

The Causes and Consequences of Community Disassembly in Human Modified Tropical Forest:  
Scarabaeine Dung Beetles as a Model System

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# The Causes and Consequences of Community Disassembly in Human Modified Tropical Forest: Scarabaeine Dung Beetles as a Model System

## ABSTRACT

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A central aim of conservation science is improving our understanding how different human activities influence the persistence of native biota and associated ecological and evolutionary processes. Meeting this applied biodiversity research challenge requires that we understand (i) patterns in biological responses to anthropogenic environmental change, (ii) what biological mechanisms influence that response, (iii) how the loss of biological diversity will impact important ecological processes, and (iv) how this information can be translated into effective and practical information useful for decision makers. Increasingly, this final translational step is met through the use of ecological indicator assemblages – suites of species whose presence and abundance in a given area provide a useful gauge for measuring and interpreting changing environmental conditions. This thesis aims to improve our understanding of the patterns, causes and consequences of community disassembly for tropical forest insect species. To do this, I have combined systematic literature reviews and empirical approaches to understand how two widespread anthropogenic drivers of environmental change in tropical forest (i.e. land-use change and degradation) influence the community disassembly of Scarabaeine dung beetles in tropical forest, at a variety of spatial scales. I outline the potential for tropical forest defaunation to negatively impact dung beetle communities, summarize the contributions of dung beetles to a range of key ecological processes, provide empirical data demonstrating how dung beetles can serve as a model system to understand terrestrial trophic cascades, discuss the ability of species traits to explain population trends in observed dung beetle community disassembly, and conclude

by demonstrating how these various lines of evidence linking dung beetle species with environmental condition strengthen their potential utility as ecological indicator taxa in applied conservation science.



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For Catherine Armstrong Joseffy.

## INTRODUCTION

Across the globe, tropical forests support a tremendous amount of biological (WCFS 1999) and cultural (Maffi 2005) diversity, much of which is imperiled by ongoing forest loss (e.g. FAO 2011) and degradation (e.g. FAO 2011, Wilkie et al. 2011). Recently, much of the conservation science community has accepted that real and enduring conservation of both diversity and its associated ecological and evolutionary processes will involve strategies that extend past reserve boundaries (e.g. Lindenmayer & Franklin 2002, Brooks et al. 2004, Rodrigues et al. 2004) to consider how human activities interface with biological diversity (Chazdon et al. 2009, Gardner et al. 2009). A robust understanding of the biodiversity consequences of environmental change is the key applied research challenge most central to the development of effective and realistic conservation strategies for tropical forest landscapes.

Understanding the consequences of environmental change for a given taxonomic group requires targeted research in four related areas, including: (i) documentation of biodiversity response patterns to specific human activities, (ii) isolation of the biological mechanisms that structure these responses, (iii) quantification of how alteration in the structure of biological communities will influence important ecosystem or evolutionary processes, and (iv) translation of the insights gained through stages i-iii into effective, efficient and practical information strategies for decision making. Increasingly, this final translational step is met through the use of ecological indicator assemblages – suites of species whose presence and abundance in a given area provide a useful gauge for measuring and interpreting changing environmental conditions (McGeoch 2007, Gardner 2010).

The historic focus of such applied conservation science research on a limited array of vertebrate and plant taxa (Fazey et al. 2005) has left our current understanding of the patterns, drivers and consequences of community disassembly especially lacking for the invertebrates and insects (Samways 2002) that represent the vast majority of life on earth (Dobson et al. 2008), are responsible for a wide array of ecosystem processes (e.g. Roubik et al. 2002, Nichols & Gómez 2011, and are often exceptionally sensitive to environmental change (Koh et al. 2004, Winfree et al. 2009). Basic information on geographic distribution and species trait information is frequently missing for invertebrate groups (Samways 2002, Pawar 2003) – a byproduct of challenges that range from taxonomic chauvinism in funding streams, insufficient taxonomic expertise (Samways 1994, Samways 2002, Pawar 2003, Samways 2006), and a weak understanding of how invertebrate-mediated ecological functions are affected by both changing horizontal diversity (i.e. within a trophic level) and vertical diversity (i.e. across trophic levels) (Srivastava and Bell 2009). Resolving the causes and consequences of community disassembly for insect and invertebrate taxa is essential if conservation science is to deliver robust and comprehensive information to decision makers across the global tropics.

#### THESIS AIMS

This thesis aims to improve our understanding of the patterns, causes and consequences of community disassembly for tropical forest insect species. To do this, I have used a combination of complementary conceptual and analytical approaches; combining both systematic literature reviews and novel quantitative approaches to understand how two widespread anthropogenic drivers of environmental change (i.e. tropical forest land-use and degradation) influence the

community disassembly of Scarabaeine dung beetles in tropical forest.

#### THESIS FOCAL TAXA

Scarabaeine dung beetles are a globally distributed and dominant component of tropical terrestrial insect fauna (Scholtz et al. 2009a). They play several key functional roles in a range of fecal detritus-burial related processes (Mathison and Ditrich 1999, Andresen and Feer 2005, Bang et al. 2005, Bertone et al. 2006) and have been proposed as effective indicators of environmental change in tropical habitats (Spector 2006a). While the community-level (e.g. Nichols et al. 2007) and species-level (McGeoch 2007) responses of dung beetles to land-use change in tropical forests suggest that dung beetles are highly sensitive to human activities, our ability to draw reliable inference from land-use change studies is confounded by the persistent confounding influence of land-use on mammal diversity and abundance (Nichols et al. 2007, Parry et al. 2007). While nearly all of the ca 6,000 species of dung beetles depend upon mammal fecal resources for feeding and/or reproduction (Halffter and Edmonds 1982a, Hanski and Cambefort 1991c), the challenges in tracking dung beetle-mammal interactions has contributed to an exceptionally poor understanding of dung beetle diet breadth and plasticity (Bustos Gomez et al. 2003, Dormont et al. 2004, Martinez and Suarez 2006). This persistent knowledge gap is particularly relevant when attempting to predict the response of dung beetle communities to tropical forest defaunation – one of the most extensive and poorly understood drivers of habitat degradation across the world's remaining tropical forests (Wilkie et al. 2011).

#### THESIS STRUCTURE

This thesis aims to improve our understanding of the patterns, causes and consequences of dung beetle community disassembly in five ways, each corresponding to a single chapter. First, by

reviewing our current understanding of mammal-dung beetle interactions, and patterns in the co-variation in both abundance and occupancy patterns, Chapter 1 highlights the potential dung beetle community-level response to changing mammal abundances as a consequence of hunting-induced defaunation, as well as the biases and limitations of existing research. Second, through an extensive review of dung beetle influences on detritus burial-related ecological functions, Chapter 2 sets a broader context for understanding the potential functional consequences of dung beetle community disassembly. Third, through the analysis of a novel field dataset, Chapter 3 provides the very first spatially-extensive quantification of dung beetle community-level response to hunting-induced defaunation in tropical forest, and demonstrates how human predation on wild vertebrates may strongly cascade through the fecal-detrital pathway to influence the future structure and function of tropical forest. Fourth, a combination of novel and mined data is combined in Chapter 4 to examine the mechanistic basis for dung beetle disassembly in tropical forest, through a global meta-analysis of the species trait-correlates associated with population responses for over 200 dung beetle species on three continents. Finally, Chapter 5 assesses the case for the use of Scarabaeine dung beetle communities as an ecological indicator taxon for applied biodiversity conservation science in tropical forest. The five chapters were each written directly in the form of scientific papers (Chapters 1-4) or book chapters (Chapter 5). Three chapters were published at the time of submission (Chapters 1, 2, 5), one has been submitted for review (Chapter 4, Ecology) and one is in preparation (Chapter 3). Individual chapters are presented in accordance with their content, and not by chronological order of their publication.



## CHAPTER 1 - CO-DECLINING MAMMALS AND DUNG BEETLES: AN IMPENDING ECOLOGICAL CASCADE

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EN and SHS were responsible for the original concept, EN wrote the first draft of text. EN and TAG developed Figure 1.1 and all authors significantly contributed to revisions.

## ABSTRACT

Biodiversity loss can precipitate extinction cascades and impair ecological processes. These ‘downstream’ effects will be exacerbated if functionally important taxa are tightly linked with species threatened by extinction or population decline. We review the current evidence that such a scenario is currently playing out in the linked declines of persistently hunted mammal populations and the dung beetle communities (Coleoptera: Scarabaeidae: Scarabaeinae) that depend on them for adult and larval food resources. Through a close evolutionary association, mammal assemblages have played a fundamental role in structuring extant dung beetle communities. Today many game mammal species’ populations are severely depleted by subsistence or commercial hunting, especially in tropical forest systems. Multiple lines of evidence from temperate and tropical systems indicate that the regional-scale decline or extirpation of medium and large bodied mammal faunas can severely disrupt the diversity and abundance of dung beetle communities through alterations in the composition and availability of dung resources. These observed community disassemblies have significant short- and long-term implications for the maintenance of key ecosystem processes including nutrient recycling and secondary seed dispersal. Identifying the species- and community-level traits that buffer or exacerbate these species and functional responses is essential if we are to develop a better understanding of the cascading ecological consequences of hunting in tropical forests.



## INTRODUCTION

Biodiversity loss research has predominantly focused on the direct impacts of human activity, while comparatively little attention has been given to cascade effects across dependent species groups and associated ecological functions (Brook et al. 2008, Tylianakis et al. 2008a). However, in co-evolved systems the decline or loss of even a single keystone species can instigate a cascade of ‘downstream’ extinctions among dependent taxa, with dramatic implications for subsequent patterns of community structure (Koh et al. 2004) and functional capacity (Eklöf and Ebenman 2006). The ecological consequences of these downstream impacts may be particularly insidious in cases where functionally important taxa are closely dependent upon imperiled keystone resource providers (Scheffer et al. 1993, Van de Koppel et al. 1997). We posit that the preconditions for such a scenario are becoming increasingly prevalent in tropical forests with regard to linked declines in game mammal populations and the dung beetles that depend on them for adult and larval food resources.

The decline of large-bodied game vertebrates is currently at a crisis level in many tropical countries (Fa and al. 2006, Corlett 2007, Peres and Palacios 2007). Rural hunters preferentially hunt large-bodied frugivorous primate and ungulate species when available, but resort to smaller-bodied prey as large game becomes scarce (Fa et al. 2000, Jerozolinski and Peres 2003). Massive abundance declines in large-bodied game species have been recorded in Amazonian (Peres 2000a, Peres and Palacios 2007), African (Fa and al. 2006) and southeast Asian forests (Corlett 2007), even within the most inaccessible regions (Peres and Lake 2003).

This often sets into motion a predictable sequence of size related declines, if not local

extinctions, in persistently overhunted forests (Jerozolinski and Peres 2003) sometimes followed by partial compensation by usually smaller-bodied mammal species with higher reproductive rates (i.e. small ungulates, primates and rodents) (Peres and Dolman 2000). Extremely heavy hunting pressures can lead to an ‘empty’ or ‘half-empty’ forest scenario (Redford and Feinsinger 2003), a current or impending phenomenon for many tropical forest regions, particularly in Africa (Fa et al. 2002) and southern Asia (Corlett 2007).

The extent and scale of large mammal removal has spurred concern about the trophic consequences of hunting for plant communities through altered patterns of zoochory and herbivory (Peres and van Roosmalen 2002, Stoner et al. 2007, Nunez-Iturria et al. 2008, Terborgh et al. 2008) However mammal removal has at least two additional potential cascade effects: the secondary extinction of dependent taxa and the subsequent decline of the ecological processes that are mediated by associated species. Scarabaeine dung beetles use primarily mammal dung as an adult and larvae food resource, the latter by laying eggs within the dung itself, or within brood balls buried under the soil surface (Halffter and Edmonds 1982a, Hanski and Cambefort 1991c). This manipulation, relocation and consumption of mammal feces contributes to a series of ecological functions, including nutrient cycling, parasite suppression, soil aeration and secondary dispersal of intact seeds expelled in mammal dung.

A growing body of evidence demonstrates that these ecological functions are highly sensitive to the shifts in dung beetle community structure that accompany widespread habitat modification (Klein 1989b, Andresen 2003, Horgan 2005b). However, dung beetle communities also undergo significant changes following mammal defaunation (Andresen and Laurance 2007) in otherwise

undisturbed forests, with declining dung resources affecting beetle reproduction and survival. Despite the severity and scale of mammal overhunting in tropical forests, surprisingly few studies have documented the fate of dependent dung beetle assemblages, and none have assessed the consequences of mammal removal on dung beetle functional capacity.

Here we evaluate the potential for declines in mammal diversity and overall biomass to instigate population declines and an extinction cascade within associated dung beetle communities, outline the potential functional consequences of beetle community disassembly, and identify the knowledge gaps that currently confound our ability to make predictions about wider ecosystem effects. We focus our review on tropical forests systems, but draw upon studies from other biomes to provide a wider context for discussion.

#### CONSEQUENCES OF HUNTING ON BEETLE COMMUNITY STRUCTURE

To our knowledge, only one tropical forest study has documented the potential effects of hunting and changes in mammal communities on dung beetles, reporting that mammal hunting had a marked impact on dung beetle community structure on Barro Colorado Island in Panama (Andresen and Laurance 2007). Across a gradient of hunting intensity, the species richness and overall abundance of dung beetles declined with decreasing mammal abundance; with two-thirds of beetle species demonstrating a significant negative response to mammal decline. In Los Tuxtlas, Mexico, Estrada et al. (1998) reported a positive association between non-volant mammal richness and abundance and both dung beetle species richness and abundance, in continuous tropical forest, forest fragments and plantation forestry sites. Another study that compared forest fragments with and without howler monkeys in the same system revealed that

monkey occupancy was associated with significantly higher beetle richness and overall abundance (Estrada et al. 1999), driven by changes in the dominance of dung beetle species with known affinities for howler monkey dung (Estrada et al. 1993). Caution should be taken, however, in inferring relationships between mammals and beetles from forest fragments, as the effects of area and isolation influence both communities (Feer and Hingrat 2005) in ways that may confound our ability to isolate the drivers of dung beetle community change (Nichols et al. 2007).

Three other comparative studies outside of the tropics also illustrate the potential for strong, if idiosyncratic, dung beetle responses to changing mammal assemblages. In Mexico, Halffter and Arellano (Halffter and Arellano 2002) reported that reduced cattle stocking rates reduced total abundance, significantly decreased total biomass, and decreased the representation of large-bodied dung beetle species, while species richness, guild structure and species composition remained similar. In contrast, Carpaneto et al. (2005) reported that the removal of wild and domestic herbivores from an urban Italian park drove a 60% decline in dung beetle species richness but a 77% increase in total abundance. In Madagascar, the ability of at least three *Helictopleurus* species to shift to using introduced cattle dung in open habitats has led to their rapid range expansion over the past 1500 years compared to other native forest-dwelling species (Hanski et al. 2008)

Drawing upon historical data, comparisons among dung beetle collections across parts of Africa and the Mediterranean provide circumstantial evidence of strong, linked changes in mammal-dung beetle assemblages, typically within a context of broader land-use change. The partial

replacement of native Mediterranean mammals by livestock after human colonization was largely successful in maintaining endemic dung beetle communities on the Iberian Peninsula (Verdu and Galante 2002). However, changes in traditional grazing regimes have led to recent declines in several dung beetle species in the region (Lumaret and Kirk 1991, Carpaneto et al. 2007). In addition, 70 years of dung beetle collection records from the French regions of Languedoc and Provence reveals the local extinction of two previously common species, and strong population declines in at least seven more (Caillol 1908, Théron 1980). Along a gradient of historical persecution of large mammal populations in three tropical savanna sites in Africa, Cambefort (1991c) reported an increase in total dung beetle abundance, accompanied by a decline in overall species richness. In west and southern Africa, overhunting of savannah elephants has had a particularly dramatic effect on the structure of dung beetle communities (Hanski & Cambefort 199b; Gardiner 1995 cited in Bote 2006) . The extirpation of large-bodied elephant-specialist *Heliocopriss* species across parts of Côte d'Ivoire has been attributed to the national decline in elephant populations (Cambefort 1982). *Heliocopriss* populations are still rare in other African reserves where elephants were hunted to local extinction before park boundaries were delimited (Cambefort 1982), yet abundant in regions that have historically retained higher elephant densities, such as Kruger National Park, the Zambezi Valley in Zimbabwe (Doubé 1990) and Ankasa Conservation District in Ghana (T. K. Philips pers. comm). Finally, *Circellium bacchus*, a large, flightless, dung generalist with clear preferences for elephant dung (feeding) and buffalo dung (nesting) has disappeared from virtually its entire southern African range as a combined consequence of habitat transformation and replacement of native herbivores with livestock (Chown et al. 1995, Kryger et al. 2006).

## MECHANISMS OF BEETLE COMMUNITY DISASSEMBLY

This diverse group of studies points strongly to the potential for linked mammal-dung beetle decline with changes observed across different historical and contemporary disturbance regimes and involving distinct native mammal and beetle faunas. Our current understanding of the dominant response patterns of dung beetles and related functions to mammal decline in tropical forests and other ecosystems remains limited. Nevertheless, it is possible to make certain predictions regarding the effects of persistent mammal hunting on dung beetles, by linking our understanding of mammal extinction order in hunted systems with available ecological information on patterns of dung beetle resource preference, plasticity and functional capacity. An understanding of such linkages is key to developing a conceptual framework to evaluate, and ultimately predict, the cascading effects of mammal declines on dung beetle community structure and function (Fig. 1.1).

A particularly critical challenge in the development of such a framework lies in partitioning those aspects of dung beetle community disassembly driven by changes in mammal diversity (i.e. losses of species that once specialized on extirpated mammals), from those driven by declines in overall mammal biomass (losses of species to a general reduction in resources). In overhunted Neotropical forests, the total biomass of mammal game that produce large, moist feces (e.g. ateline primates and large ungulates) is often significantly depressed, while the representation of non-hunted species that produce small amounts of dry, pelleted dung (e.g. rodents, small armadillos, small primates) can increase (Fig. 1.1; Peres and Dolman 2000, Peres and Palacios 2007). For an individual beetle species, the implications of these changes in dung diversity and availability will depend upon its original level of resource specialization, the extent

to which its dietary requirements are plastic over ecological timescales, and the relationship between dung availability and fitness.

Drawing firm conclusions regarding the impacts of reduced dung diversity in persistently hunted forests is complicated by the dearth of empirical information on the feeding ecology of individual dung beetle species (Holter and Scholtz 2007). While the majority of coprophagous dung beetles are broad generalists capable of feeding on dung from multiple species, others display an intermediate degree of preference for a particular species or species groups, and relatively few are highly specialized on the dung of a single species (Hanski and Cambefort 1991a, Larsen et al. 2006). However, even generalist species have been observed to discriminate differences in major dung ‘types’ (Chame 2003), as portrayed along axes of water/fiber content (Verdu and Galante 2004, Lopez-Guerrero and Zunino 2007), nutritional value (Verdu and Galante 2004), dung shape (Gordon and Cartwright 1974, Chame 2003), and dung size (Peck and Howden 1984a). The relative impact of lowered dung diversity on a given beetle species will depend upon the level of stenophagy in that species for dung provided by a preferred game species, and its level of resource plasticity in the absence of the favored resource (Brown 1927, Gordon and Cartwright 1974). In persistently hunted systems, depressed mammal diversity is therefore likely to impact dung beetles in three ways; (1) by lowering the overall diversity of available dung types, (2) by shifting the dominant dung type away from large, moist depositions towards smaller, drier, pelleted depositions, and (3) by directly affecting the beetle species with strict or near strict obligate associations with hunted game mammal species (Fig. 1.1).

Persistent hunting in tropical forests may also affect overall dung resource availability in at least

two ways. First, the disproportionate removal of large-bodied mammals drives marked declines in overall mammal biomass (Peres and Palacios 2007), which can be expected to correspond with declines in overall resource availability. This reduction in overall dung biomass will reduce the density and increase the spatial variance (clumping) of individual dung depositions across a given area, with the effect of lowering the probability of encountering a suitable deposition for an individual beetle. This will differentially affect species pursuing either the ‘perch and wait’ approach common to small-bodied species, versus the active foraging of larger depositions that is a common strategy among larger-bodied beetle species (Peck and Howden 1984b, Gill 1991). Perching species often feed on pelleted droppings with a higher density and more reliable distribution across the forest floor (Gill 1991, Louzada 1998). In persistently overhunted forests, these species may remain at pre-hunting levels, or potentially increase, if compensation (or undercompensation) by non-hunted rodents and small ungulates occurs.

In contrast, larger species may be heavily impacted by the overall reduction in large, wet dung that results from; (1) the reduced probability of encountering dung, (2) elevated levels of competition at individual dung pats, or (3) negative effects on fitness from accepting lower quality resources (Davis 1989). Second, the decline in body size across target game species driven by selective hunting (Bodmer 1995), (Jerozolinski and Peres 2003) is likely to reduce the average deposition size both among and within species, as body size and fecal output are related (Blueweiss et al. 1978). The level of exploitative competition faced by dung beetles at a dung pat is often extreme, and can result in removal of the entire dung resource, sometimes within just minutes of deposition (Hanski and Cambefort 1991c). While larger-bodied beetles are attracted to larger-sized depositions (Peck and Howden 1984), the influence of changing individual



deposition size on beetle competition dynamics and fecundity remains poorly known. Smaller individual depositions of large, moist dung types may favor those species capable of reproducing at low resource levels (i.e. those requiring less dung per brood ball) relative to those larger-bodied species that create substantially larger brood balls and are likely to secure greater benefits from larger dung pats (Hanski and Cambefort 1991).

#### CONSEQUENCES OF HUNTING ON BEETLE COMMUNITY FUNCTION

The restructuring of dung beetle communities following extensive mammal removal is likely to have profound implications for the maintenance of several key ecosystem functions (Fig. 1.1; Srinivasan et al. 2007). For example, within a given community, the largest dung beetles remove a disproportionate amount of dung (Lindquist 1933, Larsen et al. 2005, Slade et al. 2007), implying a similarly larger role in nitrogen mineralization (Yokoyama et al. 1989) and suppression of pestiferous flies through exploitation competition (Horgan 2005b). In addition, these species bury a larger proportion of excreted plant seeds, bury larger seeds than smaller beetles, and bury seeds deeper (reviewed by Andresen and Feer 2005). The removal of the largest community members may also initiate a cascading series of changes in community assembly rules and patterns of interspecific competition (Horgan and Fuentes 2005) with unknown functional consequences. The importance of differences in the size of dung beetles for predicting both the responses of beetle communities to hunting, and the functional implications of these changes, points to emergent relationships between dung beetle disturbance response traits (Larsen et al. 2005, Gardner et al. 2008b) and functional effect traits (Slade et al. 2007). Achieving a better understanding of the correlation between these traits will help better prescribe the overall functional prognosis of shifts in dung beetle communities across hunting gradients

and alternative habitat change scenarios (Larsen et al. 2005).

#### CURRENT CAPACITY FOR PREDICTION

Our ability to disentangle the downstream effects of mammal declines on dung beetle communities through the restructuring of available dung resources is confounded by complex interactions that are often unrelated to the effects of hunting. For example, a given beetle's requirement or preference for specific dung features may correspond to seasonal changes in environmental conditions and dung quality, reproductive status or feeding purpose (adult or larvae provisioning) (Hanski and Cambefort 1991). Physical habitat modification can result in superficially similar changes in both mammal (e.g. fragmentation, fire: Estrada et al. 1993) and dung beetle communities (e.g. decreases in average beetle size: Larsen et al. 2005; altered community structure: Nichols et al. 2007) as those elicited by overhunting. Partitioning the relative importance of habitat modification and shifting dung availability represents one of the most challenging aspects of dung beetle applied ecology. Finally, changes in the availability of non-dung resources (rotting fruit, fungi, carrion) may further influence the structure of dung beetle communities in hunted areas of tropical forest through 'resource-switching' (Hanski and Cambefort 1991a) during adult feeding. However, as few dung beetle species can use non-dung resources for nesting material (Gill 1991), it is unlikely that such changes could be fully compensatory. Finally it is important to recognize that as the number of dung producing mammals in tropical forests and other ecosystems changes, so too may the 'demand' for dung related ecosystem functions. For example, if a decline in large game-vertebrates precipitates a decline in the number of excreted seeds (Wright et al. 2007b), the requirement for secondary seed dispersal may also decrease. Alternatively, as seed-predation pressures by non-game, small rodents increase (Dirzo et al. 2007), so too may the demand for dung beetle secondary burial, to

protect the few remaining incoming seeds. The expected decline in mammal excreta in overhunted systems will potentially alter the ecological relevance of dung beetle mediated nutrient mobilization and parasite suppression roles that are poorly understood even in intact ecosystems (Nichols et al. 2008). Ultimately these chronic second-order effects of intense hunting pressure may result in long-term changes in tree species composition and the overall functional capacity of impacted sites, regardless of the presence or absence of dung beetles (Stoner et al. 2007). Nevertheless, it should be remembered that maintaining the functional capacity of dung beetle assemblages is likely to be a key ingredient in efforts to restore degraded lands, such as enriching agricultural lands with animal-dispersed forest trees (Martinez-Garza and Howe 2003). It remains unclear the extent to which density compensation by non-target small primates, rodents and didelphid marsupials occurs in heavily hunted forests (Peres and Dolman 2000, Peres and Palacios 2007) and whether such shifts could support even partial numerical and functional compensation by beetles that are able to process the dung of non-game vertebrates. A related, but completely unexplored aspect of compensatory mechanisms in mammal-beetle relationships is the likely dung ‘subsidy’ provided by increasingly larger human populations in tropical forests. Increased human fecal input into hunted systems may play a role in offsetting or buffering the effects of declining large mammal feces. Finally, at larger spatial and temporal scales, the influence of shifting source sink dynamics in mammal densities on the maintenance of dung beetle assemblages remains completely unknown. Even persistently hunted areas often retain high densities of dispersing (rather than resident) mammals (Novaro et al. 2000), which may contribute to apparently species rich and abundant dung beetle assemblages even in sites where mammal hunting is intense (Howden and Nealis 1975, Peck and Forsyth 1982).

#### FUTURE CHALLENGES

Overall, while the evidence supporting the ecological importance of dung beetles for many functional processes is strong, our understanding of the long-term ecological consequences of disrupting linkages between mammals, beetles and processes is still limited. Many of these questions can be partially addressed through the collation of species-specific natural history data, but can only truly be resolved with additional field and experimental research. A first step will be documenting the patterns of dung beetle response across hunted and non-hunted forests using multiscale, comparative field programs that employ standardized dung beetle collection methods. Combined with relevant, site-level data on environmental conditions, these studies will provide the empirical context necessary to help disentangle the confounding drivers of change in dung beetle communities that have been subject to both landscape modification and the depletion of resident mammal populations.

By linking this work with research on the functional capacity of dung beetle species and communities, we can examine the potential for mammal hunting to impair dung beetle mediated ecological functions and processes. Paired experimental diversity-function manipulations (Slade et al. 2007) will further clarify the mechanisms linking dung beetle community assembly to key ecological functions and how such relationships may be impaired in the context of realistic scenarios of biodiversity loss. The combination of such observational and experimental field-based work in a non-plant based system will represent a significant expansion into realism for studies of biodiversity-ecosystem function (Cardinale et al. 2006).

Connecting data on dung beetle abundance and function patterns to species traits is key to

scaling up the generalizability of ecological inference across studies (McGill and Enquist 2006). Beetle body size, diel activity, dung handling method, dispersal ability, habitat specificity and population density are well-defined, easily measurable characteristics, that can be compared across species to assess response and effect traits that correspond to the impact of changing mammal populations and alterations in ecosystem function (Lavorel and Garnier 2002, Larsen et al. 2005, Larsen et al. 2008). Finally, particular attention to the spatial scale of sampling in empirical field studies is critical, as dung beetle diversity is strongly linked to habitat composition and heterogeneity at landscape scales (Arellano and Halffter 2003), to tree cover and soil type at sub-regional scales (Halffter et al. 1992, Halffter and Arellano 2002) and inter and intra-specific competition associated with resource variability at local scales (Doubé 1990). Multi-scale and cross-site analyses will be invaluable in identifying the relative importance of different factors and constraints in structuring the compositional and functional responses of dung beetles to mammal declines.

The fact that dung beetles can be sampled more cost effectively than almost any other species group in tropical ecosystems (Gardner et al. 2008a) indicates that while daunting, such a challenge is not insurmountable further highlighting the fact that coprophagous dung beetles represent a ideal focal taxon for pure and applied ecological research (Spector 2006a). While our understanding of the ecological importance of dung beetle-mediated functions remains incomplete, our current understanding of their dependency on mammal communities is sufficient to warrant considerable concern about their future decline. We hope that this paper will stimulate renewed research efforts to tackle both the specific issue of cascading effects of mammal overhunting on dung beetle populations, and the broader challenge of understanding the indirect

effects of species loss on the structure and function of natural ecosystems (Tylianakis et al. 2008a).

## TABLES AND FIGURES

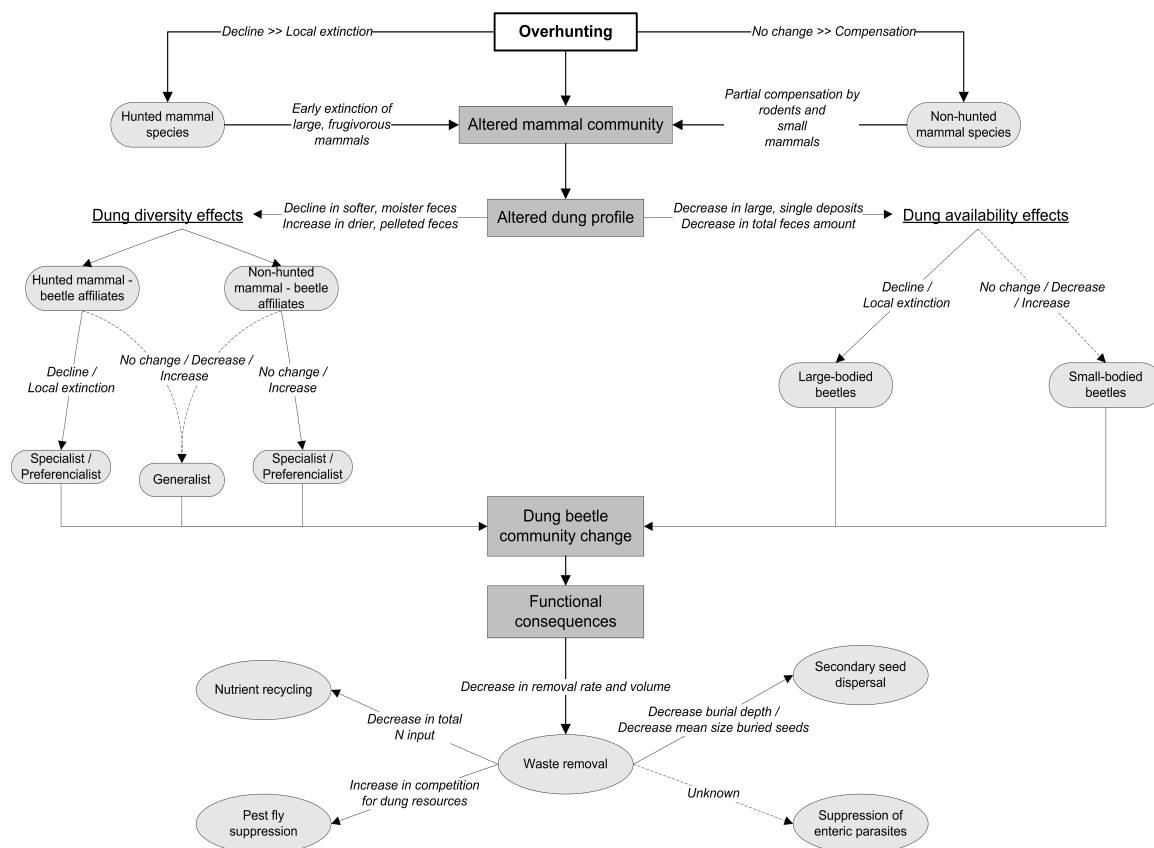


Figure 1.1 Conceptual model of pathways by which overhunting in tropical forests impacts coprophagous dung beetle community structure and dung beetle-ecosystem function. Text along each arrow describes the potential direction or mechanism driving each effect.

## CHAPTER 2 - ECOLOGICAL FUNCTIONS AND ECOSYSTEM SERVICES PROVIDED BY SCARABAEINAE DUNG BEETLES

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## ABSTRACT

Clear understanding of the links between ecological functions and biodiversity is needed to assess and predict the true environmental consequences of human activities. Several key ecosystem functions are provided by coprophagous beetles in the subfamily Scarabaeinae (Coleoptera: Scarabaeidae), which feed on animal excreta as both adults and larvae. Through manipulating feces during the feeding process, dung beetles instigate a series of ecosystem functions ranging from secondary seed dispersal to nutrient cycling and parasite suppression. Many of these ecological functions provide valuable ecosystem services such as biological pest control and soil fertilization. Here we summarize the contributions of dung beetles to nutrient cycling, bioturbation, plant growth enhancement, secondary seed dispersal and parasite control, as well as highlight their more limited role in pollination and trophic regulation. We discuss where these ecosystem functions clearly translate into ecosystem services, outline areas in critical need of additional research and describe a research agenda to fill those gaps. Due to the high sensitivity of dung beetles to habitat modification and changing dung resources, many of these ecological processes have already been disrupted or may be affected in the future. Prediction of the functional consequences of dung beetle decline demands functional studies conducted with naturally assembled beetle communities, which broaden the geographic scope of existing work, assess the spatio-temporal distribution of multiple functions, and link these ecosystem processes more clearly to ecosystem services.

## INTRODUCTION

Human economy, health and wellbeing are intimately linked to functionally intact ecosystems (MEA 2005) and well characterized relationships between biodiversity and ecosystem function are key to predicting the ecological and economic impacts of human activities (Armsworth et al. 2007). In terrestrial systems, insects play important ecological roles in diverse ecological processes such as nutrient cycling, seed dispersal, bioturbation and pollination. Dung beetles in the coleopteran subfamily Scarabaeinae mediate several of these processes. Dung beetles are a globally distributed insect group, with their highest diversity in tropical forests and savannas (Hanski and Cambefort 1991c). Largely coprophagous, dung beetle species feed on the microorganism-rich liquid component of mammalian dung (and less commonly that of other vertebrates, as well as rotting fruit, fungus and carrion) and use the more fibrous material to brood their larvae (Halffter and Matthews 1966a, Halffter and Edmonds 1982a). Most dung beetles use one of three broad nesting strategies, each with implications for ecological function. Paracoprid (tunneler) species bury brood balls in vertical chambers in close proximity to original deposition site. Telocoprid (roller) species transport balls some horizontal distance away, before burial beneath the soil surface. Endocoprid (dweller) species brood their young inside the dung mass itself (Halffter and Edmonds, 1982). Ecological linkages between dung beetles and mammals have played an important role in shaping the evolution of the Scarabaeinae and the structure of extant dung beetle communities for at least the last 40 million years (Cambefort 1991a). Recent fossil evidence of dung-provisioned burrows strongly suggests that dung beetles evolved coprophagy through association with dinosaurs even before the diversification of mammals (Chin and Gill 1996).

The amount of dung buried by a beetle species is primarily related to mean female body size (Horgan 2001), though factors such as soil type and moisture (Sowig 1995b), pair cooperation (Sowig 1996) and dung quality ((Dadour and Cook 1996) also play a role. These varied patterns of consumption and relocation of dung by beetles drive a series of ecological processes that include nutrient cycling, soil aeration, secondary seed burial, and parasite suppression. Where they are directly relevant to humans, these ecosystem functions often provide important and/or economically beneficial ecosystem services (De Groot et al. 2002). Here we summarize our current knowledge about dung beetle ecosystem functions. We outline the circumstances wherein these functions become ecosystem services and highlight areas in need of further empirical study. We frame the importance of these ecological processes with a discussion of the numerous threats to dung beetle persistence.

## ECOLOGICAL FUNCTIONS

### *NUTRIENT CYCLING*

A significant proportion of the nutrients consumed by vertebrates are voided in excreta (Steinfeld et al. 2006) and the extent to which these nutrients can be returned to the plant growth cycle has strong implications for plant productivity. The transfer of freshly deposited waste below the soil surface by tunneler and roller dung beetle species physically relocates nutrient rich organic material and instigates micro-organismal and chemical changes in the upper soil layers.

Nitrogen is an often critically limiting element that structures plant productivity (Vitousek et al. 1997). A recent FAO report estimates that 12 of 30 million tons of N excreted by extensive

livestock production systems in the mid-1990s were lost through  $\text{NH}_3$  volatilization (Vitousek et al. 1997). By burying dung under the soil surface, dung beetles prevent the loss of N through ammonia ( $\text{NH}_3$ ) volatilization (Gillard 1967), and enhance soil fertility by increasing the available labile N available for uptake by plants through mineralization (Yokoyama et al. 1991a). While a high estimate of  $\text{NH}_3$  volatilization from livestock excreta (ca. 80%, Gillard 1967, 1967) has been cited in studies estimating the impacts of dung beetle activity on soil fertility (e.g. (Bang et al. 2005) (Losey and Vaughan 2006), more recent estimates from the Food and Agriculture Organization of the United Nations and the Intergovernmental Panel on Climate Change project more moderate rates of around 22% (FAO/IFA 2001).

One mechanism by which dung beetles affect the nitrogen cycle is by accelerating mineralization rates. Nitrogen volatilization and mineralization are bacteria-mediated processes, and dung beetles alter the microorganism fauna in dung pats and brood balls during feeding and nesting (Yokoyama et al. 1991a). Several studies suggest that the aerobic conditions in dung and elevated C and N levels in the upper soil layers stimulated by dung beetle activity foster bacterial growth, including ammonifier bacteria responsible for continued N mineralization (Yokoyama et al. 1991a, Yokoyama et al. 1991b, Yokoyama and Kai 1993). In the absence of dung beetle activity, nitrogen mineralization rates in freshly deposited dung initially increase, accompanied by a release of inorganic N (Yokoyama et al. 1989, Yokoyama et al. 1991a, Yokoyama and Kai 1993, Yamada et al. 2007). This mineralization processes declines or ceases within 5–7 days, yet continues to increase in beetle-colonized dung and brood balls (Yokoyama et al. 1989, Yokoyama et al. 1991a, Yokoyama and Kai 1993). Dung beetles may also affect N-volatilization rates by physically diluting the available concentration of inorganic N as they incorporate it into

the soil (Yokoyama et al. 1991b). This action may enhance N-fixing activity through increasing the availability of easily decomposable organic matter, but the net positive benefits of this mobilization remain unknown (Yokoyama et al. 1991b).

The influence of dung beetle action on denitrification rather than  $\text{NH}_3$  volatilization remains uncertain. Yokoyama et al. (1991a) demonstrated that dung beetles significantly inhibited the volatilization of  $\text{NH}_3$ , principally from brood balls. However, denitrification in brood balls caused an N loss significantly greater than that from un-manipulated dung. They postulated this was a consequence of dung beetles increasing the endogenous  $\text{NO}_3\text{-N}$  pool, enhancing denitrifying activity. Increased denitrification rates in dung beetle-colonized dung could partially offset the benefits of increased N-mineralization, however a full accounting of the influence of dung beetles on nitrogen flows and distributions has yet to be done. Work by Rougon et al. (1991) reported high concentrations of amino acids in dung beetle brood ball casings, which potentially accumulate following gaseous nitrogen fixation by microorganisms in the digestive tracts of dung beetle larvae.

Several authors have reported an increase in soil nutrients (P, K, N, Ca and Mg) found in soils exposed to dung beetle activity in experimental dung masses (Bertone 2004) (Galbiati et al. 1995, Lastro 2006, Yamada et al. 2007). Bertone (2004) also found dung beetle activity spurred an increase in soil pH and cation exchange capacity of soils, though had little effect on humic matter content. Yamada et al. (2007) report a significant positive relationship between the magnitude of released inorganic N and available P and K in cattle dung and dung beetle abundance.

Our understanding of dung beetles' role in soil fertility comes exclusively from pasture and grassland studies, and the importance of these processes is poorly understood for other natural systems. Further research is needed in tropical forests, where dung beetles are typically capable of transferring all deposited mammal feces into the soil within hours after deposition (Arrow 1931, Slade et al. 2007), and highly localized differences in soil fertility are important in structuring plant communities in nutrient-poor soils (John et al. 2007). Necrophagous dung beetles may also affect nutrient cycling by relocating carrion below the ground surface. Carrion consumption is most strongly developed in Neotropical Scarabaeines (Gill 1991), though no present estimates exist for the amount of vertebrate or invertebrate typically biomass consumed.

Finally, dung beetles are not exclusively responsible for the relocation of fecal material into the soil. Many wood, litter and soil feeding termites are also documented coprophages, though dung does not appear to be a preferential food source (Freyman et al. 2008). Termites may proportionally remove more waste in arid areas and dry seasons relative to dung beetles (Coe 1977, Herrick and Cambefort 1995). Termites impact nutrient cycling through the comminution and spatial redistribution of dung, which increases its availability to microbial decomposers. Termite modified soil is often richer in nitrogen, organic carbon, and exchangeable cations than non-modified soil, but these impacts have not been clearly attributed to feeding on dung, rather than other detritus (Freyman et al. 2008). Earthworms also incorporate faeces into the soil, and alter organic materials that pass through their gut – spurring microbial interactions that alter N availability in complex ways (Groffman et al. 2004). In north-temperate systems where

coprophagous beetle communities are dominated by the genus *Aphodius* (Coleoptera: Scarabaeidae), earthworms often play a significant role in waste burial (Holter 1977, 1979, Gittings et al. 1994).

### *BIOTURBATION*

Bioturbation (the displacement and mixing of sediment particles by animals or plants) may influence soil biota and plant productivity by increasing soil aeration and water porosity. Tunneler dung beetles play a role in bioturbation through moving large quantities of earth to the soil surface during nesting (Mittal 1993). While particular nesting styles vary greatly among tunneler species, most construct underground tunnels with branching brood chambers. These tunnels can be up to several meters deep, and are often lightly backfilled with soil to protect the developing larvae. The tunnel depth and amount of soil removed are positively related to beetle body size (Lindquist 1933, Halffter and Edmonds 1982a, Edwards and Aschenborn 1987). While this tunneling activity is generally assumed to increase soil aeration and water porosity in the upper soil layers, these effects have rarely been empirically assessed (Miranda 2006). A single study has measured the impact of dung beetles on soil permeability beneath dung pats, and reported that of three species (*Copris ochus*, *C. tripartitus* and *Onthophagus lenzii*), only the largest-bodied species (*C. ochus*) had a significant positive effect on permeability (Bang et al. 2005). Their results also indicated that beetle activity did not affect soil permeability at depths greater than 10 cm. We found no studies that assessed whether soil aeration by dung beetles is sufficient to offset soil compaction by grazing livestock (Fincher et al. 1981). Neither were there studies that empirically separated the relative effects of soil aeration and nitrogen mobilization

on plant growth. In situ studies assessing the physical affects of dung beetles on soil structural properties and subsequent impacts on plant productivity and biodiversity are needed, given that dung beetle behaviors that affect soil structure are often altered in the laboratory environment (Mittal 1993). Other organisms, specifically termites and earthworms also create tunnels and redistribute soil. The mass of dung buried and soil removed by termites has a strong linear relationship with an average 2–1 ratio (Herrick and Lal 1996). While several studies have demonstrated that some earthworms are efficient dung removers in Europe (Holter and Scholtz 2005, Holter and Scholtz 2007) Australia and New Zealand (Baker 1994), their dung related contribution to bioturbation in areas with a higher diversity of Scarabaeine dung beetles is unknown.

#### *PLANT GROWTH ENHANCEMENT*

A series of experimental studies link dung beetles' role in bioturbation and nutrient mobilization to increases in plant biomass. These experiments often contrast the biomass of plants grown in soil with dung mixed by hand, mixed by dung beetles, and with chemical fertilizer applications. Studies have reported that dung mixing actions by dung beetles result in significant increases in plant height (Kabir et al. 1985, Galbiati et al. 1995) above-ground biomass (Bang et al. 2005, Lastro 2006), grain production (Kabir et al. 1985), protein levels (Macqueen and Beirne 1975a) and nitrogen content (Bang et al. 2005). Galbiati et al. (1995) also reported that dung beetle activities had positive (though inconsistently significant) effects on corncob diameter and below ground biomass. Bornemissza and Williams (1970) reported a two-factor yield increase in above-ground biomass of millet planted in soil mixed with cow dung relative to dung-free soil,



but biomass was not influenced by the mechanism of dung burial. In some studies, the positive impacts of dung beetle activity on both above and below ground plant biomass required several months to manifest (Miranda et al. 1998, Miranda et al. 2000). In the only *in situ* study conducted with both natural vegetation and un-manipulated dung beetle abundances, Borghesio (1999) found that dung beetle mixing significantly increased net primary productivity (NPP) of heathland plants in Italy over dung without beetle activity, or dung-free controls. A repetition of their experiment the following year found significant differences in NPP between the control and both dung treatments, but could not distinguish between the effects of the latter. They attributed this to the comparatively lower number of dung fauna in the second year, possibly as a consequence of lowered cattle stocking rates in the area.

In several studies, the effects of nutrient mobilization by dung beetles on plant growth rival that of chemical fertilizers. Miranda et al. (2000) found dung beetle activity outperformed chemical fertilizer application in increasing plant height and leaf production at an application of 100 kg/ha of N, 100 kg/ha of P<sub>2</sub>O<sub>5</sub> and 100 kg/ha of K<sub>2</sub>O. In an *in situ* pasture study, Fincher et al. (1981) contrasted the yield of Bermuda grass fertilized with two levels of ammonium nitrate application (112 kg/ha and 224 kg/ha) or cattle dung exposed naturally to dung beetles

Dung beetle activity resulted in significantly higher yield than the lower fertilizer application and dung unmanipulated by beetles, but could not be distinguished from the yield found in the higher fertilizer treatments. In a second study, Fincher et al. (1981) reported that dung beetle activity significantly elevated the yield of wheat plants relative to chemical fertilizers and unmixed dung in one of three trials, though results in the other two trials were equivocal. Maqueen and Beirne

(1975a) reported that while dung-beetle mixing of cattle dung increased crude protein levels in bearded wheatgrass by 38% relative to a hand-mixed control, both low (67 kg/ha) and high chemical fertilizer application (269 kg/ha) had a much greater effect (increases of 95% and 144%, respectively). The studies outlined above predominantly consisted of single dung beetle/single plant species experimental systems, in laboratory settings. Incorporating naturally assembled dung communities with multi-species plant assemblages and non-crop plant species will be important for future work. There is a conspicuous lack of dung beetle nutrient mobilization studies in tropical forests. Non-native earthworms often have demonstrable effects on nutrient cycling in natural positive effects on yields in agroecosystems (Baker 1994) but these effects have not been linked to coprophagy. Similarly, termite effects on plant yield as a consequence of dung consumption have been inconclusive (Freyman et al. 2008).

#### *SECONDARY SEED DISPERSAL*

Vertebrate seed dispersal mechanisms are extremely widespread in tropical and temperate ecosystems (Howe and Smallwood 1982, Jordano 1992, Willson and Traveset 2000). For seeds, the risks between initial deposition in frugivorous animals' dung and final seedling emergence include predators, pathogens and unsuitable placement for future germination (Chambers and MacMahon 1994). Secondary seed dispersal is believed to play an important role in plant recruitment through interactions with these post-primary dispersal risk factors (Chambers and MacMahon 1994). From a dung beetle's perspective, most seeds present in dung simply represent contaminants, since they occupy space in the dung and are not consumed by the larvae. However, with competition for dung usually intense and burial occurring rapidly, dung beetles

often bury seeds, perhaps accidentally, as they bury dung for their larval brood balls. At other times, dung beetles purposefully remove seeds before or after burying dung, typically ‘cleaning’ the dung from a seed and abandoning it on the soil surface or within the tunnel (Andresen and Feer 2005).

Dung beetles relocate seeds both horizontally and vertically from the point of deposition. The combined impact of this dispersal by tunneler and roller species benefits seed survival (and therefore plant recruitment) by (i) reducing seed predation and mortality due to seed predators and pathogens (Janzen 1983b, Estrada and Coates-Estrada 1991, Chambers and MacMahon 1994, Shepherd and Chapman 1998, Andresen 1999, Feer 1999, Andresen and Levey 2004) (ii) directing dispersal to favorable microclimates for germination and emergence (Andresen and Levey 2004); and (iii) decreasing residual postdispersal seed clumping (Andresen 1999, 2001) with potential effects on density dependent seed mortality, seedling competition, and predation risk (Andresen 2005). The probability and depth of a seed’s vertical burial by a dung beetle depends on seed size (Andresen and Levey 2004) the composition of the dung beetle community (Andresen 2002b, Vulinec 2002, Slade et al. 2007), and both the amount (Andresen 2001, 2002b), and type of dung (Ponce-Santizo et al. 2006). Dung beetle communities bury between 6 and 95% of the seeds excreted in any given fecal pile, and this percentage ranges widely across studies (13–23% Feer, 1999; 26–67%; Andresen and Levey, 2004; 35–48%; Andresen, 2003; 6–75% Andresen, 2002; 47–95% Shepherd and Chapman, 1998). As they bury a disproportionate amount of dung, larger bodied and nocturnal species perform a disproportionate amount of secondary seed burial (Andresen 2002a, Slade et al. 2007).

The horizontal movement of seeds away from the original deposition site may increase seed fitness by (i) reducing density dependent predator or pathogen attack or by (ii) increasing seedling survival by reducing seedling density and competition (Howe 1989, Peres 1997). The probability and distance of a seed's horizontal dispersal depends on seed size (Andresen, 2002, but see Andresen and Levey, 2004) and the beetle community composition. Both the amount and origin of dung deposits affect the composition of the attracted dung beetle assemblage, but not the probability or distance of horizontal seed burial (Andresen 2001, 2002b, Ponce-Santizo et al. 2006). Overall, dung beetles communities move approximately 5–44% of available seeds horizontally (Andresen 2001, 2002b, Andresen and Levey 2004). Maximal recorded distances of dung beetle brood balls (presumably containing seeds) up to 15m in the Afrotropics ( Heymons and von Lengerken, 1929 cited in Halffter and Matthews, 1966) and 10.6m in the Neotropics have been reported (*Canthon pilularius*, Halffter and Matthews, 1966, though shorter distances are more common (6–17 cm Andresen, 2002; 18 cm Andresen and Levey, 2004; 82–112 cm Andresen, 1999; 200–500 cm *Canthon humectus* and *Canthon indigaceus* Halffter and Matthews, 1966).

Both vertical and horizontal secondary dispersal assist seeds to avoid the extremely high seed predation rates often seen in tropical forests due to rodents (Estrada and Coates-Estrada 1991, Sánchez-Cordero and Martínez-Gallardo 1998). Seed detection and predation risks decline with deeper seed burial depths (Estrada and Coates-Estrada 1991, Shepherd and Chapman 1998, Andresen 1999). Seed 'cleaning' during brood ball creation may reduce the likelihood of rodent predation of those seeds by reducing the attractive dung scent (Andresen 1999), though this impact remains speculative. While deeper seed burial depths decreases rodent detection and

predation, buried seeds must also be shallow enough to permit germination and emergence (Dalling et al. 1995, Andresen and Feer 2005). The ability of a seed to emerge from a given depth depends on seed size, cotyledon morphology and microclimate requirements (Estrada and Coates-Estrada 1991, Shepherd and Chapman 1998, Andresen 1999). While the emergence success of most seeds is greatly reduced at depths below 3 cm ((Feer 1999, Hingrat and Feer 2002, Pearson et al. 2002), a recent review by Andresen and Feer (2005) found that dung beetles bury most seeds at depths of 1–5 cm. Consequently, the secondary burial of a seed by a given dung beetle may impact that seed positively or negatively.

Determination of the net effect of dung beetle seed dispersal on plant recruitment will require studies that (i) track seed fate through germination and emergence, (ii) assess the response of small seeds to dung beetle burial, (iii) relate changes in beetle community structure to overall profiles of burial depth and (iv) assess the effect of dung beetle burial on invertebrate seed predation and fungal pathogens. The germination of a seed secondarily dispersed by a dung beetle may be influenced by local physical alteration of the soil, the seeds' final dispersal location (within a brood ball or within the tunnel itself), or the size of the brood ball in which it was incorporated, but these factors remain uninvestigated. The effect of dung beetles on small seeds (63 mm) is broadly unknown given the logistic challenges in following the fate of very small seeds (Andresen and Feer, 2005). Many small seeds are light demanding pioneer species (Dalling 2005) that represent a large proportion of the seed bank (Murray and Garcia 2002). Dung beetles bury nearly all the small seeds present in dung, but as small seeds face real constraints on maximal burial depth for successful germination (Dalling et al., 1995), the average burial depth by dung beetles may contribute more to small seed death than survival. The

relative importance of beetle seed dispersal in areas with elevated rodent seed predator densities, such as partially defaunated or secondary forests (Asquith et al. 1997) will be important information for predicting the quality of recovering forests (Gardner et al. 2007).

The importance of dung beetle secondary seed dispersal outside of the Neotropics (and Afrotropics to a lesser extent) is poorly known, particularly in savannas, temperate and Mediterranean systems and the (primarily wind-dispersed) Dipterocarp forests of south-east Asia (McConkey 2005). While there are several reports of dispersion of invasive plant species by livestock (Campbell and Gibson 2001, Constible et al. 2005) and wild mammals ((Myers et al. 2004, Shiponeni and Milton 2006) in anthropogenic and natural ecosystems worldwide, it is not known whether dung beetles play a role in the seedling establishment and success of invasive plants. In northeastern Brazil *Phanaeus kirbyi* and *Dichotomius (Selenocopris) aff. bicuspis* are known to positively affect germination rates through scarring pequi seeds (*Cariocar brasiliensis*) (Vaz de Mello pers. comm), but it is unknown if scarification is a common dung beetle function.

Secondary seed dispersal is not unique to dung beetles. Earthworms may have a strong effect on seeds, as seeds are occasionally ingested and re-deposited in surface-level casts or deep within the soil profile, though the net effects of these movements are unknown (Dalling 2005).

Secondary dispersal by ants (myrmecochory) is also relatively common in tropical forest systems (Dalling 2005, Pizo and Oliveira 2005).

## PARASITE SUPPRESSION

Through feeding and nesting, adult and larval dung beetle activity serves to control the abundance of dung-breeding hematophagic and detritivorous flies and dung-dispersed nematodes and protozoa. As these ecological processes potentially have enormous implications for livestock, wildlife and human health and wellbeing (Miller 1954, Byford et al. 1992). Much of our understanding of these functions has arisen from the study of livestock parasites and pests.

## ENTERIC PARASITES

From an early study in Australian cattle pastures, Bryan (1973) reported a significant decrease in emergent strongyle nematode larva from cattle dung manipulated by *Digitonthophagus gazella*. In a subsequent study, Bryan (1976) reported that control pats with no dung beetles contained 50 times more helminth larvae than those with 10 or 30 *D. gazella* pairs. Fincher (1973) experimentally elevated the dung beetle population 5-fold in a cattle pasture in the southeastern United States and reported a nearly 15-fold reduction in the emergence in *Ostertagia ostertagi* relative to dung beetle free-pastures and a 3.7-fold reduction relative to pastures with natural dung beetle levels. In a second experiment, Fincher reported that calves grazed on pastures without dung beetles acquired nine times more endoparasites (*Ostertagia* and *Cooperia*) than those in pastures with experimentally elevated levels dung beetles and four times more than pastures with natural beetle abundances (Fincher 1975). Bergstrom (1976) reported an 84.7% reduction in the number of emerging elk lungworm larvae (*Dictyocaulus hadweni*) when elk dung was manipulated by an *Aphodius* dominated dung beetle community. Dung beetles have

also been implicated in the reduction in abundance of the exploding fungus *Pilobolus sporangia*, which forcefully disperses nematodes in pasture systems along with its own spores (Gormally 1993).

Laboratory studies reveal that passage through certain dung beetle species significantly reduces the abundance of viable helminth eggs and protozoan cysts, including *Ascaris lumbricoides*, *Necator americanus*, *Trichuris trichiura*, *Entamoeba coli*, *Endolimax nana*, *Giardia lamblia* (Miller et al. 1961) and *Cryptosporidium parvum* (Mathison and Ditrach, 1999). Miller et al. (1961) reported the feeding actions of four *Canthon* and *Phanaeus* species reduced the passage of hook and roundworm eggs by nearly 100%, while *Dichotomius carolinus* had little effect. Miller understood dung beetle feeding to involve a grinding action between the molars and attributed the reduced control of helminth eggs by *D. carolinus* to its large molar size and spacing (Miller 1961). Subsequent work indicates that Scarabaeine beetles strain out, rather than comminute large particles, using their soft, filtering setae to ingest only minute particles (8–50  $\mu$ m) and squeezing the smaller remainder between the molar surfaces to remove excess liquid (Holter 2002), consequently the specific mechanism for this parasite suppression remains poorly understood. Additional research is also needed to assess the relative impacts of adult dung beetle feeding versus nesting on the survival rate of parasitic eggs and cysts, and extent to which these actions reduce disease incidence or parasite load in wild and domestic animals. Male *Canthon cyanellus cyanellus* are known to produce an antifungal compound that protects brood balls. It is not known if this chemical protection is widespread, nor has implications for fungal or other pathogen control (Cortez-Gallardo 2007). While dung beetles have been conjectured to be important suppressors of human endoparasites (Miller 1954), we know of no publication



empirically relating dung beetles and human endoparasite transmission. Hingston (Hingston 1923) reported that dung beetles in rural India were capable of interring 40–50 thousand tons of human feces in the months of May and June. Under similar removal rates, dung beetles use of human faeces may reduce transmission of fecal–oral pathogens, particularly in rural areas with inadequate sanitation.

#### *PARASITE DISPERSAL*

Several studies have alternatively suggested that dung beetles may transmit dung-borne pathogens within their gut or upon their exoskeleton, acting as intermediate, incidental or paratenic hosts. However few studies present convincing evidence of the role of dung beetles in transmission. Other coprophagous invertebrates (e.g. earthworms) have been investigated for their role as endoparasite hosts, also with generally inconclusive results (Roepstorff et al. 2002). Without targeted epidemiological study of the parasites in question, it remains unknown if dung beetles commonly amplify parasite transmission as frequently suggested. Species in various dung beetle genera (including *Anomiopsoides*, *Eucranium*, *Megathopa*, *Canthon*, *Phanaeus*, *Dichotomius*, and *Ateuchus*) have been reported as intermediate hosts of swine parasites (e.g. *Ascarops strongylina*, *Physocephalus sexalatus*, *Macracanthorhynchus hirudinaceus* and *Gongylonema verrucosum*) (Alicata 1935, Martínez 1959, Stewart and Kent 1963), however simple presence of infectious or non-infectious larval stages within adult dung beetles is an insufficient demonstration of a dung beetle's role as host in a parasite's development cycle. Stumpf (1986) suggested that *M. hirudinaceus* used scarabaeine beetle adults as intermediate hosts in Brazil, though he reported more larvae in non-infective (IV & V) than infective (VI)

stages in adult beetles. This suggests that *M. hirudinaceus* larvae may not develop within the dung beetle, but simply be consumed at the later infective stage.

Saitoh and Itagaki (1989) concluded that two species of Onthophagus that emerged from cat feces infected with feline coccidia (*Toxoplasma gondii*) carried infective oocysts both in their feces and on their bodies. Mice that then consumed these beetles were capable of infecting kittens (Saitoh and Itagaki 1989). Saitoh and Itagaki additionally detected two additional strains of feline coccidia, *Isopora felis* and *Isopora rivolta* on dung beetles collected from urban dog feces; these dung beetles were also able to transmit feline coccidia to three of four kittens via dung beetle-mouse consumption, presenting a potential incidental or intermediate host role for some beetle species in feline coccidia. In contrast, Xu et al. (2003) tested 113 *Catharsius molossus* dung beetles for two *E. coli* strains (O157:H7 and the virulent Shiga-toxin), both with principle reservoirs in domestic pigs and cattle. Only six beetles (ca. 5%) tested positive for *E. coli* O157:H7 and four of the six for the Shiga-toxin 2 strain. They concluded that dung beetles likely play no epidemiological role in *E. coli* O157:H7.

#### *FLY CONTROL*

Fresh mammal dung is an important resource for a variety of dung-breeding flies as well as dung beetles. Several pestiferous, dung-dwelling fly species (principally *Musca autumnalis*, *M. vetustissima*, *Haematobia thirouxi potans*, *H. irritans exigua* and *H. irritans irritans*) have followed the introduction of livestock globally. Fly infestations reduce livestock productivity (Haufe 1987) and hide quality (Guglielmone et al. 1999) and represent an enormous financial

burden to livestock producers (Byford et al. 1992).

When and where dung beetles and dung flies co-occur, fly survival tends to decline as a consequence of asymmetrical competition for dung resources, mechanical damage of eggs by beetles, and fly predation by mites phoretic on dung beetles. A series of experimental manipulations of dung beetle and fly densities in artificial dung pats report elevated fly mortality in the presence of Scarabaeine beetles, both in the laboratory and field (Bishop et al. 2005)(Bishop et al., 2005; (Bornemissza 1970, Blume et al. 1973, Feehan et al. 1985, Doube 1986) (Macqueen and Beirne 1975b, Hughes et al. 1978a, Moon et al. 1980, Ridsdill-Smith 1981, Ridsdill-Smith et al. 1986, Ridsdill-Smith and Hayles 1987, Mariategui 2000) (Wallace and Tyndale-Biscoe 1983, Ridsdill-Smith and Matthiessen 1984). Fly mortality caused by dung beetle activity is a combined consequence of (i) direct mechanical damage to fly eggs and early instars caused during adult beetle feeding (Ridsdill-Smith and Hayles 1990, Bishop et al. 2005), (ii) unfavorable microclimates for fly eggs and larvae caused by dung disturbance (Ridsdill-Smith and Hayles 1987) and (iii) resource competition with older larvae, primarily from removal of dung for brood balls (Hughes 1975, Ridsdill-Smith and Hayles 1987, Ridsdill-Smith and Hayles 1990). The relative impact of these dung beetle activities is modulated by several factors, including dung quality (Macqueen and Beirne 1975b, Ridsdill-Smith and Matthiessen 1986, Ridsdill-Smith and Hayles 1990), beetle abundance (Bornemissza 1970, Hughes et al. 1978a, Ridsdill-Smith and Matthiessen 1986, Ridsdill-Smith and Matthiessen 1988, Ridsdill-Smith and Hayles 1989, Tyndale-Biscoe 1993), activity period (Fay et al. 1990), nesting strategy (Edwards and Aschenborn 1987) and importantly, arrival time (Hughes et al. 1978a, Edwards and Aschenborn 1987, Ridsdill-Smith and Hayles 1987). Phoretic predatory macrochelid mites have

also been implicated in fly control (Axtell 1963) (Doubé 1986). These mites rely on dung beetles for transport between dung pats (Krantz 1998) and consume significant numbers of fly eggs and young larvae (Wallace et al. 1979) when sufficiently abundant (Glida et al. 2003). Anecdotal reports from Australia suggest that the level of fly control achieved in dung pats with both mites and beetles is superior to those with only beetles (Dadour 2006).

Experimental simulations of field conditions typically report a strong reduction in fly abundance by dung beetles in individual dung pats (Hughes et al. 1978a, Ridsdill-Smith and Hayles 1990)- yet attempts to link the activity of a single dung beetle species to demonstrable reductions of natural fly populations have been unsuccessful to date (*Eoniticellus intermedius*, Hughes et al., 1978; *Onthophagus granulatus*, Feehan et al., 1985, *Digionthophagous gazella*, Bishop et al., 2005). For example, Tyndale-Biscoe and Walker (1992) found that experimentally elevated densities of *Onthophagus australis* reduced bush fly survival by 74% and fly puparia size by 18% – however *O. australis* densities were not observed to reach this critical density in the spring, when bush flies populations first began to grow. Fly abundance did not significantly differ before or after the 1971 introduction of dung beetles and successful establishment of *Eoniticellus intermedius* in 1974 to Australia (Hughes and Morton 1985), despite anecdotal evidence to the contrary (Hughes et al. 1978b).

While dung beetles have a clear and negative impact on fly breeding success under experimental conditions, in natural settings this relationship is more complex. An entire dung beetle assemblage (rather than a single species) is less likely to demonstrate the mismatches in habitat use and seasonal and daily flight activity that would reduce their effectiveness in fly suppression.

The two in situ field studies that have measured fly success after exposure to the entire dung beetle assemblage (Fay et al. 1990, Horgan 2005b) both report a strong fly reduction by dung beetles in individual dung pats. Rather than concluding from these single species interactions that dung beetles offer no practical pest fly control at the landscape level (i.e. Macqueen and Beirne, 1975b), we advocate that future investigations assess these functions with the entire dung beetle assemblage.

Expanded future research on fly–beetle interactions to novel ecosystems (e.g. outside of pastures or savannas), geographic regions (e.g. outside of Australia, southern Africa and to a lesser extent Brazil) and fly groups (e.g. disease vectors and wild mammal pests, though see Bishop et al., 2005) would strengthen our understanding of the true role of dung beetles as fly competitors in both natural and managed landscapes. While dung beetles are important competitors of pestiferous flies, fly predators (e.g. Macrochelid mites, histerid and staphylinid beetles) and parasites (e.g. parasitic wasps) are also key biological control agents. This entire suite of organisms likely produces the function of truly effective fly control, and both the relative contribution by dung beetles and the underlying functional relationships among these coprophagous organisms (e.g. resource partitioning, facilitation or a selection effect) are poorly known.

#### *TROPHIC REGULATION AND POLLINATION*

Some dung beetle species have additional unique ecological roles in trophic regulation and pollination. Dung beetle predation potentially contributes to population regulation of leafcutter

ants (*Atta spp.*) – one of the Neotropics' principal herbivores (Costa et al. 2008). *Canthon virens* (misidentified as *C. dives* sensu Borgmeier, 1937) individuals attack leaf-cutter queens during nuptial flights to provision their larvae (Halffter and Matthews 1966b, Hertel and Colli 1998, Forti et al. 1999, Silveira et al. 2006). Forti et al. (1999) estimated that a single dung beetle individual could predate dozens of queens during a reproductive period, representing up to 10% of the recently hatched individuals. Vasconcelos et al. (2006), observed that 61.8% of the predation events resulting in nest establishment failure were instigated by *Canthon virens*. As *Atta* ants strongly impact plant community structure and dynamics, soil properties and nutrient cycling (Farji-Brener 1992, Hull-Sanders and Howard 2003, Moutinho et al. 2003), the enormous predation pressure they face during nuptial flights may play an important role in ecological processes. Further research on *Atta* predation by dung beetle species is needed to determine the relative trophic importance of these predation events.

While restricted to only a few plant species, Scarabaeine beetles are important (and often obligate) pollinators of decay-scented flowers in the families Araceae and Lowiaceae. Two species of Onthophagus dung beetles (*O. ovatus* and *O. sellatus*) are pollinators of the dung/carrion scented *Arum dioscoridis* (Araceae) in Lebanon (Gibernau et al. 2004) (Meeuse and Hatch 1960). Gleghorn, cited in Arrow (1931) reported the pollination of the carrion-scented *Typhonium tribolatum* (Araceae) in India by *Onthophagus tarandus* and *Caccobius diminitivus*. Sakai and Inoue (1999) described the obligate pollination of carrion-scented *Orchidantha inquei* (a member of the highly relictual Lowiaceae family) by carrion feeding *Onthophagus* species. While these tight co-evolutionary relationships may be rare, their obligate nature merits appropriate conservation action.

## ECOSYSTEM SERVICES

Ecosystem services are the subset of ecological functions that are directly relevant or beneficial to the human condition (De Groot et al. 2002). The few studies evaluating dung beetle ecosystem services have predominantly outlined their value to the livestock industry, particularly in the context of the Australian Dung Beetle Project.

Following European colonization, Australian livestock production in the absence of a native ruminant-adapted dung beetle fauna resulted in an estimated deposition of 33 million tons of dung yr<sup>-1</sup> (Bornemissza, 1960; Bornemissza, 1976). This vast fecal deposition increased pest fly populations (Hughes, 1975) and caused extensive pasture loss (Ferrar 1975), as livestock avoided grazing in the fouled areas surrounding deposits (Anderson et al. 1984). In response, 55 species of dung beetles were imported between 1968 and 1982, principally from southern Africa. Eight species have successfully established (Macqueen and Edwards 2006), and several are widely distributed across the productive livestock regions (Elphinstone 2006). These introduced beetles have reduced the area physically covered by cattle waste by approximately 4 percent (Hughes 1975), representing a tremendous gain in pasture, since an additional 6–12% of the area surrounding each dung pat is generally avoided by grazing livestock (Fincher et al. 1981). However, while successfully increasing dung removal services, introduced beetles appear to have failed to successfully suppress fly population at the landscape level (Feehan et al. 1985).

Beyond Australia, dung beetles play a key role in the sustainability of extensive livestock production globally. Extensive pasture systems account for 78% of all agricultural land use and currently cover nearly 2.0 billion hectares – some 15% of the earth's ice-free surface (Steinfeld

et al. 2006). As chemical additives and curative (rather than preventative) veterinary care are often economically and logistically infeasible in these areas, their long-term sustainability rests upon natural ecological processes to avoid forage fouling, suppress livestock pests and maintain forage productivity through prevention of N-volatilization (Miranda 2006). Losey and Vaughan (2006) estimate the net value of dung beetles to the extensively pastured beef cattle industry in the United States at USD \$380 million yr<sup>-1</sup>, based largely on estimates first published by Fincher (1981) and Anderson et al. (1984). This sum represents the estimated avoided costs in fertilizer application and production losses from forage fouling, enteric parasites and flies. An extrapolation of these values to extensive cattle ranching globally is beyond the scope of this paper, but may portend a significant economic role for dung beetles in maintaining sustainable livestock production (Steinfeld et al. 2006).

Aside from the relevance of dung beetles to livestock production, we can only conjecture about the importance of other dung beetle ecosystem services. Soil conditioning and nutrient recycling by dung beetles may increase crop yield and plantation productivity as suggested by laboratory studies (Yokoyama et al. 1991b, Miranda et al. 2000)(Miranda et al., 2000; Yokoyama et al., 1991b). Isolation and synthesis of the chemical compounds that suppress pathogenic fungal growth on dung beetle brood balls may have horticultural applications. Secondary seed dispersal likely contributes to the timber and non-timber forest product industries as well as reforestation or restoration projects (Vulinec et al. 2007).

As with most ecosystem services, before dung beetle services can be properly integrated with conservation planning or practice, additional research on dung beetle biodiversity ecosystem



function (BEF) relationships and links between ecosystem functions and services will be required. A bridging research agenda suggested by Kremen (2005) provides a near perfect fit to this task, suggesting future work that would identify: (1) the key species or traits providing ecosystem functions, (2) the relationships between ecosystem function and community assembly and disassembly processes, (3) the environmental factors influencing the production of ecosystem functions, and (4) the spatio-temporal scales relevant to both providers and their functions (Kremen and Ostfeld 2005). The most recent dung beetle BEF work has begun to advance our understanding of points 1–3, by identifying the specific-specific and community traits responsible for both ecological function (effect traits) and sensitivity or resistance to environmental change (response traits) (Horgan 2005b, Larsen et al. 2005, Slade et al. 2007).

To this we suggest a necessary fifth step, the specific relation of ecosystem functions to ecosystem services, through identifying those socio-economics and ecological contexts where a given function is directly relevant to humans. It is unlikely that all dung beetle functions are relevant to humans in all natural and socio-economic contexts. For example, dung beetle secondary seed dispersal is unequivocally an ecosystem function in a Neotropical forest. Is the burial of that seed relevant or useful to humans, and therefore a service? If that dispersal is important for the regenerative capacity of a national park that contributes to atmospheric and hydrologic regulation, or has cultural values, is it then an ecosystem service? Declaring an ecological process “important” to the human condition is heavily subjective to spatial, temporal and even ethical considerations (Srivastava and Vellend 2005, McCauley 2006, Wallace 2007) compelling researchers to clearly delimit the scale and intent of their study.

## DUNG BEETLE RESPONSE TO ANTHROPOGENIC THREATS

Multiple lines of evidence from temperate and tropical systems indicate that local and regional-scale changes in land-use and mammal faunas can severely alter patterns of dung beetle species diversity and abundance. The decline or local extinction of dung beetles will likely have significant short and long-term implications for the maintenance of the ecosystem processes outlined above.

Globally, tropical forest loss, modification and fragmentation are driving high rates of local extinction across forest-restricted dung beetle communities (Nichols et al. 2007), effects that are likely exacerbated by concomitant declines in food resources as mammal populations respond both to habitat change and hunting. Natural grasslands modified for livestock pasturing offer altered vegetation density, soil temperature and moisture support – leading to range expansion for some dung beetles species and contraction for others (Davis et al. 2004). New evidence demonstrates that re-forested habitats often perceived as ‘conservation friendly’ (e.g. secondary or plantation forests) provide low conservation value for dung beetles (Gardner et al. 2008b) – a finding that increases concern over continued primary forest loss. Since 1953, even comparatively low annual rates of deforestation (1.4–2.0%) in Madagascar have resulted in the apparent extinction of 43% endemic forest-dwelling species in the tribe Helictopleurini (Coprinae)(Hanski et al. 2007). Compounding these concerns is evidence that conservation area networks may be insufficient to conserve dung beetle biodiversity. Over 23% of Costa Rica’s land surface is under conservation protection (UNEP-WCMC 2003), yet this protected area network encompasses less than 13% of Costa Rica’s areas of highest dung beetle species richness and endemism (Kohlmann et al. 2007). Over 35 years of dung beetle records from a

single Costa Rican protected area (the La Selva Biological Station) indicate community changes over time are most affected by the loss, rather than the gain of species, a trend the authors associate with the isolating effect of regional agriculture intensification (Escobar et al., unpublished data).

It is in the Mediterranean however, where the strongest empirical evidence of dung beetle decline can be found (Lobo 2001) often associated with the replacement of extensive livestock grazing by intensive agriculture and afforestation, or ivermectin use in grazing animals. Across Italy, from the first to the last quarter of the 20th century the relative capture frequency of rolling species has declined over 31%, while the number of 30 · 30m grid cells occupied by a rolling species declined by nearly 24% (Carpaneto et al. 2007). In the Iberian Peninsula over the same time period, the probability of finding a roller in the decreased by 21.48% and the number of UTM cells with rollers present declined by 20.04% (Lobo 2001).

## CONCLUSION

In natural systems, dung beetles appear to play an important role in maintaining ecosystem integrity, especially through secondary seed dispersal and nutrient cycling. With the high sensitivity of dung beetles to many kinds of human activities and habitat disturbance, it is imperative to understand and protect these processes. In agricultural systems, dung beetles play an important role in increasing primary productivity and suppressing parasites of livestock. Improved understanding of the linkages between dung beetle ecological functions and ecosystem services is critical to the future management of these services.

We suggest four future lines of dung beetle ecological function research. First, as outlined in the above sections several basic gaps remain in our understanding of dung beetle ecological processes. A focus on in situ studies that use naturally assembled communities and assess specific functions in novel geographic regions (e.g. seed dispersal in the Australian tropics) and interactions with novel taxa (e.g. endoparasite control in Neotropical primates) would be particularly useful in filling in these gaps.

Second, significant trade-offs likely exist both in space and time for dung beetle-mediated ecological functions (Rodriguez et al., 2006), with other species playing more dominant functional roles under specific geographic areas and seasonal conditions. Termites for example perform the majority of waste removal in arid (Nakamura 1975, Anderson et al. 1984, Herrick and Lal 1996), and seasonally arid areas (Janzen 1983a), while earthworms play a key role in temperate regions (Holter 1977, 1979). Dung beetles have also been implicated in increasing seed mortality and dispersing pathogens – ecological functions that inherently cannot provide ecosystem services since they are not beneficial to humans.

Third, greater emphasis on the mechanisms of function responses to environmental change will help us to predict the ecological implications of dung beetle biodiversity loss (Larsen et al. 2005, Nichols et al. 2007). Understanding how the functional consequences of species loss are buffered by compensatory mechanisms operating at the community level or exacerbated by non-random extinction orders will be key. Trait-based approaches are a tangible way to determine the ecological correlates of success (compensation) and extinction- proneness (extinction order) and directly relate those factors to ecological function (e.g. Larsen et al., 2005; Slade et al., 2007).

Finally, the economic value of dung beetle communities is an important and exciting area for future study (Mertz et al. 2007). Dung beetles and their functions are not evenly distributed across space or time, which will present challenges to understanding the dynamics of service production, even in those habitats where ecosystem service values can be clearly delimited (e.g. cattle pastures) (Anduaga and Huerta 2007). Studies that articulate the supply and demand for dung beetle services in a given socio-ecological context such as ecological restoration projects and managed forests will be especially useful (Boyd and Banzhaf 2007).

The declining global trends in habitat and food availability for Scarabaeine dung beetles are of great conservation concern (Carpaneto et al. 2007, Nichols et al. 2007). An improved understanding of the ecological importance of dung beetles is one contribution to understanding the consequences of diversity loss in natural and human dominated ecosystems.

CHAPTER 3 - HUNTING-INDUCED TROPHIC CASCADES IN TROPICAL FOREST: LANDSCAPE-  
LEVEL EVIDENCE FOR COMMUNITY-LEVEL CASCADES IN THE ‘BROWN WORLD’.

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## ABSTRACT

While evidence that vertebrate predators can regulate food webs and initiate terrestrial trophic cascades has been demonstrated in many systems, three key aspects have received scarce research attention to date: (1) the potential for cascades within fecal-detritus-based food webs, (2) the ability of vertebrate predators to initiate community-wide cascades, and (3) whether strong cascade effects often reported in experimental work occur at landscape-levels. These questions are central to understanding the impacts of tropical forest defaunation - an important driver of anthropogenic environmental change. We used data collected across 880,000 ha of tropical forest in the western Brazilian Amazon to conduct the first landscape-level assessment of hunting-induced cascade effects in tropical forest on community-level detritivore diversity and biomass, and fecal detritus process rates. To do this, we coupled data on human hunting pressure, game mammal and detritivore (dung beetle) abundance together with rate measurements of two detritus-pathway processes relevant for primary producers: (i.e. fecal detritus burial and secondary seed dispersal). We found evidence of vertebrate effects on community-level beetle biomass, but not diversity. These impacts were dependent upon forest type, and were present in seasonally flooded (*várzea*) forest but not unflooded (*terra firme*). The strength of cascade effects varied across trait-defined subsets of the detritivore community, and hunting pressure corresponded to significant declines in smaller-bodied and diurnal species, while larger-bodied beetle species were unaffected. Finally, we found that the impacts of mammal hunting did influence dung beetle-mediated burial of large and medium sized seeds, however in the opposite direction expected. We posit that this strongly positive relationship between hunting and the proportion of seeds buried is driven by a hunting-mediated decline in resource availability that

increased the attractiveness of the experimental feces used to measure seed burial (i.e. the scarcity effect). Our findings suggest that the potential for hunting-induced cascades through the fecal detrital web is strong. We discuss the implications of these results for our understanding of hunting-induced trophic cascades, how the use of trait-defined subsets can highlight the specific pathways by which these effects occur, and highlight key knowledge gaps in our understanding of trophic interactions in tropical fecal detrital food webs.



## INTRODUCTION

The existence of trophic cascades – predator-prey effects that alter the biomass or diversity of species across more than one trophic level - is now well established in many ecosystems (e.g. Schmitz et al. 2000, Shurin et al. 2002, Borer et al. 2005). Empirical evidence for trophic cascades predominantly comes from manipulative experiments (e.g. Shurin et al. 2002) that test the ability of invertebrate predators in plant-based food webs (Halaj and Wise 2001) to initiate *species-level* cascades (sensu Polis 1999, Schmitz et al. 2010). More recently, vertebrate-induced trophic cascades in terrestrial habitats have also been demonstrated for plant-based webs (Schmitz et al. 2000, Royo and Carson 2005, Schmitz 2006).

As our understanding of vertebrate predator regulation of terrestrial system improves, several key questions remain. First, to what extent do the diversity and biomass cascades demonstrated in plant-based food webs also occur along the ‘brown world’ pathways of the detritus system? Trophic cascades in detrital food webs have received less research attention than plant-based food webs (Wu et al. 2011), though detritus is a major contributor to terrestrial nutrient cycling (Moore et al. 2004). Vertebrate control of the fecal detrital pathway has perhaps received the least study (Wardle and Bardgett 2004, Schmitz et al. 2010). Understanding the role of predator regulation in detritus-based food webs is particularly important, as these effects are expected to have opposite outcomes for ecosystem process rates than traditional plant-based food webs (Srivastava et al. 2009; Wu et al. 2011). Enhanced predation in plant-based food webs leads to the indirect facilitation of plant biomass or diversity, as predator-induced reductions in herbivores drive a reduction in plant damage and loss to herbivory (Hairston et al. 1960, Schmitz et al. 2000, Duffy et al. 2007). In fecal detritus-based webs however, increased predation is

expected to indirectly *reduce* plant biomass or diversity, as predator-induced herbivore declines correspond with co-declines in the feces-dependent detritivores responsible for mediating two key fecal detritus processes: feces burial and secondary seed dispersal (Nichols et al. 2009; Nichols et al. 2008; Wu et al. 2011).

Second, is there evidence that vertebrate predation can induce community-level cascades? The existence of terrestrial community-level cascades - those that substantially alter the biomass or diversity of an entire trophic level (*sensu* Polis 1999, in contrast to species-level cascades) - remains controversial. Some researchers consider community-wide cascades unlikely under the high trophic complexity, species diversity and spatial heterogeneity that characterize many terrestrial habitats (Strong 1992, Polis 1999) . A principal reason why community-level responses may be rare in diverse terrestrial systems is that with greater species diversity comes greater heterogeneity in species trait values (e.g. Powers 1992) within a given trophic level (Polis and Strong 1996, Persson 1999). When these species traits are relevant to trophic interactions, this complexity enhances the capacity for compensatory responses between functional groups (i.e. Holt 1997's 'community-modules') (Carvalho et al. 2010; Otto et al. 2008; Wardell et al. 2001). The occurrence of density or biomass compensation (i.e. an inverse relationship between density or biomass and species richness) within trophic levels can then mask the detection of community-level change (Persson 1999). Complementarity in key species traits (e.g. phenotype and phenology) between trophically interacting species is an important predictor of the probability and strength of both individual trophic interactions (Werner and Peacor 2003, Vazquez et al. 2009) as well as overall trophic cascade strength (Bascompte et al. 2005). Such trait-defined indirect interactions are ubiquitous throughout food webs (Berlow et al. 2004). Trait-defined indirect interactions (hereafter TDIIIs) operate in both density-mediated (e.g.

Abrams 1995) or behavioral trait-mediated fashions (e.g. Werner and Peacor 2003).

Documenting the identity of which TDIs are most susceptible to altered predation pressure can provide important information on which trophic interactions are most likely to drive community-level effects (Carpenter et al. 1985, Persson 1999, Bascompte et al. 2005).

A third unresolved question is the extent to which the trophic cascade effects often revealed in experiments can scale up to realistic food webs at larger spatial scales. The broad spatial and temporal extent of landscape-level observational studies are a useful complement to experimentation, particularly to assess potential cascade effects at the scales at which vertebrate predators and their prey operate (Persson 1999). To date, few spatially extensive examinations of the evidence for predator-induced trophic cascades exist (Beschta & Ripple 2009). Resolving this uncertainty is critical to understanding the cascading effects of one of the most extensive drivers of anthropogenic environmental change in tropical forests – the removal of wild vertebrates for human consumption (Stoner et al. 2007, Wilkie et al. 2011).

Trait-defined subsets may be particularly useful in understanding a key pathway by which vertebrate predators may induce community-wide trophic cascades in tropical fecal detrital foodwebs: the persistent harvesting of game mammal species by humans. Mammal hunting is a near ubiquitous activity throughout tropical forests (Fa et al. 2002, Corlett 2007, Peres and Palacios 2007). Rural hunters exhibit strong body size preferences in target game mammals (Jerozolinski and Peres 2003). In Neotropical forests, this selectivity leads to local size-ordered depletion in large-bodied and frugivorous primates and granivorous ungulate and rodent species,

and can lead to regional defaunation of these species in persistently hunted forests (Bodmer et al. 1997, Peres 2000a, Fa et al. 2002, Corlett 2007, Peres and Palacios 2007). Evidence for compensation between hunted and unhunted species is weak (Peres 2000b), though may occur between primate species (Peres and Dolman 2000), between frugivorous primates and terrestrial mammals that consume fallen fruit (Terborgh 1992, Wright et al. 2000) and between hunted mammals and unhunted insectivorous mesopredators (e.g. coatis, common opossums) (Da Fonseca and Robinson 1990, Galetti et al. 2009) or small-bodied rodents (e.g. Dirzo et al. 2007). Given the magnifying impacts of selective predation on community-wide trophic cascades (Bascompte et al. 2005), and the keystone roles of large-bodied mammals in plant-based food webs via seed dispersal and predation (Howe and Smallwood 1982, Poulsen et al. 2002, Terborgh and Nuñez-Iturri 2006) and detritus-based food webs via donations of fecal resources to detritivores (Nichols et al. 2009), understanding the potential for hunting-induced trophic cascades in tropical forests is a key ecological priority (Bodmer et al. 1997, Wright et al. 2007b). Yet to date, assessments of the potential for human hunting pressure to induce trophic cascade have (i) largely ignored fecal-detritus-based food webs, (ii) seldom sought evidence of both community-wide and trait-defined trophic cascades, and (iii) rarely documented cascade effects across extensive spatial scales (Dirzo and Miranda 1990, Terborgh et al. 2001, Andresen and Laurance 2007, Stoner et al. 2007, Wright et al. 2007b).

To examine the evidence for trophic cascade effects associated with human hunting in tropical forests, we conducted a landscape-level observational study along a gradient of hunting pressure in the western Brazilian Amazon. Across a 320-km section of the Juruá River (Fig. 3.1), we linked a three-year census of medium and large mammals with surveys of Scarabaeine dung

beetles, and rate measurements of two key detritus-pathway processes: the underground relocation of mammal feces, and the secondary burial of excreted seeds. Scarabaeine dung beetles mediate burial of herbivore feces during feeding and reproduction. This burial is demonstrated to have significant influences on plant biomass via enhanced nutrient cycling (reviewed in Nichols et al. 2008) and on plant recruitment through reduced safe-site limitation of excreted seeds (reviewed by Andresen and Feer 2005). We relied on these data to address three questions.

- (1) First, we tested for the existence of hunting-induced cascade effects on community-level changes in the diversity and biomass of the detritivore (dung beetle) trophic level. We expected community-level effects to be prevalent, given the strong dependence of Scarabaeine beetles on mammal feces (Nichols et al. 2009) and demonstrated lack of density or biomass compensation in perturbed dung beetle communities (e.g. Larsen et al. 2005, Gardner et al. 2008).
- (2) Second, we sought evidence that trait-defined indirect interactions might drive these detritivore effects. We hypothesized that the selective removal of diurnal game mammals would have size-dependent effects across the beetle community. Larger-bodied species may suffer disproportionate declines in hunted areas, as these species require larger individual dung resources for reproduction (Hanski and Cambefort 1991a) and are often only attracted to large dung deposits (Peck and Howden 1984a) provided by targeted game mammals (Nichols et al. 2009). Alternatively, hunting may more strongly influence smaller-bodied species, given that their lower energy reserves and dispersal power reduce their ability to emigrate to more optimal foraging conditions, in contrast to the active foraging strategies and

long distance dispersal capacities of larger species that may buffer them from declining fecal resource density in overhunted forest (Larsen et al. 2008, Nichols et al. submitted). Hunting pressure may also have nesting strategy-specific effects across the beetle community. Three principal nesting strategies are recognized: *paracoprid* (i.e. tunneler) species locate their nests directly underneath the fecal deposit, *telocoprid* (i.e. roller) species locate their nests at often great horizontal distances from the fecal deposit, and *endocoprid* (i.e. dweller) species nest directly within fecal deposits (Halffter and Edmonds 1982a). Each of these three nesting strategies include large and small species; however whether or not the distinctive leg morphologies associated with different nesting strategies (i.e. Inward et al. 2011) influence feces preference or plasticity remains broadly unknown (Nichols et al. 2009).

- (3) Finally, we sought evidence that human hunting pressure can further impact rate changes in two detritus-pathway processes that are important influences on primary producers. We quantified the magnitude of two detritus-pathway processes: the proportion of detritus (i.e. mammal feces), and excreted seeds buried by natural dung beetle communities across the hunting gradient. We expected that reductions in community-level dung beetle biomass would correlate with pronounced declines in both seed and feces burial rates, and that larger-bodied beetle species would be more strongly correlated with detritus process rates than smaller-bodied species (e.g. Slade et al. 2011).

## METHODS

### STUDY SITE

We conducted the study in the Médio Juruá Extractive Reserve (ResEx; 253,227 ha) and Uacari Sustainable Development Reserve (RDS; 632,949 ha) in the state of Amazonas, Brazil. The reserves are contiguous and bisected by the Juruá River, a large white-water tributary of the Amazon (Solimões) River (3.1). The region is classified as lowland tropical forest, composed of a mosaic of seasonally flooded várzea forest along main river channels and higher elevation *terra firme* forest further from the main river channel and along smaller tributaries. Elevation across the study region ranges from 65 – 170 m.a.s.l. Meteorological data collected daily at the Bauana Ecological Field Station, near the center of the study region, indicate that annual rainfall averaged 4,154 mm from 2008-2009 and is seasonal, with a prolonged rainy season (December-May) and subsequent flood pulse (January-June).

Approximately 4,000 people inhabit the study area, distributed across 74 settlements. Reserve residents variously engage in hunting, fishing and forest extraction as well as small-scale agriculture for both subsistence and local sale (Newton et al. in press-b). Subsistence hunting is legal in mixed-use protected areas, with the exception of specific CITES-listed species (i.e. jaguars and caiman). Reserve residents hunt with rifles, shotguns, and to a lesser extent snares, to supplement an otherwise fish- and manioc-based diet. *Terra firme* forests across the study site have no documented history of logging, while várzea forests have experienced the historical, selective removal of the largest adult trees of commercial timber species between 1970 and 1995 (Scelza 2008). The federally managed ResEx and state-managed RDS were decreed in 1997 and 2005 respectively. Although administered by different government agencies, here we consider

them a single system as they share near-identical extractive history, and ecological, socioeconomic and cultural contexts (Derickx 1992).

### Hunting pressure

Wild vertebrates in tropical forest are typically at very low abundances in the immediate vicinity of permanent human habitation, from the combined effects of increased local hunting pressure, and behavioral and foraging shifts by hunted game species (Levi et al. 2011). Human hunters are central-place foragers, and these faunal depletion zones radiating from permanent gun-hunting settlements are persistent features of most tropical forest landscapes (Levi et al. 2009, Parry et al. 2010a). The size of these zones is asymptotically related to human settlement size (Levi et al. 2011), and rarely extends past 10-14 kilometers for communities where forest access is primarily gained on foot (Levi et al. 2011) though can be much wider for rural communities with motorized boat access (Parry et al. 2010a). Human settlement size and distance to urban centers are typically correlated across rural Amazonia with decreasing settlement sizes at further distances from urban centers that provide access to markets (Parry et al. 2010a). We used the size of each permanent human settlement (i.e. number of households) nearest to censused transect (Franzen 2006) as a proxy for these combined effects of hunting pressure, mammal avoidance of hunted areas and urban access. This proxy (henceforth referred to as hunting pressure) from provides an estimate of the magnitude of the potential human resource pressure independent of the status of hunted populations (Rist et al. 2008), unlike hunting intensity (Peres and Palacios 2007, Fa and Brown 2009, Poulsen et al. 2011), effort (e.g. hours hunting/km<sup>2</sup>) (Franzen 2006, Parry et al. 2009), frequency (Wilkie and Carpenter 1999) or volume offtake (Refisch and Kone 2005).



### *Vertebrate surveys*

Between January 2008 and December 2010, we characterized the medium and large-bodied terrestrial mammal community across a total of 86 sites (*terra firme* N=52, *várzea* N=33) distributed across the ResEx and RDS, using standardized line-transect surveys (Peres 1999a). We focused on medium to large-bodied mammals ( $\geq 1\text{ kg}$ ), as these species represent the preferred game species among traditional hunters (Parry et al. 2009) and compose a disproportionate fraction of the total vertebrate biomass in tropical forests (Peres 1999b). Each 5,000m transect was surveyed between 0630–1030 h over a period of 4-5 consecutive rainless days by two trained individuals (a wildlife biologist and local hunter) at a mean velocity of 1.2 km/h (Peres 1999a). Species identity, group size and location were recorded for each animal encounter. For each transect, we pooled data on mammal encounters across space (i.e. along the 5,000m transect length) and time (i.e. across all census events 2008-2010).

### *Dung beetle surveys*

Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) were sampled using standardized baited pitfall traps (20 cm diameter, 15 cm depth) buried flush with the ground and baited with 20g of fresh human dung, a broad-spectrum attractant for Neotropical dung beetles (Nichols and Gardner 2011). We placed 15 traps in each of 15 *terra firme* and 11 *várzea* forest sites, along the first 750m of the same 5,000m linear transect used for surveying mammals. Traps were separated by 50m. Trapping was conducted twice at each site, coinciding with the late dry (August-September 2009) and early-wet (December-January 2010) seasons. Fewer sites were sampled in

the wet season due to accessibility issues (*terra firme* N= 10, *várzea* N = 8). Traps were operated for one 24-h period at each site. Captured specimens were separated to species (Vaz-de-Mello et al. 2011). To obtain body mass estimates for each species, a sample of between 1 and 30 individuals (median = 20) was dried in a constant-temperature oven at 60 °C for one week prior to weighing on a balance accurate to 0.0001g. Further information on nesting strategy was obtained from the literature and corroborated by experts (See Nichols et al. submitted).

#### *Detritus and seed burial rates*

During the dry season, we quantified dung beetle-mediated feces and seed burial across 14 of the *terra firme* transects described above. In each transect, we placed four ‘arenas’, separated by 100m. Each arena was composed of a 1m diameter, 15cm tall plastic netting with a single 150g experimental fecal deposit made of fresh human feces, placed in the arena center. Each fecal deposit was mixed with 70 plastic seed mimics in three size classes (1cm diameter, N=10, 10mm diameter, N=20, 5mm diameter, N=40). Seed mimics (rather than real seeds) are an ideal proxy for real seeds in tropical forest as they are not subject to rodent seed predation and have similar burial rates by beetles (Andresen and Feer 2005). After a 24hr exposure period to the detritivore community we measured the (i) change in fecal deposit wet-weight, and (ii) the number of seed mimics of each size class buried  $\geq 1$ cm under the soil surface.

#### DATA ANALYSES

We used linear regression to quantify the impacts of human hunting on the abundance of medium and large tropical forest mammals, modeling abundance as a function of human hunting

pressure and including census month as a covariate. We conducted separate analyses for ungulates and target and non-target game species of primates and rodents (all ungulate species are targeted in this system, Endo unpublished data). As human hunting pressure (i.e. community size) and distance from the central municipal town were highly correlated ( $r_{24}=-0.59$ ,  $p=0.001$ ), we used only hunting pressure in this and all subsequent regression analyses.

To quantify the impact of mammal hunting on the detritivore trophic level, we modeled dung beetle species richness and biomass as a function of hunting pressure, mammal abundance and environmental covariates with generalized linear mixed models. Following the first two main hypotheses, we looked for hunting-induced changes in dung beetle biomass and diversity at: (i) the community-level, and (ii) within trait-defined subsets based on both beetle body size (i.e. small: 0.001-0.92g and large: 0.10-0.79g) and nesting strategy (i.e. roller, tunneler or dweller). This size division was chosen for comparability with previous dung beetle studies (i.e. Slade et al. 2007).

We modeled the impact of human hunting pressure separately for *terra firme* and *várzea* forests, as these two forest types differ strongly in the seasonality of hunting (Puertas and Bodmer 2004), and other aspects of human livelihood strategies (Newton et al. in press-a), edaphic factors related to productivity (Peres 2000b) and vertebrate community structure (Haugaasen and Peres 2005). Ungulates and rodents were excluded from *várzea* forest models, due to their extreme rarity in seasonally flooded forest. In all models, we included the season in which beetles were sampled (i.e. wet or dry) as an additional covariate, incorporated transect identity as a random

effect (Z) and assumed a Poisson error structure for the response variables.

To compare the proportion of seeds removed among sites with differing hunting pressures, mammal abundance and detritivore community composition, we fit separate logistic regression models for each seed size class (i.e. small, medium, large and all sizes pooled). We represented seed burial as a function of hunting pressure, game mammal abundance (as above), and the six different representations of the dung beetle community (i.e. species richness and biomass of (i) the entire detritivore community, (ii) size-defined, and (iii) nesting strategy-defined community subsets). We included each of these six distinct representations individually in separate models, where the remaining predictor variables were identical, and used AIC model comparison to select which model (and beetle community representation) best explained the probability of seed burial. An identical model comparison approach was used to compare the proportion of fecal detritus buried in 24hrs across sites, using normally distributed linear regression models.

## RESULTS

Across the 26 forest sites sampled for both mammals and dung beetles, a total of 8,430km of mammal census walks were conducted ( $324 \pm 344$  km; mean  $\pm 1$  SD, range 80-1260km). These forest sites were associated with fifteen neighboring human communities, varying in size from five to 100 households ( $21.2 \pm 25.9$  households; mean  $\pm 1$  SD). Community size was similar between communities adjacent to *terra firme* or *várzea* forest sites (*terra firme*  $22.5 \pm 29.5$  households, *várzea*  $19.3 \pm 23.3$  households, mean  $\pm$  SD,  $t_{24} = 0.3$ ,  $p = 0.76$ , bootstrapped 95% CI = -1.9 - 1.7).

Mammal censuses resulted in observations of 42 mammal species (see Table S3.1 in the supplementary material). Primates totaled 55 percent of all individual animal encounters, followed by rodents (31 percent) and ungulates (10 percent). Sixty-one percent of all mammals encountered in census walks are considered target game species in the region (Peres 2000a). Mean mammal abundance was similar between *terra firme* and várzea sites (*terra firme*  $2.1 \pm 0.9$  individuals/km, várzea  $1.3 \pm 1.4$  individuals/km, mean  $\pm$  SD,  $t_{23} = 0.8$ ,  $p > 0.1$ , bootstrapped 95% CI = 0.6 - -2.6), while *terra firme* sites supported significantly higher mammal species richness (*terra firme*  $2.1 \pm 0.008$  species/km, várzea  $0.01 \pm 0.004$  species/km, mean  $\pm$  SD,  $t_{22} = 3.3$ ,  $p < 0.0001$ , bootstrapped 95% CI = 0.0001 - -1.96). In terra firme forest, the abundance of hunted primates and rodents was positively correlated ( $r_{24}=0.68$ ,  $p=0.0001$ ), while ungulate abundance was unrelated to both primates and rodents (primates  $r_{24}=0.30$ ,  $p=0.14$ , rodents  $r_{24}=0.34$ ,  $p=0.08$ ; Fig. 3.2).

We captured a total of 10,819 dung beetle individuals in 90 species, with 5,887 individuals and 83 species in *terra firme* forest, and 5,513 individuals and 57 species in várzea forests (see Table S3.2 in the supplementary material). The total biomass and richness of dung beetles per trap was significantly higher in the dry season (August and September) than the wet season (January and February) (biomass: dry season  $2.05 \pm 1.87$ g, wet season  $0.89 \pm 0.856$ g, mean  $\pm$  SD,  $t_{560} = 9.4$ ,  $p < 0.0001$ , bootstrapped 95% CI = -2.0 - 1.9; species richness: dry season  $7.0 \pm 3.9$  species, wet season  $3.9 \pm 2.4$ g, mean  $\pm$  SD,  $t_{560} = 11.0$ ,  $p < 0.0001$ , bootstrapped 95% CI = -1.9 - 1.7). Most dung beetle species were diurnal (67%) and used a tunneling food relocation strategy (58%).

Beetle body mass ranged widely (0.0001 – 0.79 g,  $0.096 \pm 0.152$ g mean  $\pm$  SD). The mean body mass of diurnal dung species was significantly smaller than nocturnal species (diurnal  $0.067 \pm 0.13$ g; nocturnal  $0.21 \pm 0.20$ g, mean  $\pm$  SD,  $t_{24} = -3.61$ ,  $p < 0.0001$ , bootstrapped 95% CI = -1.11 - 2.11).

### *Mammal response to hunting*

Across the study region, human hunting pressure had a negative, but non-significant effect on community-level mammal abundance ( $t_{24} = -1.97$ ,  $p = 0.061$ ). This negative influence was largely driven by the sharply negative response of hunted primates (target primates:  $t_{24} = -3.4$ ,  $p = 0.003$ ), while hunting pressure was not significantly related to either hunted or non-hunted rodents (target rodents  $t_{24} = -0.752$ ,  $p = 0.459$ ; non-target rodents  $t_{24} = -0.767$ ,  $p = 0.451$ ), ungulates ( $t_{24} = -0.446$ ,  $p = 0.659$ ) or non-target primates ( $t_{24} = -1.435$ ,  $p = 0.164$ ). These relationships were qualitatively similar when modeled separately for *terra firme* and várzea forests. We found no evidence for hunting induced changes to mammal mesopredator (i.e. coati, *Nasua nasua*) abundance across the study region.

### *(1) Hunting-induced cascade effects on community-level changes in the diversity and biomass of the detritivore dung beetle community*

Human hunting pressure had a significant negative influence on community-level biomass ( $z_{275} = -2.1$ ,  $p = 0.04$ ) but not species richness of dung beetles in várzea forest ( $z_{275} = -1.5$ ,  $p = 0.138$ ). In *terra firme* forest, neither community-level biomass nor species richness was significantly

correlated with hunting pressure (all  $p > 0.05$ , see Table S3.3). The abundance of hunted primates was unrelated to both dung beetle community-level biomass and species richness in *várzea* forest (all  $p > 0.05$ ), though was positively correlated with community-level biomass in *terra firme* forests ( $z_{367} = 2.9$ ,  $p = 0.004$ ). The abundance of hunted rodents in *terra firme* forest was also negatively correlated with community-level beetle biomass ( $z_{367} = -2.3$ ,  $p = 0.019$ ). The abundance of hunted ungulates was independent of all community-level measures of the detritivore community (all  $p > 0.05$ , see Table S3.3). Detritivore community-level species richness was positively related to both abundance and biomass both within and across the two forest types (all  $p < 0.001$ ), suggesting little density compensation at the community level.

## (2) Do trait-defined indirect interactions drive these detritivore effects?

### *Body size*

A total of 68 small-bodied species ( $0.022\text{g} \pm 0.02$ ; mean  $\pm 1$  SD, range 0.0001 – 0.092g) and 31 large-bodied species ( $0.256\text{g} \pm 0.187$ ; mean  $\pm 1$  SD, range 0.103 – 0.79g) were captured across the study region. Nearly 80% of small species were diurnal. Over half of small species used a tunneling nesting strategy, while 30 percent were rollers and six percent dwellers. Larger-bodied species were distributed more evenly across activity periods (42% nocturnal, 42% diurnal, 7% crepuscular). The majority of large species used a tunneling strategy (68%), while 20 percent were rollers and 13 percent were dwellers.

In *terra firme* forest, human hunting pressure was negatively associated with the biomass and species richness of small species, while large species were unaffected by hunting (small species biomass  $z_{367}=-3.6$ ,  $p<0.001$ ; species richness  $z_{367}=-2.1$ ,  $p=0.038$ ; large species all  $p>0.05$ , see Table S3.3). In contrast, in várzea forests, the biomass and species richness of both size classes was independent of hunting pressure (all  $p>0.05$ , see Table S3.3). The abundance of hunted primates positively co-varied with the biomass and species richness of large species in *terra firme* forest (biomass  $z_{367}=3.1$ ,  $p=0.002$ ; species richness  $z_{367}=2.3$ ,  $p=0.02$ ), while hunted rodents demonstrated a negative correlation (biomass  $z_{367}=-2.1$ ,  $p=0.037$ , species richness  $z_{367}=-2$ ,  $p=0.05$ ). Smaller-bodied species in both forest types as well as larger-bodied species in várzea forests were unrelated to all measures of mammal abundance ( $p>0.05$ , see Table S3.3). As with community-level measures of the dung beetle community, the abundance of hunted ungulates was unrelated to both body-size defined subsets (all  $p>0.05$ , see Table S3.3). In *terra firme* forest, the species richness of small beetle species was positively related to both the biomass and abundance of large beetles, suggesting an absence of density or biomass compensation with the hunting-induced loss of small beetles (biomass  $r_{13}=0.70$ ,  $p=0.004$ , abundance  $r_{13}=0.71$ ,  $p=0.002$ ).

### *Nesting strategy*

A total of 27 roller, 58 tunneler, and 8 dweller species were sampled across the study region. Human hunting pressure was negatively correlated with the species richness of beetles with a tunneling nesting strategy in várzea forest ( $z_{275}=-2.1$ ,  $p=0.04$ ), and was otherwise unrelated to the biomass or species richness of any nesting strategy in either forest type (all  $p>0.05$ , see Table S3.3). Altered tunneler species richness did not appear to correspond with compensation in roller



species (abundance  $r_9=0.57$ ,  $p=0.068$ , biomass  $r_9=0.39$ ,  $p=0.23$ ) or dweller species (abundance  $r_9=0.10$ ,  $p=0.97$ , biomass  $r_9=0.06$ ,  $p=0.86$ ). The abundance of hunted primates was positively correlated with the biomass of dweller species ( $z_{367}=2.8$ ,  $p=0.005$ ) in *terra firme* forests and a positive but non-significant association with dweller species richness ( $z_{367}=1.8$ ,  $p=0.079$ ), but was unrelated to all other *nesting strategies* in both forest types (all  $p>0.05$ ). In *terra firme* forests rodent abundance negatively covaried with roller species richness and biomass (species richness  $z_{367}=-2.5$ ,  $p=0.011$ ; biomass  $z_{367}=-2.2$ ,  $p=0.026$ ). The abundance of hunted ungulates remained independent of all nesting-strategy defined subsets (all  $p>0.05$ , see Table S3.3).

### (3) Can human hunting pressure impact rate changes in detritus-pathway processes important for plants?

The proportion of seeds removed was greatest for large seeds, lowest for medium seeds and intermediate for small seeds (large  $0.22 \pm 0.27$ ; medium  $0.19 \pm 0.18$ ; small  $0.20 \pm 0.1$ , mean  $\pm$  SD;  $n = 15$  in each case). No single explanatory model for the probability of any seed (pooled across size classes) being buried by a dung beetle was clearly supported. The model including the biomass of body-size subsets of the dung beetle community was the AIC top model in the set of six candidate models, although its Akaike weight of 0.30 suggests considerable model selection uncertainty (Table 1). The probability of seed burial was strongly related to the biomass of small-bodied beetles ( $z_{59}=4$ ,  $p<0.0001$ ), while the biomass of large species remained independent ( $z_{59}=-0.3$ ,  $p=0.759$ ). The probability of community-wide seed burial was further negatively correlated with primate abundance ( $z_{59}=-2.5$ ,  $p=0.011$ ) and positively correlated with both hunting pressure ( $z_{59}=2.3$ ,  $p=0.022$ ) and ungulate abundance ( $z_{59}=4.9$ ,  $p<0.0001$ , Fig. 3.4).

The probability of burial for both large- and medium-sized seeds was best explained by a single model, based on the same body-size subsets of the detritivore community (Table 1). We found a strong *positive* relationship between human hunting pressure and the probability of large seeds removed by dung beetles ( $z_{59}=3.5$ ,  $p<0.0001$ ). Large seed removal was further positively related to the biomass of small-bodied beetles ( $z_{59}=4.7$ ,  $p<0.0001$ ) and ungulate abundance ( $z_{59}=5.6$ ,  $p<0.0001$ ) and negatively correlated with the biomass of large bodied species ( $z_{59}=-2.6$ ,  $p=0.011$ ). The biomass of small-bodied beetles also was a strong predictor of burial for medium sized seeds ( $z=4.2$ ,  $df=59$ ,  $p<0.0001$ ) as was hunting pressure ( $z_{59}=2.7$ ,  $p=0.007$ ). Medium seed burial demonstrated a positive correlation with ungulate abundance ( $z_{59}=3.3$ ,  $p=0.001$ ), negatively correlated with the biomass of large bodied species ( $_{59}z=-2.2$ ,  $p=0.03$ ), and was independent of primate abundance ( $p>0.05$ ; Fig. 3.4).

The burial of small seeds was equally well explained by both community-level beetle biomass and species richness, with species richness having a marginally lower AIC value (Table 1). Beetle species richness was positively related to the probability of small seed burial ( $z_{59}=2.7$ ,  $p=0.007$ ). The probability of small seed burial was positively related to ungulate abundance ( $z_{59}=2.9$ ,  $p=0.003$ ), negatively correlated with primate abundance ( $z_{59}=-3$ ,  $p=0.003$ ) and unrelated to both human hunting pressure and hunted rodent abundance all  $p>0.05$ , Fig. 3.4). Though the proportion of detritus buried by beetles over a 24hr period was best explained by a model with the biomass of each nesting strategy of the dung beetle community (Table 1), detritus burial was independent of beetle biomass (biomass dwellers  $z_{47}=1.0$ ,  $p=0.344$ ; biomass rollers  $z_{47}=0.3$ ,  $p=0.804$ ; biomass tunnelers  $z_{47}=0.4$ ,  $p=0.688$ ). The only significant predictor of detritus burial was primate abundance ( $z_{47}=-2$ ,  $p=0.05$ ).

## DISCUSSION

Large vertebrate predators play an important role in terrestrial food web structure and subsequent function (Duffy 2003, Meserve et al. 2003, Dunham 2008, Salo et al. 2010, Schmitz et al. 2010). The ubiquity and intensity of human predation on wild vertebrate herbivores in tropical forests (Peres 2000b, Fa et al. 2002, Peres and Lake 2003) has long been suspected to drive cascading changes in tropical tree diversity and biomass by altering seed dispersal (Wright et al. 2000, Roldán and Simonetti 2001, Galetti et al. 2006, Beckman and Muller-Landau 2007, Stoner et al. 2007, Wright et al. 2007a) and predation rates (Roldán and Simonetti 2001, Wright and Duber

2001, Dirzo et al. 2007, Wright et al. 2007b). While the detritus-based foodweb is also expected to be sensitive to predation effects via direct consumption and release of nutrients by predators, and indirect alteration of nutrient release patterns by herbivore prey (Schmitz et al. 2010), predator-induced trophic cascades along the detrital chain have received far less study to date (Dunham 2008, Schmitz et al. 2010, Wu et al. 2011). We have demonstrated here that human hunting of wild vertebrates produced significant trophic cascading effects through a tropical forest detritivore community, and in turn, these changes influenced secondary seed burial processes mediated by detritivores across the study region. To our knowledge, this study represents the first large-scale evidence that vertebrate predators can influence the fecal detrital pathway.

We found evidence for community-level hunting-induced effects on detritivore biomass in hunted várzea but not *terra firme* forests, and no evidence for community-wide diversity effects (*sensu* Dyer and Letourneau 2003) in either forest type. Similar to other Neotropical studies, we found strong correlations between community-level detritivore abundance, biomass and species richness, suggesting an absence of compensation both at the community-level and across trait-defined subsets (e.g. Gardner et al. 2008, Klein 1989).

An explanation for the disproportionately strong cascading influence of hunting in várzea forest may be associated with the composition of the vertebrate assemblage. The primarily arboreal vertebrate assemblage in várzea is dominated by the three genera of large-bodied ateline primates most preferred by rural hunters (Peres 2000b, Jerozolinski and Peres 2003, Haugaasen

and Peres 2005a). While vertebrate biomass in general and primate biomass in particular (Peres 1997) in these nutrient rich seasonally flooded forests typically exceeds that of terra firme forest (Haugaasen and Peres 2005b), the same degree of hunting pressure tends to force a disproportionate decline in vertebrate biomass in várzea relative to terra firme in the face of hunting pressure (Peres 2000b). While there is no contemporary difference in size of human communities between the two forest types, várzea forests have historically been subject to heavier extraction of timber and non-timber forest products (e.g. aromatic oils and rubber; Newton et al. 2011). As opportunistic hunting and extractive activities typically go hand in hand in tropical forests (Peres and Lake 2003, Parry et al. 2009), these effects may indicate a lingering signature of beetle-mammal co-decline as a consequence of historical hunting pressure. Alternatively or in addition, the relationship between actual hunting pressure and our use of household size as a proxy may be decoupled in the two forest types, as both human access to and primate occupancy within várzea forest shifts seasonally, and aquatic protein from fish declines with increasing flood stage (Puertas and Bodmer 2004).

In addition to the strong community-level cascade effects in várzea forests, we found that body-size defined subsets of the detritivore community responded differently to both hunting and hunting-induced abundance changes in game mammals. Smaller-bodied dung beetles were negatively impacted by hunting, yet did not covary with the abundance of target game mammals. Andresen and Laurance (2007) also found a disproportionately negative response by the small bodied, diurnal beetle community of Barro Colorado Island, even 15 years after hunting activity had ceased. While we cannot tease apart the mechanism for this size-structured decline with the present dataset, we suggest that these effects may be driven by a combination of declining

diurnal game mammal abundance (Wright et al. 2000, Andresen and Laurance 2007), and potentially increased predation on diurnal beetles via elevated densities of insectivorous rodents that remained unsampled here, due to our focus on medium and large-bodied mammals (Terborgh 1992, Wright et al. 2000, Wright 2003).

We also observed a decoupling of the influences of hunting and mammal abundance for larger-bodied *terra firme* forest beetles, although in the opposite direction reported for smaller-bodied species. Large beetles were positively correlated with the abundance of hunted primates (i.e. the one mammal group that demonstrated an exceptional sensitivity to hunting) and yet were not sensitive to higher hunting pressure themselves. This likely points towards the high vagility of large dung beetles, which enables them to detect and pursue fecal resources of wide-ranging primate groups. The highly mobile ateline primates (e.g. woolly, spider and howler monkeys) are believed to be keystone providers of fecal resources for Scarabaeine beetles where present (Castellanos et al. 1999), and are heterogeneously distributed at local and regional scales (Anzures-Dadda and Manson 2007, Palminteri et al. 2011). Across the focal reserves, hunting drove strong reductions in ateline monkey densities, but no change in occupancy rates across the 26 forest sites. This may suggest that the strong source-sink dynamics that typically influence game primates near human settlements (e.g. Sirén et al. 2004) differentially influence primates and the large dung beetles that track them in space. The demographic consequences of dispersal through the faunal depletion zone surrounding human communities are consistently negative for targeted primates (Jerozolinski and Peres 2003), yet may range from neutral to positive for large mobile dung beetles if declines in wild primate fecal resources are offset by increased subsidies from local human populations (e.g. Miller 1954).

We found stronger support for body-size defined trophic effects than nesting strategy-defined effects. Dung beetles with dwelling nesting strategies were significantly correlated with the abundance of primates in *terra firme* forest, while the species richness of tunnelers in várzea forest declined sharply with increasing hunting pressure. We found no other evidence of specific co-variation between hunting or mammal abundance and beetle trait groups. As each of these three nesting strategies encompass both species across both the size and diel activity spectrum, we speculate that the cascading effects of mammal hunting may be principally leveraged against body size and diel activity, and remain relatively agnostic with respect to nesting strategy.

Finally, we found that hunted rodent abundance was persistently negatively correlated with both beetle biomass and diversity, particularly for those species with a roller nesting strategy and larger-bodied species. We suspect that these relationships are a product of increased consumption of dung beetles by small rodents which were not sampled in our line transect censuses, a speculation dependent upon similar habitat selection criteria for the caviomorph rodents selected by rural hunters (i.e. common agouti, *Dasyprocta fulginosa*, green acouchi, *Myoprocta pratti* and paca, *Agouti paca*) and smaller and insectivorous rodents. Evidence from central Panama and the Brazilian Atlantic forest suggests that increased hunting pressure in tropical forests may lead to increases in the abundance of un hunted insectivorous mesopredators (e.g. coatis, common opossums) (Da Fonseca and Robinson 1990, Terborgh 1992, Wright et al. 2000, Galetti et al. 2009) and small-bodied rodents (e.g. Dirzo et al. 2007) that are likely to feed on dung beetles (Larsen et al. 2008). However for the single mesopredator species recorded

across these 26 sites (i.e. coatis, *Nasua nasua*), we found no correlation between mesopredator abundance and hunting pressure.

In addition to the strong evidence that mammal hunting can influence both diversity and biomass in the detritivore trophic layer, we found evidence that these effects may further influence primary producers by altering the probability of secondary seed burial by dung beetles. As expected, we found strong, positive effects of the detritivore community on the probability of burial across all seed classes. For large and medium sized seeds (as well as seeds pooled across size classes), burial rate was positively correlated with the biomass of small-bodied dung beetles, and negatively correlated with the biomass of large-bodied beetles. We also documented a strong and positive influence of hunting pressure on seed burial – in direct contradiction with our original expectations. In contrast to these strong relationships between detritivore biomass and seed burial, we found detritus burial rate unrelated to the dung beetle community (i.e. the biomass of roller, tunneler and dweller species). These results are particularly interesting as they (i) suggest that hunting has a *positive* influence on the likelihood of seed burial, despite the fact that higher rates of seed burial are correlated with the subset of the beetle community most sensitive to hunting (i.e. small-bodied, diurnal species), (ii) contradict previous findings that the burial of both large seeds and detritus is predominantly related to the large-bodied and nocturnal portion of the dung beetle community (Andresen and Feer 2005, Slade et al. 2007, Slade et al. 2011), and (iii) imply that unique beetle biodiversity-ecosystem function relationships may influence seed and burial processes.



While these patterns initially appear contradictory, they can be explained by a single sampling artifact. The large (i.e. 150g) experimental fecal deposits used in this study to measure function are likely to create exceptionally large scent plumes (Tribe and Burger 2011), and disproportionately attract those largest bodies, mobile, primate preferring dung beetle species that have been noted in previous studies to conduct the majority of both waste removal and large seed burial (Larsen et al. 2005, Slade et al. 2007). This attraction may be disproportionately effective in areas where hunting or human activity has driven local reductions in fecal resource availability (Horgan 2005b). Such resource-driven ‘scarcity effects’ have been noted previously for both dung beetles (Burger and Petersen 1991, Cambefort and Walter 1991b, Estrada et al. 1998, Horgan 2005b), and small rodents sampled with baited traps in resource limited tropical forests (Wright et al. 2000). However, the biodiversity sample data used here to relate to detritus process rates was collected through the use of baited pitfall traps with smaller baits (i.e. 20g) and therefore smaller scent plumes. These traps are likely to more accurately reflect community structure, however they fail to represent the actual dung beetle community acting upon experimental fecal resources, effectively decoupling measurements of detritus process rates from estimates of the community structure of beetles assumed to have conducted that processing. This line of reasoning is also commensurate with the strongly negative correlation between seed dispersal rates and primate abundance: in areas of lower hunting pressure, the background abundance of primate feces likely decreased the attraction rates to experimental fecal deposits (made of human feces). The strong, consistent and positive influence of ungulate abundance on seed burial rates is harder to explain, given the lack of correlation between ungulates and hunting, any measure of dung beetle community structure, or the abundance of other hunted species groups.

The present study is novel in its demonstration that significant and community-wide trophic-cascading effects can occur in terrestrial, fecal detritus-based food webs. The primary mechanism for cascade effects on the detritivore trophic level is a reduction in the quality or quantity of donor-based fecal resources (Nichols et al. 2009), while two complementary mechanisms underlie the top-down effect of hunting on detrital processing relevant to primary producers in this system: the “top-down is bottom-up” effect (*sensu* Moore et al. 2003) where predator influence on the throughput of donor-based fecal resources influences plant growth in a traditional bottom-up manner, and the top-down regulation of multiple stages within diplochorous seed dispersal. In our system, we found that human predation exerted a stronger influence on secondary seed dispersal than detritus burial processes. We caution that while the observational approach to understanding ecological functions taken here realistically reflects the outcome of interacting vertical (i.e. trophic) and horizontal influences on dung beetle-detrital processes (e.g. Duffy 2002; Duffy et al. 2007), further study should be conducted to disentangle to what degree the scarcity effects noted here influence detritus burial rates, and served to decouple the magnitude of detritus and seed burial. We also note that this study supports recent ideas that predators may play multiple, if distinct roles in interacting food webs (Schmitz et al. 2010, Wu et al. 2011), and that changes in predation rates in terrestrial ecosystems likely drive simultaneously decreases (Wu et al. 2011) and increases (Schmitz 2006) in plant biomass, either through “top-down is bottom-up” effects along the detrital chain, or more traditional top-down effects along the plant-based chain (Schmitz and Suttle 2001). These complementary roles simultaneously decrease the likelihood of observing ‘community-wide’ cascades in diverse terrestrial plant communities (Polis 1999, Polis et al. 2000), yet clarify that these effects likely

cascade along specific, trait-defined pathways (Persson 1999, Royo and Carson 2005).

Accounting for the heterogeneity across trait-based subsets of a given trophic level proved useful to disentangle the sign and strength of indirect effects of predators on community-wide trophic cascades (Carpenter et al. 1985, Bascompte et al. 2005).

Our study has several implications for our understanding of the impacts of hunting in tropical forests at the landscape level. We found that mammal hunting can instigate trophic cascades in the detritus pathway in tropical forest and, most importantly, that these changes can occur even in the absence of measurable alterations to the mammal community itself. These findings emphasize the importance of extending inquiry about defaunation beyond the population responses of target game animals themselves (Bodmer et al. 1997, Wright et al. 2007b). We found that the size of human settlements was not strongly correlated with mammal abundance, either at the community level, or within specific mammal groups defined by taxonomy and hunter selectivity. This is often the case in studies along hunting gradients (e.g. Urquiza-Haas et al. 2011, De Souza-Mazurek et al. 2000) which highlights the heterogeneity in vulnerability to hunting across game mammals (e.g. Linder and Oates 2011), the complex roles of competitive and compensatory interactions across mammals (Peres 2000b, Wright 2003, Ives and Cardinale 2004) and perhaps most strikingly, the strong capacity for even weak direct effects of hunters on game vertebrates to influence adjacent trophic levels.

Looking forward, improving our understanding of vertebrate predators on the detrital fecal web will require a specific focus on the spatial dimension of these effects, in particular how space

influences the probability and strength of trait-defined indirect interactions, as well as influences compensatory dynamics between trait-defined subsets (Loreau et al. 2003, Gonzalez and Loreau 2009). Key knowledge gaps include information on the spatial scales over which hunters, game mammals, and individual beetles interact, and greatly improved data on dung beetle fecal resource use, preference and plasticity (Nichols et al. 2009). Recent developments in the use of DNA barcoding analysis of insect gut contents to resolve ecological interaction networks may be a promising avenue for future research (e.g. Zeale et al. 2011). Determining if these observed differences in the relationship between detritivore community and detritus processes relevant to primary producers are related to methodological differences in studies, or context-dependency across biogeographic regions (e.g. Nichols et al. submitted, Slade et al. 2011) should be a key additional focus of future research.

Understanding how the implications of human removal of mammal biomass from tropical forests can propagate through food webs and influence both their structure and function is an ecological priority. Our landscape-level approach allowed us to detect the effect of human predation in a realistic socio-ecological context at the spatial scales at which scientific information on the consequences of ecosystem change is most relevant (Carpenter et al. 2006). That we detected both community-level and trait-defined trophic cascades suggests that the lasting impacts of persistent mammal hunting on dung beetles may accrue through two distinct trait-defined subsets: early declines of small-bodied diurnal species, compounded by later declines of larger-bodied primate specialists. Together, these findings suggest that human hunting has strong impacts on the structure of the detritivore trophic layer in tropical forests, and that these structural changes to the dung beetle community have strong impacts on the likelihood of safe

site limitation for larger sized seeds. Further observational and experimental research on the role of species traits in mediating cascade dynamics will be required to better understand how vertebrate predators on trophic cascades in tropical detrital food webs.

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## FIGURES AND TABLES

Table 1. Results of AIC model selection across six competing models of dung beetle community structure (see Methods), for four related detritus processes: the probability of seed burial pooled across three size classes, large, medium, and small seeds independently, and the proportion of feces buried. Dung beetle community structure and detritus process rates were measured between August and October 2009, in 15 terra firme forests in the Medio Jurua Extractive Reserve and the Uacari Sustainable Development Reserve, Amazonas State, Brazil.

Process	Metric	Community-level or trait	<i>k</i>	<i>L</i>	AIC	<i>i</i>	<i>w<sub>i</sub></i>
All seeds	Biomass	Body size	9	1.00	325.4	0.00	0.51
	Species richness	Community-level	8	0.34	327.6	2.14	0.17
	Species richness	Body size	9	0.19	328.7	3.30	0.09
	Species richness	Nesting strategy	1	0.15	329.3	3.83	0.07
	Biomass	Community-level	8	0.14	329.3	3.87	0.07
	Biomass	Nesting strategy	1	0.12	329.7	4.24	0.06
Large	Biomass	Body size	9	1.00	126.4	0.00	1.00
	Species richness	Body size	9	0.00	159.2	32.7	0.00
	Species richness	Community-level	8	0.00	159.8	33.3	0.00
	Biomass	Nesting strategy	1	0.00	160.3	33.9	0.00
	Biomass	Community-level	8	0.00	161.2	34.8	0.00
	Species richness	Nesting strategy	1	0.00	163.8	37.3	0.00
Medium seeds	Biomass	Body size	9	1.00	218.2	0.00	0.99
	Species richness	Community-level	8	0.00	234.7	16.5	0.00
	Species richness	Body size	8	0.00	236.0	17.8	0.00
	Biomass	Nesting strategy	9	0.00	236.4	18.2	0.00
	Species richness	Nesting strategy	1	0.00	237.1	18.9	0.00
	Biomass	Nesting strategy	1	0.00	237.9	19.7	0.00
Small	Biomass	Community-level	8	1.00	283.6	0.00	0.46
	Species richness	Community-level	8	0.69	284.3	0.73	0.32
	Species richness	Body size	9	0.22	286.6	3.03	0.10
	Biomass	Body size	9	0.09	288.3	4.77	0.04
	Species richness	Nesting strategy	1	0.09	288.5	4.90	0.04
	Biomass	Nesting strategy	1	0.06	289.1	5.47	0.03
Feces	Biomass	Nesting strategy	1	1.00	0.00	-	0.91
	Species richness	Nesting strategy	1	0.09	4.82	-	0.08
	Species richness	Community-level	9	0.00	18.51	-	0.00
	Biomass	Community-level	9	0.00	18.80	-	0.00
	Species richness	Body size	1	0.00	19.45	-	0.00
	Biomass	Body size	1	0.00	20.37	-	0.00

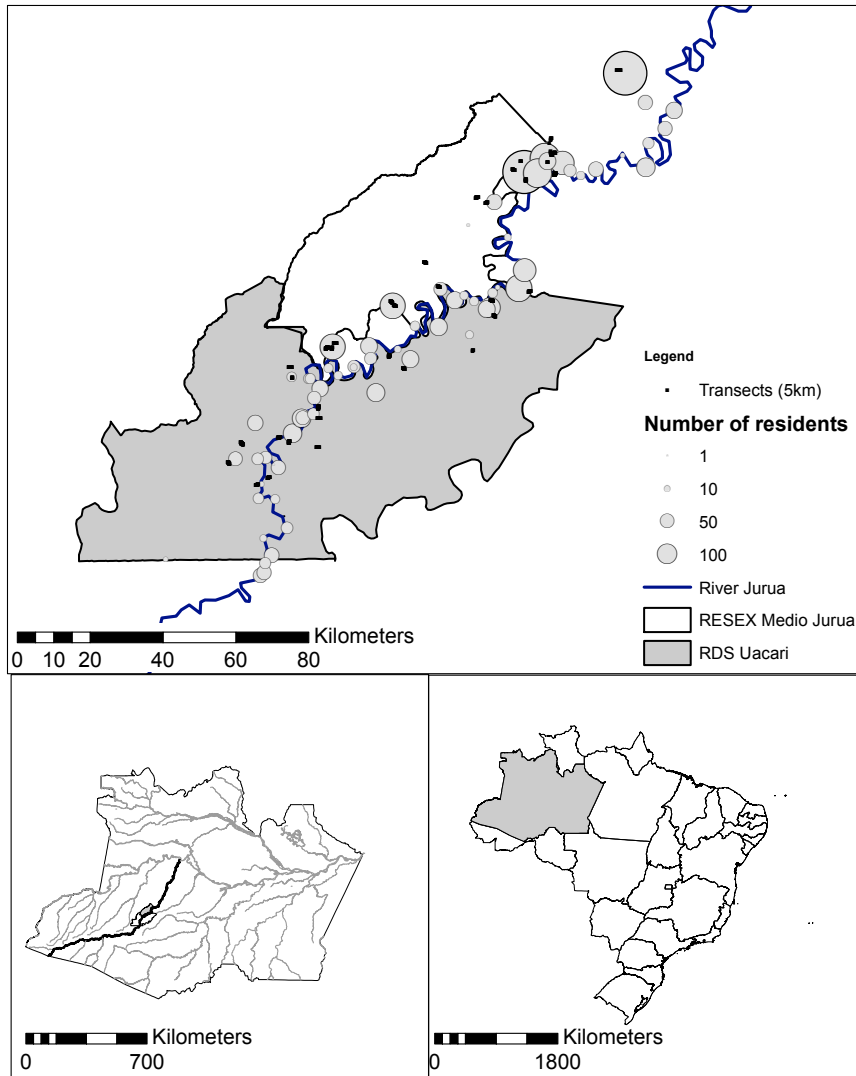


Figure 3.1. Map of study region, highlighting the two focal reserves (the Medio Jurua Extractive Reserve and the Uacari Sustainable Development Reserve), the location of the reserve system within the state of Amazonas (bottom left), and the location of the state of Amazonas within Brazil (bottom right).

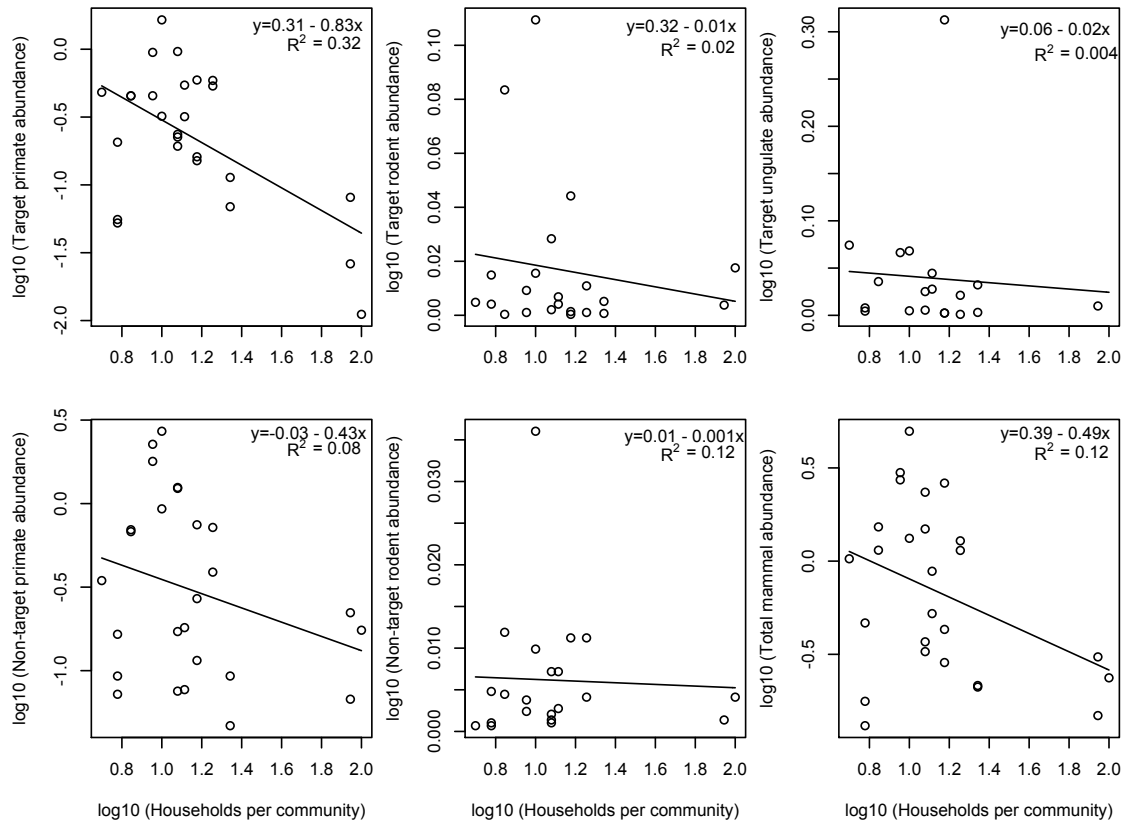


Figure 3.2. The relationship between human hunting pressure and the abundance of target game species of primates, ungulates and rodents (upper panel), non-target species primates and rodents and the entire mammal community (lower panel), across both *terra firme* and *várzea* forests in the Medio Jurua Extractive Reserve and the Uacari Sustainable Development Reserve, Amazonas State, Brazil.



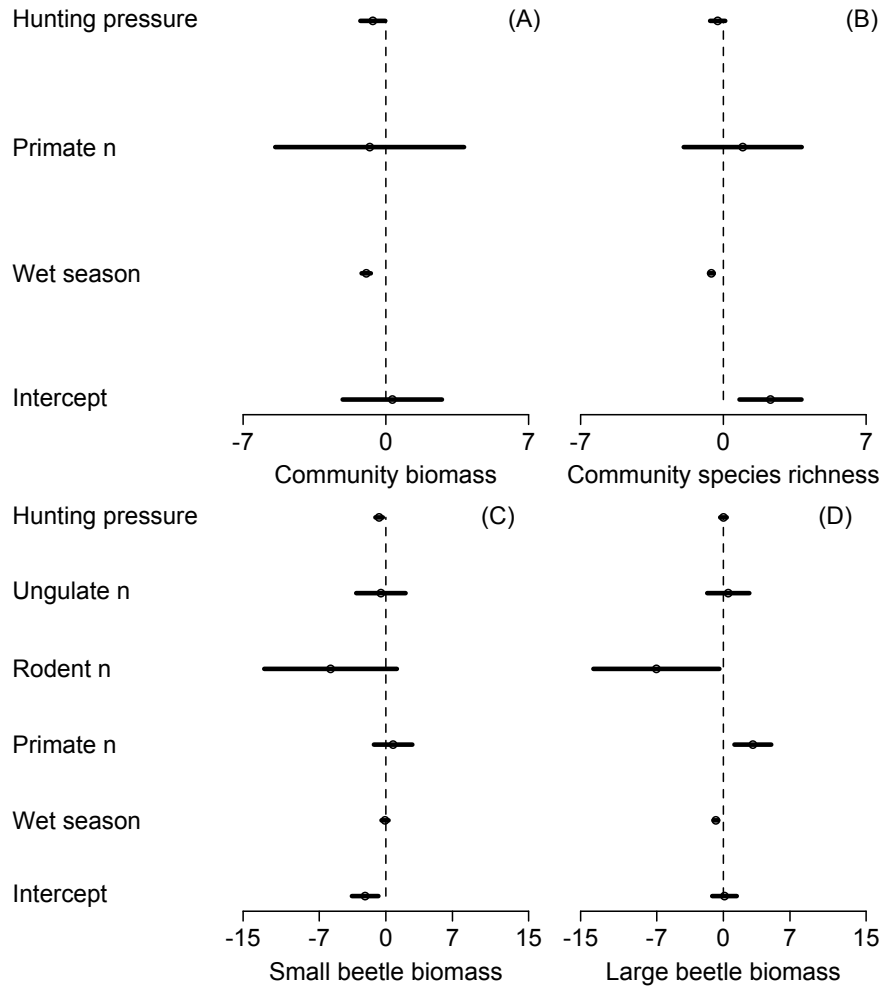


Figure 3.3. Standardized regression coefficients ( $\beta$ ) for linear regression models of the influence of human hunting pressure (number of households per community), target game mammal abundance and season (wet or dry) on the diversity and biomass of detritivores (Scarabaeine dung beetles). Panel (A) and (B) represent the community-wide detritivore response in várzea forest. Panel (C) and (D) represent the response across trait-defined subsets based on body size. All data was collected in the Medio Jurua Extractive Reserve and the Uacari Sustainable Development Reserve, Amazonas State, Brazil.

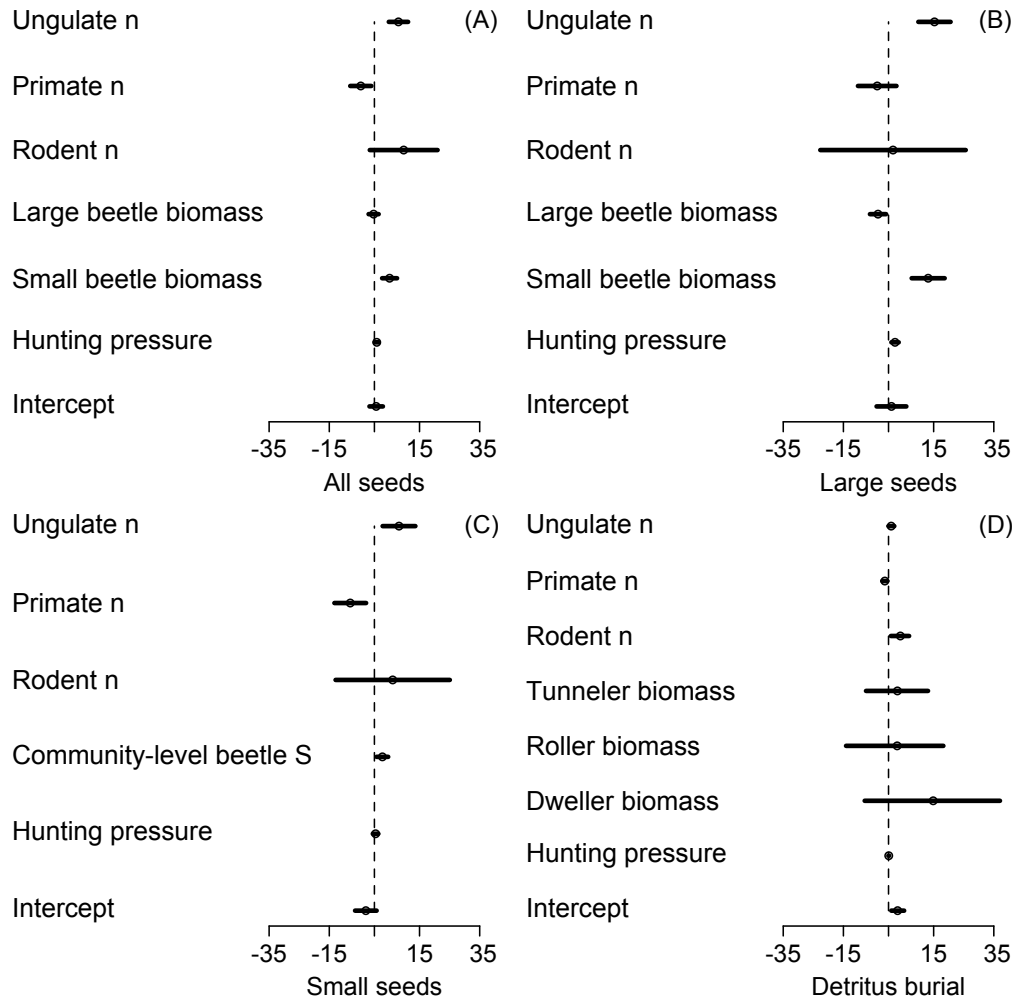


Figure 3.4. Standardized regression coefficients ( $\beta$ ) for the top AIC linear regression models relating the probability of burial of (A) large seeds, (B) medium seeds, (C) small seeds, and (D) fecal detritus as a function of the detritivore community, target game mammal abundance and human hunting pressure (see Table 1). All data was collected August-October 2009 in 15 *terra firme* forest sites in the Medio Jurua Extractive Reserve and the Uacari Sustainable Development Reserve, Amazonas State, Brazil.

## CHAPTER 4 - TRAIT-DEPENDENT RESPONSE OF DUNG BEETLE POPULATIONS TO TROPICAL FOREST CONVERSION AT LOCAL TO GLOBAL SCALES

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## ABSTRACT

Comparative analyses that link information on species' traits, environmental change and organism response have rarely identified unambiguous trait correlates of vulnerability. We tested if species' traits could predict habitat-scale changes in dung beetle population response to three distinct levels of forest conversion intensity within and across two biogeographic regions (the Neotropics and Afro-Eurasian tropics). We combined biodiversity surveys, a global molecular phylogeny and information on three species' traits hypothesized to influence vulnerability to forest conversion to examine (i) the consistency of beetle population response across regions, (ii) if species traits could predict this response, and (iii) the cross-regional consistency of trait-response relationships. Most beetle populations declined following any degree of forest conversion; these declines were strongest for Neotropical species. The relationship between traits and population trend was greatly influenced by local and biogeographic context. We discuss the ability of species traits to explain population trends and suggest several ways to strengthen trait-response models.

**Keywords:** extinction risk, population response, fitness, trait-based approaches, body size, extrinsic factors, functional traits, context-dependency, tropical forest, land-use change

## INTRODUCTION

Contemporary species extinctions are seldom random. Rather, species with similar phenotypes or high degrees of relatedness tend to exhibit similar responses to environmental change (Turvey and Fritz 2011). Comparative analyses that combine information on species phenotype and phylogeny have become an important tool in trait-based efforts to understand and predict the distribution and abundance of species across environmental gradients and the threat status of species (Fisher and Owens 2004). To date however, comparative research on animal taxa has largely failed to uncover consistent and strong associations between species' traits and to extinction risk (Cardillo et al. 2008) or response to environmental change (Jones et al. 2003, Angert et al. 2011, Collen et al. 2011).

Recent lessons learned from comparative analyses suggest that several factors may obscure strong trait-environment-response relationships. First, analyses that link traits to population-level response metrics may be more successful than those linking traits to species-level metrics (e.g. extinction risk). This is largely because extinction represents the culmination of a long sequence of local population declines and extinctions, each with distinct trait-environment dynamics (Collen et al. 2011, Yackulic et al. 2011). Second, trait-response relationships may be easier to identify at local spatial scales, where population-level metrics reflect response to highly localized environmental conditions (Fisher and Owens 2004, Collen et al. 2011). In contrast, regional or global analyses necessarily encompass multiple, and often interacting anthropogenic environmental changes (Yackulic et al. 2011) which may each produce unique trait-response relationships (Isaac and Cowlishaw 2004).

Third, both the magnitude of population response to localized environmental change, and the relationship between species' trait and population response can be highly context dependent, and specific to a given environmental change or management practice (Cardillo et al. 2008, Pocock 2011). For species traits to be a useful predictor of response to environmental change, interactions between traits and the environmental conditions associated with a given management practice must produce distinct, and measureable changes in population size. This requires that species' traits are capable of producing population responses that are neither overly idiosyncratic (i.e. site-specific), nor overly generalized across sites with clearly different management practices. Such clear links between traits, the local environment and population response are of particular importance for management and policy applications of trait-based research. Context dependency may occur at regional scales as well (Fritz et al. 2009, Pocock 2011). At this scale, context dependency may be driven by geographic differences in species composition, historical exposure to anthropogenic or climatic extinction filters, or the distribution of contemporary anthropogenic threats (Lee and Jetz 2011), all of which can influence observed relationships between traits and responses to contemporary environmental change (Balmford 1996). Cross-regional comparisons of trait-environment-response relationships are an increasingly powerful tool to determine the generality of trait-environment relationships, and how they may be modulated by biogeographic history.

Finally, weak associations between traits, environment and response to environmental change may simply arise from the use of uninformative species' traits, rather than uninformative

associations between traits, environment and response. Relative to other taxa (e.g. plants) animal ecologists often have a limited set of traits from which to predict extinction risk. Animal-based comparative analyses are seldom based on strict functional traits, defined as that subset of heritable, morphological, physiological or phenological (M-P-P) features that are measurable at the individual level, and affect growth, reproduction and survival (Arnold 1983). More common is the use of ‘proxy’ traits (soft traits, *sensu* Hodgson et al. 1999) that represent easily measurable characteristics (e.g. body size) that often represent true functional traits in a one-to-many fashion (e.g. fecundity, dispersal distance, life-span). Determining if available species’ trait data are useful in signaling significant population responses to environmental change is fundamental, both for predicting response to anthropogenic change and highlighting where the collection of additional trait data may be necessary (Nylin and Bergstrom 2009, Diamond et al. 2011).

Comparative analyses that target population response to localized environmental change will therefore be necessary to addressing three related topics. First, to what degree are local population responses context dependent across individual management practices or biogeographic regions? Second, of the available information on species traits for a given taxon, which traits are the best predictors of those local population responses to environmental change? Finally, can context-dependency in observed trait-population response relationships explain difference in population response across biogeographic regions?

We explored these questions with a global dataset of Scarabaeine dung beetle population

response to the conversion of lowland tropical forest to agriculture. We combined this information with a global compilation of species' trait information and a molecular phylogeny (Monaghan et al. 2007) to conduct a comparative analysis of the trait correlates of local population response to tropical forest conversion, both within and across biogeographic regions.

Dung beetles are a cosmopolitan insect group, highly sensitive to the direct impacts of tropical forest conversion (Nichols et al. 2007) and the indirect effects that conversion has on mammalian fecal resources (Nichols et al. 2009). Beetle fauna in different biogeographical regions have experienced strikingly different historical climatic and vegetation conditions over evolutionary time, which may contribute to differential sensitivity to the conditions that accompany forest conversion. Glacial cycles across the last several million years have influenced the relative areal extent of forest and grasslands in South America, Africa and Asia in distinct ways, contributing to greater periodic exposure to open-formation vegetation in the Afrotropics and Asia (Heaney 1991, Colinvaux et al. 2000) than in the Neotropics. Tropical Africa and Asia are considered a cohesive biogeographical unit (the Afro-Eurasian region), given their largely shared evolutionary history and significant faunal overlap at the generic level (Scholtz et al. 2009b).

Several studies demonstrate that three dung beetle species traits are associated with response to tropical forest conversion ((i.e. activity period, body size and food relocation strategy, Table S1). However these traits have never been linked with population-level responses across multiple studies, corrected for phylogenetic autocorrelation, nor evaluated across biogeographic regions with contrasting climatic and ecological histories. We collated information on dung beetle



response to forest conversion at three distinct levels of land management intensity, and replicated across two distinct biogeographic regions, which allowed us to explore the possibility of site-level and regional context-dependency in trait-response relationships. Given their demonstrated sensitivity to forest conversion (Nichols et al. 2007) and key functional roles (Nichols et al. 2008), these questions are of broad, practical importance. To our knowledge, this is the first global assessment of local trait-population abundance response relationships of any taxon.

## MATERIALS AND METHODS

### *Dung beetle surveys*

We compiled 24 biodiversity studies that each comparatively sampled dung beetle communities in ‘intact’ moist lowland (< 2,000m) tropical rainforest and neighboring areas of human-modified forest across the Neotropics (n=18), and Afro-Eurasian tropics (n=6) (Table S2). As several biodiversity studies reported multiple, independent habitat comparisons, a total of 36 datasets were incorporated into the analyses (Table S2). The converted habitats sampled across these studies can be categorized along a gradient of canopy openness, spanning: (1) ‘modified’ forest with a native, closed canopy (e.g. selective logging or secondary regrowth), (2) ‘forested agriculture’ with an open native or non-native canopy (e.g. agroforestry and tree plantations), and (3) ‘non-forested agriculture’, or cleared agricultural habitats (e.g. areas of annual crops, cattle pasture and clearcuts). All studies used standardized collection methods, and were conducted at the habitat scale (average observation extent <5 km<sup>2</sup>). Further details on the studies included in this analyses can be found in Nichols et al. (2007).

### *Trait data*

We obtained information on three dung beetle proxy traits hypothesized to correlate with sensitivity to tropical forest conversion (Table S1).

*Body size* in dung beetles has been positively correlated with sensitivity to tropical forest modification (Gardner et al. 2008b) and fragmentation (Larsen et al. 2005). In the cooler understories of intact tropical forest, larger-bodied beetles have an advantage in resource acquisition (Horgan and Fuentes 2005) and competitive outcomes (Chown and Klok 2011). Higher body temperature, however, may become a liability in modified tropical forests, where higher air and soil temperatures can push larger beetles towards their maximum sustained temperature (approximately 42° C Verdu et al. 2006, Chown & Klok 2011). Larger beetle size is also associated with a greater capacity for landscape-level dispersal (Larsen et al. 2008). At low levels of habitat degradation, greater vagility may translate into greater survival rates, as large species can more easily locate and access patchily distributed fecal resources. However in severely degraded habitat, the combination of lower survival due to thermointolerance and enhanced emigration rates may drive a decline in population size and occupancy rates for larger-bodied species (Larsen et al. 2005, Larsen et al. 2008). Compounding these effects, larger-bodied beetles may favor feces deposits from the larger-bodied mammals most likely to be rare in degraded tropical forests (Nichols et al. 2009).

*Food relocation strategy* may alter the relative fitness consequences faced by larval and adult dung beetles in converted forests, as a consequence of both abiotic and biotic changes. Dung beetles provide nests and a food supply for their progeny (Halffter and Edmonds 1982a). *Tunneler* species construct linear or branching burrows directly beneath the dung deposition site,

while *roller* species construct shallower tunnels some distance away from the deposition site. These shallower nests of roller species are likely to be less buffered against the increased temperature and decreased humidity characteristic of converted forest (Larsen 2011). Anecdotal observations suggest that roller nesting activities are also heavily influence by the physical structure of the forest floor, and can be negatively impacted by increased leaf litter, characteristic of arid forested landscapes with slow decomposition rates.

*Activity period* may interact with the higher daytime temperatures and lower humidity of modified tropical forests to strongly penalize diurnal species (Daily and Ehrlich 1996, Larsen 2011). Diurnal activity is often associated with smaller body size (e.g. Feer & Pincebourde 2005; Slade et al. 2007), which may help smaller species cope with ambient nighttime temperatures too low to allow for flight initiation (Verdu et al. 2006). Conversely nocturnal species are often larger, and therefore potentially less constrained by lower night temperatures (Chown and Klok 2011) which tend to be more consistent between intact and converted habitats (Larsen 2011).

Information on species' body mass, food relocation strategy and activity period was compiled from published and unpublished sources (Table S3). We used mean trait values collated from the literature when site-specific trait values were unavailable. For species with unknown body mass, we estimated body mass ( $y$ ) from body length ( $x$ ) ( $y = 0.01x^{3.28}$ ,  $R^2 = 0.86$ ) from a set of 79 species in 22 genera for which both body length and body mass data were available.

### *Species response*

From each dataset we extracted the per-trap abundance for every beetle species, from both intact forest and each forest conversion class. To quantify the difference in species before and after

forest conversion, we calculated a log response ratio:

$$\text{Log response ratio} = \ln\left(\frac{N_{\text{Converted forest}+1}}{N_{\text{Intact forest}+1}}\right) \quad [\text{Eqn. 1}]$$

Species that *increased* in abundance following the conversion of intact forest have positive values, species with identical abundances in intact and converted habitats have a value of 0, and species that *decreased* from their original abundance or went locally extinct have negative values. As our objectives centered on understanding the traits associated with the response of forest-dwelling dung beetle species, we excluded from the dataset species that were not originally detected in intact forest.

### *Phylogeny*

We used a global molecular phylogeny based upon 214 species from six biogeographical regions (Monaghan et al. 2007). As this phylogeny encompassed most of the genera, but few of the species present in our dataset, we modified the phylogeny by collapsing the terminal taxa of the consensus tree into generic-level tips, and representing species phylogeny below the genus level with the addition of a single branch length unit (e.g. Bielby et al. 2008).

### *Analyses*

To explore if dung beetle population responses to forest conversion were consistent across biogeographic regions, we calculated the response ratio (Eqn. 1) of each dung beetle species to the conversion of tropical forest in all converted forest classes, and compared the mean

population response between the Neotropical and Afro-Eurasian tropical regions using a bootstrapped t-test.

To investigate which species traits were associated with this population response, we conducted a phylogenetic comparative analysis across the pooled dataset. We modeled log response ratios (Eqn. 1) as a function of three species' traits (i.e. body mass, food relocation strategy, activity period), forest conversion class (i.e. modified forest, forested agricultural habitat or non-forested agricultural habitat), and two-way trait-habitat interactions using a generalized linear model. We included intact forest as a baseline, and judged the effect of forest conversion class (habitat type) on abundance response as the difference from zero. As some studies included more than one dataset, we also included study as a covariate. Body mass was logged and centered to the mean to facilitate interpretation.

To incorporate the lack of independence among species while accommodating multiple and categorical species traits, we used a generalized estimating equation (GEE) approach (Paradis 2006). Here, phylogenetic autocorrelation is taken into account with a fixed correlation matrix based on branch lengths taken from the global molecular phylogeny (Monaghan et al. 2007). All GEE analyses were conducted using the *APE* package (Paradis et al. 2004) in R (R Development Core Team 2011). We used the phylogenetic degrees of freedom (Paradis 2006) to reduce the potential risk of inflated Type I error rates, given as:

$$df_p = \frac{\sum_{Tree} \text{branch length}}{\sum_{i=1}^n \text{distance from root to tip}} \times n \quad [\text{Eqn. 1}]$$

We used the drop1 command for model simplification, following the recommendation of Paradis (2006), and assessed the degree of phylogenetic signal in these traits with Blomberg's K for body mass (Blomberg et al. 2003) and the Madison and Slatkin (1991) approach for the discrete traits of food relocation strategy and activity period.

Finally, we examined whether differences in trait-environment relationships between the Neotropical and Afro-Eurasian biogeographic centers could explain regional differences in population response to forest conversion. We could not conduct separate models for Neotropical and Afro-Eurasian tropical regional fauna due to low sample size for one specific trait-habitat type combination in the Afro-Eurasian dataset. Consequently, we calculated the mean abundance response of species in each trait-habitat type pair, and compared means across regions with a bootstrapped t-test.

## RESULTS

A total of 655 Scarabaeine species in 61 genera were recorded across the 36 datasets. After removing species with incomplete trait information, or from genera not represented in the phylogeny, a total of 1,119 observations of 265 species in 24 genera were incorporated into subsequent analyses. The final pooled dataset was heavily dominated by Neotropical species (Neotropics n=206, Afro-Eurasian tropics n=57). Most species were nocturnal (61%) and used a

tunneling food relocation strategy (74%). Beetle body mass ranged widely ( $110 \pm 14\text{mg}$ , mean  $\pm\text{SE}$ ,  $n = 265$ , range 1.1 – 1,920.75mg) and was significantly higher for nocturnal species (nocturnal  $171.48 \pm 260\text{mg}$ , mean  $\pm\text{SE}$ ,  $n = 103$ ; diurnal  $71.19 \text{ mg} \pm 185$ , mean  $\pm\text{SE}$ ,  $n = 165$ ;  $t_{272} = 3.64$ ,  $p < 0.0001$ , bootstrapped 95% CI = -1.92 - 1.72) as well as tunneler species (tunneler  $116.51 \pm 244\text{mg}$ , mean  $\pm\text{SE}$ ,  $n = 198$ ; roller  $91.67 \pm 142\text{mg}$ , mean  $\pm\text{SE}$ ,  $n = 70$ ;  $t_{272} = 3.64$ ,  $p < 0.0001$ , bootstrapped 95% CI = -1.82 – 1.78). Species activity period and food relocation strategy were independent ( $X^2 = 1.252$ ,  $df = 1$ ,  $p = 0.26$ ).

Across the pooled dataset, dung beetle abundance was sharply affected by the conversion of intact tropical forest (Fig. 1). Nearly half of all species (47%) went locally extinct in at least one converted forest class. Over 73% of species captured in the least severe conversion class (i.e. modified forest) declined from their original abundance in intact forest. A similar number of species captured in forested agriculture areas demonstrated abundance declines (74%). In the most severe forest conversion class (i.e. non-forested agriculture), approximately 97% of all species declined in abundance.

Food relocation strategy, but not activity period or body mass, demonstrated significant phylogenetic signal (Madison & Slatkin method: food relocation strategy,  $p = 0.022$ ; activity period  $p = 0.082$ ; Bloomberg's  $K$ : body mass,  $K = 0.85$ ,  $p = 0.26$ ; Fig. 2). The frequency of food relocation strategies and activity periods differed significantly across American and Afro-Eurasian fauna (relocation  $X^2 = 6.12$ ,  $df = 1$ ,  $p = 0.013$ ; activity period  $X^2 = 10.6$ ,  $df = 1$ ,  $p = 0.001$ ). Activity period and food relocation strategy frequencies were distributed evenly across

the fauna of the Neotropical dataset (NT), while the Afro-Eurasian dataset (AET), was heavily dominated by diurnal and tunneling species. Body mass was similar between regions (NT  $109.86 \pm 205.06$  mg, mean  $\pm$  1SE; AET  $110.91 \pm 279.67$  mg, mean  $\pm$  1SE;  $t_{73} = -0.03$ ,  $p > 0.9$ , bootstrapped 95% CI = 0.983 – 2.21).

*(1) Are species responses to forest conversion context dependent across biogeographic regions at the global scale?*

Neotropical dung beetles were more sensitive to forest conversion than Afro-Eurasian tropical species, as demonstrated by the lower mean log response ratio of Neotropical species pooled across converted forest types (NT  $-0.42 \pm 0.65$ , mean  $\pm$  1SE; AET  $-0.21 \pm 0.51$ , mean  $\pm$  1SE;  $t_{234} = -3.23$ ,  $p = 0.001$ , bootstrapped 95% CI =  $-0.43 - -0.32$ , Figure 1). This overall effect was largely driven by stronger regional differences in response in the most severe conversion class (i.e., non-forested agriculture;  $t_{38} = -2.06$ ,  $p = 0.09$ , bootstrapped 95% CI =  $-0.65 - -0.42$ ). Within the Afro-Eurasian dataset however, these open, permanent agricultural habitats were represented by a single study. Mean species responses to modified forest and forested agriculture were similar between the two regions (modified forest:  $t_{135} = -1.66$ ,  $p = 0.116$ , bootstrapped 95% CI =  $-0.36 - -0.29$ ; forested agriculture;  $t_{77} = -0.79$ ,  $p = 0.438$ , bootstrapped 95% CI =  $-0.41 - -0.21$ ).



*(2) Which functional traits are associated with local population response to forest conversion?*

The final phylogenetically corrected model explaining abundance response of dung beetles to tropical forest conversion included all the original predictor variables (Table 1; Fig. 3). Not surprisingly, dung beetle population response to forest conversion was significantly affected by the severity of forest conversion (Fig. 3). The average difference in population response from the intact forest level baseline was strongest in non-forested agriculture habitats and intermediate in modified forest habitats. Species captured in forested agricultural habitats also declined in abundance from intact forest levels, although this reduction was not significant (Fig. 3).

We found significant interactions with forest conversion class for all three traits (body mass:  $F(3, 1118) = 9.13, p < 0.0001$ ; activity period:  $F(3, 1118) = 9.24, p = 0.0001$ ; and food relocation strategy  $F(3, 1118) = 17.54, p < 0.0001$ ). Contrary to our initial expectations, with the increasing intensity of tropical forest conversion there was an increase in the abundance of larger-bodied beetles. The population responses of species with rolling or tunneling food relocation strategies were highly dependent upon habitat type. Roller species suffered greater declines in abundance compared to tunnelers in forested agricultural areas but had moderately higher abundances in non-forested agricultural areas. Nocturnal species declined more severely than diurnal species across all forest conversion classes, and significantly so in forested agricultural habitats (Table 1).

*(3) Do differences in trait-response relationships among biogeographical regions explain differences in the magnitude of species response to forest conversion?*

Several regional differences in dung beetle trait-environment relationships may explain the observed regional context dependency in population response (Fig 5). Diurnal Neotropical species were more significantly sensitive to the conversion to modified forests than diurnal Afro-Eurasian species while nocturnal Neotropical species declined more sharply in non-forested agricultural areas (Fig 4). Neotropical species with tunneling food relocation strategies were significantly more sensitive than Afro-Eurasian tunnelers to all three levels of forest conversion. In contrast, Afro-Eurasian roller species performed significantly worse than Neotropical roller species in forested agricultural areas (Fig 4).

## DISCUSSION

We summarized existing data on dung beetle population response to the conversion of tropical forest and contrasted the magnitude of these responses for taxa found in the Neo and Afro-Eurasian tropics. In tropical land-uses that retained some forest canopy, such as secondarily logged areas or agroforests, we found weak evidence of regional differences in the magnitude of dung beetle response. In land-uses that completely removed forest canopy, such as cattle pastures and permanent agriculture, Neotropical species fared significantly worse than Afro-Eurasian tropical species, though this result must be interpreted with caution given the paucity of available Afro-Eurasian studies in open agricultural habitats.

We found species' trait differences did explain variation in population response to forest conversion, and that the relationship between traits and population trends was greatly influenced by local and biogeographic context. At a global scale, we found the influence of food relocation strategy on population response depended on the severity of forest conversion. Dung beetles with rolling and tunneling strategies demonstrated similar declines in mildly modified forests (e.g. selectively logged areas) and areas where the forest canopy was completely removed (e.g. permanent agricultural areas). Yet in forested agriculture areas, only roller species demonstrated significant population declines. This global pattern was driven by a significantly stronger decline by roller species from the Afro-Eurasian biogeographic region. The strongly negative population trends of roller species in agroforestry habitats are likely a consequence of both changing abiotic and biotic environmental conditions. Larval survival rates can be strongly reduced at low soil moisture levels (Sowig 1995b), and the higher air and soil temperatures and lower soil moisture of degraded habitats may disproportionately influence rollers due to their shallower burial depth (Halffter and Edmonds 1982a). The increased leaf litter in plantation forests may additionally impede the ball-making activities of rollers, and potentially reduce reproductive success (Larsen pers comm).

The influence of dung beetle activity period on population response demonstrated similar local and regional context dependency. Globally, diurnal species were less sensitive than nocturnal species to all degrees of forest conversion, though the magnitude of this difference was only significant in forested agriculture habitats. At the regional level, the conversion of intact forest

into modified forests and non-forested agriculture had a significantly more negative influence on diurnal Neotropical species relative to Afro-Eurasian species. In the most severe class of forest conversion (i.e) non-forested agriculture, the observed population decline of Neotropical species was independent of activity period, suggesting that the abiotic conditions in these areas likely exceed the thermoregulatory tolerances of most species alike, regardless of diel activity (Chown and Klok 2011).

Finally, beetle body mass was positively related to population response across all habitats, although the magnitude of this relationship was dependent upon habitat type. This finding was contrary to initial expectations, given that large body size is associated with a range of species' traits (e.g. lower fecundity, longer generation time (Halffter and Edmonds 1982a, Chown and Gaston 2010) that theoretically reduce a population's ability to compensate for increased rates of mortality arising from unfavorable abiotic conditions (Chown and Klok 2011) and decreased food availability (Nichols et al. 2009) in modified forests. Comparable positive body mass-abundance relationships have been reported from comparative analyses of bird (Laurance et al. 2011, Pocock 2011) and primate (Cowlshaw et al. 2009) population response to forest conversion. We believe these results arise from a combination of larger-bodied beetle's greater capacity for dispersal and resource detection. It should be emphasized, that this is only expected to occur in those cases where the abiotic conditions of degraded forest do not exceed their thermoregulatory limits.

The observed regional differences in both population response to forest conversion and trait-population trend relationships are consistent with the hypothesis that historical differences in climate and vegetation-based extinction filters operating across the Neo and Afro-Eurasian tropics during the Late Pleistocene may have influenced the sensitivity of modern dung beetle fauna to contemporary forest conversion (Turvey & Fritz 2011). Historically, the Neo and Afro-Eurasian tropics have been shaped by distinctive climate and vegetation cycles. Across the Afrotropics, periodic reductions in the areal extent of forest driven by Pleistocene climate oscillations have been proposed as a mechanism to explain the limited number of Afrotropical forest-obligate genera, and the comparatively low diversity within those genera (Scholtz et al. 2009b). In Southeast Asia, climate further interacted with reduced sea levels to contribute to similar periodic expansion of open-formation vegetation in areas that are defined as lowland rainforest areas today (Heaney 1991). In contrast, these same glacial cycles acted to largely maintain Neotropical lowland forest under continuous forest cover (Colinvaux et al. 2000). Consequently, a lower number of genera in the Americas have been exposed to open-formation vegetation across their evolutionary history relative to the Afro-Eurasian tropics (Scholtz et al. 2009b).

This study contributes to mounting evidence suggesting that intrinsic species' traits do not influence the response of organisms to environmental change in isolation, but rather when coupled with the influences of extrinsic habitat characteristics and biogeographic history (Isaac and Cowlshaw 2004, Cowlshaw et al. 2009, Angert et al. 2011, Collen et al. 2011, Pocock 2011). Given the implications of such context dependency on the usefulness of trait-based research for policy and management, there is a clear need to examine how data availability and

sampling design influence our understanding of the trait correlates of vulnerability. While understanding the generality of trait-response relationships across different biogeographic contexts is crucial (Pocock 2011), the robustness of cross-regional analyses may be strongly influenced by the data quality-coverage trade-offs that commonly plague global analyses (Fritz et al. 2009). As demonstrated here, comparative biodiversity sample data may be a rich and widely available source of information on population trends from which to expand our understanding of trait-environment-response relationships across biogeographic contexts.

The ultimate success of trait-based approaches to modeling extinction risk requires understanding which traits are important predictors of significant population response. In meeting this challenge, trait-based population forecasts face the key challenge of quantifying relevant functional trait information across large numbers of species and sites (Angert et al. 2011). As for many animal taxa, community-wide morphological, physiological and phenological (M-P-P) traits of dung beetles are nearly non-existent. In this study we used a set of ‘proxy’ species traits selected for their global-scale availability, rather than their explicit relationship to fitness. For example, for dung beetles and other taxa, body mass is a well-described proxy for fecundity, maximum dispersal distance and thermoregulatory capacity (Halffter and Edmonds 1982a, Chown and Gaston 2010), while the association of activity period and food relocation strategy with specific functional traits is less clear. When such proxy traits represent such a ‘one-to-many’ relationship with functional traits more explicitly related to fitness, unambiguous trait-environment-response associations could be expected to be rare.

A return to the Arnold (1983) hierarchical performance paradigm as a framework for the application of existing traits may increase the predictive value of trait-based models of animal vulnerability, by enabling more transparent and operational choices about which functional traits may be represented by proxy traits. This framework can also be used as a practical roadmap to highlight important gaps in existing trait data as part of the systematic collection of new traits. Diet breadth and plasticity for example, consistently emerge as important predictors of response across many animal taxa (e.g. butterflies (Diamond et al. 2011), Passeriforme birds (Angert et al. 2011), bees (Bommarco et al. 2010), and can be tied to several functional traits (Lind and Barbosa 2010), yet is broadly unknown for dung beetles at the community level (Nichols et al. 2009). Ultimately, linking true M-P-P traits, to fitness along anthropogenic environmental gradients may provide a useful context to integrate community ecology more strongly with ongoing ecophysiology research (e.g. Chown 2011), build meaningful links from functional traits to population dynamics (McGill and Enquist 2006) and identify which functional traits are also important for ecosystem function (Larsen et al. 2005, Slade et al. 2007).

Predicting species vulnerability to anthropogenic environmental change is essential for avoiding or mitigating future species loss. This ultimately will depend equally on our ability to distinguish between uninformative species traits, and unsuccessful associations between traits, environmental change and response. The results of this study and others suggest the importance of interactions between species' traits, habitat characteristics and biogeography in predicting population responses to globally important environmental change drivers, such as conversion of tropical forest. Further effort is needed to develop a robust framework to refine our understanding of the roles of context-dependency and trait quality on observed species' response

to environmental change.



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## TABLES AND FIGURES

Table 4.1. Predictors of dung beetle response to tropical forest conversion. Significant results from a phylogenetically corrected multiple linear model are marked with an asterisk ( $p < 0.05$ ). Phylogenetic df (dfP) = 1,118. Baseline values for human-modified habitat type, activity period and food relocation strategy were intact forest, diurnal and tunneler, respectively.

Model predictors	Estimate	se	<i>t</i>	<i>p</i> -value
(Intercept)	-0.24	0.20	-1.19	0.235
Modified forest	-0.11	0.11	-0.96	0.335
Forested agriculture	0.00	0.15	-0.02	0.988
Non-forested agriculture	-0.52	0.14	-3.67	0.000*
Body mass	0.00	0.02	0.11	0.913
Activity period	0.02	0.04	0.49	0.627
Food relocation strategy	0.00	0.04	0.07	0.947
Modified forest * body mass	0.08	0.04	2.06	0.039*
Forested agriculture * body mass	0.09	0.04	2.09	0.037*
Non-forested agriculture * body mass	0.12	0.05	2.44	0.015*
Modified forest * activity period	-0.10	0.06	-1.73	0.084
Forested agriculture * activity period	-0.19	0.07	-2.92	0.004*
Non-forested agriculture * activity period	-0.09	0.07	-1.28	0.199
Modified forest * food relocation strategy	-0.10	0.06	-1.62	0.105
Forested agriculture * food relocation strategy	-0.24	0.07	-3.38	0.001*
Non-forested agriculture * food relocation strategy	0.10	0.08	1.26	0.209

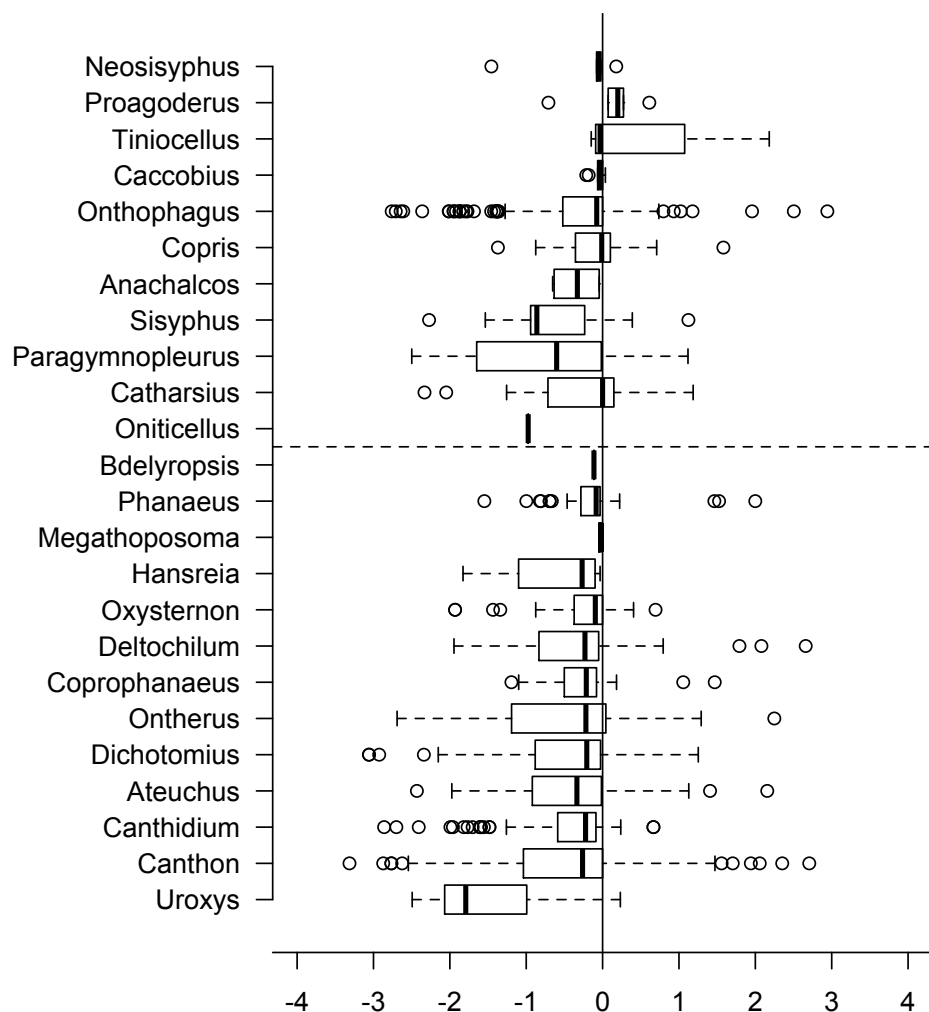


Figure 4.1. Abundance response to the conversion of lowland tropical forest for 24 Scarabaeine dung beetle genera across three continents. Species that increased in abundance following the conversion of intact forest have positive values; species those that declined from their original abundance following the conversion of intact forest have negative values. The dashed line separates genera from the Afro-Eurasian tropics (above) and Neotropics (below). *Copris* and *Onthophagus* are found globally.

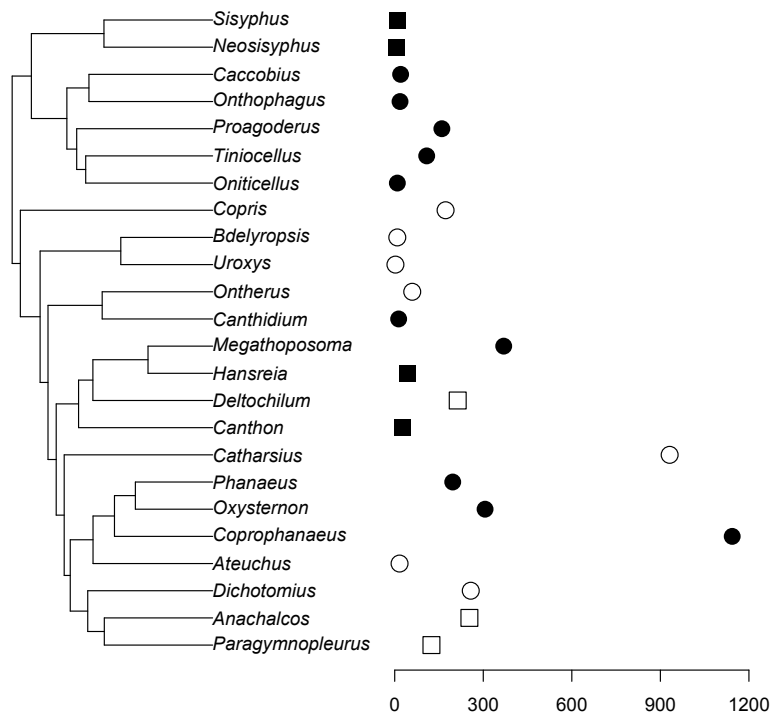


Figure 4.2. Phylogenetic relationships for 24 Scarabaeine dung beetle genera, and trait information taken from a subset of 265 species. See Methods for details on trait values and tree simplification, and Monaghan et al. (2007) for tree construction. The plot to the right represents the mean generic body mass of the species (mg) incorporated into all analyses (see Methods). Symbol shape and color reflect the dominant species trait value across all species that entered the analysis for food relocation strategy (circles: tunnelers, squares: rollers) and activity period (white: diurnal, black: nocturnal).

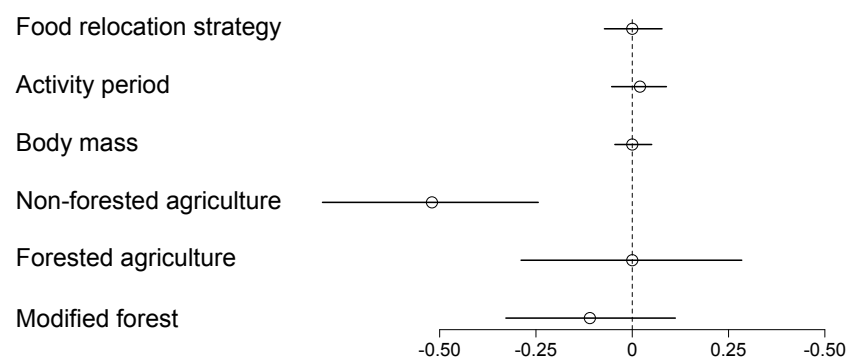
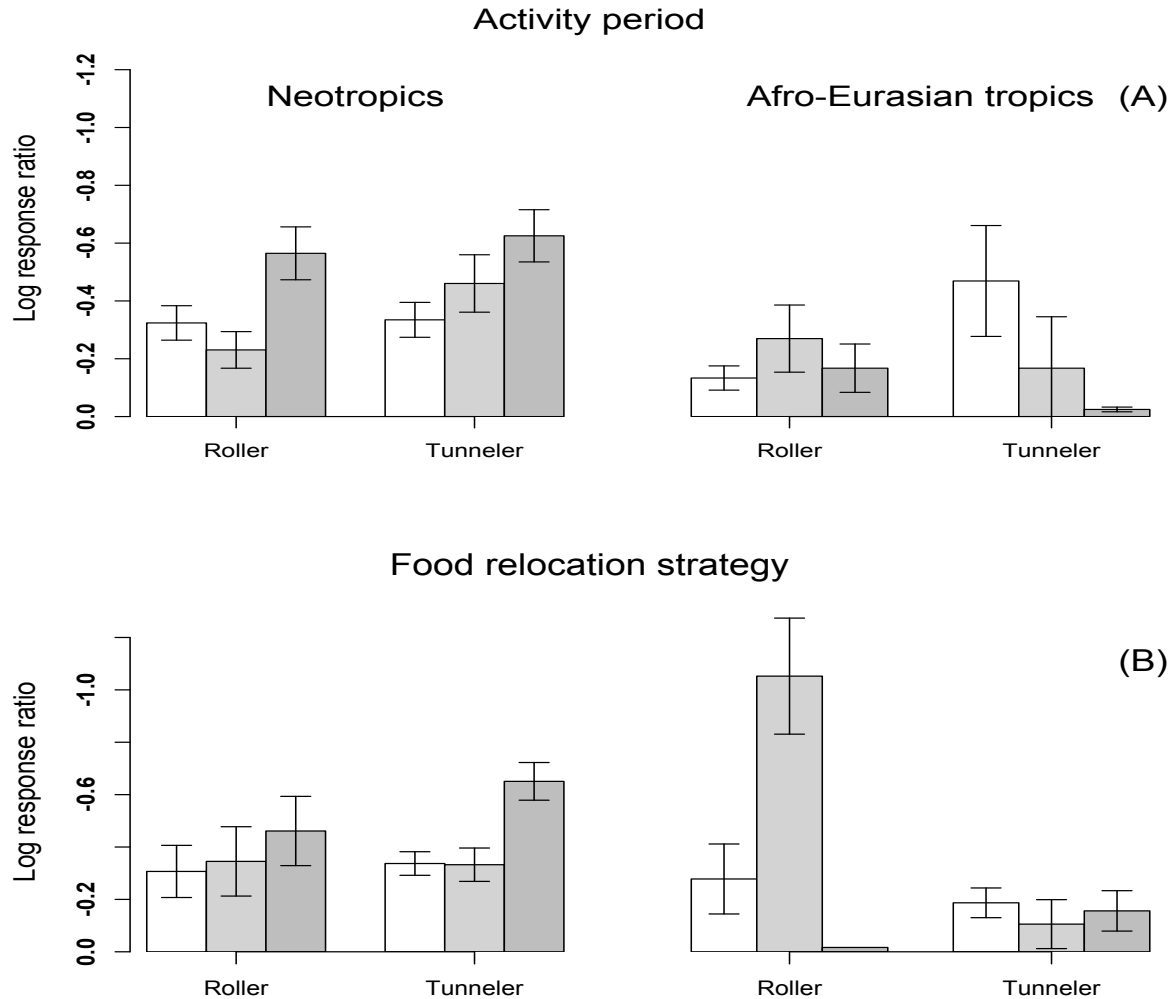


Figure 4.3. Standardized regression coefficients ( $\beta$ ) for a phylogenetic multiple linear model relating dung beetle population response to tropical forest conversion to beetle traits and modified forest type. Responses less than zero indicate a decline in relative abundance moving from intact forest to a human-modified habitat; values above zero indicate an increase.



**Figure 4.4.** Interactions between dung beetle population decline, species traits and degree of forest conversion severity in two biogeographic regions. Three degrees of severity of tropical forest conversion are represented by modified forest (white), forested-agriculture (light grey) and non-forested agriculture (dark grey). **(A)** Diurnal Neotropical species were more sensitive to the conversion to modified forests than Afro-Eurasian species (NT  $-0.32 \pm 0.57$ ; AET  $-0.13 \pm 0.28$ , mean  $\pm$  1SE;  $t_{137} = -2.12$ ,  $p=0.039$ , bootstrapped 95% CI =  $-0.34 - -0.17$ ). Nocturnal Neotropical species were also significantly more sensitive to the conversion to non-forested agriculture (NT  $-0.63 \pm 0.73$ ; AET  $-0.02 \pm 0.01$ , mean  $\pm$  1SE;  $t_{65} = -1.16$ ,  $p<0.0001$ , bootstrapped 95% CI =  $-0.65 - -0.57$ ). **(B)** Neotropical tunneler species were significantly more sensitive to all levels of forest conversion (modified forest: NT  $-0.34 \pm 0.49$ , AET  $-0.19 \pm 0.40$ , mean  $\pm$  1SE;  $t_{112} = -1.91$ ,  $p=0.04$ , bootstrapped 95% CI =  $-0.36 - -0.22$ ; forested agriculture: NT  $-0.33 \pm 0.53$ ; AET  $-0.11 \pm 0.58$ , mean  $\pm$  1SE;  $t_{73} = -2.06$ ,  $p=0.025$ , bootstrapped 95% CI =  $-0.35 - -0.15$ ; non-forested agriculture: NT  $-0.65 \pm 0.72$ ; AET  $-0.16 \pm 0.27$ , mean  $\pm$  1SE;  $t_{35} = -2.35$ ,  $p<0.0001$ , bootstrapped 95% CI =  $-0.66 - -0.50$ ). In contrast, Afro-Eurasian roller species performed significantly worse in forested agricultural areas (NT  $-0.35 \pm 0.65$ ; AET  $-1.05 \pm 0.59$ , mean  $\pm$  1SE;  $t_{11} = 2.59$ ,  $p<0.0001$ , bootstrapped 95% CI =  $-0.70 - -0.30$ ).

## CHAPTER 5 - DUNG BEETLES IN APPLIED BIODIVERSITY CONSERVATION RESEARCH

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## Abstract

A concern of conservation science is understanding how different human activities influence the persistence of native biota and associated ecological and evolutionary processes. Increasingly, such applied biodiversity research challenges are met through the use of ecological indicator assemblages – suites of species whose presence and abundances in a given area provide a useful gauge for measuring and interpreting changing environmental conditions. In this chapter we review the case for the use of Scarabaeine dung beetle assemblages as an ecological indicator taxon. We outline a general framework for selecting indicator taxa that can deliver robust and cost-effective information, and build upon the insights of previous researchers to demonstrate why dung beetles represent such an appealing candidate study group. We draw upon existing research from a diverse array of ecosystems but particularly tropical forests where the majority of our own field experience lies. Finally we consider the conservation status of dung beetles themselves, and discuss some of the practical opportunities and challenges that lie ahead for the conservation of the approximately 6,000 Scarabaeine species described to date.

## INTRODUCTION

To safeguard a significant proportion of the world's biodiversity, it is necessary to integrate conservation efforts with other human activities. On the one hand, protected areas represent an important, yet grossly inadequate component of a wider conservation strategy, with many endangered species (Rodrigues et al. 2004) and ecoregions (Schmitt et al. 2008) falling outside the existing reserve networks. On the other hand, it is also clear that conservation is not an “all or nothing” game, and many human land-uses (e.g. regenerating secondary forests, and responsibly



managed agroforestry systems) are compatible with conserving at least part of the native biota of a given region (see Chazdon et al. 2009 and references therein).

Given this reality, a central problem faced by conservation science is to understand how different types of human-modified land-use are able to support the maintenance of native biota, and associated ecological and evolutionary processes (Chazdon et al. 2009, Gardner et al. 2009). To improve our understanding of conservation opportunities in the face of rapid land-use intensification and severe funding limitations, our research methods must be effective, efficient and practical. Increasingly, applied biodiversity research challenges are met through the use of ecological indicator assemblages – suites of species whose presence and abundances in a given area provide a useful gauge for measuring and interpreting changing environmental conditions.

In this chapter we review the case for the use of Scarabaeine dung beetle assemblages as an ecological indicator taxon. We outline a general framework for selecting indicator taxa that can deliver robust and cost-effective information, and build upon the insights of previous researchers to demonstrate why dung beetles represent such an appealing candidate study group (Halfpter and Favila 1993, Spector and Forsyth 1998, Davis et al. 2001b, Davis et al. 2004, Spector 2006b). We draw upon existing research from a diverse array of ecosystems but particularly tropical forests where the majority of our own field experience lies. Finally we consider the conservation status of dung beetles themselves, and discuss some of the practical opportunities and challenges that lie ahead for the conservation of approximately 6,000 Scarabaeine species described to date.

## SATISFYING DATA NEEDS TO INFORM CONSERVATION PRACTICE

Two basic, allied concepts form the conceptual foundation of modern conservation science - biodiversity and ecological integrity (Noss 1990, Noss 2004). Biodiversity can be defined as the variety of life forms at all levels of biological systems (i.e., from genes through species, populations and ecosystems) (Wilcox 1984). Given the intractable nature of such a broad concept, many conservation projects target only a subset of biodiversity – e.g. specific species or vegetation types that are associated with a particular conservation value. In contrast to the notion of biodiversity, ecological integrity is defined broadly as an ecosystem's capacity to maintain biotic communities that have a structural, compositional and functional organization comparable to that of relatively undisturbed ecosystems in the same region (Karr 1991, 1993). The maintenance of ecological integrity invokes a much broader challenge for conservation than a more narrow focus on the preservation of particular biodiversity elements (Folke et al. 2004, Noss 2004).

For the purposes of conserving biodiversity in human-dominated landscapes, distinguishing between these two concepts is important as they underpin distinct approaches for management and monitoring (Lindenmayer and Hobbs 2007, Lindenmayer et al. 2007, Gardner 2010). While it is often easier to draw attention to the needs of individual species (which frequently represent the cornerstone of efforts to mobilize interest and investment in conservation action) it is impossible to develop species-based approaches to satisfy the conservation requirements of all taxa. Indeed for most of the world we have little idea of the identity of species in need of

conservation attention, let alone their specific resource requirements or how they interact in important ways with other taxa. Alternative conservation approaches that instead focus on the integrity or condition of human-modified ecosystems themselves can provide an arguably much richer source of information for which to guide ecological management (Angermeier and Karr 1994, Gardner 2010)

Nevertheless, measuring and interpreting changing patterns of ecological integrity remains a major scientific challenge. We generally have a very poor understanding of the processes and functions that are necessary to maintain resilient ecological systems (Angermeier and Karr 1994, Naeem 2008a). It is often the case that carefully selected biological species themselves can provide the most effective indicators of ecological integrity. This is because we have some understanding of the factors that drive changes in species distribution and abundance patterns, and because individual organisms (compared to process rates) are often less expensive to monitor, and may be more sensitive to human activities than ecosystem processes or functions themselves (Angermeier and Karr 1994).

Taxa that serve this function are termed ecological indicators (McGeoch 1998, 2007), or more specifically ecological disturbance indicators (Caro 2010, Gardner 2010). The purpose of ecological disturbance indicators is to provide reliable and interpretable information on the ecological consequences of human activities (compared against some acceptable reference condition) for a measured component of biodiversity. In a practical sense, the concept of such taxa is to help us move beyond a simple classification of areas based on physical habitat

measurements, and translate the meaning of land use changes into measures that capture changes in the ecological integrity of the system. This is only possible for taxa that can be sampled cost-effectively and for which we have some *a priori* ecological understanding of disturbance response patterns. The concept of ecological disturbance indicators is quite distinct from the notion of “biodiversity indicators” (McGeoch 2007), “biodiversity surrogates” (Moreno et al. 2007), or “cross-taxon response indicators” (Caro 2010), all of which depend upon the (largely unfounded) belief that observations of one species group can provide reliable inferences about changes in other (unstudied) species (Cushman et al. 2009).

Despite various selection criteria for ecological disturbance indicators (Greenslade and Greenslade 1987, Noss 1990, Kremen 1992, Pearson and Cassola 1992, Halffter and Favila 1993, Pearson 1994, McGeoch 1998, Davis et al. 2004), very few studies have adopted a systematic approach that accounts for both the practical and theoretical factors influencing the value of such data in addressing conservation problems (McGeoch 1998, Spector 2006a, Gardner 2010). Figure 5.1 outlines three basic criteria that can be used to systematically assess the potential of any candidate ecological disturbance indicator group, namely *viability*, *reliability* and *interpretability* (Gardner 2010).

First and foremost it is necessary for any candidate indicator group to be *viable* for study. Do the necessary field, laboratory and taxonomic expertise exist to ensure that a project has a viable chance of success?

Second, a potential candidate indicator group must provide a *reliable* and practically relevant measure of the ecological consequences of human activity. By reliable, we mean both responsive

to human-induced environmental heterogeneity at spatial and temporal scales commensurate with human management practices, and measurable within a standardized sampling protocol and limited budget. Ideally such a species group will be comprised of individual species that vary significantly in their sensitivity to human activities (i.e. response diversity, *sensu* Elmqvist et al. 2003), thereby allowing the evaluation of a wide range of land management practices.

A third general criterion for selecting ecological disturbance indicators is that biodiversity sample data must be interpretable - insofar as we have sufficient prior ecological knowledge to understand something about observed patterns of abundance and occupancy, and link changes in these patterns to measured environmental variables. Ultimately an understanding of such cause-effect relationships is necessary to develop a predictive capacity for linking human activities to changing patterns of ecological integrity (Landres et al. 1988). In situations where species-mediated ecological functions have demonstrable effects on human well-being we can further use biodiversity sample data to evaluate the consequences of human activities for the provision of ecosystem services - an area that remains a major knowledge gap in conservation science (Nicholson et al. 2009).

#### THE ROLE OF DUNG BEETLES IN APPLIED BIODIVERSITY RESEARCH IN HUMAN-MODIFIED LANDSCAPES

While no single group of species can fully satisfy these three criteria of viability, reliability and interpretability, Scarabaeine dung beetles present a very strong candidate. Accordingly, they have received substantial interest in applied biodiversity research (Halfpeter and Favila 1993,

Spector and Forsyth 1998, Davis et al. 2001b, Spector 2006a). In this section we employ this same three-tiered selection framework (Fig. 5.1) to discuss why.

#### *DUNG BEETLES AS A VIABLE CANDIDATE FOR BIODIVERSITY RESEARCH*

Comparable, standardized estimates of local species distribution and abundance form the cornerstone of applied biodiversity research. The employment of standardized, cost-effective sampling approaches can go a long way towards maximizing the information return gained from the field surveys that are typically time-limited and budget constrained (Gardner et al. 2008a). In this regard dung beetles are appealing because representative samples of a given locality can be collected within days, rather than weeks. This contrasts starkly with the challenges associated with sampling many other species groups. In the case of terrestrial vertebrates for example, rapid assessment of the distribution of species or patterns of abundance is often hampered by high detection biases and a lack of adequately trained experts (Landres et al. 1988, Feinsinger 2001).

Standardized sampling methods can also help ensure a minimum level of methodological consistency to support the kinds of meta-analyses that are needed to draw generalizations at regional or global scales. While to date no single dung beetle collection protocol has been uniformly adopted, there is considerable coherence in methodologies employed across different studies. The vast majority of comparative dung beetle studies are conducted with human dung baited pitfall traps (comprising a simple collecting vessel sunk flush with the ground and the bait suspended above). Bovine or pig dung is often used in African and Asian biogeographic contexts (Boonrotpong et al. 2004, Davis and Philips 2005) and trap arrays of feces, carrion (and occasionally fruit and fungus) are increasingly popular in the Neotropics (Escobar S. et al. 2007,

Horgan 2008, Larsen et al. 2008). Efforts to investigate the quantitative efficiencies of different collecting protocols (Larsen and Forsyth 2005) and create an actual standardized sampling protocol are underway (ScarabNet 2007). It is important to note that not all Scarabaeine beetles are attracted to baited pitfall traps, and where the objective is to conduct a species inventory it is necessary to employ a suite of complementary methods, including hand collection and passive flight intercept traps (FITs) (Davis et al. 2000). That said, the global use of human dung baited pitfall traps has created a truly tremendous potential data source from which to explore patterns in beta-diversity (Viljanen et al. 2010) as well as community (Nichols et al. 2007) and trait-based responses to land use change (Nichols et al. in review).

Once material has been collected, the ability to reliably and consistently identify specimen material to the species level is a critical requirement for any study group used in biodiversity research. Taxonomic challenges represent a major barrier to the development of time-efficient and cost-effective field research projects on the ecology of many hyperdiverse invertebrate groups (Samways 2002). While Scarabaeinae dung beetles are diverse, levels of both local and global diversity are tractable. A global taxon database managed by the Scarabaeine Research Network currently has just over 5,700 valid species names from 225 genera (ScarabNet 2009), and an ever-increasing variety of identification tools are available to facilitate the accurate processing of new material by specialist and non-specialist workers (Vaz-de Mello and Edmonds 2007, Larsen and Génier 2008, Mann 2008).

### *DUNG BEETLES AS RELIABLE INDICATORS OF ENVIRONMENTAL CHANGE*

Given our current understanding on the sensitivity in response of dung beetles to (i) natural environmental gradients, as a basis for disentangling the importance of human disturbances in driving observed patterns, (ii) land-use change and intensification gradients in tropical forests (an ecosystem that has received particular research attention within the dung beetle research community in recent years), and (iii) declines in resource diversity and availability as a consequence of mammal hunting, dung beetles can provide a valuable gauge of changes in ecological integrity in human-modified systems. Our ability to collect cost-effective and representative samples of underlying patterns of Scarabaeinae distribution and abundance further enhances their utility as an ecological disturbance indicator taxon.

### *DUNG BEETLE RESPONSE PATTERNS ACROSS NATURAL ENVIRONMENTAL GRADIENTS*

The impacts of human activities on biodiversity, whether local, regional or global, negative or positive, are invariably conditioned by the natural environmental and biophysical characteristics of the spatial scale of interest. Dung beetles are highly responsive to environmental heterogeneities across multiple scales and levels of ecological organization (Hanski and Cambefort 1991c). These associations provide the basis for understanding the structure of local species assemblages in both natural and human-modified ecosystems.

At the regional scale, dung beetle associations with specific climate and edaphic conditions often demonstrate strong patterns of fidelity, or biogeographic distinctness (Hanski and Krikken 1991, Davis 1993, Davis and Dewhurst 1993, Davis 1994, 1997, Davis et al. 2000). Indeed, biogeographic circumstances play an important role in filtering those species that are capable of



surviving in human-modified lands (see also Chapter 12 of this volume). This was very clearly demonstrated by Davis and Phillips (2009) who found high densities of dung beetles inhabiting the matrix of plantation and farmland in fragmented forest landscapes of the Ivory Coast that are dominated largely by a subset of species originating from neighboring savannah areas (Fig. 5.2). Similarly, Scarabaeine communities in areas of introduced pastures adjacent to native Brazilian savannah (Cerrado) are more likely to overlap in their community structure and composition (Vidaurre and Louzada unpublished), than communities found in introduced pastures in Central America, due to the historical lack of such native open areas in the latter region (Horgan 2007).

Understanding how dung beetle assemblage structure changes in response to natural vegetation gradients at finer spatial scales can also provide vital clues as to the appropriate spatial scales at which to assess species-abundance relationships in disturbed habitats. Remarkably high rates of species turnover have been found across neighboring habitat types, and often over very short distances (hundreds of meters). From directly adjacent savannah and forest sites in Bolivia, Spector and Ayzama (2003) reported that 24 of the 50 most common species were restricted to a single vegetation type. Only two species were present in both vegetation types with patterns being remarkably consistent over time. Working in Sabah Borneo, Davis et al. (2001b) reported not only a clear distinction in species composition for dung beetle assemblages sampled in riverine and interior rainforest, but also a finer-scale subdivision within riverine forest, with species being clustered into river-edge, river-bank, and riverine non-edge/bank components, each occupying a slightly different microclimate.

Edaphic differences likely underlie many of the patterns associated with vegetation changes described above (Davis 1997). As soil structure and consistency can directly affect reproductive site selection (Vessby and Wikteliuss 2003), and reproductive success of individual dung beetle species (Lumaret and Kirk 1987, Sowig 1995a), soil plays a direct role in structuring local dung beetle assemblages and determining local population viabilities even in the absence of any changes in vegetation (Nealis 1977, Lumaret and Kirk 1987, Doube 1991). As with vegetation, the fidelity of beetle-soil associations varies across species; with some species demonstrating obligate associations to certain soil types, others, marked differences in species density, and still others little change in abundance (see Doube 1991 and references therein for a range of South African examples); associations that can be manifest over a range of spatial scales.

#### *DUNG BEETLE RESPONSE PATTERNS ACROSS LAND USE INTENSIFICATION GRADIENTS IN TROPICAL FORESTS*

Understanding differences in species-response patterns to a given type of human-associated disturbance or land-use change is essential if we are to generate reliable information on the causes of biodiversity loss. In some areas (e.g. tropical land use change), our understanding has benefited from both a large number of individual studies, but also from meta-analyses of key similarities and differences in community response patterns. The relative lack of such synthetic assessments of dung beetle responses to other disturbance types (i.e. ivermectin impacts on agropastoral dung beetles) more reflects a lack of research attention than a lack of importance per se.

In a recent meta-analysis, Nichols et al. (2007) brought together 33 individual studies to synthesize current knowledge concerning the responses of dung beetles to land-use change in human-modified tropical forests (Fig. 5.3). Land-uses with a high degree of forest cover such as selectively logged forest, secondary and agroforests support dung beetle communities with similar community attributes to those found in intact tropical forest (Pineda et al. 2005), indicating that these more structurally complex habitats could make an important contribution to mitigating biodiversity loss from deforestation (Dunn 2004, Wright and Muller-Landau 2006). In contrast, heavily modified habitats with little or no tree cover were shown to support species-poor dung beetle communities with high rates of species turnover, dramatically altered abundance distributions, with smaller over-all body size from species found in intact forest (see also Chapter 11 in this volume). Dung beetle communities in highly modified habitats are commonly characterized by the hyper-abundance of a few small-bodied species, including species in the genera *Trichillum* in central Amazonia (Scheffler 2005) and *Tiniocellus* in West Africa (Davis and Philips 2005, Davis and Philips 2009).

Nichols et al. (2007) found that the extent of species turnover is generally greatest in open, managed fields (annually cropped fields and cattle pastures) and likely dependent upon differences in the landscape or regional context (Howden and Nealis 1975, Davis et al. 2000). The spatial extent of disturbance may also play a critical role in determining estimates of species loss following disturbance (Avendano-Mendoza et al. 2005, Shahabuddin et al. 2005). Nichols et al. (2007) also found that forest fragments displayed similarly consistent dung beetle community response patterns to those found in human-modified areas, with fragments tending to be characterized by reduced levels of richness, abundance, community similarity and species

evenness relative to intact forest. Most often these parameters vary positively with fragment size, although the make-up of the wider landscape-matrix can also play a very important role (Gardner et al. 2009).

#### *DUNG BEETLE RESPONSE PATTERNS TO SHIFTING DUNG RESOURCE AVAILABILITY*

Because of their broad dependency on mammalian faeces as a larval and adult food resource, dung beetles are expected to be highly sensitive to shifts in mammal community composition and structure (Nichols et al. 2009). Despite substantially less documentation on their response to resource shifts than is available for changes to physical vegetation structure, there is strong evidence for global patterns of dung beetle co-decline and co-extinction following changes in native mammal assemblages through persistent human hunting pressure (Andresen and Laurance 2007) and altered grazing regimes (Carpaneto et al. 2005).

In tropical forests, persistent mammal hunting often affects even the most remote of protected areas (Peres and Lake 2003) and uninhabited areas hundreds of kilometers from remote urban centers (Parry et al. 2010b). As large frugivorous primates and ungulates are typically preferentially hunted first, persistent hunting can result in massive local reductions in overall mammal biomass (Jerozolinski and Peres 2003). The resultant declines in local abundance of ungulates and large primates have the effect of reducing the availability of large amounts of moist faeces, and possibly increasing the dry, pelleted dung produced by non-hunted rodents, small armadillos and small primates (Peres and Dolman 2000). Currently, only a single study has undertaken a preliminary investigation of such hunting-mediated resource shifts, reporting

significant declines in dung beetle species richness combined with a sharp reduction in individual abundances for over two-thirds of beetle species (Andresen and Laurance 2007).

*THE COST-EFFECTIVENESS AND RELIABILITY OF DUNG BEETLES AS ECOLOGICAL DISTURBANCE INDICATOR TAXA*

Many species of dung beetle are highly susceptible to baited pitfall traps, leading to a relatively low level of false-negative recordings that plague so many biodiversity studies, especially those focused on vertebrates (Tyre et al. 2003). In a similar sense, dung beetle sampling using baited pitfall traps is relatively insensitive to variability in study design with respect to the number and distribution of individual trapping events (Figure 5.4).

Together with the intrinsic sensitivity to environmental change of the species themselves, these characteristics render dung beetle sample data a particularly valuable source of information for applied ecological research. Moreover, field sampling techniques and specimen processing are comparatively low-cost, underpinning the fact that field research on dung beetles is far more cost (and time) effective than many other commonly studied species groups (Gardner et al. 2008a) (Figure 5.5).

*INTERPRETING DISTURBANCE RESPONSE PATTERNS: APPLICATION OF A TRAIT-BASED FRAMEWORK FOR ECOLOGICAL RESEARCH*

The extensive (and growing) knowledge of Scarabaeine ecology provides an invaluable basis from which to draw meaning from sample data and isolate the drivers that are responsible for

observed changes. Understanding the long-term drivers and consequences of biodiversity change ultimately requires a research framework within which we can translate changes in abundance or species composition into an enhanced understanding of ecological processes, and ultimately changes in ecological integrity of the study system (Chapin et al. 2000). Species traits directly mediate fluxes of energy and material as well as interact with the abiotic variables that indirectly regulate ecological process rates. Consequently, within a given community, the species present, their relative abundances, the interactions among species, and the temporal and spatial variation in all of the above, influence ecological functioning by determining the overall expression of organismal traits within a local community. Only by developing an integrated understanding of the ways in which species respond to a changing environment, and how such changes feedback into altered ecological processes is it possible to scale-up inferences drawn from individual studies to a broader understanding of how human activities can influence the structure and function of ecosystems (Didham et al. 1996).

While animal ecologists have traditionally used species traits to predict extinction risk (Cole 1954, Davidson et al. 2009) the finer-grained natural history information typically available for plants has driven the use of a more sophisticated framework that distinguishes between response and effect based traits (Lavorel and Garnier 2002, Suding et al. 2008). Response traits are those associated with a given species' Grinnelian niche, and relate species resource or environmental needs with species performance. Impact traits are expressions of an Eltonian niche concept, associated with the impacts of a species on its environment, and often measured in terms of biotic interactions or abiotic consequences (Devictor et al. 2010). Taking the view that local species communities are the product of a hierarchy of biotic (predation, competition, resource

availability, habitat configuration) and abiotic (climate, geology) filters that determine the make-up of a regional species pool, species traits can be used to develop a mechanistic and predictive understanding of how species will respond to the filters represented by human impacts, and what these responses mean in ecological terms. The degree to which these response and impact traits overlap has enormous implications for the long-term persistence of biodiversity and ecological integrity in human-modified landscapes (e.g. Larsen et al. 2005).

Dung beetle ecologists have long documented a series of easily measured morphological and behavioral differences among species and individuals. These more easily discernible ‘soft’ traits (Hodgson et al. 1999b) often represent groups of underlying yet more elusive ‘hard’ traits that are challenging to measure, yet represent actual functional mechanisms associated with fitness and ecological function (Table 5.1). Dung beetle ecologists have also tended to focus on two related filters as drivers of changes in dung beetle communities - changes in vegetation structure and associated microclimates, and changes in the availability of food and breeding resources (typically dung, but also carrion and other materials). Disentangling how the soft and hard species traits that are manifest in a given regional species pool interact with novel filters represented by local human activities, and are further conditioned by the wider biogeographical context, is at the cutting edge of ecological function research, and provides an increasingly valuable basis from which to draw meaning from biodiversity field data.

*TRAIT-BASED RESPONSES TO CHANGES IN VEGETATION STRUCTURE AND ASSOCIATED MICROCLIMATE*

Understanding how inherent trade-offs between different life-history traits (e.g. body size and reproductive rate, or heat-dissipation capacity) relate to differences in the structure and composition of dung beetle assemblages found across vegetation and resource gradients can greatly facilitate the interpretation of observed species patterns. Human-induced changes to the structure and complexity of forest canopies and understory vegetation can impose dramatic changes on local microclimatic conditions, increasing levels of radiant heat, light intensity and air and soil temperature, while decreasing humidity (Halffter and Edmonds 1982a, Duncan and Byrne 2000). The combined effects of a relatively narrow physiological tolerance to temperatures (a feature shared by many species; (Chown 2001), and see Chapter 10 in this volume), together with the influence of changes to solar radiation on adult activity patterns (Lobo et al. 1998) and soil moisture content on larval survival (Sowig 1996) likely represent strong environmental filters which restructure local dung beetle assemblages following disturbance (Table 5.1).

Dung beetles span four orders of magnitude in size (Larsen et al. 2008), and large body size is increasingly cited as a response trait that confers greater risk of local extinction in the face of forest fragmentation (Klein 1989a, Larsen et al. 2005), conversion to agriculture (Shahabuddin et al 2010; Gardner et al. 2008; Nichols et al. in review), and deforestation (Scheffler 2005). These effects may occur as a consequence of physiological intolerance to thermal stress, size-dependent response to declining diversity or abundance of dung resources, or their combined effects. As body size can have a strong effect on community assembly order (Horgan and Fuentes 2005b), and interspecific competition (Horgan 2005a), the early loss of large-bodied beetles may have



significant secondary consequences for community structure and subsequent patterns of ecological function (Larsen et al. 2005, Slade et al. 2007).

#### *TRAIT-BASED RESPONSES TO CHANGING RESOURCE AVAILABILITY*

Variability in both the amount and diversity of dung (and other resources such as carrion) are also important factors in explaining the distribution of local dung beetle assemblages (Nichols et al. 2009, Fig. 5.5). There is a growing body of evidence linking the nutritional quality of different dung types with variable parental investment in brood ball size (Hunt and Simmons 2004, Kanda et al. 2005), and several aspects of dung beetles development, from adult body size (Emlen 1994) to diet-induced allometric plasticity in certain polyphenic species (Rowland and Emlen 2009). The strength of any cascading effects on resource dependent dung beetle assemblages will depend upon species-specific differences in dietary specialization, dietary plasticity over ecological timescales, and the relationship between diet and fitness. Yet further linking these physiological ‘hard trait’ responses to soft, easily measurable traits, as well as to short and long-term population dynamics remains a major research challenge as we generally lack a species-specific understanding of dung beetle diet breadth and plasticity (Holter and Scholtz 2007, Nichols et al. 2009).

This challenge is particularly great in tropical forests where adult dung beetle diets appear to be more diverse (Cambefort and Walter 1991a, Gill 1991, Hanksi and Krikken 1991) and mammalian and food resources very hard to study. Most coprophagous dung beetles may be attracted to several dung types, though adult attraction does not necessarily equate to optimal

larval nutrition (Barbero et al. 1999, Hunt and Simmons 2004, Kanda et al. 2005), somewhat compromising the reliability of the information that can be gained from ‘buffet’ style dung-preference studies. Even generalist species have been shown to discriminate differences in water and or fiber content (Verdu and Galante 2004, Lopez-Guerrero and Zunino 2007), nutritional value (Verdu and Galante 2004), dung shape (Gordon and Cartwright 1974) and dung size (Peck and Howden 1984a). Still others are highly specialized or obligate to a single host species (Cambefort 1991b, Larsen et al. 2006). Finally, a large variety of non-mammalian dung food resources are utilized by many dung beetle species, including bird, insect and reptile faeces, carrion, fungi and rotting fruits (Young 1981, Gill 1991, Falqueto et al. 2005, Halffter and Halffter 2009). Understanding the importance of these different resources to adult and larval feeding of dung beetles is the key to understanding the long-term resilience of dung beetle assemblages in the face of complex patterns of environmental change.

Large body size is also likely to be linked to a high level of sensitivity to declining dung availability. Persistently hunted systems have lower large mammal biomass (Peres and Palacios 2007) and are likely to support disproportionately fewer large-bodied, active-foraging dung beetle species. The fitness of these larger-bodied species may be compromised by reduced encounter rates of the large individual resource patches needed to construct viable brood balls (Holter and Scholtz 2007, Nichols et al. 2009), or the overall reduction in the density of larger dung pats (that are generated by larger vertebrates) because of elevated levels of interspecific competition within each pat (Horgan and Fuentes 2005). By contrast small-bodied “sit and wait” style foragers that dominate tropical forest beetle assemblages (Gill 1991) are likely to be less affected by hunting because they are capable of exploiting smaller and more ephemeral resource

pulses from small-bodied vertebrates that are of little value to humans as food. Preliminary work along an extensive gradient of hunting pressure in the western Brazilian Amazon suggests that persistently hunted areas have fewer large bodied species, and individuals at the smaller range of body size within a species, relative to areas with reduced current-day hunting pressures (Nichols, unpublished data).

To move towards a more predictive framework that links biodiversity responses to ecological processes in human-modified landscapes, a clear understanding of how response traits interact with different environmental filters is key. Yet in the case of dung beetles (and doubtless other groups), habitat modification seldom occurs without accompanying changes to the availability and diversity of (dung) resources, resulting in multiple, potentially interacting filters that will interact with response traits, and influence the structure and composition of local dung beetle assemblages (Table 5.1, also see Lavorel and Garnier 2002). The effects of vegetation structure and subsequent microclimate appear to be consistently stronger determinants of beetle presence or absence than availability of food resources for the majority of species. However, studies that simultaneously track species occupancy and abundance across habitat and resource gradients (i.e. Macagno and Palestini 2009, Jay-Roberts et al. 2008 and Barbero et al. 1999) are critically important to disentangling these two sets of explanatory factors.

Widespread changes in dung availability and diversity associated with changing rural economies in European alpine and Mediterranean regions have driven altered composition and abundance of native (Lumaret et al. 1992, Carpaneto et al. 2005, Carpaneto et al. 2007) and introduced herbivores (Carpaneto et al. 2005, Hanski et al. 2008, Jay-Robert et al. 2008). These resource

shifts are often accompanied by extensive reforestation or succession in areas of abandoned pastures. In turn, these changes in landscape composition have led to severe declines in native open-habitat associated dung beetle faunas (Lobo 2001, Macagno and Palestini 2009). Research aimed at partitioning these effects has found that, beyond local declines in overall dung availability with the shift from livestock to native grazers, the habitat preference of native pigs and deer for closed habitats has the effect of further reducing dung resources - limiting their distribution to woody successional areas that are suboptimal for the region's open-habitat restricted dung beetle fauna (Barbero et al. 1999, Jay-Robert et al. 2008, Macagno and Palestini 2009). Within biogeographic regions where open habitats represent predominantly novel land cover types, often the few native, open habitat tolerant dung beetle species demonstrate sufficient dietary plasticity to thrive on introduced livestock faeces (Hanski et al. 2008, Louzada and Carvalho e Silva 2009).

#### *TRAIT-BASED CORRELATES OF DUNG BEETLE MEDIATED ECOLOGICAL FUNCTIONS*

Overall patterns of ecological function are determined by the combination of species-level impact traits present in a local community, species abundance distributions, and interactions among species. Ecological functions can be classified into three categories based on the mechanism of energy flow across trophic levels, namely consumption, production and incidence functions (Fig. 5.6a). Consumption functions are those that result from an organism's consumption of resources (typically from one trophic level below, i.e. herbivory), while production functions result from the secondary production of organismal biomass (Clark 1946).

However many important ecological functions come neither from direct consumption or secondary production, and are best considered as incidental functions, or by-products of these two primary function classes. For dung beetles, these include functions such as secondary seed dispersal (a by-product of faeces consumption) and alteration of parasite transmission rates (often a joint product of faeces consumption and biomass production through dung beetle predation; Fig. 5.6a).

As the selection pressures for these three function classes varies, their corresponding impact may be quite different. Large body size is likely the principal impact trait related to the consumption function of waste removal for Scarabaeine dung beetles, and multiple lines of evidence suggest larger bodied beetles can remove disproportionately more dung than smaller bodied beetles (Slade et al. 2007, Nichols et al. 2008). While nesting strategy itself may confer less variation in brood ball size, many of the largest sized beetles in a community tend to have tunneling morphologies (e.g. Slade et al. 2007). Impact traits relative to the production of dung beetle biomass are most likely to be those that motivate adult beetles to select the appropriate dung type or to create sufficiently large brood balls (Table 5.1). Impact traits most relevant to incidental functions are likely to be highly context and function-specific. For example nesting strategy plays a stronger role in secondary seed dispersal than disruption of parasite transmission.

*CHALLENGES IN A TRAIT-BASED UNDERSTANDING OF DUNG BEETLE SPECIES-FUNCTION  
RELATIONSHIPS*

Scarabaeinae beetles provide an effective mobile animal study system with which to decipher biodiversity-ecosystem function (BEF) relationships (Nichols et al. 2008). Experimental work by Slade et al. (2007) to isolate the functional contributions of different elements of a dung beetle assemblage represented a novel step in this direction. They reported that waste and seed removal rates increased with the number of different functional groups represented, although individual functional groups had largely idiosyncratic relationships with function rates, suggesting that (i) dung beetle functional groups can be highly complementary, (ii) maximum function is seldom achieved without the representation of all functional groups, and (iii) that any loss of any aspect of dung beetle biodiversity appears to precipitate some loss of functional capacity (Slade et al. 2007).

Moving from community-level patterns such as these, towards a mechanistic understanding of the functional consequences of individual species responses, will require an understanding of the impact of functional linkages and trade-offs between various traits that govern resource use (Goldberg et al. 2008). One drawback to the current emphasis on the collection and analysis of more easily measurable soft trait information to explain species response and function (Larsen et al. 2005; 2008; Slade et al 2007), is the one-to-many relationship of functional linkages between many soft and hard traits (Table 5.1; and see Lavorel and Garnier 2002), challenging our ability to tease out the actual mechanism behind species response or impact. For example, populations of larger-bodied beetles may be at higher extinction risk for multiple factors (Table 5.1), yet

determining analytically which hard trait interacts with a given environmental filter is challenging. Across species within a given community, interactions among impact traits may exhibit facilitation, complementarity, or even antagonism across different ecological functions. For example, large body size in dung beetles confers greater rates of waste removal, and therefore is likely to be positively associated with incidental functions like fly suppression. However, large beetles also may carry small seeds to such a depth that they are often unable to germinate successfully (Andresen and Feer 2005, Nichols et al. 2008), generating a fly-suppression/small seed dispersal trade-off for communities with large beetles present. The distribution of impact traits across the entire dung beetle community is also important (Slade et al, 2007). For example, species of ball-roller typically dig much shallower nests (Halffter and Edmonds 1982a), potentially improving their strengths as providers of seed dispersal functions over tunneling species, which may in turn have stronger impacts on nutrient cycling to lower soil horizons.

Another consideration in species-function relationships of dung beetles (and other mobile animal communities), is that food and nesting resources appear as discrete units in both space and time (Finn 2001, O’Hea et al. 2009). Consequently, the factors that increase or decrease the likelihood of colonization of a given resource play a major role in determining both species composition and abundance structure (Table 5.1). The growing need to include such ‘mobility-based’ traits in biodiversity-ecological function work is borne out of efforts to increase realism in manipulative and observational studies (Naeem 2008b), by expanding from artificially controlled arable plant and microbial community work, to an understanding of the functional importance of mobile

animals and real-world field conditions (Kremen et al. 2007, Naeem 2008b, Tylianakis et al. 2008b).

As a final point, we emphasize the distinction between ecological functions and the increasingly popular ‘ecosystem services’ paradigm (Armsworth et al. 2007). Functions and services are nested, but not synonymous concepts, with ecosystem services most appropriately defined as the subset of ecological functions that directly or indirectly yield an improvement in human wellbeing (Fisher et al. 2009; Fig 5.6b). While every act of waste removal by a dung beetle is itself an important ecological function that helps maintain the integrity of the ecological system, not all such functions are immediately and directly pertinent to human wellbeing at all times (Nichols et al. 2008).

#### DUNG BEETLES AS ECOLOGICAL DISTURBANCE INDICATOR TAXA: APPLIED EXAMPLES

Because of the many favorable attributes outlined in this chapter, dung beetles present an attractive and cost-effective option for conservation assessments and monitoring (Barbero et al. 1999, Celi and Dávalos 2001, McGeoch et al. 2002, Gardner et al. 2008b). Yet only a few projects have actually moved from rhetoric to on-the-ground monitoring programs (Table 5.2). Most of the studies listed in Table 5.2 looked at the viability of implementing field-based monitoring programs that link dung beetle community change to various types of management practice. The goals of these studies range from validating remote-sensing data on changes to forest structure following selective logging under different management scenarios (Aguilar-



Amuchastegui and Henebry 2007), to (more commonly) providing additional data on the specificity of dung beetle species-environment relationships under various disturbance or management regimes (Celi and Dávalos 2001, Davis et al. 2001b, McGeoch et al. 2002, Davis et al. 2004). At least one large-scale monitoring program (The Amazon Land-Use Change and Biodiversity Project; Jari Brazilian Amazonia) is currently collecting longitudinal data on Scarabaeine dung beetles across multiple native and plantation forest management regimes (Gardner & Barlow, unpub). There is an urgent need to expand efforts to include dung beetles in a greater number of biodiversity monitoring programs, and publish case studies of the successes and challenges involved in their use.

#### DUNG BEETLE CONSERVATION

Basic distribution and natural history information are often missing for poorly studied and diverse invertebrate groups (Samways 2002, Pawar 2003), which are often plagued by a set of challenges ranging from taxonomic chauvinism, lack of expertise in the description of hyper-diverse taxa, and associated bioinformatics (Samways 1994, Samways 2002, Pawar 2003, Samways 2006), to a general “public relations” crisis (Kellert 1993). Despite their charisma and well-resolved taxonomy, dung beetles are far from immune to these roadblocks.

Compounding matters, survey efforts for insect taxa are often insufficiently replicated in space, time and diversity of methodology to complete dependable species lists for a given area (Samways and Grant 2007, Cotterill et al. 2008). As a consequence, most insect groups are likely to reflect a tremendous mismatch between global threats to their conservation threat and the

extent of their inclusion in the IUCN Red List (Maudsley and Stork 1995, New 2002). For example in the entire IUCN Red List (2009) there are only 2,619 species of insect listed in any of the threat categories (of which 1,989 are Odonata and only 72 are Coleoptera). Despite the well-documented decline and loss of several species, particularly across the Mediterranean region (Hanski and Cambefort 1991c), there is currently not a single Scarabaeine dung beetle species on the global IUCN Red List (IUCN 2009).

In the case of dung beetles, one ambitious step towards rectifying these gaps has recently begun in the form of their inclusion in the IUCN Sampled Red List Index (Baillie et al. 2008). The Sampled Red List Index (SRLI) program seeks to conduct global assessments for 1,500 randomly selected species of several taxonomic groups that are currently underrepresented on the IUCN Red List. By re-conducting these global assessments at regular intervals, the SRLI program can measure the rate at which species move through extinction risk categories over time. As this volume goes to press, expert assessors from The Scarabaeine Research Network (a National Science Foundation funded, international consortium of Scarabaeine systematists, ecologists and conservationists) have just completed the first round of assessments. Consequently, we now have some extremely preliminary numbers on the global extinction risk faced by the nearly 6,000 species found around the globe.

Extrapolating from the 1,500 species randomly selected for assessment, over 12% of all dung beetle species on Earth are currently threatened with extinction, in IUCN categories EN, NE or NT. The majority of these species are known to be extremely range restricted, are often limited

to areas of high forest biomass subject to logging or charcoal production, or extremely narrow diet breadth, and extensive documentation exists of the complete loss, near loss, or extensive fragmentation of their range (S. Spector, pers comm.). In Africa, elephant, rhino and lemur specialists frequently appear in one of these three threat categories. A further 9% of assessed dung beetle species were classified as vulnerable to extinction (VU). Often these species are reported as dietary specialists, restricted to areas of high vegetative biomass, or occurring in significantly reduced population densities. A preliminary look at many of the VU species suggests that, once reviewed, many will move towards one of the three threatened categories. This could mean that as many as one in five dung beetles is in a present day state of extreme conservation concern (S. Spector, pers comm.). The remaining species are near evenly split between those of least concern (LC, 37%) and those for which we have insufficient data with which to assess their status (42%), very often represented only by a single (type) specimen.

The modern day biodiversity crisis is most often portrayed in vertebrate terms, yet is overwhelmingly a loss of invertebrate life, and those species with tight resource dependencies on other organisms facing a particularly heightened risk of extinction (Dunn 2005). At the global level, this preliminary stage of the IUCN listing process suggests that extinction risk for dung beetles is higher for those species historically and currently restricted to forest areas where human needs for timber and biomass for cooking are high, and those species with diets limited to large bodied mammal species in areas historically and currently subject to over-hunting. The huge number of data deficient species also highlights that our understanding of historical and current dung beetle distributions is extremely poor, and that sample and distribution data is often difficult to access where it exists.

How can we develop conservation strategies for Scarabaeinae dung beetles (Koch et al. 2000)?

As is often the case, the key to success may be in plurality of action. The co-dependency of dung beetles on (predominantly) intact mammal communities *and* tight habitat requirements necessitates system-level conservation approaches. Ecosystem or habitat-level includes a variety of interventions, from large-scale conservation planning to more responsible approaches to natural resource management. For dung beetles, their incorporation, alongside data on other species groups and environmental surrogates will lead naturally to their increased representation in conservation efforts.

Ecosystem-level efforts should be complemented by indirect approaches that inspire the attention and imagination of public, funding bodies, and decision makers to inspire investment in the protection of entire ecosystems. Such approaches often depend upon the existence of flagship species that operate as “social hooks” to motivate political and community engagement in difficult conservation problems (Caro and O'Doherty 1999, Lindenmayer et al. 2007). While flagship species are most commonly charismatic megafauna that are easy to “sell”, ample opportunities exist for educating about the importance of conserving dung beetles. These range from economic arguments (Losey and Vaughan 2006), potential links to human and domestic animal health (du Toit et al. 2008, Nichols et al. 2008) and cultural factors (Hanski 1988, Scholtz 2008).

## SOME WAYS FORWARD

As we have hopefully demonstrated in this chapter, our understanding of the ways in which dung beetles respond to human-induced disturbances and are can be linked to ecological processes can make a significant contribution to our understanding of opportunities for biodiversity conservation in human-modified landscapes. Many of the challenges facing applied dung beetle research could be significantly ameliorated through an increased effort to collect standardized datasets on species and functional disturbance response patterns. Over the past four years, work by individuals associated with The Scarabaeinae Research Network has made considerable progress towards closing some of these database gaps. This has included the creation of a wide range of publicly accessible resources, including an online global catalog of the Scarabaeinae, new keys to genera and species, standard survey protocols and trait information ([www.scarabnet.org](http://www.scarabnet.org)).

Since Halffter and Matthews' 1966 seminal treatise on dung beetle natural history, scarabaeine workers and enthusiasts have benefited from a series of exceptional advances in our understanding of dung beetle natural history (Halffter and Matthews 1966b), nesting behaviors (Halffter and Edmonds 1982a), basic and applied ecology (Hanski and Cambefort 1991c) and more recently, evolutionary biology and conservation (Scholtz et al. 2009a). It is to these earlier works that the expanding collection of dung beetle ecology studies owes both their inspiration and their foundation. Since *Dung Beetle Ecology* was published in 1991, the number of studies documenting dung beetle community responses to land use change has literally exploded. In conjunction with our continuously improved understanding of the actual ecological mechanisms

that underlie individual species responses to habitat change, this information base now provides a valuable opportunity to develop an integrated model study system to enhance our understanding of the drivers of biodiversity persistence in human-modified systems (Didham et al. 1996). In this International Year of Biodiversity, when the relative successes and failures of conservation are in sharp focus, the need to improve our capacity to understand the consequences of global environmental change cannot be overemphasized.

## TABLES AND FIGURES

Table 5.1. Dung beetle traits relevant to species responses to environmental change and impacts on ecosystems. The left most column indicates the easily measured 'soft' traits commonly surveyed as part of natural history and ecological field studies. All other columns briefly describe some of the example mechanisms or 'hard' traits for which soft traits are a presumed proxy. Response traits are those associated with a given species' resource or environmental needs with species performance, while impact traits are associated with the impacts of a species on its environment. Nidification behavior can be broken down into nest location (superficial or subterranean), position relative to food source (adjacent, distant or within) and complexity (simple or compound). Though not immediately intuitive, nidification behavior may be functionally linked to larval nutritional needs as some species are restricted to nesting with dung of a given morphology or type. These dung types may also be deposited only at certain times of day, linking diel activity with larval nutritional needs. \*\* Brood care is binary, fully absent or present for most species and is related to reproductive rate. \*\*\* A mobility trait is one that influences the probability of a mobile species being present in a given site. As this is intimately connected with its potential ecosystem impact, these traits can be considered an impact trait, an important difference between mobile and sessile (plant-based) trait frameworks.

Soft trait	Mechanism: hard trait				
	Response			Impact	
	Habitat disturbance	Food resource shift	Waste removal	Seed dispersal	Secondary Productivity
Body size	Thermoregulation: adult metabolism	Reproduction: larval nutritional needs	Consumption: brood ball size	Incidental: brood ball size	Production: biomass
	Conservation: adult nutritional needs	Reproduction: reproductive rate	Consumption: adult nutritional needs	Incidental: burial depth	
	Avoidance: physical escape	Reproduction: resource detection	Consumption: burial depth	Incidental: cumulative seed	
	Dispersal: colonization capacity	Conservation: resource detection	Consumption: cumulative waste removal		
Diel activity	Thermoregulation: adult metabolism	Reproduction: larval nutritional needs	Probability of presence: phenology		Production: predation
	Avoidance: palatability	Reproduction: phenology			

	Avoidance: phenology				
Wing loading	Dispersal: colonization capacity	Reproduction: resource detection	Probability of presence: colonization	Production: predation	Production: predation
	Avoidance: physical escape	Conservation: resource detection			
Nidification behavior	Reproduction: larval thermoregulation	Reproduction: larval nutritional needs	Consumption: burial depth	Incidental: probability of seed removal	Production: predation
	Avoidance: physical escape	Reproduction: reproductive rate	Incidental: burial depth		
Brood care		Reproduction: reproductive rate	Consumption: cumulative waste removal	Incidental: cumulative seed dispersal	
Habitat breadth	Thermoregulation: adult metabolism	Reproduction: larval nutritional needs			
	Reproduction: larval	Reproduction: resource			
	Reproduction: larval nutritional needs	Conservation: resource detection			
	Conservation: adult nutritional				
Dietary breadth	Conservation: adult nutritional needs	Reproduction: larval nutritional needs	Probability of presence and waste removal		
	Reproduction: larval nutritional	Reproduction: adult nutritional			



Table 5.2. Existing applications of Scarabaeinae dung beetles as ecological disturbance indicators. IndVal refers to the species indicator value method developed by Dufrêne & Legendre (1997).

Study	Location	Study Purpose	Management type	Method	Conclusions
Davis et al. 2004	South Africa	Review species-environment relationships for two disturbance types	Agricultural conversion, endectocide application	None, review of published studies	When sampled at the appropriate spatial scale Scarabaeine dung beetles can effectively discriminate between types of disturbance, and hence assist in guiding management improvements
Celi & Davalos 2001	Ecuador	Generate data on species-environment relationship in zones of varying management, develop a tool for local inhabitants to assess the environmental effects of management practices	Two selective logging practices (3/4 trees/ha & all large trees/ha), agricultural conversion.	Coupled human dung & carrion baited pitfall traps along linear transects	Dung beetle community structure and composition was differentially impacted by different management practices. Some, but not all species were robust indicators of ecological change.
Davis et al. 2001	Borneo	Generate data on species-environment relationships in disturbed and undisturbed areas	Logging, conversion to plantation forest	Human dung baited pitfall traps, flight intercept traps	Species associations demonstrate high biotope fidelity, even over extremely short physical distances
McGeoch et al. 2002	South Africa	Generate data on species-environment relationships in disturbed and	Human presence	Elephant dung baited pitfall traps	Some, not all species were robust indicators of ecological change within a given habitat and across time. IndVal

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		undisturbed areas, and understand the reliability of these relationships over time and utility of the IndVal metric to select candidate indicator species			is a useful tool to select ecological disturbance indicator species
Aguilar-Amuchastegui & Henebry 2007	Costa Rica	Establish proof of concept for use of dung beetles as ecological disturbance indicators of selective logging regimes and minimum cutting schedules	Selective logging	Human dung baited pitfall traps	Dung beetle community structure and composition can be clearly linked to changes in forest management and used to validate remote-sensing data and propose a minimum logging intensity ( $\leq 5$ trees/ha)

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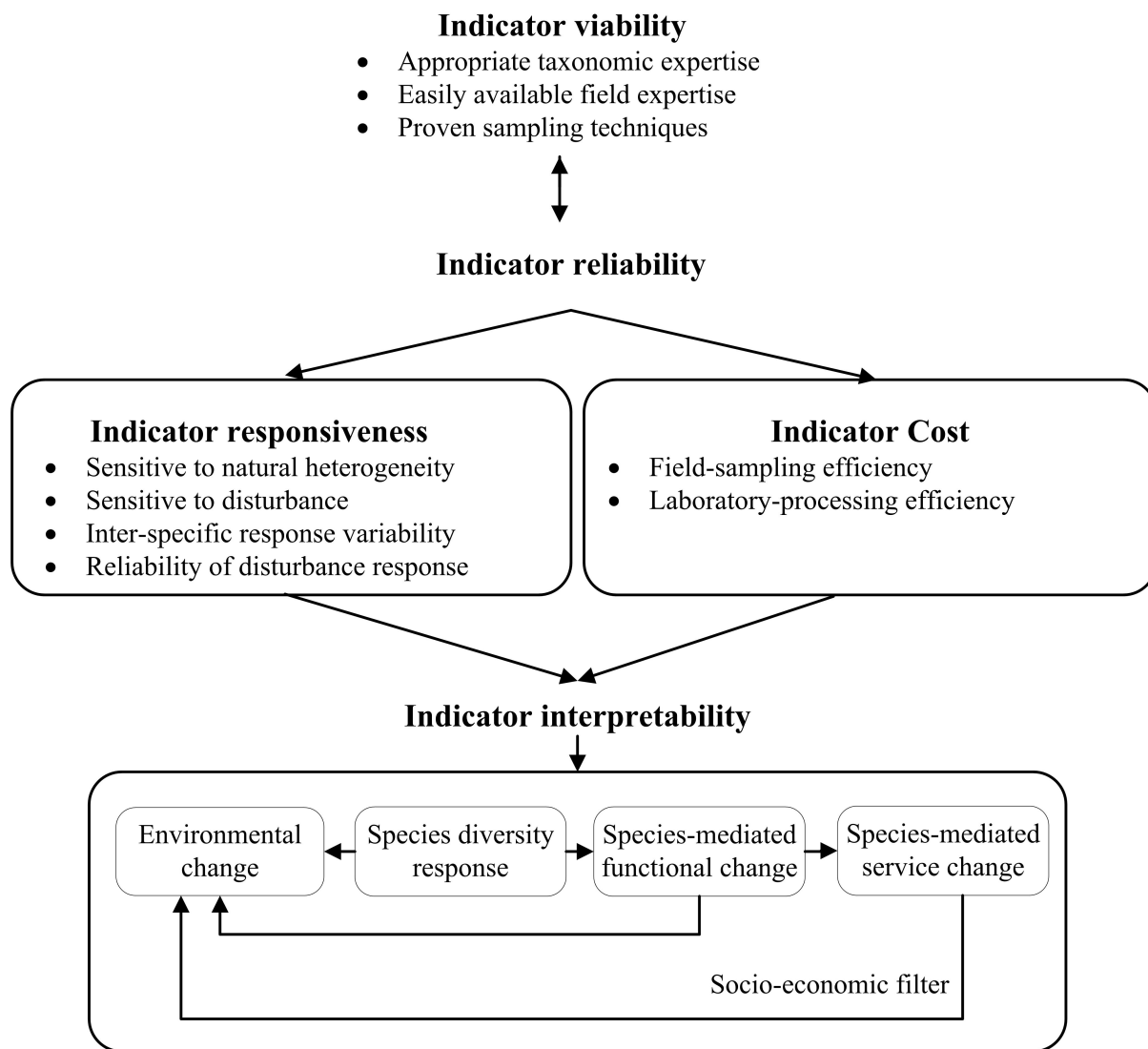


Figure 5.1. A general framework for selecting high-value ecological disturbance indicator taxa for monitoring changes in ecological condition.

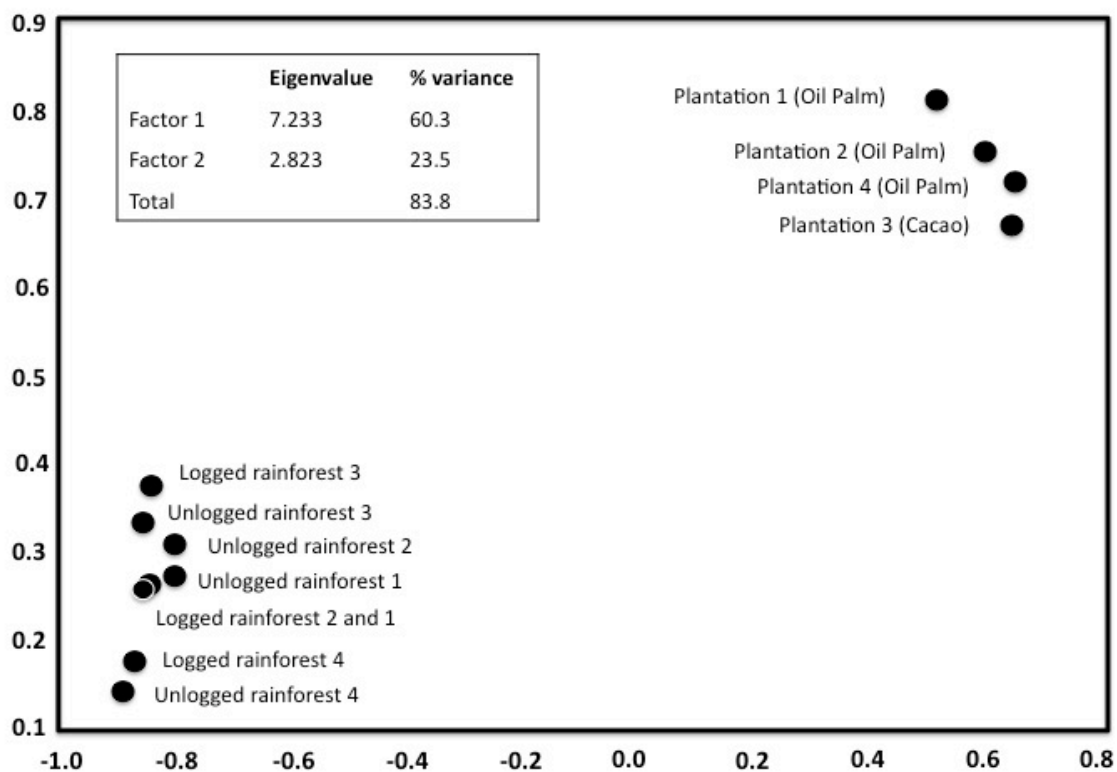


Figure 5.2. Ordination plot demonstrating the statistical distance between plantation and rainforest dung beetle faunas along the southern edge of Ankasa Conservation Area, southwest Ghana. Figure redrawn from Davis and Philips (2005).

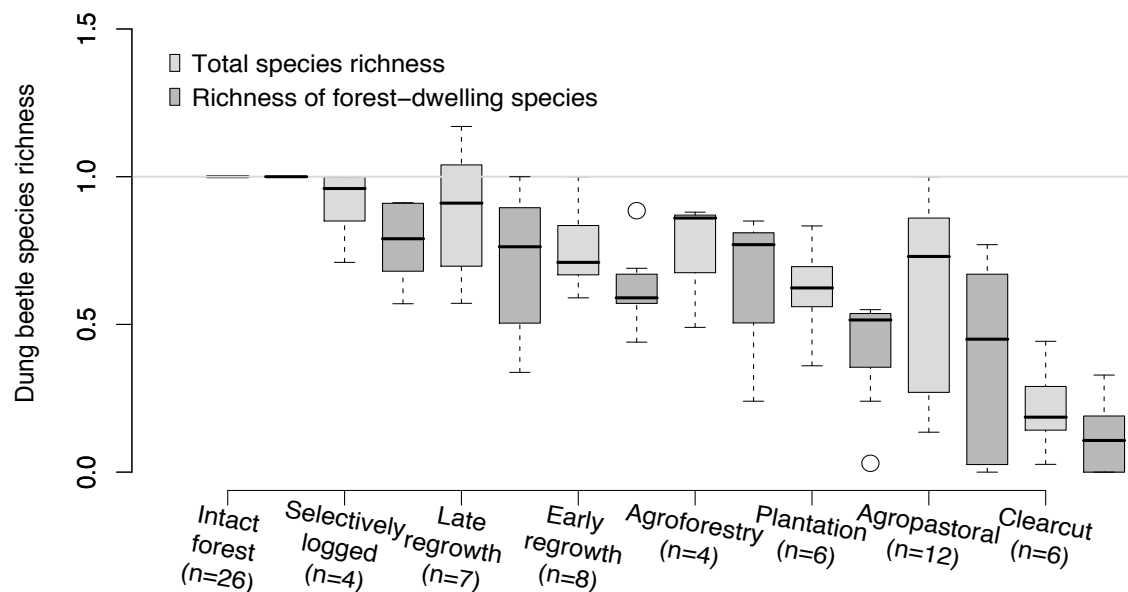


Figure 5.3. Generalized declines in dung beetle species richness across common anthropogenic land uses of moist tropical forest. Redrawn from a global meta-analysis by Nichols et al. (2007) that combined 26 independent studies of species response patterns to forest modification. Here the total number of species recorded in any given land use (light gray) is distinguished from the proportion of species recorded in that land use that were also captured in that study's intact forest (dark gray). Within a given land use, the difference between this 'complete' and 'intact forest' beetle assemblage is an indicator of turnover from forest-restricted to open-habitat adapted species.

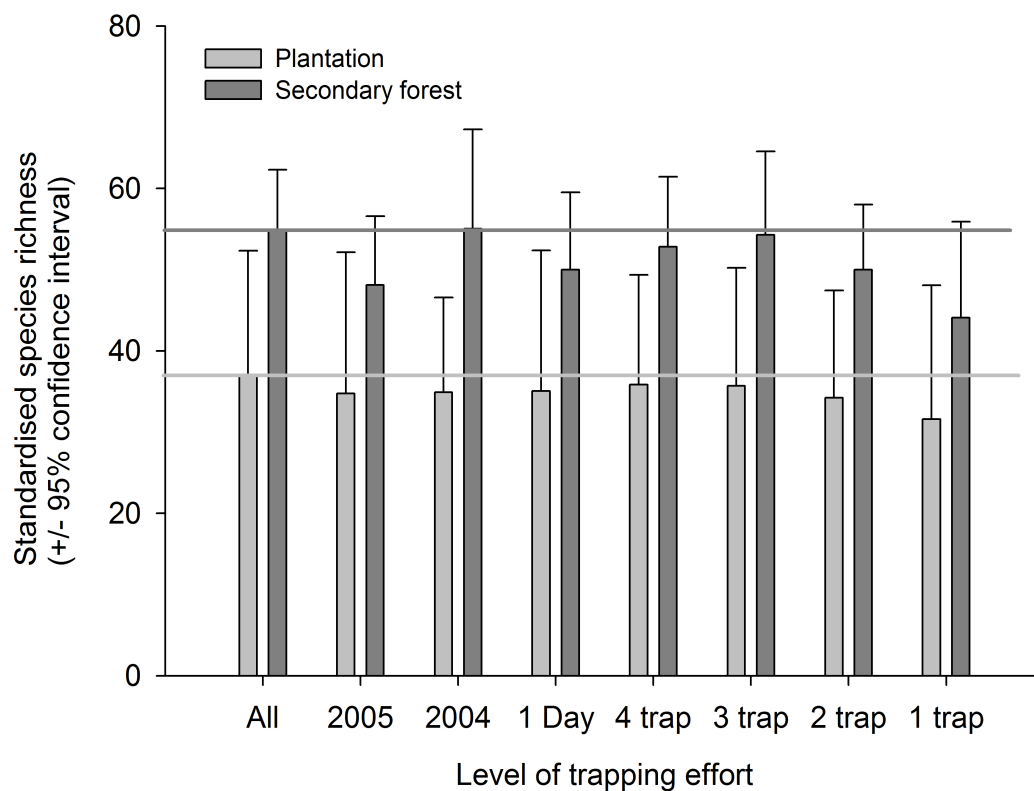


Figure 5.4. Robustness of standardized effect sizes to differences in sampling effort. Plot shows the reduction in number of dung beetle species from primary forest to plantations (light shading) and primary to secondary forest (dark shading) in Jari, Brazilian Amazonia. Different bars represent the same measurements using subsets of the data that draw on different levels of sampling effort, including only using data from one year (2004 or 2005), only using one temporal sub-sample from each site visit (rather than two), and only using data from a decreasing number of spatial sub-samples (1,2,3 or 4 traps rather than 5). Redrawn from Gardner (2010).

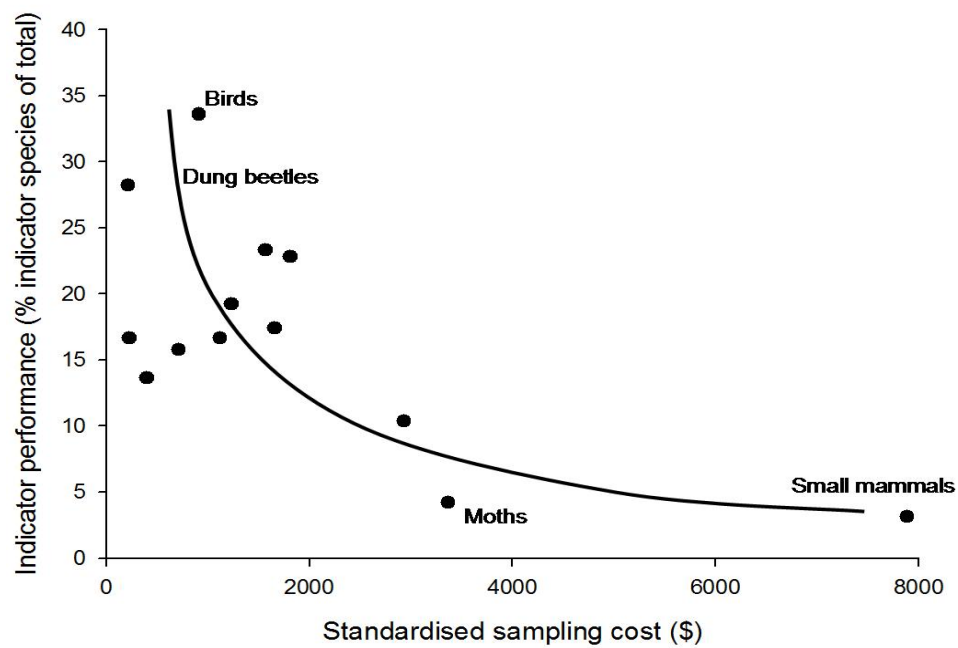


Figure 5.5. Comparing patterns of indicator value and standardized survey cost across 14 taxa sampled in an area of primary rainforest in Jari, Brazilian Amazonia. From Gardner et al. 2008.

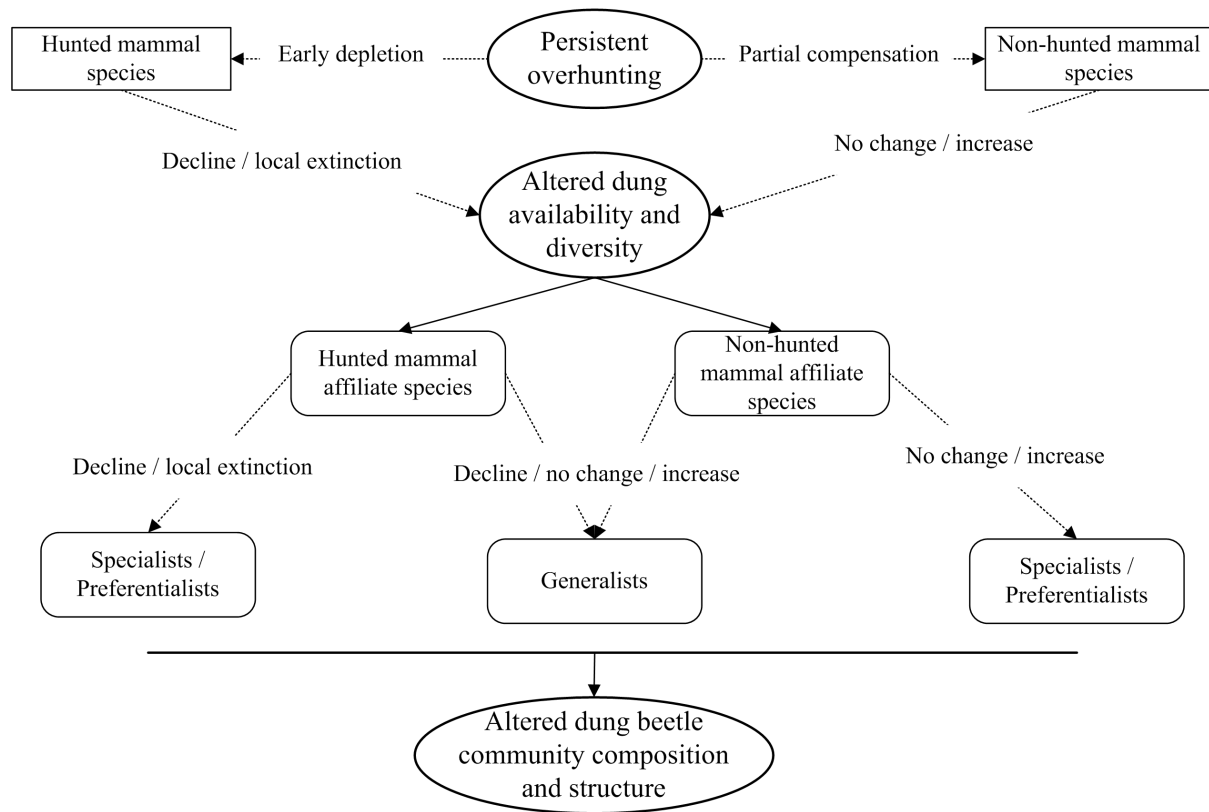


Figure 5.6. Conceptual diagram of the mechanisms likely to drive changes in coprophagous dung beetle community structure as a consequence of hunting-mediated resource shifts. Modified from Nichols et al (2009).



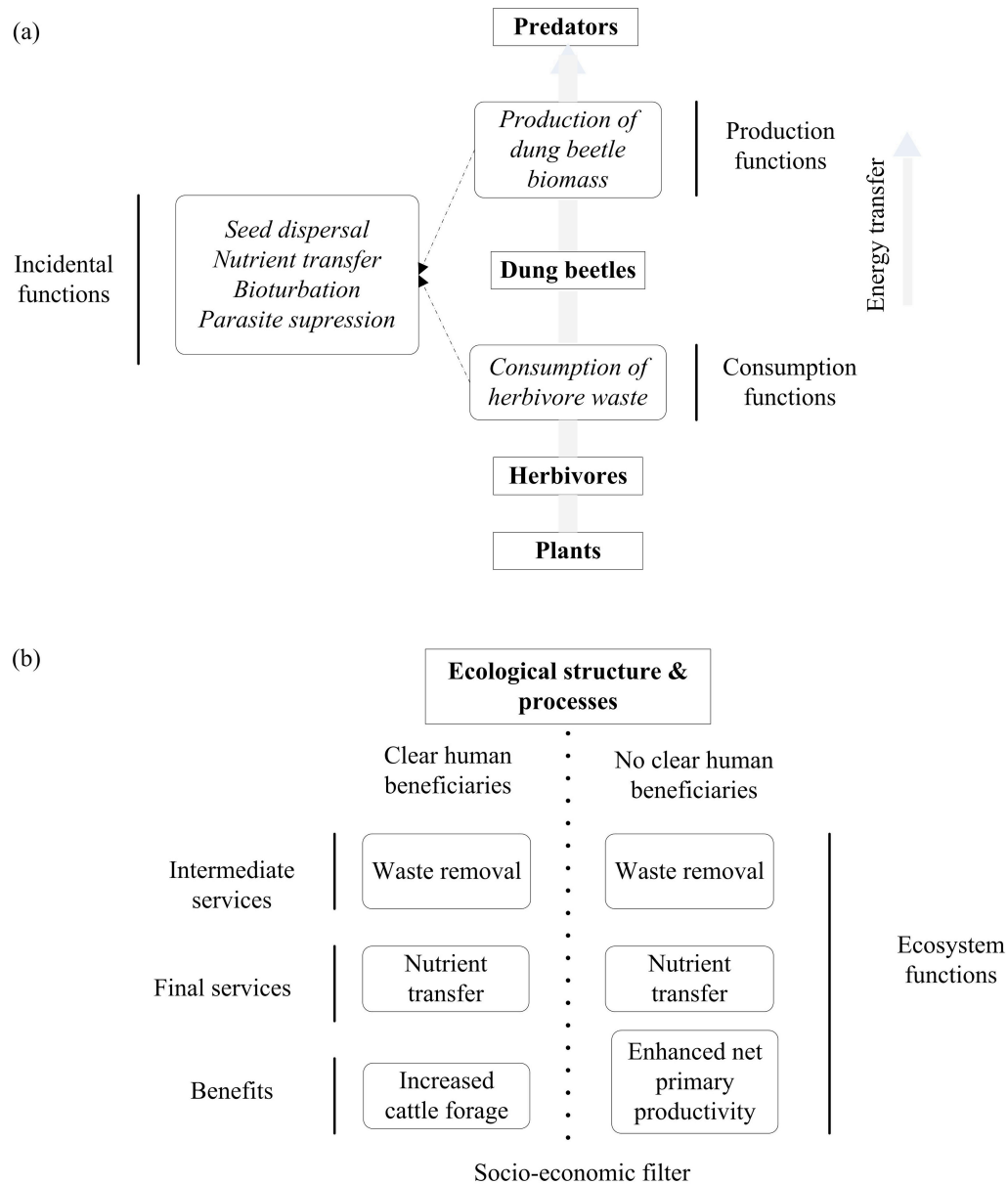


Figure 5.7a. Example of how the ecological functions mediated by Scarabaeine dung beetles can be categorized as consumption, production and incidental functions. Figure 5.7b provides an illustration of the differences between ecological functions and ecosystem services, and how one single set of dung beetle-mediated ecological functions may be categorized as services, given the appropriate socio-economic context.

## APPENDICES

SUPPLEMENTARY TABLE 3.1. Total captures per habitat type, and values of three species traits: mean body mass, activity period and food relocation strategy. Abundance totals represent total captures from a total of 369 trap nights in *terra firme* forest and 277 trap nights in várzea forests. All data collected between January 2008 and December 2010 in the Medio Jurua Extractive Reserve and the Uacari Sustainable Development Reserve, Amazonas State, Brazil

	Mammal Species	Target species?	Trait Group	No group or individual encounters
1	<i>Pecari tajacu</i>	T	Ungulate	365
2	<i>Mazama gouazoubira</i>	T	Ungulate	117
3	<i>Mazama americana</i>	T	Ungulate	111
4	<i>Tayassu pecari</i>	T	Ungulate	67
5	<i>Mazama spp</i>	T	Ungulate	59
6	<i>Tapirus terrestris</i>	T	Ungulate	14
7	<i>Mazama fub.</i>	T	Ungulate	9
8	<i>Mazama sp.</i>	T	Ungulate	1
9	<i>Dasyprocta spp</i>	T	Rodent	1038
10	<i>Sciurus spp</i>	NT	Rodent	392
11	<i>Myoprocta exilis</i>	T	Rodent	307
12	<i>Agouti paca</i>	T	Rodent	36
13	<i>Hydrochoerus hydrochaeris</i>	NT	Rodent	10
14	<i>Microsciurus spp</i>	NT	Rodent	5
15	<i>Coendou prehensilis</i>	NT	Rodent	1
16	<i>Nasua nasua</i>	NT	Procyonid	91
17	<i>Myrmecophaga tridactyla</i>	NT	Myrmecophagid	82
18	<i>Tamandua tetradactyla</i>	NT	Myrmecophagid	44
19	<i>Saimiri spp</i>	NT	Primate	714
20	<i>Saguinus spp</i>	NT	Primate	524
21	<i>Cebus apella</i>	T	Primate	501
22	<i>Alouatta seniculus</i>	T	Primate	409
23	<i>Pithecia pithecia</i>	T	Primate	364
24	<i>Callicebus sp</i>	NT	Primate	356
25	<i>Lagothrix lagothricha</i>	T	Primate	245
26	<i>Ateles paniscus</i>	T	Primate	234
27	<i>Cebus albifrons</i>	NT	Primate	137
28	<i>Cacajao sp</i>	T	Primate	120
29	<i>Saimiri sciureus</i>	NT	Primate	56
30	<i>Aotus nigriceps</i>	NT	Primate	17
31	<i>Cebuella pygmaea pygmaea</i>	NT	Primate	6
32	<i>Saguinus mystax</i>	NT	Primate	1
33	<i>Eira barbara</i>	NT	Mustelid	96
34	<i>Lontra longicaudis</i>	NT	Mustelid	5
35	<i>Leopardus wiedii</i>	NT	Felid	56
36	<i>Panthera onca</i>	NT	Felid	9
37	<i>Puma concolor</i>	NT	Felid	4
38	<i>Didelphis marsupialis</i>	NT	Didelphid	1
39	<i>Dasyus novemcinctus</i>	T	Dasypodid	24
40	<i>Priodontes maximus</i>	T	Dasypodid	7

41	<i>Cerdocyon thous</i>	NT	Canid	2
42	<i>Speothos venaticus</i>	NT	Canid	1

SUPPLEMENTARY TABLE 3.2. Total captures per habitat type, and values of three species traits: mean body mass, activity period and food relocation strategy. Abundance totals represent total captures from a total of 369 trap nights in *terra firme* forest and 277 trap nights in várzea forests. All data collected between August 2009 and February 2010 in the Medio Jurua Extractive Reserve and the Uacari Sustainable Development Reserve, Amazonas State, Brazil

	Species	N <i>terra firme</i>	N várzea	Mean bodymass	Activity period	Food relocation
1	<i>Anisocanthon aff sericinus</i>	2	124	12.97	na	R
2	<i>Ateuchus aff murrayi</i>	177	10	8.66	N	T
3	<i>Ateuchus aff. candezei</i>	3	0	24.47	N	T
4	<i>Ateuchus aff. ovalis</i>	1	0	8.25	N	T
5	<i>Ateuchus connexus</i>	51	0	25.64	N	T
6	<i>Ateuchus scatimoides</i>	5	1	10.45	N	T
7	<i>Ateuchus sp1</i>	3	0	9.61	N	T
8	<i>Ateuchus sp2</i>	34	0	19.07	D	T
9	<i>Canthidium aff collare</i>	2	22	13.23	D	T
10	<i>Canthidium aff cupreum</i>	22	0	16.33	D	T
11	<i>Canthidium aff lentum</i>	4	71	27.64	D	T
12	<i>Canthidium onitoides</i>	160	68	50.37	D	T
13	<i>Canthidium sp1</i>	18	3	17.01	D	T
14	<i>Canthidium sp10</i>	2	0	2.00	D	T
15	<i>Canthidium sp2</i>	6	33	9.82	D	T
16	<i>Canthidium sp3</i>	3	0	25.30	D	T
17	<i>Canthidium sp4</i>	214	1	9.125	D	T
18	<i>Canthidium sp5</i>	0	3	10.00	D	T
19	<i>Canthidium sp6</i>	0	5	5.36	D	T
20	<i>Canthidium sp7</i>	0	5	0.80	D	T
21	<i>Canthidium sp8</i>	2	0	14.32	D	T
22	<i>Canthidium splendidus</i>	210	32	12.79	D	na
23	<i>Canthon aff angustatus1</i>	1	0	8.73	D	R
24	<i>Canthon aff angustatus2</i>	1	3	7.93	D	R
25	<i>Canthon aff quinquemaculatus</i>	34	349	38.99	D	R
26	<i>Canthon aff sericatus</i>	0	2	8.10	D	R
27	<i>Canthon aff smargardulus</i>	135	0	138.96	D	R
28	<i>Canthon bimaculatus</i>	4	0	28.50	D	R
29	<i>Canthon coloratus</i>	1	0	21.625	D	R
30	<i>Canthon fulgidus</i>	58	0	103.34	D	R
31	<i>Canthon luteicollis</i>	245	1	57.64	D	R
32	<i>Canthon proseni</i>	246	314	92.255	D	R
33	<i>Canthon quadriguttatus</i>	3	0	20.50	D	R

34	<i>Canthon rufocoeruleus</i>	0	616	4.91	D	R
35	<i>Canthon semiopacus</i>	72	0	43.515	D	R
36	<i>Canthon triangularis</i>	246	1346	92.03	D	R
37	<i>Coprophanaeus callegarii</i>	3	0	153.52	C	T
38	<i>Coprophanaeus ensifer</i>	1	0	2754.2	na	na
39	<i>Coprophanaeus telamon</i>	30	1	453.84	D	T
40	<i>Deltochilum aff peruanum</i>	61	208	68.59	C	R
41	<i>Deltochilum aff septemstriatum</i>	29	0	44.26	C	R
42	<i>Deltochilum aff sericeum</i>	50	0	106.86	C	R
43	<i>Deltochilum amazonicum</i>	81	17	496.38	N	R
44	<i>Deltochilum orbiculare</i>	41	0	300.10	N	R
45	<i>Dichotomius aff lucasi</i>	75	0	105.10	N	T
46	<i>Dichotomius aff. fortistriatus</i>	265	18	113.77	D	T
47	<i>Dichotomius apicalis</i>	1	0	146.45	N	T
48	<i>Dichotomius mamillatus</i>	47	12	461.79	N	T
49	<i>Dichotomius melzeri</i>	2	0	529.90	N	T
50	<i>Dichotomius nimuendaju</i>	2	0	550.70	N	T
51	<i>Dichotomius ohausi</i>	7	1	162.90	N	T
52	<i>Dichotomius prietoi</i>	167	4	531.35	N	T
53	<i>Dichotomius robustus</i>	2	0	119.00	N	T
54	<i>Dichotomius sp1</i>	1	0	186.30	N	T
55	<i>Dichotomius worontzowi</i>	4	1	165.48	N	T
56	<i>Eurysternus caribaeus</i>	323	22	117.35	D	D
57	<i>Eurysternus hamaticolis</i>	47	81	185.16	D	D
58	<i>Eurysternus wittmerorum</i>	211	34	23.48	na	D
59	<i>Eurysterus cayennensis</i>	894	18	29.36	D	D
60	<i>Eurysterus foedus</i>	34	6	154.32	D	D
61	<i>Eurysterus hypocrita</i>	276	16	189.95	D	D
62	<i>Eurysterus strigilatus</i>	22	6	13.16	D	D
63	<i>Eurysterus vastiorum</i>	6	7	13.53	D	D
64	<i>Genera nova</i>	0	114	5.85	na	na
65	<i>Gromphas amazonica</i>	1	56	156.88	na	T
66	<i>Ontherus pubens</i>	8	14	76.97	N	T
67	<i>Onthophagus aff bidentatus</i>	276	263	8.85	D	T
68	<i>Onthophagus aff clypeatus</i>	3	0	13.36	D	T
69	<i>Onthophagus aff haemathopus</i>	450	40	16.55	D	T
70	<i>Onthophagus marginicollis</i>	1	1	12.76	D	T
71	<i>Onthophagus onorei</i>	147	0	4.03	D	T
72	<i>Oxysternon conspicillatum</i>	11	0	789.62	D	T
73	<i>Oxysternon lautum</i>	27	345	596.07	D	T
74	<i>Oxysternon silenus zikani</i>	17	3	135.38	D	T

75	<i>Phanaeus cambeforti</i>	22	3	142.55	D	T
76	<i>Phanaeus chalconelas</i>	89	0	264.26	D	T
77	<i>Pseudocanthon aff xanthurus</i>	0	1	3.15	D	na
78	<i>Pseudocanthon sp 1</i>	1	3	5.05	D	na
79	<i>Scybalocanthon sp1</i>	39	0	42.17	D	na
80	<i>Scybalocanthon sp2</i>	64	6	25.98	D	na
81	<i>Scybalocanthon sp3</i>	9	86	26.65	D	R
82	<i>Scybalocanthon sp4</i>	13	697	25.44	D	R
83	<i>Scybalocanthon sp5</i>	2	0	5.10	D	R
84	<i>Sylvicanthon aff bridarollii</i>	7	146	44.83	D	R
85	<i>Sylvicanthon sp2</i>	6	1	22.45	D	R
86	<i>Uroxys sp1</i>	9	6	7.18	D	T
87	<i>Uroxys sp2</i>	2	23	0.10	D	T
88	<i>Uroxys sp3</i>	14	140	2.62	D	T
89	<i>Uroxys sp4</i>	1	2	0.10	D	T
90	<i>Uroxys sp5</i>	21	102	2.75	D	T

Supplementary table S3.3. Results of generalized linear regressions relating detritivorous dung beetle communities and community subsets as a function of human hunting pressure, game mammal abundance and sampling season. Forest type abbreviations are TF (*terra firme*) and VZ (*várzea*). All data collected between January 2008 and December 2010 in the Medio Jurua Extractive Reserve and the Uacari Sustainable Development Reserve, Amazonas State, Brazil.

Forest type	Detritivore community	Coefficient	Est.	SE	<i>t</i>	<i>p-value</i>	Lower 95% CI	Upper 95% CI
TF	Diurnal species biomass	(Intercept)	-1.11	0.76	-1.46	0.143	-2.605	0.377
		Wet season	-0.21	0.13	-1.65	0.099	-0.463	0.040
		Primate abundance	2.03	1.12	1.81	0.071	-0.173	4.234
		Rodent abundance	-8.48	3.84	-2.21	0.027	-15.994	-0.956
		Ungulate abundance	0.29	1.32	0.22	0.826	-2.302	2.883
		Hunting pressure	-0.49	0.20	-2.40	0.016	-0.883	-0.090
	Nocturnal species biomass	(Intercept)	0.32	0.60	0.54	0.591	-0.846	1.487
		Wet season	-1.36	0.22	-6.28	<0.0001	-1.783	-0.936
		Primate abundance	2.75	0.96	2.86	0.004	0.866	4.644
		Rodent abundance	-2.63	3.23	-0.82	0.415	-8.954	3.691
		Ungulate abundance	0.39	1.05	0.38	0.707	-1.661	2.450
		Hunting pressure	0.27	0.17	1.58	0.114	-0.065	0.614
	Dweller species biomass	(Intercept)	-1.36	1.07	-1.27	0.203	-3.451	0.732
		Wet season	-0.71	0.24	-3.02	0.003	-1.172	-0.250
		Primate abundance	4.56	1.61	2.83	0.005	1.402	7.709
		Rodent abundance	-10.20	5.48	-1.86	0.063	-20.949	0.543
		Ungulate abundance	-0.15	1.98	-0.08	0.940	-4.023	3.724
		Hunting pressure	-0.53	0.32	-1.66	0.097	-1.155	0.097
	Roller species biomass	(Intercept)	-2.67	0.96	-2.78	0.005	-4.550	-0.786
		Wet season	0.04	0.18	0.23	0.818	-0.312	0.395
		Primate abundance	1.91	1.39	1.38	0.167	-0.800	4.630
		Rodent abundance	-10.95	4.93	-2.22	0.026	-20.602	-1.289
		Ungulate abundance	0.43	1.56	0.27	0.784	-2.627	3.481
		Hunting pressure	-0.31	0.24	-1.29	0.198	-0.794	0.164
	Tunneler species biomass	(Intercept)	0.10	0.63	0.16	0.872	-1.137	1.341
		Wet season	-0.95	0.16	-5.77	<0.0001	-1.271	-0.627
		Primate abundance	1.28	0.97	1.32	0.187	-0.622	3.185
		Rodent abundance	-1.90	3.27	-0.58	0.561	-8.314	4.510
		Ungulate abundance	0.55	1.08	0.51	0.613	-1.569	2.660
		Hunting pressure	0.02	0.17	0.12	0.904	-0.310	0.351
	Small species biomass	(Intercept)	-2.18	0.71	-3.07	0.002	-3.566	-0.787
		Wet season	-0.09	0.19	-0.46	0.645	-0.456	0.283
		Primate abundance	0.76	1.03	0.74	0.458	-1.254	2.781
		Rodent abundance	-5.81	3.55	-1.64	0.102	-12.777	1.154
		Ungulate abundance	-0.52	1.32	-0.39	0.694	-3.112	2.071
		Hunting pressure	-0.71	0.20	-3.56	<0.0001	-1.098	-0.318

Forest type	Detritivore community	Coefficient	Est.	SE	<i>t</i>	<i>p</i> -value	Lower 95% CI	Upper 95% CI
TF	Large species biomass	(Intercept)	0.12	0.66	0.18	0.859	-1.171	1.405
		Wet season	-0.79	0.13	-6.22	<0.0001	-1.037	-0.540
		Primate abundance	3.10	0.99	3.14	0.002	1.164	5.028
		Rodent abundance	-7.04	3.38	-2.09	0.037	-13.657	-0.422
		Ungulate abundance	0.51	1.13	0.46	0.648	-1.696	2.725
		Hunting pressure	0.01	0.17	0.05	0.959	-0.334	0.352
	Community-level biomass	(Intercept)	0.09	0.55	0.17	0.865	-0.978	1.164
		Wet season	-6.53	2.80	-2.34	0.019	-12.011	-1.052
		Primate abundance	2.35	0.82	2.88	0.004	0.752	3.948
		Rodent abundance	0.24	0.95	0.25	0.804	-1.627	2.100
		Ungulate abundance	-0.59	0.11	-5.53	<0.0001	-0.793	-0.378
		Hunting pressure	-0.19	0.15	-1.31	0.190	-0.475	0.094
	Community-level species richness	(Intercept)	1.85	0.53	3.50	<0.0001	0.814	2.894
		Wet season	-2.84	2.69	-1.06	0.291	-8.107	2.431
		Primate abundance	1.11	0.78	1.41	0.158	-0.430	2.645
		Rodent abundance	0.03	0.93	0.04	0.970	-1.792	1.861
		Ungulate abundance	-0.55	0.05	-10.86	<0.0001	-0.652	-0.453
		Hunting pressure	-0.15	0.13	-1.15	0.252	-0.412	0.108
	Diurnal species richness	(Intercept)	1.55	0.52	2.99	0.003	0.535	2.567
		Wet season	-0.44	0.06	-7.61	<0.0001	-0.552	-0.326
		Primate abundance	0.89	0.77	1.16	0.246	-0.616	2.403
		Rodent abundance	-2.07	2.63	-0.79	0.431	-7.220	3.081
		Ungulate abundance	-0.38	0.92	-0.41	0.681	-2.177	1.423
		Hunting pressure	-0.21	0.13	-1.59	0.111	-0.463	0.048
	Nocturnal species richness	(Intercept)	-0.09	0.61	-0.15	0.881	-1.277	1.095
		Wet season	-1.14	0.13	-8.47	<0.0001	-1.399	-0.873
		Primate abundance	1.77	0.90	1.98	0.048	0.014	3.523
		Rodent abundance	-6.74	3.11	-2.16	0.031	-12.841	-0.635
		Ungulate abundance	1.63	0.98	1.66	0.097	-0.293	3.560
		Hunting pressure	0.04	0.15	0.27	0.785	-0.258	0.342
	Dweller species richness	(Intercept)	0.72	0.75	0.95	0.341	-0.760	2.194
		Wet season	-0.41	0.10	-4.15	<0.0001	-0.597	-0.214
		Primate abundance	1.99	1.13	1.75	0.079	-0.233	4.212
		Rodent abundance	-3.33	3.85	-0.87	0.387	-10.869	4.215
		Ungulate abundance	0.01	1.33	0.01	0.992	-2.593	2.620
		Hunting pressure	-0.17	0.19	-0.87	0.386	-0.547	0.211
	Roller species richness	(Intercept)	-0.77	0.52	-1.49	0.136	-1.779	0.242
		Wet season	0.01	0.10	0.07	0.942	-0.181	0.195
		Primate abundance	1.23	0.77	1.60	0.109	-0.275	2.729
		Rodent abundance	-6.72	2.64	-2.55	0.011	-11.887	-1.545
		Ungulate abundance	-0.30	0.90	-0.33	0.739	-2.070	1.468
		Hunting pressure	-0.18	0.13	-1.37	0.172	-0.433	0.077



Forest type	Detritivore community	Coefficient	Est.	SE	<i>t</i>	<i>p</i> -value	Lower 95% CI	Upper 95% CI
	Tunneler species richness	(Intercept)	1.28	0.56	2.28	0.023	0.179	2.374
		Wet season	-0.90	0.08	-11.35	<0.0001	-1.059	-0.747
		Primate abundance	0.91	0.83	1.10	0.271	-0.714	2.541
		Rodent abundance	-2.46	2.83	-0.87	0.386	-8.015	3.095
		Ungulate abundance	0.51	0.98	0.52	0.604	-1.408	2.423
		Hunting pressure	-0.08	0.14	-0.60	0.551	-0.360	0.192
	Small species richness	(Intercept)	1.46	0.55	2.64	0.008	0.376	2.551
		Wet season	-0.51	0.06	-7.95	<0.0001	-0.635	-0.384
		Primate abundance	0.50	0.83	0.61	0.544	-1.116	2.118
		Rodent abundance	-0.61	2.81	-0.22	0.827	-6.130	4.900
		Ungulate abundance	-0.79	1.00	-0.79	0.429	-2.740	1.164
		Hunting pressure	-0.29	0.14	-2.08	0.038	-0.565	-0.017
	Large species richness	(Intercept)	0.71	0.68	1.05	0.292	-0.613	2.035
		Wet season	-0.63	0.08	-7.63	<0.0001	-0.795	-0.470
		Primate abundance	2.34	1.00	2.33	0.020	0.373	4.310
		Rodent abundance	-6.74	3.43	-1.96	0.050	-13.476	-0.012
		Ungulate abundance	1.14	1.16	0.98	0.326	-1.130	3.403
		Hunting pressure	0.10	0.17	0.59	0.558	-0.234	0.434
VZ	Diurnal species biomass	(Intercept)	0.06	1.36	0.05	0.964	-2.614	2.736
		Wet season	-0.93	0.12	-7.70	<0.0001	-1.168	-0.694
		Primate abundance	-1.05	2.60	-0.41	0.685	-6.141	4.032
		Hunting pressure	-0.63	0.34	-1.85	0.065	-1.292	0.038
	Nocturnal species biomass	(Intercept)	-3.22	2.98	-1.08	0.279	-9.061	2.617
		Wet season	-1.22	0.64	-1.90	0.058	-2.474	0.041
		Primate abundance	-1.27	5.64	-0.23	0.822	-12.328	9.785
		Hunting pressure	-0.13	0.79	-0.16	0.871	-1.671	1.415
	Dweller species biomass	(Intercept)	-0.02	2.23	-0.01	0.992	-4.401	4.356
		Wet season	0.55	0.43	1.27	0.204	-0.300	1.403
		Primate abundance	5.55	4.33	1.28	0.200	-2.945	14.043
		Hunting pressure	-0.31	0.76	-0.40	0.688	-1.801	1.188
	Roller species biomass	(Intercept)	-0.68	1.56	-0.44	0.664	-3.729	2.375
		Wet season	-0.90	0.16	-5.53	<0.0001	-1.218	-0.580
		Primate abundance	-1.09	2.96	-0.37	0.712	-6.894	4.711
		Hunting pressure	-0.53	0.41	-1.31	0.189	-1.328	0.262
	Tunneler species biomass	(Intercept)	-1.14	2.17	-0.52	0.601	-5.398	3.122
		Wet season	-1.26	0.19	-6.75	<0.0001	-1.632	-0.897
		Primate abundance	-2.08	4.13	-0.50	0.614	-10.174	6.014
		Hunting pressure	-0.70	0.52	-1.35	0.178	-1.723	0.319
	Small species biomass	(Intercept)	-0.10	1.44	-0.07	0.943	-2.935	2.727
		Wet season	-0.93	0.16	-5.76	<0.0001	-1.244	-0.612
		Primate abundance	-0.04	2.75	-0.01	0.989	-5.429	5.353
		Hunting pressure	-0.63	0.39	-1.63	0.104	-1.393	0.129

Forest type	Detritivore community	Coefficient	Est.	SE	<i>t</i>	<i>p</i> -value	Lower 95% CI	Upper 95% CI
VZ	Large species biomass	(Intercept)	-0.99	1.79	-0.56	0.579	-4.506	2.517
		Wet season	-0.99	0.17	-5.96	<0.0001	-1.314	-0.664
		Primate abundance	-2.01	3.40	-0.59	0.555	-8.679	4.662
		Hunting pressure	-0.66	0.44	-1.51	0.132	-1.512	0.198
	Community-level biomass	(Intercept)	0.32	1.24	0.25	0.799	-2.119	2.750
		Wet season	-0.96	0.12	-8.34	<0.0001	-1.190	-0.737
		Primate abundance	-0.79	2.36	-0.34	0.737	-5.424	3.835
		Hunting pressure	-0.64	0.31	-2.05	0.040	-1.250	-0.029
	Community-level species richness	(Intercept)	2.31	0.78	2.98	0.003	0.791	3.831
		Wet season	-0.59	0.06	-9.76	<0.001	-0.705	-0.469
		Primate abundance	0.95	1.48	0.64	0.520	-1.944	3.841
		Hunting pressure	-0.28	0.19	-1.48	0.138	-0.649	0.090
	Diurnal species richness	(Intercept)	1.89	0.84	2.26	0.024	0.253	3.533
		Wet season	-0.50	0.07	-7.68	<0.0001	-0.632	-0.375
		Primate abundance	0.60	1.59	0.38	0.705	-2.517	3.723
		Hunting pressure	-0.26	0.20	-1.30	0.194	-0.663	0.135
	Nocturnal species richness	(Intercept)	-1.06	2.87	-0.37	0.711	-6.687	4.561
		Wet season	-0.75	0.33	-2.30	0.022	-1.385	-0.111
		Primate abundance	1.23	5.46	0.23	0.821	-9.467	11.936
		Hunting pressure	-0.53	0.78	-0.68	0.495	-2.049	0.991
	Dweller species richness	(Intercept)	1.45	2.14	0.68	0.499	-2.750	5.649
		Wet season	0.60	0.20	2.97	0.003	0.203	0.992
		Primate abundance	5.89	4.10	1.44	0.151	-2.155	13.931
		Hunting pressure	-0.67	0.69	-0.97	0.330	-2.016	0.677
	Roller species richness	(Intercept)	0.62	0.91	0.68	0.494	-1.167	2.417
		Wet season	-0.50	0.08	-6.05	<0.0001	-0.666	-0.340
		Primate abundance	-0.97	1.74	-0.56	0.578	-4.370	2.439
		Hunting pressure	0.00	0.22	-0.01	0.989	-0.431	0.426
	Tunneler species richness	(Intercept)	1.67	1.25	1.34	0.181	-0.774	4.116
		Wet season	-1.03	0.11	-9.56	<0.0001	-1.239	-0.817
		Primate abundance	1.51	2.37	0.64	0.525	-3.146	6.163
		Hunting pressure	-0.65	0.32	-2.06	0.040	-1.272	-0.030
	Small species richness	(Intercept)	1.99	0.84	2.35	0.019	0.333	3.643
		Wet season	-0.67	0.07	-9.91	<0.0001	-0.805	-0.539
		Primate abundance	0.70	1.61	0.43	0.665	-2.453	3.846
		Hunting pressure	-0.23	0.20	-1.14	0.256	-0.633	0.168
	Large species richness	(Intercept)	1.22	0.86	1.43	0.154	-0.458	2.894
		Wet season	-0.27	0.13	-2.13	0.033	-0.527	-0.022
		Primate abundance	2.26	1.63	1.39	0.166	-0.939	5.468
		Hunting pressure	-0.42	0.25	-1.69	0.092	-0.910	0.069

SUPPLEMENTARY TABLE 4.1. Results of previous investigations of dung beetle species' trait correlates of response to the fragmentation (F) or modification (M) of moist tropical forests, using non-phylogenetically corrected analyses. Species traits significantly associated with species response are in bold. Traits marked with an asterisk are considered extrinsic *sensu* Violle et al. (2007). Study abbreviations are as follows: Chapman et al. 2003 (1), Klein 1989 (2), Larsen et al 2008 (3), Larsen et al. 2005 (4), Estrada & Coates Estrada 2002 (5), Andresen 2003 (6), Escobar & Chacon de Ulloa 2000 (7), Escobar 2004 (8), Pineda et al. 2005 (9), Shahabuddin et al. 2005 (10), Slade et al. 2011 (11). \*\* Estrada & Coates Estrada 2002 reported that food relocation strategy and diel activity were non-significant predictors of species occupancy in forest fragments, yet were significantly associated with species abundance.

Reference	Country	Study	Species' traits tested	Species response
1	Uganda	F	Functional group	Abundance
			(Body mass/ Food relocation)	
2	Brazil	F	Weighted mean length	Abundance
3	Venezuela	F	Food relocation strategy	Occupancy
			Activity period	
			Diet breadth	
			Body size	
			Population density*	
			Forest specificity*	
4	Venezuela	F	Body mass	Occupancy
			Population density*	
5	Mexico	M, F	Food relocation strategy	Occupancy, abundance**
			Diel activity	
6	Brazil	M	Body size	Abundance
7	Colombia	M	Food relocation	Abundance
			Diel activity	
8	Colombia	M	Functional group (Body mass/ Food relocation, Activity period)	Abundance
9	Mexico	M	Body size	Abundance
			Diet breadth	
10	Indonesia	M	Body size	Occupancy,
11	Borneo	M	Functional group (Body mass/ Food relocation, Activity period)	Abundance

SUPPLEMENTARY TABLE 4.2. Providence of original data, final number of species (S) and individual observations N) from each dataset that entered into the analysis, land-use types represented by each dataset (MF: modified forest, FA: forested agriculture, NFA: non-forested agriculture) and description of those land-uses as provided by the original reference.

Land-use								
	Dataset	S	N	Country	MF	FA	NFA	Land-use description
Avendano-Mendoza et al. 1996	1	18	54	Guatemala	x		x	MF: Early secondary forest; NFA: Average of two <i>Zea mays</i> fields
Boonrotpong et al. 2004	2	7	14	Thailand	x			MF: 10 yr. secondary forest
Davis et al. 2001	3	25	75	Borneo	x	x		MF: Selectively logged forest; FA: Shade <i>Theobroma cacao</i> plantation
Davis et al. 2001	4	26	78	Borneo		x	x	MF: Selectively logged forest; FA: <i>Acacia mangium</i> and <i>Swietenia macrophylla</i> plantations
Davis & Philips 2005	5	6	18	Ghana	x	x		MF: Average of 4 selectively logged forest sites; FA: Average of 3 oil palm plantation and 1 cacao plantation sites
Escobar 2004	6	1	3	Colombia	x		x	MF: Secondary forest; NFA: cattle pasture
Estrada & Coates-Estrada 2002	10	20	40	Mexico		x		FA: Mosaic of shaded coffee & cocoa, citrus and banana groves
Gardner et al. 2008	11	28	84	Brazil	x	x		MF: 14-19 yr. secondary forest; FA: mature Eucalyptus
Gardner et al. 2008	12	31	96	Brazil	x	x		MF: 14-19 yr. secondary forest; FA: mature Eucalyptus
Gardner et al. 2008	13	37	111	Brazil	x	x		MF: 14-19 yr. secondary forest; FA: mature Eucalyptus
Gardner et al. 2008	14	35	105	Brazil	x	x		MF: 14-19 yr. secondary forest; FA: mature Eucalyptus
Gardner et al. 2008	15	31	93	Brazil	x	x		MF: 14-19 yr. secondary forest; FA: mature Eucalyptus
Harvey et al. 2006	16	30	60	Costa Rica		x		FA: Cocoa agroforestry
Harvey et al. 2006	17	30	60	Costa Rica		x		FA: Banana agroforestry
Harvey et al. 2006	18	30	55	Costa Rica		x		FA: Plantain monocultures

Harvey et al. 2006	19	1938	El Salvador		x	NFA: Average of 7 recently cleared agriculture fields.
Klein 1989	20	2244	Brazil		x	NFA: Average of 3 clear-cut sites
Lopera & Larsen unpub	21	9 35	Costa Rica	x	x	MF: Average of 2 secondary forest sites; FA: <i>Gmelina</i> tree
Larsen unpub	22	36 108	Peru	x	x	NFA: Cattle pasture
Larsen & Lopera unpub	23	2346	Peru		x	MF: Young secondary forest; NFA: Clear-cut site
Nummelin & Hanski 1989	24	4 12	Uganda	x	x	MF: Selective logging; FA: <i>Pinus spp.</i> timber plantation
Nummelin & Hanski 1989	25	5 15	Uganda	x	x	MF: Selective logging; FA: <i>Cupressus sp.</i> plantation
Quintero & Roslin 2005	26	1938	Brazil	x		MF: 5 yr. secondary forest
Quintero & Roslin 2005	27	1428	Brazil	x		MF: 10 yr. secondary forest
Quintero & Roslin 2005	28	1937	Brazil	x		MF: 14 yr. secondary forest
Scheffler 2005	29	34 102	Brazil	x	x	MF: Average of 2 selectively logged sites; NFA: Average across 4 clear-cut sites
Shahabuddin et al. 2005	30	1352	Indonesia	x	x	MF: Average of 4 secondary forest sites; FA: Average of 4 shaded cacao forest; NFA: average of 4 <i>Zea mays</i> fields
Slade et al. 2011	31	2754	Borneo	x		MF: Selective logging
Slade et al. 2011	32	2142	Borneo	x		MF: Selective logging
Vaz de Mello unpublished	33	1938	Brazil	x		MF: Secondary forest
Vulinec unpublished.a	34	48 144	Brazil	X	X	MF: 10-15 yr. secondary forest; NFA: Cattle pasture
Vulinec unpublished.b	35	2781	Brazil	x	x	MF: Late secondary forest; NFA: Average of 2 clear-cut sites
Vulinec unpublished.c	36	1836	Brazil	x		MF: Average of 3 sites of late secondary growth

SUPPLEMENTARY TABLE 4.3. Identity and trait values for 265 species of Scarabaeine dung beetles incorporated into phylogenetically corrected comparative analyses to understand the trait-correlates of population response to tropical forest degradation (see Methods). Trait values were taken from both published sources (Halffter and Edmonds 1982b, Hanski and Cambefort 1991b, Halffter et al. 1992, Kirk 1992, Halffter et al. 1995, Montes de Oca and Halffter 1995, Favila and Diaz 1996, Favila 1997, Villalobos et al. 1998, Escobar and Chacón de Ulloa 2000, Andresen 2002a, Vulinec 2002, Kohlmann et al. 2003, Kohlmann and Moron 2003, Feer and Pincebourde 2005, Scheffler 2005), as well as unpublished contributions from the authors (M.E Favila, S. H. Spector, K. Vulinec, and F. Vaz de Mello). Biogeographic region abbreviations are as follows: NT (Neotropical), AET (Afro-Eurasian tropical).

	Species	Activity period	Food relocation strategy	Region	Mean body mass (mg)
1	<i>Anachalcos cupreus</i>	N	R	AET	253.02
2	<i>Ateuchus sp1</i>	N	B	NT	1.10
3	<i>Ateuchus aff. irinus</i>	N	B	NT	14.77
4	<i>Ateuchus aff. murrayi</i>	N	B	NT	6.52
5	<i>Ateuchus candezei</i>	N	B	NT	24.48
6	<i>Ateuchus cereus</i>	N	B	NT	25.65
7	<i>Ateuchus connexus</i>	N	B	NT	25.65
8	<i>Ateuchus frontalis</i>	N	B	NT	24.60
9	<i>Ateuchus illaesum</i>	N	B	NT	9.94
10	<i>Ateuchus laevicollis</i>	N	B	NT	11.18
11	<i>Ateuchus murrayi</i>	N	B	NT	8.66
12	<i>Ateuchus pauki</i>	N	B	NT	24.60
13	<i>Ateuchus sp2 prox. connexus</i>	N	B	NT	19.81
14	<i>Ateuchus setulosus</i>	N	B	NT	28.79
15	<i>Ateuchus solisi</i>	N	B	NT	13.49
16	<i>Ateuchus sp nr pygidialis</i>	N	B	NT	7.80
17	<i>Ateuchus sp1</i>	N	B	NT	8.48
18	<i>Ateuchus sp2</i>	N	B	NT	10.00
19	<i>Ateuchus sp3</i>	N	B	NT	24.75

20	<i>Ateuchus sp4</i>	N	B	NT	36.00
21	<i>Ateuchus sp5</i>	N	B	NT	2.36
22	<i>Ateuchus sp6</i>	N	B	NT	28.00
23	<i>Ateuchus sp7</i>	N	B	NT	16.00
24	<i>Ateuchus sp8</i>	N	B	NT	3.00
25	<i>Bdelyropsis newtoni</i>	N	B	NT	8.75
26	<i>Caccobius binodulus</i>	D	B	AET	20.00
27	<i>Caccobius unicornis</i>	D	B	AET	20.00
28	<i>Canthidium sp1</i>	D	B	NT	1.10
29	<i>Canthidium sp2</i>	D	B	NT	1.10
30	<i>Canthidium sp3</i>	D	B	NT	10.05
31	<i>Canthidium sp4 aff. deyrollei</i>	D	B	NT	6.10
32	<i>Canthidium sp5 aff. gerstaeckeri</i>	D	B	NT	16.40
33	<i>Canthidium annagabrielae</i>	D	B	NT	1.10
34	<i>Canthidium ardens</i>	D	B	NT	3.04
35	<i>Canthidium atricolle</i>	D	B	NT	16.23
36	<i>Canthidium aurifex</i>	D	B	NT	2.19
37	<i>Canthidium bicolor</i>	D	B	NT	3.20
38	<i>Canthidium centrale</i>	D	B	NT	17.86
39	<i>Canthidium cupreum</i>	D	B	NT	13.20
40	<i>Canthidium deyrollei</i>	D	B	NT	6.10
41	<i>Canthidium dorhrini</i>	D	B	NT	43.62
42	<i>Canthidium gerstaeckeri</i>	D	B	NT	33.10
43	<i>Canthidium haroldi</i>	D	B	NT	15.90
44	<i>Canthidium lentum</i>	D	B	NT	27.65
45	<i>Canthidium pinotoides</i>	D	B	NT	3.19
46	<i>Canthidium sp6 nr bicolor</i>	D	B	NT	3.20
47	<i>Canthidium sp7 nr deyrollei</i>	D	B	NT	11.40
48	<i>Canthidium sp7</i>	D	B	NT	25.71
49	<i>Canthidium sp8</i>	D	B	NT	5.20
50	<i>Canthidium sp9</i>	D	B	NT	2.06
51	<i>Canthidium sp10</i>	D	B	NT	18.60
52	<i>Canthidium sp11</i>	D	B	NT	27.79
53	<i>Canthidium sp12</i>	D	B	NT	30.00
54	<i>Canthidium sp13</i>	D	B	NT	25.00
55	<i>Canthidium sp14</i>	D	B	NT	25.00
56	<i>Canthidium sp15</i>	D	B	NT	7.90
57	<i>Canthidium sp16</i>	D	B	NT	6.00

58	<i>Canthidium sp17</i>	D	B	NT	4.65
59	<i>Canthidium sp18</i>	D	B	NT	2.30
60	<i>Canthidium sp19</i>	D	B	NT	5.00
61	<i>Canthidium sp20</i>	D	B	NT	3.00
62	<i>Canthidium splendidum</i>	D	B	NT	12.80
63	<i>Canthidium vespertinum</i>	D	B	NT	1.39
64	<i>Canthon sp1</i>	D	R	NT	1.10
65	<i>Canthon sp2</i>	D	R	NT	3.33
66	<i>Canthon sp3</i>	D	R	NT	10.05
67	<i>Canthon sp4</i>	D	R	NT	10.05
68	<i>Canthon aequinoctialis</i>	D	R	NT	50.00
69	<i>Canthon angustatus</i>	D	R	NT	8.73
70	<i>Canthon bicolor</i>	D	R	NT	4.11
71	<i>Canthon cyanellus</i>	D	R	NT	26.77
72	<i>Canthon cyanellus cyanellus</i>	D	R	NT	25.00
73	<i>Canthon euryscelis</i>	D	R	NT	8.67
74	<i>Canthon femoralis</i>	D	R	NT	15.68
75	<i>Canthon femoralis bimaculatus</i>	D	R	NT	15.68
76	<i>Canthon fulgidus</i>	D	R	NT	103.34
77	<i>Canthon laesum</i>	D	R	NT	27.00
78	<i>Canthon leechi</i>	D	R	NT	5.03
79	<i>Canthon lituratus</i>	D	R	NT	9.00
80	<i>Canthon luteicollis</i>	D	R	NT	57.64
81	<i>Canthon moniliatus</i>	D	R	NT	12.00
82	<i>Canthon morsei</i>	D	R	NT	8.40
83	<i>Canthon sp5 prox. femoralis</i>	D	R	NT	17.30
84	<i>Canthon sp6 prox. sericatus</i>	D	R	NT	9.20
85	<i>Canthon quadrigattatus</i>	D	R	NT	9.35
86	<i>Canthon semiopacus</i>	D	R	NT	43.52
87	<i>Canthon septemmaculatus histrion</i>	D	R	NT	42.00
88	<i>Canthon shiny black tibia</i>	D	R	NT	8.60
89	<i>Canthon shiny brown</i>	D	R	NT	8.60
90	<i>Canthon silvaticus</i>	D	R	NT	1.96
91	<i>Canthon smaragdulus</i>	D	R	NT	280.00
92	<i>Canthon sp1 nr angustatus</i>	D	R	NT	8.73
93	<i>Canthon sp7</i>	D	R	NT	4.00
94	<i>Canthon sp8</i>	D	R	NT	12.00



95	<i>Canthon sp9</i>	D	R	NT	14.00
96	<i>Canthon sp10 grp sericatus</i>	D	R	NT	4.20
97	<i>Canthon sp11</i>	D	R	NT	15.00
98	<i>Canthon subhyalinus</i>	D	R	NT	8.40
99	<i>Canthon triangularis</i>	D	R	NT	25.51
100	<i>Canthon sp12</i>	D	R	NT	12.85
101	<i>Canthon sp13</i>	D	R	NT	12.85
102	<i>Canthon virens chalybaeus</i>	D	R	NT	19.00
103	<i>Canthon viridis vazquezae</i>	D	R	NT	12.85
104	<i>Catharsius dayacus</i>	N	B	AET	725.00
105	<i>Catharsius molossus</i>	N	B	AET	1881.46
106	<i>Catharsius ninus</i>	N	B	AET	250.00
107	<i>Catharsius renaud pauliani</i>	N	B	AET	735.00
108	<i>Copris agnus</i>	N	B	AET	297.69
109	<i>Copris incertus</i>	N	B	NT	9.17
110	<i>Copris laeviceps</i>	N	B	NT	24.72
111	<i>Copris lugubris</i>	N	B	NT	112.24
112	<i>Copris ramosiceps</i>	N	B	AET	67.42
113	<i>Copris sinicus</i>	N	B	AET	322.14
114	<i>Coprophanaeus callegarii</i>	D	B	NT	153.52
115	<i>Coprophanaeus dardanus</i>	D	B	NT	346.61
116	<i>Coprophanaeus jasius</i>	D	B	NT	405.36
117	<i>Coprophanaeus lancifer</i>	D	B	NT	1920.75
118	<i>Coprophanaeus parvulus</i>	D	B	NT	618.00
119	<i>Coprophanaeus telamon</i>	D	B	NT	453.84
120	<i>Coprophanaeus telamon corythus</i>	D	B	NT	453.84
121	<i>Deltochilum amazonicum</i>	N	R	NT	496.39
122	<i>Deltochilum burmeisteri</i>	N	R	NT	298.00
123	<i>Deltochilum carinatum</i>	N	R	NT	189.47
124	<i>Deltochilum enceladum</i>	N	R	NT	313.00
125	<i>Deltochilum gibbosum</i>	N	R	NT	180.00
126	<i>Deltochilum gibbosum sublaeve</i>	N	R	NT	405.88
127	<i>Deltochilum granulatum</i>	N	R	NT	46.40
128	<i>Deltochilum sp1 nr granulatum</i>	N	R	NT	46.40
129	<i>Deltochilum guyanensis</i>	N	R	NT	65.60
130	<i>Deltochilum icarus</i>	N	R	NT	476.98

131	<i>Deltochilum laevigatum</i>	N	R	NT	65.40
132	<i>Deltochilum lobipes</i>	N	R	NT	426.00
133	<i>Deltochilum orbiculare</i>	N	R	NT	358.41
134	<i>Deltochilum pseudoicarus</i>	N	R	NT	617.27
135	<i>Deltochilum pseudoparile</i>	N	R	NT	67.35
136	<i>Deltochilum scabriusculum</i>	N	R	NT	332.25
137	<i>Deltochilum septemstriatum</i>	N	R	NT	44.27
138	<i>Deltochilum sp1</i>	N	R	NT	68.33
139	<i>Deltochilum sp2</i>	N	R	NT	52.28
140	<i>Deltochilum sp3</i>	N	R	NT	28.49
141	<i>Dichotomius sp4 grp lucasi</i>	N	B	NT	132.40
142	<i>Dichotomius sp5</i>	N	B	NT	76.59
143	<i>Dichotomius annae</i>	N	B	NT	526.03
144	<i>Dichotomius apicalis</i>	N	B	NT	136.42
145	<i>Dichotomius batesi</i>	N	B	NT	73.00
146	<i>Dichotomius boreus</i>	N	B	NT	564.40
147	<i>Dichotomius carbonarius</i>	N	B	NT	99.60
148	<i>Dichotomius carinatus</i>	N	B	NT	508.00
149	<i>Dichotomius carolinus colonicus</i>	N	B	NT	791.95
150	<i>Dichotomius favi</i>	N	B	NT	30.14
151	<i>Dichotomius globulus</i>	N	B	NT	56.00
152	<i>Dichotomius imitator</i>	N	B	NT	364.00
153	<i>Dichotomius inachus</i>	N	B	NT	58.91
154	<i>Dichotomius latilobatus</i>	N	B	NT	256.78
155	<i>Dichotomius lucasi</i>	N	B	NT	105.11
156	<i>Dichotomius mamillatus</i>	N	B	NT	434.14
157	<i>Dichotomius melzeri</i>	N	B	NT	513.00
158	<i>Dichotomius sp6 nr cuprinus</i>	N	B	NT	277.00
159	<i>Dichotomius ohausi</i>	N	B	NT	162.90
160	<i>Dichotomius podalirius</i>	N	B	NT	656.00
161	<i>Dichotomius prietoi</i>	N	B	NT	531.36
162	<i>Dichotomius sp7 prox. lucasi</i>	N	B	NT	50.74
163	<i>Dichotomius robustus</i>	N	B	NT	114.01
164	<i>Dichotomius satanas</i>	N	B	NT	190.70
165	<i>Dichotomius subaeneus</i>	N	B	NT	121.51
166	<i>Dichotomius worontzowi</i>	N	B	NT	147.08
167	<i>Hansreia affinis</i>	D	R	NT	43.62
168	<i>Megathoposoma candezei</i>	D	B	NT	369.26

169	<i>Neosisyphus angulicolis</i>	D	R	AET	6.06
170	<i>Oniticellus tessellatus</i>	D	B	AET	8.92
171	<i>Ontherus sp1</i>	N	B	NT	32.39
172	<i>Ontherus alexis</i>	N	B	NT	64.00
173	<i>Ontherus appendiculatus</i>	N	B	NT	65.00
174	<i>Ontherus azteca</i>	N	B	NT	89.50
175	<i>Ontherus carinifrons</i>	N	B	NT	49.06
176	<i>Ontherus laminifer</i>	N	B	NT	57.99
177	<i>Ontherus mexicanus</i>	N	B	NT	76.59
178	<i>Ontherus pubens</i>	N	B	NT	76.97
179	<i>Ontherus sulcator</i>	N	B	NT	112.23
180	<i>Onthophagus sp1</i>	D	B	AET	11.03
181	<i>Onthophagus sp2</i>	D	B	AET	88.81
182	<i>Onthophagus sp3</i>	D	B	AET	7.12
183	<i>Onthophagus sp4</i>	D	B	AET	3.79
184	<i>Onthophagus sp5</i>	D	B	AET	21.30
185	<i>Onthophagus sp6</i>	D	B	AET	26.44
186	<i>Onthophagus sp7</i>	D	B	AET	6.75
187	<i>Onthophagus sp8</i>	D	B	AET	44.28
188	<i>Onthophagus sp9</i>	D	B	AET	40.00
189	<i>Onthophagus acuminatus</i>	D	B	NT	8.00
190	<i>Onthophagus angustatus</i>	D	B	AET	30.00
191	<i>Onthophagus aphodioides</i>	D	B	AET	47.14
192	<i>Onthophagus batesi</i>	N	B	NT	8.69
193	<i>Onthophagus bidentatus</i>	D	B	NT	8.85
194	<i>Onthophagus borneensis</i>	D	B	AET	8.57
195	<i>Onthophagus cervicapra</i>	D	B	AET	53.42
196	<i>Onthophagus cervicapra complex</i>	D	B	AET	53.42
197	<i>Onthophagus clypeatus</i>	D	B	NT	23.35
198	<i>Onthophagus coscineus</i>	D	B	NT	1.10
199	<i>Onthophagus crinitus</i>	D	B	NT	32.00
200	<i>Onthophagus deplanatus</i>	N	B	AET	9.14
201	<i>Onthophagus fuscidorsis</i>	D	B	AET	6.06
202	<i>Onthophagus gazella</i>	N	B	NT	21.52
203	<i>Onthophagus sp10 gr. clypeatus</i>	D	B	NT	11.07
204	<i>Onthophagus haematopus</i>	D	B	NT	11.79
205	<i>Onthophagus hanksins</i>	D	B	AET	10.05

206	<i>Onthophagus hirculus</i>	D	B	NT	21.20
207	<i>Onthophagus incisus</i>	N	B	AET	16.20
208	<i>Onthophagus laeviceps</i>	D	B	AET	2.92
209	<i>Onthophagus laevis</i>	D	B	AET	30.00
210	<i>Onthophagus marginicollis</i>	D	B	NT	6.79
211	<i>Onthophagus mulleri</i>	D	B	AET	13.33
212	<i>Onthophagus ochromerus</i>	D	B	AET	11.67
213	<i>Onthophagus onthochromus</i>	D	B	NT	21.20
214	<i>Onthophagus pacificus</i>	D	B	AET	16.00
215	<i>Onthophagus pavidus</i>	D	B	AET	10.00
216	<i>Onthophagus poenicoerus</i>	D	B	AET	97.67
217	<i>Onthophagus praecellens</i>	D	B	NT	6.40
218	<i>Onthophagus rhinolophus</i>	N	B	NT	9.08
219	<i>Onthophagus rorarius</i>	D	B	AET	10.00
220	<i>Onthophagus rubescens</i>	D	B	NT	7.18
221	<i>Onthophagus rugicollis</i>	D	B	AET	53.06
222	<i>Onthophagus sarawacus</i>	D	B	AET	17.14
223	<i>Onthophagus semiaureus</i>	D	B	AET	9.00
224	<i>Onthophagus sharpi</i>	N	B	NT	13.45
225	<i>Onthophagus sp11</i>	D	B	AET	62.00
226	<i>Onthophagus sp12 grp</i>	D	B	AET	18.00
227	<i>Onthophagus sp13 cf babirussa</i>	D	B	AET	10.65
228	<i>Onthophagus stockwelli</i>	D	B	NT	11.18
229	<i>Onthophagus sumatranus</i>	D	B	AET	32.39
230	<i>Onthophagus taeniatus</i>	D	B	AET	12.50
231	<i>Onthophagus tiniatus</i>	D	B	AET	12.50
232	<i>Onthophagus vulpes</i>	D	B	AET	15.64
233	<i>Onthophagus waterstradti</i>	D	B	AET	10.00
234	<i>Oxysternon conspicillatum</i>	D	B	NT	789.62
235	<i>Oxysternon durantoni</i>	D	B	NT	189.11
236	<i>Oxysternon festivum</i>	D	B	NT	326.58
237	<i>Oxysternon macleayi</i>	D	B	NT	222.51
238	<i>Oxysternon silenus</i>	D	B	NT	172.58
239	<i>Oxysternon smaragdinum</i>	D	B	NT	177.00
240	<i>Oxysternon spiniferum</i>	D	B	NT	48.20
241	<i>Oxysternon striatopunctatum</i>	D	B	NT	98.00
242	<i>Paragymnopleurus maurus</i>	D	R	AET	130.90
243	<i>Paragymnopleurus sparsus</i>	D	R	AET	80.00

244	<i>Paragymnopleurus striatus</i>	N	R	AET	150.57
245	<i>Phanaeus alvarengai</i>	D	B	NT	78.00
246	<i>Phanaeus bispinus</i>	D	B	NT	156.00
247	<i>Phanaeus cambeforti</i>	D	B	NT	136.00
248	<i>Phanaeus chalcomelas</i>	D	B	NT	230.81
249	<i>Phanaeus endymion</i>	D	B	NT	136.57
250	<i>Phanaeus meleagris</i>	D	B	NT	250.00
251	<i>Phanaeus pyrois</i>	D	B	NT	192.00
252	<i>Phanaeus sallei</i>	D	B	NT	163.52
253	<i>Phaneus endymion</i>	D	B	NT	136.57
254	<i>Proagoderus multicornis</i>	D	B	AET	163.52
255	<i>Proagoderus wantanabei</i>	D	B	AET	154.04
256	<i>Sisyphus eburneus</i>	D	R	AET	10.70
257	<i>Sisyphus thoracicus</i>	D	R	AET	9.04
258	<i>Tiniocellus sarawacus</i>	D	B	AET	108.33
259	<i>Uroxys boneti</i>	N	B	NT	1.30
260	<i>Uroxys sp1</i>	N	B	NT	6.10
261	<i>Uroxys sp2</i>	N	B	NT	1.27
262	<i>Uroxys sp3</i>	N	B	NT	2.45
263	<i>Uroxys sp4</i>	N	B	NT	10.00
264	<i>Uroxys sp5</i>	N	B	NT	2.45
265	<i>Uroxys sp6</i>	N	B	NT	10.00

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