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Act locally, think globally. Ant studies in Argentina in the context of ecological theory

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Abstract. Building and testing general principles is key to accelerate scientific progress. Here, we review the studies performed in Argentina in which ants were used as model organisms, in the context of ecological theories, hypotheses and concepts. Specifically, we focus on ant studies performed under the conceptual frameworks of ecological engineering, indirect interactions, seed dispersal, community assembly rules, biological invasions and integrated pest management. Those studies contributed to 1) supporting the concept of ecological engineers through the study of the physical changes in the environment caused by ants through the building and maintenance of their nests, and their consequences on other organisms such as soil biota, plants and herbivores; 2) questioning the convergence hypothesis, which proposes that independently assembled communities in similar, but geographically distant habitats converge in composition and functioning under similar environmental pressures; 3) showing that directed seed dispersal is an important process to increase plant performance in desert ecosystems; 4) understanding the type of control which prevails in communities (top-down or bottom-up); 5) emphasizing the relevance of indirect interactions in the structure and functioning of ecosystems with examples of trophic cascades, indirect facilitation, exploitative competition and trait-mediated effects; 6) a better understanding of the causes of success or failure of biological invasions, via the study of the behavioral and demographic characteristics of invasive ant species in their native area, and the role of biotic resistance and mutualism facilitation; and 7) exploring the concept of integrated pest management via the study of the use of natural enemies, repellents and attractants, and the knowledge about the feeding and foraging behavior of pests. This body of work reinforces the key role of ants as model organisms to test ecological hypotheses and highlights the importance of using conceptual frameworks as guidance to better understand the complexity of natural systems.

[Keywords: ants, biological invasions, ecological hypotheses, ecological engineering, seed dispersal, pest control, indirect interactions]

Resumen. Actuar localmente, pensar globalmente. Estudios de hormigas en la Argentina en el contexto de la teoría ecológica. Construir y probar principios generales es clave para acelerar el progreso científico. En este trabajo revisaremos los estudios realizados en la Argentina en los que las hormigas se usaron como organismo modelo para probar teorías, hipótesis y conceptos ecológicos. Específicamente, nos enfocaremos en los marcos conceptuales de ingeniería ecológica, interacciones indirectas, dispersión de semillas, ensamble de comunidades, invasiones biológicas y manejo integrado de plagas. Estos estudios contribuyeron a: 1) apoyar el concepto de ingenieros ecológicos al estudiar las modificaciones en el ambiente realizadas por las hormigas al construir y mantener sus hormigueros, y las consecuencias de estas modificaciones sobre la biota del suelo, las plantas y los herbívoros; 2) cuestionar la hipótesis de convergencia, que propone que comunidades independientes en ambientes parecidos, pero distantes geográficamente, convergen en composición y funcionamiento; 3) demostrar que la dispersión directa es un proceso que incrementa la adecuación de las plantas en sistemas desérticos; 4) comprender el tipo de control que prevalece en las comunidades (de arriba hacia abajo o de abajo hacia arriba); 5) enfatizar la relevancia de las interacciones indirectas, con ejemplos de cascadas tróficas, facilitación indirecta, competencia por explotación y efectos mediados por rasgos; 6) comprender mejor las causas del éxito o fracaso de las invasiones biológicas, a través del estudio de las características comportamentales y demográficas de las hormigas invasoras en su área nativa, y el papel de la resistencia biótica y la facilitación por mutualismos; y 7) explorar el concepto de manejo integrado de plagas estudiando el uso de enemigos naturales, repelentes y atrayentes, y el comportamiento de la alimentación de plagas. Todos estos trabajos refuerzan el papel clave de las hormigas como organismo modelo para poner a prueba hipótesis ecológicas, y enfatizan la importancia de usar marcos conceptuales como guía para comprender mejor la complejidad de los sistemas naturales.

[Palabras clave: control de plagas, dispersión de semillas, hipótesis ecológicas, hormigas, ingeniería ecológica, interacciones indirectas, invasiones biológicas]

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Ecological theory matters

Ecology progresses faster when researchers operate within an explicit framework of concepts, hypotheses and theories. Without them, ecology would be merely the accumulation of particular knowledge with a limited predictive ability (Lawton 1999; Scheiner and Willig 2019). Ecological theory reduces the complexity of the natural world because it captures the essential features of a system, provides abstract characterizations and makes predictions for phenomena that can be tested with additional data (Marquet et al. 2014). Therefore, working in the context of general ecological principles is key to accelerate scientific progress, enhance the ability to address environmental challenges and improve the design of experiments and large-scale environmental-monitoring programs.

Ecological science has a long history of building theories, hypotheses and concepts. Foraging theory, ecological niche, predator-prey interactions, resource availability and plant anti-herbivore defense, competitive exclusion principle, island biogeography, and macro-ecological rules are some examples of ideas that helped to improve our understanding of the natural world (MacArthur and Wilson 1967; Coley et al. 1985; Schoener 1987; Tilman 1990; Brown 1995; Hubbell 2001; Mukherjee and Heithaus 2013). These ideas were based on or tested by observation and experimentation with various types of organisms. Ants are an ideal model organism to work in the context of ecological theory. Ants are abundant, diverse, worldwide distributed and feasible to manipulate in field and lab conditions (Hölldobler and Wilson 1990). For example, ants were used to build and test the ideas of ecological engineering (De Almeida et al. 2020), trade-off among plant defense strategies (Heil et al. 2002), the size-grain hypothesis (Kaspari and Weiser 1999), island biogeography and meta-population dynamics (Morrison 2002), competition and niche theory (Savolainen and Vepsäläinen 1988), directed dispersal hypothesis (Rice and Westoby 1986; Berg-Binder and Suárez 2012), macroecology (Segev et al. 2015), and Rapoport's rule (Sanders 2002). In Argentina, apart from a large number of studies on ant taxonomy and natural history (e.g., Cuezzo 2000; Cuezzo et a. 2015; Lanteri and Martínez 2012; Vittar and Cuello 2017), there is a vast amount of research where ants are used as model organisms in the context of ecological theories, hypotheses, and concepts. Here, we review some of these studies. In particular, works in which ants were used under the conceptual frameworks of ecological engineering, indirect interactions, seed dispersal, community assembly rules, biological invasions and integrated pest management. We hope this review illustrates how ants can help to better understand and build ecological theories and stimulates further research using these "little things that run the world" (Wilson 1987; Del Toro et al. 2012).

Ant studies in Argentina in the context of ecological theory

Ecosystem engineers. Ants as habitat builders

The concept of ecological engineering helps ecologists to develop conceptual tools to better understand general patterns and to build models of how nature works (Wright and Jones 2006). Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species by causing physical state changes in biotic or abiotic materials (Jones et al. 1994). Engineering can affect other species and may involve the construction of a physical structure by an organism (Jones et al. 1997). Several animals are considered key ecological engineers, such as beavers (*Castor canadensis*), which cut and use trees to construct dams, altering hydrology and creating wetlands that may persist for centuries (Wright et al. 2002). Ants can also be relevant ecosystem engineers by creating habitats for other organisms and controlling their activities through physical and biochemical processes (Farji-Brener 1992; Farji-Brener and Silva 1995; Folgarait 1998; Farji-Brener and Werenkraut 2015; Lavelle et al. 2016; Farji-Brener and Werenkraut 2017; Farji-Brener et al. 2017; De Almeida et al. 2020; Elizalde et al. 2020). Specially, the chemical and physical changes produced by ants in the soils around their nests may affect the abundance and distribution of plants and animals, both at local and at regional geographical scales (Jonkman 1978; Farji-Brener and Silva 1995; Sosa and Brazeiro 2012; Farji-Brener and Werenkraut 2017).

Ant studies in Argentina have well exemplified the concept of ecological engineers via the study of the physical changes they cause in the environment and their consequences on other organisms. Firstly, ants affect soil conditions both by building and maintaining their nests and by accumulating organic matter (Farji-Brener and Werenkraut 2017). For example, in the Argentinian subtropical dry forests and Mesopotamian Espinal, leaf-cutting ants are important soil modifiers through their effects on soil profile, distribution of organic matter, and micro-relief conditions (Bucher and Zucardi 1967; Bucher 1982; Diaz et al. 2016). It is estimated that *Atta wollenveideri* activity removes about 1100 kg of soil.ha^{-1}.year^{-1} (Bucher 1982). In arid Patagonian regions (steppe and Monte deserts), *Acromyrmex lobicornis* nests show a greater nutrient content and water retention capacity than surrounding soils (Quiran and Pilati 1998; Farji-Brener and Ghermandi 2000, 2004, 2008; Tadey and Farji-Brener 2007; Farji-Brener and Tadey 2009; Lescano et al. 2012). Besides leaf-cutting ants, other ants that build mound-nests have large effects on soil properties. For example, the canonical mounds of *Camponotus punctulatus* produce soil alterations mainly due to physical disturbance of profiles (i.e., they remove fine materials from deep soil horizons to the surface) through changes in the distribution of organic matter and by the creation of a micro-relief associated with the presence of a considerable nest-mound density (Bucher 1982; Folgarait et al. 2002). This nest-mound environment differs from the surrounding ground environment in soil texture, structure and chemical composition (Bonetto et al. 1961; Pire et al. 1991; Folgarait et al. 2002). Finally, relatively small ant nests can also modify soil properties in their surroundings. In northern Patagonia, nest soils of the three abundant and widespread ant species in the steppe (*Dorymyrmex tener*, *Pogonomyrmex carbonarius* and *Pheidole spininodis*) showed higher soil conductivity, K, and Mg than non-nest soils (Pirk et al. 2020). All these edaphic changes affect soil dynamics and can spread along other trophic levels, affecting plants that grow near nests, their herbivores and the natural enemies of those herbivores.

Changes in soil properties and accumulation of organic matter due to ant activities can further affect soil biota, modifying nutrient cycling. In greenhouse and laboratory experiments, the rate of soil decomposition was greater in nest soils and refuse dump samples of *Ac. lobicornis* than in non-nest soil samples (Farji-Brener and Ghermandi 2000; Farji-Brener 2010) because of an enhanced microbial activity (Farji-Brener 2010; Fernández et al. 2014a,b). However, under natural conditions, the decomposition rate in nests was significantly lower than that in non-nest soils probably due to the scarcity of soil water typical of desert habitats such as the Monte desert (Romero et al. 2018). In a subtropical pasture from Argentina, nest-mounds of *C. punctulatus* showed higher proportion of bacterial activity, mesofauna abundance, and soil decomposition than non-nest soils (González-Polo et al. 2004; Paris et al. 2008). Increased soil biota activity usually improves soil nutrient content, which affects plants growing on ant nest proximities and animals that feed on those plants.

The presence of ant nests increases plant richness and/or enhances plant growth, survival and reproduction. In eastern and central Chaco savannas, trees only develop on flat *Atta* mound nests. Abandoned nest-mounds allow woody plant invasions of grasslands (Bucher 1982). In the Patagonian steppe, *Ac. lobicornis* nests increase plant diversity at a local scale (Farji-Brener and Margutti 1997; Farji-Brener and Ghermandi 2000, 2004). Moreover, a few native and several exotic plants showed greater growth and fitness when growing in nest-soils compared to non-nest soils (Farji-Brener and Ghermandi 2008; Farji-Brener et al. 2010; Cerda et al. 2012). In subtropical habitats, nest-mounds of the ant *C. punctulatus* increase the floristic richness at small spatial scales and provide micro-sites for particular species (Lewis et al. 1991), affecting plant composition assemblage (Folgarait et al. 2002). Finally, nest soils from *D. tener* and *P. carbonarius* increase seedling recruitment and plant growth of native plant species. The effects of ant nests on plant fitness may spread to higher trophic levels affecting herbivores and their natural enemies (Lescano et al. 2012, 2019).

Finally, in agreement with the concept of ecological engineering, several other animals use the modified environment of ant nests to live and reproduce. For example, in Argentinian pastures, leaf-cutting ant nests of the genus *Acromyrmex* are inhabited by a variety of arthropods such as spiders, opilions, beetles, acari, and collembola (Quirán and Pilatti 1998; Peralta and Martínez 2013). Samples from nests of *Acromyrmex lundii* and *Ac. ambiguus* revealed the presence of 1440 oribatids belonging to 18 families, 25 genera and 34 species, including three new species (Peralta and Martínez 2013). In sum, ant nests drastically affect their surroundings by modulating the availability of resources to other species, causing changes in the physical state of biotic or abiotic materials (Figure 1).

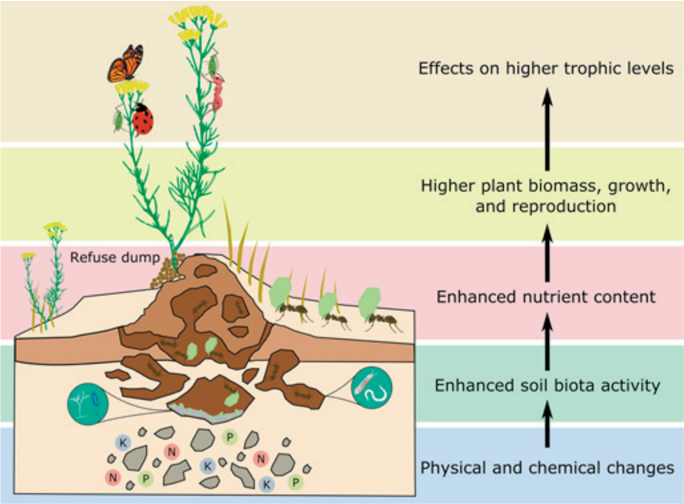

Figure. 1. Scheme of ants as ecological engineers and their potential effects. Ants modify the physical and chemical properties of soil by building and maintaining their nests, modulating the availability of resources to other organisms. These soil alterations often increase soil biota activity, soil nutrient content and performance of plants that grow nearby. This, in turn, may affect higher trophic levels. Figure credit: A. Devegili.

Figura 1. Esquema de las hormigas como ingenieros ecológicos y sus efectos potenciales. Las hormigas modifican las propiedades físicas y químicas del suelo al construir y mantener sus hormigueros, modulando la disponibilidad de recursos para otros organismos. Estas alteraciones suelen incrementar la actividad de la biota del suelo, el contenido de nutrientes del suelo y el desarrollo de las plantas que crecen cerca del hormiguero. A su vez, esto puede afectar niveles tróficos más altos. Crédito de la figura: A. Devegili.

There is still a need to accumulate empirical data from comparative and experimental studies to better understand the concept of ecosystem engineering (Wright and Jones 2006). We believe that the studies we summarized here offer valuable information to illustrate and predict effects of ecosystem engineering on biogeochemical processes and species distributions. This research indicates both the important role of ants in diverse communities of Argentina and their value as model organisms to explore the concept of ecosystem engineering. Furthermore, since these studies were conducted in various habitats, they can help to understand and predict how the ecosystem engineering activities can vary in different environmental contexts.

Granivory. The convergence hypothesis

The convergence hypothesis is based on the idea that independently assembled communities in similar but geographically distant habitats converge in composition and functioning under similar environmental pressures (Orians and Solbrig 1977). Granivory, seed consumption by animals, is especially common in arid areas and has been the main topic of studies aiming at finding patterns of convergent evolution among deserts. An increasing number of intercontinental comparisons of granivory rates and composition and abundance of granivore assemblages (mainly ants, rodents and birds) in deserts has challenged the convergence paradigm (Mares and Rosenzweig 1978; Abramsky 1983; Kerley and Whitford 1994). Studies performed by Argentine ecologists on seed removal rates by ants in arid regions of Argentina have made relevant contributions to this debate.

Seed bait experiments in the Patagonian steppe and in the Monte desert showed that seed removal by ants is lower than in similar deserts around the world (i.e., North America, Australia and South Africa). In the Patagonian steppe, insects (most likely ants) removed more seeds than rodents and birds. However, the removal rates by insects were much lower than those found in the Great Basin in North America, a climatically equivalent desert (Folgarait and Sala 2002). In the northwest Patagonian steppe, it was found that ten ant species interacted with native and exotic seeds, being *P. cabonarius* and *Dorymyrmex* spp. the ones with the highest proportion of interactions (Pirk and Lopez de Casenave 2017). In the southern Monte desert, removal rates of ants were also low and the only species seen removing seeds was *Ac. lobicornis* (Saba and Toyos 2003). However, in the central Monte desert, ants were the most important granivores in spring-summer, with higher removal rates under canopy than in exposed areas, similar to those found in Australian deserts (Lopez de Casenave et al. 1998). In fact, field observations revealed that around 40 ant species are capable of removing seeds (Lopez de Casenave et al., unpublished data). These studies challenged previous assertions that ants were depauperate in the Monte desert and also revealed that the assemblage is mainly constituted by omnivorous species, contrasting the highly specialized ant granivore assemblage in other deserts such as North American deserts (Marone et al. 2000). Altogether, research performed in Argentinian deserts shows that ant assemblages and granivory rates are far from being convergent intercontinentally, and that they even exhibit high variations within the same habitat (Southern *vs.* central Monte desert). These studies also highlight the importance of using different approaches to achieve a higher robustness in observed patterns (Marone et al. 2000).

Directed seed dispersal, far and safe

Seed dispersal is a key process for most plant populations. Seeds which land far from parent plants have multiple advantages over seeds which fall close to them: they escape from density-dependent mortality from pathogens or seed predators near parent plants and avoid sibling competition (Figure 2). These advantages were independently proposed by Janzen (1970) and Connell (1971) in what was later known as the Janzen-Connell hypothesis, and it has gathered evidence since then (Comita et al. 2014). In addition, seeds that arrive at safe and suitable sites could increase plant fitness even more, a process known as directed dispersal (Howe and Smallwood 1982) (Figure 2). For directed dispersal to occur, plants must have a predictable dispersal vector that takes seeds disproportionately to suitable sites. It has been suggested that directed dispersal is more common than previously believed even in the absence of plant adaptations to promote it, and especially frequent in arid ecosystems (Wenny 2001). Ant species are involved in directed dispersal when they transport undamaged seeds to their nests, which are often more nutrient-rich than non-nest soils (Farji-Brener and Werenkraut 2017). There are some studies in Argentina on seed dispersal by ants, so-called myrmecochory, showing evidence that directed seed dispersal could be an important process, at least in desert ecosystems.

In the Northern Monte desert, myrmecochorous seeds of *Jatropha excisa* bear an elaiosome rich in fatty acids (Aranda-Rickert and Fracchia 2010). These seeds attract

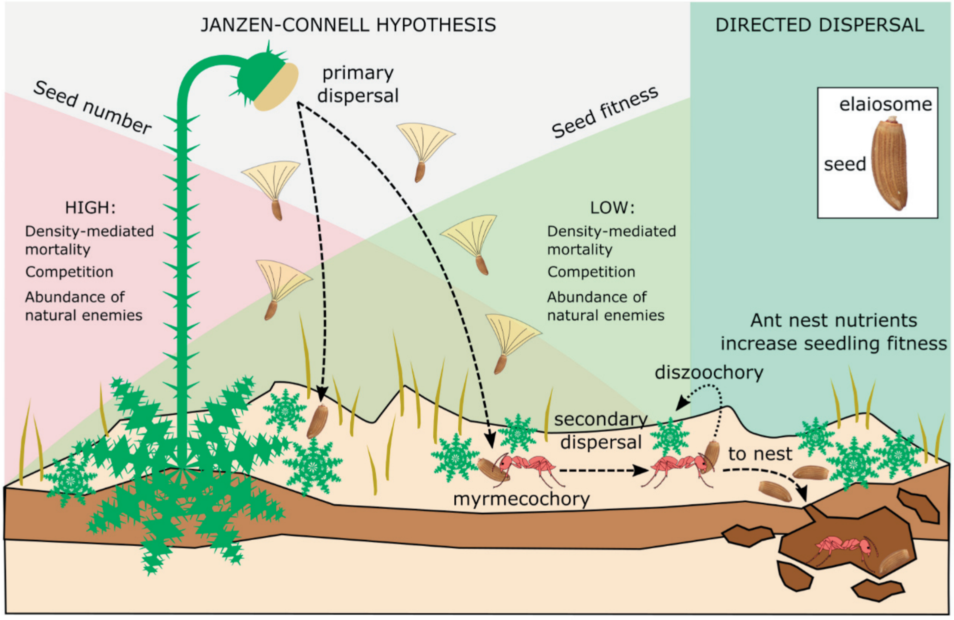

Figure 2. Scheme of the role of ants on seed dispersal and its consequences on plant performance under the Janzen-Connell hypothesis. Ants can move seeds away from parent plants decreasing mortality via the reduction of density-mediated competition and incrementing the probability of escape from natural enemies. Furthermore, ants can relocate seeds in the nutrient-rich nest soils near their ant nests, increasing seedling fitness (i.e., directed dispersal). Figure credit: A. Devegili.

Figura 2. Esquema del papel de las hormigas en la dispersión de las semillas y sus consecuencias en el desarrollo de las plantas bajo la hipótesis de Janzen-Connell. Las hormigas mueven semillas lejos de la planta madre reduciendo la mortalidad al disminuir la competencia denso-dependiente e incrementar la probabilidad de escapar de los enemigos naturales. Más aun, las hormigas pueden relocalizar las semillas en los suelos ricos en nutrientes cerca de sus hormigueros, aumentando la adecuación de las plántulas. Crédito de la figura: A. Devegili.

several ant species but are mainly removed by *Pogonomyrmex cunicularius*, which takes the seeds to the nest, consumes the elaiosome and leaves the seeds undamaged at an appropriate depth for emergence (Aranda-Rickert and Fracchia 2011). Workers of *P. cunicularius* can move these seeds up to 18 m (Aranda Rickert and Fracchia 2011), so they constitute effective seed dispersers (*sensu* Schupp et al. 2010) in terms of quantity (number of seeds removed) and quality (transport distance and seed fate) of dispersal. Another recent study in the Patagonian steppe shows that the generalist species of the genus *Dorymyrmex* also take seeds with nutritive structures, especially of exotic species, to their nests (Ortiz et al. 2021), which are enriched in some nutrients and may favor plant growth (Pirk et al. 2020). Ongoing studies (Ortiz et al., unpublished data) show that the germination potential of seeds discarded around the nests remain intact or is only slightly diminished. Finally, a study in the central Monte desert shows that ants can place seeds around their nests by mistake, a process also known as diszoochory (Milesi and Lopez de Casenave 2004). In particular, as a by-product of their predation on fruits and seeds, leafcutter ants (*Ac. lobicornis* and *Ac. striatus*) redistribute *Prosopis flexuosa* seeds by removing them from below the parental tree and dropping closed pod segments (with apparently viable seeds) around their nests. This implies a high benefit to this species since seedlings are negatively affected by shade (Vilela and Ravetta 2000) and soil (Vilela and Ravetta 2001) under adult trees and they could escape from predators that search preferentially under the parent tree. All these studies performed in arid areas of Argentina suggest that directed dispersal by ants might affect the abundance, distribution and establishment of plants.

Resources and consumers. Down to up or up to down?

Another interesting topic in community ecology concerns the study of the type of control which prevails in communities, either top-down (i.e., established by consumers/predators) or bottom-up (i.e., influenced by resource availability and/or abiotic factors which limit producers/herbivores). Arid ecosystems were traditionally believed to be controlled by abiotic factors, especially water availability which limit producers (Noy-Meir 1973). However, the importance of biotic interactions such as granivory or predation, has been highlighted in numerous studies (Brown et al. 1979; Meserve et al. 2003). More recently, it has been proposed that the prevalence of the type of control depends on precipitation levels, which show a great variability in desert ecosystems. Specifically, during high precipitation, and thus high productivity periods, the control by consumers on plants is more relevant than during drier periods (Meserve et al. 2003). Some studies on the ecology of harvester ants of the genus *Pogonomyrmex* in the Monte desert have explored the reciprocal effects (top-down and bottom-up) that ants and seeds have on each other throughout their activity season (from spring to early autumn).

Pogonomyrmex is a harvester ant genus which inhabits mostly arid areas in North, Central and South America. Until the early 2000s, the only information on this genus in South America came from the pioneer articles by N. Kusnezov (Kusnezov 1951, 1963), who stated that these species had smaller colonies and populations than their North American counterparts. In North American deserts, *Pogonomyrmex* spp. are important granivores and play an important ecological role (MacMahon et al. 2000; Johnson 2000, 2001). Studies in the central Monte desert show that both activity levels (Pol and Lopez de Casenave 2004) and colony size (Nobua-Behrmann et al. 2010, 2013) of three *Pogonomyrmex* species are indeed lower than the North American species. However, these species have specialized diets and concentrate their foraging on seeds of a few preferred species (Pirk and Lopez de Casenave 2006; Pirk and Lopez de Casenave 2011), which show lower abundance around their nests by the end of their foraging season (Pirk and Lopez de Casenave 2014). Thus, colonies of *Pogonomyrmex* spp. exert a top-down effect on seed abundance which could enhance the heterogeneity of soil seed banks, but the effect on adult plant populations might depend on the degree to which seed abundance limits their recruitment.

Reciprocally, several aspects of the ecology and behavior of *Pogonomyrmex* spp. are affected by variations in seed abundance, but in a species-specific fashion. The activity of *Pogonomyrmex inermis*, the species with a narrower diet and group foraging, is concentrated both in space and time (i.e., when and where the resources are abundant). *Pogonomyrmex mendozanus*, and to a lesser extent *P. rastratus*, have wider diets and more flexible foraging strategies, and they both keep on foraging when resources are scarce, including higher proportions of suboptimal items (Pirk et al. 2009; Pol et al. 2011, 2015). Moreover, a low abundance of seeds triggers a numerical decline in some *Pogonomyrmex* ant species in some regions of the Monte desert (Pol et al. 2017). Altogether, these behavioral responses to seed abundance may allow ants to maximize collective search and seed removal, and may buffer the effects of ants on preferred seeds when they are scarce. Thus, there is an alternation between the prevalence of bottom-up and top-down influences between harvester ants and their resources, something similar to the proposed fluctuation between control types (Meserve et al. 2003) but at a smaller spatial and temporal scale. However, in order to establish if these effects translate into a control of one trophic level on the other, studies on population abundances at longer temporal scales should be performed.

Indirect interactions involving ants. We are much more than two

Indirect interactions are critical for the structure and functionality of ecosystems because the effect induced by one species on a second one often requires the presence of a third species (Wootton 1994). These interactions can include physical or chemical changes in the environment, and affect community assembly, species coexistence, and ecological processes such as herbivory, pollination, and species invasion (Bronstein et al. 2007; McInire and Fajardo 2014). Different mechanisms have been proposed for indirect interactions: trophic cascades, indirect facilitation, exploitative competition, and trait-mediated effects (Ohgushi et al. 2012). These mechanisms have been reported in most geographic regions and ecosystems worldwide and illustrated with diverse animal and plant species (McIntire and Fajardo 2014). Several studies carried out in Argentina provide empirical evidence on the mechanisms of trophic cascades, indirect facilitation, exploitative competition, and trait-mediated indirect effects. Here, we synthesize the contributions of most of these studies.

In the Patagonian steppe of Argentina, aphid-tending ants modulate top-down trophic cascades by attacking aphid predators and enhancing aphid infestation, with negative consequences for plant fitness (Chalcoff et al. 2019; Devegili et al. 2021). They may also have positive indirect effects on plant fitness by preying on hemipteran or on other non-hemipteran herbivores (Devegili et al. 2021). Conversely, in the Monte desert in northwestern Argentina, hemipteran tending-ants do not affect the abundance of non-hemipteran herbivores and have no effects on plant fitness (Aranda-Rickert et al. 2017a). Nectarivorous ants can also provide anti-herbivory defense to host plants and trigger top-down trophic cascades. For example, in central Argentina, ants that visit the extrafloral nectaries of *Dyckia floribunda* or *Croton lachnostachyus* may increase plant fitness by defending plants against herbivores (Vesprini et al. 2003; Pereyra et al. 2015). However, nectarivorous ants may not provide anti-herbivory services to host plants in other systems (Freitas et al 2000; Alma et al. 2015; Simonetti and Devoto 2018). Finally, in the Monte desert ants seek sugary secretions from wasp galls on *Prosopis* sp. and may provide anti-herbivory services to the host plant (Aranda-Rickert et al 2017b), illustrating another insect association that may trigger top-down trophic cascades to host plants. Contrary to top-down trophic cascades, bottom-up trophic cascades are triggered at lower trophic levels (e.g., primary producers) and are propagated to higher trophic levels (e.g., predators) (Figure 3a). For example, in northwestern Patagonia, refuse dumps of the leaf-cutting ant *Ac. lobicornis* increase plant fitness (Farji-Brener and Ghermandi 2004, 2008), enhance aphid infestation on plants and increase aphid-tending ant activity (Lescano et al. 2012), which may further impact on aphid predators (Devegili et al. 2020). In sum, ants belonging to different functional groups (hemipteran-tending, nectarivores, and leaf-cutting ants) modulate and trigger top-down and bottom-up trophic cascades with an important impact on community composition and ecosystem function.

Indirect facilitation occurs when one species benefits a second one by suppressing its antagonists, such as predators or competitors (White et al. 2006). For example, in northwestern Patagonia, the aggressive aphid-tending ant *Dorymyrmex tener* deters ladybugs and syrphid larvae which in turn increases aphid fitness (Devegili et al. 2020). Indirect facilitation also occurs when one species relaxes competition between two other species (Sotomayor and Lortie 2015; Figure 3b). For example, in the Patagonian steppe, the leaf-

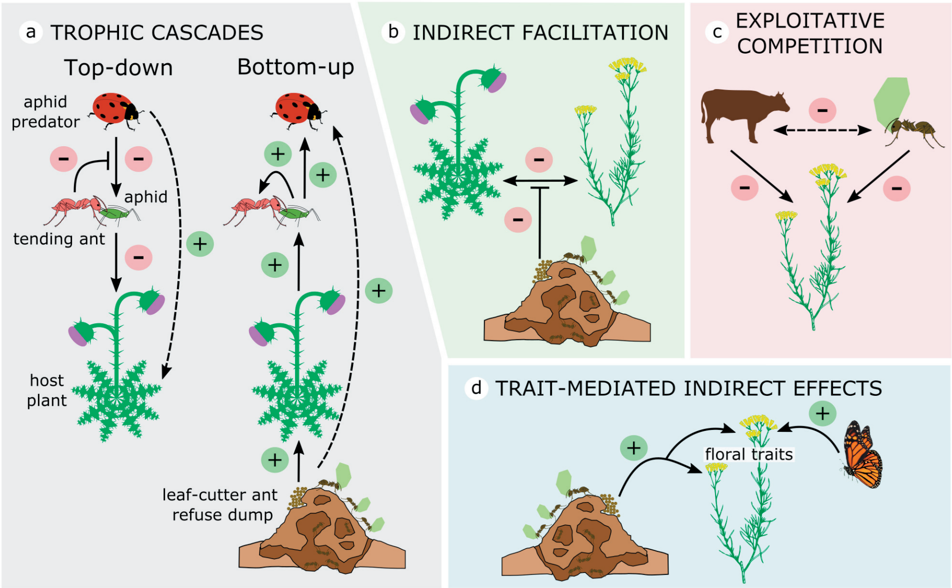

Figure 3. Indirect interaction mechanisms arising from ant studies in Argentina. a) Top-down trophic cascade mediated by aphid-tending ants (Devegili et al. 2021); bottom-up trophic cascades triggered by leaf-cutting ant refuse dumps (Lescano et al. 2012). b) Indirect facilitation provided by ant refuse dumps to plants via the relaxation of plant competition for soil nutrients (Farji-Brener and Lescano 2017). c) Exploitative competition between cattle and leaf-cutting ants through the consumption of plant resources (Tadey and Farji-Brener 2007). d) Trait mediated indirect effects involving ant refuse dumps, floral traits, and pollinators (Fernandez et al. 2019). Figure credit: A. Devegili.

Figura 3. Mecanismos de interacciones indirectas que surgen de algunos estudios de hormigas en la Argentina. a) Cascadas tróficas de arriba hacia abajo medidas por hormigas que cuidan áfidos (Devegili et al. 2021); cascadas tróficas de abajo hacia arriba determinadas por los basureros de las hormigas cortadoras de hojas (Lescano et al. 2012). b) Facilitación indirecta ocasionada por los basureros de las hormigas cortadoras de hojas a través del relajamiento de la competencia entre plantas por los nutrientes del suelo (Farji-Brener and Lescano 2017). c) Competencia por explotación entre el ganado y las hormigas cortadoras de hojas a través del consumo de plantas (Tadey and Farji-Brener 2007). d) Efectos indirectos mediados por atributos que involucran a los basureros de las hormigas cortadoras de hojas, rasgos florales y polinizadores (Fernández et al. 2019). Crédito de la figura: A. Devegili.

cutting ant *Ac. lobicornis* relaxes competition between plant species by providing nutrients through their refuse dumps (Farji-Brener and Lescano 2017). Similarly, in the Caldén forest in central Argentina, granivorous ants may relax competition between native and exotic plants by suppressing exotic seeds to a greater extent than native ones (Pearson et al. 2014). Exploitative competition occurs when two species interact through resource consumption where the resource is a third species (Sotomayor and Lortie 2015) (Figure 3c). For example, in northwestern Patagonia, livestock herbivory negatively affects leaf-cutting ant herbivory by decreasing vegetation richness and abundance (Tadey and Farji-Brener 2007). The composition of predatory or omnivorous ant communities may also be structured by exploitative competition when ant species target the same resources. For example, in their native range in Argentina, the invasive *Linepithema humile* and *Solenopsis richteri* co-dominate while consuming similar resources (LeBrun et al. 2007). Colony removal experiments evidence that *S. invicta* and *L. humile* experience an approximately equal competitive release upon removal of the other (LeBrun et al. 2007). Similarly, ants that seek nectar or sugary rewards may experience exploitative competition when the nectar or sugary resource is consumed by other ant species or insects. These multiple-species scenarios are highly frequent in nature. For example, sugary secretion of wasp galls on *Prosopis* sp. are consumed by ant species and wasps (Aranda-Rickert et al. 2017b) and four aphid-tending ant species consume sugary excretions of an aphid species on thistles (Lescano et al. 2014). Finally, ants that visit flowers for nectar rewards may indirectly compete with pollinators through the decrease in nectar availability. For example, ants visiting flowers of *Cucurbita* sp. decreased bee visitation rate (Mazzei et al. 2020). All these studies indicate that ants can play an important role in structuring terrestrial communities through indirect facilitation and exploitative competition.

Trait-mediated indirect interactions (hereafter, TMII) are becoming increasingly evident and important in terrestrial communities (Ohgushi et al. 2012). TMII arises when one species induces trait changes in a second species and these trait changes affect the fitness of a third species (Figure 3d). For example, in the Patagonian steppe, *Ac. lobicornis*' refuse dumps induce changes in floral traits and floral display of *Eschscholzia californica*, which may impact on plant pollination (Fernández et al. 2019). Thistles growing on *Ac. lobicornis* refuse dumps increase spine length and leaf toughness, which are anti-herbivory plant traits (Farji-Brener 2007). TMII may also be driven by changes in species behavior. In summary, the interaction of ants with plants or other animals may trigger TMII with consequences on pollination, herbivory and species behavior.

These studies emphasize the relevance of ants as model organisms to study the proposed mechanism for indirect interactions (Figure 3). Ants are often considered as keystone species and often participate in indirect interactions. Ants are easy to observe and manipulate, which makes it easy to evaluate both their direct and indirect effects on other species. We believe that the different regions of Argentina and the associated rich ant fauna offer a particularly adequate scenario to continue testing the predictions of trophic cascades, indirect facilitation, exploitative competition and trait-mediated indirect effect concepts to fully understand the relevance of indirect interactions in nature.

Ants and biological invasions. Both sides of the story

Ants are an excellent model for studying biological invasions. On the one hand, invasive ants rank among the most damaging exotic species and generate socio-economic costs in the invaded areas (Angulo et al. 2021). Within the 100 most invasive species on the planet, five are ants (Lowe et al. 2000), which impact on natural ecosystems by reducing native ant diversity, displacing other arthropods, negatively affecting vertebrate populations and disrupting ant-plant mutualisms (Lach and Hooper-Bui 2010). On the other hand, native ants can establish direct and/or indirect interactions with exotic species modulating their potential invasive success (Alba-Lynn and Henk 2010; Devegili et al. 2021). In Argentina, researchers have used ants as models to address invasion ecology questions related to 1) behavioral and demographic characteristics of invasive ant species in their native area, and 2) the role of native ants on the biotic resistance and mutualism facilitation hypotheses. Below, we discuss some contributions from works in Argentina to these two lines.

Successful invasive species are usually inconspicuous in their native ranges, thus studying invasive species in their native areas may help identify factors responsible for their greater prominence where they are invasive (Felden et al. 2018). Among the 19 ants listed in the IUCN invasive species database (iucngisd.org/gisd), five are native to Argentina and three are pointed out within the 100 world's worst invaders (*Linepithema humile*, *S. invicta* and *Wasmannia auropunctata*) (Lowe et al. 2000). *Linepithema humile* is a strong competitor in the invaded areas displacing native ants through rapid recruitment and numerical dominance (e.g., Holway 1999). Unicoloniality, resource acquisition efficiency and the escape from co-evolved competitors have been proposed to be key factors for *L. humile* success as an invader (Holway et al. 2002). In central and northern Argentina, *L. humile* coexists with other ant species such as the competitive dominants *S. invicta* and *Solenopsis richteri* (Calcaterra et al. 2008, 2016). The ecological dominance of *L. humile* is disrupted when *S. invicta* or *S. richteri* are present in the native area (LeBrun et al. 2007; Calcaterra et al. 2016), suggesting that the absence of these species could be a key factor for *L. humile*'s invasive success. Like *L. humile*, the red imported fire ant *S. invicta* co-dominates with other ant species in north-western Argentina, where it is native (Calcaterra et al. 2008). However, *S. invicta* becomes ecologically dominant in introduced ranges, possibly due to the escape from co-evolved competitors (LeBrun et al. 2007).

Alternatively, the escape from natural enemies such as nematodes, parasitoids and parasitic ants may also contribute to *S. invicta*'s invasive success (Briano et al. 2012). The little fire ant *W. auropunctata* is behaviorally submissive when coexisting with other ant species in its native range (north-western Argentina) (Calcaterra et al. 2008). Its invasive success could be explained by its reproductive characteristics, such as clonality, and physiological adaptations to disturbed habitats (Chifflet et al. 2018). Finally, examining invasive ant species in their native ranges is critical for identifying effective biocontrol agents (Folgarait et al.

2007; Briano et al. 2012). Resident ants are successful invaders and may interact with exotic species and help stop or reduce their spread in the new area.

Biotic interactions play an important role in the establishment and spread of exotic species (Traveset and Richardson 2014). The biotic resistance hypothesis states that exotic species fail to invade communities because strong biotic interactions with native species hinder their establishment and spread (Elton 1958). Support for the biotic resistance hypothesis has been found in native ant assemblages in Argentina. For example, in Patagonia, native ants can exclude the exotic wasp *Vespula germanica* from food baits; this asymmetric competition may explain the lower degree of invasion of this exotic wasp in Patagonia compared to other invaded regions (Masciocchi et al. 2010). In the Caldén forest in central Argentina, seed-harvesting ants consume mainly exotic seeds, acting as strong filters to exotic plant establishment and recruitment (Pearson et al. 2014). A different outcome occurs in the Argentine Patagonian steppe, where *Pogonomyrmex carbonarius*, a seed predator, avoids exotic seeds and instead prefers the native ones (Pirk and Lopez de Casenave 2017; Aput et al. 2019). The biotic resistance of native seed-harvesting ants may thus depend on species identities and habitat type. In the Patagonian steppe, a native aphid-tending ant, *Dorymyrmex tener*, decreases exotic thistle fitness by protecting aphids against their predators and increasing aphid infestation and damage (Chalcoff et al. 2019; Devegili et al. 2020, 2021). Therefore, through positive effects on aphid populations, native aphid-tending ants may trigger indirect biotic resistance toward exotic plants. Finally, while tending aphids, ants show strong aggression towards the invasive ladybug *Harmonia axyridis* in northwestern Patagonia (Devegili et al. 2020), suggesting that native aphid-tending ants contribute to decrease ladybug invasion. Much evidence supports that native ants in Argentina have a great potential for resisting exotic species invasion, however, native ants may still do the opposite by enhancing exotic species invasion.

The mutualist facilitation hypothesis asserts that the substitution of mutualists from the native range by mutualists from the introduced range is important for the establishment and spread of exotic species (Richardson et al. 2000). Mutualistic associations between native and introduced species can lead to the rapid growth of exotic populations and thus turn exotic species into invasive species in a short time (Richardson et al. 2000). Native ants may provide new mutualistic associations to exotic species. Myrmecochory is an excellent example of ant-plant mutualism that enhances species invasion. In northwestern Patagonia, the numerically dominant *D. tener* could promote the spread of invasive plants such as *Carduus thoermeri* and *Cytisus scoparius* (Ortiz et al. 2021). Likewise, leafcutter ants from the Chaco dry forests of central Argentina, may aid the spread of the invasive *Ligustrum lucidum* by transporting fleshy fruits into their nests and disposing the viable seeds on nutrient-enriched sites (Ferreras et al. 2008). Food-for-protection mutualisms between native ants and exotic species can be also important for species invasion. For example, in the Argentine Patagonian steppe, the exotic aphid *Brachycaudus cardui* is visited by aphid-tending ants that protect aphids in exchange of a sugary reward (Devegili et al. 2020). The most aggressive ant species increase exotic aphid fitness on thistles (Devegili et al. 2020), possibly triggering the colonization and infestation of new host plants in the area (Lescano and Farji-Brener 2011). Ants can also facilitate species invasion in biotic interactions that are not necessarily mutualistic. For example, in Patagonia the refuse dumps of leaf-cutting ants act as fertility islands that enhance mainly exotic plant recruitment and reproduction (Farji-Brener and Ghermandi 2004, 2008; Farji-Brener et al. 2010). Further, exotic thistles growing on refuse dumps improve anti-herbivore physical defenses (Farji-Brener 2007). In summary, through mutualistic associations and facilitative interactions, native ants may enhance the establishment, spread, survival, and reproduction of exotic species and, ultimately, increase species invasion (Figure 4).

We synthesize some of the main contributions in Argentina that, using ants as model organisms, try to understand why biological invasions can succeed or fail. There are still a number of knowledge gaps that ant studies in Argentina may contribute to fill. Roadsides can be excellent scenarios to test hypotheses regarding anthropogenic changes and species invasions (Farji-Brener and Ghermandi 2008). In Argentina, seed-harvesting ants can be excellent models for understanding exotic seed bank dynamics as well as exotic plant dispersal (e.g., Ortiz et al. 2021). Finally, there is a lack of studies assessing exotic species invasion at

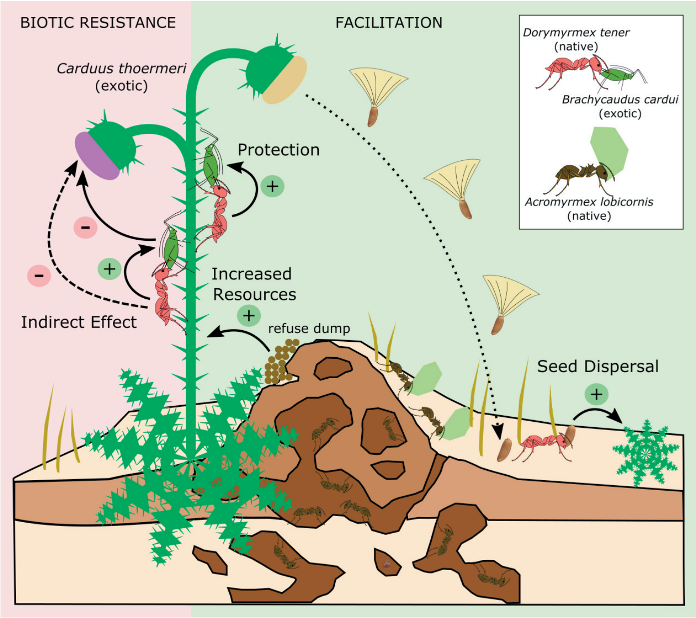

Figure 4. Native ants as drivers of biotic resistance and facilitation of invasive organisms in the Patagonian steppe (Argentina). Biotic resistance: protection provided by *Dorymyrmex tener* to aphids indirectly reduces *Carduus thoermeri* reproduction by increasing aphid infestation and damage. Facilitation: protection provided by *D. tener* to *Brachycaudus cardui* increases aphid population growth rate; nutrient-enriched refuse dump of *Acromyrmex lobicornis* increases *C. thoermeri* establishment, growth and reproduction; secondary seed dispersal by *D. tener* may increase *C. thoermeri* spread and establishment. Figure credit: A. Devegili.

Figura 4. Hormigas nativas como protagonistas de resistencia biótica y facilitación de organismos invasores en la estepa patagónica. Resistencia biótica: la protección de parte de la hormiga *Dorymyrmex tener* hacia los áfidos reduce indirectamente la reproducción del cardo exótico *Carduus thoermeri* al facilitar el aumento en la infestación y daño foliar por parte de los áfidos. Facilitación: la protección por parte de la hormiga nativa *D. tener* al áfido exótico *Brachycaudus cardui* fomenta la tasa de crecimiento poblacional de los áfidos; los basureros ricos en nutrientes de la hormiga cortadora de hojas *Acromyrmex lobicornis* incrementa el establecimiento, crecimiento y reproducción del cardo exótico *C. thoermeri*; la dispersión secundaria de semillas por la hormiga *D. tener* puede aumentar la propagación y establecimiento del cardo exótico *C. thoermeri*. Crédito de la figura: A. Devegili.

the population level. This is crucial, as species invasion is a population-based phenomenon (Sakai et al. 2001; Simberloff 2003). Ants have a great potential to answer relevant questions related to species invasion, both from a theoretical and practical standpoint, and ecosystems in Argentina offer a valuable scenario for this research.

Integrated pest management. Ants under control

The concept of integrated pest management (IPM) arose as an alternative to the predominant paradigm of insecticide use to control pests, as evidence accumulated showing that insect pests rapidly adapt to pesticides and that its excessive use poses serious threats both to the ecosystem and human health (Devine and Furlong 2007). IPM is an ecosystem-based strategy that focuses on long-term prevention of pests through a combination of techniques such as biological control, habitat manipulation, modification of cultural practices, and use of resistant varieties. Thus, understanding the biology of the target pest is key for IPM to be successful (Barzman et al. 2015).

Ants, especially leaf-cutting ants, are recognized as important pest species in the Neotropics (Montoya-Lerma et al. 2012), and as with other insect pests, IPM should reduce the need for pesticides. Several studies in Argentina have contributed to IPM for pest ant control, mainly, on three general points: 1) use of natural enemies, 2) use of repellents and attractants with promising results in push-pull systems, and 3) knowledge about ant feeding and foraging behavior. Most of these studies were conducted with leaf-cutting ants, in particular, species such as *Ac. lobicornis*, *Ac. ambiguus*, *Ac. lundii*, and *A. vollenweideri*, that might turn as native pests in important economic plantations in Argentina, including forestations, vineyards, crops and pastures (Pérez et al. 2011; Elizalde et al. 2016; Jimenez et al. 2021).

Some natural enemies that regulate populations of leaf-cutting ant pest species might be important biological control agents in agroecosystems, including vertebrates such as armadillos and anteaters (Superina et al. 2009; Gallo et al. 2017; Elizalde and Superina 2019), parasitoids (Folgarait and Gilbert 1999; Folgarait et al. 2002; Elizalde and Folgarait 2011, 2012; Briano et al. 2012; Folgarait 2013; Elizalde et al. 2018b), pathogens like entomopathogenic fungi, microsporidia, nematodes (Briano et al. 2012; Goffré and Folgarait 2018; Folgarait et al. 2020), and diseases (Valles et al. 2018). Some of these natural enemies are highly specialized in consuming one or a few ant species (Elizalde et al. 2018b; Goffré and Folgarait 2018), while others consume diverse animals and plants (Superina et al. 2009; Gallo et al. 2017), thus allowing managers to select the species that are better suited to their needs for pest-ant control. The effects of ant natural enemies might be direct, causing increased mortality (Elizalde and Folgarait 2011; Elizalde and Superina 2019), or indirect, affecting their foraging behavior or disrupting their nest (Guillade and Folgarait 2015; Elizalde and Superina 2019). Some ant natural enemies interact by complementing each other (Elizalde and Superina 2019), segregating in their use of the pest thus reducing competition among them (Elizalde et al. 2018a) or aiding in the spread of a disease (Oi et al. 2009). This interaction among enemies may increase their potential as biological control agents of ant pest populations and allow for the use of several natural enemies in an IPM program (Walter 2005). However, there are some examples of negative effects among pathogens (Folgarait et al. 2011), highlighting the need to carry out detailed studies of the natural history, physiology, and ecological interactions before considering them for IPM (Elizalde and Folgarait 2011, 2012).

Another tool for management of pest ants is the use of repellent and attractant stimuli. Different plant-based compounds, plant species, and even waste generated by the ants themselves have been demonstrated to modulate ant foraging behavior (Farji-Brener and Sasal 2003; Ballari and Farji-Brener 2006; Medina et al. 2012; Perri et al. 2017; Alma et al. 2019; Buteler et al. 2021). Among those with repellent action, tea tree oil (a complex mixture of terpene hydrocarbons and tertiary alcohols distilled mainly from plantation stands of the Australian native plant *Melaleuca alternifolia*) and farnesol (present in many essential oils, such as *Pluchea dioscoridis* and *Pittosporum undulatum*) repel leaf-cutting ants at short distance in both laboratory and field assays (Perri et al. 2017; Buteler et al. 2021). Their low toxicity and persistence make them environmentally safer than other pesticides, but their high volatility might reduce their repellent power. The 'jarilla' (*Larrea cuneifolia*) phenolic resin is another plant-based compound that can repel or attract leaf-cutting ants depending on their previous experience (Medina et al. 2012). Leaf-cutting ants inhabiting the ecotone between the biogeographical provinces of Chaco (characterized by thick profuse forests with large-sized species) and Monte (characterized by xerophilous vegetation and by resinous and prickly shrubs), where *Larrea* spp. are present prefer the phenolic resin, while ants from areas where *Larrea* spp. are absent show an extreme avoidance to this resin (Medina et al. 2012). In addition, the refuse that leaf-cutting ants produce from exhausted cultivars have been shown to protect plants from damage in the field (Farji-Brener and Sasal 2003; Ballari and Farji-Brener 2006). Even though its repellent effect is short-lived, further research identifying the compounds that cause the effect could lead to a novel ant repellent. In addition, heptyl butyrate, a volatile compound found in fresh apples and plums, and orange pulp can be used as attractant stimuli (Perri et al. 2017; Alma et al. 2019). Attractants and repellents could be combined in an IPM strategy termed push-pull, which involves the manipulation of ant foraging behavior by integrating stimuli that turns crops unsuitable or unattractive to the insect pest (push) and simultaneously attracts them towards another resource (pull) from where the pest is subsequently removed (Cook et al. 2007). Although the use of repellents and attractants separately can have low effectiveness, they have been proven particularly useful when used together in a push-pull system avoiding leaf-cutting ants to attack forestations in the Delta area of Río de la Plata (Perri et al. 2017, 2021).

The study of ant behavior that contributes to the implementation of management tools within an IPM framework involves understanding how pest-ants feed and forage. One such technique to control urban ants, which are worldwide household pests, involve the use of food baits containing slow-acting insecticides (Sola et al. 2013). Behavioral studies conducted by Argentine researchers using the Argentine and carpenter ants as models demonstrate the importance of considering the foraging and feeding response in low-motivation scenarios (Sola et al. 2013) or understanding how information is processed by ants to enhance potential bait deterrence (Josens et al. 2016). Furthermore, these studies highlight the importance of species-specific preferences to develop the proper tool to control the pest ant we are dealing with (Sola et al. 2013). This knowledge is key for controlling urban ants (Josens et al. 2017), especially in sensitive places such as hospitals, where there are often restrictions on the methods and toxicants that can be applied (Josens et al. 2014).

Understanding the complex biology and ecological interactions with natural enemies of ants that have become pests is key in developing IPM strategies. Research performed in Argentina has contributed to important studies on how to manage pest ant populations, mainly of leaf-cutting ants, reducing reliance on traditional insecticides. These studies point towards the potential of IPM to manage ant pests, although they still need to be implemented by producers.

CONCLUDING REMARKS: LITTLE THINGS CAN SUSTAIN BIG CONCEPTS

Advances in ecology are largely due to the iterative process of induction and deduction, prediction, and testing. A recognition of the role of this interplay significantly enhances scientific progress in the understanding of how species interact among themselves and with their environment (Marquet et al. 2014). Here we summarized ant studies performed in Argentina that helped to illustrate and test key ecological concepts such as ecological engineering, directed dispersal, convergence hypothesis, indirect interactions, biological invasions, and integrated pest management. These studies were performed through observations, lab or greenhouse experiments, and field manipulations in different habitats, offering a wide range of evidence to support or question these concepts. Taken together, all these works reinforce the key role of ants as model organisms to test ecological hypotheses, and highlight the importance of being guided by conceptual frameworks to better understand the complexity of ecological systems and predict their behavior in the next future.

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