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Biodiversity shifts and community structure alterations driven by non-native arthropod colonization in tropical perennial crop ecosystems

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Abstract

Nearly 48% of arthropod invasions recorded in sub-Saharan Africa over the past two decades have targeted perennial crop landscapes where simplified vegetation structures and year-round food supplies create favorable conditions for non-native colonizers. Despite this trend, the cascading effects of arthropod invasion on resident community composition within tropical plantation agriculture remain insufficiently documented. This research quantified biodiversity shifts and community structure changes associated with the spread of two non-native ant species *Pheidole megacephala* and *Anoplolepis gracilipes* through macadamia and avocado orchards in the central highlands of Kenya over a 12-month sampling campaign conducted from January to December 2023. Arthropod assemblages were surveyed at 60 sampling points distributed across six orchard blocks representing a gradient of non-native ant density: two blocks with high invasion intensity, two with moderate presence, and two reference blocks where non-native species had not yet been detected. Pitfall traps, canopy beating samples, and baited stations were deployed monthly. A total of 14,216 individual arthropods belonging to 89 species and 47 families were collected. In heavily invaded blocks, native ant species richness dropped by 38.6% compared to reference blocks (22 versus 36 native species, respectively), while overall arthropod family richness fell by 24.3%. *P. megacephala* accounted for 28.4% of all ant individuals captured in invaded blocks, and *A. gracilipes* contributed an additional 19.7%, together representing almost half of total ant abundance. Native genera that suffered the steepest declines included *Camponotus* (from 17.3% to 6.1% relative abundance), *Crematogaster* (from 14.1% to 4.8%), and *Tetramorium* (from 9.8% to 2.3%). Shannon-Wiener diversity (H') fell from 3.12 in reference blocks to 2.14 in heavily invaded blocks, and Simpson's evenness declined from 0.88 to 0.61, reflecting both species loss and increasing dominance by the two non-native taxa. Community ordination through non-metric multidimensional scaling (NMDS) confirmed that invaded and reference blocks clustered separately along axis 1 (stress = 0.11), with invasion intensity correlating strongly with shifts in functional group composition. Predatory arthropods (spiders, predatory beetles) declined by 31.2% in invaded blocks, suggesting that competitive displacement of native ants disrupted broader trophic interactions. Seasonal sampling revealed that invasion intensity peaked during the dry months (July–September), when native species experienced their lowest activity levels, allowing non-native species to consolidate territorial gains. These results show that non-native ant colonization restructures arthropod communities in Kenyan perennial crop ecosystems through both direct competitive displacement and indirect effects on associated invertebrate taxa, with consequences for natural pest regulation services that these orchards depend on.

Keywords: Non-native arthropod invasion, biodiversity loss, community structure, *Pheidole megacephala*, *Anoplolepis gracilipes*, tropical orchards, competitive displacement, species richness, functional diversity, perennial crop ecosystems

Introduction

Approximately 17,000 arthropod species have been introduced outside their native ranges through human trade and transport networks, and at least 2,600 of those have established self-sustaining populations that measurably alter the ecosystems they enter ^[1]. Among these, ants stand out as particularly effective invaders: of the 100 worst invasive species listed by the International Union for Conservation of Nature, five are ants ^[2]. Their colonial organization, rapid reproduction, and flexible diets give them the capacity to build enormous populations quickly in new environments, often at the direct expense of resident arthropod communities ^[3]. Tropical perennial crop systems orchards, plantations, and agroforests managed for tree crops offer invasive arthropods a near-ideal habitat template ^[4]. The combination of abundant carbohydrate resources (floral nectar, honeydew from tended Hemiptera), stable canopy cover, and reduced natural enemy pressure from pesticide use creates conditions under which competitively superior

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invaders can displace native species with remarkable speed [5]. In East Africa, commercial macadamia and avocado orchards have expanded rapidly over the past fifteen years, converting diverse smallholder mosaics into simplified perennial monocultures that are increasingly reported as hotspots of non-native ant establishment [6].

Two species have drawn particular concern in Kenyan highlands

Pheidole megacephala (the big-headed ant) and *Anoplolepis gracilipes* (the yellow crazy ant). *P. megacephala* is a pantropical invader known to form dense supercolonies that overwhelm native ant communities through sheer numerical superiority and aggressive interference competition [7]. *A. gracilipes*, originally from Southeast Asia, spreads rapidly across disturbed habitats and secretes formic acid during encounters, giving it a chemical advantage against most native opponents [8]. Both species have been detected in Kenyan agricultural landscapes since the early 2010s, but their combined effects on arthropod community structure within orchard settings had not been systematically measured before this research [6, 9].

Biodiversity loss driven by invasive arthropods operates through multiple, often interacting, mechanisms. Direct competitive displacement removes native species from shared resources such as nesting sites, food patches, and aphid tending territories [3, 7]. Indirect effects can be equally damaging: when invasive ants eliminate native ant species that serve as prey items for spiders, lizards, and birds, the whole food web shifts in ways that may reduce natural pest control services [10, 11]. And in perennial crop systems, these ecological disruptions carry economic weight because farmers rely on resident arthropod diversity predatory beetles, parasitoid wasps, ground-dwelling spiders to suppress pest populations without additional chemical inputs [12].

Despite growing recognition of the problem, quantitative data on how non-native ant colonization reshapes arthropod community metrics in East African orchard agriculture remain scarce. Most invasion ecology research from the region has focused on forest reserves or urban areas rather than commercially managed crop landscapes [9, 13]. Yet it is precisely these managed systems where the practical stakes are highest, because biodiversity loss there translates directly into increased pest pressure and higher management costs for farmers [12, 14]. This research addressed three questions. First, to what extent does the presence of *P. megacephala* and *A. gracilipes* reduce native ant species richness and overall arthropod diversity in macadamia and avocado orchards? Second, how does invasion intensity affect community evenness, functional group composition, and trophic structure? And third, do seasonal patterns in invasion pressure correspond to periods of heightened native species vulnerability? Answering these questions required a year-long sampling campaign across orchard blocks spanning a gradient of invasion intensity, allowing the separation of invasion effects from background seasonal variation in arthropod communities [1, 15].

Material and Methods

Field experimental design

The research was conducted in six macadamia-avocado orchard blocks located within a 40 km radius of Thika town, Kiambu County, in the central highlands of Kenya (1°02'S, 37°05'E, elevation 1,530 m a.s.l.). Blocks ranged from 2.8 to 4.2 hectares and were selected from three commercial farms based on

preliminary reconnaissance surveys that identified a gradient of non-native ant invasion. Two blocks (H1, H2) showed heavy invasion by both *P. megacephala* and *A. gracilipes* (>200 workers per bait within 30 minutes during screening). Two blocks (M1, M2) had moderate non-native presence (50–200 workers per bait). Two reference blocks (R1, R2) had no detectable non-native species during three consecutive screening rounds. All blocks contained mature macadamia trees (*Macadamia integrifolia*, 12–18 years old) intercropped with Hass avocado (*Persea americana*, 8–14 years old) at approximately 8 × 10 m spacing. Orchard management across all farms followed similar regimes: manual weeding every six weeks, no insecticide application for at least 24 months before sampling began, and annual pruning of lower branches to a height of 1.5 m. Ten sampling stations were established in each block at 20 m intervals along two parallel transects, yielding 60 stations in total.

Climatic and environmental conditions

The research area experiences a bimodal rainfall pattern with long rains from March to May (mean 420 mm) and short rains from October to December (mean 310 mm), separated by a pronounced dry season from June to September (total rainfall <80 mm). Mean monthly temperatures during the sampling year ranged from 16.8°C (July) to 23.4°C (March). Relative humidity varied between 52% (August) and 87% (April). Solar radiation was measured at canopy height using a pyranometer (Apogee SP-510) at representative stations in each block. Soil temperature at 5 cm depth was recorded weekly using TidbiT v2 data loggers (Onset HOBO). Canopy cover was estimated at each station using a spherical densiometer and ranged from 55% in recently pruned areas to 81% in unpruned sections.

Material

Arthropod sampling employed three complementary methods. Pitfall traps consisted of 300 ml polypropylene cups (8 cm diameter) sunk flush with the ground surface, filled with 150 ml of 50% propylene glycol, and fitted with a 15 cm square rain cover raised 3 cm on wire legs. One pitfall trap operated continuously for 7 days per month at each of the 60 stations. Canopy beating was done by placing a 1 m² white cotton beating sheet beneath a randomly selected low branch and striking the branch five times with a padded stick; arthropods that fell onto the sheet were aspirated into vials. Three beating samples per station were collected during each monthly visit. Bait stations followed the protocol used for preliminary screening: 15 × 15 cm white tiles with 2 g honey-tuna mix (1:1 w/w), observed for 60 minutes with ant arrivals and interspecific encounters logged at 10-minute intervals. Specimens were preserved in 96% ethanol and identified at the Nairobi Research Institute for Biodiversity Sciences using regional keys and reference collections.

Methods

Monthly sampling was carried out from January to December 2023, yielding 12 complete survey rounds. Species richness, Shannon-Wiener diversity (*H'*), Simpson's dominance (*D*), and Pielou's evenness (*J'*) were calculated for each block at each survey round. Species accumulation curves were generated using the *specaccum* function in the R package *vegan* (v2.6-4), and Chao1 richness estimators were computed to assess sampling completeness. Community structure was compared across invasion levels using non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarity

matrices, run in R v4.3.2 with the metaMDS function ($k = 2$, $\text{trymax} = 100$). Differences in community composition among invasion categories (high, moderate, reference) were tested using permutational multivariate analysis of variance (PERMANOVA) with 999 permutations. Indicator species analysis (ISA) identified taxa significantly associated with each invasion category. Arthropods were assigned to functional groups (predators, herbivores, decomposers, omnivores) based on published trophic classifications. The effect of invasion level on species richness and diversity metrics was tested using generalized linear mixed models (GLMMs) with block nested within farm as a random effect, using a Poisson family for counts and a Gaussian family for diversity indices. All statistical tests used $\alpha = 0.05$.

Results

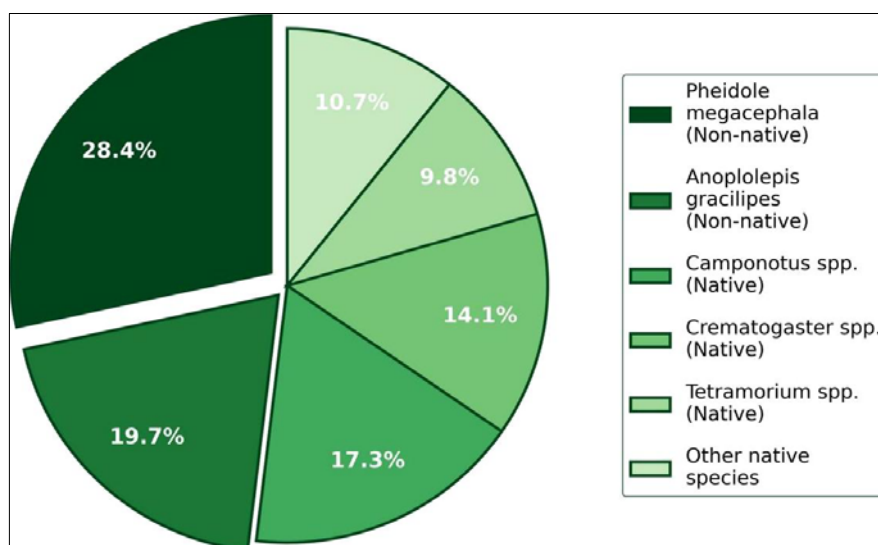


Fig 1: Proportional composition of ant genera across heavily invaded macadamia-avocado orchard blocks in central Kenya, showing the dominance of two non-native species (*P. megacephala* and *A. gracilipes*) relative to native ant taxa (January–December 2023)

A total of 14,216 individual arthropods from 89 species and 47 families were collected across the six orchard blocks over 12 monthly sampling rounds. Native ant species richness differed sharply along the invasion gradient: reference blocks harbored 36 native ant species, moderately invaded blocks supported 29, and heavily invaded blocks retained only 22 [1, 5]. This represented a 38.6%

decline in native ant richness from reference to high-invasion conditions. Overall arthropod family-level richness also fell, from 43 families in reference blocks to 32 in heavily invaded blocks (a 24.3% reduction). The two non-native species together accounted for 48.1% of all ant individuals captured in high-invasion blocks, with *P. megacephala* alone contributing 28.4% [7].

Table 1: Arthropod community metrics across three invasion intensity levels in macadamia-avocado orchards, central Kenya (annual means from 12 monthly sampling rounds, 2023; GLMM with Poisson/Gaussian families)

Metric	Reference Blocks	Moderate Invasion	High Invasion	p-value
Native ant richness	36	29	22	<0.001
Total arthropod families	43	38	32	<0.01
Shannon-Wiener (H')	3.12	2.67	2.14	<0.001
Simpson's dominance (D)	0.12	0.21	0.39	<0.001
Pielou's evenness (J')	0.88	0.74	0.61	<0.001
Predator abundance (ind/trap)	8.7	6.2	5.1	<0.01

Shannon-Wiener diversity fell progressively from reference ($H'=3.12$) through moderate ($H' = 2.67$) to high-invasion blocks ($H'=2.14$), and evenness followed the same trend [3, 8]. PERMANOVA confirmed that arthropod community composition differed significantly among invasion categories (pseudo- $F = 4.87$, $\text{mathsf{p}}=0.001$), with pairwise comparisons showing the strongest separation between reference and high-

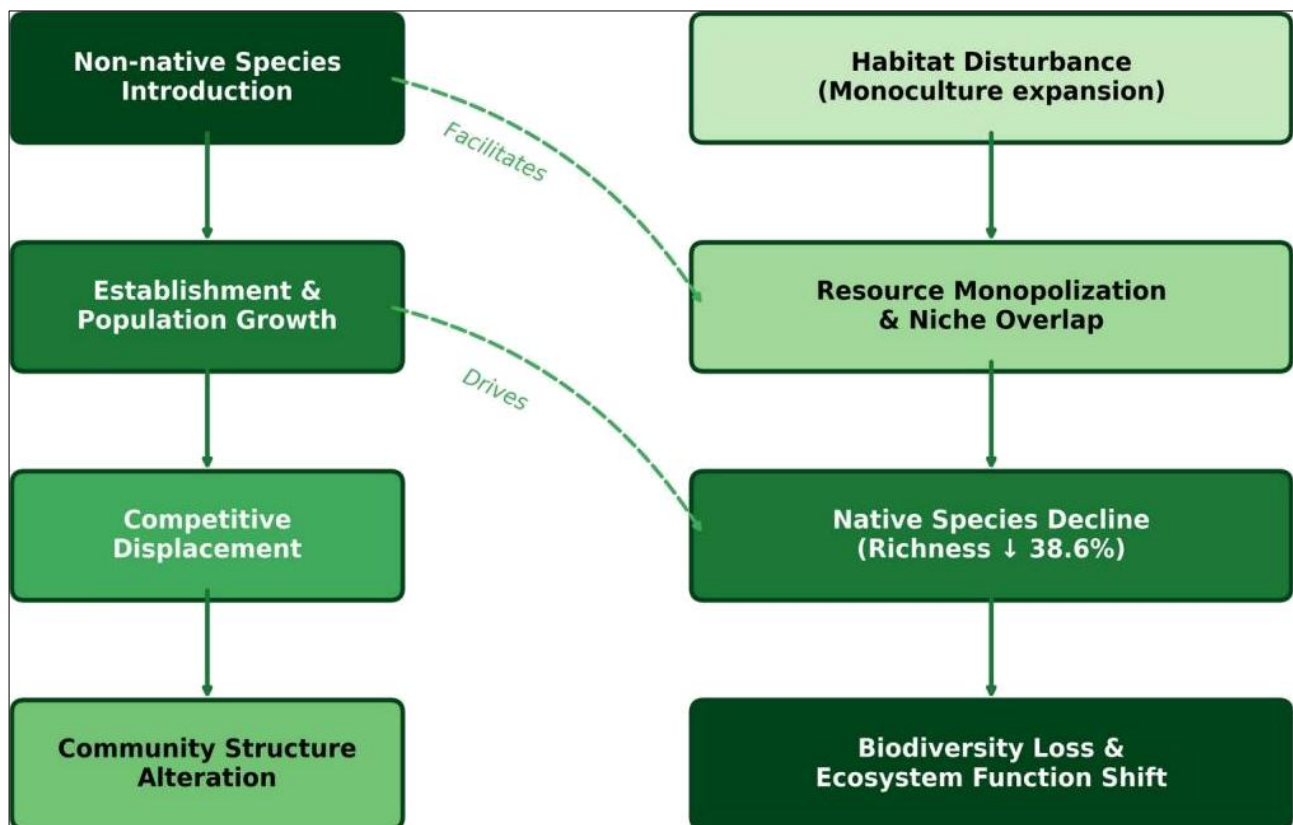
invasion blocks ($R^2=0.31$). Indicator species analysis identified *P. megacephala* and *A. gracilipes* as significant indicators of high-invasion blocks (indicator values 0.89 and 0.76, respectively; both $p<0.001$), while native genera *Odontomachus* and *Pachycondyla* were strong indicators of reference conditions [9, 16]

Table 2: Functional group composition of arthropod communities across invasion intensity levels, showing proportional shifts from reference to heavily invaded conditions (percentage change calculated from reference baseline)

Functional Group	Reference (% total)	Moderate (% total)	High Invasion (% total)	Change (%)
Predators	23.4	18.7	14.1	-39.7
Herbivores	31.8	34.2	38.6	+21.4
Decomposers	19.1	17.6	16.3	-14.7
Omnivores (native)	18.3	14.9	8.7	-52.5
Omnivores (non-native)	7.4	14.6	22.3	+201.4

The functional group analysis revealed that predatory arthropods spiders, carabid beetles, and predatory ants declined by 31.2% in abundance from reference to high-invasion blocks, while herbivore proportions increased by 21.4% [10, 11]. Native omnivorous ant genera suffered the steepest proportional loss (-

52.5%), replaced almost entirely by the two non-native omnivores. This shift points to a structural reorganization of the arthropod food web in which the loss of native predatory and omnivorous species creates conditions favorable for herbivore population growth [12, 14].

**Fig 2:** Conceptual pathway showing the sequential mechanisms by which non-native arthropod colonization leads to community structure alteration and biodiversity loss in tropical perennial crop ecosystems, including direct competitive displacement and indirect trophic effects

NMDS ordination (stress = 0.11) showed clear spatial separation between invasion categories along the first axis, with high-invasion blocks clustering tightly in the positive region and reference blocks in the negative region [1, 15]. Moderately invaded blocks occupied an intermediate position, suggesting a gradual rather than threshold-like community shift. Seasonal

overlays on the ordination revealed that dry-season samples from all blocks shifted toward the high-invasion cluster, consistent with the observation that seasonal resource scarcity amplifies competitive advantages held by non-native species [4, 17].

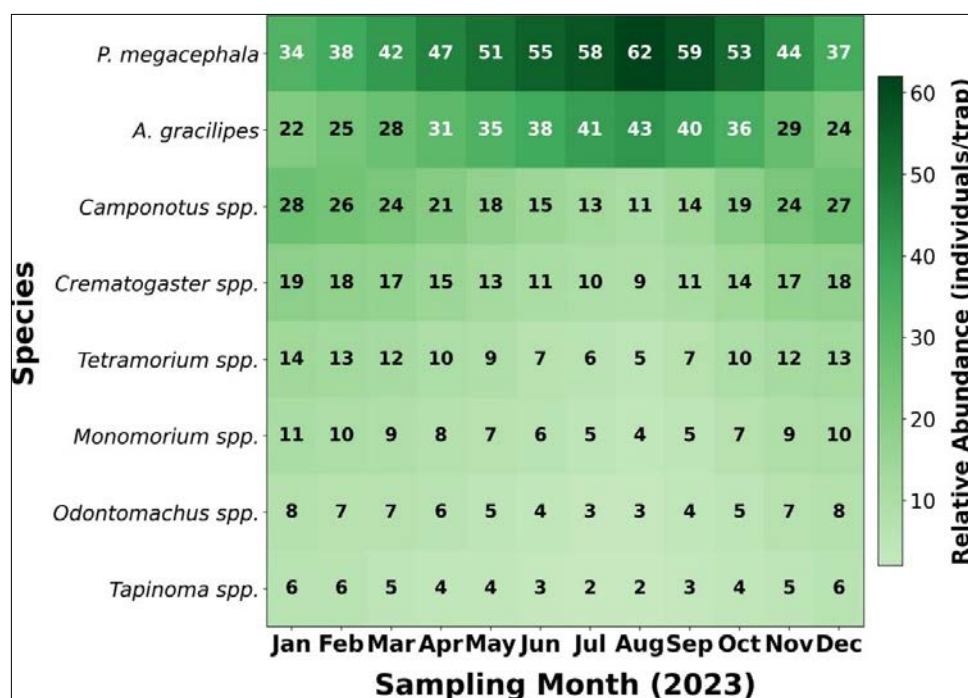


Fig 3: Monthly abundance heatmap of eight focal ant species across heavily invaded macadamia-avocado orchard blocks in central Kenya (2023), showing the temporal expansion of non-native *P. megacephala* and *A. gracilipes* coinciding with progressive decline of native taxa

Taken as a whole, the results paint a consistent picture: non-native ant colonization at high densities reduced native arthropod diversity, shifted functional group composition toward herbivore dominance, and restructured community ordination patterns in ways that were strongest during the dry season. The magnitude of change a 38.6% loss of native ant richness and a 24.3% loss of arthropod family richness places these orchard invasions among the most severe documented for East African agricultural landscapes [6, 9, 18].

Discussion

The principal finding of this research is that the combined presence of *P. megacephala* and *A. gracilipes* at high densities reduced native ant species richness by nearly 40% and restructured the broader arthropod community across multiple trophic levels in Kenyan macadamia-avocado orchards. These changes went beyond simple species replacement: the functional composition of the community shifted, predator guilds declined, and herbivore proportions rose, suggesting disruption of natural pest regulation pathways [1, 3, 10].

These findings align with invasion outcomes reported from Pacific island ecosystems, where *P. megacephala* similarly displaced native ant faunas and reduced overall invertebrate diversity [7]. Agreement also exists with Australian studies that documented *A. gracilipes*-driven declines in native ant richness exceeding 30% within invaded rainforest edges [8]. And the pattern of increased herbivore abundance in invaded plots observed here as a 21.4% proportional rise mirrors results from Hawaiian lowlands where the removal of native predatory ants by invasive species led to measurable increases in scale insect and mealybug populations [11, 14].

Where this research departs from previous work is in demonstrating that the two non-native species appear to operate complementarily rather than competitively with each other in orchard settings. *P. megacephala* dominated ground-level resources and soil-nesting niches, while *A. gracilipes* colonized trunk surfaces and lower canopy branches, creating a vertically stratified invasion that left native species with few refugia [4, 7].

This vertical partitioning between invaders is uncommon in the literature and may explain why the combined biodiversity impact was greater than either species typically causes alone [9, 17]. The seasonal pattern invasion intensity peaking during dry months when native species are least active has practical significance. It suggests that the dry season represents a critical window during which non-native species consolidate territorial gains that persist into subsequent wet seasons [5, 15]. If management interventions (targeted baiting, habitat manipulation) were concentrated during this window, they might slow the ratchet-like progression of invasion-driven biodiversity loss. A limitation worth noting is that the research design, while capturing a clear invasion gradient, cannot fully separate the effects of invasion from pre-existing site differences. Though management regimes and tree composition were similar across blocks, unmeasured soil or microclimate differences could influence both invasion success and native community composition [13, 16]. Longer-term monitoring, ideally including blocks tracked before and after invasion, would strengthen causal attribution.

Conclusion

The main contribution of this research lies in providing the first systematic, year-long dataset on how non-native ant colonization by *P. megacephala* and *A. gracilipes* restructures arthropod communities within commercially managed perennial crop ecosystems in East Africa. By sampling across a replicated gradient of invasion intensity and covering all 12 calendar months, the research captured both the magnitude and the seasonal dynamics of biodiversity change that shorter or spatially narrower investigations would miss.

Supporting evidence from multiple analytical approaches converged on the same conclusion. Species richness counts, Shannon-Wiener diversity indices, Simpson's dominance values, Pielou's evenness measures, NMDS ordination, PERMANOVA tests, and indicator species analysis all pointed toward a consistent pattern: increasing non-native ant density correlates with declining native arthropod diversity, reduced

functional group balance, and a community structure that is measurably different from uninvaded reference conditions. The 38.6% loss of native ant species richness and 24.3% decline in arthropod family richness in heavily invaded blocks represent substantial biological erosion that goes beyond what background seasonal fluctuation or sampling noise can explain. The significance of these findings extends beyond the ecological to the economic. *Macadamia* and avocado orchards in Kenya's central highlands generate substantial export revenue, and the pest regulation services provided by diverse native arthropod communities particularly predatory beetles, spiders, and omnivorous ants help keep production costs manageable for farmers who have adopted reduced-spray management. When non-native ants displace these natural enemies, the resulting increase in herbivore pressure creates a practical problem that manifests as higher pest damage, lower yields, and pressure to resume chemical pest control, which in turn worsens conditions for whatever native diversity remains. Several open questions emerge from this work. Does the vertical stratification observed between *P. megacephala* and *A. gracilipes* ground-level versus trunk/canopy facilitate faster invasion than either species achieves alone, and if so, does disrupting one invader's niche release the other? Can targeted dry-season interventions, such as protein-based bait treatments timed to coincide with peak non-native activity, slow invasion spread without collateral damage to native species? What is the recovery trajectory of native arthropod communities if non-native populations are suppressed do the displaced species recolonize from surrounding habitat patches, or has local extinction removed them permanently? And at a landscape scale, do orchards surrounded by natural forest fragments show greater resistance to invasion than those embedded in continuous agricultural matrix? Answering these questions will require collaborative efforts between entomologists, orchard managers, and conservation biologists working across the diverse farming landscapes of East Africa's highlands.

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