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Review

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.

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1. 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, 1991). 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 Edmonds, 1982; Halffter and Matthews, 1966).

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, 1991). 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, 1995), pair cooper-

ation (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.

2. Ecological functions
2.1. 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 NH₃ volatilization (Steinfeld et al., 2006). By burying dung under the soil surface, dung beetles prevent the loss of N through ammonia (NH₃) 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 NH₃ volatilization from

livestock excreta (ca. 80%, Gillard, 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/IFIA, 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 and Kai, 1993; Yokoyama et al., 1991a,b). In the absence of dung beetle activity, nitrogen mineralization rates in freshly deposited dung initially increase, accompanied by a release of inorganic N (Yamada et al., 2007; Yokoyama and Kai, 1993; Yokoyama et al., 1991a, 1989). This mineralization processes declines or ceases within 5–7 days, yet continues to increase in beetle-colonized dung and brood balls (Yokoyama and Kai, 1993; Yokoyama et al., 1991a, 1989). 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 NH_3 volatilization remains uncertain. Yokoyama et al. (1991a) demonstrated that dung beetles significantly inhibited the volatilization of 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. (1990) 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 affect 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 Lal, 1996). 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 feces 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 (Gittings et al., 1994; Holter, 1977, 1979).

2.2. 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 (Edwards and Aschenborn, 1987; Halffter and Edmonds, 1982; Lindquist, 1933). 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, 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, 1977, 1979), Australia and New Zealand (Baker, 1994), their dung-related contribution to bioturbation in areas with a higher diversity of Scarabaeine dung beetles is unknown.

2.3. 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 (Galbiati et al., 1995; Kabir et al., 1985), 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 corn cob diameter and below ground biomass. Borne-missza 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, 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 P₂O₅ and 100 kg/ha of K₂O. 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 bee-

gles. 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).

2.4. Secondary seed dispersal

Vertebrate seed dispersal mechanisms are extremely widespread in tropical and temperate ecosystems (Howe and Smallwood, 1982; Jordano, 1992; Willson et al., 1990). 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 (Andresen, 1999; Andresen and Levey, 2004; Chambers and MacMahon, 1994; Estrada and Coates-Estrada, 1991; Feer, 1999; Janzen, 1983a; Shepherd and Chapman, 1998); (ii) directing dispersal to favorable microclimates for germination and emergence (Andresen and Levey, 2004); and (iii) decreasing residual post-dispersal seed clumping (Andresen, 1999, 2001), with potential effects on density dependent seed mortality, seedling competition, and predation risk (Andresen and Feer, 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, 2002; Slade et al., 2007; Vulinec, 2002) and both the amount (Andresen, 2001, 2002) 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, 2002; 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 et al., 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, 2002; Ponce-Santizo et al., 2006). Overall, dung beetles communities move approximately 5–44% of available seeds horizontally (Andresen, 2001, 2002; Andresen and Levey, 2004). Maximal recorded distances of dung beetle brood balls (presumably containing seeds) up to 15 m in the Afrotropics (Heymons and von Lengerken, 1929 cited in Halffter and Matthews, 1966) and 10.6 m 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 (Andresen, 1999; Estrada and Coates-Estrada, 1991; Shepherd and Chapman, 1998). 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 (Andresen and Feer, 2005; Dalling et al., 1995). The ability of a seed to emerge from a given depth depends on seed size, cotyledon morphology and microclimate requirements (Andresen, 1999; Estrada and Coates-Estrada, 1991; Shepherd and Chapman, 1998). 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 (≤ 3 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 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 to 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 redeposited 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 et al., 2005).

2.5. Parasite suppression

Through feeding and nesting, adult and larval dung beetle activity serves to control the abundance of dung-breeding hematophagous 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 (Byford et al., 1992; Miller,

1954). Much of our understanding of these functions has arisen from the study of livestock parasites and pests.

2.6. 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 (1983) 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 Ditrich, 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 scarabeine beetles strain out, rather than comminute large particles, using their soft, filtering setae to ingest only minute particles (8–50 µm) 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 and Favila, 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 endopara-

site transmission. 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 feces may reduce transmission of fecal–oral pathogens, particularly in rural areas with inadequate sanitation.

2.7. 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 *Anomiosoides*, *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; Fincher and Marti, 1982; 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 scarabeine 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 (1990) 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, 1990). 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.

2.8. 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; Blume et al., 1973; Bornemissza, 1970; Doube, 1986; Feehan et al., 1985; Hughes et al., 1978; Macqueen and Beirne, 1975b; Mariategui, 2000; Moon et al., 1980; Ridsdill-Smith, 1981; Ridsdill-Smith and Hayles, 1987, 1990; Ridsdill-Smith et al., 1986; Ridsdill-Smith and Matthiessen, 1984, 1988; Wallace and Tyndale-Biscoe, 1983). 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 (Bishop et al., 2005; Ridsdill-Smith and Hayles, 1990), (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, 1990). The relative impact of these dung beetle activities is modulated by several factors, including dung quality (Macqueen and Beirne, 1975b; Ridsdill-Smith, 1986; Ridsdill-Smith and Hayles, 1990), beetle abundance (Bornemissza, 1970; Hughes et al., 1978; Kirk and Ridsdill-Smith, 1986; Ridsdill-Smith and Hayles, 1989; Ridsdill-Smith and Matthiessen, 1988; Tyndale-Biscoe, 1993), activity period (Fay et al., 1990), nesting strategy (Edwards and Aschenborn, 1987) and importantly, arrival time (Edwards and Aschenborn, 1987; Hughes et al., 1978; Ridsdill-Smith and Hayles, 1987). Phoretic predatory macrochelid mites have also been implicated in fly control (Axtell, 1963; Doube, 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., 1978; 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 (*Eonticellus intermedius*, Hughes et al., 1978; *Onthophagus granulatus*, Feehan et al., 1985; *Digionthophagus 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 *Eonticellus intermedius* in 1974 to Australia (Hughes and Morton, 1985), despite anecdotal evidence to the contrary (Hughes et al., 1978).

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, 2005) 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.

2.9. 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 leaf-cutter ants (*Atta* sp.) – one of the Neotropics' principal herbivores (Costa et al., in press). *Canthon virens* (misidentified as *C. dives sensu Borgmeier, 1937*) individuals attack leaf-cutter queens during nuptial flights to provision their larvae (Forti et al., 1999; Halffter and Matthews, 1966; Hertel and Colli, 1998; 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 trilobatum* (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.

3. 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^{-1} (Bornemissza, 1960; Bornemissza, 1976). This vast fecal deposition increased pest fly populations (Hughes, 1975) and caused extensive pasture loss (Ferrari, 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, 1981; Weeda, 1967). However, while successfully increasing dung removal services, introduced beetles appear to have failed to successfully suppress fly population at the landscape level (Hughes and Morton, 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^{-1} , 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 (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, 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, 2005; 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 (McCauley, 2006; Srivastava and Vellend, 2005; Wallace, 2007) compelling researchers to clearly delimit the scale and intent of their study.

4. 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 (Nichols et al., unpublished data). Natural grasslands modified for livestock pasturing offer altered vegetation density, soil temperature and moisture support – leading to range expansion for some dung beetle 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. in press) – 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 Mediterranean however, where the strongest empirical evidence of dung beetle decline can be found (Lobo et al., 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 × 30 m 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 et al., 2001).

5. 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 (Rodríguez 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 (Anderson et al., 1984; Herrick and Lal, 1996; Nakamura, 1975), and seasonally arid areas (Janzen, 1983b), 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.

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