

RESEARCH ARTICLE

Indirect control of decomposition by an invertebrate predator

Alice E. L. Walker^{1,2}  | Mark P. Robertson³  | Paul Eggleton⁴  | Katherine Bunney³  |
Candice Lamb³ | Adam M. Fisher⁵  | Catherine L. Parr^{1,3,6} 

¹School of Environmental Sciences, University of Liverpool, Liverpool, UK; ²Department of Geography, UCL, London, UK; ³Department of Zoology & Entomology, University of Pretoria, Pretoria, South Africa; ⁴Soil Biodiversity Group, Department of Life Sciences, Natural History Museum, London, UK; ⁵School of Biological and Behavioural Sciences, Queen Mary University of London, London, UK and ⁶School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, South Africa

Correspondence

Alice E. L. Walker

Email: alicewalker24@gmail.com**Funding information**Natural Environment Research Council;
Royal Society**Handling Editor:** Verónica Ferreira**Abstract**

1. Understanding the factors that control decomposition is critical for predicting how the carbon cycle will alter with global change. Until recently, the accepted paradigm was that climate primarily drives decomposition rates, and interactions among decomposers only control variation at finer scales. Although it is now understood that biotic agents can play an important role, we know less about the importance of species interactions with a lack of field experiments at a large scale. Predation is a key ecological interaction that could influence decomposition by directly or indirectly regulating the abundances of decomposer organisms, but a comprehensive understanding of the cascading effects that predation can have on decomposition, particularly at large scales, is missing.
2. Here we report on an experiment where we suppressed the abundance of ants, which are major predators of termites, at a hectare scale in a natural African savanna and examined how this affected the decomposition of three common substrates (wood, grass and dung).
3. Our study revealed that ants exert considerable top-down control on decomposition via their predation of termites: decomposition of wood, grass and dung increased by 98%, 74% and 84% with ant suppression, respectively. Suppression of ants increased termite activity and consequently resulted in increased termite-mediated decomposition. Remarkably, for all substrates, the suppression of ants nearly doubled decomposition by termites. Additionally, for grass and dung substrates, the dominant agent of decomposition switched from microbes to termites with ant suppression.
4. Our study highlights the critical importance of considering species interactions in decomposition studies, particularly given declines in predatory species in the Anthropocene.

KEYWORDS

biotic interactions, ecosystem functioning, predator-prey, savanna, trophic cascade

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *Functional Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

1 | INTRODUCTION

Decomposition is a fundamental ecosystem process that recycles carbon and nutrients from plant litter and organic matter (Swift et al., 1979). It therefore has a major influence on carbon flux (Griffiths et al., 2021), nutrient dynamics (Freschet et al., 2013) and below-ground ecosystem functioning (Meier & Bowman, 2008; Wardle et al., 2004). Determining the biotic drivers of decomposition rates will, therefore, be vital for predicting how ecosystem change will affect ecosystem functioning. This may be particularly relevant in tropical ecosystems, which play a critical role in carbon cycling and storage (Mitchard, 2018; Scurlock & Hall, 1998), yet are undergoing rapid change.

Traditionally, climate and litter quality have been considered the dominant controls on decomposition rate, and the impact of decomposer organisms was considered to be relatively small (Swift et al., 1979). Recent studies, however, have suggested that variation in populations of decomposer organisms can influence decomposition rates globally (Bradford et al., 2017; García-Palacios et al., 2013) and that these effects can be independent of climate (Allison, 2012; McGuire & Treseder, 2010). Moreover, several studies have investigated whether interspecific interactions, via effects on decomposer organisms, can drive variation in decomposition rates (see Sitvarin et al., 2016 for a review). However, the magnitude and direction of the relationships shown is highly variable across the aforementioned studies (Sitvarin et al., 2016).

Predation is arguably one of the most ecologically influential interspecies interactions, as it can as it can indirectly and directly determine coexistence of species and alter species abundances (Salo et al., 2010; Sheriff et al., 2020). Predation can also affect the diversity of non-prey species via trophic cascades (Pace et al., 1999). Consequently, predation can strongly affect the structure and functioning of ecosystems (Duffy, 2002; Schmitz et al., 2010). Predatory species are currently in global decline (Estes et al., 2011), with climate change likely to alter predator-prey interactions further (Gilg et al., 2009; Laws, 2017; Wilmers et al., 2007). For example, increased metabolisms due to higher temperatures may lead to higher predation rates, and CO₂-induced physiological changes in predators may decrease predation rates (Laws, 2017). Therefore, having a holistic understanding of the direct and indirect ecosystem effects of predators is important for predicting future ecosystem changes.

Although there is consistent evidence to suggest that predation can regulate abundances of herbivores and have cascading effects on herbivory (the green food web; reviewed in Schmitz et al., 2000), evidence for the impact of predation on decomposers and decomposition (the brown food web) is somewhat mixed. Studies have found positive (Lawrence & Wise, 2000; Melguizo-Ruiz et al., 2020), negative (Liu et al., 2014; Wu et al., 2011; Wu et al., 2014) and neutral (Cates et al., 2021; Denmead et al., 2017; Hocking & Babbitt, 2014; Namba & Ohdachi, 2016) relationships between predation and decomposition across studies (reviewed in Sitvarin et al., 2016). Why predation has been found to have variable effects on decomposition

is not fully understood but may be caused by differences in predator trophic guild – that is, predators that directly consume decomposer species may have negative cascading effects on decomposition (Lawrence & Wise, 2000; Wu et al., 2011; Wyman, 1998), whereas higher-trophic level predators that prey on the predators of decomposers, or on microbivores, may release decomposers from predation and, therefore, have positive cascading effects (Lawrence & Wise, 2004; McGlynn & Poirson, 2012; Melguizo-Ruiz et al., 2020). Moreover, a number of studies reported no predation effect on decomposition, which was attributed to high levels of functional redundancy within brown food webs (Cates et al., 2021), the complexity of food web pathways (Miyashita & Niwa, 2006; Namba & Ohdachi, 2016) and other biotic or abiotic factors overshadowing any predation effect (Denmead et al., 2017; Hocking & Babbitt, 2014; Homyack et al., 2010; López-Rodríguez et al., 2018). Notably, there is a lack of large-scale (>8 × 8 m), open plot experiments in previous literature (though see Parr et al., 2016 and Cates et al., 2021), as the vast majority of studies employed mesocosms, which run the risk of artefacts arising due to small scales and enclosure of the study organisms (Petersen & Hastings, 2001). Previous studies are also biased towards non-tropical systems, which is a concern given the vital importance of biomes such as savannas and rainforests to carbon cycling and storage (Mitchard, 2018; Scurlock & Hall, 1998). Thus, we lack a comprehensive understanding of the factors determining the existence, direction and strength of predation effects on decomposition, and studies are needed to broaden the experimental and geographical scale upon which our knowledge is based.

Macroinvertebrates, particularly termites, play a crucial role in decomposition in tropical and subtropical ecosystems (Griffiths et al., 2019; Wood & Sands, 1978). As such, determining the controls on termite-mediated decomposition is a critical part of understanding how these ecosystems function. Research into the determinants of termite abundance and activity has largely focussed on bottom-up controls such as climate (e.g. Cerezer et al., 2020, Davies et al., 2015), and top-down controls such as predation have received little attention. Recent work suggests that termite-feeding mammals may exert top-down pressures on termite activity and decomposition rates, although it is not clear whether this is due to direct predation of termites or to physical disturbance of termites by the predator (Coggan et al., 2016). Yet, in most tropical and subtropical ecosystems ants are the major invertebrate predator of termites (Tuma et al., 2020). Being far more widespread and abundant than termite-feeding mammals, ants have the potential to influence termite-mediated processes to a much greater extent (Parr et al., 2016). However, anthropogenic pressures, such as invasive species, land-use change and climate change, are likely to alter ant abundance patterns and species distributions (Bertelsmeier et al., 2015; Bertelsmeier et al., 2018; Parr & Bishop, 2022). For example, climate change may have particularly strong negative impacts on ant abundances in tropical systems, yet potentially positive impacts in temperate regions (Parr & Bishop, 2022). This means that predator-prey interactions involving ants may shift in the future, which could have cascading

consequences for processes such as decomposition, that are mediated by prey species such as termites.

Here, we suppressed the abundance of ants on 1 ha open plots in a South African savanna and measured how this affected macroinvertebrate-mediated decomposition in three common organic substrates, which represent the dominant vegetation in the system: grass and wood, and less-well studied but common organic inputs, herbivore dung. Specifically, we quantified how ant suppression (1) affected the abundance and activity of termite decomposers; (2) affected macroinvertebrate-mediated decomposition across substrates, and evaluated the importance of termites to decomposition (to establish their role as key macroinvertebrate decomposers in our study system) and finally, (4) we determined whether ant suppression altered the balance of macroinvertebrate versus microbial decomposition rates. We predicted that ant suppression would positively influence termite abundance and activity, resulting in an increase in macroinvertebrate decomposition across all substrates. We demonstrate a strong indirect effect of ants on macroinvertebrate-mediated decomposition rates across a range of common decomposition substrates and propose that these trends are largely due to a release of the major decomposer, termites, from ant predation.

2 | MATERIALS AND METHODS

2.1 | Field site

This study was conducted at the Wits Rural Facility, University of Witwatersrand (WRF; 24°32'39S, 31°06'10 E) in the Limpopo Province, South Africa, a 350 ha area of lowveld savanna which lies 580 m above sea level. Seasonal rain occurs during the summer months (December–April), and mean annual rainfall is 652 mm ± 200 mm (1992–2018, WRF weather station). Mean monthly temperature is 21.1°C (2016–2018, WRF weather station). All elements of this study were carried out between November 2017 and February 2020. Permission to conduct the fieldwork was granted by the University of Witwatersrand.

2.2 | Ant suppression

We suppressed ants at four sites across the Wits Rural Facility, separated by at least 300 m. Within each site, we established two plots with similar vegetation and topographic characteristics: one suppression plot of 1 ha (100 m × 100 m) and one control plot of 0.25 ha (50 m × 50 m), totalling eight experimental plots. The suppression plots were larger due to a 25 m buffer zone surrounding the core 0.25 ha area to reduce the chance of ants from outside the area foraging in the core sampling area (Parr et al., 2016). Application of the ant suppression treatment began in November 2017 (and is currently ongoing) and consisted of two types of baits treated with insecticides (Appendix S1). The suppression treatment was applied to the

entire 1 ha area of the suppression plots, with sampling conducted within the core area. Following Parr et al. (2016), our ant suppression treatment minimises detrimental non-target effects: the baits were designed to appeal to ants and did not negatively affect the abundances of other invertebrates (Appendix S2), and no residual chemicals were detected in the environment (Appendices S3 and S4). To determine when re-application of the suppression treatment was needed, we monitored ant abundance on suppression and control plots every month using food baits (Appendix S5), reapplying the treatment when ant abundance on the suppression plots reached >20% of that on the control plots. This ensured we did not over-apply the poison, following integrated pest management protocols (Flint, 2012). To determine whether any ant genera were unsusceptible to the suppression treatment, we collected ants using pitfall traps in March 2019 (3 months after the start of the decomposition experiment, and 1.5 years after the start of the suppression experiment; Appendix S5). Ants were identified to genus at the Universities of Liverpool and Pretoria.

2.3 | Termite abundance and activity

Comparing savanna termite abundances is notoriously difficult at local scales because there tends to be high variability in termite activity throughout the day and across seasons, and different sampling methods vary in their efficiency (Davies et al., 2021). Nevertheless, we used the best method available given the circumstances and combined these data with other measures of activity to quantify the effect of ants on termites. In February 2020 (2 months after the last remaining decomposition bags were collected – see below – and 2.25 years after the start of the suppression experiment, which was still ongoing at this time), we assessed termite abundance in soil pits (Davies et al., 2021). Unfortunately, these data do not represent termite abundance and activity when the decomposition bags were on the plots, as we were unable to collect termite data during the decomposition experiment. However, these data were collected when the ant suppression treatment was in effect, and as such they reflect effects of ant suppression on termites, and give an indication of what termite responses during the decomposition experiment may have been. Three transects were established on each plot (10 m spacing between them) and five soil pits (20 cm length × 20 cm width × 20 cm depth) were dug per transect (15 samples per plot). Soil was carefully searched for invertebrates. Specimens were identified in the laboratory using a microscope, and termites were counted.

To determine whether termite activity levels increased in response to ant suppression, we quantified levels of sheeting on the plots in January and March 2019. Fungus-growing termite species construct runways and galleries from soil on prospective food resources, and on the ground while foraging (sheeting) to protect workers from desiccation and predation (Wood & Sands, 1978). As such, termite sheeting can be used to indicate termite activity (Cheik et al., 2019; Veldhuis et al., 2017). Five out of the seven most common termite genera in our study system are fungus-growing

termites (*Microtermes*, *Allodontermes*, *Ancistrotermes*, *Odontotermes* and *Macrotermes*), which are also highly abundant (K. Bunney, unpublished data), and thus, despite excluding non-fungus growing termites from our measurements, this method captures the activity of the majority of termites at our site. Termite sheeting was quantified along four parallel 50 m transects on each plot, spaced 10 m apart. We recorded the length of each incidence of sheeting at the beginning and end-points where sheeting crossed the transect, and the total length of sheeting was summed for each transect. The first measurements were taken in January 2019, 1 month after all decomposition bags had been deployed (mid-wet season). The second set of measurements were taken in March 2019, 4 months after the start of the decomposition experiment (end of wet season).

2.4 | Decomposition assay

The decomposition experiment took place between December 2018 and December 2019 using three substrates: grass, dung and wood. We used three substrates for several reasons: firstly, to avoid the risk of one substrate type producing anomalous results. Secondly, to appeal to a range of decomposers (particularly termites, which have differing feeding habits; Eggleton & Tayasu, 2001). Thirdly, to ensure our results are broadly relevant across a range of common substrates in African savannas. Decomposition bags (20×20 cm) were constructed from 300-micron nylon mesh (Plastok), folded twice along the edges and sealed with staples. Grass decomposition bags contained 10 g of the common native grass *Themeda triandra*, oven dried at 70°C for 48 h. Dung decomposition bags contained 20 g of elephant dung (collected from surrounding game reserves) dried at 70°C for 48 h. Wood decomposition bags contained blocks of a non-native pine, (*Pinus radiata*; 203.6 g ± SE 24.4 g), dried at 120°C for 48 h. We used this species as some of our decomposition bags contributed to a global decomposition study, with *P. radiata* as a common substrate.

To separate the contribution of termites to decomposition we used two bag designs: termite-accessible (open) and termite-inaccessible (closed), with half the bags for each substrate accessible to termites, and termites excluded from the remaining half. For the termite-accessible bags, we created access holes in half of the decomposition bags by punching nine holes (~7 mm in diameter) in the bottom with a standard hole punch (Griffiths et al., 2019). We used punched holes, as opposed to coarse mesh bags, to minimise leaching of the substrates and to maintain similar microclimates in the two bag types. Following Griffiths et al. (2019) we assumed that decomposition in closed bags is predominantly microbe-mediated, although some macroinvertebrate decomposers such as Oribatid mites and Collembola may have accessed the closed bags.

A total of 20 open and 20 closed bags containing dung ($n = 320$), 20 open and 20 closed bags containing grass ($n = 320$) and 40 open and 40 closed bags containing wood ($n = 640$) were placed on each plot in December 2018. Clusters of eight bags were spaced evenly across each plot (in a 4 × 5 grid, with grid point locations separated

by 5 m). Within each plot, at each of the 20 locations within grids, eight bags were placed on the ground in four rows: one open and one closed wood bag, one open one closed grass bag, one open and one closed dung bag, and finally another set of open and closed wood bags. Bag types were alternated so open bags were always next to closed bags, and vice versa, and each bag was separated by 10 cm. We ensured the bags were in contact with the soil surface, with open-bags placed hole-side down, so termites could access the substrates. Bags were secured to the ground using tent pegs. Decomposition bags were collected in stages at a number of time points for us to determine the optimal time point at which to perform our main analyses on the data for each substrate (i.e. where a substantial amount of mass had decomposed, but not so much that the majority of the bags had lost most of their mass, as this would obscure any effect of suppression). For grass and dung, we collected five open and five closed decomposition bags from each plot at 14, 28, 56 and 112 days, but for dung this final collection point was discarded as most bags had lost the majority of their mass. As woodblocks are slower to decompose, we collected 20 open and 20 closed bags from each plot after 6 months, and 20 open and 20 closed bags after 1 year. After collection, we separated the original substrate from any termite sheeting soil inside the bags. We distinguished termite sheeting soil from any soil that had been washed in to the decomposition bag based on colour, particle size and structure. The remaining grass and dung substrates were dried at 70°C for 48 h. The remaining woodblocks were dried at 120°C for 48 h. Total and proportional mass loss was measured and the presence or absence of termite sheeting in the open bags was noted. Bags that had been disturbed by animals or that were missing were excluded from the analysis.

2.5 | Evaluating the role of termites in decomposition

We assume that the majority of non-microbial decomposition in open bags is termite-mediated because numerous studies have shown that the dominant macroinvertebrate decomposers of wood, dead grass, and dung in African savannas are termites (e.g. Coe, 1977; Ohiagu & Wood, 1979; Freymann et al., 2008; Veldhuis et al., 2017; Leitner et al., 2018; see also Appendix S6). Additionally, in these savannas termites are the only macroinvertebrates that feed on dried grass and dung, to our knowledge (adult dung beetles eat only fresh dung; Holter, 2016). However, to establish whether termites are the dominant decomposers in this system, we assessed whether higher levels of substrate mass loss (decomposition) were linked to termite activity. We considered the presence of soil in open decomposition bags upon collection as an indication of termite activity (e.g. Stoklosa et al., 2016; Veldhuis et al., 2017) as no other animal moves soil in this way (soil was most often on the surface as sheeting, or within the wood blocks). If higher levels of mass loss are associated with the presence of termite soil, then termites are responsible for large amounts of decomposition as previous studies

in African savannas have suggested (Buxton, 1981; Collins, 1981; Ouédraogo et al., 2004).

2.6 | Data analysis

2.6.1 | Effect of ant suppression on ant abundance

We assessed whether our ant suppression treatment was effective in significantly reducing ant abundance at food baits over the course of the ant suppression experiment (October 2017–February 2020). We used a linear mixed effects model where mean ant activity score at baits for each treatment per date ($n = 44$) was our response variable, treatment (ant suppression or control) was a fixed effect and date was a random effect (Appendix S7).

2.6.2 | Responses of termites to ant suppression

We analysed the response of termites to ant suppression by determining how termite abundance in soil pit samples varied between our ant suppression and control plots. We modelled this using a Poisson generalised linear mixed effects model with log link structure, where the abundance of termites was the response variable, treatment was the fixed effect, and site was included as a random effect (Appendix S7). We included an additional 'observation-level-random effect' to account for overdispersion (Harrison, 2014). We also analysed how termite activity (termite sheeting) changed in response to ant suppression using a linear mixed effects model, where the total length of sheeting per plot was the response variable, treatment and month (January or March) were the fixed effects and plot was the random effect (Appendix S7).

2.6.3 | Role of termites in decomposition

We assessed whether the presence of termite sheeting on the substrates was linked to greater amounts of mass loss (i.e. decomposition) in open bags. As we were interested in a correlation between soil and mass loss, all collection time points were pooled to capture bags in various stages of decomposition. We conducted a generalised linear model for each substrate, where the presence or absence of sheeting per bag was the binomial response variable, percentage mass loss was the fixed effect, and the random effects structure was plot nested within site (Appendix S7).

2.6.4 | Decomposition rate

For each substrate, we determined how ant suppression affected decomposition rates by calculating the decomposition constant (k) for each combination of treatment and bag type following Olson (1963) (Appendix S8).

2.6.5 | Effect of ant suppression on decomposition in open and closed bags

For each substrate, we assessed the effect of treatment (ant suppression and control) and bag type (open and closed) on decomposition in terms of proportional mass loss. We selected the final collection time point for each substrate for these analyses (1 year for wood, 112 days for grass, and 56 days for dung), to ensure that sufficient time had passed for measurable decomposition to occur. We used a linear mixed effects model with logit-transformed proportional mass loss as the response variable, with treatment, bag type (open or closed) and their interaction as fixed effects, and plot nested within site was the random effects structure (Appendix S7). Both fixed effects were retained in the final model as these were central to the design of the experiment.

All linear (lmer function) and generalised linear (glmer function) mixed models were conducted using the LME4 package (Bates et al., 2015) in R and were visually assessed for normality of residuals, homogeneity of variance and goodness of fit. For models with more than one fixed effect, the most parsimonious model was determined by removing non-significant terms sequentially (starting with least significant first) from the maximal model. Due to low power in our experimental design, marginally non-significant effects ($p < 0.1$) were kept in models.

2.6.6 | Percentage of decomposition performed by macroinvertebrates and microbes

We determined the mean absolute percentage of each substrate that was decomposed by macroinvertebrates and microbes on the suppression and control plots. For each treatment, the percentage decomposed by microbes was taken to be the mean percentage of mass lost from the closed bags. We subtracted this from the mean percentage of mass lost from the open bags to give the macroinvertebrate contribution (% mass loss in open bags minus % mass loss in closed bags). In other words, decomposition by macroinvertebrate equals decomposition by both decomposers minus decomposition by microbes.

We calculated the relative contributions of macroinvertebrate and microbes to decomposition on ant suppression and control plots for each substrate. To do this, we used the macroinvertebrate contribution (%) and microbe contribution (%) as described above, expressing these as a percentage of total decomposition.

3 | RESULTS

3.1 | Effect of ant suppression on ant activity

On average, ant abundance at baits was 71% lower on ant suppression plots than the controls throughout the ant suppression experiment (October 2017–January 2020; $df = 71$, $t = 7.729$,

$p < 0.001$; Appendix S9). Low abundance on control plots in July–September is due to reduced activity in the dry season. In March 2019, data from pitfall traps indicated that the majority of ant genera responded negatively to ant suppression (Appendix S10). Two exceptions were the genera *Myrmecaria* and *Pheidole*, which had recently recolonised several ant suppression plots (Appendix S10). We are confident that these were recent recolonisations, because ant abundance at bait cards was substantially lower in the 3 months leading up to March 2019 (the first 3 months of the decomposition experiment; Appendix S9). This, together with our subsequent re-application of suppression treatment in March 2019 being successful in reducing ant numbers for the remainder of the experiment (Appendix S9), means we are confident that the long-term effects of ant suppression are reflected in our data for this study.

3.2 | Response of termites to ant suppression

Termite abundance in soil pits was 53.1% higher on ant suppression plots compared with control plots (mean = 49 ± 15 (SE) and 32 ± 14 (SE) for ant suppression and control respectively), although the effect of ant suppression on termite abundance was marginally non-significant, likely due to a very small sample size ($df = 5$, $Z = 1.62$, $p = 0.10$; Figure 1a). The mean length of sheeting recorded on ant suppression plots was 77% higher than on control plots on average, and the effect of ant suppression was significant (10.8 ± 2.0 m (SE) versus 6.1 ± 1.2 m (SE), respectively: $df = 12$, $t = 2.265$, $p = 0.043$, Figure 1b).

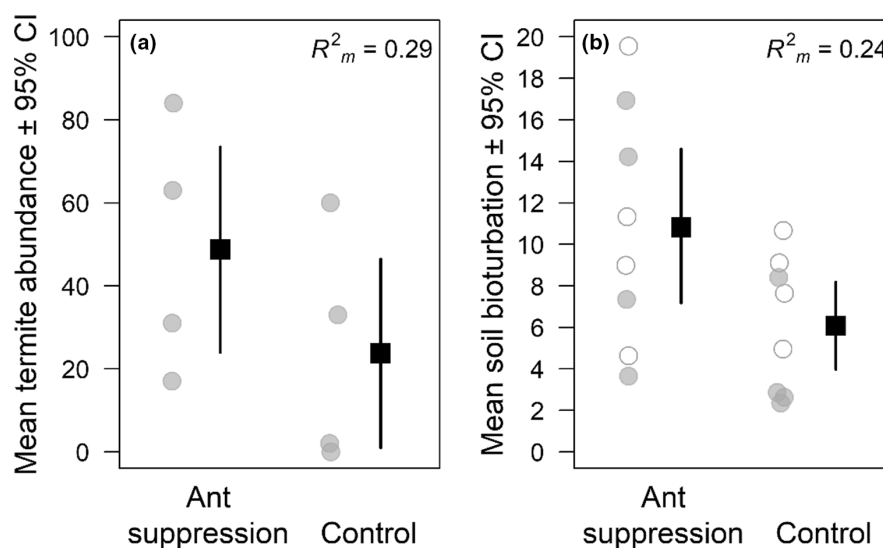


FIGURE 1 (a) Variation in the abundance of termites collected in soil pits in ant suppression and control plots, where square points represent mean abundance of termites for each treatment, and each circular point represents total abundance of termites in a plot. (b) Variation in the length of soil (i.e. sheeting) freshly bioturbated by termites in suppression and control plots, measured in January 2019 (open circular points) and March 2019 (closed points), where square points represent the mean length of sheeting for each treatment, and each circular point represent total length of sheeting in a plot. For (a) and (b), lines represent bootstrapped 95% confidence intervals.

3.3 | The role of termites in resource decomposition

In macroinvertebrate-accessible (open) decomposition bags, termite sheeting occurred in 60.3% of wood, 22.0% of grass, and 48.0% of dung decomposition bags (all time periods combined). Across the suppression and control plots, the presence of sheeting and thus, presence of termites, was associated with higher levels of mass loss (Figure 2). This was true for wood ($df = 313$, $Z = 6.08$, $p < 0.001$), grass ($df = 146$, $Z = 5.07$, $p < 0.001$) and dung ($df = 148$, $Z = 5.87$, $p < 0.001$; Figure 2). Bags with the highest levels of mass loss always contained soil (Figure 2).

3.4 | Effect of ant suppression on macroinvertebrate- and microbe-mediated decomposition

A total of 1152 undisturbed decomposition bags were collected across all substrates, treatments and collection time points (619 of wood, and 305 of grass and 305 of dung). As expected, the mass of all three substrates declined with time (Figure 3). Overall, dung decayed quickest, with wood decaying slowest. Substrates in open bags decayed faster than the same substrate in closed bags (Figures 3 and 4; Appendix S11). In all cases, substrates in open bags in ant suppression plots decayed faster (higher k value) than open bags in control plots (Appendix S11). There was no consistent trend in decay rate with closed bags.

In the open bags (decomposition by macroinvertebrates and microbes), mean mass loss was significantly higher on ant suppression

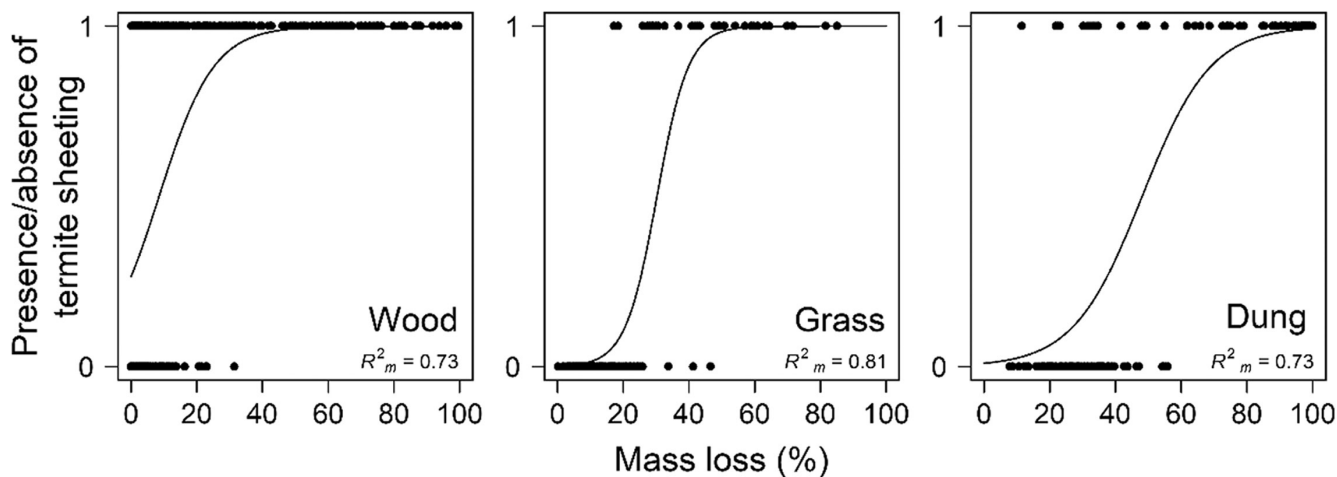


FIGURE 2 Across all ant suppression and control plots, the relationship between the presence of sheeting in termite-accessible (open) bags and mass loss (%) within open decomposition bags containing wood, grass and dung, where 0 represents the absence of sheeting and 1 represents presence. Points represent raw data, lines represent model-predicted probabilities.

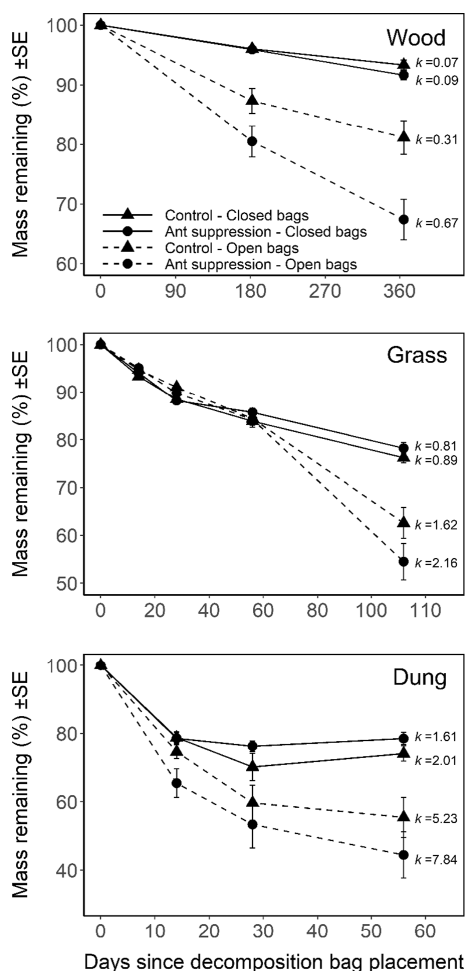


FIGURE 3 Mean mass lost over time from decomposition bags accessible to both termites and microbes (open bags) and from decomposition bags accessible only to microbes (closed bags) containing wood, grass and dung collected at different time points in the ant suppression and control plots. k values (Appendix S11) are given to indicate decomposition rate inside each set of decomposition bags.

plots than the control plots for wood and grass (wood, $32.6 \pm (\text{SE}) 3.4\%$ vs. $18.9 \pm 2.8\%$, $df = 296$, $t = 3.36$, $p = 0.01$; grass, $45.5 \pm 3.8\%$ vs. $37.4 \pm 3.2\%$, $df = 72$, $t = 2.21$, $p = 0.03$) and was also higher for dung ($55.6 \pm 6.7\%$ vs. $44.6 \pm 5.8\%$, $df = 71$, $t = 1.77$, $p = 0.08$; Figures 3 and 4; Appendix S11), although this was marginally non-significant. In the closed bags, as expected, there was no difference in mass loss between the ant suppression and the control plots for any of the substrates (wood, $8.4 \pm 0.8\%$ vs. $6.7 \pm 0.8\%$; $df = 296$, $t = 0.80$, $p = 0.45$; grass, $21.8 \pm 1.2\%$ vs. $23.8 \pm 1.2\%$, $df = 71$, $t = 0.69$, $p = 0.50$; dung, $21.5 \pm 1.8\%$ vs. $25.9 \pm 2.2\%$, $df = 71$, $t = 0.73$, $p = 0.46$; Figures 3 and 4; Appendix S11).

When comparing bag types, the increase in mass loss in open bags compared with closed bags was significant for both the suppression plots (wood, $df = 296$, $t = 7.36$, $p < 0.001$; grass, $df = 72$, $t = 6.61$, $p < 0.001$; dung, $df = 71$, $t = 5.25$, $p < 0.001$; Figures 3 and 4; Appendix S11) and control plots (wood, $df = 296$, $t = 3.89$, $p < 0.001$; grass, $df = 72$, $t = 3.79$, $p < 0.001$; dung, $df = 71$, $t = 2.65$, $p < 0.01$; Figures 3 and 4; Appendix S11). Thus, the macroinvertebrate contribution to absolute mass loss (macroinvertebrate contribution = open bag – closed bag) on suppression plots was nearly double that of control plots for wood (24.2% vs. 12.2%; 98% higher decomposition), grass (23.7% vs. 13.6%; 74% higher decomposition) and dung (34.1% vs. 18.7%; 84% higher decomposition).

3.5 | Percentage of decomposition performed by macroinvertebrates and microbes

For wood, the major decomposition agents were macroinvertebrates on both suppression and control plots. However, on control plots 65% of wood decomposition was due to macroinvertebrates and 35% was due to microbes, whereas a higher percentage of total wood decomposition was attributed to termites in suppression plots (74%) and a smaller percentage of total decomposition to microbes (26%; Figure 5b). For grass, in the control plots microbes were the

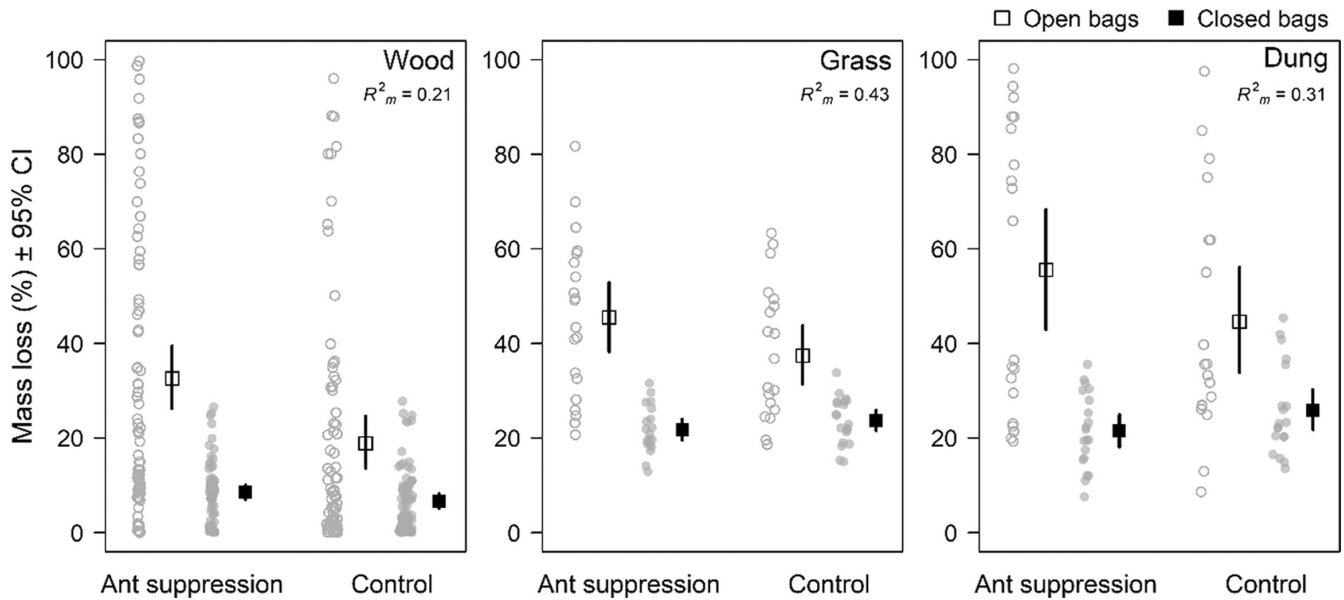


FIGURE 4 Variation in the proportion of substrate mass lost from termite-accessible (open) decomposition bags (unfilled points), and termite-inaccessible (closed) decomposition bags (filled points), in ant suppression and control plots. Bags contained dried wood (collected after 1 year), grass (collected after 112 days) and dung (collected after 56 days), and were placed in ant suppression and control plots. Open and filled square points represent mean mass loss in open and closed bags respectively, lines represent model-predicted 95% confidence intervals, and open and filled circular points represent raw mass loss within open and closed decomposition bags, respectively.

dominant agents of decomposition (63.6% of total decomposition compared with 36.4% by macroinvertebrate), whereas in suppression plots the dominant agent switched to macroinvertebrates (52.1% of total decomposition compared with 47.9% by microbes; Figure 5d). For dung, in control plots microbes were also the dominant agents of decomposition (58.1% of total decomposition compared with 41.9% attributed to macroinvertebrates), although yet again, this switched on the ant suppression plots (61.3% of total decomposition by termites compared with 38.7% by microbes, Figure 5f).

4 | DISCUSSION

We demonstrate that decomposition, a key ecosystem process, can be indirectly controlled by predation to a large extent. Suppressing ants increased termite-mediated decomposition for all three substrates that were tested (wood, grass and dung), relative to controls (Figures 3–5; Appendix S11). This led to a switch in dominant decomposer for two of the substrates tested, from microbes to termites (Figure 5c–f). Our findings add to a growing body of evidence showing that top-down pressures from interspecies interactions can have cascading effects within brown food webs and enhance our understanding of how ecosystems may respond to future changes in predator–prey interactions, which are being disrupted by climate and land-use change (Gilg et al., 2009; Laws, 2017; Schwab et al., 2021; Wilmers et al., 2007).

We show that suppressing ants led to an increase in decomposition at a large scale, and across all three of our experimental substrates (Figures 3–5). It is likely that much of the increase in

decomposition in the absence of ants can be attributed to termites for several reasons. Firstly, the presence of large amounts of termite soil within open bags (Figure 2) indicates high levels of termite activity on the substrates, as only termites move soil in this way. Secondly, we found strong evidence that soil sheeting on, and soil within, the macroinvertebrate-accessible substrates was associated with the highest levels of decomposition for all substrates (Figure 2), indicating that termites were highly active and dominant macroinvertebrate decomposers in our study system (also see Appendix S6). Thirdly, we observed no evidence of wood boring beetles in the wood blocks after collection; indeed, at our study site in another experiment using wood blocks with bark, we similarly found no evidence for wood-boring beetles (K. Bunney, unpublished data) suggesting they are a minor element in these savannas. Finally, our results are consistent with a previous study in the same system, which found that cellulose decomposition (which was attributed to termites) increased when ants were suppressed (Parr et al., 2016), suggesting that the ant–termite predator–prey system is an important aspect of decomposition pathways in African savannas.

The variation in response with substrates (wood showing the largest effect and grass showing the smallest, Figures 3–5), may be due to termite genera which feed on wood (such as *Microtermes*, *Allodotermites*, *Ancistrotermes*, *Odontotermites* and *Macrotermes*) dominating our study system (K. Bunney, unpublished data). Thus, the ecological release of this group may have caused the unexpectedly large effect of ant suppression on wood decomposition. Considering the significant role savannas play in carbon storage and cycling, with wood in particular comprising a large portion of carbon stocks in some savannas (Grace et al., 2006; Scurlock & Hall, 1998), our

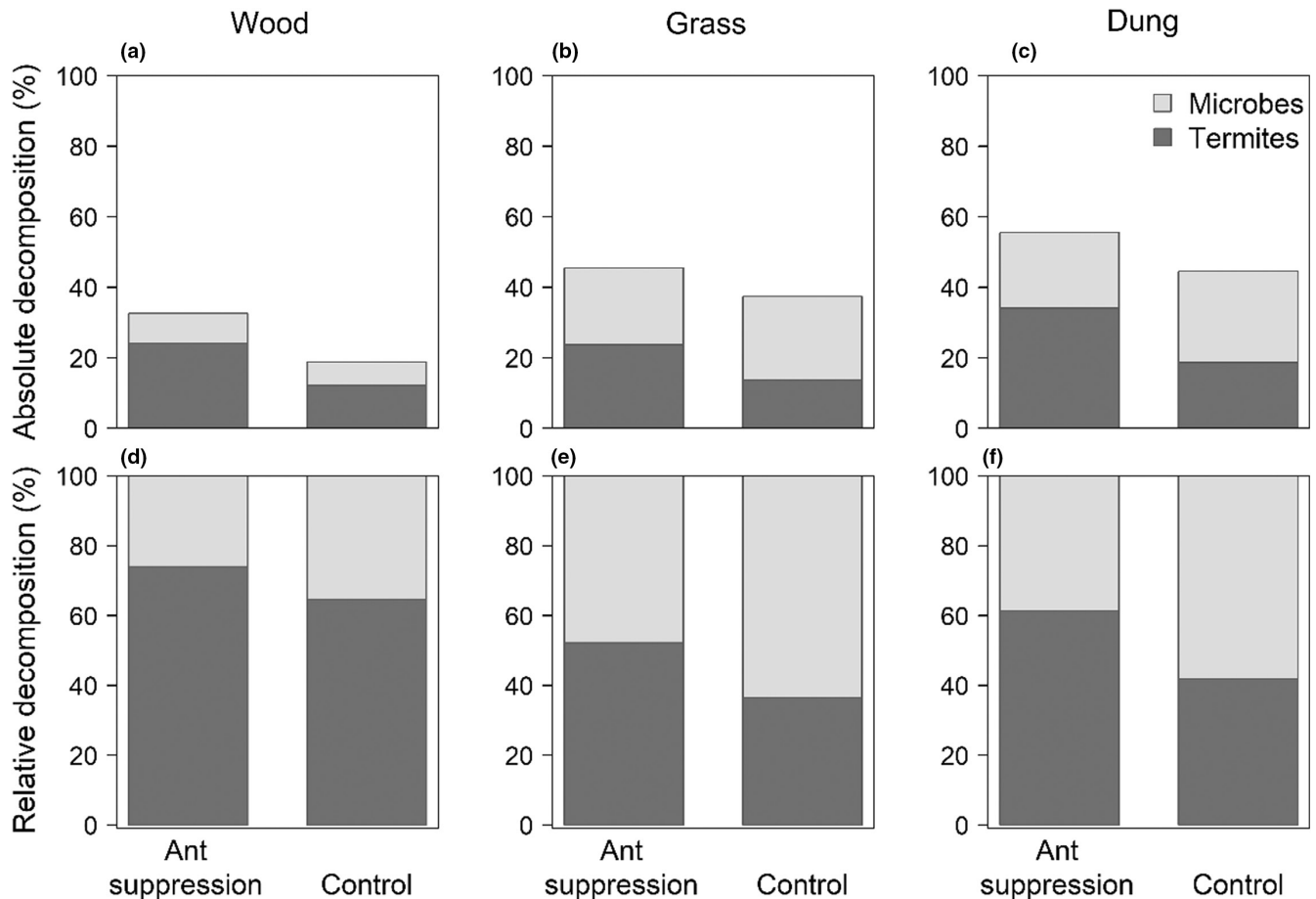


FIGURE 5 Variation in the total (a, c, e) and relative (b, d, f) contributions of termites and microbes to decomposition between ant suppression and control plots for three substrates: wood (collected after 1 year), grass (collected after 112 days) and dung (collected after 56 days). Decomposition attributable to termites was calculated by subtracting mass loss in closed bags from mass loss in open bags. Mass loss due to microbes is presumed to be the mass loss in closed bags.

findings may be important for understanding future shifts in carbon fluxes with changes in predator–prey interactions (Gilg et al., 2009; Laws, 2017). Importantly, our estimates of predation effects on decomposition are likely to be conservative: it is not possible to remove all ants with our treatment, and up to 20% of ants remained on the suppression plots at all times likely contributing to some predation. Therefore, the total effect of ant predation on decomposition is almost certainly greater than our results suggest.

The marginally non-significant increase in the abundance of termites when ants were suppressed (Figure 1a,b) is likely influenced by the small sample size and sampling challenges (as termite abundance is difficult to accurately measure and compare locally; Davies et al., 2021), but is suggestive that ants exert top-down control on termites in this environment. There may be several reasons we detected a cascading effect of predation on decomposition, where many other studies (including those on large-scales) did not (Cates et al., 2021; Denmead et al., 2017; Hocking & Babbitt, 2014; Namba & Ohdachi, 2016; Sitvarin et al., 2016). First, the extremely high abundance and ubiquity of the predators (ants) in this study far outweighs that of previous large-scale studies, which have examined effects of ants in temperate regions (where they are naturally less

abundant; Cates et al., 2021; Kendrick et al., 2015), or focused on vertebrate predators (such as salamanders and shrews; Hocking & Babbitt, 2014; Namba & Ohdachi, 2016), which are present at far lower abundances than ants. Ants are by far the most abundant predatory group in our system, comprising 80% of invertebrates collected in pitfall traps (A. Walker, unpublished data), and are much more ubiquitous than termite-feeding vertebrates such as aardvarks and lizards. Thus, our suppression of a highly active and abundant predator led to the large effects on decomposition that we observed. Moreover, when we suppressed ants, no other termite predator compensated for the loss of ants in predating termites to any great extent. This means that the ecological role of termite predation has little functional redundancy, with ants being major agents. This contrasts with a previous large-scale study by Cates et al. (2021) that found no effect of ant exclusion on decomposition, which was attributed to functional redundancy in the invertebrate predator community. Finally, there also appears to be little functional redundancy in the role of macroinvertebrate-decomposition in our study system, as termites are the dominant invertebrate decomposers of wood, grass and dung (Figure 2). This contradicts previous literature which suggests that soil communities have a high degree of functional

redundancy (Setälä et al., 2005), and suggests that decomposition in African savannas may be sensitive to changes in ant and termite assemblages.

Levels of microbe-mediated decomposition did not vary between the ant suppression and control plots. As a result, with ant suppression, the contribution of termite-mediated decomposition increased relative to microbe-mediated decomposition (Figure 5). In the case of dung and grass, the dominant agent of decomposition switched from microbes to termites (Figure 5). While microbes are often the primary biotic agent of decomposition (e.g. Donald et al., 2018), our results indicate that this balance can be determined by predator abundance. Termite and microbe-mediated decomposition may respond differently to climate change (for example, increased decomposition by termites but decreased decomposition by bacteria, during droughts; Ashton et al., 2019). As such, considering the role of predation in mediating the relative importance of these groups may be important for understanding future shifts in decomposition rates. However, our estimates of the relative contribution of microbes to decomposition must be regarded with caution for two reasons. First, our study uses microbe-mediated decomposition as measured in the absence of macroinvertebrates to infer to contribution of microbes to decomposition in the presence of macroinvertebrates. This ignores the possibility that termite decomposition of substrates can lead to increased microbial abundance (Ulyshen et al., 2016). Second, our pre-experimental treatment of the substrates (see Methods) removed all pre-existing microbes, meaning microbial decomposition was likely hindered whilst microbes recolonised the substrates. Thus, our estimate of microbe-mediated decomposition may be an underestimate of natural microbial decomposition.

Our findings that changes to predator abundance can dramatically affect key ecosystem processes such as decomposition are significant because ants and other predators are under threat. Climate change is predicted to alter ant abundances (increases in temperate regions, and decreases in the tropics; Parr & Bishop, 2022), and land-use changes such as logging can affect ant diversity and ant-mediated ecosystem functions (Luke et al., 2014; Schwab et al., 2021). Many vertebrate predators of macroinvertebrate decomposers are also under threat and are undergoing declines due to anthropogenic pressures (e.g. pangolins and anteaters, Heinrich et al., 2016; Bertassoni et al., 2019). At a global scale, predator-prey interactions across food webs are also expected to be affected by human activities, such as altering prey foraging behaviour (and thus exposure to predators), and changing the composition of predator-prey communities (Gilg et al., 2009; Laws, 2017; Wilmers et al., 2007). Our study suggests that these changes to predator populations may have strong indirect effects on decomposition. As decomposition influences carbon flux, nutrient dynamics and below-ground ecosystem processes (Freschet et al., 2013; Griffiths et al., 2021; Wardle et al., 2004), these effects may cascade to other aspects of ecosystem functioning with, unknown consequences. We, therefore, highlight the critical importance of assessing the indirect effects of changes in predator abundance on key ecosystem processes, particularly in light of the

threats posed to predator and prey communities by anthropogenically induced global change (Bertelsmeier et al., 2016; Laws, 2017; Wilmers et al., 2007).

AUTHOR CONTRIBUTIONS

Alice E. L. Walker, Katherine Bunney, Catherine L. Parr, Mark P. Robertson and Paul Eggleton conceived the study. Alice E. L. Walker, Katherine Bunney and CL 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 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.

ACKNOWLEDGEMENTS

We are grateful to the fantastic field assistants at the Wits Rural Facility, particularly Frank Nyathi whose unyielding hard work has made this project possible. We thank Wayne Twine and Cameron Watt for their logistical support at the Wits Rural Facility, which has been hugely helpful over the course of this long-term project. We also thank Thomas Bishop for comments on analysis and manuscript. We are grateful to Monica Leitner for assistance with project planning and logistics. We kindly acknowledge the LC-MS Synapt Facility (Department of Chemistry, University of Pretoria) for chromatography and mass spectrometry services provide by Madelien Wooding. The experiment was funded through a Royal Society-DCDO African Capacity Building Initiative award to C.L.P. and M.P.R., and a NERC ACCE Doctoral Training Partnership studentship to AELW.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and R codes needed to reproduce the analysis are available in the Zenodo Digital Repository <https://doi.org/10.5281/zenodo.6385484> (Walker et al., 2022).

ORCID

Alice E. L. Walker  <https://orcid.org/0000-0002-5193-6357>

Mark P. Robertson  <https://orcid.org/0000-0003-3225-6302>

Paul Eggleton  <https://orcid.org/0000-0002-1420-7518>

Katherine Bunney  <https://orcid.org/0000-0002-6079-3319>

Adam M. Fisher  <https://orcid.org/0000-0002-9532-9575>

Catherine L. Parr  <https://orcid.org/0000-0003-1627-763X>

REFERENCES

- Allison, S. (2012). A trait-based approach for modelling microbial litter decomposition. *Ecology Letters*, 15, 1058–1070.
- Ashton, L. A., Griffiths, H. M., Parr, C. L., Evans, T. A., Didham, R. K., Hasan, F., Teh, Y. A., Tin, H. S., Vairappan, C. S., & Eggleton, P. (2019). Termites mitigate the effects of drought in tropical rainforest. *Science*, 363(6423), 174–177. <https://doi.org/10.1126/science.aau9565>

- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, arXiv:1406.5823v1.
- Bertassoni, A., Costa, R. T., Gouvea, J. A., Bianchi, R. d. C., Ribeiro, J. W., Vancine, M. H., & Ribeiro, M. C. (2019). Land-use changes and the expansion of biofuel crops threaten the giant anteater in southeastern Brazil. *Journal of Mammalogy*, *100*, 435–444.
- Bertelsmeier, C., Blight, O., & Courchamp, F. (2016). Invasions of ants (Hymenoptera: Formicidae) in light of global climate change. *Myrmecological News*, *22*, 25–42.
- Bertelsmeier, C., Luque, G. M., Hoffmann, B. D., & Courchamp, F. (2015). Worldwide ant invasions under climate change. *Biodiversity and Conservation*, *24*, 117–128.
- Bertelsmeier, C., Ollier, S., Liebhold, A. M., Brockerhoff, E. G., Ward, D., & Keller, L. (2018). Recurrent bridgehead effects accelerate global alien ant spread. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 5486–5491.
- Bradford, M. A., Veen, G. F., Bonis, A., Bradford, E. M., Classen, A. T., Cornelissen, J. H. C., Crowther, T. W., De Long, J. R., Freschet, G. T., Kardol, P., Manrubia-Freixa, M., Maynard, D. S., Newman, G. S., Logtestijn, R. S. P., Vikeftoft, M., Wardle, D. A., Wieder, W. R., Wood, S. A., & Van Der Putten, W. H. (2017). A test of the hierarchical model of litter decomposition. *Nature Ecology & Evolution*, *1*, 1836–1845.
- Buxton, R. (1981). Termites and the turnover of dead wood in an arid tropical environment. *Oecologia*, *51*, 379–384.
- Cates, A. M., Wills, B. D., Kim, T. N., Landis, D. A., Gratton, C., Read, H. W., & Jackson, R. D. (2021). No evidence of top-down effects by ants on litter decomposition in a temperate grassland. *Ecosphere*, *12*, e03638.
- Cerezer, F. O., Azevedo, R. A., Nascimento, M. A. S., Franklin, E., Morais, J. W., & Dambros, C. (2020). Latitudinal gradient of termite diversity indicates higher diversification and narrower thermal niches in the tropics. *Global Ecology and Biogeography*, *29*, 1967–1977.
- Cheik, S., Bottinelli, N., Soudan, B., Harit, A., Chaudhary, E., Sukumar, R., & Jouquet, P. (2019). Effects of termite foraging activity on topsoil physical properties and water infiltration in Vertisol. *Applied Soil Ecology*, *133*, 132–137.
- Coe, M. (1977). The role of termites in the removal of elephant dung in the Tsavo (East) National Park Kenya. *African Journal of Ecology*, *15*, 49–55.
- Coggan, N. V., Hayward, M. W., & Gibb, H. (2016). Termite activity and decomposition are influenced by digging mammal reintroductions along an aridity gradient. *Journal of Arid Environments*, *133*, 85–93.
- Collins, N. (1981). The role of termites in the decomposition of wood and leaf litter in the southern Guinea savanna of Nigeria. *Oecologia*, *51*, 389–399.
- Davies, A. B., Eggleton, P., van Rensburg, B. J., & Parr, C. L. (2015). Seasonal activity patterns of African savanna termites vary across a rainfall gradient. *Insectes Sociaux*, *62*(2), 157–165. <https://doi.org/10.1007/s00040-014-0386-y>
- Davies, A., Parr, C., & Eggleton, P. (2021). A global review of termite sampling methods. *Insectes Sociaux*, *68*, 1–12.
- Denmead, L. H., Darras, K., Clough, Y., Diaz, P., Grass, I., Hoffmann, M. P., Nurdiansyah, F., Fardiansah, R., & Tschantke, T. (2017). The role of ants, birds and bats for ecosystem functions and yield in oil palm plantations. *Ecology*, *98*, 1945–1956.
- Donald, J., Weir, I., Bonnett, S., Maxfield, P., & Ellwood, M. D. F. (2018). The relative importance of invertebrate and microbial decomposition in a rainforest restoration project. *Restoration Ecology*, *26*, 220–226.
- Duffy, J. E. (2002). Biodiversity and ecosystem function: The consumer connection. *Oikos*, *99*, 201–219.
- Eggleton, P., & Tayasu, I. (2001). Feeding groups, lifestyles and the global ecology of termites. *Ecological Research*, *16*, 941–960.
- Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., & Jackson, J. B. (2011). Trophic downgrading of planet Earth. *Science*, *333*, 301–306.
- Flint, M. L. (2012). IPM in practice. In *Principles and methods of integrated pest management* (2nd ed.). University of California Agriculture and Natural Resources.
- Freschet, G. T., Cornwell, W. K., Wardle, D. A., Elumeeva, T. G., Liu, W., Jackson, B. G., Onipchenko, V. G., Soudzilovskaia, N. A., Tao, J., & Cornelissen, J. H. (2013). Linking litter decomposition of above- and below-ground organs to plant–soil feedbacks worldwide. *Journal of Ecology*, *101*, 943–952.
- Freyman, B. P., Buitenwerf, R., Desouza, O., & Olf, H. (2008). The importance of termites (Isoptera) for the recycling of herbivore dung in tropical ecosystems: A review. *European Journal of Entomology*, *105*, 165–173.
- García-Palacios, P., Maestre, F. T., Kattge, J., & Wall, D. H. (2013). Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. *Ecology Letters*, *16*, 1045–1053.
- Gilg, O., Sittler, B., & Hanski, I. (2009). Climate change and cyclic predator–prey population dynamics in the high Arctic. *Global Change Biology*, *15*, 2634–2652.
- Grace, J., Jose, J. S., Meir, P., Miranda, H. S., & Montes, R. A. (2006). Productivity and carbon fluxes of tropical savannas. *Journal of Biogeography*, *33*, 387–400.
- Griffiths, H. M., Ashton, L. A., Evans, T. A., Parr, C. L., & Eggleton, P. (2019). Termites can decompose more than half of deadwood in tropical rainforest. *Current Biology*, *29*, R118–R119.
- Griffiths, H. M., Eggleton, P., Hemming-Schroeder, N., Swinfield, T., Woon, J. S., Allison, S. D., Coomes, D. A., Ashton, L. A., & Parr, C. L. (2021). Carbon flux and forest dynamics: Increased deadwood decomposition in tropical rainforest tree-fall canopy gaps. *Global Change Biology*, *27*, 1601–1613.
- Harrison, X. A. (2014). Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*, *2*, e616. <https://doi.org/10.7717/peerj.616>
- Heinrich, S., Wittmann, T. A., Prowse, T. A., Ross, J. V., Delean, S., Shepherd, C. R., & Cassey, P. (2016). Where did all the pangolins go? International CITES trade in pangolin species. *Global Ecology and Conservation*, *8*, 241–253.
- Hocking, D. J., & Babbitt, K. J. (2014). Effects of red-backed salamanders on ecosystem functions. *PLoS ONE*, *9*, e86854.
- Holter, P. (2016). Herbivore dung as food for dung beetles: Elementary coprology for entomologists. *Ecological Entomology*, *41*, 367–377.
- Homyack, J. A., Sucre, E. B., Haas, C. A., & Fox, T. R. (2010). Does *Plethodon cinereus* affect leaf litter decomposition and invertebrate abundances in mixed oak forest? *Journal of Herpetology*, *44*, 447–456.
- Kendrick, J. A., Ribbons, R. R., Classen, A. T., & Ellison, A. M. (2015). Changes in canopy structure and ant assemblages affect soil ecosystem variables as a foundation species declines. *Ecosphere*, *6*, art77.
- Lawrence, K. L., & Wise, D. H. (2000). Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. *Pedobiologia*, *44*, 33–39.
- Lawrence, K. L., & Wise, D. H. (2004). Unexpected indirect effect of spiders on the rate of litter disappearance in a deciduous forest. *Pedobiologia*, *48*, 149–157.
- Laws, A. N. (2017). Climate change effects on predator–prey interactions. *Current Opinion in Insect Science*, *23*, 28–34.
- Leitner, M., Davies, A. B., Parr, C. L., Eggleton, P., & Robertson, M. P. (2018). Woody encroachment slows decomposition and termite activity in an African savanna. *Global Change Biology*, *24*, 2597–2606.
- Liu, S., Chen, J., He, X., Hu, J., & Yang, X. (2014). Trophic cascade of a web-building spider decreases litter decomposition in a tropical forest floor. *European Journal of Soil Biology*, *65*, 79–86.
- López-Rodríguez, M. J., Martínez-Megías, C., Salgado-Charrar, A. C., Cámara-Castro, J. P., & Tierno De Figueroa, J. M. (2018). The effect

- of large predators on the decomposition rate and the macroinvertebrate colonization pattern of leaves in a Mediterranean stream. *International Review of Hydrobiology*, 103, 90–98.
- Luke, S. H., Fayle, T. M., Eggleton, P., Turner, E. C., & Davies, R. G. (2014). Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo. *Biodiversity and Conservation*, 23, 2817–2832.
- McGlynn, T. P., & Poirson, E. K. (2012). Ants accelerate litter decomposition in a Costa Rican lowland tropical rain forest. *Journal of Tropical Ecology*, 28, 437–443.
- McGuire, K. L., & Treseder, K. K. (2010). Microbial communities and their relevance for ecosystem models: Decomposition as a case study. *Soil Biology and Biochemistry*, 42, 529–535.
- Meier, C. L., & Bowman, W. D. (2008). Links between plant litter chemistry, species diversity, and below-ground ecosystem function. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 19780–19785.
- Melguizo-Ruiz, N., Jiménez-Navarro, G., De Mas, E., Pato, J., Scheu, S., Austin, A. T., Wise, D. H., & Moya-Laraño, J. (2020). Field exclusion of large soil predators impacts lower trophic levels and decreases leaf-litter decomposition in dry forests. *Journal of Animal Ecology*, 89, 334–346.
- Mitchard, E. T. A. (2018). The tropical forest carbon cycle and climate change. *Nature*, 559, 527–534.
- Miyashita, T., & Niwa, S. (2006). A test for top-down cascade in a detritus-based food web by litter-dwelling web spiders. *Ecological Research*, 21, 611–615.
- Namba, T., & Ohdachi, S. D. (2016). Top-down cascade effects of the long-clawed shrew (*Sorex unguiculatus*) on the soil invertebrate community in a cool-temperate forest. *Mammal Study*, 41, 119–130.
- Ohiagu, C., & Wood, T. (1979). Grass production and decomposition in Southern Guinea savanna, Nigeria. *Oecologia*, 40, 155–165.
- Olson, J. S. (1963). Energy storage and the balance of producers and decomposers in ecological systems. *Ecology*, 44, 322–331.
- Ouédraogo, E., Mando, A., & Brussaard, L. (2004). Soil macrofaunal-mediated organic resource disappearance in semi-arid West Africa. *Applied Soil Ecology*, 27, 259–267.
- Pace, M. L., Cole, J. J., Carpenter, S. R., & Kitchell, J. F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution*, 14, 483–488.
- 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., & Bishop, T. R. (2022). The response of ants to climate change. *Global Change Biology*, 28, 3188–3205.
- Petersen, J. E., & Hastings, A. (2001). Dimensional approaches to scaling experimental ecosystems: Designing mousetraps to catch elephants. *The American Naturalist*, 157, 324–333.
- Salo, P., Banks, P. B., Dickman, C. R., & Korpimäki, E. (2010). Predator manipulation experiments: Impacts on populations of terrestrial vertebrate prey. *Ecological Monographs*, 80, 531–546.
- Schmitz, O. J., Hambäck, P. A., & Beckerman, A. P. (2000). Trophic cascades in terrestrial systems: A review of the effects of carnivore removals on plants. *The American Naturalist*, 155, 141–153.
- Schmitz, O. J., Hawlena, D., & Trussell, G. C. (2010). Predator control of ecosystem nutrient dynamics. *Ecology Letters*, 13, 1199–1209.
- Schwab, D., Wurz, A., Grass, I., Rakotomalala, A. A. N. A., Osen, K., Soazafy, M. R., Martin, D. A., & Tschardtke, T. (2021). Decreasing predation rates and shifting predator compositions along a land-use gradient in Madagascar's vanilla landscapes. *Journal of Applied Ecology*, 58, 360–371.
- Scurlock, J. M. O., & Hall, D. O. (1998). The global carbon sink: A grassland perspective. *Global Change Biology*, 4, 229–233.
- Sheriff, M. J., Peacor, S. D., Hawlena, D., & Thaker, M. (2020). Non-consumptive predator effects on prey population size: A dearth of evidence. *Journal of Animal Ecology*, 89, 1302–1316.
- Sitvarin, M. I., Rypstra, A. L., & Harwood, J. D. (2016). Linking the green and brown worlds through nonconsumptive predator effects. *Oikos*, 125, 1057–1068.
- Setälä, H., Berg, M. B., & Jones, T. H. (2005). Trophic structure and functional redundancy in soil communities. In *Biological diversity and function in soils* (pp. 236–249). Cambridge University Press.
- Stoklosa, A. M., Ulyshen, M. D., Fan, Z., Varner, M., Seibold, S., & Müller, J. (2016). Effects of mesh bag enclosure and termites on fine woody debris decomposition in a subtropical forest. *Basic and Applied Ecology*, 17, 463–470.
- Swift, M. J., Heal, O. W., & Anderson, J. M. (1979). *Decomposition in terrestrial ecosystems*. Blackwell.
- Tuma, J., Eggleton, P., & Fayle, T. M. (2020). Ant-termite interactions: An important but under-explored ecological linkage. *Biological Reviews*, 95, 555–572.
- Ulyshen, M. D., Diehl, S. V., & Jeremic, D. (2016). Termites and flooding affect microbial communities in decomposing wood. *International Biodeterioration & Biodegradation*, 115, 83–89.
- Veldhuis, M. P., Laso, F. J., Olf, H., & Berg, M. P. (2017). Termites promote resistance of decomposition to spatiotemporal variability in rainfall. *Ecology*, 98, 467–477.
- Walker, A., Robertson, M., Eggleton, P., Bunney, K., Lamb, C., Fisher, A., & Parr, K. (2022). Indirect control of decomposition by an invertebrate predator. *Zenodo*, <https://doi.org/10.5281/zenodo.6385484>.
- Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., Van Der Putten, W. H., & Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. *Science*, 304, 1629–1633.
- Wilmers, C. C., Post, E., & Hastings, A. (2007). The anatomy of predator-prey dynamics in a changing climate. *Journal of Animal Ecology*, 76, 1037–1044.
- Wood, T. G., & Sands, W. A. (1978). The role of termites in ecosystems. In M. V. Brian (Ed.), *Production ecology of ants and termites* (pp. 245–292). Cambridge University Press.
- Wu, X., Duffy, J. E., Reich, P. B., & Sun, S. (2011). A brown-world cascade in the dung decomposer food web of an alpine meadow: Effects of predator interactions and warming. *Ecological Monographs*, 81, 313–328.
- Wu, X., Griffin, J. N., & Sun, S. (2014). Cascading effects of predator-detritivore interactions depend on environmental context in a Tibetan alpine meadow. *Journal of Animal Ecology*, 83, 546–556.
- Wyman, R. L. (1998). Experimental assessment of salamanders as predators of detrital food webs: Effects on invertebrates, decomposition and the carbon cycle. *Biodiversity and Conservation*, 7(5), 641–650. <https://doi.org/10.1023/a:1008856402258>

SUPPORTING INFORMATION

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

How to cite this article: 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. <https://doi.org/10.1111/1365-2435.14198>