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An invasive ant reduces diversity but does not disrupt a key ecosystem function in an African savanna

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Abstract. Understanding the consequences of anthropogenic biodiversity decline has become an increasingly urgent priority for ecologists. Biological invasions are a common result of anthropogenic habitat change, and numerous studies have established the negative impact of invasions on the diversity and abundance of native species. But fewer studies have directly examined the effect of biological invasions on ecosystem functions and services. We leveraged a recent invasion by the big-headed ant (*Pheidole megacephala*) in an East African savanna to evaluate the impact of invasion on arthropod diversity, and on dung decomposition, an ecosystem function provided by a subset of these arthropods. We found that invaded sites had lower overall arthropod diversity, but these diversity changes did not extend to a functional group of detritivorous insects (e.g., dung beetles and termites), which play key roles in dung decomposition. In a manipulative experiment, we found that rates of dung pile decomposition did not differ significantly in invaded vs. non-invaded sites. Our study provides evidence that these invaded savannas are undergoing large changes in arthropod diversity, while maintaining resilience in decomposition function, suggesting that diversity alone may be an insufficient impact assessment tool. By monitoring functional guilds and their attendant services, we may better understand the broader structural and functional consequences of invasion.

Key words: big-headed ant; decomposition; ecosystem services; insect diversity; invasive ant species; *Pheidole megacephala*.

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INTRODUCTION

Biological invasions are a significant driver of biodiversity loss worldwide (Lowe et al. 2000, Molnar et al. 2008) and can cause disruptive and long-lasting changes in ecosystems (Vitousek 1990, Strayer 2012, Prior et al. 2015). Human activity has introduced exotic species to virtually all ecosystems around the globe, and it is difficult to identify a non-invaded ecosystem (van Kleunen et al. 2015). Many biological invasions have strong impacts on native species abundance and diversity (e.g., Dejean et al. 2007, Fournier et al. 2012), and recent studies highlight the strong link between species diversity and ecosystem functions (e.g., carbon and nitrogen cycling, and decomposition; reviewed in Nielsen et al. 2011, Strayer 2012, Kitz et al. 2015). To better understand the effects of biological invasion on ecosystem functions, we must closely examine changes that occur in systems currently experiencing invasions.

Biological invasions can directly influence ecosystem function by altering nutrient pools or disturbance frequency and intensity (reviewed in Vitousek 1990). Invasive species may also indirectly alter ecosystem function by preying on or outcompeting native species and altering trophic structure (Vitousek 1990). These effects of biological invasion can be especially strong if the biological invasion impacts species that play key functional roles.

In savanna ecosystems, dung beetles and termites play large roles in driving rates of decomposition and nutrient cycling (Nichols et al. 2008, Sitters et al. 2014). Invertebrate detritivores contribute to carbon and nitrogen storage, soil aeration, and the conversion of detritus to bioavailable soil nutrients (e.g., Nichols et al. 2008, Sitters et al. 2014), and these arthropod-mediated processes have been shown to directly influence nutrient cycling and primary productivity (e.g., Lumaret et al. 1992, Nichols et al. 2008). In addition, termite activity generates spatial heterogeneity, increases plant diversity and productivity, and potentially lends stability and drought resilience to these systems at landscape scales (e.g., Pringle et al. 2010, Bonachela et al. 2015).

Tropical and subtropical ecosystems worldwide have been invaded by the "big-headed ant" *Pheidole megacephala* (Wetterer 2012). Listed by the International Union for the Conservation of Nature as one of the world's "100 worst invasive species" (Lowe et al. 2000), this ant species preys upon a broad range of arthropods (e.g., Vanderwoude et al. 2000, Holway et al. 2002). *Pheidole megacephala* likely originates from Ethiopia or Madagascar and has invaded tropical and subtropical regions on all continents except Antarctica (Wetterer 2012). Like other invasive ant species, this species can form large polydomous (multiple nest) and polygynous (multiple queen) colonies (Fournier et al. 2012). The major and minor workers of *P. megacephala* exhibit pronounced dimorphism, and both castes aggressively prey on native invertebrates (Holway et al. 2002, Dejean et al. 2007). Strong local recruitment of major and minor workers for foraging and potential recruitment from regional supercolonies makes *P. megacephala* a successful predator and extirpator of native insect species (Holway et al. 2002, Dejean et al. 2008).

The Laikipia Plateau in central Kenya is a diverse tropical ecosystem that has been invaded by *P. megacephala* in the last 5–10 yr (Riginos et al. 2015). Studies in other subtropical and tropical regions have shown that *P. megacephala* significantly reduces arthropod species abundance and diversity (e.g., Dejean et al. 2007, Fournier et al. 2012). However, we have little understanding of whether and how these effects may influence ecosystem processes.

Here we examine the effects of *P. megacephala* invasion on arthropod diversity and abundance, on decomposer diversity and abundance, and on dung decomposition rates, addressing three questions. First, is overall arthropod diversity and abundance lower in invaded vs. non-invaded sites? Second, is arthropod decomposer abundance and diversity negatively affected by *P. megacephala* invasion? And third, are rates of dung decomposition lower in invaded vs. non-invaded sites? Given the strong link between community diversity and ecosystem function (e.g., Nielsen et al. 2011 Kitz et al. 2015, Ulyshen 2016), we predicted that native decomposers would decrease in abundance and/or diversity, causing a reduction in decomposition rates of herbivore dung.

METHODS

Study location

We conducted this study in Laikipia, Kenya, at Mpala Research Centre (MRC) (0°17′ N, 36°52′ E, 1600–1800 m elevation). This region comprises two main soil types: dark "black cotton" vertisols and sandy clay loam "red soils" (Ahn and Geiger 1987). Our study was conducted on the red soils, which at MRC have been more extensively influenced by human activity and *P. megacephala* invasion.

Site selection

The invasion front of *P. megacephala* appears to have radiated outward from the main research and living quarters at MRC, and was mapped in 2013 along the unpaved road network on Mpala ranch (C. Stone, *unpublished data*). In 2014, we confirmed and updated these invasion sites by establishing belt transects parallel to the road, 15 m from the roadside. We placed peanut butter baits (Beardsley et al. 1982) every 30 m onto bare soil along this belt transect, extending 150 m in both directions. After 2 h, baits were checked for the presence of native ants and *P. megacephala*. We used these data to estimate the current "invasion front." We chose six study blocks that straddled this invasion front, consisting of an invaded site 100 m from the invasion front, and a paired non-invaded site 400 m from the leading edge of the invasion front (12 sites in total). Each study block was >500 m from the next nearest study block and >100 m from human establishments.

Arthropod community and dung decomposition surveys

We collected dung from a local cattle herd. To prevent arthropod decomposers from colonizing the freshly deposited dung, we followed cows and immediately collected dung as it was defecated. Dung was then sealed in a large plastic bin to prevent insect colonization and mixed thoroughly. We then shaped the homogeneous mixture into circular 90-cm^3 dung pile molds and recorded initial wet mass ($\bar{x}$ = 96.1 ± 6.2 g). At each of the 12 sites (two per block), we constructed three 24-m parallel belt transects, separated by 30 m, positioned at least 30 m away from the nearest road. From 08:00 to 11:00 on two consecutive days, dung samples were placed at intervals of 6 m along the center of transects, with a meter leeway in any direction to set the piles specifically onto shaded, bare soil (n = 12 dung piles per site). Seventy-two piles were randomly selected for collection after 3 d, to search for resident detritivores that recruit quickly after deposition (Lee and Wall 2006). The remaining 72 piles were collected after 25 d, to record final dry weight. Within site types, decomposition rate was highly variable for the first three weeks after deposition, perhaps due to differential liquefaction and drying of non-cellulose dung materials. We chose to collect dung piles after 25 d to examine the longer-term effect of arthropods on rates of dung breakdown: Mass losses were on average 86.6% ± 8.7%.

Arthropod decomposers exhibit a wide range of dung foraging behavior, which occurs both inside and around dung piles (dung beetles, Lee and Wall 2006, termites, Freymann et al. 2008). Thus, we collected arthropods from both inside dung piles and from the area surrounding the dung piles. Twenty-four hours before dung sample collections, we placed two soap-water pitfall traps (8 cm diameter by 8.5 cm tall) on opposite sides of every sample, 10 cm from the center of the sample. The pooled contents of these pitfall traps constituted one pitfall "survey." We set out our pitfall traps associated with dung baits on days 8, 15, 19, and 22, for collection 24 h later, to sample the insect community across multiple stages in the decomposition process. These dung baits were also uniform 100 g dung piles, and were placed in the field at the beginning of the study. These dung baits aged in line with the experimental dung piles, and we used adjacent pitfall traps to sample the associated insect community at multiple stages of decomposition.

We collected a total of 144 dung piles and 272 pitfall surveys. We carefully dissected each dung pile to search for resident insects, which consisted of mature adult termites (*Odontotermes* spp.) and beetles (Order Coleoptera). We sorted all dung and pitfall-captured insects into morphospecies and recorded species abundances in pitfalls and dung piles. We stored multiple specimens of each morphospecies in 95% ethanol and later identified them to the lowest taxonomic resolution possible. We further designated species as decomposers (detritivores) or non-decomposers (i.e., non-detritivorous residents) based on these identifications.

On day 25, dung material was collected after all arthropods were removed, dried for 12 h at 60°C (after which, piles lost no appreciable mass), and then weighed for final dry mass (n = 72).

Arthropod exclosures

To account for differences in environmental variables among blocks, we established control dung piles which were exposed to desiccation, but from which detritivores were excluded. We constructed 24 arthropod exclosures, using 12 cm diameter polyethylene tubes, cut into 5 cm long segments, and sealed on both ends with 1-mm gauge plastic gauze and an interior layer of fine mesh netting. Dung piles were placed in exclosures and sealed with fast-drying glue, and the exclosures were then externally coated with Tree Tanglefoot Insect Barrier. The layers of gauze and netting prevented entry by any insects larger than 0.1 mm in diameter. These barriers were checked every 3 d.

Two exclosures were randomly placed on shaded, bare soil in the 30 m × 24 m area at each site, at the same time as the other dung piles. After 25 d, dung piles were searched for insects and weighed for final dry mass, following our previously described protocols. Four exclosures were destroyed by wildlife and were omitted from analysis.

Statistical analysis

We calculated arthropod community diversity (using the Shannon–Weiner diversity index) separately for species collected in the pitfalls and dung samples. We only calculated arthropod diversity from the dung samples that were collected on day 3; there were no arthropods in the dung collected on day 25. We used a repeated-measures ANOVA to test for "time" as a factor in our pitfall survey analyses.

To establish that our sites accurately reflected invaded vs. non-invaded areas, we first tested for significant changes in invasive ant abundance at the two site types. We then tested whether there were changes in the diversity and abundance of arthropods at each site type. We conducted mixed-model ANOVAs to test for the effects of block and site type (invaded or non-invaded) on (1) *P. megacephala* abundance in pitfall traps (very few were found in dung piles); (2) overall arthropod diversity and abundance in pitfalls; (3) detritivore diversity and abundance in pitfalls; and (4) arthropod diversity and abundance in dung piles. We included site type as a fixed effect and block as a random effect. In all analyses, we considered blocks as replicates. Our repeated-measures ANOVA revealed no effect of "time" on pitfall diversity ($P = 0.21$) nor abundance ($P = 0.14$); we therefore pooled the species abundance data of all pitfall traps in a given block for all collection days, producing longitudinal estimates for diversity and abundance.

We conducted an ANOVA to test for the effects of arthropod exclusion and block on dung decomposition rates. This test revealed no significant variation in background decomposition rates between blocks ($P = 0.15$), so we excluded the "block" effect from subsequent tests concerning dung decomposition. We conducted a nested ANOVA to test for the effects of site type and arthropod exclusion (as a factor nested within "site type") on decomposition after 25 d.

We conducted all tests with JMP 12.0 (SAS Institute, Cary, North Carolina, USA).

RESULTS

Insect surveys

Two of our study blocks did not accurately reflect the invasion front, contrary to the findings of our peanut butter bait surveys: One site designated as "non-invaded" had a significant presence of *P. megacephala* ($\bar{x} = 72$ individuals per pitfall), and one site designated as "invaded" had very few *P. megacephala* ($\bar{x} = 2.4$ individuals per pitfall). We excluded these sites from our analyses.

Our dung pile surveys contained only detritivorous insects, while pitfall surveys contained both detritivores and non-detritivores. In pitfalls, we collected 4759 insects from 38 species across four orders (Coleoptera, Hemiptera, Hymenoptera, and Isoptera; see Appendix S1: Table S1): Six were detritivores, and 32 were non-detritivores. In dung piles, we collected 509 insects from 12 species across two orders (Coleoptera and Isoptera; see Appendix S1: Table S2): All 12 species were detritivorous dung beetles and termites.

We found no effect of block on any community abundance or diversity data: of dung pile-associated species ($F_{3,4} = 2.84$, $P = 0.17$; $F_{3,4} = 0.83$, $P = 0.54$; resp.), of pitfall-surveyed decomposer species ($F_{3,5} = 0.77$, $P = 0.56$; $F_{3,5} = 0.84$, $P = 0.53$; resp.), or of the pitfall-surveyed detritivore subgroup ($F_{3,4} = 0.52$, $P = 0.69$; $F_{3,4} = 0.41$, $P = 0.76$; resp.). We found no effect of collection date on the diversity ($F_{6,11} = 1.72$, $P = 0.21$) and abundance ($F_{6,11} = 2.08$, $P = 0.14$) of arthropods in pitfall surveys, so we pooled pitfall abundance data to produce longitudinal abundance and diversity estimates at each block.

High *P. megacephala* abundance in invaded sites was associated with low native insect diversity and abundance in pitfall traps. Mean *P. megacephala* abundance in pitfall traps was significantly higher at invaded sites ($\bar{x} = 72$) than at non-invaded sites ($\bar{x} = 2.8$; $F_{1,3} = 59.7$, $P < 0.01$; Fig. 1A). In pitfall surveys, native arthropod diversity was reduced by 55% ($F_{1,4} = 38.61$, $P < 0.01$; Fig. 1B), and abundance was reduced by 59% in invaded sites ($F_{1,4} = 8.63$, $P = 0.039$; Fig. 1C). We found *P. megacephala* individuals in four dung piles in invaded sites, but *P. megacephala* abundance was not significantly higher in dung piles ($F_{1,4} = 0.22$, $P = 0.67$). Site type did not affect diversity ($F_{1,3} = 0.52$, $P = 0.52$) or abundance ($F_{1,3} = 1.66$, $P = 0.29$) of detritivores found in pitfalls. Further, site type did not affect diversity ($F_{1,3} = 0.95$, $P = 0.40$) or abundance ($F_{1,3} = 3.38$, $P = 0.16$) of insects in dung piles.

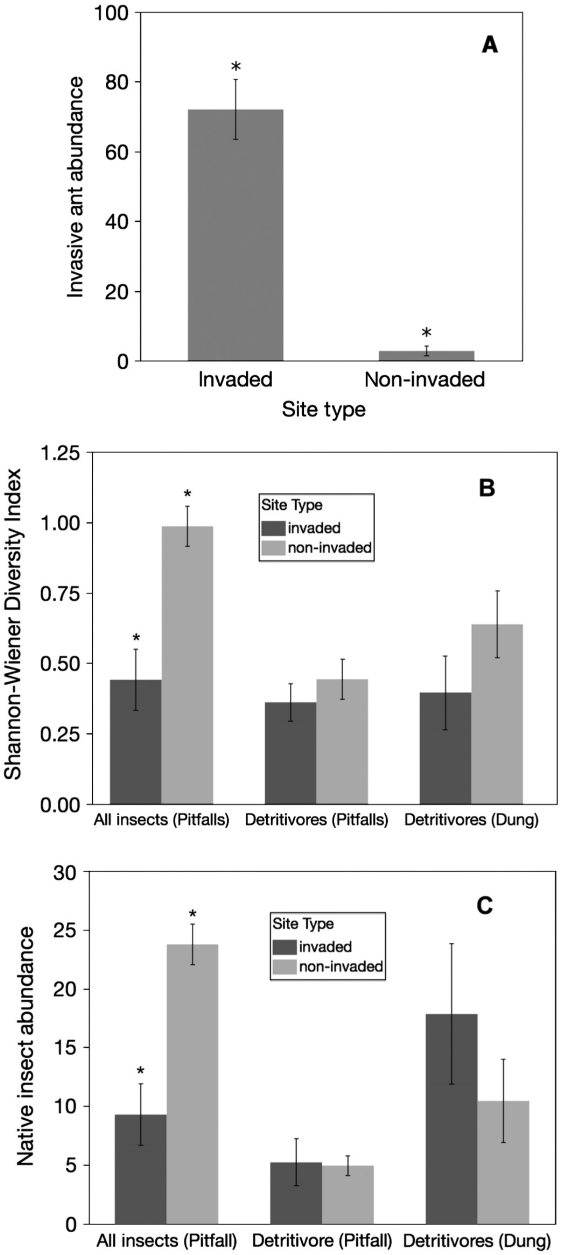

Fig. 1. (A) Abundance of *Pheidole megacephala* in pitfall traps, and (B) diversity and (C) abundance of native arthropods in pitfall traps and dung piles in invaded and non-invaded sites (mean ± SEM; $n = 4$). “All insects” refers to all detritivores and non-detritivores sampled in pitfall traps; “Detritivores” are designated by sampling method. Significant differences are denoted by an asterisk ($P < 0.05$).

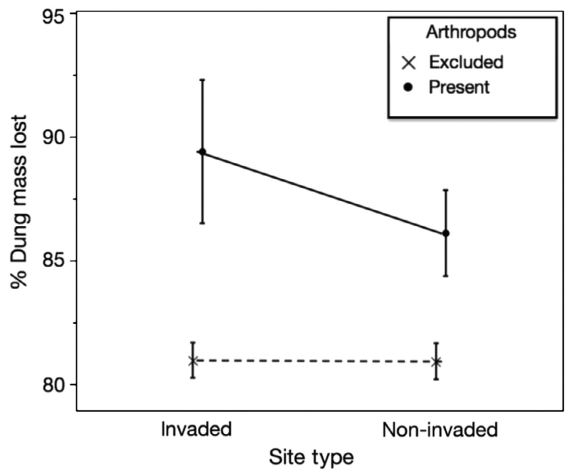

Fig. 2. Variation in dung mass loss between site types and arthropod exclusion treatments (mean ± SEM, $n = 4$). Dung mass loss was significantly lower in arthropod exclosures (a nested effect, $P < 0.01$), but was not affected by ant invasion.

Dung decomposition analysis

We found no effect of block on dung decomposition ($F_{10,11} = 5.29$, $P = 0.23$), so we removed it from the nested ANOVA model. Arthropod exclusion, as a nested effect within site type, significantly reduced rates of dung decomposition ($F_{2,7} = 5.79$, $P < 0.01$; Fig. 2), but we found no significant difference in decomposition rates between invaded and non-invaded sites for dung piles from which arthropods had been excluded ($F_{1,7} = 0.83$, $P = 0.69$; Fig. 2).

DISCUSSION

Our results suggest that *Pheidole megacephala* invasion is driving a strong decline in overall arthropod diversity and abundance, while having no detectable effects on the diversity and abundance of dung-decomposing detritivore beetles, or the decomposition functions they provide. Biological invasions often reduce native species richness and diversity, but such declines may not occur across all taxa or functional guilds. *Pheidole megacephala* invasion in other study systems often strongly reduces overall abundance and diversity of native arthropods

(Vanderwoude et al. 2000, Dejean et al. 2007, Fournier et al. 2012), and our pitfall survey results confirm that such strong changes also occur in this savanna ecosystem. Despite this substantial impact on the invertebrate community, invasion had no detectable effect on the decomposer insect guild found in pitfall and dung pile surveys. Resilient taxa include coprophagous beetles and termites (*Odontotermes* spp.), none of which experienced significant declines in abundance in the face of invasion.

The detritivore community not only was resilient with respect to species diversity and abundance, but also continued to maintain the same rates of dung decomposition in invaded savannas when compared to non-invaded areas. The abundance and diversity of detritivores has been shown to be an important factor in dung decomposition in tropical and subtropical ecosystems (Lee and Wall 2006, Slade et al. 2007, Nichols et al. 2008, Sitters et al. 2014, Kitz et al. 2015), because the tunneling and feeding action of detritivores can increase surface area in dung material, which in turn facilitates its microbially mediated breakdown. Our results demonstrate that at least in the short term (i.e., one to several years postinvasion), *P. megacephala* has little direct influence on a primary service provided by these detritivores.

The resilience of the detritivore community might be a result of the foraging preferences of *P. megacephala*. This species largely focuses its attacks on native ant taxa (e.g., Holway et al. 2002, Dejean et al. 2008), and quickly recruits soldiers to overcome native ant nests through sheer numbers. Termites form large colonies and are frequently preyed upon by *P. megacephala* in other ecosystems (Dejean et al. 2007), but some termite taxa can effectively resist their predation (Chouvenc et al. 2015); this may explain why termite (*Odontotermes* spp.) dung visitation was unchanged in invaded plots. In our study system, termite colonies consist of large numbers of workers and soldiers, and this native species may be able to effectively resist attacks by *P. megacephala*.

Invasion by *P. megacephala* was also not associated with a decline in the abundance and diversity of dung-decomposing beetles. Although *P. megacephala* can overpower and consume native insects through group attacks on a single prey (Dejean et al. 2008), we did not observe predation by *P. megacephala* on any dung beetle species. Group attack by *P. megacephala* may be more effective against taxa with relatively low mobility; it may be that the high mobility of decomposer beetles, necessitated by foraging on widely dispersed resources, allows them to avoid capture and predation.

Considering the near-complete lack of *P. megacephala* individuals found inside of experimental dung piles, it is possible that dung piles provide some form of refuge from *P. megacephala* predation for decomposer taxa. Recently deposited dung material may be a difficult medium in which to forage, or a dung pile's associated community may be sufficiently ephemeral or spatially concentrated to avoid predation by *P. megacephala*. Closer observation of dung material in *P. megacephala* invasion areas will be necessary to clarify this hypothesis and would help us to understand the effect (or lack thereof) of ant invasion on early-stage dung decomposition.

Our study documents the short-term impact of *P. megacephala* invasion, and it is possible that these effects could change over time. Our "invaded" plots had likely been invaded for 1–2 yr, and our results therefore capture the initial impacts of *P. megacephala* invasion on arthropod community structure and decomposition function in these savannas. However, *P. megacephala* colonies can continue to increase in abundance long after their initial invasion (Hoffmann and Parr 2008). If *P. megacephala* colonies increase in size and number across our study landscape, they may begin to impact a broader range of arthropod taxa. Due to time and material constraints, we focused on dung decomposition as a measurement of ecosystem function provided by invertebrate detritivores. Other ecosystem services, provided by other functional guilds, may be more strongly affected by big-headed ant invasion. Further monitoring will be necessary to record and understand these effects.

A large literature documents the relationship between biodiversity and ecosystem function (reviewed in Nielsen et al. 2011, Hooper et al. 2012), and there is increasing interest in the role of functional traits in driving these relationships (Diaz and Cabido 2001, Srivastava and Vellend 2005). Congruent with these findings, our results highlight the importance of examining linkages between ecosystem function and diversity at the level of functional groups. In our study system, a sharp decline in insect diversity did not cause a similarly abrupt change in insect-mediated dung decomposition; this resilience ostensibly exists because a subgroup of insect detritivores was largely resistant to the effects of invasion. Comprehensive studies are needed to identify and monitor individual functional guilds over time, as they can provide valuable insights into the mechanisms underlying the effects of invasion on functional attributes of natural systems.

Pheidole megacephala appears to have arrived rather recently in Laikipia, and their sustained presence in the region may continue to reduce invertebrate diversity. Sustained loss of biodiversity in this region could have both ecological and economic impacts in this highly productive landscape. Considering the continuing anthropogenic spread of *P. megacephala* to globally important ecosystems, a deeper understanding of the indirect and non-trophic effects of their invasion will be valuable for future conservation efforts.

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SUPPORTING INFORMATION

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