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RESEARCH ARTICLE

Functional compensation in a savanna scavenger community

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Abstract

1. Functional redundancy, the potential for the functional role of one species to be fulfilled by another, is a key determinant of ecosystem viability. Scavenging transfers huge amount of energy through ecosystems and is, therefore, crucial for ecosystem viability and healthy ecosystem functioning. Despite this, relatively few studies have examined functional redundancy in scavenger communities. Moreover, the results of these studies are mixed and confined to a very limited range of habitat types and taxonomic groups.
2. This study attempts to address this knowledge gap by conducting a field experiment in an undisturbed natural environment assessing functional roles and redundancy in vertebrate and invertebrate scavenging communities in a South African savanna.
3. We used a large-scale field experiment to suppress ants in four 1 ha plots in a South African savanna and paired each with a control plot. We distributed three types of small food bait: carbohydrate, protein and seed, across the plots and excluded vertebrates from half the baits using cages. Using this combination of ant suppression and vertebrate exclusion, allowed us explore the contribution of non-ant invertebrates, ants and vertebrates in scavenging and also to determine whether either ants or vertebrates were able to compensate for the loss of one another.
4. In this study, we found the invertebrate community carried out a larger proportion of overall scavenging services than vertebrates. Moreover, although scavenging was reduced when either invertebrates or vertebrates were absent, the presence of invertebrates better mitigated the functional loss of vertebrates than did the presence of vertebrates against the functional loss of invertebrates. There is a commonly held assumption that the functional role of vertebrate scavengers exceeds that of invertebrate scavengers; our results suggest that this is not true for small scavenging resources.
5. Our study highlights the importance of invertebrates for securing healthy ecosystem functioning both now and into the future. We also build upon many previous studies which show that ants can have particularly large effects on ecosystem

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functioning. Importantly, our study suggests that scavenging in some ecosystems may be partly resilient to changes in the scavenging community, due to the potential for functional compensation by vertebrates and ants.

KEYWORDS
ecosystem functioning, functional compensation, functional redundancy, savanna, scavenging

1 | INTRODUCTION

Functional redundancy is the potential for the functional deficit created by the loss of a species to be mitigated by other species with similar ecological roles or overlapping niches (Naeem, 1998). Functional redundancy enhances the stability of ecosystems: when a species is lost from the community, other species with overlapping niches may be able to functionally compensate for the loss of this species in performing the same ecological processes (Biggs et al., 2020; Gonzalez & Loreau, 2009; Naeem, 1998; Rosenfeld, 2002). Crucially, functional redundancy is likely to be an important determinant of ecosystem stability in response to the ever-increasing human pressures imposed on landscapes and habitats (Dornelas et al., 2014; Elahi et al., 2015). As such, determining which ecosystem functions are likely to be disrupted by species declines is critical for predicting how ecosystems will respond to future disturbances (Barlow et al., 2018).

Scavenging—the removal of food resources such as fallen fruit, seeds and carcasses, by animals—is an important ecosystem function (Beasley et al., 2019). Scavengers transport nutrients from resources throughout the environment, which influences nutrient heterogeneity and nutrient recycling (Beasley et al., 2019; Frouz & Jilková, 2008). Scavenging is also a significant component of food webs, as scavengers take up energy from dead resources and make it available to predators (Wilson & Wolkovich, 2011). A substantial amount of energy in food webs is transferred through scavenging activity, due to the large number of links between scavenger and prey species (Wilson & Wolkovich, 2011). However, studies exploring the effects and functional roles of native scavengers are limited in both geographical and taxonomic scope. Also, many previous studies have focussed on vertebrate scavengers (e.g. Gerke et al., 2022; Orihuela-Torres et al., 2022; Walker et al., 2021; reviewed in Beasley et al., 2019), or invasive scavengers (Abernethy et al., 2016; Angulo et al., 2011; Brown et al., 2015; Turner et al., 2021). However, our knowledge of the role the role of native invertebrate scavengers is relatively incomplete, particularly for certain ecosystems. Of the studies that have investigated invertebrate scavengers, most were conducted in urban environments (Hosaka et al., 2019; Tan & Corlett, 2012; Youngsteadt et al., 2015), degraded habitats (Ewers et al., 2015; Fayle et al., 2011; Olson et al., 2012), or on a small-scale, with studies in natural environments limited to prairies and tropical forests (Bestelmeyer & Wiens, 2003; Griffiths et al., 2018). Hence, for the majority of biomes, we do not fully understand the roles that invertebrates play as scavengers.

Previous observational studies assessing the roles of different scavengers suggest that scavenger communities are often dominated by one scavenger species or group, such as raptors, crows, vultures and ants (Huijbers et al., 2015; Inger, Per, et al., 2016; Tan & Corlett, 2012), indicating that there may be limited functional compensation amongst scavenging groups. Indeed, two prior studies which experimentally removed scavenger species or groups to assess functional redundancy have suggested that there is little redundancy in scavenger assemblages (Griffiths et al., 2018; Hill et al., 2018). In contrast, several other exclusion studies found that the remaining scavengers can sometimes compensate almost fully when a scavenger group is excluded (Ewers et al., 2015; Olson et al., 2012; Youngsteadt et al., 2015). Experimentally excluding specific scavenger groups from resources is the best method by which to measure the compensatory responses of other scavengers in the assemblage, rather than simply comparing sites with naturally different abundances of scavenger groups or by using direct observations (e.g. Brown et al., 2015; Huijbers et al., 2015; Sugiura & Hayashi, 2018); this is because the response of scavengers to the removal of other groups can be directly measured.

Studies using large-scale exclusion approaches are not common in the literature, and existing studies have largely neglected tropical ecosystems, despite the fact that tropical ecosystems are experiencing rapid changes in species composition. Only two studies from tropical ecosystems have assessed whether there is functional redundancy amongst scavengers by excluding groups from food resources, and the results were inconsistent. Griffiths et al. (2018) found that ants in a tropical forest dominated the scavenger assemblage scavenging small food resources such as seeds and dead insects, and there was no functional compensation by other scavengers when ants were excluded. In contrast, in a similar system Ewers et al. (2015) found that invertebrates could completely fulfil the seed scavenging deficit created by the exclusion of vertebrates in a primary forest, but vertebrates only partially compensated when invertebrates were excluded. However, this study was conducted in forests with contrasting levels of disturbance and only used seeds, so it is not known whether compensatory responses would have been observed with other types of small food resource or in less disturbed habitats. That these types of manipulative experiments have rarely been carried out is concerning because these ecosystems, particularly tropical ones, are undergoing rapid environmental change and biodiversity loss (Parr et al., 2014). It is critical that we evaluate the vulnerability of functions such as scavenging to changes in biodiversity, particularly in rapidly changing ecosystems (Barlow et al., 2018).

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Another pitfall of previous work exploring contributions of different groups to scavenging services is the limited range of bait types (though see Griffiths et al., 2018; Youngsteadt et al., 2015). The majority of previous studies have measured scavenging contributions using a single (often protein-based) bait (e.g. Bond & Breytenbach, 1985; Ewers et al., 2015; Hill et al., 2018; Huijbers et al., 2015; Olson et al., 2012; Sugiura & Hayashi, 2018)—given that mammalian scavengers often specialise in scavenging protein-rich resources (Beasley et al., 2015), this approach may overestimate the contribution of vertebrates to total ecosystem-wide scavenging. This approach also captures a narrower range of scavengers compared with studies using a range of bait types and underestimates the influence of non-protein scavenging taxa.

Here, we conducted the first investigation into the contribution of ants, non-ant invertebrates and vertebrates in scavenging small food resources in a tropical grassy biome—a South African savanna—and explored the potential for ant and vertebrate scavengers to functionally compensate for the loss of the other. We focused on ants and vertebrates specifically, because these are the dominant scavenger groups across various habitat types, particularly those in the tropical and subtropical regions (Griffiths et al., 2018). In addition, invertebrates and vertebrates often respond differently to different environmental pressures. Thus, investigating the compensatory responses of ants and vertebrates provides a taxonomically balanced indication of how scavenging as a function will respond to a range of anthropogenic pressures. As ant abundance is typically highest in the tropical savannas and rainforests (Schultheiss et al., 2022), we predicted that the relative contribution of ants to scavenging would be similar to the findings of Griffiths et al. (2018). Because South African savannas, including our study system, are dominated by predatory and generalist ant genera such as *Pheidole*, *Myrmicaria*, *Tetramorium*, *Ocymyrmex*, *Monomorium* and ponerines such as *Bothroponera*, (A. Walker et al. unpublished data), we also predicted that ant suppression would have a greater effect on protein bait removal relative to the removal of seed or carbohydrate baits. We also expected that our choice to use a range of bait types would capture the feeding habits of a range of vertebrate, ant and non-ant invertebrate scavengers.

2 | MATERIALS AND METHODS

2.1 | Field site

This study was conducted at the Wits Rural Facility (24°32′39 S, 31°06′10 E), which is situated 25 km from Hoedspruit, Limpopo province, South Africa. The area lies 580 m above sea level, and the vegetation type is classified as Granite Lowveld savanna (Mucina & Rutherford, 2006). Dominant tree species include *Terminalia sericea*, *Dichrostachys cinerea*, *Combretum collinum* and *Sclerocarya birrea*. Dominant grass species include *Panicum maximum*, *Heteropogon contortus* and *Hyperthelia dissoluta*. Seasonal rain occurs during the summer months (December–April), and mean annual rainfall is 652 ± 200 mm (data from 1992 to 2018). Mean monthly temperature between 2016 and 2018 was 21.1 ± 0.6°C, with mean maximum and minimum temperatures of 28.3 ± 0.45°C and 14.0 ± 0.8°C, respectively. Maximum temperature regularly exceeds 35°C in the summer months (data from Wits Rural Facility weather station, 2016–2018). Permission to conduct this experiment at the Wits Rural Facility was obtained from the relevant managers and University of Witswatersrand staff members. Ethical approval was not required for this experiment.

The vertebrate scavengers in this study system include small animals such as lizards, and many bird and rodent species; medium-sized scavengers including banded mongoose (*Mungos mungo*) and vervet monkeys (*Chlorocebus pygerythrus*)—and the largest scavengers of small resources are chacma baboons (*Papio ursinus*). The ant scavenger community includes many opportunistic generalist taxa such as *Pheidole*, *Myrmicaria* and *Monomorium*. Non-ant invertebrate scavengers included orthopterans (e.g. bush crickets), carabid an tenebrionid beetles and flies.

2.2 | Ant suppression treatment

Four sites spatially separated by at least 300 m, were designated for the experiment. Within each site, two experimental plots were established in November 2017, each measuring 50 × 50 m. One of each pair of plots was allocated as a control plot and the other as an ant suppression plot. The ant suppression plots were surrounded by an additional buffer zone of 25 m, which the suppression treatment was applied to but sampling was conducted solely within the inner 50 × 50 m of these plots. The buffer zone was intended to prevent ants from outside the suppression plots foraging and nesting within the plots. Two types of poison baits were applied to suppression plots: Maxforce®, a commercial ant bait (active ingredients: Hydramethylnon 10 g/kg), and a custom bait which was created by soaking Whiskas® dry cat food in water containing imidacloprid (100 ppm, Premise®), then mixing with jelly (gelatine and sugar) made with a water solution containing imidacloprid (50 ppm). Using a low dose of imidacloprid ensures that foraging ants are not killed, which allows the insecticide to bioaccumulate in the nest and destroy the entire colony within a few weeks. To apply the poison baits to the plots, transects with a width of 5 m were set up across the plot so that the whole plot was covered. Field staff were assigned one transect at a time, and applied the bait granules by hand, walking along the transects at constant pace and scattering the baits in a standardised fashion within their assigned transect. This procedure was repeated twice (once for the commercial bait and again for the custom bait). The ant suppression treatment was first applied in November 2017. Three kilograms of Maxforce® and 6 kg of the cat food jelly bait was applied to each treatment plot. In January 2018, ant activity had increased to 25% of control plots; therefore, to continue suppression, the treatment was re-applied. The scavenging experiment took place in March 2018, during the summer wet season when ant activity is high.

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The suppression baiting technique was designed by Parr et al. (2016) to minimise non-target effects on other organisms. Both the insecticides used have low toxicity to terrestrial vertebrates and plants (Bayer Environmental Science, 2017a, 2017b). The poison baits were applied in the morning and early afternoon when ants are active, giving time for the baits to be taken by ants to their nests and making them unavailable to small foraging mammals (the majority of which are nocturnal) and invertebrates. The quantity of insecticide applied to each treatment plot was too low to kill even the smallest vertebrates. For example, if a mouse were to find and eat all the bait spread over its foraging territory, the quantity of insecticide would be less than its LD50 and would be insufficient to kill it. In addition, the technique has no detrimental effect on any epigeic or ground-active invertebrate taxa (Figure S1) and does not leave residual poison in the soil, grass or tree leaves (Figure S2). Following initial suppression, ant activity was assessed every 1–2 months using monitoring baits: to monitor ant abundances in a given plot, a teaspoon of moistened Wiskas® dry cat food was placed on pieces of white card (5 × 7 cm) distributed along two 25 m transects, and cards were separated by at least 10 m (30 monitoring cards in total per plot). Due to high ant abundances at baits, ant numbers were estimated using a ranked scale (0 = 0 ants; 1 = 1 ant; 2 = 2–5 ants; 3 = 6–10 ants; 4 = 11–20 ants; 5 = 21–50 ants; 6 = more than 50 ants) (following Griffiths et al., 2018; Parr et al., 2016).

2.3 | Food resource removal experimental setup

We used a factorial experimental design that enabled us to quantify the amount of food resources removed when: baits were accessible to all scavengers; when vertebrates and non-ant invertebrates had access, in the absence of ants; when ants and non-ant invertebrates had access, in the absence of vertebrates; and when non-ant invertebrates had access, in the absence of ants and vertebrates.

Within the 50 × 50 m inner zone of each of the four control and four ant suppression plots, we placed six bait stations every 10 m along 10 transects, and each transect was separated by 5 m. We caged 30 of the bait stations (Figure 1a) on each plot at random and left 30 uncaged (Figure 1b). We constructed cylindrical cages out of chicken mesh (mesh size 1.2 cm × 1.2 cm, diameter 20 cm, height 20 cm), closing the top of the cages with cable ties and securing each cage to the ground with two tent pegs (Figure 1b). The size of the mesh allowed most invertebrates to access the bait but excluded vertebrates. One of three food baits was randomly placed at each bait station: 3.07 g (±0.05 g) of dried biscuit (carbohydrate-biased); 3.02 g (±0.03 g) of dried mealworm (protein-biased); and 3.04 g (±0.03 g) of dried seed (sunflower seed, which is non-myrmecochorous). Hereafter baits will be referred to as carbohydrate, protein and seed, respectively. The seeds were broken up into smaller pieces as some of the granivorous ants in the study system were very small and may not have been able to remove an entire sunflower seed. Each bait was placed in a plastic dish (8 cm diameter; 1 cm depth) on the floor. While some may disagree with our choice of bait size, we chose these baits and bait sizes for several reasons: (1) to enable direct comparison with the tropical rainforest experiment by Griffiths et al. (2018), (2) to mimic nutrients found in detrital resources and (3) because we are measuring the scavenging contributions of small- to medium-sized scavengers, which readily eat small resources that would be ignored by larger animals. Moreover, few scavenging studies have used small food resources: most have employed vertebrate carcasses (Brown et al., 2015; Gerke et al., 2022; Hill et al., 2018; Huijbers et al., 2015; Inger, Cox, et al., 2016; Inger, Per, et al., 2016; Olson et al., 2012; Sugiura & Hayashi, 2018; Walker et al., 2021), which overlooks the role of scavengers that are attracted to smaller resources.

In total, each of the eight plots (4 × control and 4 × suppression) had 60 bait stations (20 × carbohydrate, 20 × protein, 20 × seed). Ten of each bait type were caged and 10 were uncaged. Caged stations and bait types were alternated so that caged stations were always next to uncaged stations, and bait types were always next to

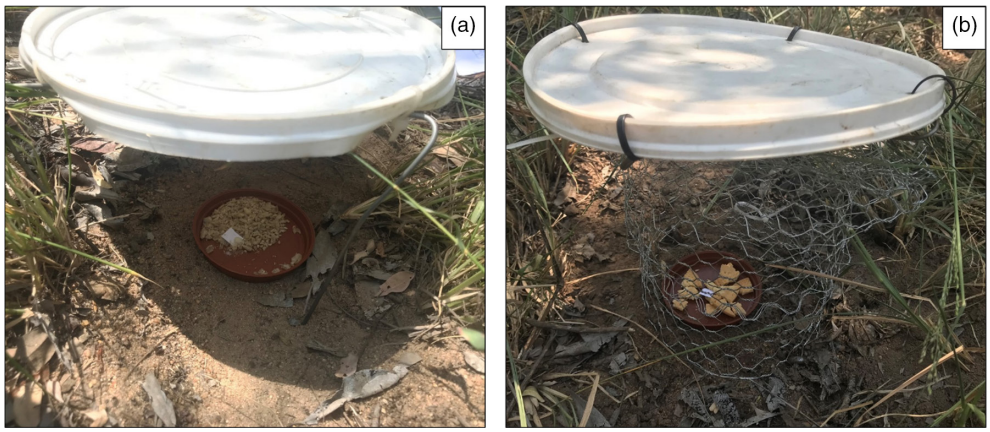


FIGURE 1 (a) Uncaged bait station containing seed, which is accessible to all foragers and (b) caged bait station containing carbohydrate (biscuit), which restricted access by vertebrates.

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a different bait type. Baits were dried at 70°C for 2 days to reach constant mass (measured using a Vibra AB3202 balance, 0.01 g precision). The baits were placed at the bait stations between 7:00 and 14:00 and were protected from the rain by a white plastic cover (25 cm diameter), which was suspended 10 cm above the uncaged baits on wire legs and secured to the cages using cable ties. Baits on each plot were collected 24 h after they had been put out. The baits were dried in the laboratory at 70°C to constant mass, and the remaining bait was weighed.

2.4 | Data analysis

To determine whether ant suppression was effective in reducing ant abundance, we analysed ant monitoring scores between 1 December 2017 (1 month after the start of the ant suppression treatment) and 1 May 2018, which includes the date of the resource removal experiment (March 2018). We performed a linear mixed effects model (lmer) in the lme4 package (Bates et al., 2015), with abundance score per bait card as the response variable ($n = 1440$ data points in total), treatment as the fixed effect and date nested within plot nested within site as the random effects structure, to account for non-independence of scores from bait cards from the same plots, within the same sites and sampled on the same dates.

To quantify the effect of our predictors on bait removal, we modelled the effects of ant suppression (ant suppression/control), vertebrate exclusion (caged/uncaged), bait type (carbohydrate/protein/seed), and the interactions between these predictors, on the mean mass (grams) of bait removed after 24 h, using a linear mixed effects model (lmer from lme4). To deal with the large number of pseudoreplicates (bait stations) and to ensure the residual errors were normally distributed to meet assumptions of linear mixed effects models, observations from each plot were averaged to obtain the group means for each combination of the three factors (ant suppression treatment, vertebrate exclusion, bait type). For example, within each suppression and control plot, we took the average mass (g) of bait removed from the 10 caged carbohydrate baits and treated it as one observation for the analysis. The response variable was mean mass loss (g) ($n = 6$ per plot; $n = 48$ data points in total). The random effects structure was plot nested within site, to account for lack of spatial independence of observations from the same plot and from plots within the same site. The model structure was: mean mass loss (g) ~ ant suppression treatment + vertebrate exclusion + bait type + (ant suppression treatment × vertebrate exclusion) + (ant suppression treatment × bait type) + (bait type × vertebrate exclusion) + (1|site/plot). As we were interested in the effects of all three fixed factors (ant suppression treatment, vertebrate exclusion and bait type), we retained all three in the model. We retrieved model coefficients for the effect of each bait type by specifying the reference bait type level in the model, by running the 'relevel' function on the bait type variable (Liang et al., 2020). For example, we retrieved coefficients for carbohydrate and seeds by setting the reference level to protein. We determined whether either ants or vertebrates displayed a compensatory response to the exclusion of the other by looking at the interaction coefficients. A significant ant suppression treatment × vertebrate exclusion interaction indicated that there was some functional compensation by scavengers.

For each bait type, means were plotted on an interaction plot, along with their bootstrapped confidence intervals (calculated from the raw data, as there is no need to use normally distributed data for bootstrapped CIs). This allowed us to visualise the amount of bait scavenged by each group in the presence and absence of the other groups and, therefore, assess whether any group was able to compensate for the loss of other group (i.e. determine whether there is any functional redundancy).

All analyses were conducted using R v.3.5.0 (R Core Team, 2018). Quantile-quantile plots, histograms of residual errors, residuals versus fitted plots were visually inspected to confirm that the assumptions of homoscedacity and normality were not violated.

3 | RESULTS

3.1 | Ant suppression

Ant monitoring scores at bait cards between November 2017 and May 2018 indicated that our ant suppression treatment was effective in reducing ant activity, as mean ant monitoring scores were 80% lower on ant suppression than control plots ($df = 6.0$, $t = -18.7$, $p < 0.001$, $R^2_m = 0.67$; Figure 2). When looking only at the month of the resource removal experiment (March 2018), ant activity was 85% lower on ant suppression than control plots (Figure 2).

3.2 | Bait depletion and discovery rates

In total, 462 undisturbed bait stations were collected from plots during this experiment. Of these, 33 had not been discovered by scavengers (no mass lost), and 122 were fully depleted (all mass lost). If too many bait stations became completely depleted it would be difficult to assess foraging efforts of the scavenging groups, but many bait stations were not fully depleted ($n = 340$). Hence, we felt confident that the results of our analyses provide a reliable estimate of scavenger effort in taking small resources.

3.3 | The role of non-ant invertebrates

When non-ant invertebrates had sole access to baits (caged baits in ant suppression plots), this group removed an average of 22.2% (Figure 3). This suggests that non-ant invertebrates played a small role in bait removal, particularly as this rate of scavenging was achieved in the absence of competition with other scavengers. Thus, we assume a small and constant role of non-ant invertebrate scavengers in removing baits, and our focus is on the roles of ant and vertebrate scavengers henceforth.

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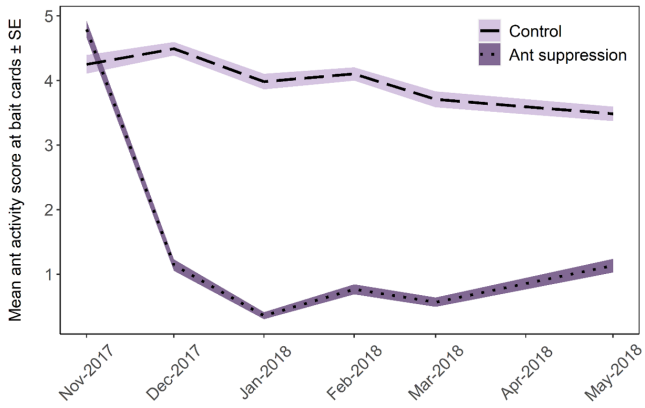


FIGURE 2 Ant monitoring scores at bait cards from November 2017 (time period immediately before the first suppression treatment was applied) until May 2018. This includes March 2018 when the resource removal experiment took place.

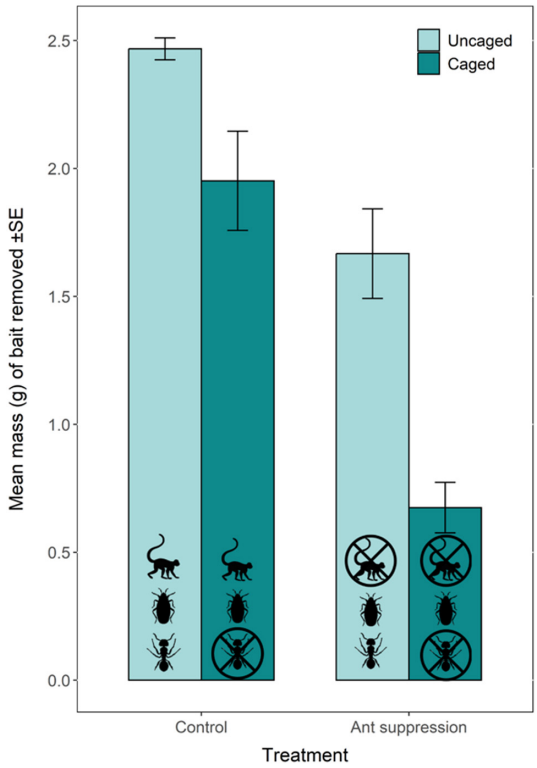


FIGURE 3 The mean mass (g) of food resources (±SE; *y*-axis), and percentage of total food resources removed from bait stations that were either caged (vertebrate exclusion) or uncaged (open to all foragers: invertebrates and vertebrates) within ant suppression and control plots. The symbols indicate which groups had access to the baits in each treatment.

TABLE 1 Linear regression results for the effects of ant suppression treatment (ant suppression or control), vertebrate exclusion (caged or uncaged) and bait type (protein, seed and carbohydrate) on the mass of bait mass removed from bait stations. Significant results ($p < 0.05$) are denoted in bold. The reference levels for each factor (treatment, cage treatment, bait type) were set to 'control', 'uncaged' and 'carbohydrate', respectively.

Fixed effect	Estimate	SE	*t*-Value	df	*p*
(Intercept)	2.39	0.18	12.99	36.26	<0.001
Treatment (ant suppression)	−0.30	0.23	−1.25	33.37	0.22
Vertebrate exclusion (caged)	**−1.01**	**0.23**	**−4.60**	**32.00**	**<0.001**
Bait type (protein)	0.13	0.24	0.55	**32.00**	0.59
Bait type (seed)	0.09	0.24	0.36	**32.00**	0.72
Treatment (ant suppression) × vertebrate exclusion (caged)	**−0.48**	**0.23**	**−2.10**	**32.00**	**0.044**
Treatment (ant suppression) × bait type (protein)	−0.49	0.28	−1.78	**32.00**	0.09
Treatment (ant suppression) × bait type (seed)	**−1.03**	**0.28**	**−3.69**	**32.00**	**<0.001**
Vertebrate exclusion (caged) × bait type (protein)	**0.66**	**0.28**	**−2.37**	**32.00**	**0.02**
Vertebrate exclusion (caged) × bait type (seed)	**0.93**	**0.28**	**−3.36**	**32.00**	**0.002**

Note: The model structure was mean mass loss (g) ~ ant suppression treatment + vertebrate exclusion + bait type + (ant suppression treatment × vertebrate exclusion) + (ant suppression treatment × bait type) + (bait type × vertebrate exclusion) + (1|site/plot). Ant suppression treatment, vertebrate exclusion, bait type and their interactions were included as fixed effects, and the random effects structure was plot nested within site. To meet assumptions of normality for linear mixed effects models, we took the average mass loss from each combination of treatment, vertebrate exclusion and bait type, were within each plot. A significant ant suppression treatment × vertebrate exclusion interaction indicates that there was some functional compensation by scavengers. The R^2 of the model was 0.77.

3.4 | The roles of ants and vertebrates in scavenging different bait types

The effect of ant suppression and vertebrate exclusion on bait removal varied depending on bait type (significant interactions between ant suppression treatment × bait type and vertebrate exclusion × bait type; Table 1). In the case of our protein baits (when we set the bait type reference level to 'protein' in the model), suppressing ants had a significant negative effect on the amount of bait removed (comparing mass lost from uncaged protein baits in ant suppression plots in Figure 4; df = 33.37, $t = -3.35$, $p = 0.002$), whereas the effect of excluding vertebrates was not significant (comparing mass lost from uncaged and caged protein baits in control plots in Figure 4; df = 40.00, $t = -1.70$, $p = 0.1$). Similarly, for our seed bait, suppressing ants had a significant negative effect on the amount of bait removed (comparing mass lost from uncaged seed baits in ant suppression plots in Figure 4; df = 33.37, $t = -5.6$, $p < 0.001$), and the effect of vertebrate exclusion was again not significant (comparing mass lost from uncaged and caged seed

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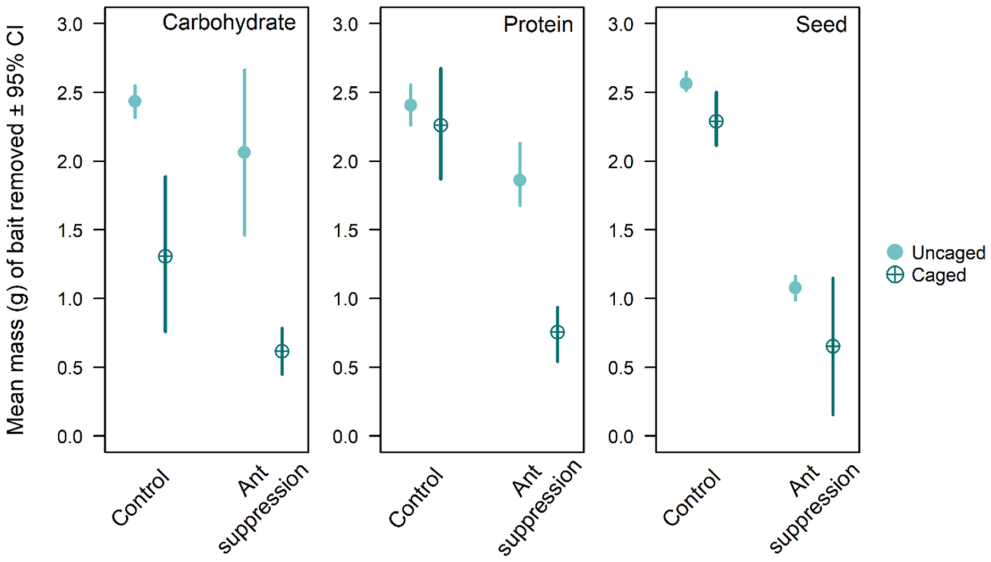


FIGURE 4 Means and bootstrapped 95% confidence intervals for the effect of treatment (ant suppression or control) and cage treatment (caged or uncaged) on the mean mass loss of each bait type (carbohydrate, protein and seed). Bootstrapped CIs were calculated from the averaged data.

baits in control plots in Figure 4; df = 32.0, $t = -0.49$, $p = 0.63$). These results suggest that ants are the dominant scavengers of small protein and seed resources in our study system. However, for our carbohydrate bait (biscuit), this trend was reversed such that vertebrate exclusion had a significant negative effect on bait removal (comparing mass lost from uncaged and caged carbohydrate baits in control plots in Figure 4; df = 32.0, $t = -4.60$, $p < 0.001$), but the effect of ant suppression was not significant (comparing mass lost from uncaged carbohydrate baits in ant suppression plots in Figure 4; df = 32.0, $t = -1.25$, $p = 0.22$). This suggests that vertebrates are the dominant scavengers of small carbohydrate resources.

3.5 | Functional compensation

Considering all bait types together, there was a significant interaction between the ant suppression and vertebrate exclusion treatments, meaning that the effect of vertebrate exclusion on bait removal depended on whether ants were suppressed or not and vice versa (df = 40, $t = -2.34$, $p = 0.024$; Table 1). Specifically, excluding vertebrates led to a 20.8% reduction in the mass of baits removed when ants were present (comparing mass loss from caged baits to uncaged baits in control plots; Figure 3), compared with a 59.3% reduction in bait removal when ants were suppressed (comparing mass loss from caged baits to uncaged baits in ant suppression plots; Figure 3). Thus, the presence of ants can reduce the functional deficit in scavenging (i.e. functional compensation) created by vertebrate exclusion by 64.9%. Furthermore, excluding ants led to a 32.8% reduction in the mass of baits removed when vertebrates were present (comparing bait mass loss between ant suppression and control plots for uncaged stations; Figure 3) compared with a 65.4% reduction when vertebrates were excluded (comparing bait mass loss between ant suppression and control plots for caged stations; Figure 3). Thus, the presence of vertebrates can reduce the functional deficit in scavenging created by the suppression of ants by 49.8% (Figure 3).

In summary, the suppression of ants had an overall greater negative impact on the *absolute* mass of bait removal than did the exclusion of vertebrates. Moreover, the presence of ants mitigated the *relative* change in bait removal associated with vertebrate exclusion to a greater extent than the presence of vertebrates mitigated the *relative* change in bait removal associated with ant suppression. However, as bait removal was still reduced when vertebrates were excluded, we cannot say that ants fully mitigated the functional loss associated with vertebrate exclusion.

4 | DISCUSSION

Quantifying the functional roles of species and their ability to compensate for the functional loss of other species is vital for determining the vulnerability of ecosystem functioning to biodiversity changes. Our results suggest that in our African savanna study system, ants are more important for scavenging small food resources than vertebrates (Figure 3). This result was consistent for two bait types: ants were the dominant scavengers of protein and seed baits, but vertebrates were the dominant scavengers of carbohydrate baits (Figure 4). Our results also indicate that scavenging ants can partially compensate for the loss of vertebrate scavengers, as ants reduced the functional deficit in scavenging created by vertebrate exclusion by 64.9%. Vertebrates were also able to compensate for the loss of ants, but to a lesser extent—vertebrates reduced the functional deficit in scavenging created by the suppression of ants by 49.8%. However, neither group was able to fully mitigate the loss of the

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other, as less bait was taken in both treatments than when all scavengers had access to the baits (Figure 3).

4.1 | Contribution of different scavenger groups

We found that in general, ants were more important for scavenging than vertebrates. At uncaged stations, when we suppressed ants, bait removal declined by 32.8%, but when we excluded vertebrates, bait removal declined by only 20.8% (Figure 3). One of the main drivers of this result is likely to be fundamental differences in ant and vertebrate ecology. Ants have been reported as important scavengers of small food resources in both temperate and tropical forests (Fayle et al., 2011; Fellers & Fellers, 1982; Griffiths et al., 2018), urban environments (Tan & Corlett, 2012) and deserts (Mares & Rosenzweig, 1978). The ubiquity and abundance of ants in many ecosystems means they can have large impacts on ecosystem functioning (Griffiths et al., 2018; Parr et al., 2016; Walker et al., 2022). Moreover, although vertebrates are often able to scavenge larger quantities of food per individual than ants, ants can rapidly discover and remove food resources due to their typically pervasive distribution within habitats (Bond & Breytenbach, 1985; Fellers & Fellers, 1982; Tan & Corlett, 2012). Furthermore, the cooperative nature of ant colonies means ant foraging can be highly efficient: in many ant species, foragers communicate the location, quantity and quality of food resources back to nestmates, which are then recruited to exploit several resource patches simultaneously (Traniello, 1989). However, each vertebrate individual (which are far fewer in number) can visit only one resource at a time, and their foraging range may be limited by the availability of safe refuges (Cooper, 2000; Orrock & Danielson, 2004). These differences in abundance and foraging efficiency may help to explain why ants were the dominant scavengers in our study.

Our findings are consistent with a similar previous study in a Bornean forest, which found that ants were the dominant scavenger group (Griffiths et al., 2018), although that study reported a larger contribution of ants to food resource removal (52%). This larger effect reported by Griffiths et al. (2018) may be due to the activity periods of ants differing in savannas and rainforests: in savannas, most ant species avoid foraging for several hours during the hottest parts of the day, reducing foraging time by ~20%, whereas they can be active all day in the cooler rainforest, resulting in ants removing a larger proportion of resources in the rainforest than in the savanna. Our finding that ants are the dominant scavengers of small food resources indicates their vital importance as scavengers and thus in redistributing nutrients from food resources, in savannas. It should also be noted that our study is likely to underestimate the role of ants; this is because it is not possible to exclude all ants from a natural experimental plot (we reduced ants by approximately 80%), meaning that the scavenging effort of residual ants in ant suppression plots will be counted as part of the contributions of vertebrates and non-ant invertebrates.

Non-ant invertebrates removed 22% of bait when competition with other scavengers was reduced (caged bait stations in ant suppression plots; Figure 3). We observed a diversity of non-ant invertebrates removing resources in our experiment, including orthopterans (e.g. bush crickets), flies, wasps and ground beetles (e.g. carabids and tenebrionids). However, it our results may overestimate the contribution of non-ant invertebrates, as ants were never fully suppressed (Figure 2), meaning some of the bait removal recorded in the caged/suppressed plots would have been due to residual ant activity.

4.2 | Bait-specific effects

We found that the impact of ant suppression and vertebrate exclusion varied amongst the three different bait types: ants were the dominant scavengers of protein and seed, and vertebrates were the dominant scavengers of carbohydrate. That ants were the dominant protein scavengers is likely due to the very high abundances of opportunistic predatory ants in our study system which are reliant on nitrogen resources such as the mealworm carcasses we used as protein baits—the ant community is dominated by genera such as *Pheidole* and *Myrmicaria* (A. Walker, unpublished data), which will readily prey and scavenge on insects and are likely not reliant on carbohydrate. These dominant feeding habits may have evolved due to a general lack of liquid carbohydrate—honeydew and plant exudates—in our study system (particularly that available to ground-active species), although studies evidencing this directly are unfortunately not available. That ants were the dominant scavengers of seeds could be due to a higher proportion of vertebrate scavengers being largely insectivorous. *Pheidole* and *Monomorium* are common genera in our system and are known to take seeds (Bond & Breytenbach, 1985; Hölldobler & Wilson, 1990). That vertebrates scavenged more carbohydrate may be because the dominant ants are not reliant on carbohydrate, and there is, therefore, reduced competition for this resource, and may also be due to the higher metabolic requirements of vertebrates compared with invertebrates leading to a greater reliance of vertebrates on this nutrient. The variation in bait preference of different scavenger types highlights the need to use a variety of bait types when quantifying the functional roles of different scavenger taxa. In addition, a better understanding of the availability of different food resources present in natural habitats would help to give natural context to our findings.

In this study, we opted to use small baits for two main reasons. Firstly, to appeal to small- and medium-sized scavengers such as ants, beetles, birds and rodents, which will readily take small resources. Second, the current literature is biased towards the use of large baits (e.g. animal carcasses: Brown et al., 2015; Hill et al., 2018; Huijbers et al., 2015; Olson et al., 2012; Sugiura et al., 2013; Sugiura & Hayashi, 2018), even though small-sized food resources are a crucial energy supply relied on by many species (Bestelmeyer & Wiens, 2003; Ewers et al., 2015; Griffiths et al., 2018; Youngsteadt et al., 2015). However, because the size of scavenged resources are likely to be positively correlated with scavenger size (i.e. large bait types will be favoured by larger scavengers), the results of any study

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using size-specific baits are may be biased. Consequently, our study, which uses small baits and no vertebrate carrion, is likely to underestimate the scavenging contribution of larger vertebrate scavengers meaning we cannot equivocally say across all bait types and sizes, that ants are more important than vertebrates. Nonetheless, our results are still valuable in revealing ants as the dominant agents of small resource scavenging, particularly given the ubiquity of small resources (e.g. seeds, fruits, dead insects) throughout most habitats.

4.3 | Functional compensation

We found that, when ants were present at natural abundances (control plots), the negative effect of excluding vertebrates on bait removal was lower (20.8%; Figure 3) than when ant abundance was suppressed (59.3%; Figure 3) and that the presence of ants, therefore, mitigated the functional loss created by excluding vertebrates by 64.9%. There are two possible explanations for this result. First, it is possible that the exclusion of vertebrates in control plots freed ants from competition with vertebrates (e.g. direct competition for food or relief from predation by facultative insectivorous mammals), which allowed ants to compensate by increasing their scavenging activity—leading to a smaller effect of vertebrate exclusion on bait removal in control plots relative to ant suppression plots. Second, it is also possible that in ant suppression plots, a release from competition with ants allowed vertebrates to compensate by increasing their scavenging activity—which would also lead to vertebrate exclusion having a smaller impact on bait removal in control plots than ant suppression plots. Both of these scenarios may have occurred to some extent, which would imply that scavenging may be somewhat resilient to diversity shifts in both ants and vertebrates. However, it seems likely that ants have a greater potential for functional compensation than vertebrates in our study system. This is because ants are ubiquitous in subtropical environments, compared with vertebrate distributions which are sparser and more stochastic. Ants are frequently the first scavengers to discover and remove small food resources, as previously mentioned (Bond & Breytenbach, 1985; Fellers & Fellers, 1982; Tan & Corlett, 2012). Thus, there may be a greater chance that ants will discover the food resources left over when vertebrates are excluded, than the chance vertebrates will discover the resources left over when ants are suppressed—leading to a lower capacity for functional compensation in vertebrates. However, it should be noted that our study took place over 24-h periods, and a longer period would have given vertebrates a larger window of opportunity for bait discovery—but this approach would have increased the likelihood of the complete depletion of baits across plots, making it impossible to quantify differences in ant and vertebrate scavenging roles.

To date, the evidence has been highly mixed regarding the capacity for scavenger groups to functionally compensate. Some studies show that there is little functional compensation by scavenger groups when others are excluded (e.g. Griffiths et al., 2018; Hill et al., 2018), while others have shown that certain scavengers can compensate for the loss of others (e.g. Ewers et al., 2015; Olson et al., 2012; Youngsteadt et al., 2015). Our results agree with a desert study (Brown et al., 1979), in which the exclusion of mammals had a greater positive impact on the relative abundance of ants than the exclusion of ants did on the relative abundance of mammals. However, Brown et al. (1979) did not measure any functional responses of ants and mammals in terms of bait removal efforts.

By showing that ants have a greater capacity for functional compensation than vertebrates, our results contrast with Griffiths et al. (2018) which found no functional compensation between ants and vertebrates, but corroborates, another similar study which found that invertebrates (likely to be mostly ants) compensated almost fully in removing seeds when vertebrates were excluded (Ewers et al., 2015). It is not clear why these differences occurred, but may be due to differences in local assemblages of vertebrate scavengers. There is yet to be a global analysis of scavenger activity and abundances across biomes, which is necessary to compare scavenging rates in different areas. In addition, a previous study exploring vertebrate scavenging of large carrion did not detect compensatory responses when dominant scavengers (vultures) were excluded (Hill et al., 2018), and hence our findings may only be relevant to scavengers of small food resources. Two studies in temperate environments have also suggested that scavengers of small food resources and small carrion can exhibit compensatory responses when dominant scavenger groups are experimentally excluded (Olson et al., 2012; Youngsteadt et al., 2015). Thus, our results support some previous research in suggesting that some scavenger groups can functionally compensate for the loss of others—indicating that the impact of biodiversity loss on scavenging as an ecosystem function may be buffered to some extent.

It is important to note that any compensation that may occur in the case of scavenger declines is not likely to buffer the impact on ecosystems, as different scavenger species have varying effects on ecosystem functioning. For example, ants are critical for the maintenance of healthy soils due to their nest-building and nutrient redistribution activities (Frouz & Jilková, 2008). Neither ant nor vertebrate scavengers could fully mitigate the loss of the other group, meaning scavenging in our study system is not fully resilient to biodiversity change. In addition, the variation of results shown across similar studies carried out in different localities suggest that the scavenging contribution of invertebrates and vertebrates is biogeographic. Further scavenger exclusion studies are needed to assess the stability of scavenging across ecosystems. Nonetheless, our results highlight the remarkable role ants play in scavenging food resources, despite their small size. Our study adds to the ever-growing body of evidence that underlines the critical importance of ants in ecosystem functioning.

AUTHOR CONTRIBUTIONS

Alice E. L. Walker, Catherine L. Parr, Mark P. Robertson and Paul Eggleton conceived the study. Alice E. L. Walker collected data. Alice E. L. Walker and Adam M. Fisher conducted the analysis and produced the figures. Alice E. L. Walker wrote the first draft

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of the manuscript and Catherine L. Parr, Adam M. Fisher, Mark P. Robertson and Paul Eggleton contributed to critical evaluation of the manuscript for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Zenodo data repository https://doi.org/10.5281/zenodo.8383092 (Walker et al., 2023).

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REFERENCES

Abernethy, E. F., Turner, K. L., Beasley, J. C., DeVault, T. L., Pitt, W. C., & Rhodes, O. E., Jr. (2016). Carcasses of invasive species are predominantly utilized by invasive scavengers in an Island ecosystem. *Ecosphere*, *7*, e01496.

Angulo, E., Caut, S., & Cerdá, X. (2011). Scavenging in Mediterranean ecosystems: Effect of the invasive Argentine ant. *Biological Invasions*, *13*, 1183–1194.

Barlow, J., França, F., Gardner, T. A., Hicks, C. C., Lennox, G. D., Berenguer, E., Castello, L., Economo, E. P., Ferreira, J., Guénard, B., Gontijo Leal, C., Isaac, V., Lees, A. C., Parr, C. L., Wilson, S. K., Young, P. J., & Graham, N. A. J. (2018). The future of hyperdiverse tropical ecosystems. *Nature*, *559*, 517–526.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Bayer Environmental Science. (2017a). *Maxforce® Ant Bait Granules material safety data sheet BES/SA0064*.

Bayer Environmental Science. (2017b). *Premise® 200SC material safety data sheet BES/SA0076*.

Beasley, J. C., Olson, Z. H., & DeVault, T. L. (2015). Ecological role of vertebrate scavengers. In M. E. Benbow, J. K. Tomberlin, & A. M. Tarone (Eds.), *Carrion ecology, evolution and their applications* (pp. 107–127). CRC Press.

Beasley, J. C., Olson, Z. H., Selva, N., & Devault, T. L. (2019). *Ecological functions of vertebrate scavenging*. Springer International Publishing.

Bestelmeyer, B. T., & Wiens, J. A. (2003). Scavenging ant foraging behavior and variation in the scale of nutrient redistribution among semi-arid grasslands. *Journal of Arid Environments*, *53*, 373–386.

Biggs, C. R., Yeager, L. A., Bolser, D. G., Bonsell, C., Dichiera, A. M., Hou, Z., Keyser, S. R., Khursigara, A. J., Lu, K., Muth, A. F., Negrete, B., & Erisman, B. E. (2020). Does functional redundancy affect ecological stability and resilience? A review and meta-analysis. *Ecosphere*, *11*, e03184.

Bond, W., & Breytenbach, G. (1985). Ants, rodents and seed predation in Proteaceae. *African Zoology*, *20*, 150–154.

Brown, J. H., Davidson, D. W., & Reichman, O. J. (1979). An experimental study of competition between seed-eating desert rodents and ants. *American Zoologist*, *19*(4), 1129–1143. https://doi.org/10.1093/icb/19.4.1129

Brown, M. B., Schlacher, T. A., Schoeman, D. S., Weston, M. A., Huijbers, C. M., Olds, A. D., & Connolly, R. M. (2015). Invasive carnivores alter ecological function and enhance complementarity in scavenger assemblages on ocean beaches. *Ecology*, *96*, 2715–2725.

Cooper, W. (2000). Tradeoffs between predation risk and feeding in a lizard, the broad-headed skink (*Eumeces laticeps*). *Behaviour*, *137*, 1175–1189.

Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., & Magurran, A. E. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science*, *344*, 296–299.

Elahi, R., O'Connor, M. I., Byrnes, J. E., Dunic, J., Eriksson, B. K., Hensel, M. J., & Kearns, P. J. (2015). Recent trends in local-scale marine biodiversity reflect community structure and human impacts. *Current Biology*, *25*, 1938–1943.

Ewers, R. M., Boyle, M. J., Gleave, R. A., Plowman, N. S., Benedick, S., Bernard, H., Bishop, T. R., Bakhtiar, E. Y., Chey, V. K., & Chung, A. Y. (2015). Logging cuts the functional importance of invertebrates in tropical rainforest. *Nature Communications*, *6*, 6836.

Fayle, T. M., Bakker, L., Cheah, C., Ching, T. M., Davey, A., Dem, F., Earl, A., Huaimei, Y., Hyland, S., & Johansson, B. (2011). A positive relationship between ant biodiversity (Hymenoptera: Formicidae) and rate of scavenger-mediated nutrient redistribution along a disturbance gradient in a south-east Asian rain forest. *Myrmecological News*, *14*, 5–12.

Fellers, G. M., & Fellers, J. H. (1982). Scavenging rates of invertebrates in an eastern deciduous forest. *American Midland Naturalist*, *107*, 389–392.

Frouz, J., & Jilková, V. (2008). The effect of ants on soil properties and processes (Hymenoptera: Formicidae). *Myrmecological News*, *11*, 191–199.

Gerke, H. C., Hinton, T. G., Okuda, K., & Beasley, J. C. (2022). Increased abundance of a common scavenger affects allocation of carrion but not efficiency of carcass removal in the Fukushima Exclusion Zone. *Scientific Reports*, *12*, 8903.

Gonzalez, A., & Loreau, M. (2009). The causes and consequences of compensatory dynamics in ecological communities. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 393–414.

Griffiths, H. M., Ashton, L. A., Walker, A. E., Hasan, F., Evans, T. A., Eggleton, P., & Parr, C. L. (2018). Ants are the major agents of resource removal from tropical rainforests. *Journal of Animal Ecology*, *87*, 293–300.

Hill, J. E., Devault, T. L., Beasley, J. C., Rhodes, O. E., & Belant, J. L. (2018). Effects of vulture exclusion on carrion consumption by facultative scavengers. *Ecology and Evolution*, *8*, 2518–2526.

Hölldobler, B., & Wilson, E. O. (1990). *The ants*. Harvard University Press.

Hosaka, T., Di, L., Eguchi, K., & Numata, S. (2019). Ant assemblages on littered food waste and food removal rates in urban–suburban parks of Tokyo. *Basic and Applied Ecology*, *37*, 1–9.

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Huijbers, C. M., Schlacher, T. A., Schoeman, D. S., Olds, A. D., Weston, M. A., & Connolly, R. M. (2015). Limited functional redundancy in vertebrate scavenger guilds fails to compensate for the loss of raptors from urbanized sandy beaches. *Diversity and Distributions*, *21*, 55–63.

Inger, R., Cox, D. T. C., Per, E., Norton, B. A., & Gaston, K. J. (2016). Ecological role of vertebrate scavengers in urban ecosystems in the UK. *Ecology and Evolution*, *6*, 7015–7023.

Inger, R., Per, E., Cox, D. T. C., & Gaston, K. J. (2016). Key role in ecosystem functioning of scavengers reliant on a single common species. *Scientific Reports*, *6*, 29641.

Liang, J., Bi, G., & Zhan, C. (2020). Multinomial and ordinal logistic regression analyses with multi-categorical variables using R. *Annals of Translational Medicine*, *8*, 982.

Mares, M. A., & Rosenzweig, M. L. (1978). Granivory in North and South American deserts: Rodents, birds, and ants. *Ecology*, *59*, 235–241.

Mucina, L., & Rutherford, M. C. (2006). *The vegetation of South Africa*. Lesotho and Swaziland.

Naeem, S. (1998). Species redundancy and ecosystem reliability. *Conservation Biology*, *12*, 39–45.

Olson, Z. H., Beasley, J. C., Devault, T. L., & Rhodes, O. E. (2012). Scavenger community response to the removal of a dominant scavenger. *Oikos*, *121*, 77–84.

Orihuela-Torres, A., Pérez-García, J. M., Sánchez-Zapata, J. A., Botella, F., & Sebastián-González, E. (2022). Scavenger guild and consumption patterns of an invasive alien fish species in a Mediterranean wetland. *Ecology and Evolution*, *12*(8), e9133.

Orrock, J. L., & Danielson, B. J. (2004). Rodents balancing a variety of risks: Invasive fire ants and indirect and direct indicators of predation risk. *Oecologia*, *140*, 662–667.

Parr, C., Eggleton, P., Davies, A., Evans, T., & Holdsworth, S. (2016). Suppression of savanna ants alters invertebrate composition and influences key ecosystem processes. *Ecology*, *97*, 1611–1617.

Parr, C. L., Lehmann, C. E. R., Bond, W. J., Hoffmann, W. A., & Andersen, A. N. (2014). Tropical grassy biomes: Misunderstood, neglected, and under threat. *Trends in Ecology & Evolution*, *29*, 205–213.

R Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rosenfeld, J. S. (2002). Functional redundancy in ecology and conservation. *Oikos*, *98*, 156–162.

Schultheiss, P., Nooten, S. S., Wang, R., Wong, M. K., Brassard, F., & Guénard, B. (2022). The abundance, biomass, and distribution of ants on earth. *Proceedings of the National Academy of Sciences of the United States of America*, *119*, e2201550119.

Sugiura, S., & Hayashi, M. (2018). Functional compensation by insular scavengers: The relative contributions of vertebrates and invertebrates vary among islands. *Ecography*, *41*, 1173–1183.

Sugiura, S., Tanaka, R., Taki, H., & Kanzaki, N. (2013). Differential responses of scavenging arthropods and vertebrates to forest loss maintain ecosystem function in a heterogeneous landscape. *Biological Conservation*, *159*, 206–213.

Tan, C. K. W., & Corlett, R. T. (2012). Scavenging of dead invertebrates along an urbanisation gradient in Singapore. *Insect Conservation and Diversity*, *5*, 138–145.

Traniello, J. F. (1989). Foraging strategies of ants. *Annual Review of Entomology*, *34*, 191–210.

Turner, K. L., Conner, L. M., & Beasley, J. C. (2021). Effects of red imported fire ant (*Solenopsis invicta*) control on carrion use by vertebrate scavengers. *Food Webs*, *29*, e00212.

Walker, A. E. L., Robertson, M. P., Eggleton, P., Bunney, K., Lamb, C., Fisher, A. M., & Parr, C. L. (2022). Indirect control of decomposition by an invertebrate predator. *Functional Ecology*, *36*, 2943–2954.

Walker, A. E. L., Robertson, M. P., Eggleton, P., Fisher, A. M., & Parr, C. L. (2023). Data from: Functional compensation in a savanna scavenger community. *Zenodo Data Repository*. https://doi.org/10.5281/zenodo.8383092

Walker, M. A., Uribasterra, M., Asher, V., Getz, W. M., Ryan, S. J., Ponciano, J. M., & Blackburn, J. K. (2021). Factors influencing scavenger guilds and scavenging efficiency in Southwestern Montana. *Scientific Reports*, *11*, 4254.

Wilson, E. E., & Wolkovich, E. M. (2011). Scavenging: How carnivores and carrion structure communities. *Trends in Ecology & Evolution*, *26*, 129–135.

Youngsteadt, E., Henderson, R. C., Savage, A. M., Ernst, A. F., Dunn, R. R., & Frank, S. D. (2015). Habitat and species identity, not diversity, predict the extent of refuse consumption by urban arthropods. *Global Change Biology*, *21*, 1103–1115.

SUPPORTING INFORMATION

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

Figure S1. Variation in non-ant invertebrate abundances in ant suppression and control plots.

Figure S2. Poison residue analyses of soil, grass and tree leaves in ant suppression plots.

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