Co-declining mammals and dung beetles: an impending ecological cascade

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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 beetles 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.

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. 2008). 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 (Eklof 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 et 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, Jerozolimski and Peres 2003). Massive abundance declines in large-bodied game species have been recorded in Amazonian (Peres 2000, Peres and Palacios 2007), African (Fa et 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 (Jerozolimski 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-Iturri 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 1982, Hanski and Cambefort 1991a). 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 (Nichols et al. 2008).

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 1989, Andresen 2003, Horgan 2005, Larsen et al. 2005). 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 (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, Thérond 1980). Along a gradient of historical persecution of large mammal populations in three tropical savanna sites in Africa, Cambefort (1991) 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 and Cambefort 1991a, Gardiner 1995 cited in Botes et al. 2006). The extirpation of large-bodied elephant-specialist *Heliocopris* species across parts of Côte d'Ivoire has been attributed to the national decline in elephant populations (Cambefort 1982). *Heliocopris* 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 (Doube 1991) 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).

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; 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
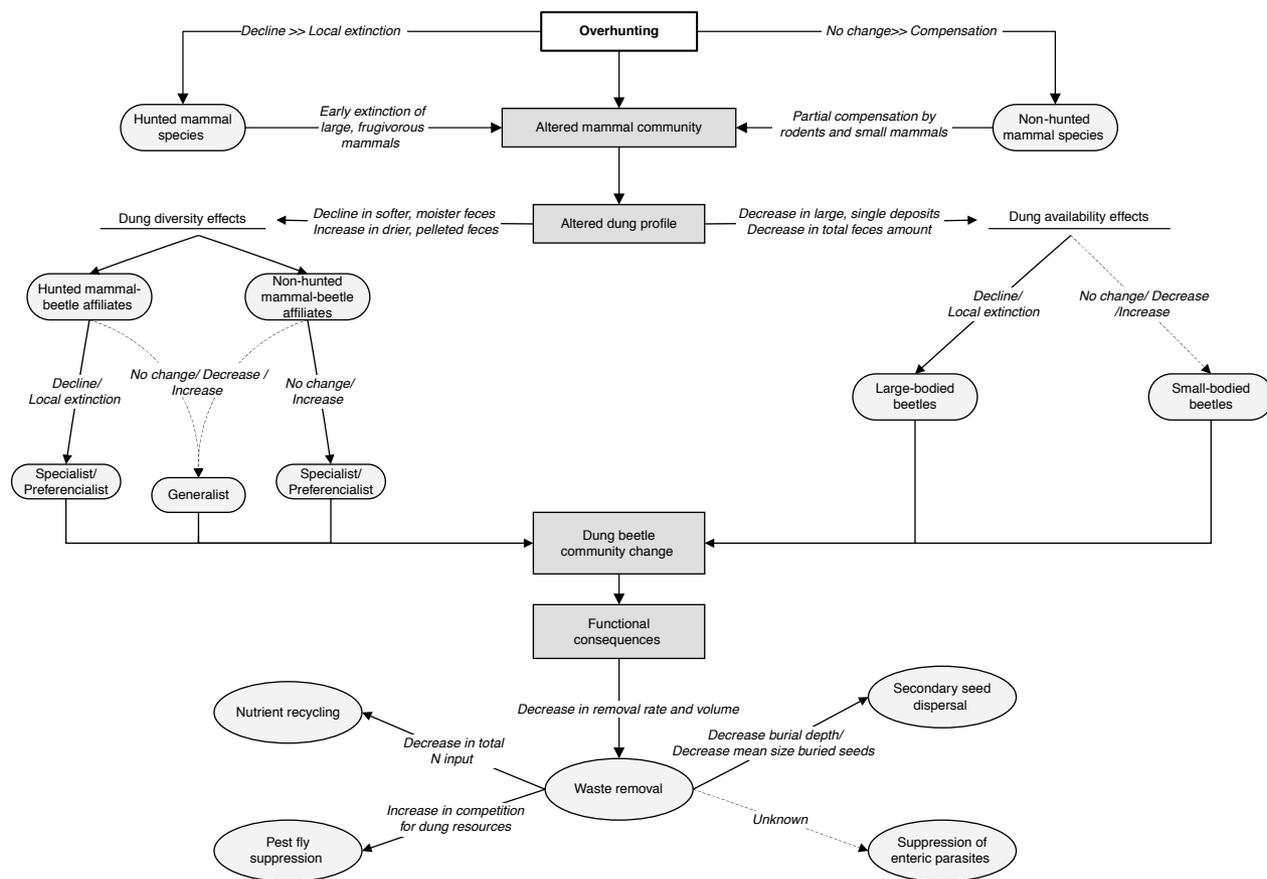

Figure 1. Conceptual model of pathways by which overhunting in tropical forests impacts coprophagous dung beetle community structure and dung beetle-ecosystem function. Text along arrows describe the potential direction or mechanism driving each effect.

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 (Cambefort 1991, 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 1984). 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, Hanski et al. 2008). 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).

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 1984, 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, Jerozolimski 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 1991a). 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 1991a).

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; 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 2005). 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. 2008a) 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 beetles' 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 1991b). 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, Gardner et al. 2008a; 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. 2007), 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 multi-scale, 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, 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 (Doube 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. 2008b) 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 2006). 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. 2008).

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