# Disruption of a protective ant-plant mutualism by an invasive ant increases elephant damage to savanna trees

Corinna Riginos, <sup>1,4</sup> Megan A. Karande, <sup>2</sup> Daniel I. Rubenstein, <sup>2</sup> and Todd M. Palmer<sup>3</sup>

<sup>1</sup>Teton Research Institute, Teton Science Schools, Jackson, 83001 Wyoming USA
<sup>2</sup>Department of Ecology and Evolutionary Biology, Princeton University, Princeton, 08544 New Jersey USA
<sup>3</sup>Department of Biology, University of Florida, Gainesville, 32611 Florida USA

Abstract. Invasive species can indirectly affect ecosystem processes via the disruption of mutualisms. The mutualism between the whistling thorn acacia (Acacia drepanolobium) and four species of symbiotic ants is an ecologically important one; ants strongly defend trees against elephants, which can otherwise have dramatic impacts on tree cover. In Laikipia, Kenya, the invasive big-headed ant (Pheidole megacephala) has established itself at numerous locations within the last 10-15 years. In invaded areas on five properties, we found that three species of symbiotic Crematogaster ants were virtually extirpated, whereas Tetraponera penzigi co-occurred with P. megacephala. T. penzigi appears to persist because of its nonaggressive behavior; in a whole-tree translocation experiment, Crematogaster defended host trees against P. megacephala, but were extirpated from trees within hours. In contrast, T. penzigi retreated into domatia and withstood invading ants for >30 days. In the field, the loss of defensive Crematogaster ants in invaded areas led to a five- to sevenfold increase in the number of trees catastrophically damaged by elephants compared to un-invaded areas. In savannas, tree cover drives many ecosystem processes and provides essential forage for many large mammal species; thus, the invasion of big-headed ants may strongly alter the dynamics and diversity of East Africa's whistling thorn savannas by disrupting this system's keystone acacia-ant mutualism.

Key words: Acacia drepanolobium; big-headed ant; Crematogaster spp.; elephant; Laikipia, Kenya; Pheidole megacephala; tree cover; whistling thorn acacia.

#### Introduction

Mutualisms are ubiquitous and ecologically important species interactions (Bronstein 1994) that play key roles in community and ecosystem processes such as seed dispersal, pollination, and nutrient cycling (van der Heijden et al. 1998, Traveset and Richardson 2010). Invasive species can disrupt these ecologically important relationships, with potential ecosystem-wide consequences (Christian 2001, Kiers et al. 2010, Aslan et al. 2013). The whistling thorn acacia (Acacia drepanolobium) maintains a complex mutualistic relationship with multiple species of ants (Young et al. 1997, Palmer et al. 2000, 2002, 2008; see Plate 1). However, the invasive big-headed ant (Pheidole megacephala) has recently been observed in the A. drepanolobium-dominated savannas of Laikipia, Kenya (Visitacao 2011). Here, we sought to elucidate the consequences of the P. megacephala invasion on an A. drepanolobium savanna via its effects on four species of mutualistic acacia ants.

The ant symbionts of *Acacia drepanolobium* differ substantially in their interactions with each other and with their tree hosts. Individual trees are typically

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occupied by one species, and interspecific competition for host trees is intense (Young et al. 1997, Palmer et al. 2000). In direct competitive encounters, there is a strong dominance hierarchy (sensu Schoener 1983), with Crematogaster sjostedti > C. mimosae > C. nigriceps > Tetraponera penzigi (Palmer et al. 2000). The nonaggressive T. penzigi, however, resists takeover by removing the trees' carbohydrate-producing extrafloral nectaries (sought-after by the Crematogaster ants) and by taking refuge inside the trees' hollow "swollen thorn" domatia behind entry holes that are too small for the larger Crematogaster ants to enter (Palmer et al. 2002). All four ant species defend their host trees against invertebrate and vertebrate consumers; however, C. mimosae and C. nigriceps provide much stronger protection than do T. penzigi and C. sjostedti (Stanton and Palmer 2011).

The role of these ants in defending trees against elephants is particularly important. Elephants can have devastating effects on trees by browsing, breaking tree branches, stripping bark, and pushing over entire trees. On *A. drepanolobium*, however, mutualistic ants substantially reduce the amount of damage that elephants inflict, stabilizing tree cover across the entire landscape (Goheen and Palmer 2010). In contrast, acacia species that do not harbor mutualistic ants have suffered sharp declines in areas of high elephant density.

<sup>&</sup>lt;sup>4</sup> E-mail: corinna.riginos@tetonscience.org

The invasive big-headed ant has established itself at multiple centers of human habitation throughout the Laikipia region, probably within the past 10–15 years, based on local informants' memories. Invasions of P. megacephala have been highly disruptive in other ecosystems, particularly in the tropical and sub-tropical zone, where they have devastated populations of native ants and other arthropods via both predation and competition (Hoffmann et al. 1999, Dejean et al. 2007, Hoffmann and Parr 2007, Wetterer 2007, Fournier et al. 2012). We predicted two possible alternative effects of the P. megacephala invasion on the native acacia ants: either (1) the behaviorally dominant and aggressive species (particularly C. sjostedti and C. mimosae) would be less vulnerable to displacement than the subordinate C. nigriceps and T. penzigi, or (2) the nonaggressive T. penzigi would be less vulnerable to displacement due to the unique behaviors it has adopted to prevent exclusion by its native competitors. We tested these predictions and examined possible impacts of the big-headed ant invasion on native ants and their tree hosts. In this study, we specifically asked: (1) Is P. megacephala able to invade the native ant-defended acacia overstory? (2) Are there differences among the native ants in their ability to defend themselves against P. megacephala invasion? And, (3) what are the effects of the invasion on A. drepanolobium trees?

### **M**ETHODS

## Study system

This research was carried out on six properties in Laikipia, Kenya: Ol Pejeta Conservancy, Lewa Conservancy, Segera Ranch, El Karama Ranch, Ol Jogi Ranch, and Mpala Research Center. All properties harbor relatively high abundances of large wild mammals, including elephants. Here, as in other parts of East Africa, *A. drepanolobium* forms a near-monospecific overstory at sites underlain by heavy clay, vertic soils. Nearly all *A. drepanolobium* trees are ant occupied, except for the smallest saplings (Young et al. 1997).

Pheidole megacephala has been present in the region since at least 2000 (J. Lemboi, personal observation), but was not observed in association with A. drepanolobium in East Africa in a 1970 survey of multiple sites (Hocking 1970). Although the origin of this species is unclear (likely Afrotropical or Malagasy; Fischer and Fisher 2013), all indications are that it is a new arrival in Laikipia and is an invasive species (Visitacao 2011). Like most of the Pheidole genus, the big-headed ant exhibits a complete dimorphism between its smaller minor workers and larger major workers. The ant generally nests in the ground and appears to form unicolonial supercolonies (Fournier et al. 2012).

## Tree occupancy surveys

To determine whether the four species of native ants differed in their vulnerability to invasion, we surveyed trees on five different properties (Ol Pejeta, El Karama, Segera, Lewa, and Ol Jogi) where the big-headed ant appears to have established in areas of human occupation and spread radially into relatively undisturbed A. drepanolobium savanna. At each property, we located an invasion front (minimum 200 m from human structures, except at Segera where P. megacephala were only found <100 m from human structures) and sampled trees along a series of parallel, randomly located  $2 \times 50$  m belt transects (20 m apart) originating on either side of the invasion front ( $\sim$ 20–50 m from the front on either side). Invaded and un-invaded areas were otherwise comparable in terms of soil type and tree species composition and size distribution. On Ol Pejeta, Lewa, and El Karama, we sampled 200 trees: 100 on the P. megacephala-invaded side of each front and 100 on the un-invaded side. The handful of trees that were not A. drepanolobium were excluded from analyses. On Segera we found only 34 A. drepanolobium trees within the invaded area; 34 additional trees were sampled on the un-invaded side of the front. At the Ol Jogi site, the entire patch of trees (mixed species dominated by A. drepanolobium) was invaded by P. megacephala, and there was no comparable un-invaded patch within reasonable distance; thus we report results for 143 A. drepanolobium sampled in the invaded area. Data were collected in July 2012 (Ol Pejeta, Ol Jogi, Segera) and May 2014 (Lewa, El Karama), both during the prolonged semi-wet season (late May-July) that follows the April–May wet season.

Trees provide carbohydrate rewards to native *Crematogaster* ants via nectaries (whereas *T. penzigi* removes nectaries); we sampled nectaries to assess whether *P. megacephala* might be obtaining carbohydrates from the trees. For every tree, we recorded the presence or absence of *P. megacephala*, as well as the presence of native ants. On each of four randomly chosen branches per tree, we scored extrafloral nectaries as active (at least one nectary with red or green tissue) or dry (all nectaries with brown or grey tissue and a withered appearance) based on 10–20 nectaries, following the methods in Palmer et al. 2008; this method provides an accurate indication of whether nectaries are producing nectar (Palmer et al. 2008).

We used chi-squared tests to examine differences between the invaded and un-invaded areas on each property with respect to the proportion of *A. drepanolobium* trees in each of five occupancy states (occupied by one of the four native ant species or unoccupied by native ant species), and the proportion of trees bearing active nectaries. For the analysis of nectary activity, we excluded trees occupied by *T. penzigi*, as this species destroys all nectaries on its host tree (Palmer et al. 2002).

## Ant interactions in direct conflict

In order to explore the behavioral mechanisms underlying patterns of native ant persistence and extirpation in invaded field sites, we simulated the interactions of native ants defending their host trees against the invader by translocating whole A. drepanolobium trees (all 1.4–2.0 m in height) from an un-invaded location to an invaded location. This work was conducted at the Mpala Ranch in July 2012; trees were translocated from an un-invaded field site on the ranch to the Mpala Research Center, where the density of P. megacephala is very high around the research center buildings. A total of 16 trees were translocated: four of each native ant species on four different days. Trees were cut at the base, and the bottom of each tree was wrapped with duct tape coated with Tanglefoot (Contech, Spartanburg, South Carolina, USA) to prevent ants from leaving the tree during transport. Trees were transported upright. At the research center, their trunks were "planted" into augured holes in the ground on a flat, low, grassy lawn surrounded by Acacia ethaica (not a myrmecophyte) woodland. Each replicate set of four trees was arrayed in a  $4 \times 4$  m square.

We observed trees at 20-min intervals for three hours after removing the Tanglefoot tape. During each observation period, we recorded the presence or absence of both native and invasive ants at three locations on the tree: the base, trunk, and branch tips. After three hours the majority of the conflict was over; however, we continued to check trees daily for 30 days, scoring them for any ant occupants. Several domatia on each tree were checked nondestructively each day. To ensure that the behavior displayed by native ants was a consequence of P. megacephala presence and not just a reaction to the tree transplantation, the same protocol (n = 4, one of each native ant species occupant) was repeated in a different flat, grassy location on Mpala Ranch where no P. megacephala were present. All native ants exhibited normal behavior (calmly moving about leaves and branches) for the entire three-hour observation period.

We used univariate survival analyses to model the time elapsed until *P. megacephala* had fully occupied (native ants no longer present) three different locations on the tree (base, trunk, and branches). A chi-squared test was then used to test whether the response curves differed across the trees based on their native ant occupant.

To further explore the interactions between native ants and P. megacephala in direct conflict, we staged a series of controlled, replicated battles in the laboratory. This allowed us to examine ant-ant interactions while holding the number of ants constant; something that was not possible in the tree translocation experiment. A total of 20 ten-on-ten battles were performed for each native ant species. Ten replicates used only P. megacephala minor workers and the other ten used only major workers. Battles were staged inside 30.48 cm (12 inch) diameter "arenas" rimmed with Fluon (Bioquip Products, Rancho Dominguez, California, USA). Each battle was observed for 30 minutes; every five minutes the number of ants engaging in aggressive interactions (prolonged biting and stinging) and the number of dead ants were recorded. We used analysis of variance

(ANOVA) to test whether the mean number of native ants (1) fighting after a 5-min interval, and (2) dead after the 30-min observation period varied among the four species. Because responses were similar for major and minor workers, we pooled data across the two castes. Means were compared using Tukey's test.

## Elephant damage

We compared levels of elephant damage to trees between invaded and un-invaded areas on Ol Pejeta, El Karama, and Lewa (the sites where there was an adequate number of trees to sample under both conditions). All A. drepanolobium trees surveyed (see Tree occupancy surveys) were scored for recent elephant damage (stem tissue still yellow or bark tissue still red) on a 1–5 scale: 1 for light or no damage (branch tips exhibit slight browsing); 2 for mild damage (branches browsed and broken); 3 for medium damage (20-50% of canopy was destroyed); 4 for substantial damage (>50% of canopy was destroyed); and 5 for catastrophic damage (tree completely pushed over or 100% canopy destroyed). Given the spatial proximity of each invaded and un-invaded area (<100 m, on opposites sides of each invasion front), there is no reason to believe that elephant presence or activity levels would differ between invaded and un-invaded areas. We used chi-square tests to evaluate whether levels of elephant damage varied between the invaded and un-invaded areas of each site. To further explore the mechanisms underlying the observed patterns, we assessed ant aggression on 28 randomly chosen A. drepanolobium trees (15 occupied by P. megacephala, 7 by C. mimosae and 6 by C. nigriceps) on Mpala Ranch in June 2014. A single swollen thorn was tapped on each tree and the number of workers swarming onto the stipule was counted over a 30-s interval. Data were analyzed as a one-way ANOVA with ant species as a fixed effect and tree height as a covariate. All analyses were conducted using JMP version 9.0 (SAS Institute 2010).

# RESULTS

## Tree occupancy patterns

Pheidole megacephala ants were present on almost all A. drepanolobium trees in the five invaded areas surveyed (100% occupancy at all sites, except El Karama with 87% occupancy). The presence of *P. megacephala* on trees was associated with dramatic shifts in the occurrence of native ants (Fig. 1). Whereas C. mimosae, C. sjostedti, and C. nigriceps dominated in un-invaded areas, the only native ant species consistently found in P. megacephala-invaded areas was T. penzigi. Further, T. penzigi occupied 10-12 times more trees in invaded areas compared to un-invaded areas (Fig. 1). In invaded areas, there were also numerous trees with no native ants on them (only *P. megacephala* present): a state rarely seen in the un-invaded areas. A higher percentage of trees also had active extrafloral nectaries in un-invaded areas than in *P. megacephala*-invaded areas (Table 1).

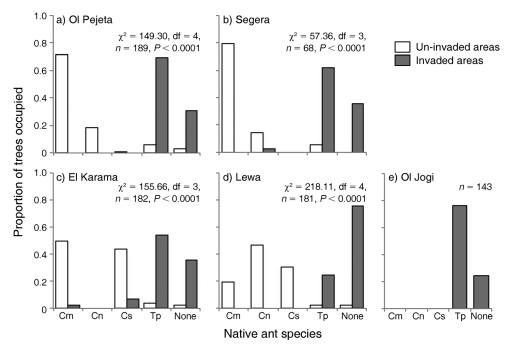


Fig. 1. Native ant presence on *Acacia drepanolobium* trees at five sites in control areas (un-invaded; white bars) and areas invaded by the big-headed ant (*Pheidole megacephala*; gray bars) in Laikipia, Kenya. Trees in control areas on all properties had zero presence of *P. megacephala*. No control area was available for Ol Jogi. Trees in invaded areas had 100% *P. megacephala* presence at the Ol Pejeta, Segera, Lewa, and Ol Jogi sites, and 87% presence at the El Karama site; in almost all cases (except 11 trees on El Karama), native ants in the invaded areas were co-occupying the tree along with *P. megacephala*. Abbreviations are: Cm, *Crematogaster mimosae*; Cn, *C. nigriceps*; Cs, *C. sjostedti*; and Tp, *Tetraponera penzigi*.

## Ant interactions in direct conflict

In the tree translocation experiment, T. penzigi exhibited very different behaviors from the three Crematogaster ants. While the Crematogaster ants streamed down the tree trunks and engaged P. megacephala in intense fighting at the base of the tree, T. penzigi retreated to the host tree's domatia within the first 20 minutes, allowing P. megacephala to occupy the tree with limited conflict. On T. penzigi trees, P. megacephala fully occupied the base ( $\chi^2 = 16.56$ , df = 3, n = 16, P < 0.001; Fig. 2a), trunk ( $\chi^2 = 19.90$ , df = 3, n= 16, P = 0.002), and branches ( $\chi^2 = 20.65$ , df = 3, n = 16, P < 0.0001; Fig. 2b) significantly faster than on trees occupied by the other ants, in about half the time compared to C. sjostedi trees and one-fifth the time compared to C. nigriceps and C. mimosae trees. Once inside the domatia, however, T. penzigi were able to block P. megacephala from entering. Over the next 30 days, P. megacephala workers continued to patrol these trees, while T. penzigi persisted inside the domatia. In contrast, once P. megacephala ants occupied the branches of the Crematogaster trees (within hours), they met little resistance, quickly entering the domatia and removing the brood.

In staged battles in the laboratory, *T. penzigi* was also less likely to be in direct conflict with *P. megacephala*. While the *Crematogaster* ants typically approached the *P. megacephala* ants and engaged in aggressive interac-

tions, *T. penzigi* avoided *P. megacephala*, often flattening their gasters and letting the invasive ant walk over them. After five minutes, *T. penzigi* was stinging or being bitten by, on average, one-third as many *P. megacephala* ants as were the three *Crematogaster* species ( $F_{3,76} = 21.60$ , df = 3, P < 0.0001; Fig. 2c). After 30 minutes of fighting, *T. penzigi* also experienced less than half the mortality of *C. mimosae* and *C. sjostedti*, and a little more than half as much as *C. nigriceps* ( $F_{3,76} = 8.23$ , df = 3, P < 0.0001; Fig. 2d).

## Elephant damage

Acacia drepanolobium trees in the P. megacephala-invaded areas on Ol Pejeta, El Karama, and Lewa all

Table 1. The percentage of trees with active nectaries (and  $\chi^2$  test results) in un-invaded areas and areas invaded by the big-headed ant (*Pheidole megacephala*) at four sites in Laikipia, Kenya.

	Trees with nectaries (%)				
Site	Un-invaded	Invaded	$\chi^2$	n	P
Ol Pejeta Segera El Karama Lewa	64.1 93.7 96.7 97.9	0 38.5 20.0 0	61.41 15.38 85.67 194.85	132 45 131 159	<0.0001 <0.0001 <0.0001 <0.0001

*Note:* Trees occupied by *Tetraponera penzigi* were excluded from these analyses since these ants remove nectaries.

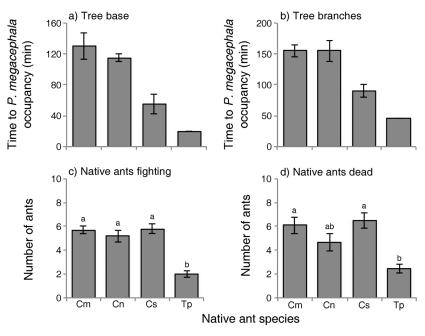


Fig. 2. Results of experimental conflicts between native acacia ants and P. megacephala. Mean ( $\pm$ SE) time until P. megacephala had completely occupied the (a) base and (b) branches of translocated A. drepanolobium trees. Occupation was indicated when native ants had completely evacuated each section of the tree. Mean number ( $\pm$ SE) of native ants (c) fighting after five minutes and (d) dead after 30 minutes in ten-on-ten staged battles. Different letters above the bars indicate significant differences in Tukey's test post hoc comparisons among the four native ant species. See Fig. 1 for abbreviations.

had much higher levels of moderate to catastrophic elephant damage compared to trees in un-invaded areas, which mostly had little to no elephant damage (Fig. 3). At both Ol Pejeta and El Karama, catastrophic damage was five times more common in the invaded areas than un-invaded areas. Elephant damage in the invaded area on Lewa was generally less than on Ol Pejeta and El Karama, but still distinctly greater than damage levels on the other side of the invasion front on Lewa. The ant aggression survey showed that far fewer P. megacephala  $(0.13 \pm 0.09$  ants [mean  $\pm$  SE]) swarmed in response to disturbance than either C. mimosae  $(17.17 \pm 6.45$  ants) or C. nigriceps  $(20.71 \pm 3.25$  ants;  $F_{2,25} = 18.71$ , df = 2, P < 0.0001).

## DISCUSSION

Although invasive species have been shown to disrupt a variety of mutualistic relationships, the indirect and cascading consequences of mutualism breakdowns are less well understood (Lach 2003, Ness and Bronstein 2004, Aslan et al. 2013). In a Kenyan savanna where an invasion by *Pheidole megacephala* appears to be occurring, we found that the invader is capable of disrupting the mutualism between *A. drepanolobium* and at least three species of native ants, threatening to fundamentally alter ecosystem dynamics by facilitating increased levels of elephant damage to trees.

In this region, *P. megacephala* appears to be spreading radially from centers of human disturbance. This ground-dwelling species forms a contiguous invasion

front made up of a single supercolony (Fournier et al. 2012). In contrast, colonies of native acacia ants typically occupy between one and six individual trees. In the presence of *P. megacephala*, we found that this patchy mosaic of native ants almost completely breaks down. Virtually all trees in *P. megacephala*-invaded areas were occupied by the invasive ant, with native *Crematogaster* ants (*C. mimosae*, *C. nigriceps*, and *C. sjostedti*) almost completely absent from these sites (Fig. 1). In contrast, *T. penzigi* was found co-occurring with *P. megacephala* on 24–76% of invaded trees.

Based on the strong dominance hierarchy among the four native acacia ants (Palmer et al. 2000), we initially predicted that the competitive dominant C. sjostedti would best be able to withstand a P. megacephala invasion and that the competitive subordinate T. penzigi would least be able to persist. Instead, we found that T. penzigi was best able to persist, likely because of its nonaggressive interspecific behavior. In tree translocation trials, T. penzigi retreated into the trees' domatia, allowing the big-headed ants to completely occupy the trees' trunk and branches within 20 minutes (Fig. 2a, b). Once inside, however, T. penzigi ants were able to prevent the invaders from entering by blocking the domatia holes with their stinging gasters. This sting is lethal to Crematogaster ants (Palmer et al. 2002), and similarly, we observed its lethal effects on P. megacephala. Additionally, the big-headed major workers were unable to enter the small domatia holes made by T. penzigi. Tetraponera penzigi ants were able to mount a

lasting defense; we found ants inside the trees' domatia even 30 days after the trees were translocated, while *P. megacephala* continued to patrol these trees and attempt to enter the domatia.

The three *Crematogaster* species had a more proactive defense strategy, recruiting aggressively to the base of the tree to fight the big-headed ants. Although they were able to inflict substantial mortality and delay the bigheaded ant's occupation of the tree, the *Crematogaster* ants were eventually overwhelmed by the invasive ant. Once in the branches, *P. megacephala* were able to enter the large holes in the *Crematogaster* domatia and remove larvae, brood, and any remaining adult native ants.

These tree translocation trials are an imperfect simulation of the dynamics along an actual invasion front; nevertheless, the extirpation of the three Crematogaster species, as well as the persistence of T. penzigi, in experimental conflicts provides a clear mechanism for the patterns of ant occupancy we observed in the field. At an invasion front the fighting between P. megecephala and Crematogaster ants would likely be much more prolonged, since the invader would be less well established and the native ants would, collectively across multiple colonies, have many more ants fighting the invader. Further, as the invasion progresses, it appears to create opportunities for T. penzigi to occupy trees it did not occupy before (see next paragraph), which was not predictable from the translocation trials. A more thorough test of these dynamics would be to observe ant-ant interactions along the invasion front and compare the native ant communities on known trees over time as the invasion front progresses (Krushelnycky and Gillespie 2009).

As noted, *T. penzigi* was found on a disproportionately high fraction of trees in invaded areas in the field (Fig. 1). It appears that, in the absence of its native competitors, foundress *T. penzigi* queens can colonize trees not formerly occupied by this species. However, *T. penzigi* were only found on the distal domatia of the trees. While *P. megacephala* were found streaming up and down the trunks and major branches of these trees, they were rarely observed in the distal branches; thus *P. megacephala* and *T. penzigi* seem to co-occur, at least in part, by partitioning the tree spatially. The net effect of *P. megacephala* on *T. penzigi* populations is not yet clear.

It is also not entirely clear why *P. megacephala* ants continue to occupy *A. drepanolobium* trees at relatively high densities long after they have eliminated the native occupants. It is possible that the invasive ants are initially attracted to the nectar produced by *A. drepanolobium*'s extrafloral nectaries, as is the case with *A. saligna* (Lach et al. 2009). However, the invasive ant does not appear to be able to stimulate *A. drepanolobium* trees to produce nectar, consistent with observations for *A. saligna* (Lach et al. 2009), and we found high densities of *P. megacephala* even on trees where all nectaries were

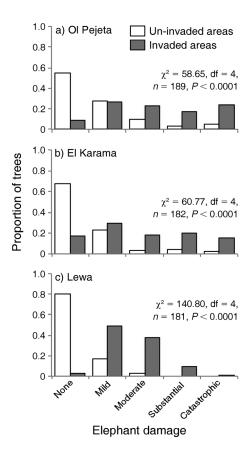


Fig. 3. The proportion of *A. drepanolobium* trees in control (white bars) and *P. megacephala*-invaded areas (gray bars) at three sites that experienced different levels of elephant damage. Mild damage was defined as branch tips browsed and/or broken; moderate as 20–50% canopy damage; substantial as 50–99% canopy damage; and catastrophic as tree pushed over, 100% canopy damage.

dry. Thus, it is unlikely that extrafloral nectaries provide any lasting benefit to the big-headed ants. It is possible that *P. megacephala* benefit from the trees in other ways; for example, by consuming honeydew from sap-sucking scale insects.

The invasion of *P. megacephala* into the savannas of Kenya may have important consequences for the biodiversity, structure, and function of these ecosystems. While native ants defend trees against herbivores, we found that P. megacephala did not respond to simulated browser disturbance. Further, T. penzigi is a relatively poor defender of its host tree (Stanton and Palmer 2011). In P. megacephala-invaded areas on three separate ranches, we found, on average, five times more trees that had experienced moderate, substantial, and catastrophic elephant damage compared to trees in un-invaded areas (Fig. 3). By contrast, 50-80% of trees in the un-invaded areas had experienced no elephant damage. These results support the hypothesis that the mutualism between A. drepanolobium and its native ant symbionts plays a



PLATE 1. Native Crematogaster mimosae ants march up and down the trunk of an Acacia drepanolobium tree. Photo credit: T. M. Palmer.

critical role in stabilizing landscape-scale savanna tree cover in the face of high elephant densities (Goheen and Palmer 2010). Thus, by disrupting the keystone ant–plant mutualism, the *P. megacephala* invasion is likely to result in substantial reductions in tree cover over the coming years.

A significant loss of tree cover has the potential to cause important changes in ecosystem function. Tree cover in savannas regulates a host of ecosystem processes, including carbon storage, grass production, fire return-intervals, nutrient cycling, soil—water relations, and herbivore habitat use (Belsky 1994, Caylor et al. 2005, Riginos and Grace 2008, Staver et al. 2011, Sitters et al. 2013). Moreover, in this region of high conservation value, *A. drepanolobium* is an important food source for a variety of large mammals, including rare and threatened species such as black rhino (*Diceros bicornis*) and reticulated giraffe (*Giraffa camelopardalis reticulata*).

The invasion of *P. megacephala* in Laikipia appears to be in its early stages; however, this ant is capable of spreading over large areas (Hoffmann and Parr 2007). If such spread occurs in the *A. drepanolobium* savannas of East Africa, the consequences could be far-reaching. These savannas constitute some of the most productive and iconic landscapes of East Africa, including large portions of the Serengeti and Maasai Mara National Parks, Nairobi National Park, and the private conservancies of Laikipia. While the extent and long-term consequences of landscape alterations caused by *P. megacephala* are as yet unknown, its potential to destabilize woody cover in this region of high conservation value are cause for concern.

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