

Extinctions of interactions: quantifying a dung beetle–mammal network

ELIZABETH H. RAINE,^{1,†} SANDRA B. MIKICH,² OWEN T. LEWIS,¹ PHILIP RIORDAN,^{1,3}
FERNANDO Z. VAZ-DE-MELLO,⁴ AND ELEANOR M. SLADE^{1,5}

¹*Department of Zoology, University of Oxford, Oxford, OX1 3PS UK*

²*Embrapa Florestas, P.O. Box 319, Colombo, 83411-970 PR Brazil*

³*Marwell Wildlife, Colden Common, Winchester SO21 1JH UK*

⁴*Departamento de Biologia e Zoologia, Instituto de Biociências, Universidade Federal de Mato Grosso, Av. Fernando, Corrêa da Costa, 2367, Boa Esperança, 78060-900 Cuiabá MT Brazil*

⁵*Lancaster Environment Centre, University of Lancaster, Lancaster LA1 4YQ UK*

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

Key words: co-extinction; commensalism; defaunation; food webs; interaction networks; mammals; Scarabaeinae; tropical forest.

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† **E-mail:** elizabeth.raine@zoo.ox.ac.uk

INTRODUCTION

Habitat loss, defaunation, climate change, and other large-scale anthropogenic disturbances

continue to drive species extinctions across the globe, with particularly rapid biodiversity loss in tropical forests (Canale et al. 2012). While the majority of research has focused on species as the

unit of biodiversity loss, an overlooked component is the extinction of ecological interactions (Valiente-Banuet et al. 2015). These extinctions are important as they often accompany or precede the loss of species and may have direct effects at the ecosystem level (Koh et al. 2004). Loss of large-bodied mammals across the globe through hunting, habitat degradation, and fragmentation is one of the most significant anthropogenic impacts on the environment (Peres and Palacios 2007, Wright et al. 2007). Cascading effects of these extinctions through ecosystems have been little studied, although correlative studies have revealed co-extinctions in closely linked groups, with implications for ecosystem structure and function (Colwell et al. 2012, Kurten 2013, Nichols et al. 2016).

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

Quantitative interaction networks have been employed widely to document plant–herbivore and plant–pollinator interactions (e.g., Kaiser-Bunbury et al. 2010, Novotny et al. 2010). However, most such studies of plant–animal interaction networks have been phytocentric, i.e., compiling data from focal plant species in the form of, for example, visitation frequencies of pollinators or attack rates by herbivores or predators (King et al. 2013), rather than zoo-centric, i.e., sampling animal activity, such as the analysis of fecal samples (Jordano et al. 2007), or pollen samples from the body of pollinators (Bosch et al. 2009). Of those interaction networks

that do include vertebrates, most focus on birds as frugivores dispersing seeds, and only a few include bats (Mello et al. 2011) and fewer still, other mammals (Donatti et al. 2011). Thus, despite their important roles in seed dispersal and hence seedling recruitment, mammals have been largely neglected in network studies (Vidal et al. 2013). Moreover, there have been few studies of networks of commensal species (Sayago et al. 2013, Nichols et al. 2016) and the role of secondary seed dispersers, such as ants and dung beetles, remains largely unexplored.

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

Despite numerous studies addressing dietary preference in dung beetles, few have used methods that enable the interactions between dung beetles and mammalian dung sources to be quantified reliably. Most sampling of dung beetle communities use standardized human- or pig dung-baited pitfall traps (Marsh et al. 2013), a method that may not accurately represent species' use of different resources (Amézquita and Favila 2010). Furthermore, dung size influences the abundance and size of dung beetles attracted

(Peck and Howden 1984). Several recent studies have attempted to ascertain dung beetle feeding preferences and have suggested that defaunation has strong effects on dung beetles (Martín-Piera and Lobo 1996, Culot et al. 2011, Enari et al. 2013, Bogoni and Hernández 2014). However, no previous work has used wild animal dung at the realistic sizes necessary to enable the incidence and frequency of interactions between individual dung beetle and mammal species to be calculated and to construct whole interaction networks. In addition, the dung type used for breeding influences brood mass and adult beetle size (Arellano et al. 2015), and dung beetle selectivity could vary between dung used for feeding or breeding.

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

METHODS

Study area

Fieldwork took place between 6 November 2015 and 13 April 2016 within a large remnant of Atlantic Forest in the Serra do Mar mountain range, in southeast Brazil (25°27'11" S, 48°52'57" W). The Atlantic rainforest supports high levels of endemic flora and fauna, but only 12% of the original forested area now remains (Ribeiro et al. 2009, Tabarelli et al. 2010). There are records of local extinctions of medium- and large-bodied mammal species from the area, resulting in impoverished mammal assemblages in many remaining fragments (Canale et al. 2012). The Serra do Mar mountain range is recognized as a center of species endemism and is the second largest area of continuous Atlantic forest remaining with an extent of 41,000 km² (Ribeiro et al. 2009). The study was conducted in three

sampling sites separated by 0.5–1 km within continuous lowland tropical forest, with an altitude of 40–100 m. Sites were predominantly primary forest but with signs of hunting or heart-of-palm (*Euterpe edulis*) harvesting.

Data collection

Dung beetle sampling.—Dung samples from seven mammal species native to the Atlantic forest were obtained from the Municipal Zoo of Curitiba, and the natural mass of each dung sample was recorded before use (Table 1; Appendix S1). All dung was stored at –18°C until use to keep it fresh and to kill any beetles or beetle predators.

Dung beetles use olfactory cues to locate dung (Dormont et al. 2004, 2010), and the odor profile of dung is a crucial aspect of its attractiveness. Pitfall trapping with unrealistic dung sizes is likely to provide odor cues that differ substantially from those generated by the spatiotemporally ephemeral distribution of dung in a tropical forest (Filgueiras et al. 2009, Whipple and

Table 1. Atlantic forest mammal species, mean dung mass, mammal status for Paraná state (Mikich and Bérnils 2004), and trophic guild feeding group for the dung used in this study.

Species	Dung mass (g)	Mammal status	Trophic guild
<i>Myrmecophaga tridactyla</i> (Linnaeus, 1758) Giant anteater	23–28†	Critical	Insectivore
<i>Sapajus nigritus</i> (Linnaeus, 1758) Black capuchin	37.2 ± 5.3	Not at risk	Frugivore
<i>Cerdocyon thous</i> (Linnaeus, 1766) Crab-eating fox	32.5 ± 14.5	Not at risk	Carnivore
<i>Panthera onca</i> (Linnaeus, 1758) Jaguar	73.6 ± 5.4	Critical	Carnivore
<i>Leopardus pardalis</i> (Linnaeus, 1758) Ocelot	33.0 ± 3.3	Vulnerable	Carnivore
<i>Galictis cuja</i> (Molina, 1782) Lesser Grison	11.9 ± 1.0	Not at risk	Carnivore
<i>Procyon cancrivorus</i> (Cuvier, 1798) Crab-eating raccoon	46.1 ± 2.9	Not at risk	Omnivore

Note: Dung mass is expressed as mean ± SE.
† Only two dung samples obtained. For all other dung types, n = 11–25.

Hoback 2012, Enari et al. 2013, da Silva and Bogoni 2014). Therefore, we used mammal dung of realistic sizes in our sampling. To distinguish between the functional use of dung, we deployed two types of trap, to identify dung beetle visitation (pitfall trap) and dung removal (bag trap). Pitfall traps attract coprophagous dung beetles that would both feed and breed on a dung source. We buried 700-mL plastic cups (10 cm top diameter, 7 cm bottom diameter, 15.5 cm depth) flush with the ground, half-filled with a water, salt, and detergent solution. The dung bait was suspended over the cup, protected with a rain cover, and left for 48 h before collection. Bag traps (Arellano 2016, Goh and Hashim 2018), designed to capture dung beetles exploiting the dung to form brood balls or balls buried for feeding, were made from large agricultural plastic bags with drainage holes in the bottom, buried in the ground, and back-filled with approximately 70 L of soil (0.45 × 0.45 m). Bags were buried flush with the soil surface; mammal dung was placed on top of the soil inside the bag and left for 24 h. Upon collection, the bags were sealed, and dung beetles collected by sifting through the soil onto a white sheet. Bag traps capture a realistic abundance and biomass of dung beetles attracted to a dung type as dung burial limits the period that the dung is attractive to beetles. This method does not reliably capture dung beetles that roll away dung balls from a dung pad for burial (rollers), but these make up a small proportion the dung beetle fauna in the Atlantic forest (Filgueiras et al. 2011), which mainly consists of tunneling dung beetles (that bury dung directly beneath the dung pad). Dung of all seven mammal species was used for pitfall trapping, and six dung types were used in the bag traps due to insufficient quantities of giant anteater dung (Appendix S1: Table S1 and Appendix S2).

In each of the three sites, two 1400-m line transects were established spaced at least 150 m apart and starting at least 100 m from the forest edge. One transect was used for pitfall traps and the other for bag traps. Each line transect had eight sampling points spaced 200 m apart, to limit interference between traps (Appendix S1: Fig. S1). Both types of traps were set once per month, on three occasions for the bag traps and four occasions for the pitfall traps. Dung from

each mammal species in naturally occurring volumes (Table 1) was randomly allocated to sampling positions along each transect. All traps were set in the morning between 0900 and 1100.

Dung beetles from both trap types were stored in 70% ethanol in a freezer until they were identified by a dung beetle taxonomist (F. Vaz-de-Mello) and using genus-specific keys (Vaz-de-Mello and Edmonds 2011). Voucher specimens were deposited at the Universidade Federal de Mato Grosso (UFMT) and Embrapa Florestas, Paraná. Dung beetle dry biomass was quantified by weighing up to 30 individuals per species (depending on the abundance of the species) with a microbalance accurate to 0.001 g.

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

Data analysis

As the three sites were not spatially independent in terms of mammals or dung beetles, data were pooled to produce two matrices, the first (from the bag trap data) representing dung beetles using dung as a resource for their offspring (breeding) and the second representing dung beetle–mammal interactions based on attraction to pitfall traps (feeding).

The total number of camera sightings, sign, and visual sightings per species was used to

calculate the relative abundance of each mammal species across the three sites. Due to the mismatch between the detection of animals and the dung used (e.g., jaguar dung was used in trapping; puma but not jaguar was recorded in the field), the categories large felid and small felid were used in place of species as nodes in the interaction network, indicative of the mammal trophic guild (Bogoni and Hernández 2014).

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

To test whether the dung beetle–dung networks differed in structure from a random network with similar structural properties, linkage density (L/S), specialism (H2'; Blüthgen et al. 2006), and nestedness were compared between the observed network and 10,000 random networks. Linkage density (L/S), specialism (H2'; Blüthgen et al. 2006), and nestedness were compared between the bag network and the resampled pitfall network using a one-sample *t*-test (Tylianakis et al. 2010). Nestedness values range from 0 to 100 where 0 is perfectly nested, and H2' values range from 0 (no specialization) to 1 (perfect specialization). Linkage density is the mean number of links per species (Dormann et al. 2009). Random networks were simulated using the *bipartite* package (Dormann et al. 2008), constraining the total species abundance and links, and compared to the empirically observed networks using a one-sample *t*-test (Dormann et al. 2009). To identify whether there were differences in structure between the feeding and breeding network, while controlling for sampling intensity, subsets of beetles were selected at random 1000 times from the pitfall network to create networks of the same size as the bag network. In addition, to test whether there were differences in the dung beetle community attracted to each trap type, a permutational multivariate analysis of variance (MANOVA) was calculated and visualized using nonmetric multidimensional scaling (NMDS).

Quantifying dung beetle–mammal interaction networks.—The feeding and breeding dung beetle–mammal dung networks created were based on the relative volume of dung available in the ecosystem. This was estimated based on the abundance of each mammal species recorded that also had dung available to use for dung beetle trapping. Dung volume (g) produced per mammal species per day (d_j) was estimated based on the mammal species body mass (m_j ; Blueweiss et al. 1978, Emmons and Feer 1997) and raw proportional occupancy (a_j), following Nichols et al. (2016): $d_j = (0.85m_j^{-0.37}) m_j a_j$. The interaction frequency between dung beetle species i and mammal species j was based on dung beetle numbers recorded, defined for each trap type as: $I_{ij} = \frac{d_j}{p_j} \times B_{ij}$ where p_j is the total volume of dung of mammal species j in one trap type (bag or pitfall), and B_{ij} represents the number of beetles captured through trapping of dung beetle species i on dung from mammal species j in one trap type. The relative abundance of a dung beetle species is therefore the sum of the interactions it is a part of: $b_i = \sum_{j=1}^n \frac{d_j}{p_j} \times B_{ij}$.

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

We simulated network responses to four alternative mammal extinction scenarios. Scenarios were selected to reflect extinction risk on the basis of (1) rarity, where the least abundant mammal species goes extinct first (Cardillo et al. 2006), based on relative mammal abundance from this study; (2) local status of extinction-proneness from the Paraná Red Book (Mikich and Bérnils 2004), where the most endangered mammal species goes extinct first; (3) body size, with the largest mammal species going extinct first,

which has been used as an indicator of extinction risk (Cardillo et al. 2006); (4) dung volume, where mammal species extinction was based on total volume of dung produced per day by mammal species d_j (mammal species with the largest dung volume removed first; Appendix S1: Table S1 and Appendix S2). Based on the generalist interactions of many dung beetles with mammal dung (Hanski and Cambefort 1991), the simulations incorporated the potential for dung beetle individuals to change their feeding interactions to alternative resources following mammal extinctions. Where jr represents the mammal species that are removed from the network, the dung beetle individuals feeding on this dung type (I_{ijr}) were reallocated to other remaining dung types available (I_{ij}), in proportion to that species' use of each dung type as recorded from the combined bag and pitfall traps. Thus, the reallocation of dung beetles to the mammal species remaining in the network is represented as:

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

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

Each mammal loss scenario (1000 iterations) was compared with a null model (1000 iterations) with a random order of mammal species extinction. For simplicity, we assumed that mammal species extinctions would not result in any compensatory response from other mammal

species. For each simulated network, we calculated dung beetle species richness, dung beetle abundance, total dung beetle biomass, and average biomass per beetle individual. These metrics were compared between the realistic scenarios and random null scenarios of mammal species extinction using confidence intervals. Code for extinction scenarios is available in the Supporting Information. All data analyses were carried out in R (R Core Team 2016), and interaction networks visualized using Food Web Designer (Sint and Traugott 2016).

RESULTS

Dung beetle and mammal data

In total, 435 dung beetles of 15 species were collected using 69 dung-baited pitfall traps and 44 dung-baited bag traps (Appendix S1: Table S2). The majority of dung beetle species captured were coprophagous or generalist in their feeding preferences according to the existing literature (Appendix S1: Table S3). Rolling dung beetles made up only 6.8% of individuals. Mammal surveys identified 17 mammal species through 151 camera records, 40 animal signs, and five visual sightings (Appendix S1: Table S4).

Trophic networks

The networks for breeding (Fig. 1a) and feeding (Fig. 1b) interactions of Atlantic forest mammals and dung beetles incorporated half of the mammal species identified at the site through the mammal census. All mammal dung types had high sample completeness (76–100%), indicating that the data are robust in terms of the number of dung beetle species attracted to each bait type. Equally, dung beetle species had high sample completeness (>90%), with the exception of *Canthidium punctatostriatum* (73%), indicating that diet breadth detected for dung beetle species was also robust. The interaction accumulation curve showed that sample size, as expected, is an important influence on the number of interactions detected for each dung beetle species (Appendix S1: Fig. S2). There were no specialist dung beetles interacting with a single dung type, other than those with very low abundances (two or fewer individuals).

The feeding interaction network included 15 dung beetle species and seven mammal species,

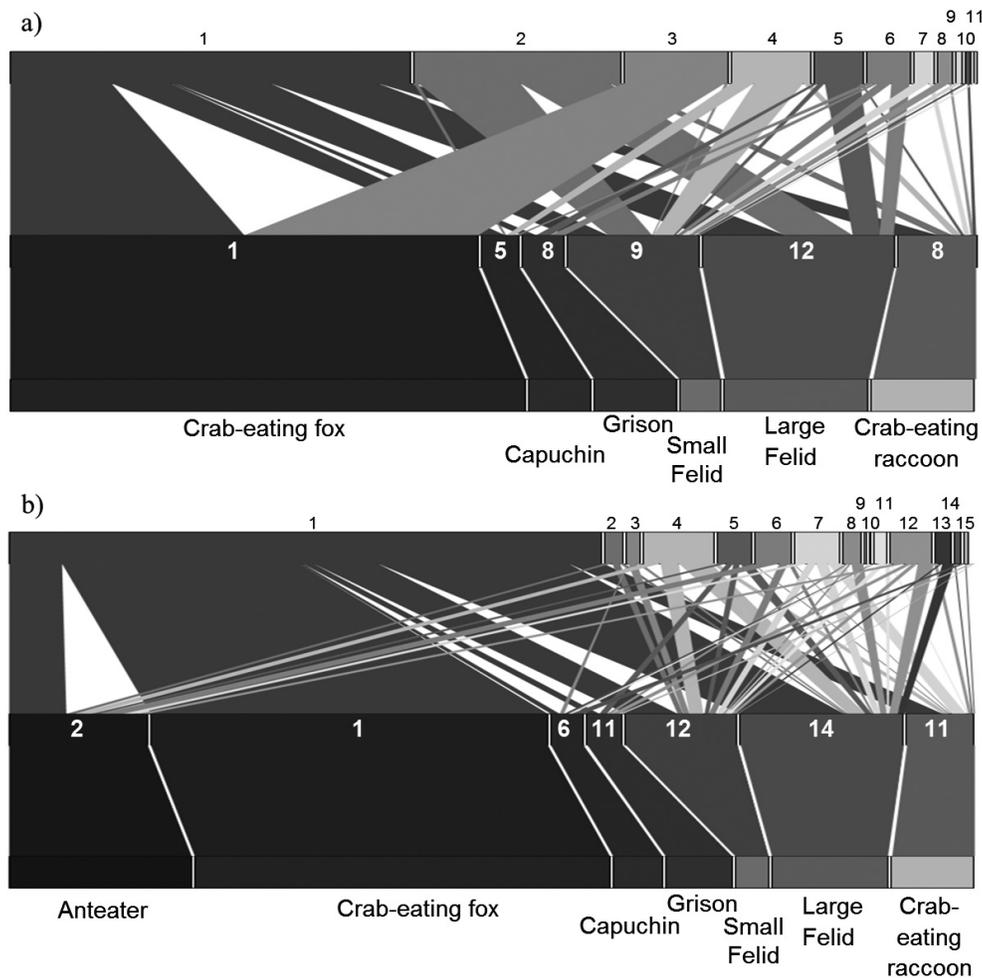


Fig. 1. (a) Dung beetle breeding interaction network. (b) Dung beetle feeding interaction network. Networks depict the dung beetle–dung–mammal interactions based on relative mammal abundance. Bottom level: relative mammal species abundance; mid-level: dung volume produced per day per mammal species,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

and the breeding interaction network included 11 dung beetle species and six mammal species. Connectance (the realized proportion of possible links, from 0 to 1) was 0.49 for both networks. For the feeding network, nestedness, specialism, and linkage density did not differ significantly from the null expectation under random association ($P > 0.05$). In contrast, in the breeding interaction network both linkage density ($P = 0.19$)

and specialism ($P = 0.011$), but not nestedness ($P > 0.05$), were significantly different from the null model expectation (Appendix S1: Table S5). The metrics for the feeding network subsampled to the same number of beetles as the breeding network revealed significant differences in nestedness ($P = 0.002$), specialism ($P = 0.001$) and linkage density ($P = 0.001$), all of which were larger in the feeding network.

Dung beetle biomass increased significantly with dung volume ($F_{1,47} = 14.43$, $R^2 = 0.22$, $P = 0.00042$), and the fitted regression was used to calculate maximum biomass of dung beetles attracted to each dung type in the equation for I_{ij} (see *Methods*). There was a small, but significant, effect of the trap type—dung bait interaction on dung beetle species composition ($F_{16, 161} = 1.85$, $R_2 = 0.16$, $P = 0.001$): The dung beetle species composition captured in bag traps overlapped but was distinct from the composition found in pitfall traps (Appendix S1: Fig. S3). We therefore pooled the bag and pitfall trap data for simulations of mammal species extinction scenarios.

Extinction scenarios

The effects of mammal extinctions differed among scenarios and for each measure of the dung beetle community (Fig. 2). The mammal extinction scenarios based on local mammal status, dung volume, and body mass all showed higher predicted losses of dung beetle abundance, biomass, and species richness than the random extinction scenarios. The extinction scenario based on local mammal status showed a greater range of predicted effects on dung beetle abundance, biomass, and species richness from the third species extinction onwards. This can be accounted for by the low-risk status of four mammal species, which were removed at random following removal of the higher risk species (see Table 1). Extinction due to mammal rarity, as based on the mammal survey data collected in this study, resulted in declines in dung beetle abundance, biomass, and species richness that were within the confidence intervals of the random extinction scenarios. However, extinction scenarios based on mammal body mass and dung volume resulted in dung beetle average biomasses that fell below the 95% quantile of the random extinction scenarios, whereas the extinction scenarios based on mammal rarity and local mammal status resulted in average dung beetle biomasses within the confidence intervals found in the random extinction scenarios.

DISCUSSION

Structure and specialization of dung beetle–mammal networks

We present the first documented dung beetle–mammal networks that quantify dung beetle

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

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

Differences in dung preference for breeding and feeding could be driven by increased

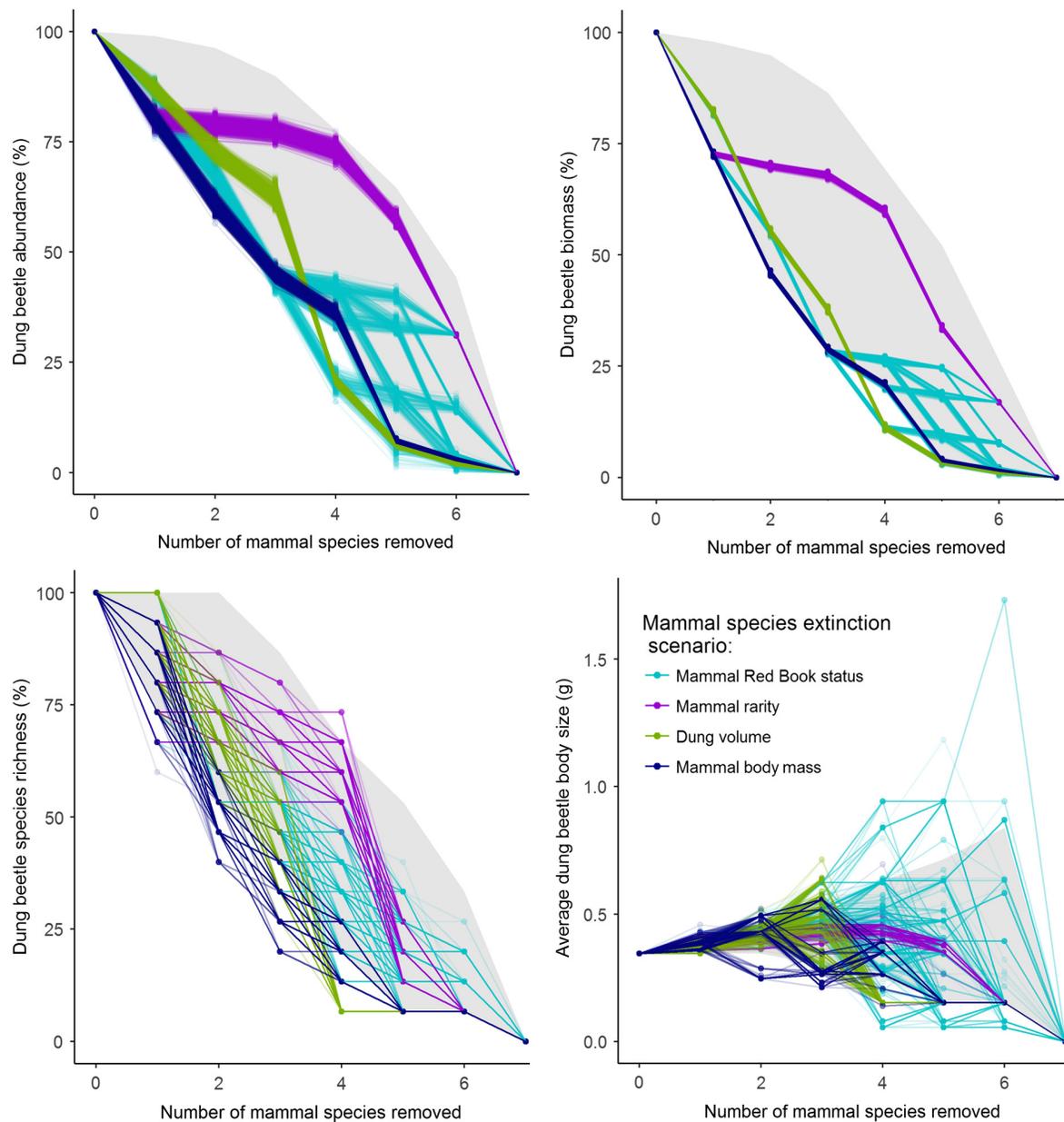


Fig. 2. Mammal species extinction scenarios (1000 iterations per scenario) plotted against dung beetle population metrics of abundance, biomass, species richness (as a percentage of the intact community), and average dung beetle body size (g). Gray areas represent the 95% quantiles produced from the 1000 random mammal species extinction scenarios. See *Methods* for explanation of extinction scenarios.

resource selectivity for the formation of brood balls where dung quality is of high importance (Shafiei et al. 2001, Moczek and Nijhout 2004, Arellano et al. 2015). This is relevant for the construction of interaction networks: by burying dung, rather than just feeding on the liquid

component, the breeding networks represent the ecosystem function contributions of dung beetles to a greater extent than feeding networks. This is analogous to pollination networks, which can identify ecosystem functioning in plant–pollinator systems more reliably than visitation

networks (King et al. 2013, Popic et al. 2013), and help predict functional consequences of species extinctions (Anderson et al. 2011). The feeding network had higher specialization and lower connectance than the breeding network, when comparing networks of equal size. However, comparison of the fully sampled feeding network revealed very similar structure to the breeding network, with the same specialization and connectance. The dung beetle community of the breeding network overlapped with the feeding network, which suggests that more dung beetle species choose to feed than breed on any dung particular type. This suggests that standardized pitfall trapping approaches to gathering data on dung beetle species dung preferences can also reliably identify the functional interactions of dung beetles. However, using bag traps can reveal realistic numbers of dung beetles breeding in a dung source, unlike pitfall traps (Arellano 2016), and so may be useful when linking dung beetle communities to ecosystem functioning measures. In both networks, the number of interactions documented between resources and dung beetle species increased with sample size (i.e., the number of individuals of a species that were recorded), again indicating a highly generalist feeding ability.

Consequences of mammal species extinctions for dung beetles

Mammal extinction scenarios based on total dung volume available in the system, the local extinction status of the mammal species, and mammal body mass resulted in patterns of secondary extinctions in dung beetles where abundance, species richness, and total biomass declined more rapidly than the majority of random extinction scenarios. This suggests that the extinction of mammals will have severe impacts on dung beetles in this system, despite the model accounting for their trophic flexibility. For two of the scenarios, dung volume and mammal body mass, mammal extinction resulted in greater declines in individual dung beetle biomass than the random extinction scenarios. As the total biomass of dung beetles is closely related to dung removal (Nichols et al. 2016), these extinction scenarios indicate the potential for the loss of the associated ecosystem functions provided by dung beetles, such as declines in seed dispersal

(Culot et al. 2015), seed burial (Lugon et al. 2017), and seed germination (Lawson et al. 2012) at rates higher than predicted for random extinction scenarios. As mammal body size is closely correlated with dung size (Blueweiss et al. 1978), the extinction scenario based on mammal body size represents the community-level effect on the dung beetle population of loss of dung source by size. Both the abundance and size of dung beetles decrease with decreasing bait sizes (Peck and Howden 1984, Andresen 2002), trends that were also found in our analysis. A reduction in the average body size of beetles would reduce the amount of dung buried per beetle and could reduce the potential for complementarity in dung removal between dung beetle functional guilds (Slade et al. 2007).

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

Assumptions and uncertainties

The dung used for this study came from animals fed diets which may not be realistic for wild animals, which could have impacted the attractiveness of the dung to dung beetles (Edwards 1991, Bogoni and Hernández 2014). However, the generally broad dietary preference detected in this study suggests minor changes in consistency,

odor, or nutritional quality of dung would not have had great effects on the dung beetle composition detected. The networks represented here consider dung beetles attracted to fecal material. We note that carrion, fungi, and rotting fruit are also important food sources for some dung beetle species (Hill 1996, Halffter and Halffter 2009). In addition, the displayed interaction network is a case study and not a systematic analysis of the dung beetle–mammal interaction network in the Atlantic Forest, and repeated sampling would be needed to elucidate the variation in network structure over time or environmental gradients (Tylianakis and Morris 2017).

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

CONCLUSIONS

By developing the first quantitative mammal–dung beetle networks, we have addressed several important knowledge gaps. In particular, we contribute to the understanding of how interactions in networks involving mammals and secondary insect seed dispersers are structured and may respond to extinctions of interactions. Crucially, the dung beetle–mammal networks presented here demonstrate the utility of including quantitative information on species-specific interactions, which can enable the exploration of alternative functional interactions under differing realistic extinction scenarios. There was no evidence of

higher selectivity in the breeding network compared to the feeding network, and both networks showed a similar structure to other commensalist systems that have been previously quantified. However, despite this low trophic specialism, simulations of mammal extinction scenarios suggest that dung beetle populations will be strongly negatively impacted by mammal extinctions, with the potential for cascading consequences for ecosystem functioning.

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