Frenemy at the gate: Invasion by *Pheidole megacephala* facilitates a competitively subordinate plant ant in Kenya

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Abstract. Biological invasions can lead to the reassembly of communities and understanding and predicting the impacts of exotic species on community structure and functioning are a key challenge in ecology. We investigated the impact of a predatory species of invasive ant, *Pheidole megacephala*, on the structure and function of a foundational mutualism between Acacia drepanolobium and its associated acacia-ant community in an East African savanna. Invasion by *P. megacephala* was associated with the extirpation of three extrafloral nectar-dependent Crematogaster acacia ant species and strong increases in the abundance of a competitively subordinate and locally rare acacia ant species, Tetraponera penzigi, which does not depend on host plant nectar. Using a combination of long-term monitoring of invasion dynamics, observations and experiments, we demonstrate that P. megacephala directly and indirectly facilitates T. penzigi by reducing the abundance of T. penzigi's competitors (Crematogaster spp.), imposing recruitment limitation on these competitors, and generating a landscape of low-reward host plants that favor colonization and establishment by the strongly dispersing T. penzigi. Seasonal variation in use of host plants by P. megacephala may further increase the persistence of T. penzigi colonies in invaded habitat. The persistence of the T. penzigi-A. drepanolobium symbiosis in invaded areas afforded host plants some protection against herbivory by elephants (Loxodonta africana), a key browser that reduces tree cover. However, elephant damage on T. penzigi-occupied trees was higher in invaded than in uninvaded areas, likely owing to reduced T. penzigi colony size in invaded habitats. Our results reveal the mechanisms underlying the disruption of this mutualism and suggest that P. megacephala invasion may drive long-term declines in tree cover, despite the partial persistence of the ant-acacia symbiosis in invaded areas.

Key words: Acacia drepanolobium; ant-plant; biodiversity; elephants; facilitation; herbivory; invasive species; mutualism breakdown; Pheidole megacephala; plant defense.

INTRODUCTION

Biological invasions are a leading driver of biodiversity decline worldwide (Murphy and Romanuk 2014, Bellard et al. 2016, Mollot et al. 2017, Blackburn et al. 2019, Kortz and Magurran 2019) and invasive species can strongly alter both native species assemblages (Mack et al. 2000) and the ecological processes that supply

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ecosystem services (Vila et al. 2011). A key challenge for invasion ecology is thus to understand and predict the effects of species invasions on both the structure and function of communities. While comparisons of assemblages and ecological processes in invaded vs. non-invaded habitats can reveal the outcomes that are correlated with species invasions, such comparisons do not establish causality, and can thereby obscure whether community changes are driven by the invader or by other environmental factors correlated with the occurrence of the invader (MacDougall and Turkington 2005). Pinpointing the mechanisms by which invasive

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species impact native communities can help in developing a predictive framework for identifying not only the traits that promote invasiveness (Drenovsky et al. 2012, Ordonez and Olff 2013), but also the traits that determine how constituent species will be impacted by invasion (Gibson et al. 2012, Godoy 2019).

Invasive species may reduce the abundance of native species through both direct (e.g., competition [Mack et al. 2000], predation [Crowder and Snyder 2010], parasitism [Meeus et al. 2011]), and indirect (Grosholz 2005, Preston et al. 2012, Feit et al. 2018) mechanisms. While there is an extensive literature on the negative effects of invasive species on native flora and fauna (Ruiz et al. 1997, Mack et al. 2000, Holway et al. 2002), invasive species also can have positive effects on native species (Rodriguez 2006). This facilitation can occur via a number of mechanisms; for example, invasive species can exert direct positive effects on native species by creating or modifying habitat (Wonham et al. 2005, Thomsen 2010, Norkko et al. 2012, Ramus et al. 2017, Fill et al. 2019), or by providing food (Chittka and Schurkens 2001, Shapiro 2002) or mutualistic services such as pollination (Moragues and Traveset 2005) or seed dispersal (Cumberland and Kirkman 2013). Alternatively, invasive species may indirectly benefit native species, for example by enhancing the services of shared mutualists (reviewed in Traveset and Richardson 2006, Bjerknes et al. 2007; but see Morales and Traveset 2009), or by reducing the abundance or impact of a native species' predators (Nelson et al. 2010, Doody et al. 2013) or competitors (Grosholz et al. 2000, Kindinger 2018).

Here we examine the impact of the invasive *Pheidole megacephala* (the "big headed" ant) on the structure and function of a mutualism between the ant-plant *Acacia* (*Vachellia*) *drepanolobium* and its four resident ant symbionts in the central highlands of Kenya. Invasion within this ecosystem results in communities in which three of the four acacia ant species are extirpated, while a fourth and previously subordinate species becomes a codominant along with *P. megacephala* (Riginos et al. 2015). Our aim in this study was to evaluate both the mechanisms underlying this dramatic shift in species composition, as well as the impact of the invasion on the functioning of the ant–plant mutualism.

Pheidole megacephala is one of the world's "worst invasive species" (Lowe et al. 2008), occurring across all seven biogeographic realms (Wetterer 2012). These predatory ants form ground-dwelling supercolonies (Fournier et al. 2012) that can spread across entire landscapes (Wilson 2003), suppressing invertebrate diversity and abundance by preying on a broad range of arthropods (Hoffmann 1998, Holway et al. 2002), and posing threats to both biodiversity (Hoffmann 1998, Vanderwoude et al. 2000, Wetterer 2007, Krushelnycky and Gillespie 2010) and agriculture (reviewed in Wetterer 2012, but see, e.g., Milligan et al. 2016*a*). Over the past ~20 yr, *Pheidole megacephala* has invaded the savannas and bushlands of central Kenya's Laikipia plateau, establishing around centers of human habitation (Riginos et al. 2015, Milligan et al. 2016*b*), and spreading at rates of up to 50 m/yr (A. G. Pietrek et al., unpublished manuscript).

The mutualism between A. drepanolobium and its resident ants is widespread throughout Laikipia, occurring in areas underlain by heavy-clay "black cotton" soils. In these areas, A. drepanolobium occurs in virtual monoculture (Young et al. 1997), hosting (in non-invaded areas) a suite of four species of mutually exclusive symbiotic ants (Crematogaster sjostedti, C. mimosae, C. nigriceps, and Tetraponera penzigi), which compete for the possession of host trees. Coexistence among these species is mediated in part by competition-colonization trade-offs; while the dominance hierarchy among mature colonies competing for host plants is C. sjostedti > C. mimosae > C. nigriceps > T. penzigi (Palmer et al. 2000),the more subordinate species (T. penzigi and C. nigri*ceps*) allocate disproportionately more resources to the production of foundress queens (Stanton et al. 2002, Boyle 2017), which are competitively superior at the colony-founding stage (Stanton et al. 2002).

In most areas of Laikipia where it occurs, the density of A. drepanolobium is sufficiently high that much competition occurs between mature colonies, with neighboring colonies competing for limited nest space within these space-limited communities. When empty host plants are not colonized by mature neighboring colonies (e.g., due to isolation, disturbance, or poor environmental conditions that do not favor colony expansion), foundress queens and incipient colonies compete for sole occupation of the host plant, and the competitive hierarchy is inverted, with T. penzigi dominating at early stages of colony development (Stanton et al. 2002). Within uninvaded habitat on Ol Pejeta Conservancy, C. mimosae and C. nigriceps are the most abundant ant occupants of A. drepanolobium (72% and 19% of occupied trees, respectively), while T. penzigi and C. sjostedti occur at low abundance (4% and 5% of occupied trees, respectively; T. M. Palmer, unpublished data). All four symbionts provide protection to the tree from herbivory, although the level of protection varies among them (Palmer and Brody 2007). In exchange for this protection, trees provide nest space within swollen spine domatia, and extrafloral nectar that is an important diet component for the three Crematogaster species (Palmer et al. 2000, Palmer and Brody 2007, Goheen and Palmer 2010. Martins 2010).

In invaded habitats, the predatory *P. megacephala* extirpates all three *Crematogaster* species, which includes the two most aggressive protectors of *A. drepanolobium*, *C. mimosae* and *C. nigriceps*. Invaded trees have far fewer active nectaries than host plants occupied by native symbionts, presumably because the invasive ant does not stimulate nectar flow (Riginos et al. 2015, see also Lach et al. 2009). While *P. megacephala* does not nest within host tree domatia, it appears to use host trees as foraging habitat, preying on invertebrates that occupy

the empty swollen spine domatia. Unlike the native ants, *P. megacephala* does not display aggression toward large browsing mammals. As a consequence, elephants are causing much higher rates of catastrophic tree damage (i.e., pushing entire trees over) in invaded areas, with potentially large impacts on landscape tree cover (Riginos et al. 2015).

A consistent feature of areas invaded by P. mega*cephala* is a pronounced increase in the proportion of host trees occupied by T. penzigi (average increase of 11.7×; Riginos et al. 2015). The mechanisms underlying this increase in T. penzigi presence, often on trees co-occupied by P. megacephala, within invaded areas are not known. Among the native ants, T. penzigi is not aggressively territorial toward heterospecifics (Palmer 2004), and during experimentally staged P. megacephala invasion it retreated into domatia where it persisted on invaded host trees for >30 d (Riginos et al. 2015). These non-aggressive behaviors may allow T. penzigi to co-exist with P. megacephala. Additionally, unlike the three Crematogaster species, T. penzigi does not rely on nectar from host trees (Palmer et al. 2002); this gives T. penzigi the unique potential among the suite of native ants to colonize and persist within invaded areas despite diminished nectar production.

The high occurrence of T. penzigi on trees in invaded areas suggests the potential for this native acacia ant to provide benefits to A. drepanolobium similar to those it confers in uninvaded landscapes, where it reduces elephant herbivory on plants of all size classes (T. Palmer unpublished data) and increases host plant survival (Palmer et al. 2010). However, since the presence of aggressive P. megacephala may disrupt T. penzigi behavior, whether the latter species provides protective benefits within invaded areas is not known. Because A. *drepanolobium* is the dominant tree where it occurs, the fate of the mutualism in the face of P. megacephala invasion has consequences for the structure and function of these ecosystems including habitat and forage provisioning for herbivores (Riginos 2015) and arboreal fauna, nitrogen cycling (Fox-Dobbs et al. 2010), and local biodiversity (Martins et al. 2013, Baker et al. 2017).

We combined field experiments and long-term observations along multiple invasion fronts to evaluate whether the high occurrence of *T. penzigi* following invasion is a consequence or correlate of *P. megacephala* invasion, and to assess whether *T. penzigi* remains an effective mutualist of *A. drepanolobium* within invaded areas. In particular, we asked three interrelated questions. (1) How do species composition of acacia ants and host tree traits change over the course of *P. megacephala* invasion? (2) Does *P. megacephala* indirectly facilitate *T. penzigi* by (a) differentially suppressing colonization of host plants by *Crematogaster* queens, and/or (b) modifying host plant traits in ways that favor *T. penzigi* colonization and establishment? (3) Does *T. penzigi* confer mutualistic benefits to *A. drepanolobium* in invaded

areas, and how does the degree of benefit compare to those offered by *T. penzigi* in non-invaded areas?

METHODS

Study site

We conducted this study on Ol Pejeta Conservancy (hereafter OPC), located in the central highlands of Kenya (0.0043° S, 36.9637° E) on the Laikipia plateau at an elevation of 1,800 m. OPC receives ca. 900 mm of rainfall distributed in a bimodal pattern each year. Approximately 32% of OPC is characterized as *A. drepanolobium* woodland or *A. drepanolobium–Euclea divinorum* mixed bushland (Adcock 2007), which serves as important foraging habitat for the conservancy's grazer and browser populations, including ~80 black rhinoceros (*Diceros bicornis*, as well as more common African savanna herbivores such as plains zebra, Cape buffalo, gazelles, elephants, and giraffes. A complete list of OPC's mammal species can be found in Wahungu et al. 2010).

Long-term monitoring of invasion effects on acacia ant community

To evaluate how the native acacia ant community and host plant traits are affected by P. megacephala invasion, we established a Multiple Before-After-Control-Impact (M-BACI, Stewart-Oaten et al. 1986) experiment on OPC in 2016. We identified three separate, active invasion fronts (North, South, and Morani sites) through a broad survey of the conservancy, visually inspecting trees for P. megacephala occupation, and surveying ant recruitment to tuna baits placed on the ground. A front was defined as an area where P. megacephala was present on baits, trees, or both with an intact community of A. drepanolobium and its native acacia ants immediately adjacent. Our impact plots were established ~ 50 m into uninvaded A. drepanolobium habitat from the leading edge of each invasion front. Because invasion fronts can spread at rates of ~50 m/yr (A. G. Pietrek et al., unpublished manuscript), we anticipated that these plots would be invaded within 1-2 yr. Uninvaded control plots were established at least 1 km ahead of the invasion front at each of our three sites, such that they were unlikely to be invaded over the course of our 3-yr study. In addition, to evaluate whether occupancy of host plants was changing over time within invaded areas, we also established invaded plots at each of our three sites, located at least 1 km behind each invasion front. In each of these habitats, we demarcated 50×50 m plots, and surveyed 40-60 mature trees (>1 m) within each plot for ant species composition.

To assess differences in species composition between invaded and uninvaded plots, we built community composition matrices with the number of trees occupied by each of the five species in each plot. We used our 4-yr data set and ran a PERMANOVA (1,000 permutations) with invasion status as a predictor and site ID as a stratum using the vegan package (Oksanen et al. 2019). In addition, following Naughton et al. (2019) we used nonmetric multidimensional scaling (NMDS) ordination to compare changes in ant community assemblages within uninvaded, invaded, and BACI impact plots between 2017 (prior to the invasion of BACI impact plots) and 2020 (after BACI impact plots had been invaded).

Ant occupancy of saplings in uninvaded, invaded and invasion front habitats

In addition to surveying ant occupancy of mature trees, we also examined ant species composition on *A. drepanolobium* saplings. To do so, we established a 100-m transect immediately adjacent to our uninvaded control, invaded, and impact plots, at each of our three sites. Along each transect, an observer located the nearest sapling (<0.40 m tall) to each 3-m demarcation point on a 100-m tape, and destructively sampled each plant, recording the identity of all live queens or developing colonies (N = 30-33 saplings per site). Surveys were conducted in January 2018, after *P. megacephala* had begun to take over host plants within Impact plots. We performed a chi-square analysis to evaluate differences in the occupancy of saplings across the three habitat types.

Does P. megacephala differentially suppress colonization by Crematogaster species?

To evaluate the role of predation by P. megacephala vs. propagule limitation in limiting colonization of host plants by Crematogaster vs. T. penzigi queens, we planted eight greenhouse-raised A. drepanolobium trees (0.75-1.0 m tall) at both invaded and uninvaded control plots at all three study sites (N = 48 trees total). For each group of eight trees, we randomly assigned half as "sticky barrier" plants and applied a layer of Tanglefoot (The Scotts Company, Marysville, OH, USA) insect barrier to duct tape on the main stem to prevent access by P. megacephala. We applied duct tape but no sticky barrier to the remaining four trees and designated them as control plants. All saplings were planted into 50 \times 50 m electrified herbivore exclusion fences, and placed at least 3 m from neighboring mature trees to minimize colonization by expansion from neighboring mature Crematogaster colonies (T. penzigi does not colonize new host plants via ground expansion; Palmer et al. 2002). After 4 months, we censused all saplings, and counted the number and identity of queens present within swollen spine domatia. We analyzed the effect of habitat type (uninvaded vs. invaded) and sticky barrier treatments on the number of T. penzigi and Crematogaster spp. queens colonizing experimental saplings using MANOVA, and then conducted separate GLMs analyzing the effects of habitat type (invaded vs. uninvaded), sticky barrier treatment, and their interaction on the colonization success of each queen type, using an α_{m-1} adjustment for

significance levels (Frane 2015). All statistical analyses were performed in JMP Pro v15 (SAS Institute, Cary, North Carolina, USA).

Does host plant nectar production change over the course of invasion?

To establish whether P. megacephala invasion affected the production of extrafloral nectar on A. drepanolobium, we surveyed our marked mature (>1 m) trees within uninvaded control and impact plots for nectar production, counting the number of active nectaries (correlated with nectar production; Palmer et al. 2008) on each of five fully expanded leaves per branch for a total of four arbitrarily chosen branches (one in each cardinal direction) per tree. Active nectaries were defined as nectaries consisting of green or red tissue, whereas inactive nectaries have a brown and dried appearance; prior study in our system (Palmer et al. 2008) has shown that nectaries on A. drepanolobium classified as "inactive" do not secrete nectar (N = 55), while nectaries classified as "active" consistently secreted nectar over a 48-h period. We conducted four surveys in each plot for ant species composition (February 2017, January 2018, January 2019, March 2020), and two surveys (February 2017 and January 2019) for active nectary production. To establish whether the change in the production of active nectaries over time (2017-2019) differed between uninvaded control and impact plots, we used a repeatedmeasures ANOVA, with plot type as a fixed effect and site as a random effect, and evaluated the plot \times time interaction term.

Do host plants with low nectar production favor establishment by T. penzigi vs. Crematogaster queens?

If host trees in P. megacephala invaded areas have diminished extrafloral nectar production, such trait variation could differentially influence the establishment success of Crematogaster species, which depend on hostplant nectar, vs. T. penzigi, which does not depend on host-plant nectar. To evaluate whether colonization success of T. penzigi and Crematogaster queens differed on host plants with low vs. high nectar production, we chose 40 greenhouse-grown A. drepanolobium saplings, matched for height (~30 cm), leafiness, and number of swollen spine domatia. We randomly assigned one-half of these saplings to a "low-reward" group, and the remainder to a "high-reward" group. On low-reward saplings, we brushed a small dot of Tanglefoot tree wound pruning and grafting sealer on the extrafloral nectaries of all but five leaves of each plant $(40.25 \pm 5.82 \text{ leaves; mean} \pm \text{standard error of mean})$ [SEM]). We brushed a similar quantity of the sealer onto the upper rachis of all but five leaves of each high-reward plant (41.6 \pm 6.13 leaves) as a procedural control, leaving all extrafloral nectaries intact. Trees were then planted into uninvaded habitat along a linear transect in August 2019, alternating high- and low-reward treatments, and ensuring that all saplings were at least 5 m from neighboring mature *A. drepanolobium* to prevent ground colonization by existing mature *Crematogaster* colonies. We maintained the treatments on these saplings at biweekly intervals for the ensuing 22 weeks, recording the identity of workers of successfully establishing colonies at the experiment's end. We used logistic regression to evaluate whether experimental manipulation of host plant nectaries influenced the colonization success of *T. penzigi* and *Crematogaster* queens at the experiment's end, and calculated odds and their associated confidence intervals to compare colonization outcomes on experimental saplings.

Does P. megacephala *use of* A. drepanolobium *vary over time*?

Spatiotemporal variation in the use of A. drepanolobium by P. megacephala is a potential mechanism that might increase the persistence of T. penzigi within invaded habitats (Melbourne et al. 2007). To assess whether P. megacephala movement onto host plants varied over time, we counted the number of workers caught in duct tape traps placed around the stems of 20 mature A. drepanolobium at each of our three Invaded study sites at five different times corresponding to peak wet and dry seasons (June 2017, July 2018, September 2018, November 2018, and February 2019). The traps were constructed by wrapping duct tape around relatively smooth portions of the stems with the sticky side of the tape facing outward. Any gaps that formed under the tape were sealed with Tanglefoot. To be certain there was only a single path to the canopy, we set the barriers above any intersections with other trees or grass. We checked the traps after 24 h and counted workers stuck to either side of the tape.

We compared abundances of *P. megacephala* on sticky traps placed on trees with plot "greenness" as measured by Normalized Difference Vegetation Index (NDVI) values in satellite imagery. NDVI is a longstanding remotesensing metric of greenness of vegetation, with higher value pixels corresponding to green plants on the ground. Raster data from the Sentinel 2 satellite (10-m² pixel resolution) of the study area was downloaded from the USGS' Earthexplorer site for five dates (June 2017; November, July, and September 2018; February 2019; data *available online*).¹⁰ We then processed the imagery using ArcGIS 10.6 (ESRI, Redlands, CA, USA), extracting our experimental plots from the larger study area and applying the NDVI to produce a time series of vegetation greenness for individual experimental plots.

To assess temporal variation in *P. megacephala*'s use of host plants across seasons, we regressed the log number of *P. megacephala* workers against the log NDVI (a measure of the "greenness" of each site) for each of our three study sites across the five sampling periods, and compared the average slope of the three regression lines to the null (slope = 0) using a *t* test.

Does T. penzigi provide protective benefits to host A. drepanolobium trees in invaded habitats?

To evaluate whether T. penzigi remained an effective protective mutualist of A. drepanolobium in invaded habitats, we compared measures of T. penzigi colony size and aggression in invaded vs. uninvaded habitats. We evaluated two measures of colony size: the number of occupied swollen spine domatia and the average worker numbers per swollen spine domatium in invaded vs. uninvaded habitats. To do this, we arbitrarily chose five T. penzigi-occupied trees in invaded and uninvaded habitats at each of our three study sites (N = 30 trees total), separated from one another by at least 20 m to minimize potential spatial autocorrelation. On each host plant, we arbitrarily chose a single swollen spine domatium on the distal-most portion of five different branches, and plugged all entry holes with window caulk. For all remaining swollen spine domatia on each tree, we opened all domatia and recorded whether the domatium was occupied or unoccupied. Caulked domatia were clipped, and transferred to a sub-zero freezer to immobilize ants for evaluation of domatium contents. After freezing, we counted the number of workers present in each domatium.

To establish whether T. penzigi was equally aggressive in defending host plants in invaded vs. uninvaded areas, we evaluated T. penzigi responses to simulated browsing on six to eight trees in both invaded and uninvaded habitats at each of our three study sites. Ant defensive levels were assessed by raking a leather gloved hand across the distal-most 30 cm of four separate arbitrarily chosen branches (one in each cardinal direction), and recording the number of ants swarming onto a leather glove over the course of 30 s (Palmer et al. 2008). Sampled trees were at least 20 m apart from one another to minimize spatial autocorrelation. We analyzed T. penzigi colony parameters (number of workers per swollen spine domatium, percent occupancy of swollen spine domatia, and levels of aggressive response to simulated disturbance) using linear mixed models, with plot type (invaded vs. uninvaded) as a fixed effect, and site as a random effect.

Finally, we surveyed elephant damage on host plants in invaded and uninvaded areas to evaluate whether *T. penzigi*-occupied trees sustained differing levels of damage in these two habitat types. Surveyed trees ranged from 0.3–4.8 m in height (N = 41 and 70 trees for invaded and uninvaded habitats, respectively). For comparative purposes, we also measured elephant damage within invaded habitats on trees exclusively occupied by *P. megacephala* (N = 30) and unoccupied trees (N = 95). We focused on elephant damage, since acacia ant symbionts are effective at protecting host plants from elephants (Stanton and Palmer 2011, Palmer and Brody 2013), but relatively ineffective at deterring feeding by

¹⁰ https://earthexplorer.usgs.gov

other mammalian browsers (Palmer and Brody 2013). We scored a tree as "elephant damaged" if it showed typical signs of elephant browsing (large broken branches or branch systems, and/or extensive bark stripping), which is distinct from feeding damage inflicted by other browsers (Stanton and Palmer 2011, Palmer and Brody 2013). The frequency of elephant damaged trees occupied by *T. penzigi* in invaded vs. uninvaded habitat was analyzed using logistic regression.

RESULTS

Effects of P. megacephala invasion on ant species composition

Results from the PERMANOVA confirmed strong differences in species composition between invaded and uninvaded plots ($F_{1,23} = 36.18$, P < 0.001). Ordination (NMDS) further suggested that BACI plots resembled uninvaded plots pre-invasion and moved to a species assemblage similar to that of invaded plots after the invasion (Appendix S1: Fig. S1, stress = 0.06). Species composition on adult host plants in Impact plots changed sharply from Crematogaster dominated to P. megacephala dominated over the 4 yr course of our study (Fig. 1b). Uninvaded Control plots, in contrast, underwent only slight changes in species composition, with some formerly Crematogaster-occupied host plants transitioning to an empty state between 2017 and 2019, many of which were colonized by 2020 (Fig. 1a). Invaded plots also shifted in composition over the 4-yr monitoring period, with marked increases in the proportion of host plants occupied by T. penzigi (Fig. 1c).

Occupancy of saplings in uninvaded, invaded and invasion front habitats

Sapling occupancy by *T. penzigi* and *Crematogaster* spp. queens and colonies differed strongly between invaded, uninvaded, and invasion front habitats (Fig. 2, likelihood ratio chi-square = 109.29, 6 df, P < 0.0001). *Tetraponera penzigi* queens were found less frequently than expected on saplings in uninvaded and invasion front habitats, while *T. penzigi* queens and small colonies were more abundant than expected in invaded habitats (Fig. 2). In contrast, *Crematogaster* queens were very rare on saplings in invaded areas, and were found more frequently than expected at the invasion front (Fig. 2b, c). Small *Crematogaster* colonies, which were absent in invaded habitats, were found more frequently than expected on saplings in uninvaded habitat (Fig. 2a, c).

Effects of P. megacephala invasion on acacia ant colonization and establishment

Crematogaster spp. queens were very rare in invaded habitat, compared to *T. penzigi* queens, which were



FIG. 1. Changes in ant species composition on *Acacia drepanolobium* from 2017–2020 in uninvaded control (top panel A), impact (middle panel B), and invaded (bottom panel C) plots. Ant species occupying host plants are indicated in legend, and *P. meg/T. pen* indicates host plants co-occupied by both *Pheidole megacephala* and *Tetraponera penzigi*.

10x more abundant on experimental saplings in invaded areas (Fig. 3). There was a significant overall effect of both invasion and the presence of sticky barriers on the overall number of T. penzigi and Crematogaster spp. queens that colonized experimental saplings (MANOVA, habitat type $F_{2,5} = 12.03$, P = 0.01; sticky barrier treatment $F_{2,5} = 7.27$, P = 0.03). There was no significant interaction between habitat type and the presence of sticky barriers on overall queen colonization ($F_{2.5} = 0.05$, P = 0.95). Crematogaster spp. queens were significantly more abundant in uninvaded than invaded habitats (chi-square = 11.62, 1 df, P < 0.001), but were not more abundant on saplings protected by sticky barriers than on unprotected saplings (chisquare = 2.01, 1 df, P = 0.16). Tetraponera penzigi queens were more abundant in invaded vs. uninvaded habitats, although these differences were not significant (chi-square = 3.80, 1 df, P = 0.051). Significantly more T. penzigi queens were found on saplings protected from ground colonization by other ants vs. those that were not protected (chi-square = 7.99, 1 df. P = 0.004).



FIG. 2. Observed (black bars) vs. expected (gray bars) number of saplings occupied by queens and small colonies of *T. penzigi* and *Crematogaster* spp. in (A) uninvaded, (B) before-aftercontrol-impact (BACI, or impact), and (C) invaded habitats. Surveys were conducted in January 2018 (after invasion of impact plots had begun). N = 41, 53, and 69 saplings for uninvaded, impact, and invaded plots, respectively.



FIG. 3. Average number of *T. penzigi* and *Crematogaster* spp. queens colonizing protected (sticky barrier) and unprotected (control) experimental saplings planted in invaded vs. uninvaded habitat. *Tetraponera penzigi* queens are more abundant in invaded habitats, while *Crematogaster* spp. is more abundant in uninvaded habitats. Overall queen numbers were higher on saplings protected by sticky barriers than on unprotected saplings.

Effects of P. megacephala *invasion on host tree nectar production*

The proportion of active nectaries on host plants was reduced by 72% in Impact plots over the course of *P. megacephala* invasion from 2017 to 2019, while active nectary production in uninvaded control plots remained relatively constant over the same time period (Appendix S1: Fig. S2; repeated-measures ANOVA, plot × year $F_{1.6} = 13.03$, P = 0.01).

Effects of host plant nectar reduction on acacia ant colonization

Species occupancy on low- vs. high-reward hosts differed significantly after 12 weeks (Fig. 4, logistic regression, chi-square = 11.45, 2 df, P = 0.003). *Crematogaster* spp. occupied saplings were 2.4× more likely to be high reward compared to *T. penzigi* and empty saplings (odds = 2.43, 95% CI = 1.05–6.28, z = 1.98, P < 0.05), while *T. penzigi* occupied saplings were 86% less likely to be high reward compared to *Crematogaster* spp. saplings (odds = 0.14, 95% CI = 0.02 - 0.76, z = -2.13, P = 0.03), and empty saplings were 94% less likely to be high reward compared to *Crematogaster* spp. saplings (odds = 0.06, 95% CI = 0.02–0.41, z = -2.44, P = 0.01).

Temporal heterogeneity in P. megacephala use of A. drepanolobium host plants

We found a negative relationship between the mean NDVI (an index of "greenness") of our experimental plots and the number of *P. megacephala* workers caught in sticky barriers on *A. drepanolobium* stems (Appendix S1: Fig. S3), indicating that movement of the invasive ant onto host plants is higher during relatively



FIG. 4. Percentage of high-vs. low-reward saplings successfully colonized by *Crematogaster* spp. and *T. penzigi* colonies in uninvaded habitat. High-reward saplings had \geq 30 active nectaries per plant, low-reward saplings had five active nectaries per plant.

TABLE 1. Tetraponera penzigi colony parameters on host plants in invaded vs. uninvaded plots.

Parameter	Invaded	Uninvaded	F	df	Р
No, swollen spine domatia occupied	48.67 ± 9.06	79.39 ± 10.42	8.52	1,26	< 0.01
No. workers per swollen spine domatia	70.36 ± 43.35	63.11 ± 38.04	0.13	1,24.1	0.72
No. workers swarming onto glove/30 s	0.44 ± 0.14	1.82 ± 0.30	8.03	1,3.46	0.05

Note: Values are mean \pm SEM.

dry vs. wet periods (slope = -1.67 ± 0.46 ; t = -3.64,2 df, P = 0.03).

Defense of host plants by T. penzigi in invaded areas

Tetraponera penzigi occupied 1.7× more swollen spine domatia on average on host plants in uninvaded than invaded areas $F_{1,26} = 8.52$, P < 0.01) and the average number of workers per occupied swollen spine domatium did not differ significantly between invaded and uninvaded areas ($F_{1,24,1} = 0.13$, P = 0.72; Table 1). Defensive activity by T. penzigi in response to simulated herbivory was low overall, but 2.6× higher in uninvaded than invaded areas $(F_{1,3.46} = 8.03, P = 0.05;$ Table 1). The frequency of elephant damage was significantly higher on T. penzigi trees within invaded habitat than uninvaded habitat (logistic regression, chi-square = 4.70, 1 df, P = 0.03), and increased with height for all trees (logistic regression, chi-square = 10.58, 1 df, P < 0.001, Fig. 5). Elephant damage on P. megacephala-occupied and unoccupied trees in invaded habitats was higher than that observed for T. penzigi-occupied trees in either habitat type (Fig. 5).

DISCUSSION

Our results demonstrate that *P. megacephala* invasion sharply reduces the diversity of the acacia ant assemblage on *A. drepanolobium*, consistent with studies conducted elsewhere showing strong negative impacts of *P. megacephala* on both native ant assemblages (Heterick 1997, Hoffmann et al. 1999, Vanderwoude et al. 2000, Callan and Majer 2009) and arthropods more broadly



FIG. 5. Predicted probability (ordinal logistic regression) of elephant damage on host plants of different sizes occupied by *T. penzigi* in invaded vs. uninvaded habitats. Predicted probability of elephant damage to *Pheidole megacephala* occupied and unoccupied trees in invaded habitat is shown for comparison.

(Krushelnycky and Gillespie 2010). Contrasting with these negative effects, however, we also found that P. megacephala strongly facilitates the establishment and spread of the competitively subordinate T. penzigi within invaded habitats. By initially eliminating virtually all mature colonies of acacia ants, P. megacephala invasion shifts the ontogenetic stage at which competition among acacia ants for host plants is most intense. Within intact communities where A. drepanolobium density and occupancy are both high, interspecific competition occurs largely at the mature colony stage, with neighboring colonies competing intensely for limited nest sites, favoring the most competitively dominant Crematogaster species (Palmer et al. 2002, Palmer 2003, 2004). In contrast, P. megacephala invasion generates a landscape of unoccupied, low-reward host plants, which shifts competition among acacia ants to the colony founding stage, favoring more strongly colonizing species with lower energetic requirements. Our results are consistent with other studies demonstrating that invasive species can facilitate natives (Rodriguez 2006, Collins et al. 2017, Kindinger 2018, Goodman and Warren 2019, Rees et al. 2019). For example, Kindinger (2018) showed that invasive lionfish (Pterois volitans) facilitated the native blackcap basslet (Gramma melacara) through differential predation on the basslet's competitor on Bahamian reefs. Reductions in the competitor's abundance allowed the blackcap basslets to occupy more favorable foraging territories on the reef, leading to higher growth rates of this fish in the presence of the invader. In our system, where competition for space is similarly strong as in reef systems, suppression of Crematogaster spp. by P. megacephala opens up space, allowing T. penzigi to increase in abundance.

To achieve viable populations within *P. megacephala* invaded habitats, acacia ants must both successfully colonize unoccupied host plants, and then persist on host plants until at least some colonies reach reproductive maturity. *Tetraponera penzigi* possesses traits that allow it to succeed in both of these phases. First, "ruderal" traits (Grime and Pierce 2012), including a disproportionate investment in the production of reproductive alates (Stanton et al. 2002), and queens that are competitively dominant in contests with *Crematogaster* spp. queens (Stanton et al. 2002) enhance the colonization success of *T. penzigi* relative to its competitors. Second,

"stress tolerance" traits including *T. penzigi*'s lower dependence on host plant nectar (Palmer et al. 2002, 2017), and avoidance and escape behaviors allow for longer persistence times on host plants, allowing

colonies to reach reproductive maturity. Although *C. nigriceps* is also a strong colonist (Stanton et al. 2002), its strong dependence on host plant nectar and high levels of interspecific aggression (Palmer 2004) likely underlie its inability to persist within invaded habitats. The persistence of *T. penzigi* in *P. megacephala*-occupied habitats accords with prior work demonstrating the persistence of innocuous and less aggressive ant species in habitats dominated by highly aggressive invasive ants (Porter and Savignano 1990).

We found that Pheidole megacephala facilitates T. penzigi through both direct and indirect mechanisms. During the initial phases of invasion, P. megacephala's predation on Crematogaster colonies eliminates the nest site limitation that constrains the expansion of competitively subordinate T. penzigi populations within uninvaded areas (Palmer 2001, Palmer et al. 2002). The elimination of mature Crematogaster colonies appears to limit recruitment for these species within invaded areas; we found only two Crematogaster spp. queens on our experimental saplings in invaded habitats, and Crematogaster queen presence on naturally occurring saplings in invaded habitats was very low. The nearest mature Crematogaster colonies were at least 1 km from our experimental saplings, suggesting that while Crematogaster queens can disperse across these distances, the majority of dispersal events may occur at shorter distances. In contrast, colonization of both experimental and naturally occurring saplings by T. penzigi queens occurred frequently within invaded habitats, likely because reproductively mature colonies of T. penzigi are present within P. megacephala invaded areas.

Tetraponera penzigi queens were capable of colonizing unprotected experimental saplings within invaded areas, while Crematogaster queens were not. While we could not identify the mechanisms underlying this disparity, the strong entry-hole seals created by claustral T. penzigi queens in their domatia may be more effective at preventing P. megacephala incursion than the coarser and weaker seals created by Crematogaster queens (Stanton et al. 2005). However, we found very few small T. penzigi colonies on naturally occurring saplings in invaded areas, suggesting that the majority of these developing colonies are killed by P. megacephala. Results from our study of experimental sapling colonization are consistent with this hypothesis; queen colonization by both T. penzigi and Crematogaster spp. in both invaded and uninvaded habitats was higher overall on saplings protected by sticky barriers than on unprotected saplings, suggesting that predation by ants – both P. megacephala in invaded areas, and native acacia ant workers in uninvaded areas - can limit new colony establishment on small host plants (see Stanton et al. 2002). In invaded areas, we have observed P. megacephala workers attacking and killing acacia ant queens attempting to establish on saplings, and we have observed C. mimosae and C. nigriceps workers from mature colonies displaying the same behaviors within uninvaded areas.

Because P. megacephala does not induce nectar production on A. drepanolobium, its invasion also is likely to indirectly facilitate T. penzigi by generating a landscape of low-reward host plants, a process that may "screen" out the more energetically demanding, nectardependent Crematogaster mutualists (see Archetti et al. 2011, Heil 2013). Our experimental manipulation of host plant nectaries showed that establishment success was higher for T. penzigi queens and lower for Crematogaster queens on low-reward host plants, consistent with a prior study demonstrating greater persistence of T. penzigi vs. C. mimosae colonies on saplings with lower reward levels (Palmer et al. 2017). Coupled with the recruitment limitation we observed for Crematogaster spp. in invaded areas, the reduction in host plant reward that accompanies P. megacephala invasion disproportionately favors colonization and establishment by T. penzigi.

The persistence of T. penzigi colonies in invaded habitats on larger trees may also be enhanced in part by the temporal variation we observed in P. megacephala occupancy of these host plants. Counts of the invasive ant in sticky trap barriers on host plant stems were highest during dry periods, and lowest during wet periods, despite the fact that *P. megacephala* abundance does not appear to be sensitive to variation in rainfall at this study site (A. G. Pietrek et al., unpublished manuscript). These results suggest that P. megacephala focuses its foraging activity on the ground during periods of higher rainfall, while increasing its use of A. drepanolobium during dry periods when ground resources may become more scarce. This temporal variation in host plant use may reduce the ability of P. megacephala to completely displace T. penzigi from adult host plants, providing a temporal refuge for the acacia ant during wet periods and increasing its persistence within invaded habitats (e.g., see Melbourne et al. 2007).

We also found that invasion by P. megacephala reduced levels of biotic defense in A. drepanolobium, consistent with other studies showing that invasion-driven declines in native ant assemblages can disrupt mutualistic services including seed dispersal (reviewed in Ness and Bronstein 2004, Lach and Thomas 2008), plant protection (Lach 2003, Lach and Hoffmann 2011, Ludka et al. 2015) and the pruning of encroaching vegetation (Mikissa et al. 2013). The partial reassembly of the symbiosis between A. drepanolobium and T. penzigi within invaded habitats appears to offer some protective benefit to host plants relative to unoccupied and P. mega*cephala*-occupied trees, but these benefits were strongly reduced compared to the those offered by T. penzigi in uninvaded habitats. Elephant damage on trees occupied by T. penzigi was higher within invaded habitats than uninvaded habitats, potentially a consequence of T. penzigi's reduced colony sizes within invaded landscapes [although we cannot rule out the possibility that the higher overall rates of elephant browsing on P. megacephala-occupied A. drepanolobium in invaded areas led to associational susceptibility (Barbosa et al. 2009) of neighboring trees occupied by T. penzigi]. Through its incursions onto A. drepanolobium, P. megacephala likely suppresses T. penzigi colonies through opportunistic predation and/or by reducing foraging activity of T. penzigi on hosts, reducing the protective benefit of this acacia ant. Further, the low frequency of T. penzigi colonies on saplings makes host plants in this size class highly vulnerable to browsing, which may curtail recruitment of A. drepanolobium over the long-term. Whether the protection offered by T. penzigi is sufficient to stabilize cover of A. drepanolobium in the face of elephant herbivory is not yet known, but will be important to establish to understand the landscape-scale consequences of this invasion. Because tree cover regulates a number of key ecosystem processes in savannas, including food web dynamics, carbon storage, nutrient cycling, and soil-water relations (Belsky et al. 1989, Pringle and Fox-Dobbs 2008, Holdo et al. 2009), the effects of P. megacephala invasion may cascade to affect ecosystem function, a consequence observed in a number of other invaded ecosystems (Ehrenfeld 2010).

Given that strong negative effects of invasive ants on native ant assemblages can persist across many decades (Menke et al. 2018), an important unanswered question in our study system is whether P. megacephala will continue to persist in these savanna habitats over the long term, and at what densities. In many areas of the world where it has established, P. megacephala has remained at high densities over time scales from decades (e.g., northern Australia; Hoffmann and Parr 2008) to over a century (e.g., Hawaii; Wetterer 2012). Contrastingly, collapses of high-density populations have been recorded at other locations, including the islands of Culebrita, Puerto Rico (Torres and Snelling 1997) and Madeira, Portugal (Wetterer et al. 2006). On Ol Pejeta conservancy, P. megacephala is currently expanding its range at rates of up to ~50 m/yr, suggesting that strong population declines are unlikely in the near term (A. G. Pietrek et al., unpublished manuscript). However, in a recent modeling study, Bertelsmeier et al. (2013) found that future climate change may contract P. megacephala's range in East Africa and elsewhere, emphasizing the potential importance of abiotic factors in limiting the spread of invasive ants (e.g., see Holway 1998).

On Ol Pejeta Conservancy where we conducted our study, A. drepanolobium provides important forage for threatened species including black rhino (Diceros bicornis), and the tree population may be at risk as a result of P. megacephala invasion. Effective restoration and mitigation efforts in this system will need to address not only the control of P. megacephala, but also the barriers to reestablishment that exist for the Crematogaster species, including both propagule limitation and low host plant productivity. As exotic species continue to drive the assembly of novel communities worldwide (Seebens et al. 2017), tests of the mechanisms through which invasive species impact resident communities will enrich our understanding of how invaded ecosystems reorganize, and may be helpful in guiding environmental management.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3230/suppinfo

DATA AVAILABILITY

Data are available from the University of Florida Institutional Repository at: https://ufdc.ufl.edu/IR00011249/00001