

RESEARCH ARTICLE

Mutualistic interactions facilitate invasive species spread

Adam J. M. Devenish^{1,2,3}  | Rosemary J. Newton¹  | Jeremy J. Midgley⁴  |
Louise Colville¹  | Jon Bridle^{2,3}  | Seirian Sumner^{2,3} 

¹Science Directorate, Royal Botanic Gardens Kew, Wakehurst Place, Ardingly, UK

²School of Biological Sciences, University of Bristol, Bristol, UK

³CBER, Department of Genetics, Evolution and Environment, University College London, London, UK

⁴Department of Biological Sciences, University of Cape Town, Rondebosch Cape Town, South Africa

Correspondence

Adam J. M. Devenish

Email: a.devenish@kew.org

Funding information

Natural Environment Research Council, Grant/Award Number: NE/K007076/1; Varley-Gradwell Travelling Fellowship in Insect Ecology

Handling Editor: Guillaume Chomicki

Abstract

1. Invasive species are major drivers of global ecosystem change. They often displace native species through competitive exclusion, creating novel species interactions. These interactions can lead to ecological cascades, where the presence of one invasive species enhances the fitness of another. Despite this, the mechanisms that underpin these mutualistic interactions and promote secondary invasions remain poorly understood.
2. We assessed how the introduction of the invasive Argentine ant (*Linepithema humile*) alters mutualistic interactions within the recipient community, enhancing the dispersal and fitness of species of a secondary invasive plant genus (*Acacia* spp.). Our study examines these interactions at the community, individual species, and trait levels for a range of native and non-native ant and plant species. Specifically, we aimed to investigate the direct and indirect effects of *L. humile* on seed dispersal mutualisms.
3. We found that in *L. humile* invaded locations, seeds of the invasive *Acacia* plant species were approximately three times more likely to be dispersed than seeds of native endemic plant species. This preference is driven by indirect changes in the community structure of native seed-dispersing ants, rather than direct interactions between the invasive ant and plant species. Moreover, we found that native ant species that co-exist with *L. humile*, such as *Tetramorium sericeiventre*, respond to a narrower range of seed traits—traits which the invasive *Acacia* seeds possess.
4. Our findings suggest that the invasion of *L. humile* has cascading effects on ant-plant mutualisms, potentially increasing community permeability to secondary invasions. These results highlight that the impact of invaders like the Argentine ant may be greater than initially perceived, driving losses in both biological and functional plant diversity.

KEYWORDS

Acacia, invasive species, *Linepithema humile*, mutualisms, plant-animal interactions, seed dispersal

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

© 2024 The Author(s). *Functional Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

1 | INTRODUCTION

Invasive species are one of the defining characteristics of the Anthropocene (Lewis & Maslin, 2015) and are widely associated as one of the leading drivers of global biodiversity loss (Bellard et al., 2016; Doherty et al., 2016). The displacement of native species through invasion not only threatens the complexity (Valiente-Banuet et al., 2015) and function (David et al., 2017; Simberloff et al., 2013) of native ecosystems but also drives the creation of novel species interactions (Vizentin-Bugoni et al., 2021). These novel species interactions can form between existing species, and/or invasive and native species. Understanding how invasive species reshape communities, and the implications of these changes for other native and invasive species, is vital for predicting and mitigating the impacts of future invasions.

Increasing evidence suggests that the presence of one invasive species can facilitate the entry and spread of another, a process known as 'secondary invasions' (Adams et al., 2003; Grosholz, 2005; O'Loughlin & Green, 2017; Pearson et al., 2018). These secondary invasion events can be mediated through various direct and indirect pathways (see review in Kuebbing, 2020). For example, mutualistic interactions can be directly impacted, as seen in examples of invasive bird species dispersing seeds of invasive plant species (Chimera & Drake, 2010; Foster & Robinson, 2007; LaFleur et al., 2009; MacFarlane et al., 2015; Spotswood et al., 2012). Alternatively, indirect pathways can also play a role, such as the case of the yellow crazy ant (*Anoplolepis gracilipes*) preying on native herbivorous red land crabs (*Gecarcoidea natalis*), which allows for the invasion of non-native plant species (Green et al., 2011). While there is increasing empirical evidence on these secondary invasions, especially in the context of invasion meltdown scenarios (Baron & Rubin, 2021; Grosholz, 2005; Nsikani et al., 2020; Simberloff & Von Holle, 1999; Walsh et al., 2016), these invader-invader interactions remain less studied compared to native-invasive dynamics or the impact of individual invasive species (Kuebbing & Nuñez, 2015).

Evidence from invasive plant species highlights the role of secondary invasions in enhancing their fitness (Richardson et al., 2000; Traveset & Richardson, 2014). For instance, ant-dispersed plant species in Australia and North America have been shown to benefit directly from the presence of invasive ant species, such as the Argentine ant (*Linepithema humile*) and the European fire ant (*Myrmica rubra*), which preferentially disperse invasive seeds over seeds of native species and sometimes disperse seeds further than native ant counterparts (Meadley-Dunphy et al., 2020; Prior et al., 2015; Rowles & O'Dowd, 2009). Similar mutualistic interactions have been observed with invasive pollinators, like the European honeybee (*Apis mellifera*), enhancing the reproduction of invasive plant species in North America (Barthell et al., 2001; Morales & Traveset, 2009). Additionally, invasive soil microbes can alter soil chemistry to favour invasive plants, as seen with the mycorrhizal fungi associated with invasive grasses in California (Bunn et al., 2015; Vogelsang & Bever, 2009). While substantial evidence exists regarding direct interactions, fewer studies have explored the indirect effects of secondary invasions (Kuebbing, 2020). This indicates a significant knowledge gap, highlighting the need for

more research into the indirect effects and the mechanisms that underpin these secondary invasions.

To explore invader–invader interactions, we studied ant-mediated seed dispersal (myrmecochory), a well-understood and globally widespread mutualism, involving at least 11,000 plant species (Lengyel et al., 2010). In this mutualistic interaction, omnivorous ants are attracted to a lipid-rich appendage on the seed, known as the elaiosome (Beattie, 1985; Bond & Slingsby, 1983). Ants transport seeds to their nests, consume the elaiosome, and leave the seed intact, often in sites suitable for seedling establishment and out of reach of predators and destructive forces like bush fires (Giladi, 2006). Seed dispersal outcomes depend upon both the assemblages of the ant community (Bond & Slingsby, 1984; Christian, 2001; Devenish et al., 2018; Rodriguez-Cabal et al., 2012) and the individual traits of the interacting species (e.g. body size and mandible size for ants; chemical signature and seed size for plants; Christian, 2001; Leal et al., 2015; Ness et al., 2004; Pfeiffer et al., 2010). Thus, the system has the potential to be disrupted directly due to the invasive ant's preference for specific seed traits but also indirectly if the invasive ant causes changes in the native seed-dispersing ant community structure and consequently their preferences for specific seed traits.

Invasive ants are likely to enhance the spread of invasive plant species through these mutualistic interactions. Studies have shown that invasive ant species can significantly alter seed dispersal dynamics (Bond & Slingsby, 1984; Carney et al., 2003; Devenish et al., 2018; Prior et al., 2015; Rodriguez-Cabal et al., 2012; Wendt et al., 2022). For example, Argentine ants have been observed to preferentially disperse seeds of invasive plants over native plants, due to the specific chemical cues emitted by the seeds or ratio of elaiosome to seed size (Gomez & Oliveras, 2003; Rowles & O'Dowd, 2009). Additionally, invasive ants often outcompete and displace native seed-dispersing ants, which can lead to a reduction in seed dispersal services for native plants and an increase for invasive plants (Prior et al., 2014; Rodriguez-Cabal et al., 2009; Rowles & O'Dowd, 2009). This displacement of native ants can alter the structure of the ant community, leading to changes in seed dispersal patterns and potentially facilitating secondary invasions by invasive plant species.

Based on these previous studies, our study aims to investigate the impact of the invasive Argentine ant on seed dispersal patterns and subsequent secondary invasions by invasive plant species. Specifically, we aim to:

1. Evaluate the impact of the invasive Argentine ant on seed dispersal patterns by comparing the dispersal of invasive and native plant seeds in locations where the invasive ant is present versus areas where the invasive ant is absent.
2. Investigate the mechanisms driving secondary invasions by measuring the effects of the invasive ants on the native seed-dispersing ant community.
3. Determine the extent of direct and indirect effects of the invasive ant on secondary invasions by assessing whether these invasions are driven by the seed-dispersing actions of the invasive ant or by the indirect effects on the native ant seed-dispersing community.

4. Characterise the chemical and physical traits of seeds from invasive and native plants and test whether the seed-preference traits exhibited by native and invasive ants can explain differences in dispersal success.

2 | MATERIALS AND METHODS

2.1 | Study system

In this study, we focused on the Cape Floristic Region of South Africa, a global biodiversity hotspot, with high levels of endemism and myrmecochorous plant species. This region was chosen because it has previously recorded significant impacts from both invasive ants (Bond & Slingsby, 1984; Christian, 2001; Witt & Giliomee, 2004) and invasive myrmecochorous plant species (Le Maitre et al., 2011; Richardson et al., 2004; Zenni et al., 2009), making it an ideal location to explore invader–invader interactions.

Fieldwork was conducted across six localities within Jonkershoek Nature Reserve (33°55′51″S, 18°51′16″E) in the Western Cape (Figure S1). The invasive *L. humile* ant has been found in several otherwise pristine and undisturbed sites within South Africa and was first detected in Jonkershoek in the 1980s, within the Swartboskloof region (De Kock & Giliomee, 1989). This region includes several endemic vegetation types, including Kogelberg Sandstone Fynbos, Cape Winelands Shale Fynbos, and Boland Granite Fynbos. Sampling was carried out during the summer months of November 2014 to March 2015, when both native and invasive ant species were active, and when myrmecochorous seeds were being dispersed naturally. Research permits for fieldwork were granted by CapeNature under permit numbers AAA007-00108 and AAA008-00068. No formal ethical approval was required for this research, as it involved the study of invertebrates, which are not subject to formal ethics approval processes in South Africa.

2.2 | Plant species

Ten myrmecochorous plant species (seven native and three invasive) were selected for this study. These species were chosen because they showed variable seed morphology (i.e. size and shape) and genealogy (i.e. eight genera from four plant families) and were locally abundant (Table S2). For each species, fruits and cones near maturation were collected from at least 25 plants (taken from at least three independent locations within our study sites) before being left to dehisce naturally in the laboratory. Seeds were handled with forceps and gloves throughout the study and stored in sealed plastic bags at –15°C to preserve the elaiosome and maintain its attractiveness to ants (Clark & King, 2012; Ness et al., 2009). To prevent post-dispersal germination, all invasive seeds utilised in the trials were selected from either damaged seed stock (e.g. signs of beetle damage) and/or they were mechanically damaged to ensure that the seeds were no longer viable. To ensure that this damage did not modify the

ants' seed preference, a pilot study was conducted in which both intact and damaged seeds were offered to a range of ant species. This study showed that all seeds were removed by the ants irrespective of seed condition (i.e. intact or damaged; Figures S2 and S3).

2.3 | Ant community

Two distinct ant communities were used in this research, selected based on the presence or absence of the invasive Argentine ant, and the abundance of both native large and small seed dispersing ant species (Table S1):

- Invaded ($n=2$ locations; $n=20$ pitfall traps)—Presence of *L. humile*; relative high abundance of *Tetramorium sericeiventre* and *Meranoplus peringueyi*.
- Non-invaded ($n=4$ locations; $n=40$ pitfall traps)—Absence of *L. humile*; relative high abundance of *Pheidole capensis*, *Lepisiota capensis* and *Anoplolepis* sp.

Previous research by Christian (2001) demonstrated that these native ant species can be broadly classified as either large-seed (i.e. *Anoplolepis* sp.) or small-seed (i.e. *P. capensis*) dispersing guilds. Non-invaded sites appeared to vary in terms of their abundance of these seed dispersing guilds (Devenish et al., 2021); we therefore included more non-invaded sites than invaded sites to ensure the natural range of seed dispersal responses was represented.

All sample locations were within 1.2 km of each other, with the two invaded plots within 250 m of each other, and the non-invaded plots similarly within 500 m of each other (Figure S1). These locations were selected to be away from the invasion front and are representative of sites that are either invaded or non-invaded, rather than locations in the process of being invaded.

2.4 | Community-level seed choice experiments

We tested the effect of ant community structure on seed dispersal by placing 10 seed hubs (set at 10 m intervals) along the transect utilised for ant community structure analysis (see Devenish et al., 2021). Each seed hub consisted of a 10 cm² white card with a dome wire mesh placed on top. Ants and small invertebrates were able to access the seeds, but larger vertebrates were not. In total, 60 seed hubs (10 per site) were set up in each of the two invaded and four non-invaded sites. Each hub consisted of four seeds from two randomly paired plant species, two seeds per plant species.

Seeds were placed on the seed hubs at 08:00 hours and then surveyed at 1-h intervals, up to a maximum of 3 h, after which any seeds left on the hubs were collected. Naturally dispersed seeds left longer than 3 h tend to be consumed by rodents rather than being dispersed by ants (Bond & Slingsby, 1983; Midgley et al., 2002). At each survey time point, the total number of seeds from each species remaining on the hub was recorded. The experiment was repeated

at 13:00h to test for temporal effects on ant activity. Seed choice experiments were run for three consecutive weeks, with seeds from each plant species being placed once on each hub.

We compared seed removal rates between and within invaded and non-invaded sites using a Cox Proportional Hazards Model (Cox, 1972) and Log-rank test (Bland & Altman, 2004) in the 'survival' (version 2.42–3) and 'coxme' (version 2.2–10) packages (Therneau & Grambsch, 2000). Generalised linear mixed models (GLMM) using a Poisson error distribution in the 'lme4' (version 1.1–17) package (Bates et al., 2015) were then used to analyse seed removal frequencies (portion of seeds removed from seed hubs after 3 h) in invaded and non-invaded sites (Crawley, 2012). In both the survival and GLMM analyses, the fixed effects were invasion status (invaded vs. non-invaded), sampling period (morning vs. afternoon), and plant species ID ($n = 10$); seed hub ID (nested within transect) was included as a random factor, which controlled for the effects of site and repeated sampling of seed hubs within sites. All generated p values were subjected to the Benjamini–Hochberg correction method to control for false discovery rates (Benjamini & Hochberg, 1995).

2.5 | Individual ant species experiments

To maximise detection power across communities, six ant species were selected. These species were chosen based on their abundance, as indicated by their presence in pitfall traps and at seed hubs during the community-level seed choice experiments. Three of these species were the most abundant in invaded sites (*L. humile*, *T. sericeiventre* and *M. peringueyi*), while the other three were the most abundant in non-invaded sites (*Lepisiota capensis*, *A. custodiens* and *P. capensis*; see Table S1). For each ant species, 20 independent nests (at least 10 m apart) were utilised. Each nest was presented with a seed mix consisting of three seeds from each of six plant species. This selection was made from 10 species used in earlier trials, but due to limitations in seed availability, only seven were used in this experiment. The seed mix was scattered evenly around the nest entrance (within 5 cm). Perforated Petri dish lids (150 mm × 15 mm) were placed over both the seeds and the nest entrance, with each lid being weighed down by a rock, with soil compacted around them to ensure that only the target ant nest/species was able to access and interact with these seeds. The seeds were left for 24 h. Any seeds remaining after this time were collected and recorded (stage 1 of extraction process). Dental plaster was then poured into each nest to fix seed placement within the nest (using methods described in Tschinkel, 2010). Nest casts were then excavated (stage 2) and graded according to three depth criteria (0–12 cm; 13–24 cm; >25 cm). Seeds in the nest were retrieved by soaking and physical abrasion of the plaster casts in the laboratory. Seeds placed at depths between 0 and 12 cm within the nest were deemed to be at depths favourable for seedling establishment. A maximum depth of 12 cm was selected on the basis that previous studies have shown some myrmecochorous species emerge from this depth (Christian & Stanton, 2004).

Unfortunately, the range of plant species for which these data are available is limited: germination depths were available for only one of the six plant species used in this study. In fire-prone systems such as fynbos, seeds must be buried to escape fire and predation; therefore, we classified optimal locations as those where seeds remained within the nest at depths conducive to germination (i.e. not beyond 12 cm; Bond & Keeley, 2005; Lamont, 1985).

Seeds used in nest excavation trials were split into three broad groups: invasive (*Acacia longifolia*, *A. pycnantha*, *A. saligna*), native small-seeded (*Phyllica pubescens*, *Podalyria calyprata*) and native large-seeded (*Leucospermum conocarpodendron*) species. The latter size classes for native plant species are based on the Christian (2001) classification system, with seeds that weigh more than 32 mg classified as large-seeded. To determine whether ant species, and therefore ant community status, was having effect on seed placement, we compared the placement (optimal vs. sub-optimal) of individual seeds within ant nests. In this instance, we consider the seeds to have only two possible discreet outcomes (optimal placement [1] vs. sub-optimal placement [0]); as such, a binomial GLMM model was selected where the fixed effects were ant species ($n = 6$) and plant species ($n = 6$), with nest ID ($n = 120$) included as a random factor.

2.6 | Seed-trait analysis

Data were collected on a range of physical and chemical seed traits for all 10 plant species. Physical seed traits included total diaspore weight (seed plus elaiosome), elaiosome weight and seed-elaiosome ratio. These traits are cited in the literature as the dominant physical characteristics that ants target during seed removal (Gorb & Gorb, 1999; Hughes & Westoby, 1992; Mark & Olesen, 1996). Seeds were weighed on a GR-202 five place balance (A&D Instruments Ltd., Abingdon, UK). Mean diaspore weight was calculated from the mean weight of five replicates of 50 randomly selected seeds. By contrast, elaiosome weights were obtained by calculating the difference between the five replicates of 50 randomly selected seeds before and after the elaiosome was detached. In addition, seed-elaiosome ratio was calculated by dividing the seed weight by the elaiosome weight. The lower the seed-elaiosome ratio, the higher the reward to the ant transport cost ratio.

Chemical seed traits were assayed using gas chromatography–mass spectrometry (GC–MS) on intact diaspores (see Supporting Information for full methodology). The focus was on the relative abundance of two key fatty acids, linoleic acid (C18:2) and oleic acid (C18:1). These fatty acids were selected due to their significance as signalling compounds that stimulate foraging behaviour, particularly oleic acid, as demonstrated in previous studies (Boulay et al., 2006; Fischer et al., 2008; Hughes & Westoby, 1992; Miller et al., 2020; Reifnath et al., 2012; Turner & Frederickson, 2013). Although several fatty acids were identified, including palmitic acid, stearic acid, linoleic acid and linolenic acid, linoleic acid was chosen for its high abundance and its known role in eliciting a removal response by ants in North America (Lanza et al., 1992). For each species, three replicates of 10 randomly selected diaspores were sampled.

Full diaspores (including both the seed and elaiosome) were sampled instead of just the elaiosome. This approach was necessary because, in the community experiments, it was unclear whether the ants were attracted to the seed or the elaiosome. Sampling the entire diaspore ensured that the results could be accurately related to the observed ant behaviour in these experiments.

The effects of chemical and physical seed traits on seed removal rates were analysed using a GLMM in the lme4 (version 1.1.14) package (Bates et al., 2015) with a Poisson error distribution (O'Hara & Kotze, 2010). The fixed effects were four continuous outcome variables (seed traits: oleic acid concentration, linoleic acid concentration, diaspore weight and seed: elaiosome ratio); seed hub ID (nested within transect) was included as a random factor, which controls for the effects of site and repeated sampling of seed hubs. Additional, odds ratios (OR) estimates were extrapolated from the resulting GLMM models; this information represents the odds of an event occurring (in this case seed removal) given an exposure (seed trait).

3 | RESULTS

3.1 | Invasive plant seeds are preferentially dispersed in locations invaded by the Argentine ant (Aim 1)

Using standard cafeteria-style seed-choice experiments, we found that significantly fewer seeds were dispersed in invaded locations (*L. humile* ant present) compared with non-invaded locations (GLMM: SE=0.09, $z=7.23$, $p<0.0001$; Figure S4). On average, only 30% (\pm SE 1.9%, $n=490$) of seeds placed in the invaded ant communities were dispersed, compared with 43% (\pm SE 2.0%, $n=976$) in the non-invaded ant communities. Notably, seeds of the invasive *Acacia* plant species were around three times more likely to be dispersed than those of native endemic plant species in the invaded ant communities (Figure 1 LHS top panel). In contrast, native endemic large-seeded *Leucospermum conocarpodendron* and *Serruria krausii* were preferentially dispersed in non-invaded ant communities (Figure 1 LHS bottom panel).

3.2 | Presence of Argentine ant alters native seed-dispersing ant community composition (Aim 2)

In locations invaded by *L. humile*, there was a decrease in overall ant abundance and diversity (Table S2). Native ant community composition differed substantially between invaded and non-invaded locations (ANOSIM: permutations 999, $r=0.92$, $p<0.0001$; Figure 1 RHS). At least 12 native ant species were completely displaced due to the invasion by *L. humile*, including several key native large-seed-dispersing species (*Anoplolepis custodiens* and *Anoplolepis steingroeveri*) and small-seed-dispersing species (*Pheidole capensis*). Conversely, at least two native species increased in abundance in the presence of *L. humile* (i.e. *Tetramorium sericeiventre* and *Meranoplus peringueyi*).

3.3 | Native ants preferentially disperse invasive seeds in invaded ant communities (Aim 3)

To determine whether altered seed dispersal patterns were driven directly by the invasive ant species or indirectly by their impact on co-existing native seed-dispersing ant species, we compared seed-dispersing services of ants present in invaded and non-invaded locations.

Excavation of nests revealed that seeds of invasive *Acacia* plants were placed in more favourable locations in the nests of *T. sericeiventre* which co-exist with *L. humile* (Figure 2b; top panel). Although invasive *Acacia* seeds are preferentially dispersed by *L. humile*, most seed dispersal was facilitated by the co-existing native species *T. sericeiventre* (Figure 2b; top panel). This native ant species increased in abundance in the presence of *L. humile* (Table S1).

Native small-seeded plant species were placed in favourable locations in nests of native ant species in both sites with and without *L. humile* (Figure 2b). By contrast, native large-seeded plant species were effectively dispersed only by the large-seed dispersing specialists *A. custodiens*, which were restricted to the sites not invaded by *L. humile* (Figure 2b; bottom panel).

3.4 | Seed dispersal likelihood is influenced by different seed traits in invaded and non-invaded ant communities (Aim 4)

Seed trait analysis showed that plant species clustered largely according to genus and family (Figure 3a), with no single trait clearly distinguishing invasive *Acacia* species from endemic plant species. In locations invaded by *L. humile*, the likelihood of seed dispersal was explained by variation in three distinct chemical and physical traits: diaspore weight, oleic acid, and seed-to-elaiosome ratio (Figure 3c). Importantly, ants in invaded communities did not respond to linoleic acid (Figure 3c). Instead, ants in these communities selected seeds with elaiosomes that had a higher concentration of oleic acid. Notably, the invasive *Acacia* seeds had the highest recorded amounts of this chemical among the seeds analysed (Figure 3a).

In non-invaded locations, seed dispersal likelihood was determined by linoleic and oleic acid content (Figure 3c). Diaspore weight and seed-to-elaiosome ratio had no clear influence on likelihood of seed dispersal in non-invaded locations.

4 | DISCUSSION

This study sheds light on the mutualistic mechanisms by which the invasive Argentine ant (*Linepithema humile*) affects seed dispersal dynamics and facilitates the spread of invasive *Acacia* plant species. The results indicate that sites invaded by *L. humile* exhibit significantly reduced seed dispersal compared to non-invaded sites, with a notable preference for invasive *Acacia* seeds. Importantly, this preference is not driven by the direct dispersal

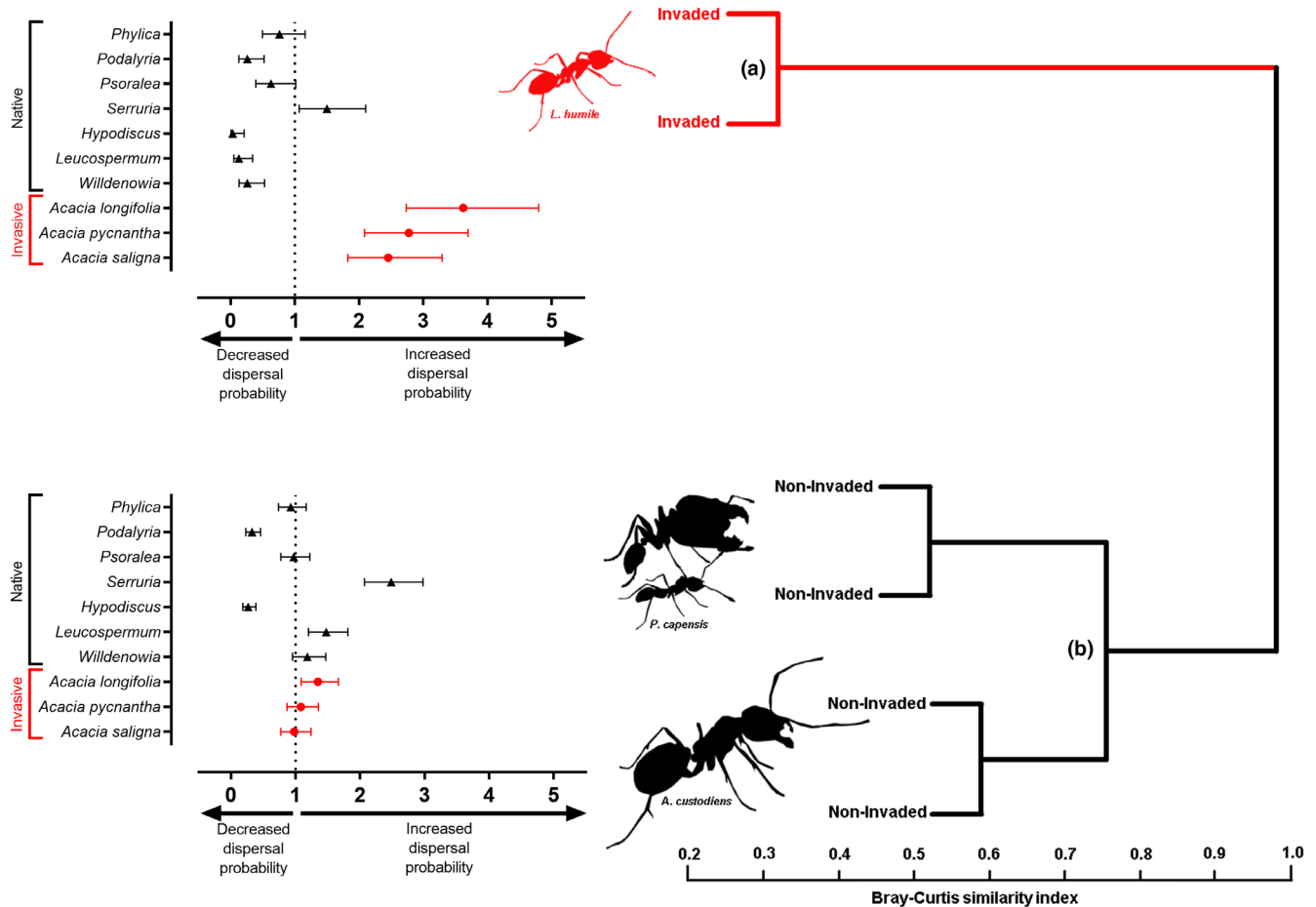


FIGURE 1 Effects of *Linepithema humile* on ant-plant myrmecochory mutualisms in the Cape Floristic Region of South Africa. Regions that were invaded by *L. humile* (top panel) showed higher dispersal probability of non-native invasive plant seeds (red circles) and lower dispersal probability of native endemic plant seeds (black triangles); there was no clear difference in dispersal probability of invasive and native plant seeds in regions without *L. humile* (bottom panel). Seed preference was determined using a Cox proportional hazards model, which compares seed dispersal probability for each plant species against the mean of all plant species. Scores greater than one indicate an increase in dispersal probability, whereas scores less than one indicate a decrease in dispersal probability [95% confidence intervals]. Regions where *L. humile* are present (a) exhibit lower levels species diversity (higher levels of similarity) than native ant communities where *L. humile* are absent (b); sites ($n=6$) were clustered according to their Bray–Curtis similarity index, which groups sites according to their compositional similarity in ant species community.

ability of *L. humile* but rather indirectly by changes in the co-existing native ant community. These findings build on previous research (Bond & Slingsby, 1984; Christian, 2001; Gomez & Oliveras, 2003; Rowles & O'Dowd, 2006), demonstrating how the presence of invasive ants can have cascading effects and extending our understanding of invasive species' mutualistic interactions in South African ecosystems.

4.1 | Alteration of seed dispersal services by *L. humile*

Linepithema humile, like other invasive ant species, disrupts native seed-dispersing ant communities, leading to a decrease in both native ant abundance and diversity (Devenish et al., 2018; Gamman et al., 2018; Gomez & Oliveras, 2003; Rodriguez-Cabal et al., 2012;

Rowles & O'Dowd, 2009; Wendt et al., 2022). In invaded sites, key native seed dispersing ant species such as *A. custodiens* and *P. capensis* are often completely displaced by *L. humile*, demonstrating the powerful competitive exclusion this invasive species exerts. This competitive exclusion has been documented in various systems (Grover et al., 2007; Holway, 1999; Human & Gordon, 1996; Rowles & O'Dowd, 2006; Sanders et al., 2001) and in other regions of South Africa (Bond & Slingsby, 1984; Christian, 2001). The disruption caused by *L. humile* reduces the number of native seed-dispersing ants and alters community composition, which in turn affects seed dispersal patterns. Specifically, there was a 13% decrease in the number of seeds dispersed in invaded communities compared to non-invaded ones. This reduction in seed dispersal capacity in invaded areas means that fewer seeds are likely to be removed from the soil surface, increasing the risk of seed predation by rodents, desiccation, and loss from bushfires.

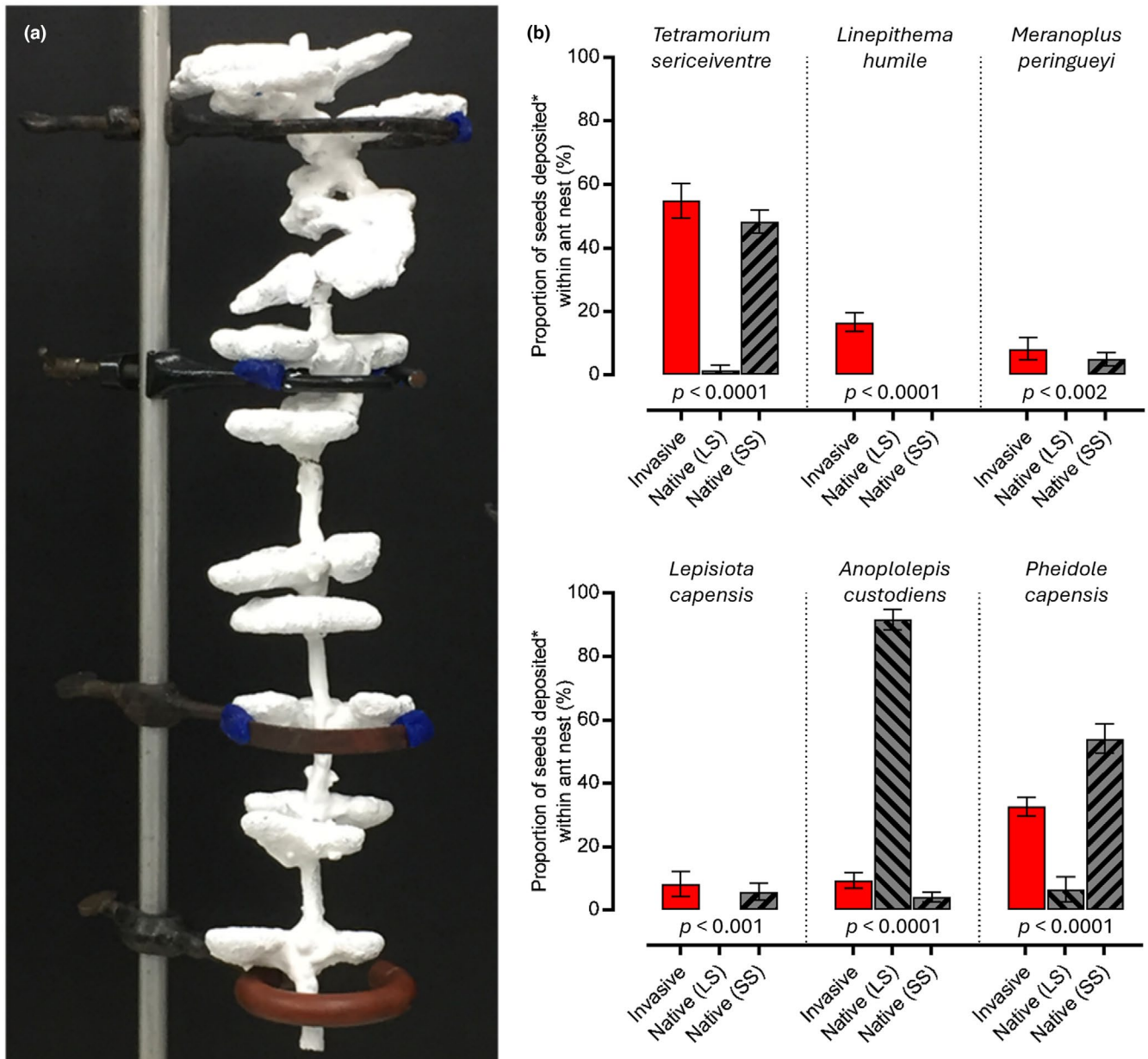


FIGURE 2 Shifts in the assemblages of seed-dispersing ant genera alters seed fate. (a) Example of an excavated nest of *Anoplolepis custodiens*. (b) Proportion of invasive (red) and native (grey hatched) seeds placed at a favourable depth (*between 0 and 12 cm) in the nests of ant communities invaded by the Argentine ant *Linepithema humile* (top panel; $n = 60$ nests), and without the invasive ant (bottom panel; $n = 60$ nests). X-axes indicate seed types: 'invasive' are the *Acacia* spp.; native (LS) and native (SS) are native plants with large seeds (*Leucospermum conocarpodendron*) and small seeds (*Phyllica pubescens* and *Podalyria calytrata*), respectively.

While previous studies have documented similar impacts of invasive ants on native ant communities and the subsequent effects on seed dispersal services, our study adds a critical layer of understanding by showing how invasive seeds are disproportionately dispersed. In other words, not only is the overall number of dispersed seeds reduced, but the remaining dispersal events favour invasive plant species, such as *Acacia longifolia* (Figure 1). This synergy between invasive ant-plant mutualists has been observed in other regions (Prior et al., 2015; Rowles & O'Dowd, 2009), suggesting a generalisable mechanism by which invasive plants benefit from the presence of invasive ants. The preferential dispersal of

invasive seeds can therefore enhance the spread and establishment of invasive plants, potentially leading to significant ecological shifts over time.

4.2 | Indirect impacts on seed dispersal mutualisms

Our study highlights the indirect impact *L. humile* has on seed dispersal mutualisms. Although *L. humile* is generally recognised as a poor-quality seed disperser (Rodríguez-Cabal et al., 2009), both in terms of the types of seeds it can disperse (Christian, 2001; Gomez

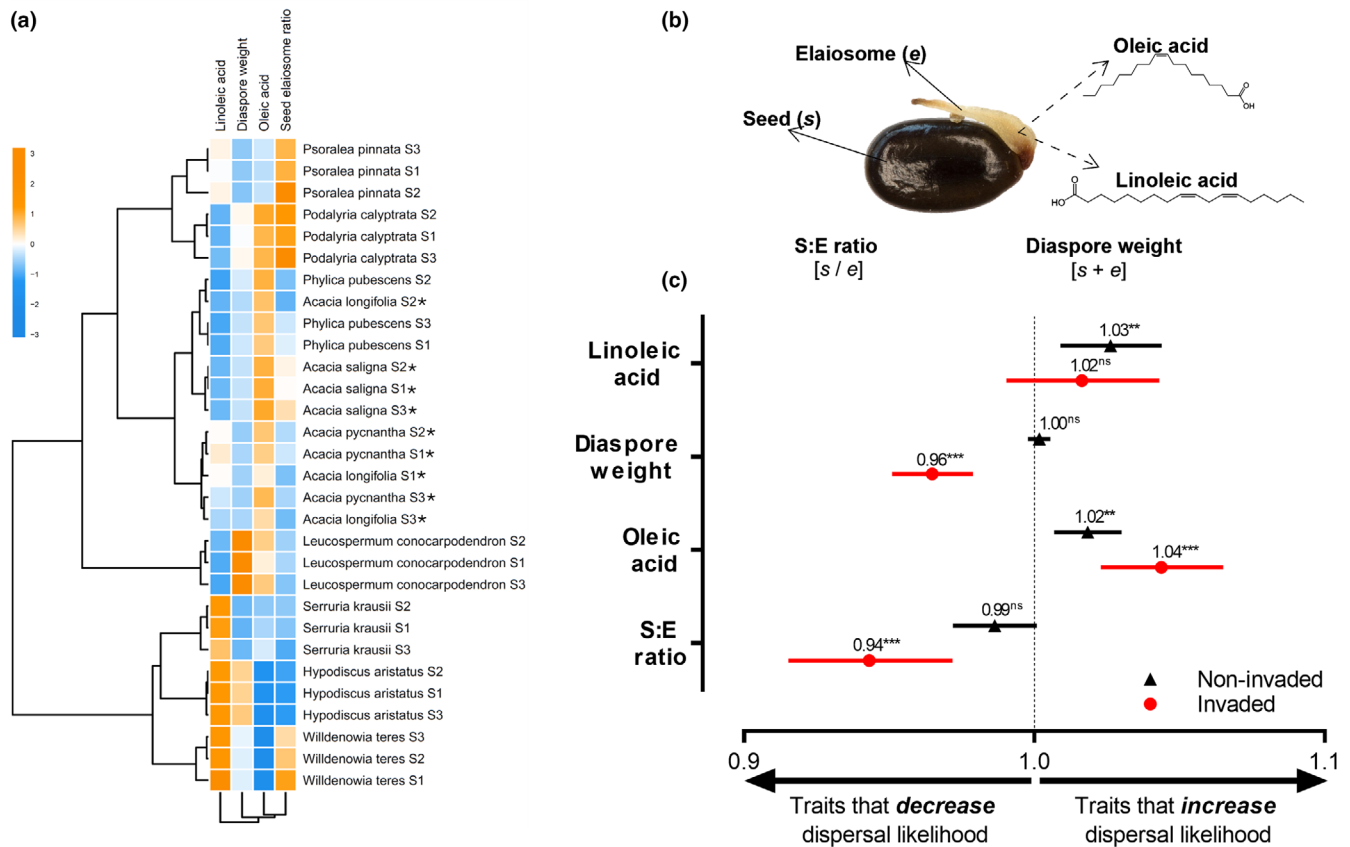


FIGURE 3 Seed dispersal within invaded regions is contingent on a wider array of physical and chemical seed traits than in non-invaded regions. Seeds of native and invasive (*) plants species (a) differ in their physical and chemical properties (b), which in turn influence dispersal probabilities by ants in invaded (red) and non-invaded (black) ant communities (c). Panel (a) shows a heat map of similarities between 10 plant species across four key traits; orange indicates a high trait value and blue a low trait value; the dendrogram clusters the plant species based on quantitative trait sharing. Panel (c) shows how these four traits influence the likelihood of dispersal in regions with *Linepithema humile* (red circles) and regions without (black triangles).

& Oliveras, 2003; Witt et al., 2004) and the distances seeds are dispersed (Devenish et al., 2018; Gomez et al., 2013), it indirectly influences seed dispersal through its effect on native ant species. Unlike previous studies that focus on the direct dispersal ability of *L. humile*, our findings suggest that the subordinate species *T. sericeiventris* plays a significant role in dispersing invasive seeds and placing them in locations suitable for germination.

Tetramorium sericeiventris is present in lower numbers in non-invaded communities and is subordinate to the more aggressive and numerically dominant *A. custodiens*, *A. steingroeveri*, and *P. capensis*. These dominant species likely exclude *T. sericeiventris* from myrmecochorous seed resources through competitive exclusion. This dominance–richness relationship at bait resources has been observed in other parts of Africa (Campbell et al., 2015; Parr, 2008) and is recognised as a factor in structuring ant communities (Davidson, 1998). While scavenging or omnivorous ants, which quickly retrieve and remove seeds, generally favour seed dispersal events (Warren et al., 2014), subordinate ants are recognised as key dispersers in other systems (Aranda-Rickert & Fracchia, 2012; Ness et al., 2009). Our results support the idea that in the absence of primary seed dispersers, *T. sericeiventris* fills this niche, thereby shifting the dispersal

potential of invaded communities to favour a different range of seed traits than those in non-invaded ant communities.

4.3 | Importance of seed placement

A notable aspect often absent from most myrmecochorous studies is the placement of seeds post-dispersal. We addressed this gap by including seed placement in our assessment of dispersal potential. Our results show that the above-ground preference for invasive seeds is mirrored below-ground. In *T. sericeiventris* nests, invasive *Acacia* seeds were placed in potentially favourable locations for germination more frequently than in nests of other native ant species. Interestingly, *L. humile* only transported invasive seeds into its nests, as shown in Figure 2.

The favourable placement of seeds is driven by a combination of factors, including seed traits (Miller et al., 2020; Wehner et al., 2020), handling behaviour of the ants (Ness et al., 2004; Penn & Crist, 2018) and the nest structure (Christian & Stanton, 2004; Renard et al., 2010). For example, some seeds are too large to be removed into ant nests (Witt et al., 2004), or their post-dispersal seed traits prevent their

removal from the nest after the elaiosome has been consumed (Gómez et al., 2005). Our findings indicate that native seeds are better adapted for dispersal by native ants, particularly large-seeded species such as *Leucospermum conocarpodendron*, which were almost exclusively dispersed by the larger *Anoplolepis* ants.

By contrast, *Acacia* seeds are smaller and have a greater seed-to-elaiosome ratio (Figure 4a). They also produce higher numbers of seeds compared to endemic Proteaceae species (Richardson & Kluge, 2008). Additionally, *Acacia* seeds exhibit plasticity in invaded ranges, producing more seeds with a more favourable seed-to-elaiosome ratio in these areas (Correia et al., 2016). The generalist nature of these invasive *Acacia* seeds allows them to exploit the altered ant community dynamics, ensuring their spread and establishment even in environments where specialist native ants have been displaced. These traits appear to be particularly attractive to subordinate ant species like *T. sericeiventris*, which have smaller colonies and shallower nests, making them more likely to place seeds in favourable locations for germination. This matching between invasive seeds and native ants, coupled with the species' adaptability, underscores the invasive potential of *Acacia* and similar species, which can thrive in new territories by leveraging their interactions with both native and invasive ant species. The ability of *Acacia* seeds to be favourably placed by a variety of ant species, including those in disrupted or invaded communities, highlights their invasion success. This adaptability not only enhances their germination and establishment but also perpetuates the displacement of native species, further altering the ecosystem dynamics.

4.4 | Influence of seed traits on dispersal dynamics

Physical and chemical traits of diaspores (seeds and elaiosomes) play a crucial role in determining their attractiveness to ants and their subsequent dispersal. Our study revealed that in locations invaded by *L. humile*, the likelihood of seed dispersal was significantly influenced by both chemical and physical traits (Figure 4c). *Acacia* seeds, which exhibited higher concentrations of oleic acid,

a more favourable seed-to-elaiosome ratio, and smaller size, were preferentially dispersed in invaded sites. This finding aligns with previous studies indicating that oleic acid is a key attractant for ants (Brew et al., 1989; Marshall et al., 1979; Reifenrath et al., 2012) and that invaded ant communities tend to disperse smaller seeds (Christian, 2001; Ness et al., 2004).

In non-invaded locations, chemical traits, particularly the abundance of both linoleic and oleic acids, appeared to be strong predictors of dispersal outcomes, rather than physical seed traits. This preference for chemical cues over physical traits among native ants is consistent with findings in other regions, where native ants prioritise chemical signals even if it comes at a potential cost to the colony (Turner & Frederickson, 2013). This strong preference might be due to the temporally restrictive nature of the food reward, as elaiosome-bearing seeds may represent a key temporally restricted resource (Alcántara et al., 2007; Warren et al., 2019).

The overall homogenisation of seed dispersal traits in invaded communities, driven by the presence of *L. humile*, likely impacts both the diversity of plant species that can be dispersed, but also the functional phenotypes of the seeds. This shift towards a narrower range of seed traits at invaded sites favours invasive species like *Acacia*, over the endemic myrmecochorous flora. The ability of *Acacia* seeds to exploit these chemical cues underscores their invasive potential. By producing seeds with higher oleic acid content, *Acacia* can effectively manipulate the foraging behaviour of ants in invaded communities, ensuring preferential dispersal. This chemical adaptability highlights the importance of seed traits in the context of biological invasions and the complex interplay between chemical signals and ecological interactions.

4.5 | Limitations and further research

Despite the insights provided by this study, several limitations must be acknowledged. First, the research was conducted within a limited number of locations in a single nature reserve, which

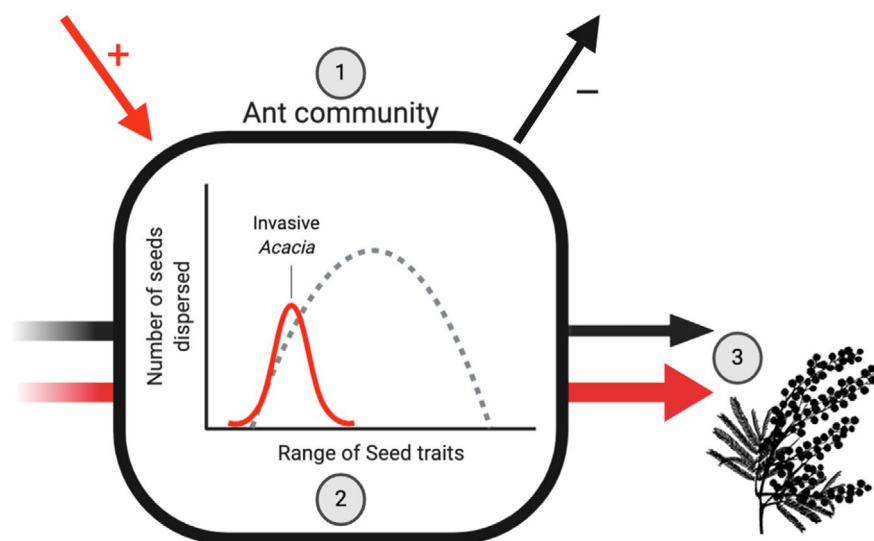


FIGURE 4 Invaders beget invasion. Invasion of *Linepithema humile* leads to a displacement of key native seed dispersers (1), leading to a rewiring of the invaded community's ant-plant networks and a change in seed trait preferences (2). This increases the permeability of these invaded communities to invasive *Acacia* plant species (3).

may not fully represent broader regional patterns. The spatial arrangement of invaded and non-invaded sites within Jonkershoek Nature Reserve was not ideal, potentially limiting the generalisability of the results. Additionally, without data on the previous ant community structure prior to invasion, we cannot be certain that the habitats compared were initially similar. Nonetheless, our findings on the impact of *L. humile* on native ant community structure are consistent with those reported in other fynbos regions (Christian, 2001).

Second, the study was based on data collected during a single season, which may not capture seasonal variations in seed traits and ant behaviour. Seasonal and geographical influences can significantly affect diaspore traits (Boeiro et al., 2012; Manzaneda & Rey, 2009, 2012), which could have implications on the dispersal outcomes. Future research should therefore include multi-seasonal data to account for these variations.

Third, while our study focused on a specific set of native and invasive ant and plant species, examining a broader range of species would help validate our findings across different ecological contexts. Investigating a variety of seeds with diverse traits could provide more insight into the relative importance of physical versus chemical cues in seed dispersal by ants. This broader approach would enhance our understanding of how different traits influence invader–invader interactions.

Fourth, understanding which aspects of *T. sericeiventris* ecology and biology make it a particularly effective disperser for *Acacia* seeds would be valuable for further investigation. Key traits such as colony size, foraging behaviour, nest structure and its ability to thrive in disturbed or invaded ecosystems might play crucial roles in how this species interacts with invasive plants. Investigating these features would not only identify why *T. sericeiventris* is more likely to favour *Acacia* seeds but also help predict and identify other ecosystems that might be vulnerable to similar invasion dynamics.

Finally, the long-term fate of dispersed seeds was not tracked in this study. Understanding whether dispersed seeds successfully germinate and establish is crucial for fully comprehending the impact of altered seed dispersal dynamics on ecosystem composition and function. Future research should aim to follow dispersed seeds through to germination and establishment, providing a more comprehensive understanding of the ecological consequences of invasive ant species. Complementing this with measurements of myrmecochorous plant abundance and seed bank dynamics alongside ant community data would offer valuable insights into long-term invasion dynamics.

Moreover, invasive species like *L. humile* can alter multiple processes within invaded communities, including pollination, seed predation, and nutrient cycling (Blancafort & Gomez, 2005; Hanna et al., 2015; Menke et al., 2010; Oliveras et al., 2007). Understanding these interconnected processes is essential for a comprehensive understanding of how invaders influence ecosystem dynamics and promote secondary invasions. While this is outside the scope of this study, without this broader understanding, it is difficult to extrapolate the true extent of the impact of this invasive species.

5 | CONCLUSIONS

Understanding how invasive species interact, and the mechanisms behind these interactions—whether it be antagonistic or synergistic—has profound implications for designing and implementing effective management strategies (Blackburn et al., 2011). This study provides key evidence supporting the secondary invasion hypothesis, demonstrating that the invasion of one species can indirectly enhance the invasion potential of another species through a restructuring of natural interaction networks between mutualistic species (Figure 4). Specifically, we found that (1) the invasion by *L. humile* significantly alters native ant community structure; (2) this alteration restricts the range of seed phenotypes that can be effectively dispersed; and (3) this shift increases the permeability and invasion success of *Acacia* plant species.

Our findings suggest that the threat posed by invasive ants such as *L. humile* may be greater than previously recognised. Their presence not only leads to a loss of biological diversity but also impacts functional seed trait diversity within ecosystems. These results underscore the importance of considering the broader ecological implications of invasive species, including their potential to drive secondary invasions and alter multiple ecological processes. Understanding these dynamics is crucial for developing effective conservation and management strategies to mitigate the far-reaching impacts of biological invasions.

AUTHOR CONTRIBUTIONS

Adam J. M. Devenish., Rosemary J. Newton, Jeremy J. Midgley, Jon Bridle and Seirian Sumner conceived the ideas and designed methodology; Adam J. M. Devenish and Louise Colville collected the data; Adam J. M. Devenish analysed the data; and Adam J. M. Devenish led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

The authors thank field assistants (Beatrice Dewenter, Cindy van Heerden, Matthew Granger, Micaela Gillespie and Nkoliso Magona) who helped with data collection, and thesis examiners for their constructive input. This work was funded by grants and awards from the Natural Environmental Research Council (NERC) Case Studentship awarded to S.S., J.B. and R.J.N. (NE/K007076/1); and Varley-Gradwell Travelling Fellowship in Insect Ecology awarded to A.J.M.D.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data used in this manuscript is available from the NERC Environmental Information Data Centre: <https://doi.org/10.5285/e4cd04881-fd86-45e2-99e1-f0ec61324329> (Devenish, 2019).

ORCID

Adam J. M. Devenish  <https://orcid.org/0000-0001-5240-622X>
Rosemary J. Newton  <https://orcid.org/0000-0003-3952-3805>

Jeremy J. Midgley  <https://orcid.org/0000-0001-7831-2301>
 Louise Colville  <https://orcid.org/0000-0003-4626-4522>
 Jon Bridle  <https://orcid.org/0000-0002-5999-0307>
 Seirian Sumner  <https://orcid.org/0000-0003-0213-2018>

REFERENCES

- Adams, M. J., Pearl, C. A., & Bury, R. B. (2003). Indirect facilitation of an anuran invasion by non-native fishes. *Ecology Letters*, 6(4), 343–351. <https://doi.org/10.1046/j.1461-0248.2003.00435.x>
- Alcántara, J. M., Rey, P. J., Manzaneda, A. J., Boulay, R., Ramírez, J. M., & Fedriani, J. M. (2007). Geographic variation in the adaptive landscape for seed size at dispersal in the myrmecochorous *Helleborus foetidus*. *Evolutionary Ecology*, 21(3), 411–430. <https://doi.org/10.1007/S10682-006-9110-3>
- Aranda-Rickert, A., & Fracchia, S. (2012). Are subordinate ants the best seed dispersers? Linking dominance hierarchies and seed dispersal ability in myrmecochory interactions. *Arthropod-Plant Interactions*, 6(2), 297–306. <https://doi.org/10.1007/s11829-011-9166-z>
- Baron, J. N., & Rubin, B. D. (2021). Secondary invasion? Emerald ash borer (*Agrilus planipennis*) induced ash (*Fraxinus* spp.) mortality interacts with ecological integrity to facilitate European buckthorn (*Rhamnus cathartica*). *Canadian Journal of Forest Research*, 51(3), 455–464. <https://doi.org/10.1139/cjfr-2020-0134>
- Barthell, J. F., Randall, J. M., Thorp, R. W., & Wenner, A. M. (2001). Promotion of seed set in yellow star-thistle by honeybees: Evidence of an invasive mutualism. *Ecological Applications*, 11(6), 1870–1883. [https://doi.org/10.1890/1051-0761\(2001\)011\[1870:POSSIV\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[1870:POSSIV]2.0.CO;2)
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using {lme4}. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Beattie, A. J. (1985). *The evolutionary ecology of ant-plant mutualisms*. Cambridge University Press.
- Bellard, C., Cassey, P., & Blackburn, T. M. (2016). Alien species as a driver of recent extinctions. *Biology Letters*, 12(4), 20150623. <https://doi.org/10.1098/rsbl.2015.0623>
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, 57, 289–300. <https://www.jstor.org/stable/2346101>
- Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., Wilson, J. R. U., & Richardson, D. M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*, 26(7), 333–339. <https://doi.org/10.1016/j.tree.2011.03.023>
- Blancafort, X., & Gomez, C. (2005). Consequences of the Argentine ant, *Linepithema humile* (Mayr), invasion on pollination of *Euphorbia characias* (L.) (Euphorbiaceae). *Acta Oecologica*, 28(1), 49–55. <https://doi.org/10.1016/j.actao.2005.02.004>
- Bland, J. M., & Altman, D. G. (2004). The logrank test. *BMJ (Clinical Research Ed.)*, 328(7447), 1073. <https://doi.org/10.1136/bmj.328.7447.1073>
- Boeiro, M. M., Espadaler, X., Gomez, C., Eustaquio, A., Gómez, C., & Eustaquio, A. (2012). Spatial variation in the fatty acid composition of elaiosomes in an ant-dispersed plant: Differences within and between individuals and populations. *Flora*, 207(7), 497–502. <https://doi.org/10.1016/j.flora.2012.06.007>
- Bond, W., & Keeley, J. (2005). Fire as a global 'herbivore': The ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution*, 20(7), 387–394. <https://doi.org/10.1016/j.tree.2005.04.025>
- Bond, W., & Slingsby, P. (1983). Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. *South African Journal of Science*, 79(6), 231–233. https://doi.org/10.10520/AJA00382353_2316
- Bond, W., & Slingsby, P. (1984). Collapse of an ant-plant mutualism: The Argentine ant (*Iridomyrmex humilis*) and myrmecochorous proteaceae. *Ecology*, 65(4), 1031–1037. <https://doi.org/10.2307/1938311>
- Boulay, R., Coll-Toledano, J., & Cerdá, X. (2006). Geographic variations in *Helleborus foetidus* elaiosome lipid composition: Implications for dispersal by ants. *Chemoecology*, 16(1), 1–7. <https://doi.org/10.1007/s00049-005-0322-8>
- Brew, C. R., O'Dowd, D. J., & Rae, I. D. (1989). Seed dispersal by ants: Behaviour-releasing compounds in elaiosomes. *Oecologia*, 80(4), 490–497. <https://doi.org/10.1007/BF00380071>
- Bunn, R. A., Ramsey, P. W., & Lekberg, Y. (2015). Do native and invasive plants differ in their interactions with arbuscular mycorrhizal fungi? A meta-analysis. *Journal of Ecology*, 103(6), 1547–1556. <https://doi.org/10.1111/1365-2745.12456>
- Campbell, H., Fellowes, M. D., & Cook, J. M. (2015). Species diversity and dominance-richness relationships for ground and arboreal ant (Hymenoptera: Formicidae) assemblages in Namibian desert, saltpan, and savannah. *Myrmecological News*, 21, 37–47.
- Carney, S. E., Byerley, M. B., & Holway, D. A. (2003). Invasive Argentine ants (*Linepithema humile*) do not replace native ants as seed dispersers of *Dendromecon rigida* (Papaveraceae) in California, USA. *Oecologia*, 135(4), 576–582. <https://doi.org/10.1007/s00442-003-1200-0>
- Chimera, C. G., & Drake, D. R. (2010). Patterns of seed dispersal and dispersal failure in a Hawaiian dry forest having only introduced birds. *Biotropica*, 42(4), 493–502. <https://doi.org/10.1111/J.1744-7429.2009.00610.X>
- Christian, C. E. (2001). Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature*, 413(6856), 635–639. <https://doi.org/10.1038/35098093>
- Christian, C. E., & Stanton, M. L. (2004). Cryptic consequences of a dispersal mutualism: Seed burial, elaiosome removal, and seed-bank dynamics. *Ecology*, 85(4), 1101–1110. <https://doi.org/10.1890/03-0059>
- Clark, R. E., & King, J. R. (2012). The ant, *Aphaenogaster picea*, benefits from plant elaiosomes when insect prey is scarce. *Environmental Entomology*, 41(6), 1405–1408. <https://doi.org/10.1603/EN12131>
- Correia, M., Montesinos, D., French, K., & Rodríguez-Echeverría, S. (2016). Evidence for enemy release and increased seed production and size for two invasive Australian Acacias. *Journal of Ecology*, 104(5), 1391–1399. <https://doi.org/10.1111/1365-2745.12612>
- Cox, D. R. (1972). Regression models and lifetables. *Journal of the Royal Statistical Society: Series B: Methodological*, 34(2), 187–220.
- Crawley, M. J. (2012). *The R book* (2nd ed.). Wiley-Blackwell.
- David, P., Thébault, E., Anneville, O., Duyck, P.-F., Chapuis, E., & Loeuille, N. (2017). Chapter one—Impacts of invasive species on food webs: A review of empirical data. In D. A. Bohan, A. J. Dumbrell, & F. Massol (Eds.), *Networks of invasion: A synthesis of concepts* (Vol. 56, pp. 1–60). Academic Press. <https://doi.org/10.1016/bs.aecr.2016.10.001>
- Davidson, D. W. (1998). Resource discovery versus resource domination in ants: A functional mechanism for breaking the trade-off. *Ecological Entomology*, 23(4), 484–490. <https://doi.org/10.1046/J.1365-2311.1998.00145.X>
- De Kock, A. E., & Giliomee, J. (1989). A survey of the Argentine ant, *Iridomyrmex humilis* (Mayr), (Hymenoptera: Formicidae) in south African fynbos. *Journal of the Entomological Society of Southern Africa*, 52, 157–164.
- Devenish, A. J. M. (2019). Impacts of Argentine ant (*Linepithema humile*) on seed dispersal services in Jonkershoek, Cape Floristic Region South Africa. NERC Environmental Information Data Centre. (Dataset). <https://doi.org/10.5285/ecd04881-fd86-45e2-99e1-f0ec61324329>
- Devenish, A. J. M., Gomez, C., Bridle, J. R., Newton, R. J., & Sumner, S. (2018). Invasive ants take and squander native seeds: Implications for native plant communities. *Biological Invasions*, 21, 451–466. <https://doi.org/10.1007/s10530-018-1829-6>
- Devenish, A. J. M., Newton, R. J., Bridle, J. R., Gomez, C., Midgley, J. J., & Sumner, S. (2021). Contrasting responses of native ant

- communities to invasion by an ant invader, *Linepithema humile*. *Biological Invasions*, 23(8), 2553–2571. <https://doi.org/10.1007/s10530-021-02522-7>
- Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G., & Dickman, C. R. (2016). Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences of the United States of America*, 113(40), 11261–11265.
- Fischer, R. C., Richter, A., Hadacek, F., & Mayer, V. (2008). Chemical differences between seeds and elaiosomes indicate an adaptation to nutritional needs of ants. *Oecologia*, 155(3), 539–547. <https://doi.org/10.1007/s00442-007-0931-8>
- Foster, J. T., & Robinson, S. K. (2007). Introduced birds and the fate of Hawaiian rainforests. *Conservation Biology*, 21(5), 1248–1257. <https://doi.org/10.1111/j.1523-1739.2007.00781.x>
- Gammans, N., Drummond, F., & Groden, E. (2018). Impacts of the invasive European Red ant (*Myrmica rubra* (L.): Hymenoptera; Formicidae) on a myrmecochorous system in the northeastern United States. *Environmental Entomology*, 47(4), 908–917. <https://doi.org/10.1093/EE/NVY069>
- Giladi, I. (2006). Choosing benefits or partners: A review of the evidence for the evolution of myrmecochory. *Oikos*, 112(3), 481–492. <https://doi.org/10.1111/j.0030-1299.2006.14258.x>
- Gómez, C., Espadaler, X., & Bas, J. M. (2005). Ant behaviour and seed morphology: A missing link of myrmecochory. *Oecologia*, 146(2), 244–246. <http://www.jstor.org/stable/20062496>
- Gomez, C., Espadaler, X., Gómez, C., & Espadaler, X. (2013). An update of the world survey of myrmecochorous dispersal distances. *Ecography*, 36(11), 1193–1201. <https://doi.org/10.1111/j.1600-0587.2013.00289.x>
- Gomez, C., & Oliveras, J. (2003). Can the Argentine ant (*Linepithema humile* Mayr) replace native ants in myrmecochory? *Acta Oecologica*, 24(1), 47–53. [https://doi.org/10.1016/S1146-609X\(03\)00042-0](https://doi.org/10.1016/S1146-609X(03)00042-0)
- Gorb, S. N., & Gorb, E. V. (1999). Dropping rates of elaiosome-bearing seeds during transport by ants (*Formica polyctena* Foerst.): Implications for distance dispersal. *Acta Oecologica*, 20(5), 509–518. [https://doi.org/10.1016/S1146-609X\(00\)86618-7](https://doi.org/10.1016/S1146-609X(00)86618-7)
- Green, P. T., O'Dowd, D. J., Abbott, K. L., Jeffery, M., Retallick, K., & Mac Nally, R. (2011). Invasional meltdown: Invader–invader mutualism facilitates a secondary invasion. *Ecology*, 92(9), 1758–1768. <https://doi.org/10.1890/11-0050.1>
- Grosholz, E. D. (2005). Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. *Proceedings of the National Academy of Sciences of the United States of America*, 102(4), 1088–1091. <https://doi.org/10.1073/pnas.0308547102>
- Grover, C. D., Kay, A. D., Monson, J. A., Marsh, T. C., & Holway, D. A. (2007). Linking nutrition and behavioural dominance: Carbohydrate scarcity limits aggression and activity in Argentine ants. *Proceedings Biological sciences*, 274(1628), 2951–2957. <https://doi.org/10.1098/rspb.2007.1065>
- Hanna, C., Naughton, I., Boser, C., Alarcón, R., Hung, K. L. J., & Holway, D. (2015). Floral visitation by the Argentine ant reduces bee visitation and plant seed set. *Ecology*, 96(1), 222–230. <https://doi.org/10.1890/14-0542.1>
- Holway, D. A. (1999). Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology*, 80(1), 238–251. [https://doi.org/10.1890/0012-9658\(1999\)080\[0238:CMUTDO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[0238:CMUTDO]2.0.CO;2)
- Hughes, L., & Westoby, M. (1992). Effect of diaspore characteristics on removal of seeds adapted for dispersal by ants. *Ecology*, 73(4), 1300–1312. <https://doi.org/10.2307/1940677>
- Human, K. G., & Gordon, D. M. (1996). Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia*, 105(3), 405–412. <https://doi.org/10.1007/BF00328744>
- Kuebbing, S. E. (2020). How direct and indirect non-native interactions can promote plant invasions, lead to invasional meltdown and inform management decisions. *CABI*, 153–176. <https://doi.org/10.1079/9781789242171.0008>
- Kuebbing, S. E., & Nuñez, M. A. (2015). Negative, neutral, and positive interactions among nonnative plants: Patterns, processes, and management implications. *Global Change Biology*, 21(2), 926–934. <https://doi.org/10.1111/GCB.12711>
- LaFleur, N., Rubega, M., & Parent, J. (2009). Does frugivory by European starlings (*Sturnus vulgaris*) facilitate germination in invasive plants? *The Journal of the Torrey Botanical Society*, 136(3), 332–341. <https://doi.org/10.3159/08-RA-111.1>
- Lamont, B. (1985). The comparative reproductive biology of three *Leucospermum* species (Proteaceae) in relation to fire responses and breeding system. *Australian Journal of Botany*, 33(2), 139–145. <https://doi.org/10.1071/BT9850139>
- Lanza, J., Schmitt, M. A., & Awad, A. B. (1992). Comparative chemistry of elaiosomes of three species of *Trillium*. *Journal of Chemical Ecology*, 18(2), 209–221. <https://doi.org/10.1007/BF00993754>
- Le Maitre, D. C., Gaertner, M., Marchante, E., Ens, E.-J., Holmes, P. M., Pauchard, A., O'Farrell, P. J., Rogers, A. M., Blanchard, R., Blignaut, J., & Richardson, D. M. (2011). Impacts of invasive Australian acacias: Implications for management and restoration diversity and distributions. *Diversity and Distributions*, 17, 1015–1029. <https://doi.org/10.1111/j.1472-4642.2011.00816.x>
- Leal, I. R., Leal, L. C., & Andersen, A. N. (2015). The benefits of myrmecochory: A matter of stature. *Biotropica*, 47(3), 281–285. <https://doi.org/10.1111/btp.12213>
- Lengyel, S., Gove, A. D., Latimer, A. M., Majer, J. D., & Dunn, R. R. (2010). Convergent evolution of seed dispersal by ants, and phylogeny and biogeography in flowering plants: A global survey. *Perspectives in Plant Ecology, Evolution and Systematics*, 12(1), 43–55. <https://doi.org/10.1016/j.ppees.2009.08.001>
- Lewis, S. L., & Maslin, M. A. (2015). Defining the Anthropocene. *Nature*, 519, 171–180. <https://doi.org/10.1038/nature14258>
- MacFarlane, A. E. T., Kelly, D., & Briskie, J. V. (2015). Introduced blackbirds and song thrushes: Useful substitutes for lost mid-sized native frugivores, or weed vectors? *New Zealand Journal of Ecology*, 40(1), 80–87. <https://doi.org/10.20417/NZJECOL.40.9>
- Manzaneda, A. J., & Rey, P. J. (2009). Assessing ecological specialization of an ant–seed dispersal mutualism through a wide geographic range. *Ecology*, 90(11), 3009–3022. <https://doi.org/10.1890/08-2274.1>
- Manzaneda, A. J., & Rey, P. J. (2012). Geographical and interspecific variation and the nutrient-enrichment hypothesis as an adaptive advantage of myrmecochory. *Ecography*, 35(4), 322–332. <https://doi.org/10.1111/j.1600-0587.2011.06923.x>
- Mark, S., & Olesen, J. M. (1996). Importance of elaiosome size to removal of ant-dispersed seeds. *Oecologia*, 107(1), 95–101. <https://doi.org/10.1007/BF00582239>
- Marshall, D. L., Beattie, A. J., & Bollenbacher, W. E. (1979). Evidence for diglycerides as attractants in an ant–seed interaction. *Journal of Chemical Ecology*, 5(3), 335–344. <https://doi.org/10.1007/BF00987919>
- Meadley-Dunphy, S. A., Prior, K. M., & Frederickson, M. E. (2020). Invasive ants disperse seeds farther than native ants, affecting the spatial pattern of seedling recruitment and survival. *Oecologia*, 192(1), 119–132. <https://doi.org/10.1007/s00442-019-04553-3>
- Menke, S. B., Suarez, A. V., Tillberg, C. V., Chou, C. T., & Holway, D. A. (2010). Trophic ecology of the invasive Argentine ant: Spatio-temporal variation in resource assimilation and isotopic enrichment. *Oecologia*, 164(3), 763–771. <https://doi.org/10.1007/S00442-010-1694-1>
- Midgley, J., Anderson, B., Bok, A., & Fleming, T. (2002). Scatter-hoarding of Cape Proteaceae nuts by rodents. *Evolutionary Ecology Research*, 4(4), 623–626.
- Miller, C. N., Whitehead, S. R., & Kwit, C. (2020). Effects of seed morphology and elaiosome chemical composition on attractiveness of five *Trillium* species to seed-dispersing ants. *Ecology and Evolution*, 10(6), 2860–2873. <https://doi.org/10.1002/ECE3.6101>

- Morales, C. L., & Traveset, A. (2009). A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecology Letters*, 12(7), 716–728. <https://doi.org/10.1111/J.1461-0248.2009.01319.X>
- Ness, J. H., Bronstein, J. L., Andersen, A. N., & Holland, J. N. (2004). Ant body size predicts dispersal distance of ant-adapted seeds: Implications of small-ant invasions. *Ecology*, 85(5), 1244–1250. <https://doi.org/10.1890/03-0364>
- Ness, J. H., Morin, D. F., & Giladi, I. (2009). Uncommon specialization in a mutualism between a temperate herbaceous plant guild and an ant: Are *Aphaenogaster* ants keystone mutualists? *Oikos*, 118(12), 1793–1804. <https://doi.org/10.1111/j.1600-0706.2009.17430.x>
- Nsikani, M. M., Geerts, S., Ruwanza, S., & Richardson, D. M. (2020). Secondary invasion and weedy native species dominance after clearing invasive alien plants in South Africa: Status quo and prognosis. *South African Journal of Botany*, 132, 338–345. <https://doi.org/10.1016/J.SAJB.2020.05.009>
- O'Hara, R. B., & Kotze, D. J. (2010). Do not log-transform count data. *Methods in Ecology and Evolution*, 1(2), 118–122. <https://doi.org/10.1111/j.2041-210X.2010.00021.x>
- Oliveras, J., Bas, J. M., & Gomez, C. (2007). A shift in seed harvesting by ants following Argentine ant invasion. *Vie et Milieu*, 57(1–2), 79–85.
- O'Loughlin, L. S., & Green, P. T. (2017). Secondary invasion: When invasion success is contingent on other invaders altering the properties of recipient ecosystems. *Ecology and Evolution*, 7(19), 7628–7637. <https://doi.org/10.1002/ece3.3315>
- Parr, C. L. (2008). Dominant ants can control assemblage species richness in a South African savanna. *Journal of Animal Ecology*, 77(6), 1191–1198. <https://doi.org/10.1111/J.1365-2656.2008.01450.X>
- Pearson, D. E., Ortega, Y. K., Runyon, J., & Butler, J. L. (2018). Secondary invasion re-redefined: The distinction between invader-facilitated and invader-contingent invasions as subclasses of secondary invasion. *Ecology and Evolution*, 8(10), 5185–5187. <https://doi.org/10.1002/ece3.3966>
- Penn, H. J., & Crist, T. O. (2018). From dispersal to predation: A global synthesis of ant–seed interactions. *Ecology and Evolution*, 8(18), 9122–9138. <https://doi.org/10.1002/ECE3.4377>
- Pfeiffer, M., Huttenlocher, H., & Ayasse, M. (2010). Myrmecochorous plants use chemical mimicry to cheat seed-dispersing ants. *Functional Ecology*, 24(3), 545–555. <https://doi.org/10.1111/j.1365-2435.2009.01661.x>
- Prior, K. M., Robinson, J. M., Meadley Dunphy, S. A., & Frederickson, M. E. (2015). Mutualism between co-introduced species facilitates invasion and alters plant community structure. *Proceedings of the Royal Society B: Biological Sciences*, 282(1800), 20142846. <https://doi.org/10.1098/RSPB.2014.2846>
- Prior, K. M., Saxena, K., & Frederickson, M. E. (2014). Seed handling behaviours of native and invasive seed-dispersing ants differentially influence seedling emergence in an introduced plant. *Ecological Entomology*, 39(1), 66–74. <https://doi.org/10.1111/EEN.12068>
- Reifenrath, K., Becker, C., & Poethke, H. J. (2012). Diaspore trait preferences of dispersing ants. *Journal of Chemical Ecology*, 38(9), 1093–1104. <https://doi.org/10.1007/s10886-012-0174-y>
- Renard, D., Schatz, B., & McKey, D. B. (2010). Ant nest architecture and seed burial depth: Implications for seed fate and germination success in a myrmecochorous savanna shrub. *Ecoscience*, 17(2), 194–202. <https://doi.org/10.2980/17-2-3335>
- Richardson, D. M., Allsopp, N., D'Antonio, C. M., Milton, S. J., & Rejmanek, M. (2000). Plant invasions—The role of mutualisms. *Biological Reviews*, 75(1), 65–93. <https://doi.org/10.1017/S0006323199005435>
- Richardson, D. M., & Kluge, R. L. (2008). Seed banks of invasive Australian *Acacia* species in South Africa: Role in invasiveness and options for management. *Perspectives in Plant Ecology, Evolution and Systematics*, 10(3), 161–177. <https://doi.org/10.1016/J.PPEES.2008.03.001>
- Richardson, D. M., Yelenik, S. G., & Stock, W. D. (2004). Ecosystem level impacts of invasive *Acacia saligna* in the South African fynbos. *Restoration Ecology*, 12(1), 44–51. <https://doi.org/10.1111/j.1061-2971.2004.00289.x>
- Rodriguez-Cabal, M. A., Stuble, K. L., Guenard, B., Dunn, R. R., Sanders, N. J., Guénard, B., Dunn, R. R., & Sanders, N. J. (2012). Disruption of ant-seed dispersal mutualisms by the invasive Asian needle ant (*Pachycondyla chinensis*). *Biological Invasions*, 14(3), 557–565. <https://doi.org/10.1007/s10530-011-0097-5>
- Rodríguez-Cabal, M. A., Stuble, K. L., Nuñez, M. A., Sanders, N. J., Nunez, M. A., & Sanders, N. J. (2009). Quantitative analysis of the effects of the exotic Argentine ant on seed-dispersal mutualisms. *Biology Letters*, 5(4), 499–502. <https://doi.org/10.1098/rsbl.2009.0297>
- Rowles, A. D., & O'Dowd, D. J. (2006). Interference competition by Argentine ants displaces native ants: Implications for biotic resistance to invasion. *Biological Invasions*, 9(1), 73–85. <https://doi.org/10.1007/s10530-006-9009-5>
- Rowles, A. D., & O'Dowd, D. J. (2009). New mutualism for old: Indirect disruption and direct facilitation of seed dispersal following Argentine ant invasion. *Oecologia*, 158(4), 709–716. <https://doi.org/10.1007/s00442-008-1171-2>
- Sanders, N. J., Barton, K. E., & Gordon, D. M. (2001). Long-term dynamics of the distribution of the invasive Argentine ant, *Linepithema humile*, and native ant taxa in northern California. *Oecologia*, 127(1), 123–130. <https://doi.org/10.1007/s004420000572>
- Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., & Vilà, M. (2013). Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution*, 28(1), 58–66. <https://doi.org/10.1016/j.tree.2012.07.013>
- Simberloff, D., & Von Holle, B. (1999). Positive interactions of nonindigenous species: Invasional meltdown. *Biological Invasions*, 1(1), 21–32. <https://doi.org/10.1023/A:1010086329619>
- Spotswood, E. N., Meyer, J. Y., & Bartolome, J. W. (2012). An invasive tree alters the structure of seed dispersal networks between birds and plants in French Polynesia. *Journal of Biogeography*, 39(11), 2007–2020. <https://doi.org/10.1111/J.1365-2699.2012.02688.X>
- Therneau, T., & Grambsch, P. (2000). Modeling survival data: Extending the Cox model. In *Stat Med* (Vol. 48). Springer-Verlag.
- Traveset, A., & Richardson, D. M. (2014). Mutualistic interactions and biological invasions. *Annual Review of Ecology, Evolution, and Systematics*, 45, 89–113. <https://doi.org/10.1146/annurev-ecolsys-120213-091857>
- Tschinkel, W. R. (2010). Methods for casting subterranean ant nests. *Journal of Insect Science*, 10(1), 88. <https://doi.org/10.1673/031.010.8801>
- Turner, K. M., & Frederickson, M. E. (2013). Signals can trump rewards in attracting seed-dispersing ants. *PLoS One*, 8(8), e71871. <https://doi.org/10.1371/journal.pone.0071871>
- Valiente-Banuet, A., Aizen, M. A., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, M., García, M. B., García, D., Gómez, J. M., Jordano, P., Medel, R., Navarro, L., Obeso, J. R., Oviedo, R., Ramírez, N., Rey, P. J., Traveset, A., Verdú, M., & Zamora, R. (2015). Beyond species loss: The extinction of ecological interactions in a changing world. *Functional Ecology*, 29(3), 299–307. <https://doi.org/10.1111/1365-2435.12356>
- Vizentin-Bugoni, J., Sperry, J. H., Kelley, J. P., Gleditsch, J. M., Foster, J. T., Drake, D. R., Hruska, A. M., Wilcox, R. C., Case, S. B., & Tarwater, C. E. (2021). Ecological correlates of species' roles in highly invaded seed dispersal networks. *Proceedings of the National Academy of Sciences of the United States of America*, 118(4), e2009532118. <https://doi.org/10.1073/pnas.2009532118>
- Vogelsang, K. M., & Bever, J. D. (2009). Mycorrhizal densities decline in association with nonnative plants and contribute to plant invasion. *Ecology*, 90(2), 399–407. <https://doi.org/10.1890/07-2144.1>
- Walsh, J. R., Carpenter, S. R., Jake, M., Zanden, V., Luecke, C., Strayer, D., & Yan, N. D. (2016). Invasive species triggers a massive loss of ecosystem services through a trophic cascade. *Proceedings of the National*

Academy of Sciences of the United States of America of the United States of America, 113(15), 4081–4085. <https://doi.org/10.1073/PNAS.1600366113>

- Warren, R. J., Elliott, K. J., Giladi, I., King, J. R., & Bradford, M. A. (2019). Field experiments show contradictory short- and long-term myrmecochorous plant impacts on seed-dispersing ants. *Ecological Entomology*, 44(1), 30–39. <https://doi.org/10.1111/EEN.12666>
- Warren, R. J., Giladi, I., & Bradford, M. A. (2014). Competition as a mechanism structuring mutualisms. *Journal of Ecology*, 102(2), 486–495.
- Wehner, K., Schäfer, L., Blüthgen, N., & Mody, K. (2020). Seed type, habitat and time of day influence post-dispersal seed removal in temperate ecosystems. *PeerJ*, 2020(3), e8769. <https://doi.org/10.7717/peerj.8769>
- Wendt, C. F., Nunes, A., Lobo Dias, S., Verble, R., Branquinho, C., & Boieiro, M. (2022). Seed removal decrease by invasive Argentine ants in a high nature value farmland. *Journal for Nature Conservation*, 67, 126183. <https://doi.org/10.1016/J.JNC.2022.126183>
- Witt, A. B. R., Geertsema, H., & Giliomee, J. H. (2004). The impact of an invasive ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae), on the dispersal of the elaiosome-bearing seeds of six plant species. *African Entomology*, 12(2), 223–230. <https://hdl.handle.net/10520/EJC32602>
- Witt, A. B. R., & Giliomee, J. H. (2004). The impact of an invasive ant, *Linepithema humile* (Mayr), on the dispersal of *Phyllica pubescens* aiton seeds in South Africa. *African Entomology*, 12(2), 179–185.
- Zenni, R. D., Wilson, J. R. U., Le Roux, J. J., & Richardson, D. M. (2009). Evaluating the invasiveness of *Acacia paradoxa* in South Africa. *South African Journal of Botany*, 75(3), 485–496. <https://doi.org/10.1016/j.sajb.2009.04.001>

SUPPORTING INFORMATION

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

Figure S1. Map showing sampling locations in Jonkershoek Nature Reserve.

Figure S2. Viability testing of mechanically damaged and insect damaged *Acacia* seeds.

Figure S3. Attractiveness of damaged and intact *Acacia* seeds.

Figure S4. Comparison of the number of seeds removed from hubs in *L. humile* invaded and non-invaded locations in the Jonkershoek Nature Reserve.

Table S1. Ant diversity in Jonkershoek Nature Reserve.

Table S2. Plant species and their respective seed weights.

Methods S1. Ant diversity and abundance sampling.

Methods S2. Viability and attractiveness of damaged *Acacia* seeds.

Methods S3. Gas chromatography–mass spectrometry seed sampling.

How to cite this article: Devenish, A. J. M., Newton, R. J., Midgley, J. J., Colville, L., Bridle, J., & Sumner, S. (2025). Mutualistic interactions facilitate invasive species spread. *Functional Ecology*, 39, 254–267. <https://doi.org/10.1111/1365-2435.14688>