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The Argentine ant, *Linepithema humile*: natural history, ecology and impact of a successful invader

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With 1 figure

Abstract: The Argentine ant, *Linepithema humile*, is one of the world's worst invasive species, with established populations in at least 40 countries on six continents. In this review, we synthesise the vast literature on this species in four areas, concentrating on its introduction to natural systems. The first section reviews its distribution, habitat preferences, and the factors promoting its invasion success. Second, we review current knowledge of its ecological impacts on invertebrates, vertebrates and ecosystem functions. The third section deals with behaviour and genetics, particularly traits promoting invasiveness. Finally, we address applied issues, emphasising the quantification of the economic costs and eradication strategies associated with *L. humile* invasion. Despite tremendous research efforts, especially over the past 40 years, numerous knowledge gaps remain in the understanding of the distribution, ecology, impacts, management, and economic costs of this species. We conclude by highlighting the most critical gaps and propose a research agenda to tackle the future challenges in the study of *L. humile* biology.

Keywords: biological invasions; climate change; Dolichoderinae; invasive species; pest control

1 Introduction

Invasive alien species are transported through human trade to new regions outside of their native range and ultimately cause adverse impacts to introduced ecosystems and their associated biota. The Argentine ant, *Linepithema humile* (Mayr 1868, syn. *Iridomyrmex humilis*; Dolichoderinae), is listed among the 100 of the world's worst invasive alien species (Global Invasive Species Database 2023). Originating from a small area in South America (Wild 2004), it was introduced into new regions since at least the mid-19th century and is now established on all continents, except Antarctica.

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The Argentine ant is one of the most widely studied ant species, being the subject of more than 1100 scientific papers published since 1945. Research on Argentine ants has been expansive since the late 1980s, peaked around the late 2010s, and inspired studies on other invasive ants (Suarez et al. 1999) (Supplementary Fig. S1). The topics covered in the literature encompass all the themes of invasion biology; however, the interest in this species extends far beyond this field, as understanding the behavioural and physiological adaptations and the genetic mechanisms that facilitate its success pose interesting questions in a broader evolutionary ecology context. Additionally, due to the ease of maintenance in the laboratory, the Argentine ant has been used as a model organism for investigating collective behaviour, decision-making and self-organisation (e.g. Goss et al. 1989).

This review summarises the current knowledge on this species to provide a synthesis of hundreds of papers on a species with widespread environmental and economic impacts and identify priorities for future research. Our review covers distribution and spread, impacts, behaviour, population biology, as well as eradication strategies. We conclude with a research agenda, highlighting specific challenges to be addressed in future studies.

2 Spread and updated distribution

2.1 Global spread (Fig. 1)

Determining the native range of introduced species can be particularly challenging, especially for widespread species whose actual distribution is the result of repeated introductions occurring over several centuries (Suarez et al. 2001; Wetterer et al. 2009). Nonetheless, with advancements in taxonomic (Wild 2004), molecular (Tsutsui et al. 2001), and species distribution modelling studies (Roura-Pascual et al. 2004), together with thorough samplings in geographically distant regions (Suarez et al. 2001), the native range of *L. humile* is now one of the best understood among globally-distributed invasive alien ants, even if some gaps may remain. *Linepithema humile* is native to the Río Paraná drainage basin and its tributaries (Río Paraguay and Río Uruguay), which span across eastern Bolivia, southern Brazil, Paraguay, Uruguay and northern Argentina. Within this area, most known records are, however, restricted to a few kilometres along the river drainage (Wild 2007), while some populations may have been introduced early on, especially within more urbanised environments (Tsutsui et al. 2001; Wild 2004).

Outside its putative native range, the Argentine ant has been recorded in 59 countries, including Argentina and Brazil, where it is considered non-native in some regions (Wild 2004; Guénard et al. 2017). It is thus among one of the most widespread invasive alien ants (Wong et al. 2023), being recorded from all 12 biogeographic realms colonised by ants.

It is paramount to discriminate among different introduction stages to discern the ant's spreading pattern, potential impacts, and prevent over-predictions in species distribution modelling. Indeed, invasion stages (introduction, establishment, spread, and impact) reflect various ecological filters, which, once overcome, may lead to the establishment and/or spread of introduced populations (Wong et al. 2023). A list of the terms and definitions used throughout the manuscript is provided in Supplementary Table S1. To date, non-native outdoor populations of *L. humile* have been recorded in 40 countries, including several overseas territories, while records for 19 other countries have been limited to quarantine interceptions or indoor populations (Guénard et al. 2017). Outdoor populations can become invasive when the population spreads and causes ecological harm. In most instances studied, the Argentine ant has been ecologically dominant and displaced most native ant species (Castro-Cobo et al. 2021); however, sometimes the Argentine ant does not achieve ecological dominance, coexisting with native species, persisting in this status for > 10y (Castro-Cobo et al. 2020b). Investigation of such establishments, without dominance, may yield important insights into the mechanisms for achieving successful invasion elsewhere.

Linepithema humile most readily invades Mediterranean and subtropical ecosystems. The invasion history of *L. humile* includes at least seven invasion events from the native to non-native regions, as well as several long-distance, human-mediated dispersal between invaded ranges (Suarez et al. 2001; Tsutsui et al. 2001; Sunamura et al. 2009a; Vogel et al. 2010).

Historical records place the Saharo-Arabian biogeographic realm as the earliest region invaded by *L. humile*, as early as 1858. The island of Madeira was invaded first, followed by other Macaronesian Islands, except for the Cape Verde archipelago (Wetterer et al. 2009). The ant established populations in the Maghreb in the early 1920s, mainly limited to coastline areas even if it now occasionally expands inland (Slimani et al. 2020). Towards the end of the 20th century, additional records were reported East within the Arabian Peninsula (Oman, Yemen) and later in Iran (Ghahari et al. 2009), while records from Turkey require confirmation (Kiran & Karaman 2020).

Following its introduction in the Western Palearctic realm as early as 1890, the ant appeared for several decades limited to a thin fringe of the southern Atlantic and Mediterranean Sea coastlines to about 25 km inland (Bernard 1983, but see Espadaler & Gómez 2003), including several islands (e.g. Balearic Islands, Corsica, Crete; Gómez & Espadaler 2006; Blight et al. 2009; Masoni et al. 2020; Salata et al. 2020). Newly established populations have, however, been recently reported farther north along the western coastal regions of France (Blatrix et al. 2018; Charrier et al. 2020), inland in Italy (Frizzi et al. 2023), and temporary outdoor populations observed in England (Fox & Wang 2016), the Netherlands (Boer et al. 2018) and Germany (Seifert 2018), apparently

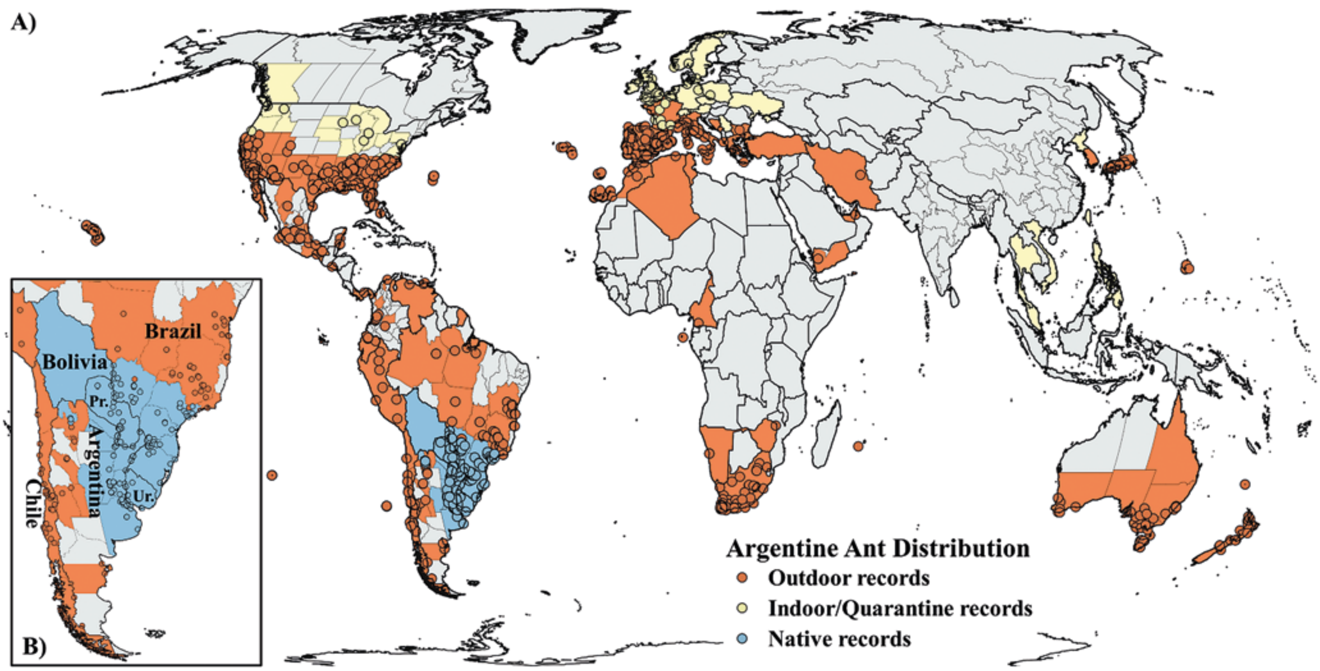

Fig. 1. **(A)** Global distribution of the Argentine ant (*Linepithema humile*) showing its native (blue) and introduced (orange and yellow) ranges. Outdoors (orange) and indoors/quarantine (yellow) records are shown separately as they illustrate dispersal and environmental limitations for the species. Individual records with available coordinates are shown as dots, while polygons, where the species is recorded, are coloured accordingly, with region definitions following Guénard et al. (2017). In regions where records of different types are reported (e.g. both established and non-established populations), priority is given to native and then established populations. Grey polygons show countries where no valid records are known. **(B)** Native range showing intermixing of potential introduced populations with native populations. Abbreviations: Pr. Paraguay, Ur.: Uruguay.

associated with buildings. For these regions, long-term survival outdoors remains to be confirmed. Biogeographic dispersion from at least three European geographic sources appears likely (Blight et al. 2010a, 2012).

In the Nearctic realm, the Argentine ant was first recorded in 1891 in New Orleans, Louisiana (Suarez et al. 2001), and is now found from Mexico to northern California on the West coast, and from Florida to North Carolina on the East Coast of the USA nearly continuously. Non-coastal populations remain patchier, likely due to multiple local introductions, and anthropogenic habitat modification creating pockets of suitable conditions in otherwise unsuitable areas (Menke et al. 2007; Brightwell et al. 2010; see section 2.2). These, in turn, provide several bridgeheads expanding the introduced range further (Espadaler & Gómez 2003; Menke et al. 2007; Brightwell & Silverman 2011).

Within the Afrotropical realm, most records are from South Africa, while other records are from Cameroon, Namibia and Zimbabwe, with population survival in these last three countries requiring confirmation (Wetterer et al. 2009). In South Africa, where *L. humile* has been well studied, it was first recorded in 1893, and again in 1901 and currently forms two distinct supercolonies (Mothapo & Wossler 2011) thought to originate from direct introductions from the native range (Tsutsui et al. 2001; Vogel et al. 2010).

In the Australian and Oceanian realms, Argentine ants were detected in 1939 and 1990 in Australia and New Zealand, respectively, with established populations in New Zealand originating from southern Australia (Corin et al. 2007b). In Australia, *L. humile* is mainly found along coastal areas in the southern half of the country, including Tasmania and Norfolk Island, and has expanded north as far as Brisbane (Hoffmann et al. 2011), from potentially two distinct introduction events (Suhr et al. 2009). In the Pacific, the species has been recorded from a few islands, including Hawaii (1916), Easter Island (1987) and the Mariana Islands, with the latter to be confirmed (Wetterer et al. 2009).

Within the Sino-Japanese realm, outdoor populations of *L. humile* have been known from Japan since 1993 (Sugiyama 2000) and have since spread within the southern part of Honshu along a 900 km long region (ranging from Yamaguchi to Tokyo prefectures), and more recently to Shikoku island (Ohara & Yamada 2012), with multiple introductions suspected within the country (Sunamura et al. 2009a). In South Korea, populations of *L. humile* were detected in 2019 in the southern part of the country (Busan and Kwangyang regions; Lee et al. 2020), where the species now appears to have become locally dominant. The lack of records from China is notable considering the presence of both suitable environments (Jung et al. 2022) and sympatric species from its native range now established in the country (e.g. *Solenopsis invicta, Wasmannia auropunctata*).

Within the Neotropical realm, the distribution of *L. humile* appears extensive, but patchy outside its native range, as the species has been recorded from southern Argentina and Chile up to the Guyana shield, Panama or Chiapas (Mexico), although some historical records (e.g. Costa Rica) are now considered dubious (Wild 2004; Wetterer et al. 2009).

In 2023, *L. humile* was recorded from Reunion Island at 1200 m elevation, representing the first population established outdoors within the Malagasy realm (Colindre 2023). Additionally, models based on environmental conditions predict further suitable areas for its spread in the region (Jung et al. 2022, but see Roura-Pascual et al. 2011).

Overall, the Argentine ant, despite being established outside its native range for over 165 years, keeps expanding globally through human-mediated long-distance dispersal (e.g., Iran, South Korea, Mascarene Islands) fuelled by both primary and secondary introductions (Vogel et al. 2010), but also through more regional spread with further expansion inland as observed in several countries such as Algeria, France, Italy or the USA.

In several regions, records of Argentine ants are restricted to indoor populations or intercepted specimens (e.g., quarantine), as observed in the northern parts of the Western Palearctic and Nearctic realms, especially beyond the northern half of the USA (from Virginia to Oregon). These records are insightful as they provide information about the human-mediated capacity of this species to reach new regions while facing environmental conditions that potentially prevent its survival and establishment outdoors. However, the situation within the Oriental realm is likely to be different. Records from Peninsular Malaysia, the Philippines, Taiwan, Thailand, and Vietnam lack evidence for outdoor establishment, despite potential climatic suitability within some of these regions (e.g. Taiwan, Vietnam; Roura-Pascual et al. 2011; Jung et al. 2022) and further studies confirming propagules arrival in those regions would be welcome. Therefore, data from biosecurity interceptions are particularly relevant for understanding propagule pressure, even in countries where the Argentine ant is already established (Australia: Suhr et al. 2019; New Zealand: Corin et al. 2007b), and to define the main introduction pathways worldwide. In Australia, surprisingly, most propagules originated from regions unknown to host outdoor or any Argentine ant populations (Suhr et al. 2019), a pattern also observed in New Zealand (Corin et al. 2007b), suggesting that viable populations may exist near trade hubs (e.g. Singapore, Fiji, Thailand), but remain undetected; or that other factors regarding the production of trade records should be evaluated critically.

2.2 Habitat preferences and factors promoting local spread

The spread of Argentine ants involves two separate processes: short-range diffusion by budding and long-range dispersal by human transport (Suarez et al. 2001). The successful establishment of an invasive species is influenced by a combination of the abiotic and biotic conditions of the recipient environment and the biological and functional traits of the invader (Blackburn et al. 2011).

Abiotic factors limit the spread of this temperate-ant into Mediterranean-type and some sub-tropical areas because the species cannot tolerate high temperatures (thermal limit CTmax: 38–40 ºC; Jumbam et al. 2008) and requires high humidity and moisture levels (Holway et al. 2002b; Menke & Holway 2006; Menke et al. 2007). It exhibits seasonal polydomy, retracting into overwintering nests during cold months and spreading out during warmer months (Heller & Gordon 2006; Diaz et al. 2014). Couper et al. (2021) reported a population retraction after an extreme 4-year drought in northern California. In South Africa, Luruli (2007) showed that *L. humile* nests close to waterways, rivers, gardens and regularly watered agricultural sites. Arnan et al. (2021) showed its ability to occupy empty European climatic niches. Indeed, *L. humile* is most abundant closer to anthropised areas (Holway & Suarez 2006), including disturbed environments like agricultural fields and clearings with loose soil providing proper nesting sites (Way et al. 1997; Vonshak & Gordon 2015).

Regarding biotic factors, interspecific competition with native ants can limit Argentine ant spread. However, evidence varies, from no evidence (Holway 1998b; Castro-Cobo et al. 2019), to specific native species slowing the invasion spread (Thomas & Holway 2005; Walters & Mackay 2005; Menke et al. 2007; Blight et al. 2010). Recently, specific traits and competitive abilities of native ants have been investigated, because the species providing resistance seem to be ecologically dominant, and with strong competitive abilities such as mass recruitment (Castro-Cobo et al. 2020a). Argentine ant spread is also facilitated by the mutualistic relationship with aphids (Grover et al. 2007; Tillberg et al. 2007; Mothapo & Wossler 2017). Local spread is limited because the species does not have nuptial flights, and spreads by budding, but it could be fostered by scavenging vertebrates (Castro-Cobo et al. 2019; Castro-Cobo et al. 2021).

Finally, dependence on abiotic factors suggests that global climate change will affect the current distribution patterns of *L. humile*, retracting in tropical areas but expanding in higher latitudes (Roura-Pascual et al. 2004; Cooling et al. 2012; Bertelsmeier et al. 2016). However, some populations have persisted for a long time (Castro-Cobo et al. 2021), while others that have declined could recover with climate change (Cooling et al. 2012): in any case, the distribution of invaded areas will change according mainly to local-scale environmental conditions (Menke & Holway 2020).

3 Ecological and environmental impacts

3.1 Impacts on ant communities

Once successfully established in a new area, the Argentine ant usually displaces much of the local ant fauna resulting in a change in the structure of communities (e.g. Holway et al. 2002a; Sanders et al. 2003; Lessard et al. 2009), with evidence for long-term impacts accumulating (Menke et al. 2018; Achury et al. 2021). Loss of local species richness and diversity have been reported both in disturbed and undisturbed areas, from urban parks (Touyama et al. 2003) and agroecosystems (Zina et al. 2020) to uninhabited islands (Naughton et al. 2020). Nevertheless, species displacement is not the rule, possibly owing to the superior competitive abilities of certain ant species (Heller 2004). For example, species of the *Tapinoma nigerrimum* complex and *Lasius niger* have comparable competitive abilities to the Argentine ant (Blight et al. 2010b; Cordonnier et al. 2020). Small and hypogeic species (e.g. *Stenamma* spp., *Solenopsis* sp. and *Heteroponera imbellis*) also appear less affected in some areas (Ward 1987; Holway 1998a; Rowles & O'Dowd 2009a). Similarly, the small Mediterranean ant *Plagiolepis pygmaea* can probably co-occurrt with *L. humile* due to its submissive behaviour during interspecific encounters (Abril & Gómez 2009; Zina et al. 2020). Other native ants can co-occur because of different thermal requirements along the day, e.g., the thermophilic *Cataglyphis floricola* and *C. tartessica* (Angulo et al. 2011) or differences in thermal breadth that reduce coexistence along the seasons, e.g., *Prenolepis imparis* (Nelson et al. 2023). In South Africa, some native ant species (*Tetramorium* spp. and *Meranoplus* spp.) show increased abundance in invaded areas than in uninvaded ones, although the facilitating role of *L. humile* remains unclear (Mothapo & Wossler 2017; Devenish et al. 2021).

The sympatry of *L. humile* with other invasive ant species has been observed and studied in several parts of the world, leading to various ecological outcomes ranging from local exclusion to co-occurrence. In the USA, the Asian needle ant *Brachyponera chinensis* may displace *L. humile* because of its broader seasonal period of foraging activity and colony expansion (Rice & Silverman 2013). Contrarily, *L. humile* can prevail on *Solenopsis invicta* by attacking its queens (Brinkman 2006). Instead, in Bermuda, the Argentine ant co-occurred for at least 25 years with *Pheidole megacephala*, which had invaded the area approximately fifty years earlier, without either of them displacing the other (Haskins & Haskins 1988). In Spain, where *Lasius neglectus* and *L. humile* overlap, coexistence is achieved through spatial segregation (Trigos-Peral et al. 2021). Future investigations should assess whether *L. humile* directly favours or impairs the invasion of other invasive ants, and under which circumstances (O'Loughlin & Green 2017).

3.2 Impacts on non-ant arthropods, plants and ecosystem functions

The substantial alteration of ant communities might affect native myrmecophilous arthropods, which may not thrive when their ant host is absent. Populations of the myrmecophilous cricket *Myrmecophilus kubotai* declined in invaded areas due to its inability to use Argentine ant colonies after native ants have been displaced (Takahashi et al. 2018). On the contrary, the brood production of the lycaenid butterfly *Narathura bazalus* was similar in invaded and uninvaded areas, thus suggesting that the butterfly larvae can also be attended by the Argentine ant (Ikenaga et al. 2020). It has been estimated that 10,000–100,000 myrmecophiles may exist; hence understanding the impact of the Argentine ant on their survival is of the utmost importance (Parker & Kronauer 2021).

Argentine ants have a wide range of impacts on other arthropods in the soil. These effects have arguably been detrimental in Hawai'i, where the native fauna has no evolutionary history with ants (Reimer et al. 2019); their introduction to the high-elevation shrublands led to a drastic reduction in diversity and biomass of many arthropod groups (Cole et al. 1992; Krushelnycky et al. 2008). Where arthropods are not naive to ants, effects vary, likely largely due to some combination of their behaviour, defences, resource overlap with Argentine ants and indirect effects. In northern California, several taxa, such as flies and collembolans, were not detected in invaded areas, whereas other taxa, such as ground beetles and isopods, increased (Human & Gordon 1997). In New Zealand, taxa in invaded sites were differently affected; for example, collembolans increased, and isopods, amphipods and fungus-feeding beetles declined (Stanley & Ward 2012). In contrast, studies in Californian riparian woodlands (Holway 1998a), Santa Cruz Island (Hanna et al. 2015), and coastal scrub in southeastern Australia (Rowles & O'Dowd 2009a) report no effects of Argentine ants on the richness and abundance of non-ant arthropods. This complex picture reveals that local factors are probably crucial in determining the effects of *L. humile* on these taxa, and their identification is not always straightforward. The behavioural plasticity of the Argentine ant to local conditions is probably one of the keys to understanding the incongruity of its effects (Sagata & Lester 2009), with future studies focusing on the differential sensitivity of non-ant arthropods to invasion needed.

As with many other invasive ant species, Argentine ants affect plant-associated arthropods, with cascading effects on plants. *Linepithema humile* often increases the abundance of honeydew-producing hemipterans by protecting them against predators and parasitoids (e.g. Powell & Silverman 2010). However, not all natural enemies are equally affected, and considerable variability in the effects has been shown. For example, Daane et al. (2007) showed that in California vineyards invaded by *L. humile*, the density of parasitoids is lowered and that of predators increased. Contrarily, Calabuig et al. (2015) found that in citrus orchards in Spain, the abundance of generalist predators decreased while that of parasitoids increased in the presence of Argentine ants. The Argentine ant may, however, reduce herbivore populations, with positive effects on plants (Stanley et al. 2013, but see Henin & Pavia 2004).

In invaded communities, the Argentine ant disrupts the benefits of myrmecochory either through the displacement of native ant species and without contributing significantly to seed dispersal (Gómez & Oliveras 2003; Frasconi Wendt et al. 2022) or by reducing seedling emergence rates (Gómez et al. 2003). In addition, *L. humile* may modify plant composition by favouring direct seed dispersal of invasive over native plant species, through a selection process relying on seed size and dispersal distance (Rowles & O'Dowd 2009b). Ultimately, these mechanisms may lead to important changes in plant community composition (Christian 2001; Devenish et al. 2019)

Linepithema humile also disrupts plant-pollinator mutualisms (Blancafort & Gomez 2005) through pollinators' displacement, competition, predation or deterrence (Lach 2007, 2008; LeVan et al. 2014; Liang et al. 2022). Consequently, a reduction in plant reproductive success has been associated with their invasion (Blancafort & Gómez 2005). Therefore, *L. humile* can threaten the conservation of pollinators and the plants relying on them (Lach 2013).

All the relationships between *L. humile* and other organisms discussed in this section might have cascading effects on several ecological processes and functions. The alteration of the community of soil invertebrates, accompanied by the reduction of the soil microbial biomass, slows the decomposition in the invaded areas, resulting in a higher C:N ratio and nutrient content in the soil of invaded sites (Stanley & Ward 2012).

3.3 Impacts on vertebrates

Recorded effects on vertebrates can be either direct or indirect, and a comprehensive list of known impacts is shown in Supplementary Table S2.

The displacement of native ants has cascading ecosystem impacts by disrupting the interactions among native ants and native predators (Pintor & Bayers 2015). For example, the displacement of native ants by Argentine ant was interpreted as one of the causes of the decline of habitat suitability for the coastal horned lizard, *Phrynosoma coronatum*, a highly specialised ant predator (Suarez & Case 2002). A similar result was found recently for amphibians, which consumed relatively fewer ants in invaded than uninvaded areas, especially for the most ant-specialist species, the natterjack toad, *Epidalea calamita* (Alvarez-Blanco et al. 2017). In these cases, the Argentine ant was more difficult to detect, capture and consume by the predators (but see Ito et al. 2009). Moreover, if the predator cannot move beyond the invaded area, the growth and survival of individuals can be compromised. A decrease in juvenile growth has been shown in *P. coronatum* under laboratory conditions, in *E. calamita* and in the spadefoot toad (*Pelobates cultripes*) when the main prey offered was the Argentine ant instead of native ants; and *E. calamita* juveniles also suffered from lower survival (Suarez & Case 2002; Alvarez-Blanco 2019). Lack of suitable prey decreases territory quality and alters behavioural patterns. For example, adults of the natterjack toad moved to uninvaded areas, being less abundant in invaded areas (Alvarez-Blanco et al. 2017). Therefore, the cascading food web consequences of Argentine ant invasions could lead to population extirpations of the most myrmecophilous vertebrates (as suggested for the horned lizard, Fisher et al. 2002).

Cascading effects of the invasion can alter the prey of other vertebrates that do not usually feed on ants. In cork oak forests in northeast Spain, insectivorous bird community composition differed in invaded and uninvaded areas (Pons et al. 2010), and there was a reduction of caterpillar biomass, an essential prey in the hatchling diet (Estany-Tigerström et al. 2010). Invaded areas represented lower breeding quality areas for the insectivorous blue tit, *Cyanistes caeruleus* with reduced clutches and growth, lighter fledglings with slightly yellower and duller plumage, but with nest and hatching success higher in these areas, possibly due to the blue tit predation shift towards alternative preys still available (Estany-Tigerström et al. 2013). In areas where environmental factors could be limiting, the negative impacts of the Argentine ant could be more pronounced. For example, a population of the great tit (*Parus major*) inhabiting a suboptimal environment at Doñana National Park (Spain), in the southern limit of the species distribution, reared poorer quality offspring in invaded areas (Alvarez-Blanco et al. 2020).

Vertebrate avoidance of invaded areas could also be caused by direct harassment by the Argentine ant, which is difficult to determine without specific experiments or observational data. For example, in the case of Argentine ant feeding on dead chicks, it is challenging to determine whether the ants caused the death or if they just recruited to the carrion (Hooper-Bui et al. 2004; Flores et al. 2017; Varela et al. 2018). Quantification of nest failure showed that the Argentine ant has limited impacts on the breeding of birds: > 2% of failed nests of the dark-eyed junco *Junco hyemalis* (Suarez et al. 2005), and even less for Bulwer's petrel *Bulweria bulwerii* (Boieiro et al. 2018). In some of these cases, ants were observed feeding on the egg contents while hatching (as also seen in California in the Least bell's vireo, *Vireo bellii pusillus*; Peterson et al. (2004)), swarmed over hatchling chicks or were seen attacking nestlings that were still living and later died.

Impacts on bird reproductive success have been linked to Argentine ant disturbance or harassment. In Spain, the quality of nestlings of the great tit was negatively affected by the Argentine ant (Alvarez-Blanco et al. 2020): chicks reared in invaded areas were smaller, lighter, had lower nutritional condition and altered oxidative stress balance compared with chicks reared in uninvaded areas. Because invaded and uninvaded territories were interspersed and shared overlapping foraging areas, direct disturbance was suggested. Similarly, in California, Nell et al. (2023) showed that the breeding success of the coastal cactus wren (*Campylorhynchus brunneicapillus sandiegensis*) was negatively related to Argentine ant abundance, with the causal mechanism being harassment. Lower nest box occupancy in invaded areas was observed in the great tit (Alvarez-Blanco et al. 2020), in contrast to the blue tit (Estany-Tigerström et al. 2013).

Direct attacks of the Argentine ant have been observed toward newly metamorphosed amphibians of three Iberian species (Alvarez-Blanco et al. 2021), using numerical dominance and spraying defensive compound from the pygidial gland. The venom's main compounds are iridomyrmecin, dolichodial and iridodial, which were considered to be mainly used as trail and alarm pheromones (Choe et al. 2012). Iridomyrmecin was demonstrated to be the venom causing amphibian death, as it penetrates the toad skin, causing paralysis and is ultimately lethal at high doses (Alvarez-Blanco et al. 2021). The effect of the defensive compound has also been tested on three amphibians in the Argentine ant's native range, for which the chemical is toxic but suggested to be ineffective in the field (Llopart et al. 2023).

4 Behaviour, physiology, and genetics

4.1 Foraging behaviour and trophic niche

Argentine ant colonies in invaded areas can contain millions of workers with interconnected nests spread over thousands of square-metres (Tsutsui & Case 2001; Pedersen et al. 2006; Heller et al. 2008). Large colonies facilitate resource discovery and retrieval through chemical communication and recruitment (Beckers et al. 1989). Observations in California estimated that over 250,000 workers foraged daily on each tree of a citrus orchard, and nearly 300,000 workers visited urban bait stations each night (Vega & Rust 2003). Extreme polydomy allows for dispersed central place foraging, facilitating rapid discovery and resource recruitment (Holway & Case 2000; Robinson 2014). Whenever a resource appears, they are typically the first species to find and monopolise it, with 24-h foraging and persistent trails observed under suitable conditions (Abril et al. 2007; Flanagan et al. 2013).

In invaded areas, Argentine ants consistently locate resources more quickly than native ants do (Human & Gordon 1996; Holway 1999; Gomez & Oliveras 2003; Angulo et al. 2011).

Another advantage of polydomy is that once workers from one nest locate resources, they can be rapidly distributed to colony mates inhabiting nearby nests. Markin (1968) used a radioactive marker (^{32}P labelled sugar water) and found the tracer "had spread almost entirely" through an 81-tree citrus grove covering 400 m^2 in just three days. Using dye in sugar solution over two weeks, Heller et al. (2008) found the food was shared up to an area of 647 m^2, and Vega & Rust (2003) found the marker in over 50% of ants up to 61 m away from the bait station (the maximum distance examined).

Argentine ants are omnivorous, and are predators of other insects and small vertebrates, scavenge on carrion, gather plant material, including small seeds, and consume liquid carbohydrate resources, including insect honeydew and plant nectar (Holway et al. 2002a; Rowles & O'Dowd 2009b). However, directly quantifying the relative contribution of different food sources to a colony can be challenging, and stable isotope analysis has allowed more insights into this topic. Using laboratory colonies of Argentine ants, Menke et al. (2010) found that workers fed an artificial animal-based diet had d15N values 5.5% greater than those fed a plant-based diet. Similarly, colonies with access to honeydew-producing aphids had d15N values 6% lower than colonies without access to aphids.

Colonies from native populations tend to be more carnivorous than colonies from introduced populations (Tillberg et al. 2007). However, there is also considerable variation in relative trophic position among Argentine ant colonies within sites. For example, in their native range, separate Argentine ant colonies can vary by an entire trophic level (d15N variation up to 3 ‰) at a single site (Tillberg et al. 2006) or up to 2.6% over one year in the introduced range (Menke et al. 2010). This variation may be related to the location of colonies relative to resources (Hanna et al. 2017, Mothapo & Wossler 2017), or the seasonal production of brood (Menke et al. 2010). Tillberg et al. (2007) tracked the leading edge of an invasion of Argentine ants over eight years and found that the relative trophic position of workers was lower behind the invasion front relative to those at the invasion front, probably because they become more dependent on plant-based resources over time (Tillberg et al. 2007). However, after another eight years, d15N of Argentine ants at this site increased, suggesting that the decline in relative trophic position was temporary or relative trophic position could fluctuate over larger time scales (Baratelli et al. 2023). These results together point to the potential for substantial spatial and temporal variation in resource assimilation and the need for more research identifying mechanisms responsible for variation in the Argentine ant diet.

Notably, the type of food source used can influence the behaviour of the Argentine ant and, in turn, have cascading effects on the interactions with other ant species and overall activity. Sucrose deprivation reduces Argentine ant worker aggression and overall activity (Grover et al. 2007). Similarly, the availability of floral nectars increases Argentine ant activity (Mothapo & Wossler 2017). The monopolisation of plant-based resources has also been linked to the invasion success. For example, access to aphid honeydew increases propagule survival, colony growth and worker activity rate (Shik & Silverman 2013), and even sucrose can increase local Argentine ant abundance and spread into forested habitats (Rowles & Silverman 2009).

4.2 Reproductive behaviour

Knowledge about the reproductive behaviour of *L. humile* comes from experimental and field studies in the invaded range. Like many invasive ants, *L. humile* displays secondary polygyny, resulting from gyne acceptance or colony fusion (Passera et al. 1988). Queen number is inversely proportional to queen fecundity (Keller 1988; Abril et al. 2008; Abril & Gómez 2020). A few queens lay almost all of the colony's eggs, while others contribute few to none (Abril & Gómez 2014; 2020). However, this inequality disappears when queens artificially experience monogynous conditions, suggesting cohabiting queens exert some form of reciprocal reproductive inhibition (Abril & Gomez 2020). The underlying mechanism could be queen pheromones since greater quantities of certain cuticular hydrocarbons (CHCs) are associated with higher rates of queen productivity and survival (e.g. Abril & Gómez 2020). Less is known about the physiological or behavioural effects of these compounds on nestmate queens, including how they affect fecundity among mature queens. Additional research must clarify whether these CHCs are queen pheromones or whether they serve to signal queen fertility.

In *L. humile*, the queen number is regulated by adopting or executing queens. Colonies seem more likely to adopt non-nestmate queens whose CHC profiles are similar to those of the host colony's queens (Vasquez et al. 2008). Execution in this species occurs in late spring; workers execute up to 90% of their colony's mature queens (Keller et al. 1989). CHCs also play an important role in this process, since the survivors display higher levels of certain compounds correlated with queen productivity (Abril et al. 2018; Abril & Gómez 2019), suggesting that workers execute less productive queens to increase colony productivity. Moreover, the number of queens executed positively correlates with the queen number (Abril & Gómez 2019). According to Vargo & Passera (1992), *L. humile* workers regulate queen numbers to control levels of queen inhibitory pheromones in the colony. Indeed, mature queens use queen pheromones to inhibit gyne development in three ways: they cause workers to behave aggressively towards queen larvae, including cannibalism (Bach et al. 1993; Passera et al. 1995); they prevent dealation and egg-laying in virgin queens (Passera & Aron 1993a); and they prompt workers to attack and kill virgin alates (Passera & Aron 1993b). The massive execution of queens in the spring coincides with the period of larval sexualisation. Therefore, by eliminating mature queens, workers cause a drastic drop in the colony's levels of queen pheromones, allowing new gynes to be produced (Vargo & Passera 1992). However, further research is needed to identify the causal link between queen pheromones and caste development in this species.

A key facet of its invasiveness is that little time elapses between sexuals emerging and the new queens laying eggs. Gynes emerge later than males; they reach sexual maturity and mate just a few hours after emergence. As in many other invasive ants, mating occurs within the natal nest, and young, mated queens start to lay eggs within a few days (Passera & Keller 1992). Work remains scarce on the species' reproductive biology in its native range, especially on queen fecundity, the regulation of queen number, and the seasonal execution of queens. This knowledge could help us better understand whether the species' reproductive biology has changed throughout its invasion history.

4.3 Aggressive interactions

Intraspecific aggression among non-nestmates in invasive populations of Argentine ants has been investigated in detail due to its impact on the formation of supercolonies via unicoloniality. Reduced aggression or its complete absence between non-nestmates can yield a numerical advantage to *L. humile*, allowing it to exert aggression on other supercolonies and towards other species.

4.3.1 Intraspecific aggression among non-nestmates

Although unicoloniality (see Supplementary Table S1) is observed within the native range of Argentine ants, supercolonies expand over short distances (0.05–6 km) compared to introduced populations (Vogel et al. 2010). Beyond these distances, fighting was commonly observed at all spatial scales, suggesting sub-structuring of populations (Suarez et al. 1999; Tsutsui et al. 2003; Heller 2004; Blight et al. 2017). In the invaded range, individuals from nests separated by hundreds or thousands of kilometres do not show aggression, forming supercolonies that spread over vast distances. Indeed, unicoloniality is common in the invaded range, as seen in the USA (Holway et al. 1998; Tsutsui et al. 2003; Thomas et al. 2006), Europe (Giraud et al. 2002; Blight et al. 2012; Castro-Cobo et al. 2021), Japan (Sunamura et al. 2009a; Inoue et al. 2013), South Africa (Mothapo & Wossler 2011), Australia (Björkman-Chiswell et al. 2008; Suhr et al. 2011), and New Zealand (Corin et al. 2007a). In these populations, aggression between non-nestmates can be completely absent (Tsutsui et al. 2003), mildly present (Giraud et al. 2002) or replaced by increased rates of allogrooming and antennation (Björkman-Chiswell et al. 2008). The aggression in these introduced populations remains significantly lower than levels observed among non-nestmates in the native populations of *L. humile* (Blight et al. 2017).

In experiments involving aggression bioassays between supercolonies from different continents, it was found that the major supercolonies of Europe, California, Japan, Australia, New Zealand and Hawai'i showed no reciprocal aggression, but showed aggression to secondary supercolonies or smaller colonies from South Africa, California and Hawai'i (Sunamura et al. 2009b; van Wilgenburg 2010b), indicating that there is one supercolony (the "main" or the "large") that has a trans-continental spread. There has been evidence for the existence of high levels of aggression between supercolonies from the same country, sometimes of the same region, as seen in the USA (Chen & Nonacs 2000; Buczkowski et al.

2004; Thomas et al. 2006; van Wilgenburg et al. 2022), Japan (Sunamura et al. 2009a), South Africa (Mothapo & Wossler 2011) and Mediterranean Europe (Blight et al. 2009; Abril & Gómez 2011; Blight et al. 2012).

There are endogenous and exogenous sources of nestmate recognition in Argentine ants, modulating aggression in the invaded range. Endogenous sources are related to low genetic diversity (see section 4.4). This causes similarity in CHC profiles and ultimately results in unicoloniality over large areas. Genetically more homogenous colonies also attack genetically diverse colonies (Tsutsui et al. 2003). Wherever genetic diversity is higher, as it occurs in native populations, or where multiple introduction events raise the genetic diversity in certain spatial pockets such as airports or ports, non-nestmates display higher levels of aggression (Suarez et al. 1999) or allogrooming and antennation (Giraud et al. 2002; Björkman-Chiswell et al. 2008) as compared to populations with low genetic diversity.

The role of non-heritable exogenous environmental components, such as diet, has been debated in lowering aggression between non-nestmates. In general, similar diets could lead to similar CHC profiles, reduced aggression among non-nestmates and may lead to colony fusion (Buczkowski et al. 2005, but see Suarez et al. 2002). Aggression has also been reduced with time under laboratory conditions (Chen & Nonacs 2000), or by the absence of certain macronutrients such as carbohydrates in the diet (see section 4.2). Inversely, processes that interfere with an individual's CHC profile, such as a different diet, or even engaging with the prey leading to the transference of the prey's CHC onto the ants, can lead to disruption of colony integrity (Liang & Silverman 2000; Liang et al. 2001; Silverman & Liang 2001; Buczkowski & Silverman 2006). Colony identity can also play a role, as different colonies respond differently to diet changes (Buczkowski & Silverman 2006). Moreover, highly aggressive colonies maintain their aggressiveness despite dietary changes, whereas medium- or low-aggression colonies reduce their aggression when diet becomes similar (Buczkowski et al. 2005). However, diet is proposed to be ineffective in creating conditions suitable for unicoloniality (Thomas et al. 2005; van Wilgenburg et al. 2022).

Other modulators of aggression are memory and prior experience of an aggressive interaction with a non-nestmate. Individuals escalate aggression in future encounters based on their prior experience of facing a non-nestmate, and, in response, showing or receiving aggression. This experience can modulate future interactions for up to a week (van Wilgenburg et al. 2010a). At the colony level, less aggressive colonies raise their aggression levels in future interactions after encounters with a hostile and highly aggressive colony, transitioning from asymmetrical to symmetrical colony interactions concerning aggression (Thomas et al. 2005).

Finally, intraspecific aggression among non-nestmates in Argentine ants is also a context-dependent process based on social and ecological contexts of discrimination of a non-nestmate. For example, increased aggression is observed when the context related to nest proximity exists in the form of numerous nestmates or familiar territory, but the aggression is reduced when such contexts are removed (Buczowski & Silverman 2005). Such context-dependent cues often give different results in dyadic interactions versus colony interactions. The role of such exogenous and context-dependent cues in modulating aggression also highlights the importance of using appropriate social and ecological context-based behavioural assays for testing aggression in *L. humile* in the future.

4.3.2 Interspecific aggression

Argentine ants are usually highly aggressive towards other species, and their ability to break the discovery-dominance trade-off (Human & Gordon 1996; Holway 1999) is part of their success as invasive species (section 3.1). There are inherent differences between different supercolonies of Argentine ants, and they are differentially aggressive towards other ant species. The differential invasion success of different supercolonies could also be a function of their inherent aggressiveness, with aggressive supercolonies attaining a wider range and milder colonies receiving more aggression, resulting in smaller territories and fewer resources, and a narrower range (Abril & Gómez 2011).

Argentine ants display a "bourgeois strategy" in fighting, behaving either as "hawks" (behaviourally aggressive) or "doves" (behaviourally submissive) depending on group size (Carpintero & Reyes-López 2008). Owing to their small size, Argentine ants usually lose one-to-one contests or numerically-matched interspecific contests between smaller colonies or groups of workers (Frizzi et al. 2023). However, as the group size grows, Argentine ants show a change in behavioural strategy, with rapid recruitment of individuals towards aggressive interactions (Buczkowski & Bennett 2008), active cooperation among individuals where multiple individuals of *L. humile* fight a single individual of the native ant (Sagata & Lester 2009; Blight et al. 2010b; Bang et al. 2017; Leonetti et al. 2019), and chemical defences combined with physical aggression (Buczkowski & Bennett 2008; Welzel et al. 2018). Native ant species who are behaviourally aggressive can withstand Argentine ant invasions, as happens in *Tapinoma* c.f. *nigerrimum* (Blight et al. 2010b), and the Australian native ant, *Iridomyrmex rufoniger* (Walters & Mackay 2005). Interestingly, unlike many native ant species, *L. humile* individuals show immunity to their nestmates' chemical defences, and these serve a dual purpose, incapacitating the opponents and simultaneously acting as an alarm pheromone to recruit more nestmates to aggressive interactions (Buczkowski & Bennett 2008; Welzel et al. 2018). Such social facilitation around aggressive interactions allows *L. humile* to advance from a local numerical advantage of fighting in groups to a global numerical advantage of higher absolute numbers, and assists in invading new areas and outcompeting larger and ecologically dominant native ants (Human & Gordon 1996; 1999; Holway 1999).

4.4 Genetic variability/population genetics

As in other invasive ants, genetic diversity is higher in native than in introduced populations, due to founder effects (e.g. genetic bottlenecks and single introductory events, Suarez et al. 2008; Vogel et al. 2010). Low genetic diversity is linked to its unicolonial social organisation, which is an important attribute of the Argentine ant's invasive potential. Sib mating, queen executions and "genetic cleansing" (i.e. the death of individuals with rare alleles) may further contribute to the reduction of genetic diversity, the decrease in the number of haplotypes, and the increase of nestmate relatedness, which nonetheless remains very low (Giraud et al. 2002; Keller & Fournier 2002; Inoue et al. 2015). Such a condition contributes to reducing intraspecific competition and aggressiveness (Inoue et al. 2015; but see Sanmartín-Villar et al. 2022) and confers these population's further local ecological dominance and an unrestricted growing potential (Holway et al. 1998), at least during the first phase of their invasive process (Lester & Gruber 2016).

The analysis of the genetic structure of *L. humile* supercolonies using both nuclear and mitochondrial DNA showed that these are characterised by i) the presence of many queens in each nest, ii) nestmates relatedness not different from zero (Pedersen et al. 2006), iii) the presence of a single mitochondrial haplotype per supercolony (Sunamura et al. 2009a; Vogel et al. 2009), and iv) a strong genetic differentiation between supercolonies, primarily in their native range (Thomas et al. 2006). All these features further support that supercolonies are closed breeding units, with no significant inbreeding and limited gene flow. The competition occurring where different supercolonies come into contact contributes to regulating the stability and evolution of unicolonial structures and their gene pool in native and invaded ranges (Sanmartín-Villar et al. 2022).

The invasion history at the global scale (section 2.1) is still debated, and genetic analysis, together with behavioural assays, can help elucidate the relationship between different populations (Corin et al. 2007b). Analysing maternally inherited mitochondrial DNA is a key tool for investigating invasion histories based on founding queen dispersal (Tsutsui et al. 2001; but see Vogel et al. 2010). The analysis of mitochondrial marker genes, such as cytochrome c oxidase (CoI, CoII) and cytochrome b (Cytb), allowed identifying more than 19 different haplotypes in both native and introduced ranges (Sunamura et al. 2009a; Vogel et al. 2010; Park et al. 2021). Several have an intercontinental distribution due to long-distance human-mediated dispersal events (Suarez et al. 2001). For example, the LH1 haplotype is widespread across Europe, North America, Australasia and Japan, while LH3 was found in South (Chile and Ecuador) and North America, but also Asia (Vogel et al. 2010; Inoue et al. 2013; Seko et al. 2021a).

5 Applied issues

5.1 Economic impacts

Although the evidence for the ecological impacts of invasive ants, including the Argentine ant, has accrued rapidly in the past few decades (section 3), the synthesis of their economic impacts have only recently been collected and analysed (Diagne et al. 2020; Angulo et al. 2022). Between 1980–2020, *L. humile* caused economic impacts worth US$ 19.2 million to the global economy (standardised to US$ 2017 values), thus causing global economic impacts of US$ 480,000 annually. However, even if no costs were recorded, the species started to become a severe urban and agricultural pest one century before, around the end of the 19th century (Newell & Barber 1913). Compared to other invasive ants, the Argentine ant is the fourth costliest species after *Solenopsis* spp. (US$ 32 billion), *W. auropunctata* (US$ 19 billion) and *A. gracilipes* (US$ 66 million). The decadal costs of *L. humile* have remained stable in the last four decades, with a spending of about US$ 3–5 million per decade (Angulo et al. 2022). However, these figures are highly underestimated, as they consider only costs reported in reliable publications, mainly in English, creating a linguistic and geographic skew in cost representation (Angulo et al. 2022).

Although *L. humile* has invaded more than 30 countries worldwide (section 2.1), the economic impact information has been reported only from 7 of these, from which 6 are high-income economies (Australia, Ecuador, Japan, New Zealand, Portugal, Spain, and the USA; Supplementary Fig. S2). Among them, the number of locations reporting costs is two to three orders of magnitude lower than the number of locations from where Argentine ants are reported in these countries (Angulo et al. 2022). Furthermore, the costs among these seven countries are highly disparate, with the highest costs coming from Australia (84% of total costs), followed by New Zealand (5%), USA (4–5%) and Japan (3–4%). The costs in Europe represent <1%, and Africa and mainland Asia do not have any reliable cost reported (Angulo et al. 2022), despite the spread of *L. humile* on these continents. The under-representation of costs from the low- and middle-income economies are likely language-related and/or related to the emerging nature of the discipline in these regions (Angulo et al. 2021; Bang et al. 2022).

Most economic costs generated by *L. humile* invasions were in human-modified environments (87% of total costs), open forests (3%) and scrub forests (2%) (Angulo et al. 2022). Over 99% of costs are due to management, and more than 90% are related to post-invasion management, including control programs, eradication campaigns and containment operations (Supplementary Fig. S2; Angulo et al. 2022). This figure contrasts with those obtained when all invasive ants or all invasive species are considered, where management accounts only for 10% or less (Diagne et al. 2021; Angulo et al. 2022). This difference could be due to a bias toward high-income countries whose governmental services or official organisations can afford management. A more uniform geographical representation of economic impact entries could mitigate this trend.

5.2 Eradications and control

Due to the high environmental impacts in its invaded range, *Linepithema humile* has been the target of several control and eradication attempts. The use of chemicals against *L. humile* dates back to the end of the 19th century (Hoffmann et al. 2009). The control of invasive ant populations, including *L. humile*, has been the subject of previous reviews, and we refer to these papers for a comprehensive description of the methods employed (Silverman & Brightwell 2008; Hoffmann et al. 2009; 2016). Here we focus on eradication attempts, trying to elucidate why some of them failed and others were successful. A summary of the literature about management published since 2010 is reported in Supplementary Table S3.

Reports of eradications for eleven species with established populations outside their native ranges exist, among which, *L. humile* has been eradicated from the greatest area (~16,000 ha) and the greatest number of times (~3,000 discrete populations) (Hoffmann et al. 2011; 2016). Most of these population-level eradications were from a single program conducted in Western Australia (Van Shagen et al. 1994), with an average population size of about 10 ha, and the largest of approximately 300 ha (Hoffmann et al. 2011). Most of those eradications were achieved using toxic sprays, primarily of organochlorines prior to their deregistration. However, sprays are now rarely used for broadscale (>tens of ha) eradications because of significant non-target issues.

Eradication attempts of *L. humile* using products other than sprays (granular baits and gels/pastes) had mixed results (Silverman & Brightwell 2008), with only two reported to have achieved eradication. The first, on Tiritiri Matangi Island in New Zealand, eradicated two populations covering 10 and 1 ha, respectively (Green 2019). The effort took 16 years, involving paste baits containing 0.01% fipronil dispersed manually at densities no less than one per 3 m^2 over the entire areas multiple times and only wherever residual populations were found. The second, in Japan, also involved two populations covering 8.5 and 16 ha, respectively (Sakamoto et al. 2017). That program primarily used paste baits containing 0.005% fipronil placed every 5–10 m along buildings, also using a spray containing 0.005% fipronil whenever brood was found. Other eradications that remain unreported in the scientific literature relate to three populations on Norfolk Island, Australia, covering 2 ha and less, that were treated with paste baits containing 0.6 g/kg fipronil placed every few m^2 over the entirety of the areas an unknown number of times. Inoue et al. (2015) used paste baits with fipronil over a period of 11 months at two doses and showed 99.8% reduction of *L. humile* populations while having limited effects on other arthropods. Buczkowski & Wossler (2019) highlighted that fipronil is effective against *L. humile* even at very low doses (ng). Interestingly, they showed that high secondary mortality can be achieved through horizontal transfer within the population; in field plots, releasing fipronil-sprayed workers led to a > 90% reduction of the *L. humile* population within 24 h (see also Hooper-Bui et al. 2015).

So why are there so few eradications of *L. humile* using products other than sprays, and what can be done to bolster change? Aside from numerous administrative and technical reasons why eradications fail (Myers et al. 2000; Simberloff 2009), the greatest issue appears to be the relatively low efficacy of individual treatments. Effective baiting can be defined as one or both scenarios leading to the extirpation of populations: the reproductive queens being incapacitated, or the workers being killed. The greater the number of queens and/or workers affected by individual treatments, the fewer repeat treatments needed to achieve eradication, but the relative merits of the two scenarios to achieve eradication remain to be determined (Silverman & Brightwell 2008).

For unknown reasons, the efficiency of individual field treatments on *L. humile* populations is lower than for some other invasive ant species often targeted for eradication. This disparity is most striking with using hydrogels as bait (Buczkowski et al. 2014). Even when using extremely low concentrations (<0.006–0.0007%) of fipronil or thiamethoxam, which allows workers to return to the nest and share the bait with nestmates before they die, *L. humile* abundance decline after each treatment is more of a noticeable drop (e.g. ~20%) than a crash (e.g. > 80%) (Boser et al. 2014; Rust et al. 2015). Notably, no eradication of an entire *L. humile* population has been achieved yet, even after 12 or more applications spaced approximately weekly to monthly apart (Boser et al. 2017; Hoffmann et al. 2023). In comparison, a single treatment using the same hydrogel bait containing fipronil will kill over 99% of yellow crazy ant, *A. gracilipes*, workers, and three treatments spaced three months apart give almost certainty of eradication (Hoffmann et al. 2023). Whether this same disparity also occurs with granular products is unclear because no eradication programs have reportedly used granular products. Ultimately, this difference between outcomes for different species suggests that it is not the concentration of the active compound that is the predominant issue, but something about biology that requires a change in baiting techniques.

One possibility is a simple difference in food dispersal within colonies between queens, brood, and workers. Markin (1970), however, showed that the number of ants to receive food, the speed and the distribution patterns among castes were similar to that of non-invasive species. Another possibility is that baits are non-preferential to environmental food sources, and therefore not enough of the active ingredient is being taken to the nests. Notably, ants often prefer complex nectars over simple sugars (Blüthgen & Fiedler 2004), and hydrogel baits used to date against *L. humile* were composed solely of sucrose. Also, when there is an abundant alternative food source, workers that have fed on a bait would have reduced opportunity to share the bait with other individuals because fewer individuals would be hungry (Markin 1970). Another possibility could be that, per standard body weight, workers require less toxicant to be killed than queens, at least for hydramethylnon (Hooper-Bui & Rust 2000); potentially with workers dying quickly before providing the lethal dose to a queen. There also seems to be a disparity between bait constituents and queen feeding preferences. Liquid and hydrogel baits are composed solely of sugar, but queens are preferentially fed protein (Markin 1970). Ultimately, this may be inconsequential if only workers need to be extirpated to achieve eradication.

6 Future research

Although Argentine ants are among the most studied ant species, this review identified several important knowledge gaps that could be important future priorities for research.

One poorly-understood phenomenon with huge management implications is why some introductions result in successful invasions, whereas others result in the establishment of the ant without spreading. The latter are underreported; however, their frequency and the factors that cause them are essential to improve our ability to predict local spread and to attempt its control. Comparative or meta-analysis studies at the global scale, including multiple invaded sites and native areas for comparison, will provide insights into the frequency of establishments that do not result in invasions and their drivers. In particular, more records could be searched in areas with long-term monitoring, such as California (Menke & Holway 2020) or Japan (Inoue et al. 2013), or obtained by extensively resampling regions invaded in the past.

Despite the vast literature on the ecological effects of *L. humile* on other species and ecosystems, there are still knowledge gaps in the comprehension of why some non-ant arthropod communities are more sensitive to the invasion than others. Regarding vertebrates, future studies should pay special attention to areas and seasons where vertebrates coexisting with the Argentine ant are at their most vulnerable stage, and to the effects on specialised ant predators. Particularly relevant are the sublethal impacts of the venom associated with reduced body condition, survival and development of juvenile amphibian and avian offspring (Alvarez-Blanco 2019; Llopart et al. 2023), which may show delayed, long-term consequences on populations that can be easily overlooked. The impact of the venom should be extensively investigated to understand its toxicity for other vertebrates, such as mammals, altricial birds or reptiles. Finally, iridomyrmecin can deter pollinators and hence have hidden cascading effects on plants that are still to be fully quantified (e.g. Wilson et al. 2020).

The link between the monopolised food sources (e.g. carbohydrates and plant-based resources vs. proteins) with ants' overall activity and aggressiveness and its effects on invasion success deserve further studies. Also, the adaptive change in dietary breadth as key to success is another mechanism worth exploring in depth (Seko et al. 2021b).

Quantifying the economic impacts of invasive species such as the Argentine ant is a necessary step in highlighting that biological invasions pose not only ecological but also socioeconomic challenges. Despite its worldwide distribution, estimating the costs of Argentine ant invasions is still in its infancy. The current figures merely represent the lower limit of the actual economic impact due to widespread gaps in reporting from several geographic areas, economies, habitats, and sectors.

Further trials and research are needed to elucidate the causes inhibiting eradication success. One important advancement could be linking genetic analysis to eradication techniques to use the most effective products for each specific population. For example, Hayasaka et al. (2015) showed that supercolonies characterised by different dominant haplotypes have differential susceptibility to fipronil baits, and this finding opens new perspectives towards targeted eradication/control strategies. Control based on RNA interference (RNAi) is also promising. This technology is based on a highly specific, post-transcriptional gene inactivation process, triggered by double-stranded RNA (dsRNA) homologous to the gene sequence to be suppressed. Ideally, it is possible to design a dsRNA that interrupts one or more vital genes, such that only the target species would be killed. RNAi is now functional as a topical spray for some agricultural pests (Hoang et al. 2022), but remains to be fully functional as an ingested toxicant just like typical ant baits. The Argentine ant could be the ideal subject for testing and developing such a technique, which is gaining attention to control invasive insects, including ants (e.g. Allen 2021).

To conclude, *L. humile*, one of the 100 worst globally invasive species, has been extensively researched, especially in the last 100 years, coinciding with its global range expansion. This review has synthesised historical and recent advances regarding the global invasion of the species, with a focus on its natural history, behaviour, genetics, ecological and socioeconomic impacts and future research directions. Such reviews have the potential to inform researchers, practitioners and policymakers on the existing knowledge and knowledge gaps on species of global concern.

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Figure S1, S2, Table S1, S2