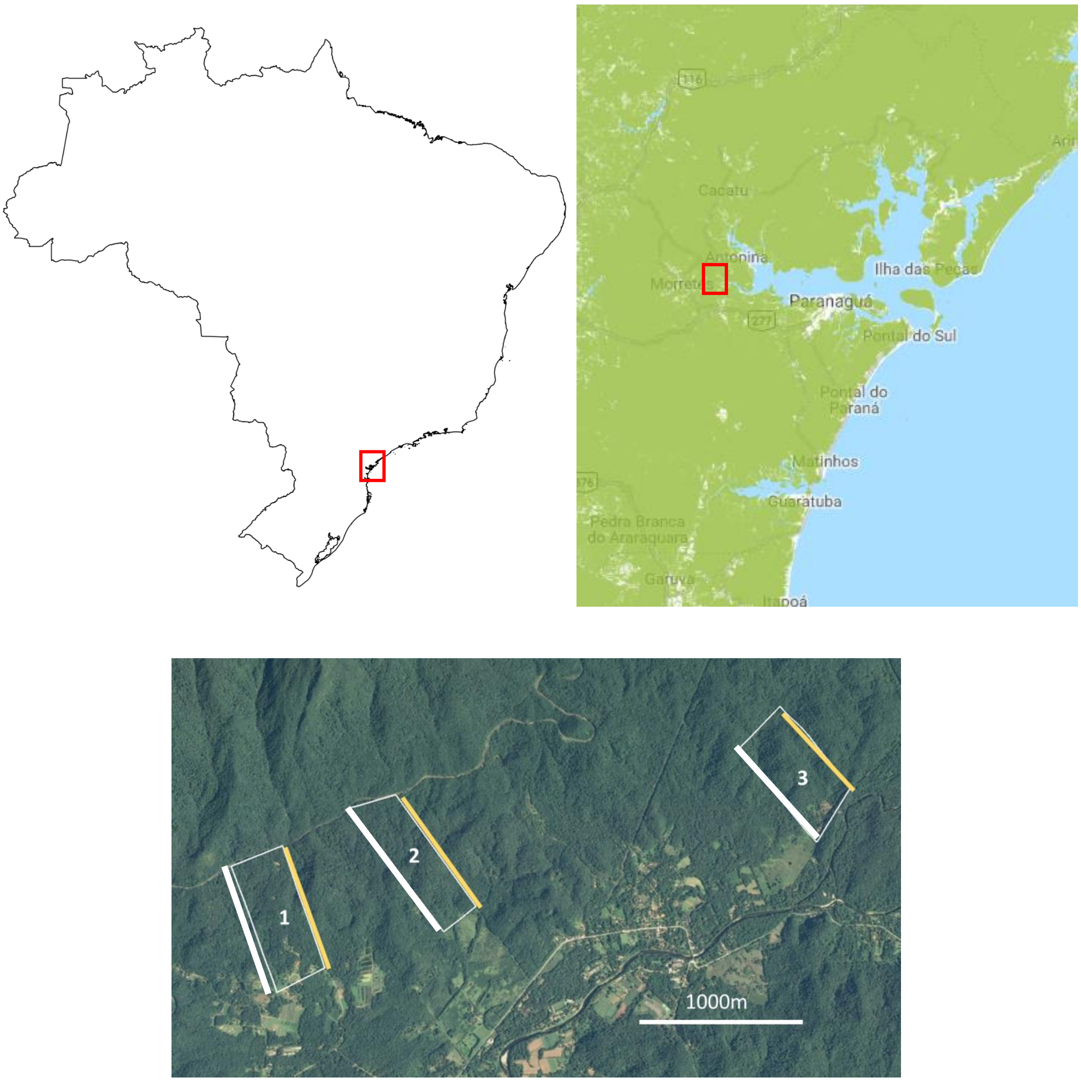


Figure B.1: Map of location of field site in Brazil and Paraná state. White lines represent site extent and yellow lines represent transect locations for pitfall traps in each of three sample sites in continuous lowland tropical forest in the Atlantic forest, Paraná state, Brazil (25’27’11"S, 48’52’57"W). Numbering references site identities in Table B2.1.

Site	**Bait type**	**Date**	*C. dardanus*	*M. saphirinus*	*P. splendidulus*	*D. mormon*	*D. sericeus*
1	H	09/12/15	13	3	5	4	12
	P	09/12/15	0	0	0	0	5
	J	09/12/15	0	3	0	0	3
2	H	10/12/15	0	2	3	0	0
	J	10/12/15	0	0	1	0	0
	P	10/12/15	0	0	0	0	2
3	H	11/12/15	0	1	0	4	3
	J	11/12/15	1	1	0	0	12
	P	11/12/15	0	0	0	5	3
2	H	14/01/16	0	0	4	21	6
	J	14/01/16	0	0	0	0	3
	P	14/01/16	0	0	3	0	6
1	H	15/01/16	0	0	2	40	4
	J	15/01/16	1	0	1	4	8
	P	15/01/16	0	0	0	7	6
3	H	20/01/16	2	0	0	3	12
	J	20/01/16	0	0	0	1	2
	P	20/01/16	0	0	2	8	8
2	H	04/02/16	0	1	1	2	7
	J	04/02/16	0	0	0	0	1
	P	04/02/16	0	0	0	10	4
1	H	05/02/16	0	0	0	2	5
	J	05/02/16	0	0	3	6	5
	P	05/02/16	0	0	5	5	1
3	H	05/02/16	0	0	1	0	0
	J	05/02/16	0	1	0	2	0
	P	05/02/16	0	0	0	0	1
2	H	02/03/16	0	0	7	0	4
	J	02/03/16	0	0	0	1	1
	P	02/03/16	0	0	0	15	4
1	H	02/03/16	0	0	3	9	11
	J	02/03/16	0	0	0	0	1
	P	02/03/16	0	0	2	8	9
3	H	03/03/16	0	2	3	4	10
	J	03/03/16	0	0	0	0	8
	P	03/03/16	0	0	5	4	18

Table B.1: Abundance of dung beetles of five species collected from dung baited pitfall traps. Numbering references site identities from Figure B1. H = Human, P=Pig, J= Jaguar.

C

Supplementary Material for Chapter 3

Mammal species	**Average dung volume (g) ±SE**	**Burial intercept trap sample completeness**	**Pitfall trap sample completeness**
Sapajus nigritus Black Capuchin	37.3 ±5.3	0.96	0.66
Panthera onca Jaguar	75.2 ±5.4	0.97	0.99
Leopardus pardalis Ocelot	33.0 ±3.3	0.94	0.95
Galictis cuja Lesser Grison	11.9 ±1.0	0.33	0.82
Procyon cancrivorus Crab-eating racoon	46.1 ±2.9	0.89	0.88
Human	202.2 ±7.6	0.98	0.99
Domesticated pig	211.6 ±10.7	1.00	0.99

Table C.1: Mammal species, dung volumes used, and sample completeness for dung beetle communities in both trap types

	Explanatory variable	
Response variable	**Trap**	**Dung type**
Dung beetle abundance	$\chi^2(1) = 7.02$ p=0.008*	$\chi^2(6) = 79.21$ p<0.005*
Species richness	$\chi^2(1) = 30.86$ p<0.005*	$\chi^2(6) = 92.92$ p<0.005*
Total biomass	$\chi^2(1) = 8.39$ p<0.005*	$\chi^2(6) = 34.28$ p<0.005*
Per-beetle biomass	$\chi^2(1) = 7.98$ p = 0.005*	$\chi^2(6) = 29.21$ p <0.005*
Proportion of rollers to tunnellers	Pitfall only	$\chi^2(6) = 12.31$ p=0.055

Table C.2: Test statistic and p-value for each term included tested against a model with the term removed. Model: response variable trap + dung type + (1|dung type: dung volume). * p-values are significant at the 0.05 level.

Table C.3: Dung beetle individuals captured in each different bait and trap type

				Burial intercept trap							**Pitfall trap**							
			Bait	**C**	**G**	**H**	**J**	**O**	**P**	**R**	**C**	**G**	**H**	**J**	**O**	**P**	**R**	**Total**
Species	**Nesting strategy**	**Biomass**	**No. traps**	5	8	17	12	9	10	8	6	11	68	14	12	12	11	203
Coprophanaeus saphirinus (Sturm, 1828)	T	0.343		0	0	2	1	0	0	0	1	0	30	5	1	0	1	41
Coprophanaeus bellicosus (Olivier, 1789)	T	1.732		0	0	1	0	0	0	0	0	2	64	4	4	0	2	77
Coprophanaeus dardanus (MacLeay, 1819)	T	0.668		0	0	2	4	0	0	1	0	1	36	2	3	0	0	49
Phanaeus splendidulus (Fabricius, 1781)	T	0.262		1	0	49	33	5	10	5	0	0	112	6	1	17	0	239
Deltochilum brasilense (Castelnau, 1840)	R	0.488		0	0	0	0	0	0	0	0	0	3	0	0	0	0	3
Deltochilum furcatum (Castelnau, 1840)	R	0.341		0	0	1	1	0	0	0	1	0	36	7	1	3	0	50
Deltochilum aff. irroratum (Castelnau, 1840)	R	0.178		0	0	0	2	0	0	0	0	0	6	2	0	0	0	10
Deltochilum morbillosum (Burmeister 1848)	R	0.091		0	0	1	0	0	0	0	0	0	3	2	3	0	1	10
Canthon smaragdulus (Fabricius, 1781)	R	0.136		0	0	0	0	0	0	0	0	1	72	1	0	2	0	76
Onthophagus catharinensis Paulian, 1936	T	0.006		2	1	37	4	1	3	0	0	0	113	7	1	34	1	204
Dichotomius mormon (Ljungh, 1799)	T	0.635		5	0	46	16	0	22	3	0	0	382	15	8	62	4	563
Dichotomius sericeus (Harold 1867)	T	0.152		13	1	41	31	6	11	14	2	3	376	53	48	67	22	688
Dichotomius fissus (Harold, 1869)	T	0.277		0	0	2	0	0	0	0	3	0	47	0	0	0	1	53
Dichotomius quadrinodosus (Felsche, 1901)	T	0.324		0	0	9	5	0	3	2	0	0	78	7	3	28	9	144
Dichotomius depressicollis (Harold, 1867)	T	0.350		0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Dichotomius ascinus (Harold, 1869)	T	0.054		0	0	0	0	0	0	0	0	0	3	0	0	0	0	3
Ontherus azteca (Harold, 1869)	T	0.032		0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Canthidium punctatostriatum (Mannerheim, 1829)	T	0.021		0	0	1	1	0	0	1	1	0	8	0	0	0	0	12
Canthidium sp1	T	0.007		0	1	8	2	2	2	1	0	2	20	5	3	15	1	62
Canthidium sp2	T	0.007		0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Eutrichilium hirsutum Boucomont, 1928	T	0.004		0	0	0	0	0	0	0	0	0	3	0	0	0	0	3
Chalocopris hesperus (Olivier, 1789)	T	0.080		0	0	0	0	0	0	0	0	0	3	0	0	0	0	3
Ateuchus subquadratus (Harold, 1868)	T	0.05		0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Eurysternus inflexus (Germar, 1824)	T	0.06		0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
			Total	**21**	**3**	**200**	**100**	**14**	**51**	**27**	**8**	**9**	**1397**	**116**	**76**	**231**	**42**	**2295**

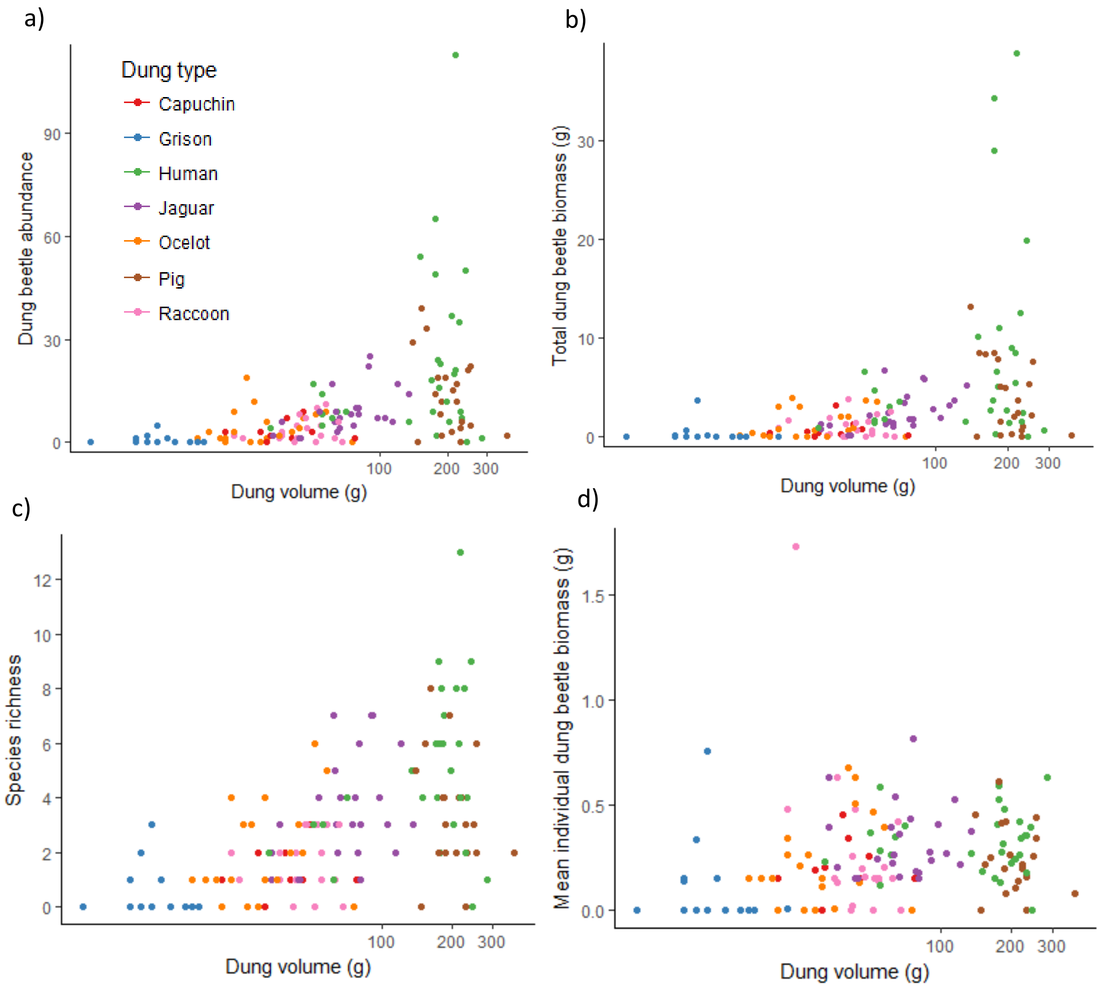


Figure C.1: Total dung beetle a) abundance and b) biomass c) species richness and d) individual beetle biomass plotted against dung volume for each dung type.

D

Supplementary Material for Chapter 4

Species	Bag trap n^o	Pitfall trap n^o	Extinction scenario orders			
			Red Book	**Dung vol.**	**Mam. rarity**	**Mam. body size**
Tamandua tridactyla (Linnaeus, 1758) Giant ant eater	1	2	1	3	6	5
Sapajus nigritus (Linnaeus, 1758) Black Capuchin	5	6	3	7	2	6
Cerdocyon thous (Linnaeus,1766) Crab-eating fox	1	1	3	1	7	3
Panthera onca (Linnaeus, 1758) Jaguar	12	14	1	4	1	1
Leopardus pardalis (Linnaeus, 1758) Ocelot	9	12	2	2	5	2
Galictis cuja (Molina, 1782) Lesser Grison	8	11	3	6	3	7
Procyon cancrivorus (Cuvier, 1798) Crab-eating raccoon	8	11	3	5	4	4
Human	17	68	Not included in extinction scenarios			
Pig	10	12	Not included in extinction scenarios			
Total	71	137				

Table D.1: Dung beetle sampling details and order of removal for extinction scenarios, Paraná red book extinction scenario (Mikich & Bérnils 2004)

Table D.2: Abundance of dung beetle species collected per bait type, percentage abundance of each dung beetle species, dry mass (g) and specialisation (d')

Species	**Anteater**	**Crab-eating fox**	**Black Capuchin**	**Lesser Grison**	**Jaguar**	**Ocelot**	**Crab-eating Raccoon**	**Total**	**%**	**d’**	**Mass ±sd (g)**
Coprophanaeus dardanus (MacLeay, 1819)				1	6	3	1	11	2.36	0.044	0.67 ±0.14
Coprophanaeus saphirinus (Sturm, 1828)			1		6	1	1	9	1.93	0.038	0.34 ±0.11
Coprophanaeus bellicosus (Olivier, 1789)	3			2	4	4	2	15	3.21	0.056	1.73 ±0.61
Phanaeus splendidulus (Fabricius, 1781)	2		1		39	6	5	53	11.35	0.018	0.26 ±0.09
Dichotomius fissus (Harold, 1869)			3				1	4	0.86	0.091	0.28 ±0.056
Dichotomius sericeus (Harold 1867)	14	2	15	4	84	54	36	217	46.47	0.031	0.15 ±0.067
Dichotomius quadrinodosus (Felsche, 1901)	3				12	3	11	29	6.21	0.032	0.32 ±0.12
Dichotomius mormon (Ljungh, 1799)	4		5		31	8	7	58	12.42	0.029	0.63 ±0.20
Deltochilum furcatum (Castelnau, 1840)		1	1		8	1		11	2.36	0.032	0.34 ±0.10
Deltochilum aff. irroratum (Castelnau, 1840)					4			4	0.86	0.076	0.18 ±0.067
Deltochilum morbillosum (Burmeister 1848)					2	3	1	6	1.28	0.108	0.091 ±0.043
Canthon smaragdulus (Fabricius, 1781)				1	1			2	0.43	0.073	0.14 ±0.045
Onthophagus catharinensis Paulian, 1936	6		2	1	11	2	1	26	5.57	0.026	0.0064 ±0.0024
Canthidium punctatostriatum (Mannerheim, 1829)			1		1		1	3	0.64	0.041	0.021 ±0.011
Canthidium sp 1	2			3	7	5	2	19	4.07	0.058	0.0068 ± 0.0024
Number of individuals	**34**	**3**	**29**	**12**	**216**	**90**	**69**	**467**			
Number of species	**6**	**2**	**8**	**6**	**14**	**11**	**12**				

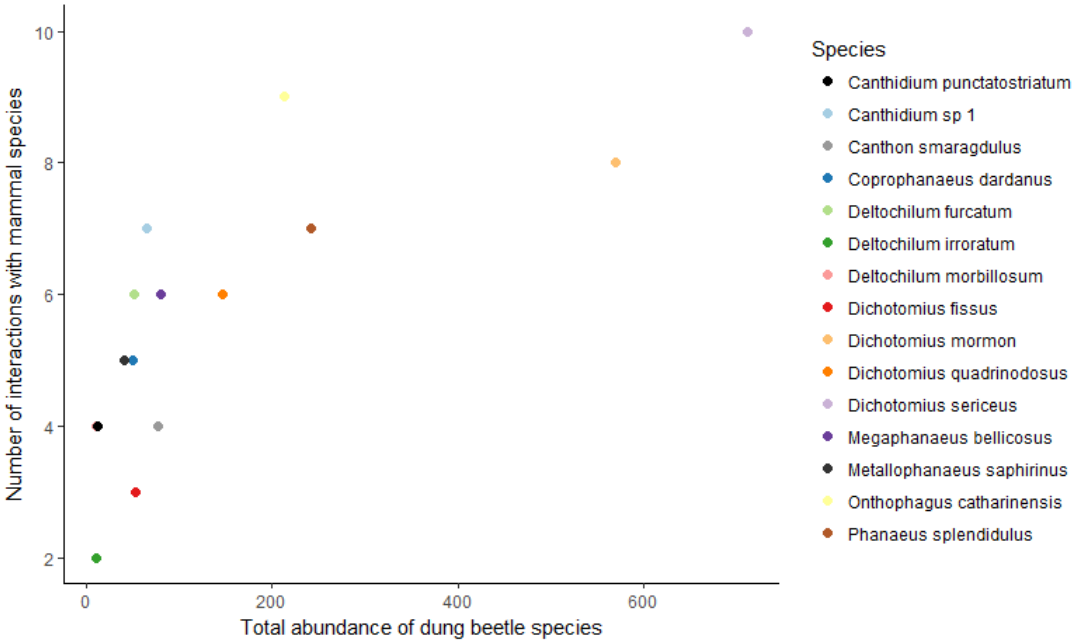


Figure D.1: Accumulation curve for dung beetle- mammal species interactions

Species	**Feeding activity**	**Feeding preference**	**Reference**
Coprophanaeus dardanus	T	Generalist	Salomão, Lira & Iannuzzi 2014
Coprophanaeus saphirinus	T	Necrophagous	Almeida et al. 2009; Silva, Vaz-de-Mello & Mare 2012
Megaphanaeus bellicosus	T	Necrophagous	Falqueto 2005
Phanaeus splendidulus	T	Generalist	Silva et al. 2012; Bogoni & Hernández 2014
Deltochilum furcatum	R	Coprophagous	Bogoni & Hernández 2014
Deltochilum irroratum	R	Generalist	Silva & Hernández 2007
Deltochilum morbillosum	R	Generalist	Silva et al. 2012; Bogoni & Hernández 2014
Canthon smaragdulus	R	Necrophagous	Almeida & Mise 2009
Onthophagus catharinensis	T	Coprophagous	Silva et al. 2012
Dichotomius mormon	T	Coprophagous	Bogoni & Hernández 2014
Dichotomius fissus	T	Coprophagous	Bogoni & Hernández 2014
Dichotomius sericeus	T	Generalist	Filgueiras et al. 2009; Bogoni & Hernández 2014; Salomão et al. 2014
Dichotomius quadrinodosus	T	Insufficient data	Falqueto et al. 2005
Canthidium sp 1	T	No data	
Canthidium punctatostriatum	T	No data	

Table D.3: Dung beetle species functional traits: feeding activity (roller =R, tunneler = T) and feeding preference

Species	**Visual encounters**	**Camera trap events**	**Signs**
Sphiggurus villosus Orange-spined haired dwarf porcupine		1	
Didelphis aurita Southeastern common opossum		22	5
Tamandua tetradactyla Southern Tamandua		11	
Sapajus nigritus Black Capuchin	1		
Alouata fusca Brown howler monkey	1		
Procyon cancrivorus Crab eating racoon		1	4
Nasua nasua South American Coati		1	
Cerdocyon thous Crab eating fox	1	13	10
Eira Barbara Tayra		6	
Lontra longicaudis Neotropical otter	1		2
Galictis cuja Lesser Grison		3	1
Felidae: Leopardus/Herpailurus Small cat		3	4
Puma concolor Puma		2	
Mazama gouazoubira Grey (brown) brocket deer	1	6	4
Hydrochaeris hydrochaeris Capybara	1	2	1
Dasyprocta azarae Azara's agouti		48	2
Dasypus novemcinctus Nine-banded long-nosed armadillo		32	4

Table D.4: Mammal species recorded in three sites over the census period

Dung beetle sampling information with mammal dung types

Pitfall trapping was carried out four times, in December (2015), January, February and March (2016). Bag trapping was carried out three times, in December

(2015), January and February (2016). Each trap type was set at each of the three sites on consecutive days, with a week interval between each method of trapping. In each transect: human, ocelot, pig and jaguar dung were used as a bait, with the trap point randomised between transects. Due to a lack of availability, the other dung types could not be used for all trapping periods. Grison and raccoon dung were included for all rounds of trapping except one pitfall and bag transect at one site in January. Capuchin dung was used for all sites and both trap types in December, and two of the three sites in January. In February, Capuchin dung was used for pitfall trapping at just one site. Anteater and Peccary dung were used three times, and crab-eating fox dung only twice. Model selection using likelihood tests ANOVA of log mass of dung beetles predicted by log mass of dung and mammal guild: A linear model was fitted to the transformed data (dung beetle mass and dung volume both log transformed, with 0 values removed). Bait type was not included as a fixed factor as there were too few replicates of several dung types (crab eating fox, anteater, black capuchin). Categories were designated as mammal feeding guilds (omnivore, carnivore, herbivore) to account for the possible differences between dung content and the biomass of dung beetles attracted to dung types. A linear model was fitted and likelihood ratio tests applied to perform model simplification. Mammal guild was found to be non significant ($F_{3,44}$=2.1038, p=0.1133) and dropped from the model. So that the equation log dung beetle biomass = log dung mass * 0.5761-2.0161 was found to be the best fit for the data. This was used to calculate a biomass of dung beetle expected per average dung produced by each bait type.

	Index value	**Mean from null networks**	**P value (df=9999)**	**Mean from subsampled pitfall network**	**P value (df=999)**
Feeding network					
Nestedness	13.18	10.76	0.28		
H2'	0.13	0.092	0.087		
Linkage density	3.84	4.09	0.082		
Breeding network					
Nestedness	16.71	12.68	0.19	17.49	0.002
H2'	0.14	0.093	0.011	0.74	0.001
Linkage density	4.57	5.00	0.019	2.81	0.001

Table D.5: Network indices for the feeding and breeding networks, and their significance values compared to randomly created null networks.

E

Supplementary Material for Chapter 5

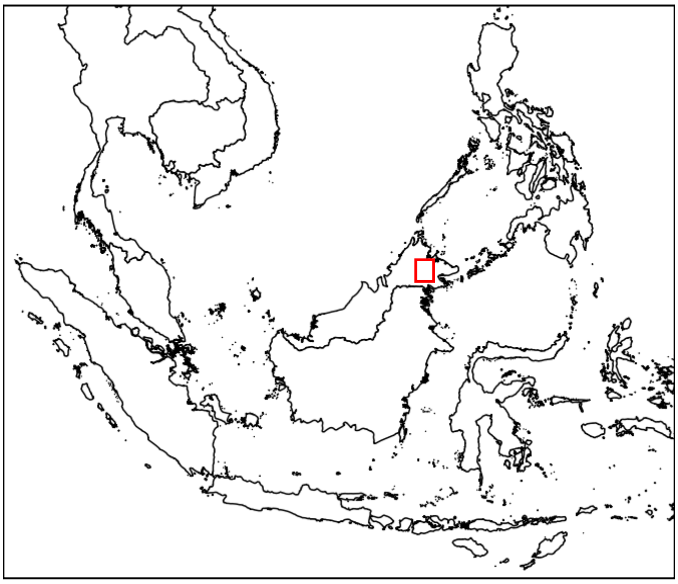


Figure E.1: Location of Stability of Altered forest ecosystems project in Sabah, Malaysian Borneo.

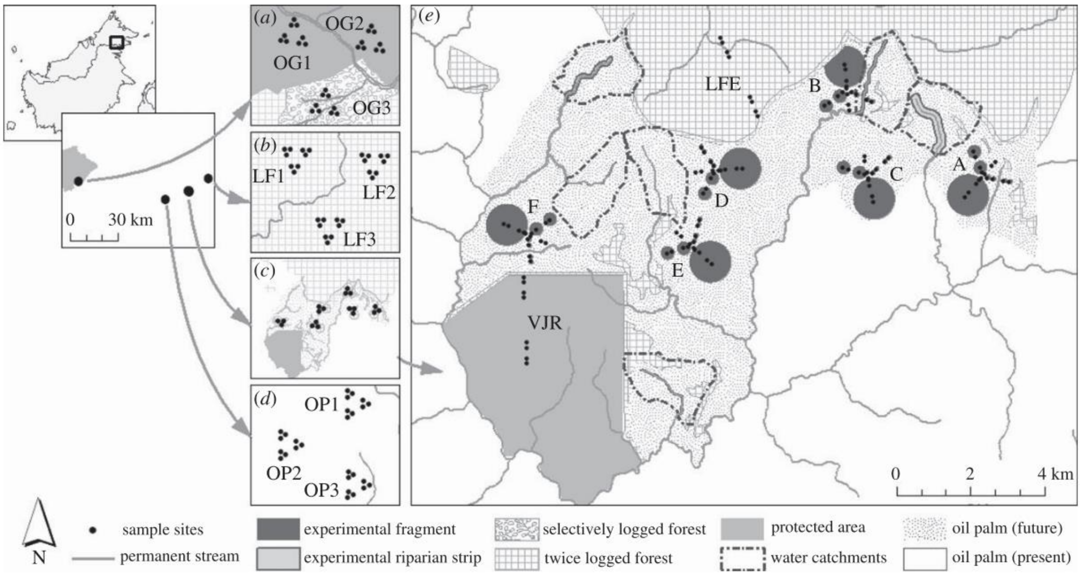


Figure E.2: Map of SAFE sites and layout reproduced from Ewers et al. (2011).

Species	**Weight (mg)**
Diurnal tunneller	
Caccobius bawangensis	1.112
Onthophagus aff. hidakai	2.980
Onthophagus aff. rutilans	32.021
Onthophagus aff. tritibiodentatus	3.107
Onthophagus angustatus	26.137
Onthophagus aphodiodes	8.169
Onthophagus borneensis	48.675
Onthophagus cervicapra	9.000
Onthophagus clivemurus	20.142
Onthophagus deliensis	3.281
Onthophagus dux	30.306
Onthophagus fujii	9.621
Onthophagus incisus	43.000
Onthophagus indecorious sp1	4.000
Onthophagus indecorious sp2	4.000
Onthophagus kawahari	1.098
Onthophagus leavis	14.608
Onthophagus mulleri	34.214
Onthophagus negrobscurior	7.750
Onthophagus nr. borneensis	48.675
Onthophagus obscurior	9.917
Onthophagus ochromurus	17.333
Onthophagus pacificus	12.194
Onthophagus pastillatus	5.214
Onthophagus pavidus	20.403
Onthophagus rorarius	48.675
Onthophagus rudis	5.724
Onthophagus rugicollis	17.000
Onthophagus sarawacus	55.572
Onthophagus semiaureus	21.533
Onthophagus semicupreus	5.325
Onthophagus sideki	5.153
Onthophagus taeniatus	13.200
Onthophagus trituber	5.623
Onthophagus vulpes	13.000
Onthophagus waterstradi	14.608
Proagaderus wantanabei	145.000
Synapsis ritsemae	443.865
Yvescamberforti sarawacus	54.130
Diurnal roller	
Ochicanthon masumutoi	6.507
Ochicanthon dytiscoides	6.271
Paragymnopleurus maurus	203.896
Paragymnopleurus sparsus	80.000
Paragymnopleurus striatus	119.869
Sysiphus thoracicus	12.000
Nocturnal tunneller	
Catharsius dayacus	733.000
Catharsius rendaupaulina	914.654
Copris agnus	240.750
Copris ramiosiceps	81.538
Copris sinicus	154.760
Microcopris doriae	61.000
Microcopris hidakai	60.410

Table E.1 Dung beetle species and weights.

Species	Weight kg
Carnivore	
Banded Linsang	0.68
Bay Cat	3.43
Sunda Clouded Leopard	14.95
Collared Mongoose	1.40
Domestic Dog	15.00
Flying Squirrel	3.53
Leopard Cat	2.78
Malay Weasel	0.57
Malay Civet	7.35
Marbled Cat	2.83
Oriental Small clawed Otter	3.53
Short tailed Mongoose	1.40
Yellow throated Marten	2.50
Frugivore	
Binturong	13.00
Bornean Gibbon	5.91
Brooke s Squirrel	0.11
Common Palm Civet	3.20
Ear spot Squirrel	0.21
Four striped Ground Squirrel	0.18
Greater Mouse deer	5.27
Horse tailed Squirrel	0.36
Lesser Mouse deer	2.25
Long tailed Macaque	4.57
Long tailed Porcupine	1.75
Malay Porcupine	8.00
Masked Palm Civet	4.30
Bornean Orangutan	53.41
Pig tailed Macaque	7.82
Plantain Squirrel	0.21
Prevost's Squirrel	0.40
Thick spined Porcupine	4.58
Tufted Ground Squirrel	1.35
Herbivore	
Asian Elephant	3269.79
Hose's Langur	6.28
Maroon Langur	6.35
Red Muntjac	17.61
Sambar Deer	177.52
Banteng	635.97
Yellow Muntjac	18.94
Insectivore	
Banded Civet	1.26
Hose's Civet	1.26
Large Treeshrew	0.18
Least Pygmy Squirrel	0.02
Lesser Treeshrew	0.07
Low's Squirrel	0.08
Moon Rat	0.76
Pen tailed Treeshrew	0.04
Slender Squirrel	0.07
Slender Treeshrew	0.11
Sunda Stink Badger	2.50
Striped Treeshrew	0.17
Sunda Pangolin	4.86
Plain Treeshrew	0.01
Western Tarsier	0.11
Omnivore	
Bearded Pig	70.00
Black Rat	0.14
Brown Spiny Rat	0.15
Chestnut bellied Spiny Rat	0.16
Dark tailed Tree Rat	0.07
Long tailed Giant Rat	0.35
Muller's Rat	0.36
Polynesian Rat	0.05
Red Spiny Rat	0.15
Small Spiny Rat	0.16
Sun Bear	57.08
Whitehead's Rat	0.05
Spiny Rat	0.09

Table E.2 Mammal species and body mass.

Explanatory variables	**Old growth**	**Fragment**	**Oil palm**
Carnivore biomass (kg)	0.71 ± 0.04	1.02 ± 0.03	2.71 ± 0.14
Frugivore biomass (kg)	2.40 ± 0.17	3.83 ± 0.18	0.52 ± 0.06
Herbivore biomass (kg)	35.40 ± 3.50	107.27 ± 13.55	11.70 ± 0.87
Insectivore biomass (kg)	0.25 ± 0.02	0.21 ± 0.01	0.03 ± 0.002
Omnivore biomass (kg)	11.42 ± 1.38	16.28 ± 0.52	1.18 ± 0.13
Forest biomass	220.32 ± 4.05	55.17 ± 4.05	14.19 ± 1.07
Soil moisture	44.74 ± 2.71	48.87 ± 1.99	59.02 ± 2.07
Soil temperature	28.80 ± 0.07	27.51 ± 0.30	27.73 ± 0.45
Canopy diversity	0.29 ± 0.02	0.28 ± 0.15	0.32 ± 0.03
Air temperature	25.59 ± 0.13	27.09 ± 0.21	30.24 ± 0.29

Table E.3 Average ± SE of explanatory variables across land use types.

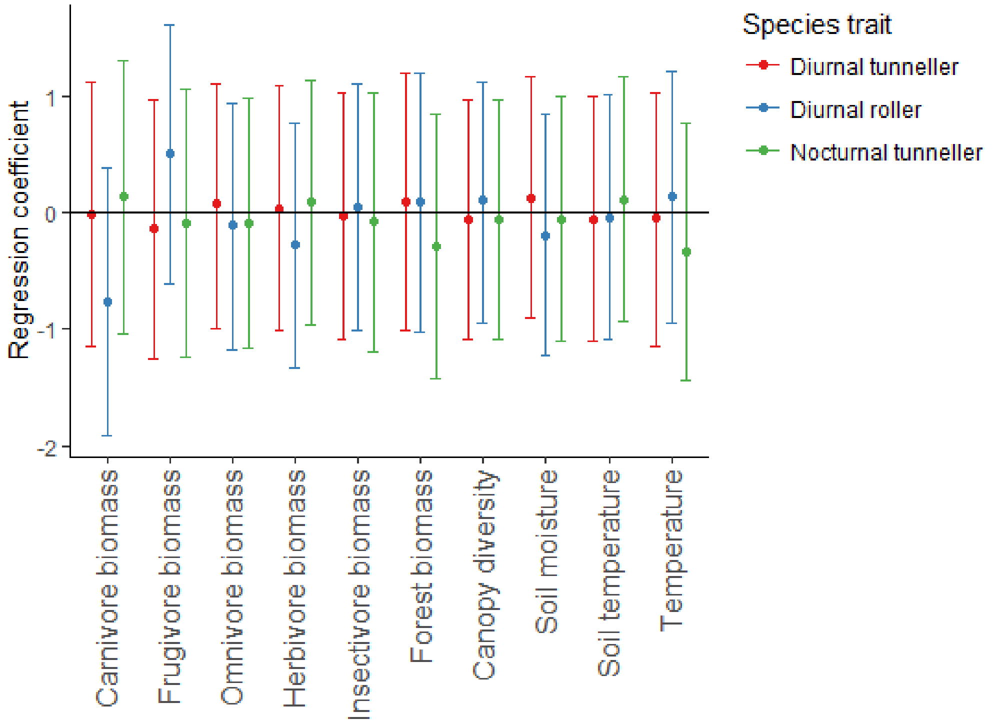
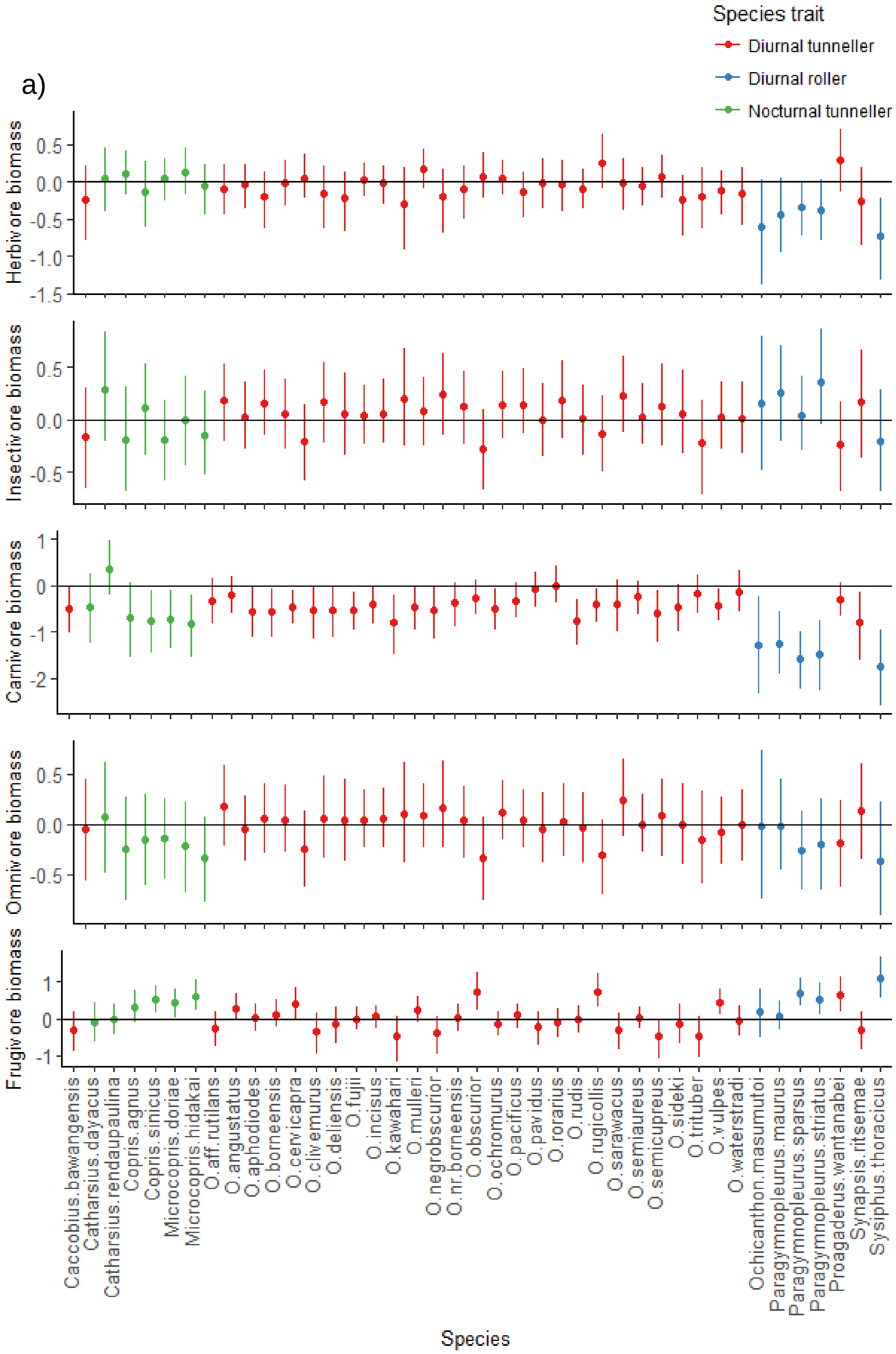


Figure E.3: Model parameter estimates for response of dung beetle species traits to explanatory variables. Mean and 95% credible intervals calculated from posterior distributions.


Species trait
Diurnal tunneller
Diurnal roller
Nocturnal tunneller
a)
Herbivore biomass
0.5
0.0
-0.5
-1.0
-1.5
Insectivore biomass
0.5
0.0
-0.5
Carnivore biomass
1
0
-1
-2
Omnivore biomass
0.5
0.0
-0.5
Frugivore biomass
1
0
-1
Caccobius.bawangensis
Catharsius.dayacus
Catharsius.rendaupaulina
Copris.agnus
Copris.sinicus
Microcopris.doriae
Microcopris.hidakai
O.aff.rutilans
O.angustatus
O.aphodiodes
O.borneensis
O.cervicapra
O.clivemurus
O.deliensis
O.fujii
O.incisus
O.kawahari
O.mulleri
O.negrobscurior
O.nr.borneensis
O.obscurior
O.ochromurus
O.pacificus
O.pavidus
O.rorarius
O.rudis
O.rugicollis
O.sarawacus
O.semiaureus
O.semicupreus
O.sideki
O.trituber
O.vulpes
O.waterstradi
Ochicanthon.masumutoi
Paragymnopleurus.maurus
Paragymnopleurus.sparsus
Paragymnopleurus.striatus
Proagaderus.wantanabei
Synapsis.ritsemae
Sysiphus.thoracicus
Species

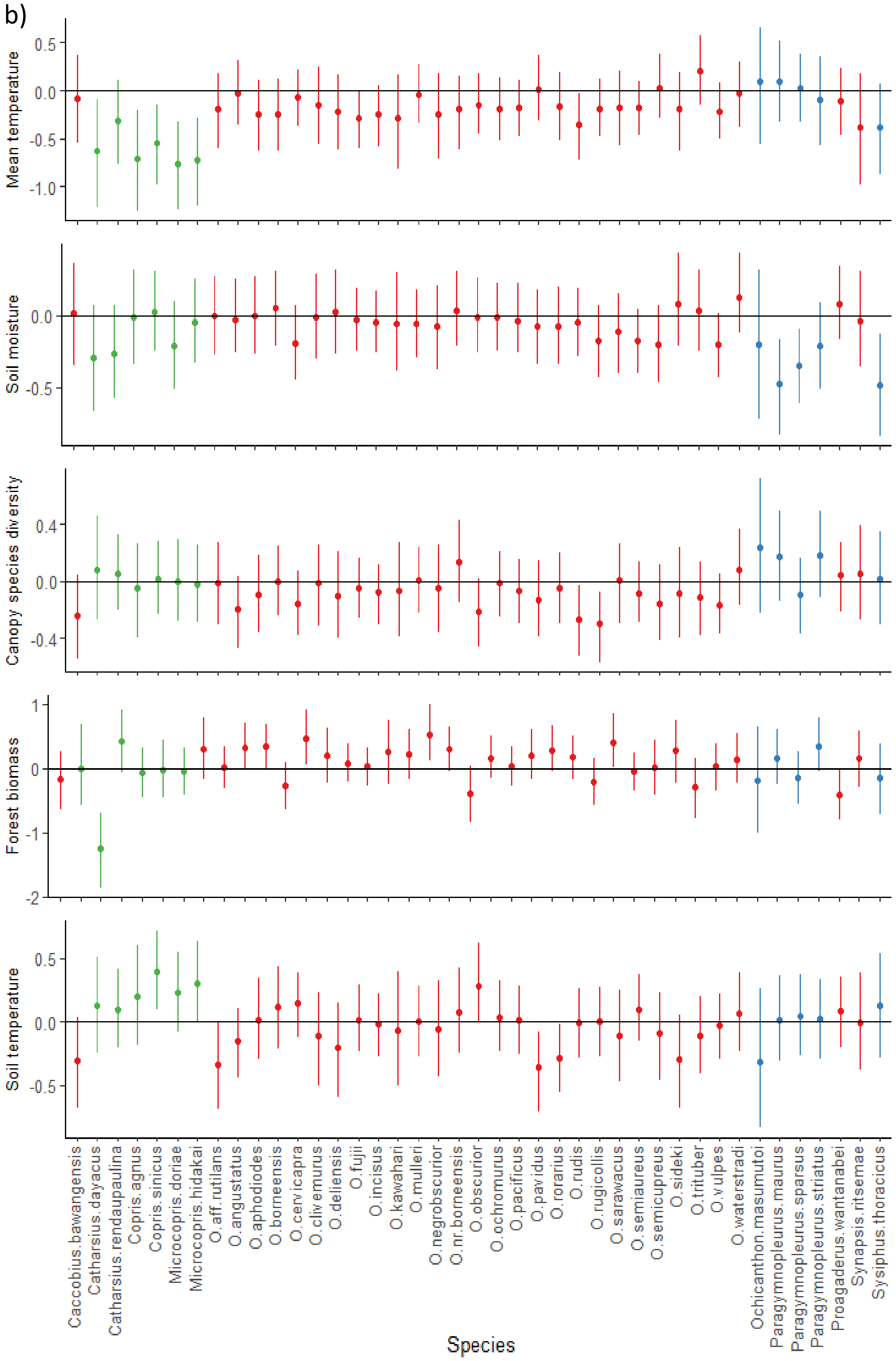
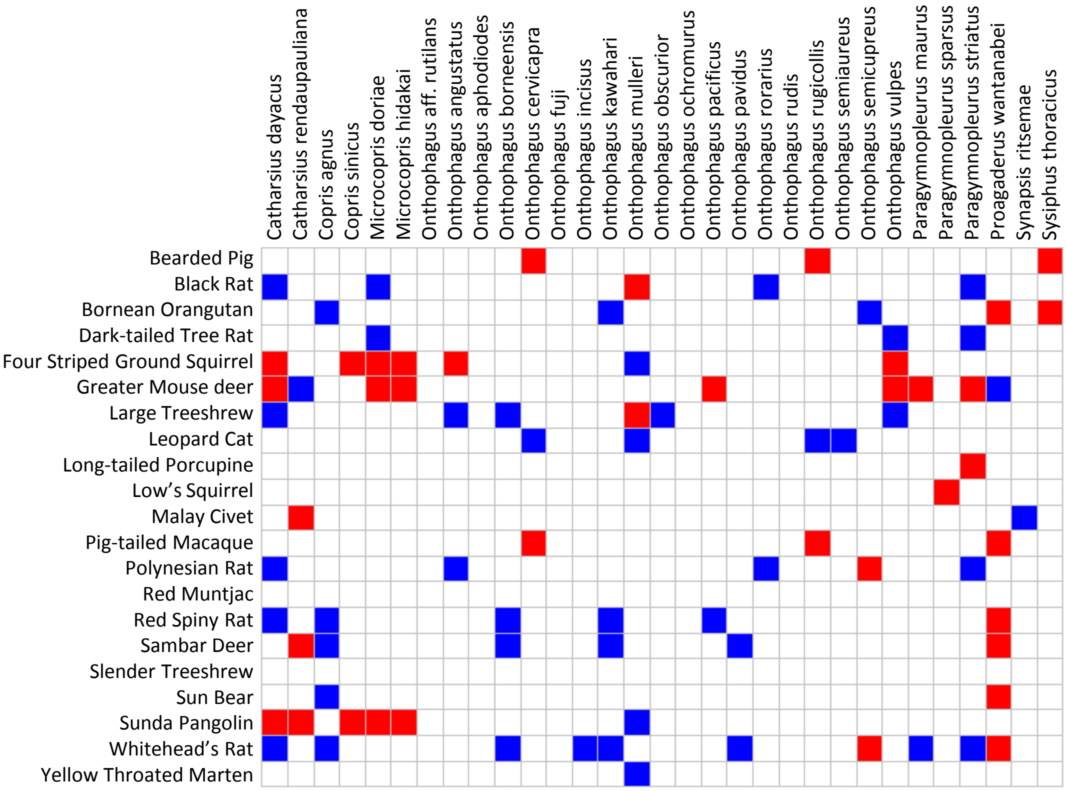
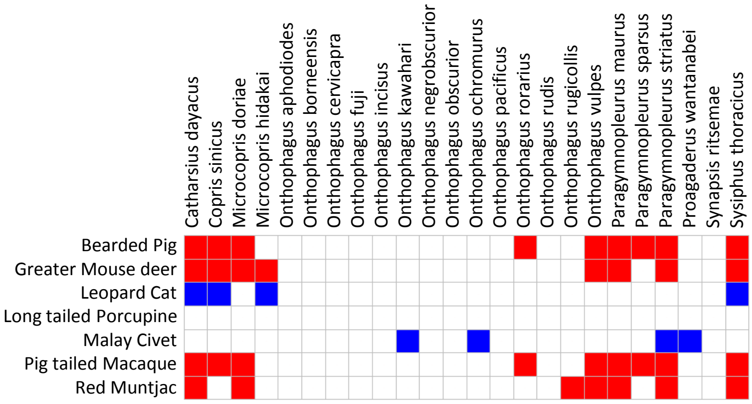


Figure E.4: Species-specific regression coefficients for a) mammal trophic group biomass and b) environmental covariates. Mean and 95% probability interval estimated from the model.



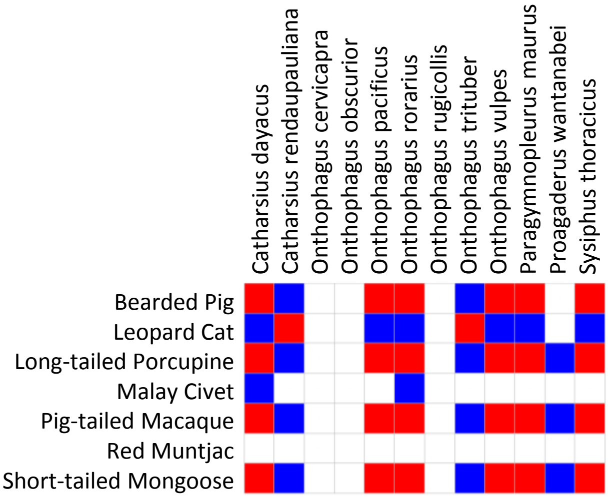
	Catharsius dayacus	Catharsius rendaupauliana	Copris agnus	Copris sinicus	Microcopris doriae	Microcopris hidakai	Onthophagus aff. rutilans	Onthophagus angustatus	Onthophagus aphodiodes	Onthophagus borneensis	Onthophagus cervicapra	Onthophagus fuji	Onthophagus incisus	Onthophagus kawahari	Onthophagus mulleri	Onthophagus obscurior	Onthophagus ochromurus	Onthophagus pacificus	Onthophagus pavidus	Onthophagus rorarius	Onthophagus rudis	Onthophagus rugicollis	Onthophagus semiaureus	Onthophagus semicupreus	Onthophagus vulpes	Paragymnopleurus maurus	Paragymnopleurus sparsus	Paragymnopleurus striatus	Proagaderus wantanabei	Synapsis ritsemae	Sysiphus thoracicus
Bearded Pig											🟥											🟥									🟥
Black Rat	🟦				🟦										🟥					🟦								🟦			
Bornean Orangutan			🟦											🟦										🟦					🟥		🟥
Dark-tailed Tree Rat					🟦																				🟦			🟦			
Four Striped Ground Squirrel	🟥			🟥	🟥	🟥		🟥							🟦										🟥						
Greater Mouse deer	🟥	🟦			🟥	🟥												🟥							🟥	🟥		🟥	🟦		
Large Treeshrew	🟦							🟦		🟦					🟥	🟦									🟦						
Leopard Cat											🟦				🟦							🟦	🟦								
Long-tailed Porcupine																												🟥			
Low’s Squirrel																											🟥				
Malay Civet		🟥																												🟦	
Pig-tailed Macaque											🟥											🟥							🟥		
Polynesian Rat	🟦							🟦												🟦				🟥				🟦			
Red Muntjac																															
Red Spiny Rat	🟦		🟦							🟦				🟦				🟦											🟥		
Sambar Deer		🟥	🟦							🟦				🟦					🟦										🟥		
Slender Treeshrew																															
Sun Bear			🟦																										🟥		
Sunda Pangolin	🟥	🟥		🟥	🟥	🟥									🟦																
Whitehead’s Rat	🟦		🟦							🟦			🟦	🟦					🟦					🟥		🟦		🟦	🟥		
Yellow Throated Marten															🟦																

Figure E.5: Pair wise species co-occurence between dung beetles and mammals in Old growth forest. Red = positive associations. Blue = negative associations.



	Catharsius dayacus	Copris sinicus	Microcopris doriae	Microcopris hidakai	Onthophagus aphodiodes	Onthophagus borneensis	Onthophagus cervicapra	Onthophagus fuji	Onthophagus incisus	Onthophagus kawahari	Onthophagus negrobscurior	Onthophagus obscurior	Onthophagus ochromurus	Onthophagus pacificus	Onthophagus rorarius	Onthophagus rudis	Onthophagus rugicollis	Onthophagus vulpes	Paragymnopleurus maurus	Paragymnopleurus sparsus	Paragymnopleurus striatus	Proagaderus wantanabei	Synapsis ritsemae	Sysiphus thoracicus
Bearded Pig	🟥	🟥	🟥												🟥			🟥	🟥	🟥	🟥			🟥
Greater Mouse deer	🟥	🟥	🟥	🟥														🟥	🟥		🟥			🟥
Leopard Cat	🟦	🟦		🟦																				🟦
Long tailed Porcupine																								
Malay Civet										🟦			🟦								🟦	🟦		
Pig tailed Macaque	🟥	🟥	🟥												🟥			🟥	🟥	🟥	🟥			🟥
Red Muntjac	🟥		🟥														🟥	🟥	🟥		🟥			🟥

Figure E.6: Pair wise species co-occurence between dung beetles and mammals in Logged forest. Red= positive associations. Blue = negative associations.



	Catharsius dayacus	Catharsius rendaupauliana	Onthophagus cervicapra	Onthophagus obscurior	Onthophagus pacificus	Onthophagus rorarius	Onthophagus rugicollis	Onthophagus trituber	Onthophagus vulpes	Paragymnopleurus maurus	Proagaderus wantanabei	Sysiphus thoracicus
Bearded Pig	🟥	🟦			🟥	🟥		🟦	🟥	🟥		🟥
Leopard Cat	🟦	🟥			🟦	🟦		🟥	🟦	🟦		🟦
Long-tailed Porcupine	🟥	🟦			🟥	🟥		🟦	🟥	🟥	🟦	🟥
Malay Civet	🟦					🟦						
Pig-tailed Macaque	🟥	🟦			🟥	🟥		🟦	🟥	🟥	🟦	🟥
Red Muntjac												
Short-tailed Mongoose	🟥	🟦			🟥	🟥		🟦	🟥	🟥	🟦	🟥

Figure E.7: Pair wise species co-occurence between dung beetles and mammals in Oil Palm. Red = positive associations. Blue = negative associations.

F

Supplementary Material: Additional published paper

Data from Chapter 4 was used in the following paper:

Frank, K., Krell, F.T., Slade, E.M., Raine, E.H., Chiew, L.Y., Schmitt, T.,Vairappan, C.S., Walter, P., Blüthgen, N. (2018) Global dung webs: high trophic generalism of dung beetles along the latitudinal diversity gradient. *Ecology Letters*, 21, 1229–1236.

ECOLOGY LETTERS

Ecology Letters, (2018) **21**: 1229–1236 doi: 10.1111/ele.13095

LETTER

Global dung webs: high trophic generalism of dung beetles along the latitudinal diversity gradient

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Abstract

At the global scale, species diversity is known to strongly increase towards the equator for most taxa. According to theory, a higher resource specificity of consumers facilitates the coexistence of a larger number of species and has been suggested as an explanation for the latitudinal diversity gradient. However, only few studies support the predicted increase in specialisation or even showed opposite results. Surprisingly, analyses for detritivores are still missing. Therefore, we performed an analysis on the degree of trophic specialisation of dung beetles. We summarised 45 studies, covering the resource preferences of a total of 994503 individuals, to calculate the dung specificity in each study region. Our results highlighted a significant (4.3-fold) increase in the diversity of beetles attracted to vertebrate dung towards the equator. However, their resource specificity was low, unrelated to diversity and revealed a highly generalistic use of dung resources that remained similar along the latitudinal gradient.

Keywords

Biodiversity, brown food web, dung beetles, Scarabaeoidea, ecological networks, meta analysis, latitudinal diversity gradient.

Ecology Letters (2018) **21**: 1229–1236

INTRODUCTION

The latitudinal gradient, particularly the pronounced increase in plant and animal diversity towards the equator, has fascinated biologists for a long time (Darwin 1859; Wallace 1878) and is still a popular research topic (Hillebrand 2004; LaManna *et al.* 2017; Roslin *et al.* 2017). A predicted *increase* in specialisation towards the tropics has been suggested as an explanation of the high diversity found there (MacArthur 1972). Consequently, for a given resource spectrum, a higher resource partitioning in the tropics could contribute to reduce interspecific competition, and a larger resource spectrum in the tropics may additionally increase this trend. Yet, only a few analyses of trophic or mutualistic interactions have revealed such a trend (Olesen & Jordano 2002; Dyer *et al.* 2007; Peguero *et al.* 2017). On the contrary, specialisation of pollinators and frugivores (Schleuning *et al.* 2012), and bark beetles (Beaver 1979) on their host plants decreases towards the equator, and the high specialisation level of herbivores and host–parasitoid networks remains similar along the latitudinal gradient (Novotny *et al.* 2006; Morris *et al.* 2014; Forister *et al.* 2015).

At the base of every food web, decomposers process organic material and provide a nutritional basis for higher trophic levels. Although plant litter is abundant, but comparably poor in nutrient quality for consumers, animal carcasses or dung – although representing already processed food – are high quality resources, with high levels of all essential nutrients such as amino acids, fatty acids and sterols (Enser *et al.* 1996; Carter *et al.* 2007; Frank *et al.* 2017a). Consequently, competition among detritivores for carcasses and dung can be pronounced, an important prerequisite for niche differentiation among competing species. Yet, there are no assessments of global specialisation patterns for detritivores on their resources.

Dung beetles (Scarabaeoidea part.) are known to use a wide range of dung types among a few other resources such as carcasses, humus and fungi. However, most species feed on vertebrate dung as their main resource (Hanski & Cambefort 1991). These beetles are almost ubiquitous in all climatic zones, including hot spots with over 80 sympatric species in tropical forests and savannahs (Hanski & Cambefort 1991; Davis 2000; Feer & Hingrat 2005; Barragan *et al.* 2011). Hence, we focused on the coprophagous groups of this cosmopolitan superfamily of insects, which evolved a detritivorous lifestyle over a hundred million years ago (Krell 2006; Philips 2011), to conduct a meta-analyses of their resource specificity. We compiled data sets from across the globe on the distribution of dung beetles occurring on two or more vertebrate dung types to quantify the extent of dung partitioning

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across beetle species, as a potential mechanism fostering coexistence and thus diversity. We assessed trends in species diversity and dung type specialisation along the latitudinal gradient and with increasing altitude. Although highly specialised tropical dung beetle species exist, often utilising resources other than vertebrate faeces and differentiated in several other niche dimensions, the global analysis for beetle communities captured with commonly available mammalian dung revealed a highly generalistic use of dung resources. This study highlights findings contrary to classical niche theory and fills a gap in current knowledge of detritivores as a basic trophic level.

MATERIAL AND METHODS

We assembled data sets from the literature that included dung beetles trapped by or surveyed from two or more types of dung in the same study area. Most surveys of dung beetle diversity include only a single type of dung, hence could not be used to quantify dung-resource specialisation. For the comparability of the dung-resource specificity, we excluded carrion and vegetable matter as resources in seven studies. We required studies that provided the total abundance of each dung beetle species on each dung type, which excluded studies that pooled species at the genus level, or where abundances were only summarised across dung types. For studies that sampled within different habitats (i.e. forests and grasslands), but with the same dung types, we conducted separate analyses for each habitat to avoid pooling habitat-specific dung beetle communities. In total, we found 34 papers published between 1966 and 2017 that fit our criteria. In addition, we also included 11 of our own unpublished data sets. All data sets including geographic coordinates, the total number beetle species, and the degree of specialisation (see below) are summarised in Table S1; additional information for separate subsets of the data (habitats) is also included therein.

Data analysis

For improved comparability and to account for variation in sampling and total abundance among the studies, we calculated rarefied diversity (based on 100 permutations), as the studies showed variation in sampling effort, beetle density, and consequently, the total number of individuals collected. Unlike species richness, the Shannon diversity H' has the advantage to account for evenness in species abundance (while being closer to richness in uneven assemblages than Simpson's); its exponential form ($e^{H'}$) converts the index to an 'effective' number of species which is equivalent to the richness of equally common species (Jost 2006). We also computed raw richness (unweighted for abundance) for comparison (Fig. S2). We set a minimum value of 100 individuals for rarefaction. In seven networks (from four studies, see Table S1), the number of individuals was below this threshold and so the non-rarefied effective Shannon diversity was used for these networks.

As a measure of complementary specialisation in networks, that is, the degree of resource partitioning across dung beetle species, the standardised two-dimensional Shannon entropy H_2' (Blüthgen *et al.* 2006) was calculated for the beetle species × dung type matrix with number of individual beetles as cell entries. The minimum ($H_2' = 0$) is defined for the case where each of the dung beetle species is utilising different dung types in similar proportions (e.g., cow 70%, horse 30%), whereas the maximum level ($H_2' = 1$) is reached if all dung types are used as exclusively as possible by different beetle species. Such minimum and maximum H_2' for each network were defined by heuristically re-distributing the beetle individuals across dung types to the highest and lowest entropy possible after fixing the marginal totals of the matrix. Hence, the total abundance of each beetle species and the total number of beetle individuals per dung type are maintained for this standardised method, facilitating comparisons across networks that vary in number of species and individuals. In a null model based on the Patefield's algorithm, also based on fixed marginal totals, the individuals were randomly distributed 10^5 times, showing that in 90% of the networks, H_2' was significantly higher than random (Table S1) (Blüthgen *et al.* 2006). To compare the degree of specialisation on each type of dung i, we also computed the species-level Kullback–Leibler distance d_i' that is related to H_2' (Blüthgen *et al.* 2006). For each dung type i, d_i' describes the exclusiveness of the beetle species attracted, that is, $d_i' = 0$ if the dung type i is used by similar proportions of each beetle species as found across all other dung types together, while $d_i' = 1$ if dung type i attracts only exclusive beetle species.

We also quantified the relative attractiveness of dung types, standardised for each network as N_i/N_{max}, where N_i is the total number of beetle individuals recorded on dung type i and N_{max} the maximum number of beetles found for any dung type in this network. In the same way, we quantified the relative number of species attracted as S_i/S_{max}, with S_i being the beetle species richness for dung type i and S_{max} the maximum richness for any dung type in this network. Note that there is no 'standard' dung or methodology across all studies, which limits the comparability, as each dung type is evaluated in a variable context of other dung types offered in the same study. Nevertheless, this analysis should be useful for understanding the role of different dung types across the data sets. We thus tested whether these parameters change along the latitudinal gradient for five of the most attractive dung types with the largest number of sampled beetles: human, wildebeest, donkey, sheep and pig.

We used a linear mixed effects model to test for effects on a latitudinal gradient, accounting for potential linear and quadratic effects of altitude. We thus employed altitude, altitude^2 and absolute latitude as fixed factors. To account for non-independence of data within studies providing multiple networks from the same region, we used the region(s) of each study (geographic coordinates) as a random factor. We used this model structure to test the following response variables: resource specificity (H_2'), rarefied effective Shannon diversity ($e^{H'}$), specialisation levels for dung types (d_i'), individual and species based attractiveness of dung ($N_i/N_{max;}$ S_i/S_{max}).

Data analyses were conducted with the statistical software R 3.3.2 (R Core Team 2016). For community analyses (species richness, Shannon diversity), we used the R package 'vegan' (Oksanen *et al.* 2007).

RESULTS

A total of 116 dung beetle networks from 45 studies used in this analysis covered 6 continents and 28 countries, ranging from 60° N to 34° S and 151° E to 103° W (Fig. 1, Table 1) with a high density of studies in Central Europe (Fig. 1b). As expected, the diversity of dung beetles (rarefied effective Shannon diversity $e^{H'}$) significantly increased towards the tropics (Table 2), with a 4.3-fold increase from the highest latitude (60.7°) to the equator (Fig. 2a and S2). Altitude did not have a significant effect on beetle diversity across the studies used for this analysis, although some studies reported a decrease in dung beetles trapped with a single dung type with increasing altitude within a region, for example Escobar *et al.* (2005) and Lobo *et al.* (2007) (Table 2).

Dung beetle-resource specificity (H_2') was relatively low (0.23 ± 0.17, range). This high level of generalisation remained constant with latitude as well as with altitude (Table 2). Moreover, variation in H_2' was unrelated to the (rarefied) Shannon diversity ($F_{1,41} = 0.16$, $P = 0.696$ (Fig. 2b). Neither the number of dung types used in a study nor the number of feeding guilds of dung producers (carnivores, omnivores and herbivores) had a significant effect on H_2' (Fig. S3).

Across the different studies, human dung attracted the highest number of beetle individuals, followed by faeces from several herbivorous (wildebeest, donkey, sheep and cattle) or omnivorous large mammals (pig and wild boar). Among carnivorous mammals, lion and lynx faeces had an intermediate attractiveness, whereas dung from puma, wolf, and bear were much less attractive (Fig. 3a). Most of the more attractive dung types also attracted the largest number of species (Fig. 3b). Variation in standardised attractiveness and species richness was highly significant across dung types (N_i/N_{max}: $F_{19,\ 286} = 4.3$, $P < 0.0001$; S_i/S_{max}: $F_{19,286} = 15.0$, $P < 0.0001$; focusing on 20 dung types that were each represented in at least five networks). Yet, most of the focal dung types attract a largely representative spectrum of beetle species in similar proportions, resulting in relatively low specialisation levels (d_i') (Fig. 3c) that were similar across dung types ($F_{19,286} = 1.1$, $P = 0.31$). Additionally, all parameters (attractiveness, richness and d_i') remained similar along the latitudinal and altitudinal gradients for each of the four dung types used in at least 10 regions (all $P \geq 0.30$), except for an increase in N_i/N_{max} for sheep dung with latitude ($F_{1,12} = 11.6$, $P = 0.005$) (Figure S1).

DISCUSSION

The latitudinal gradient for species diversity and interaction-specificity is subject of ongoing research and comparative approaches (Beaver 1979; Dyer *et al.* 2007; Schleuning *et al.* 2012; LaManna *et al.* 2017). Here, we analysed, for the first time and on a global scale, the resource specificity of dung beetles. These important detritivores, present in all climatic zones, are key biological indicators in monitoring programmes (Scholtz *et al.* 2009), and are of vital importance for many ecosystem functions and services (Nichols *et al.* 2008; Beynon *et al.* 2015). Previous studies on dung beetle diet specialisation (e.g., Philips 2011; Whipple & Hoback 2012; Bogoni and Hernandez, 2014) have been regionally restricted, resulting in contradictory results, whereas our study combines data sets across the globe based on a unified analytical approach, allowing the resource specificity of this group of detritivorous insects to be quantified and compared across larger scales.

We found dung beetle interaction networks differing widely in their degree of specialisation ($0.01 \leq H_2' \leq 0.76$), but found no evidence for an increase in specialisation towards the equator (Figs. 1 and 2). Dung beetles may be expected to be generalists in higher latitudes due to the low diversity of dung available

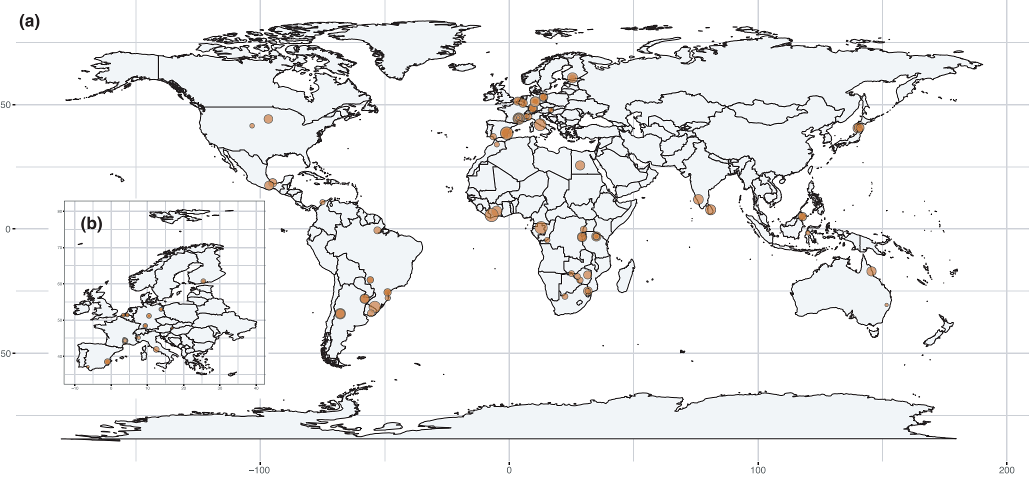

Figure 1 Global (a) and European (b) map for beetle–dung networks represented in this study. Dot positions represent the sampling region, their sizes increase with the degree of dung specificity H_2'.

Table 1 Number of networks (N_{webs}), total number of individuals ($N_{individuals}$), mean number of beetle species (S), mean number of dung types (N_{dung}) and mean resource specificity (H_2') per network for each reference used in the present study

Reference	N_{webs}	$N_{individuals}$	S	N_{dung}	H_2'
Cambefort (1991)	1	52220	123	2	0.48
Barbero *et al.* (1999)	1	2244	10	4	0.19
Bogoni & Hernandez (2014)	1	426	17	4	0.06
Carpaneto *et al.* (2005)	1	1708	20	2	0.65
Carpaneto *et al.* (2010)	1	2024	25	3	0.12
Correa *et al.* (2016)	2	7089	43	3	0.11
Da Silva & Dorneles Audino (2011)	1	121	7	3	0.59
Davis (1994)	1	14648	52	3	0.33
Davis *et al.* (2010)	1	63934	47	4	0.08
Donovan (1979)	1	456357	6	5	0.01
Dormont *et al.* (2004)	3	5672	21.67	2	0.19
Dormont *et al.* (2007)	4	6353	14.25	4	0.13
Enari *et al.* (2013)	3	1771	8	4	0.31
E. Slade & E. Raine, unpubl. data	3	1141	24	8	0.15
Errouissi *et al.* (2004)	3	6684	9.67	2	0.04
Estrada *et al.* (1993)	1	1567	22	2	0.25
Foster (1993)	8	61829	18.5	2.13	0.13
Frank *et al.* (2017b) and unpubl. data	22	19348	34	7.36	0.23
Galante & Cartagena (1999)	4	955	11	2	0.63
Gardiner (1995)	3	61112	35	3	0.14
Hernandez *et al.* (2012)	1	865	21	3	0.05
Hewavithana *et al.* (2016)	1	454	22	5	0.41
Jay-Robert *et al.* (2008)	6	7485	20.67	2	0.37
Kessler *et al.* (1974)	1	2429	14	2	0.26
E. Slade, L. Yuen Chiew, C. S. Vairappan, unpubl. data	6	9123	39.34	9.34	0.2
Cambefort & Walter (1991) and unpubl. data	1	1614	73	5	0.71
Marsh *et al.* (2013)	1	1288	53	2	0.15
Martín-Piera & Lobo (1996)	1	2477	35	9	0.1
Martinez & Suarez (2006)	1	2574	6	2	0.3
Milotic *et al.* (2017)	4	7845	17	3	0.18
Morelli *et al.* (2002)	1	1846	12	2	0.14
Nibaruta (1982)	4	10123	17.5	4.5	0.27
Paetel (2002)	2	36032	76	5.5	0.18
Rainio (1966)	2	16190	22.5	3	0.26
Ricou (1981)	2	8837	13	2	0.08
Wurmitzer *et al.* (2017) (Austria) and unpubl. data	6	14604	7.34	3	0.03
Shahabuddin *et al.* (2010)	1	1429	28	2	0.04
Cambefort & Walter (1991) and unpubl. data	1	3108	72	3	0.82
Tshikae *et al.* (2008)	1	68393	67	4	0.08
Vernes *et al.* (2005)	1	541	11	5	0.33
Vinod & Sabu (2007)	1	2657	46	2	0.38
Walter (1978); P. Walter (unpubl. data)	1	18932	100	5	0.06
Whipple & Hoback (2012)	1	7395	15	11	0.03
Wurmitzer *et al.* (2017) (Argentina) and unpubl. data	4	1050	13.75	9	0.34

to specialise on. The low specialisation in the tropics may highlight the beetles' ability to opportunistically respond to available resources, as becoming a specialist can incur trade-offs.

Table 2 Rarefied effective Shannon diversity ($e^{H'}$) increased significantly with declining latitude, while altitude had no effect. The beetles' resource specificity (H_2') showed no significant change for both altitude and latitude

	Rarefied $e^{H'}$		H_2'	
	$F_{1,45}$	P	$F_{1,45}$	P
Altitude	0.23	0.64	2.45	0.12
Altitude^2	1.03	0.32	0.50	0.48
|Latitude|	29.44	0.0001	1.52	0.22

Studies on dung beetles differ greatly in their sampling approach and particularly in the dung types used. Likewise, studies across the globe cover substantially different habitats and biomes, resulting in different dung beetle communities and variable resource specificities. Our analysis was confined to studies that used at least two different dung types, which is a relatively small subset of published dung beetle studies. The dung types analysed included livestock, wild animals, exotic (i.e., non-native) dung types and ranged from commonly used cow and human dung to faeces of the region-specific mammalian fauna. Cow and human dung are often used as standard dung types as they are thought to attract a large part of the dung beetle fauna (Hanski & Cambefort 1991; Whipple & Hoback 2012; Marsh *et al.* 2013), which was confirmed in our analysis (Fig. 3). Including dung from non-native animals and/or livestock might bias the analysis towards relatively opportunistic, generalist species. However, the diversity of dung types used for this analysis had no effect on the degree of specialisation, and native dung did not attract a more specific beetle fauna than other dung types (Fig. 3).

This study corroborates the commonly held assumption that most adult dung beetles are opportunistic and generalised, using a broad range of vertebrate dung types, yet trophic preferences of larvae of certain dung beetle species need to be examined more closely in further approaches as they can differ from adult preferences and become more specialised (Hanski & Cambefort 1991). We did not look at specialisation of dung beetles beyond vertebrate dung, but we acknowledge that there are dung beetle species that are highly specialised on particular types of dung such as sloth faeces (Young 1981), marsupial dung or other food items, such as millipede carcasses (Schmitt *et al.* 2004), or, rarely, vertebrate carrion (Larsen *et al.* 2006; Scholtz *et al.* 2009). For future studies, it may also be fruitful to investigate how such specialisation and carrion use vary across the beetles' phylogeny and mirror evolutionary shifts from ancestral saprophagy associated with changes in the shape of mandibles (Hanski & Cambefort 1991; Philips 2011).

Dung beetle-resource specificity did not change with altitude. All studies included in the analysis were conducted below 2000 m a.s.l. (except Martinez & Suarez 2006 at ~2600 m a.s.l.). The occurrence of dung beetles is driven firstly by the spatial distribution of dung producing mammals, and secondly, by the climatic conditions which constrains all ectothermic insects (Kuhn 2010; Bogoni *et al.* 2016). Thus, the major drivers of altitudinal limitations in dung beetle occurrence are the thermal conditions and altitudinal shifts in vegetation affecting the diversity of mammals the dung beetles rely on.

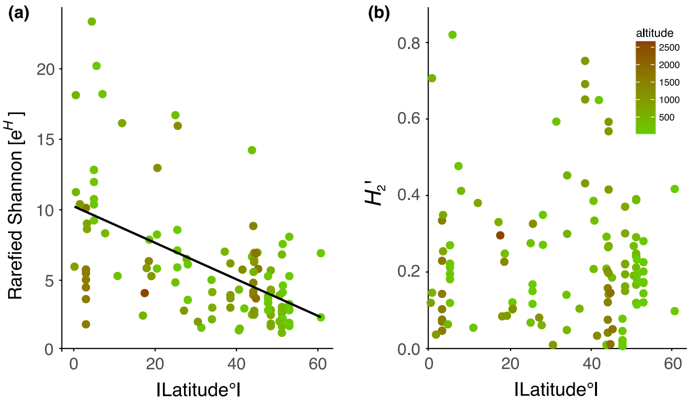

Figure 2 Changes in (a) effective Shannon diversity (rarefied $e^{H'}$ for 100 individuals per network) and (b) dung-type specificity H_2' along an absolute latitudinal gradient (0° = equator, northern and southern hemisphere plotted up to 60°). Colouring of dots represent the altitude of the study region.

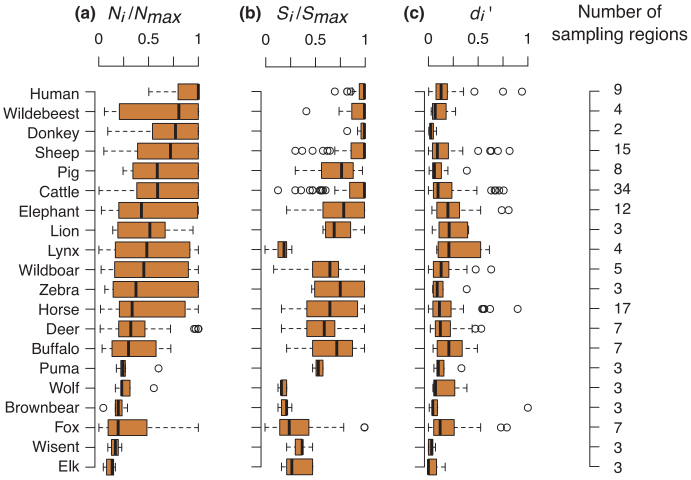

Figure 3 Dung beetle attraction to 20 commonly used dung types (all dung types represented in at least 5 networks in our analysis). (a) The attractiveness of dung was expressed as the number of beetle individuals N_i per dung type relative to the most attractive dung type in each study (N_i/N_{max}), and (b) the number of beetle species S_i was expressed in relation to the maximum found per study accordingly (S_i/S_{max}). (c) The degree of specialisation of each dung type (d_i') quantifies the relative composition of dung beetle species in comparison to the other dung types in the study.

Theory suggests that specialisation on resources provides niche partitioning and thus potentially enhances coexistence and species diversity (McKane *et al.* 2002). However, we found dung beetle communities with high diversity but a low degree of resource specificity (Tshikae *et al.* 2008, 67 species, $H_2' = 0.12$), and communities with low diversity but with high specificity (Hewavithana *et al.* 2016, 22 species, $H_2' = 0.41$). Across the gradient in dung beetle diversity, the degree of specialisation was similar (Fig 2b). This suggests that niche dimensions other than resource selectivity may be important to facilitate the coexistence of dung beetle species. These might be temporal patterns, such as variation in seasonal activity periods and day/night differentiation (Hanski & Cambefort 1991) or differences in dung discovery speed (Jacobs *et al.* 2008). Moreover, spatial partitioning into different (micro-) habitats (Hanski & Cambefort 1991; Mehrabi *et al.* 2014) may promote coexistence of species despite using similar resource types. Such niche differentiation in space, time and/or environmental conditions, for example vertical resource stratification due to arboreal mammals or ephemeral dung provided by migrating mammals, may increase towards the tropics and is likely to be particularly pronounced in more diverse mammal faunas. However, global trends of such niche dimensions remain to be tested.

Given that dung beetle species within a community show pronounced overlap in utilisation of dung resources, higher beetle diversity may improve functional complementarity and redundancy within a community (Finke & Snyder 2008), resulting in increases in the rates, stability and resilience of ecosystem functions and services provided by dung beetles.

CONCLUSION

We quantified the beetles' dung-resource specificity (i.e., the degree of specialisation in trophic networks characterised by the distribution of beetle species among dung types) across a large sample of all available studies using two or more dung types. Yet, many tropical regions such as the Amazonian basin are still missing in such a comparison of dung beetle-resource specificity. The analysis confirms a highly generalistic use of dung by dung beetle communities, at a comparable level as reported for generalised frugivores or nectar-seeking ants (Blüthgen *et al.* 2007), regardless of latitude or altitude. Additionally, we found no correlation between dung beetle specificity and dung beetle diversity. Although competition across beetle species for dung resources can be severe, and different life-history strategies exist to rapidly utilise and monopolise portions of dung piles, increased specialisation does not provide an explanation why so many dung beetle species coexist in a given habitat. This analysis is a first step to acquire global patterns for the most basal, trophic level, possibly stimulating global comparisons of other detritivorous systems.

ACKNOWLEDGEMENTS

KF and NB were funded by the German Research Foundation (DFG) Priority Program 1374 'Infrastructure-Biodiversity-Exploratories' (DFG, BL 960/3–1). For detailed acknowledgements for infrastructure and support, please see the original manuscripts. EMS, LYC, CSV were funded by the UNDP-GEF sub-contract SC-6B under SFD permit JPHTN/TKKH(PSH)100-14/18/2/JLD.35(31). ER was funded by NERC DTP studentship (grant number NE/L02612/1), and received funding for fieldwork from Embrapa Florestas.

AUTHORSHIP

K.F. and N.B. conceived the initial idea, conducted the design and formal analyses of the study, and drafted the manuscript; K.F., T.S., F.T.K., P.W., E.M.S., E.R., C.S.V. and L.Y.C. carried out the field and dung sampling, identified species and/or provided unpublished datasets; T.S., F.T.K., P.W., E.S. and E.R. commented on the manuscript; N.B. acquired funding, designed and coordinated the overall study. All authors declare no conflict of interest and gave final approval for publication.

DATA ACCESSIBILITY STATEMENT

All data sets supporting the results are available in the Figshare repository: https://doi.org/10.6084/m9.figshare.5840784.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Editor, Vojtech Novotny
Manuscript received 1 February 2018
First decision made 5 March 2018
Second decision made 8 May 2018
Manuscript accepted 12 May 2018