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Ants in restoration ecology: Why, what's and the way forward

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Abstract

Global changes call for more nature-based solutions, especially in nature conservation involving ecological restoration. Current methods essentially based on civil engineering are both expensive and costly in non-renewable energy consumption and pollution terms. The non-sustainability of these techniques is leading to the direct use of certain species to restore degraded ecosystems. Ants, because of their central role in ecosystem functioning and their occurrence on almost all terrestrial ecosystems, are promising candidates for environmental monitoring and such ecological restoration projects. We provide here a narrative review of the ecological functions performed by ants, and we take stock of how ants are currently considered in passive and active restoration. We then propose a trait-based approach to facilitate their use by practitioners in future restoration projects. We list and discuss both life-history traits relevant for environmental monitoring and functional traits known to affect abiotic (physical and chemical soil properties) and biotic (plant and fauna communities) components.

KEYWORDS

active restoration, ecological engineering, ecological functions, functional traits, life-history traits, monitoring

1 | INTRODUCTION

Ecological restoration plays a vital role in conserving biodiversity worldwide (Aronson & Alexander, 2013). The aim is to increase biodiversity and ecosystem services by recovering the structure and function of human-degraded ecosystems (Benayas et al., 2009). Removing the disturbance that degraded the ecosystem is the first step in a restoration project. Active restoration projects manage the ecosystem through a range of human interventions to accelerate/influence the successional trajectory of recovery (see glossary in Table 1 for definition of terms). The projects involve three phases: the pre-operational phase of defining the restoration objectives and the ecological functions to restore; the operational phase, which consists in setting up the project; and the post-operational phase, when the success of the restoration is monitored (Choi, 2004; Clewell & Aronson, 2013). The operational phase often involves the use of civil engineering principles and techniques based on major technical interventions such as public works machinery

(e.g., extraction, loading, and/or compacting machines). These techniques entail extensive consumption of non-renewable resources (e.g., diesel and petrol) and significant emissions of pollutants (e.g., CO₂, NO_x). To avoid the environmental consequences of such civil engineering, one component of or approach to restoration ecology, called “ecological engineering,” consists in directly using organisms to restore degraded ecosystems (Aronson et al., 2016; Mitsch & Jørgensen, 2003). This nature-based solution inspired by, supported by, or copied from nature uses internal mechanisms to change the ecosystem in the desired successional direction, thereby ensuring the provision of ecosystem services (Nesshöver et al., 2017). Since ecological engineering generally promotes the use of species that directly or indirectly modify the physics and chemistry of their habitat, thereby influencing other organisms (Jones et al., 1997), a key challenge is identifying the appropriate species to introduce and/or promote.

To ensure delivery of the ecological functions targeted, the identification of the functions provided by native species is essential

TABLE 1 Glossary of terms.

Terms	Definition
Active restoration	Where damage is intermediate or high, all causes of degradation should be removed or reversed and additional active interventions should be carried out to correct abiotic damage and trigger biotic recovery (McDonald et al., 2016)
Disturbance	“A natural or anthropogenic event that changes the structure, content, and/or function of an ecosystem, usually in a substantial manner” (Clewell & Aronson, 2013)
Ecological engineering	“The manipulation and use of living organisms or other materials of biological origin to solve problems that affect people” (Clewell & Aronson, 2013)
Ecological restoration	“The process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed” (Gann et al., 2019)
Ecosystem services	“The aspects of ecosystems utilized (actively or passively) to produce human well-being” (Fisher et al., 2009). The Millennium Ecosystem Assessment divided ecosystem services into four categories: supporting, regulation, provisioning, and cultural services (Millennium Ecosystem Assessment, 2005)
Passive restoration	“Where damage is relatively low and topsoil retained, or where sufficient time frames and nearby populations exist to allow recolonization, plants and animals may be able to recover after cessation of certain types of degradation” (Gann et al., 2019)

(Sotka & Byers, 2019). One way to do this is to study their functional traits. Functional traits that are defined as any measurable morphological, physiological, behavioral, or phenological features of an individual, from cell to whole-organism level (Pey et al., 2014; Violle et al., 2007), make it easier to link a species to the functions it performs in its habitat (Cadotte et al., 2011; Gagic et al., 2015). Traits can reflect environmental tolerance, that is, life-history traits, and/or affect ecosystem processes, that is, functional traits (Hedde et al., 2022). Thus, measuring and understanding the diversity of species traits could greatly improve restoration decision making (Cadotte et al., 2011). However, despite the recent effort to adopt such a trait-based approach, there is still a gap between their study and their actual use in restoration projects (Carlucci et al., 2020; Merchant et al., 2022), particularly with fauna.

Globally, the use of animals, particularly invertebrates, to monitor the recovery of an ecosystem or to actively restore it, has been underexplored compared with plants (Auclerc et al., 2022; Snyder & Hendrix, 2008). Among possible explanations for this neglect of invertebrates, the first may be resource limitation to the development of some invertebrates after a disturbance (Jouquet et al., 2014). Second, restoration of insect populations is sometimes based on the hypothesis that insects will follow the restoration of plant communities. However, this overlooks the importance of direct or indirect interactions

between invertebrates, with some species being key to the establishment and maintenance of others (De Almeida, Mesléard, et al., 2020). Third, collecting enough individuals may be challenging (e.g., breeding them and finding enough source populations), and such difficulties may hamper their reintroduction in active restorations (Jouquet et al., 2014). To date, earthworms, because of the key role they play in soil, are the soil organisms most frequently used in ecological engineering (Jouquet et al., 2014) and have successfully restored soils (e.g., Butt, 2008), as have termites occasionally (Jouquet et al., 2014).

By contrast, ants remain underexploited in ecological engineering. Yet, their social life and related traits, generally forming long-term sedentary colonies, as well as their recognized ecological value make them a good choice for ecological engineering projects. Ants occur throughout all continents except Antarctica and are among the most diverse and abundant organisms on Earth (Hölldobler & Wilson, 1990). In all the different terrestrial ecosystems they occupy, ants play key ecological roles as soil engineers, predators, and/or regulators of plant growth and reproduction (De Almeida, Mesléard, et al., 2020; del Toro et al., 2012). These effects suggest that ants have enormous untapped potential for applications in active restoration projects.

The aim of this paper is to highlight ants' potential for restoration ecology and to provide keys for their future use. We first provide a narrative review of the ecological functions performed by ants, and we take stock of how ants are currently considered in passive and active restoration. We made a quick review of the ISI Web of Science database by searching for “restoration ants,” “ant traits,” because our objective was not to conduct a comprehensive review. We then propose a trait-based approach to facilitate their future use. We list and discuss both life-history traits relevant for environmental monitoring and functional traits known to affect the soil (physics and chemistry), the plant community, and the soil fauna relevant in ecological engineering.

2 | ANT ECOLOGICAL FUNCTIONS

Ants play a central role in ecosystem functioning (del Toro et al., 2012; Elizalde et al., 2020). Their engineering activity affects not only each ecosystem component separately but also their relationships (De Almeida, Mesléard, et al., 2020). By their structural engineering activities, particularly during nest construction and maintenance, ants can move large amounts of underground soil to superficial layers (Dostál et al., 2005). Earthworms are considered to be more important bioturbation agents than ants in several ecosystems, as shown by Taylor et al. (2019) in cold-temperate ecosystems. In their study, Wilkinson et al. (2009) states that over half of the studies recording bioturbation rates of 10–50 t ha⁻¹ year⁻¹ and exceeding 100 t ha⁻¹ year⁻¹ in some tropical locations. However, the bioturbation role of ants is not negligible. In a recent review, Viles et al., 2021 showed that the median amount of soil moved by ants in bioturbation/mounding is about 1.5 t ha⁻¹ year⁻¹, with a minimum of 0.05 t ha⁻¹ year⁻¹ for *Lasius niger* (Persson et al., 2007) and a

maximum of $68.38 \text{ t ha}^{-1} \text{ year}^{-1}$ for *Aphaenogaster longiceps* (Richards, 2009). Ants can also concentrate organic matter and produce large quantities of organic waste that are deposited inside the nest or on the soil surface (Frouz & Jilková, 2008). Through these activities, ants can alter soil physico-chemical properties and water infiltration, indirectly affecting the surrounding vegetation (Dostál et al., 2005).

The magnitude and direction (positive, negative, or neutral) of their effects on soil physico-chemical properties vary between ant species (Frouz & Jilková, 2008) and environments (Farji-Brener & Werenkraut, 2017). Most studies show an increase in organic matter within ant nests compared with the surrounding soil (Azcárate & Peco, 2007; Cammeraat et al., 2002). Similarly, ant activity generally increases soil nitrogen, phosphorus, and potassium contents. However, no effect (Leal et al., 2007) or even a decrease in nitrogen or potassium content has also been recorded (Dostál et al., 2005). Accordingly, ants have contrasting effects on plants, positively or negatively modifying plant growth (De Almeida, Mesléard, et al., 2020; Saha et al., 2012) or diversity (Saha et al., 2012; Schütz et al., 2008) depending on their nutrient requirements.

In addition to these indirect effects on vegetation, ants can profoundly affect plant population and community structure through seed dispersal. Myrmecochory involves more than ten thousand plant species across many terrestrial ecosystems (Lengyel et al., 2009). Christian (2001) showed that the preservation of seed dispersal mutualistic interactions is essential to maintaining natural plant communities. It may shape the initial spatial distribution of plants within populations and define the context for future ecological, demographic, and genetic interactions among emerging seedlings (Kalisz et al., 1999). Granivorous ants too can disperse seeds, but the positive effects on vegetation are balanced by the predation costs to the plant population (Arnan et al., 2012). Although several studies found more seeds (Bulot et al., 2016; Schütz et al., 2008) and seed germination in ant nests than in surrounding areas, the relative effect of seed dispersal via ants depends on ant community composition (Prior et al., 2015), as well as on seed availability (Arnan et al., 2012). Ants may also act as biotic defences, protecting plants against herbivores and parasites, thus modifying plant population and community dynamics. In return, plants offer benefits such as shelter and food rewards (Rosumek et al., 2009).

Ants also impact other invertebrates. They can negatively affect populations of some species through predation and competition, while other species feed on ants themselves. For example, ants and spiders are potential mutual predators (Gajski et al., 2020; Sanders & Platner, 2007). Ants can also have a mutualistic relationship with trophobionts (e.g., aphids, mealybugs, cicadellids). In exchange for protecting trophobionts, ants collect their honeydew, sometimes as their main food source. This relationship can increase the density and diversity of trophobionts, to the detriment of plants (Elizalde et al., 2020; Styrsky & Eubanks, 2007). Ants can also indirectly affect invertebrates by modifying the abiotic component and plant communities. This impact is mostly positive for macro-, meso-, and microfauna (Boulton & Amberman, 2006; Çakır, 2019; Sanders & van

Veen, 2011), as well as bacterial and fungal communities. The higher abundance of bacteria and fungi may indirectly increase bacterial and fungal predators such as nematodes and collembolans (Boulton et al., 2003; Boulton & Amberman, 2006). An increase in plant heterogeneity and biomass in ant patches can thus be responsible for an increased abundance of detritivores such as Collembola and plant-feeding Coleoptera, and indirectly for that of their predators (e.g., Araneae and predator Coleoptera) (De Almeida, Mesléard, et al., 2020).

While we have stressed the positive effects of ants on the ecosystem, some ants can also cause disservices. For example, leaf-cutting ants can improve soil conditions (Farji-Brener & Silva, 1995) and assist in seed dispersal (Farji-Brener & Ghermandi, 2004) but can also drastically cut new growing vegetation (Corrêa et al., 2010). Similarly, wood ants (*Formica rufa* group) can positively affect soil porosity (Frouz & Jilková, 2008) and moisture content (Frouz, 2000), which may increase microbial activity (Jilkova et al., 2013; Stadler et al., 2006). They are also well known as herbivore predators, which has led to breeding them for biological control of pests such as the pine processionary moth (Pavan, 1981). However, they can also have negative effects on microarthropod density in semi-arid pine forest (Çakır, 2019). Furthermore, positive effects of ants may be not constant along degradation and restoration gradient (e.g., Holec & Frouz, 2006; Tuma et al., 2022). The costs and benefits of using a species to restore a site must always be precisely measured and depend strictly on the local context.

3 | ANTS IN RESTORATION ECOLOGY

3.1 | Environmental monitoring

Environmental monitoring is crucial in restoration ecology. A recent literature survey by Casimiro et al. (2019) found 470 articles featuring ants used to monitor environmental changes. They found that most studies on ant community response to restoration processes in degraded ecosystems were conducted in Brazil (26%) (e.g., Coelho et al., 2009), Europe (24%, including Belgium (e.g., Dekoninck et al., 2008), Germany (e.g., Dauber & Wolters, 2005), Hungary (e.g., Gallé et al., 2016), Czech Republic (e.g., Holec & Frouz, 2005), Italy (e.g., Ottonetti et al., 2006), and Spain (e.g., Arnan et al., 2013), and Australia (19%) (e.g., Majer, 1984). The use of ants as bioindicators dates from Australian mid-1970s assessments of the restoration of abandoned quarries (Andersen & Majer, 2004; Majer, 1983, 1984). Since then, it has spread to other countries, mainly Brazil and Europe (Casimiro et al., 2019). While abundance and species richness are the most commonly used ecological metrics for assessing success of ant recovery (Borges et al., 2021; Underwood & Fisher, 2006), ant functional groups seem to recover more rapidly than species richness (Casimiro et al., 2019).

A global model of ant community dynamics based on nine functional groups was developed for Australian communities according to environmental stressors (factors limiting ant productivity) and

disturbance (factors eliminating ant biomass) (Andersen, 1995; Andersen & Majer, 2004; Hoffmann & Andersen, 2003). Ant community functional composition provides information on the state of ecosystem degradation. Disturbances also have strong indirect effects on competitive hierarchies through changes in dominant species abundance.

However, the Australian functional groups developed by Andersen (1995) combine life-history traits, taxonomy, and competitive abilities, and this inclusion of taxonomy limits their application to other ant communities (Hedde et al., 2022). An approach based on quantitative traits that avoid taxonomy would allow more accurate evaluation of ant community responses to environmental change, regardless of biogeographic region.

3.2 | Ants in ecological engineering projects

Because of their multi-component impacts, ants have strong potential in ecological engineering projects (De Almeida, Mesléard, et al., 2020; Lu et al., 2019; Nicolai, 2019). However, to date, only one study has actively used ants to restore a degraded ecosystem. In 2011, Bulot et al. (2014) reintroduced mated queens of the granivorous ant *Messor barbarus* (Linnaeus, 1767) in the Plain of la Crau (South of France) to accelerate the restoration of soil physico-chemical properties and vegetation (Box 1).

Through their bioturbation and organic matter concentration activities, ants can help restore degraded soils early in the succession. As seed dispersers they may be key to the recolonization and dispersion of plants. In passive restoration, ants have been shown to accelerate restoration (Nicolai, 2019; Nicolai et al., 2008). Nicolai (2019) demonstrated that 2 years after a wildfire, *Pogonomyrmex rugosus* (Emery, 1895) ant nest edges improved resources leading to faster recovery of grass inflorescences than on burned controls. As areas of high grass reproduction during recovery, ant patches may act as a source of seed dispersal into the surrounding habitat (Nicolai, 2019). In a tropical forest, ant nest soil enrichment in microbial carbon was also found to increase with restoration age (up to 53 years) (Lu et al., 2019). Such high soil enrichment in organic matter, available nitrogen, ammonium, and nitrate at an early stage might promote spontaneous forest restorations. At a later restoration stage, ants improve plant development by strongly stimulating microbial growth and opening up space for their establishment (Lu et al., 2019).

Although ant impacts on soil physico-chemical properties are mostly small-scale and limited to the nest, they can play a significant role in maintaining spatial heterogeneity and plant species richness at site scale (Platt, 1975). For example, they impact resource heterogeneity within a landscape by creating diversity in nutrient concentrations (Dostál, 2007) and thus potentially enhancing the restoration of degraded grasslands (Lane & BassiriRad, 2005). Their nests may foster recolonization by other organisms, mainly plants but also fauna (Kachamakova et al., 2019; Nicolai, 2019), throughout the degraded ecosystem. Moreover, their impacts are detected not only during nest occupation but also up to more than 20 years after colony

BOX 1 Study case of using ants in active restoration.

In 2009, an oil leak destroyed 5.5 ha of a Mediterranean grassland (Bulot et al., 2014). After soil restoration (see Bulot et al., 2017 for details), a fine crust formed at the soil surface, limiting plant establishment. To restore soil physico-chemical properties and the vegetation component, a trait-based approach was applied to identify a candidate ant species combining all the traits required to restore the functions of interest. We determined that the selected species should exhibit a range of traits related to soil decompaction and increased soil nutrients, as well as seed dispersal, and be abundant in the original ecosystem. Of the most abundant native species, those that disperse seeds and nest in the soil were identified from the regional literature (Cerdan, 1989), and two species were selected: *M. barbarus* and *Pheidole pallidula* (Nylander, 1849). Granivorous ants are known to increase soil nutrient content, the workers' large mandible gap allows the species to displace large soil particles and seeds, their permanent nests enhance the effect on soil, and their dispersion through nuptial flight accelerates colonization. Although both species disperse through nuptial flight and have high densities of workers, *M. barbarus* was finally chosen because of its larger mandible gap and larger body size (Bulot et al., 2014; De Almeida, Blight, et al., 2020). In this case study, the degraded area was surrounded by the original grassland. Given that *M. barbarus* makes permanent and temporary trails up to 40 m long (Detrain et al., 1996), the founding queens were transplanted to a maximum of 25 m from the Mediterranean grassland to ensure that the ants were able to forage in the original ecosystem (see Bulot et al., 2014). Mated queens were reintroduced at 10-m intervals to reduce the risk of competition once colonies were established. It took about 1 h for four people to collect 600 founding queens of *M. barbarus* and 2 days to reintroduce them on the Crau plain (Bulot et al., 2014).

Seven years after introduction of mated queens, *M. barbarus* improved soil fertility, drove the soil seed bank towards the reference ecosystem, and significantly increased plant biomass, species richness, and micro-local heterogeneity. By directly and indirectly facilitating plant establishment, *M. barbarus* accelerated grassland restoration compared to controls without *M. barbarus* nests, trails, or refuse piles (De Almeida, Blight, et al., 2020).

disappearance (Kristiansen & Amelung, 2001; Lane & BassiriRad, 2005), thus increasing their spatial and temporal environmental impact.

4 | THE WAY FORWARD: A TRAIT-BASED APPROACH FOR FUTURE PROJECTS

Traits can reflect environmental tolerance, that is, life-history traits, and/or affect ecosystem processes, that is, functional traits (Hedde et al., 2022) that make easier to link a species to the functions it performs in its habitat (Cadotte et al., 2011; Gagic et al., 2015). In ecological restoration, a trait-based approach diverges from classical restoration methods that focus on restoring species composition of pre-disturbance communities to focus on restoring ecosystem functioning. The application of such methods is receiving growing attention worldwide (Carlucci et al., 2020). However, one of the reasons for their current limited use is the lack of knowledge about the link between functional traits and ecological functions performed within the ecosystem (Carlucci et al., 2020).

Because of their social life form, ant traits should be quantified at both the level of the individual and that of the colony (Elizalde et al., 2020), and selected according to the restoration needs. The type of restoration and its objectives will depend on the state of the degraded ecosystem (Table 1; Figure 1). When disturbance of the target ecosystem is slight enough to be dealt with by removing the disturbances (i.e., passive restoration), community and population changes need to be monitored to ensure that all target functions have been restored (Holl & Aide, 2011). When only the biotic component is deeply degraded, biotic interactions (e.g., seed dispersal, predation,

competition, facilitation, symbiosis) will require restoration. If disturbance has degraded both abiotic and biotic components, the priority is to restore soil physical and chemical properties (Heneghan et al., 2008) by identifying the ecological functions of interest (e.g., soil structure, water infiltration, soil fertility) and then the biotic component. After the abiotic and/or biotic components are restored, community and population changes need to be monitored, in particular ant traits characterizing the stages of the restoration (Figure 1).

4.1 | Ant traits relevant in environmental monitoring

Certain characteristics define a species as a “bioindicator species,” the most notable being ease of measurement, sensitivity to environmental disturbances, and predictable responses to environmental disturbances (Niemi & McDonald, 2004). Ants generally fulfil these three criteria.

Some ant traits can provide information on resource availability. Monitoring ant body size, by measuring the traits of individuals from local populations, as well as diet might provide information on the quantity and quality of resources available in a degraded or restored habitat. Although traits linked to feeding behaviors can reveal a species' response to environmental changes, traits directly related to a species' tolerance of environmental changes might be more

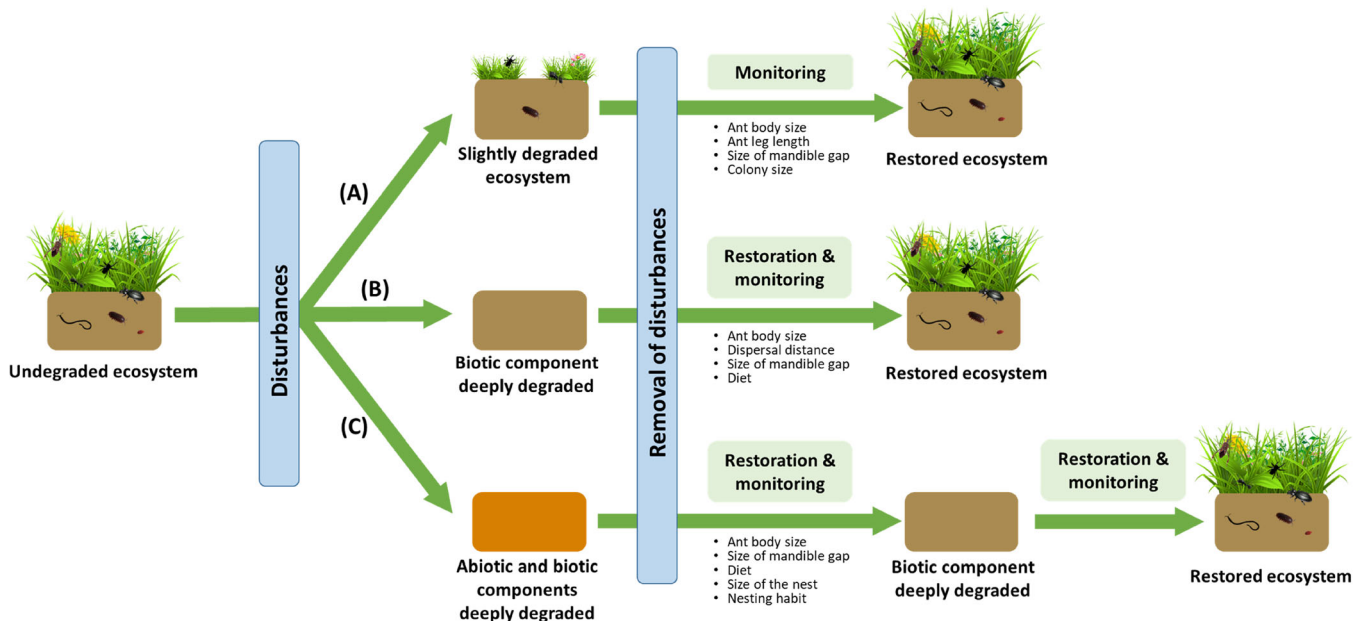


FIGURE 1 Main ant individual and colony traits relevant in restoration projects. (a) A slightly degraded ecosystem requires first removal of disturbances, then monitoring of community and population changes to ensure that restoration of all target functions is complete or ongoing. (b) A more intensely degraded ecosystem requires only the biotic component functions to be restored after disturbance removal. (c) A deeply degraded ecosystem (abiotic and biotic components) requires, after disturbance removal, first restoration of soil functions, followed by restoration of biotic component functions. In cases b and c, ant introduction will be effective only (i) when conditions for their establishment and persistence are met or (ii) if they are able to forage at an undisturbed site nearby. For example, granivorous ants should be introduced after the site has been colonized by vegetation or at a distance from an undisturbed site that does not exceed their foraging capacity. After the restoration of each component, community, and population changes also require monitoring. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

appropriate for assessing such responses (Arnan et al., 2013; Wiescher et al., 2012). For example, body size gives information on the soil compaction with a higher proportion of small ants in compacted soil (Schmidt et al., 2017). Dark colors, large bodies, and physiological tolerance of low temperatures are traits associated with low-temperature climatic zones. Ants tend to be smaller in warm and wet habitats (Gibb et al., 2018). Similarly, hair can increase tolerance of dehydration (Willot et al., 2016; Wittlinger et al., 2007). Monitoring these traits in a degraded ecosystem will provide information on the evolution of microclimate conditions in degraded and restored habitats. Monitoring requires traits to be measured directly on individuals present in the study areas, but it is important to consider that some traits are subject to seasonal variability, such as diet (Lázaro-González et al., 2013) and thermal resistance (Bujan et al., 2020). As measuring traits can be very time-consuming, body size could be the first choice for monitoring environmental changes. This trait is relatively easy to measure. It could be the first trait studied, and one or two other more tedious traits, such as hair or color, could be combined with it.

Ant traits are closely related to environmental complexity (Nooten et al., 2019). Ant body size and leg length tend to be negatively correlated with habitat complexity, with longer legs and larger heads in open spaces than in complex habitats (Weiser & Kaspari, 2006; Yates et al., 2014). Mandibular and eye traits also vary with habitat complexity: longer apical teeth and smaller mandibles in relation to their overall length were recorded in open habitats at the ant community level (Gibb et al., 2015; Yates et al., 2014). At this same scale, Salas-Lopez et al. (2018) found that mandible length and width, apical tooth length, and eye size increased with land-use intensification. Moreover, in areas disturbed by fires, average colony size, worker size, worker polymorphism, and ratio of queen to worker size were greater than in unburned areas (Arnan et al., 2013). Ants with longer antenna scapes, which are important for perceiving the environment and locating resources or prey items (Silva & Brandão, 2010; Weiser & Kaspari, 2006), prevailed in habitats with dense herb/grass layer (Nooten et al., 2019).

4.2 | Ant traits relevant to restore ecological functions

4.2.1 | Abiotic component

The first trait to consider when restoring the abiotic component is the ant nesting habit, selecting ground-nesting species. Ants' capacity to restructure soil depends on their physical capacity to transport material (Dostál et al., 2005). During nest construction and maintenance, workers use their mandibles to transport mineral particles and soil pellets outside the nest. The size of their mandible gap, which is positively correlated with body size, influences the formation of texture-contrast soils (Oliveras et al., 2005) (Figure 1; Table 2), determining the size of the soil particles excavated. The larger the mandible gap, the more able ants are to transport large particles (Dostál et al., 2005; Martín-Perea et al., 2019). Nest depth can also influence the size of soil particles excavated. Such excavation increases soil (macro)

porosity, which in turn alters the ratio between soil solid and air phases and leads to lower bulk densities (Cammeraat & Risch, 2008). Moreover, the size of ant nest biopores strongly affects water infiltration and soil erosion from water flowing overland (Lobry de Bruyn & Conacher, 1994). Higher soil pore volume in the nest mound promotes preferential flow and thus increases water content at greater depths (MacMahon et al., 2000). Water infiltration is also related to nest architecture, particularly the sizes of nests and of nest entrances (MacMahon et al., 2000) (Figure 1; Table 2), which vary among ant species (Cammeraat & Risch, 2008).

Ants also help to modify soil chemical properties. Their diet determines the magnitude of soil enrichment. Leaf-cutting and granivorous ants contribute more to soil fertility than omnivorous species, which suggests that the accumulation of food and waste generated from plant sources, for example, in ant refuse piles, may improve soil fertility more than that from animal sources (Farji-Brener & Werenkraut, 2017). This may be explained by the considerably higher amount of plant biomass than animal biomass in most terrestrial ecosystems and the differences between plants and animals (e.g., decomposition rate, nutrient composition). The enhancement of soil fertility in leaf-cutting and granivorous ant nests may also be due to their large colonies (Farji-Brener & Werenkraut, 2017; Jonkman, 1980a, 1980b).

4.2.2 | Biotic component

Ants involved in seed dispersal directly influence plant community composition and structure. The spatial effects of seed dispersal may depend on the colony foraging strategy (Lanan, 2014; MacMahon et al., 2000). Ant body size is a good predictor of seed dispersal distance (Christian, 2001; Ness et al., 2004), which influences plant establishment, seed germination, and seedling growth (Christian, 2001; Fernandes et al., 2020). Larger species disperse seeds farther (Gómez & Espadaler, 1998; Ness et al., 2004). Beyond the attractiveness of seeds, their successful transport may depend on ants' mandible gap and thus on their physical ability to carry seeds of a specific morphology or size (Oliveras et al., 2005) (Figure 1; Table 2). Leaf-cutting ants, although they can disperse seeds (Wirth et al., 2003), have attracted more attention for their ability to carry leaves. Their body size and leg size determine leaf-transport rate, relatively long legs being advantageous (Burd, 2000).

Ants' diet clearly determines their impact on the biotic component. Granivorous species produce more noticeable effects on vegetation, whereas predatory species have a stronger impact on fauna (Offenberg, 2015; Vandermeer et al., 2010). Thus, granivorous ants are expected to have a greater effect at earlier restoration stages (colonization), while predators will have greater impacts at more advanced stages (population control). For predatory or generalist species, the colony foraging strategy and worker body size and mandible gap size determine prey size (Cerdá & Dejean, 2011; Oliveras et al., 2005). Length of mandibles being related to diet; longer mandibles lead to more predation events (Parr et al., 2017) (Figure 1; Table 2).

Changes in soil physico-chemical properties and vegetation positively and indirectly influence above- and below-ground fauna

TABLE 2 Ants effect traits and their associated ecological functions on soil, vegetation and fauna components, and unit of measurement.

Components	Impacted processes	Traits	Measures	Sources
Soil	Soil structure	Size of mandibles gap	mm	(Cammeraat & Risch, 2008; Dostál et al., 2005; Martín-Perea et al., 2019; Oliveras et al., 2005)
		Mandibles length	mm	
		Ant body size	mm	
		Production of biogenic structure	Burrowing or not burrowing	
	Soil (macro) porosity	Production of biogenic structure	Burrowing or not burrowing	(Cammeraat & Risch, 2008)
	Bulk density	Production of biogenic structure	Burrowing or not burrowing	(Cammeraat & Risch, 2008)
	Infiltration rate	Size of ant biopores	mm	(Cammeraat & Risch, 2008; Lobry de Bruyn & Conacher, 1994; MacMahon et al., 2000)
		Nest depth	mm	
		Size of the nest	m	
		Nest entrance size	mm	
Soil erosion	Size of ant biopores	mm	(Cammeraat & Risch, 2008; Lobry de Bruyn & Conacher, 1994; MacMahon et al., 2000)	
Magnitude of enrichment	Diet	Generalist predator, specialist predator, generalist, seed harvester, seed harvester and generalist, sugar feeder and generalist, fungivore	(Elizalde et al., 2020; Farji-Brener & Werenkraut, 2017)	
Vegetation	Seed predation	Colony foraging strategy	Individual or group	(Cammeraat & Risch, 2008; Lobry de Bruyn & Conacher, 1994; MacMahon et al., 2000; Parr et al., 2017)
		Diet	Generalist predator, specialist predator, generalist, seed harvester, seed harvester and generalist, sugar feeder and generalist, fungivore	
	Seed dispersal	Ant body size	mm	(Ness et al., 2004; Oliveras et al., 2005; Parr et al., 2017)
		Size of mandibles gap	mm	
	Seed germination	Diet	Generalist predator, specialist predator, generalist, seed harvester, seed harvester and generalist, sugar feeder and generalist, fungivore	(Fernandes et al., 2020; Ness et al., 2004)
		Ant body size	mm	
	Seedling growth	Dispersal distance	m	(Fernandes et al., 2020; Ness et al., 2004)
		Ant body size	mm	
	Plant establishment	Dispersal distance	m	(Fernandes et al., 2020; Ness et al., 2004)
		Ant body size	mm	
Fauna	Population regulation	Size of mandibles gap	mm	(Elizalde et al., 2020; Oliveras et al., 2005)
		Prey-predator size	mm	
	Predation	Colony foraging strategy	Individual or group	(Cerdá & Dejean, 2011; Parr et al., 2017)
		Length of mandibles	mm	
	Diet	Generalist predator, specialist predator, generalist, seed harvester, seed harvester and generalist, sugar feeder and generalist, fungivor		

Note: In the literature, some authors refer to the ant body size and others to their biomass. To discuss these two traits, as they are correlated, we have chosen to use only the more commonly used and more easily measurable trait “ant body size.”

occurrence, abundance, and community structure (Sanders et al., 2008; Sanders & van Veen, 2011; Schuch et al., 2008). In ant nests, the high rates of organic material accumulation increase food resources for detritivores and indirectly increase microhabitats for soil fauna through vegetation modification. Nests are also a refuge for myrmecophilous species such as lycaenid butterflies (e.g., *Maculinea teleius* (Bergsträsser, 1779) and *M. nausithosus* (Bergsträsser, 1779)) (Wynhoff et al., 2008) or some beetles (e.g., *Amidobia talpa* (Heer, 1841) and *Monotoma conicicollis* (Aubé, 1838)) (Päivinen et al., 2004). Other species are predators of the brood or adults, such as spiders from the genus *Zodariinae* (e.g., *Zodarion elegans* (Simon, 1873)) (Traxler, 2016) or some beetles (e.g., *Pella humeralis* (Gravenhorst, 1806)) (Päivinen et al., 2004).

4.3 | Ant traits to consider to facilitate population introduction, establishment, and dispersion

Although in some cases, providing shelters (e.g., stones, wood logs) may be sufficient to reinforce populations by decreasing nesting site competition, when introduction is required, the operational phase will be facilitated by choosing a species easy to collect and introduce. The species should be common near the introduction site, generalist, and pioneer in the ecosystem dynamics. For example, in their study on brown coal mining spoil dumps in the Czech Republic, Holec and Frouz (2005) showed that two species, *L. niger* and *Manica rubida*, have a marked ability to colonize new habitats and are considered to be pioneer species in this context. Given the negative impact that some exotic ant species can have on their environment (e.g., on vegetation (Christian, 2001), native ant diversity (Wittman, 2014), arthropods, and vertebrates (Lach & Hooper-Bùi, 2010)), we highly recommend choosing native species.

The number of queens per colony and the dispersal method are also important. Collecting queens from colonies that disperse by budding may require digging out the pre-existing colony, which may degrade the donor site. With species that reproduce during nuptial flight, collecting mated queens should be easier and have less impact on the donor site.

As in any introduction process, particular attention must be paid to species involved in hybridogenesis. In this reproductive system, known as “social hybridization” and varying among species (Lavanchy & Schwandertanja, 2019; Romiguier et al., 2017), workers result from the hybridization of parents of different genetic origin. It is thus important that both lineages are still present on the site (e.g., collection and introduction of both lineages) to ensure successful population growth.

To avoid a population collapse in the years following introduction, nesting habit (hypogaeic, under stones, dead wood, litter, arboreal) is a key factor to ensure species establishment, particularly if shelters have to be created (e.g., dead wood and stone cover). Overall, the environmental conditions of the degraded site need to fulfil the species' requirements, such as thermal and moisture habitat preferences. Territoriality must also be considered to ensure that the candidate species will persist in coexistence with the species already present. Species

reproducing by mating flight, although they take more time to build a stable and mature colony than species reproducing by budding, can spread over greater distances. Finally, choosing polymorphic species—with intraspecific variation in worker body size—may be a solution. Worker polymorphism has been related to the breadth of functional roles performed by colonies (Arnan et al., 2011; Mertl & Traniello, 2009) and implies greater variability of responses to temperature, which increase the overall period of external activity, and enhances colony success (Cerdeira & Retana, 1997). As most incipient colonies from mated queens have only nanitic workers, polymorphism is only considered an advantage after the first phase of colony growth.

5 | CONCLUSION

To develop trait-based approaches in ecological restoration, it is essential to acquire general knowledge of the organisms to use, the functions they performed, the traits related to the functions, and ecosystem services. While the current knowledge on the ecological functions of ants has already been extensively studied as shown here, we have pointed out a list of key traits in ants that are valuable for environmental monitoring and/or that are related to the different functions targeted in restoration projects.

However, some limitations remain and may constrain a wide use of a trait-based approach. The access to ant trait data is one of them. Indeed, to date, only a few ant databases have been developed including GABI project, which focuses on distribution records (Guénard et al., 2017), and “GlobalAnts,” which focuses on ant traits with associated georeferenced assemblage-level data (Parr et al., 2017). While these databases appear to be interesting and powerful tools in ecological restoration, the large amount of missing data is a limit to their current use (Auclerc et al., 2022). A first step should be to complete the data on traits by focusing on the most important for ecological restoration. Future studies need to address this gap across a wide range of functional traits both at the individual and colony level.

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CONFLICT OF INTEREST STATEMENT

There is no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

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