Myrmecological News
ISSN 1997-3500
myrmecologicalnews.org
Myrmecol. News 34: 129-157 doi: 10.25849/myrmecol.news_034:129 25 September 2024
Review Article

Two sides of the same coin? Ants are ecosystem engineers and providers of ecosystem services.

Felipe P. Rocha*, Taylor A. Bogar*, Andre Ibañez Weemaels, Jiaxin Hu, Mingrong Liang, Clara Park, Roger H. Lee, Shahmshad Ahmed Khan, Shaolin Han, Yuen Lam Ng & Benoit Guénard

Abstract

Ants are well-known for their roles in ecosystem engineering and for providing multiple ecosystem services. In the past, these two roles have mainly been studied independently, and the possibility that these are two interchangeable roles just studied in different ways should be considered. In this review, we outline what is known of ant populations and communities as engineers and service providers, including disservices resulting mainly from their nesting habits. Then we consider the possibility of engineering and services being similar or contrasting roles. We argue that while both are linked through the same processes, they are effectively researched as distinct because of conceptual and methodological differences; a consequence of the historical construction of both fields and of their focus. However, considering the relevance of ants within most terrestrial ecosystems and of their widespread presence and abundance, we must start combining knowledge and practices from both fields to fully acknowledge and account for the importance of ant engineering to human well-being. Thus, we provide directions and identify areas that would benefit from the incorporation of both approaches into future studies. For example, a shift of focus from ant population to ant community studies is necessary and overdue for a holistic understanding of the role of ant communities in ecosystems. Further, another direction is the potential for ant engineering to restore degraded ecosystems. Both directions would highly benefit from applying the theory and methods of functional ecology in their approaches, and the reasons are also discussed in this review. Hopefully, growing awareness on the topic will increase the demand for conservation of the ecosystems and their derived services, as well as the proper quantification of this insect contribution to human societies.

Key words: Ecosystem services, ecosystem engineering, physical engineering, bioturbation, chemical engineering, biological engineering, scale, valuation, ecosystem disservices, restoration ecology.

Received 17 June 2024; revision received 14 August 2024; accepted 27 August 2024
Subject Editor: Nicholas J. Gotelli

Felipe P. Rocha (contact author), Taylor A. Bogar, Andre Ibañez Weemaels, Jiaxin Hu, Mingrong Liang, Shahmshad Ahmed Khan, Yuen Lam Ng & Benoit Guénard (contact author), Insect Biodiversity and Biogeography Laboratory, Kadoorie Biological Sciences Building, The University of Hong Kong, Pok Fu Lam Road, Hong Kong SAR, China. ORCID numbers: FPR 0000-0003-3968-1280, AIW 0000-0002-0316-1294, BG 0000-0002-7144-1175. E-mail: feprocha93@gmail.com; zeroben@gmail.com (last author)

Clara Park, Biodiversity and Environmental Change Laboratory, Kadoorie Biological Sciences Building, The University of Hong Kong, Pok Fu Lam Road, Hong Kong SAR, China.

Roger H. Lee, Science Unit, Lingnam University, Tuen Mun, Hong Kong SAR, China. ORCID number: 0000-0002-8023-3490.

Shaolin Han, Insect Biodiversity and Biogeography Laboratory, Kadoorie Biological Sciences Building, The University of Hong Kong, Pok Fu Lam Road, Hong Kong SAR, China; Centre for Immunology & Infection, Hong Kong SAR, China; School of Public Health, The University of Hong Kong, Hong Kong SAR, China.

* These authors contributed equally to the paper as first authors.

Introduction

In the current state of biodiversity decline, the management and valuation of ecosystem services (ES) have become central elements in conservation and policy strategies. Ecosystem services can be categorized into three main groups: provisioning of material goods, regulation of ecosystem processes (supporting and regulating services), and non-material (cultural) services such as learning and inspiration (Millennium Ecosystem Assessment 2005, IPBES 2019; Glossary in Box 1). While provisioning services often present direct, intuitive outcomes to biodiversity declines (e.g., reduced food options due to species loss) and can be quantified monetarily, the valuation of regulatory and non-material services poses significant challenges due to their complex and less tangible nature (Fisher & Turner 2008, Sterner & Persson 2008). Despite this, the increasing rate of anthropogenic diversity loss necessitates a comprehensive understanding of these underlying ES (Cardinale & al. 2012, Birkhofer & al. 2015). To address these challenges more effectively, it is beneficial to concentrate on species that have extensive interactions with other species, particularly those with well-established provisioning services. This focus provides an opportunity to express the value of non-provisioning services in terms of ecological risk, such as the probability of losing economically valuable services (Abson & Termansen 2010). Furthermore, prioritizing species that

Box 1: Glossary of relevant terms presented in this review.

Term	Definition
Ecosystem Engineer	An organism that through some physical, biological, or biochemical mechanism, alters in a system a condition or resource for another organism or community, which results in the modification of the abundance or fitness of said organism, or the diversity or composition of said community (modified from Jones & al. 1994, Jones & al. 1997).
Ecological Process	The complex interaction between organisms and elements of the abiotic environment that underpin fluxes of information, energy, and matter (Mace & al. 2012, Brockerhoff & al. 2017).
Ecosystem Process	The interaction between ecological processes and ecosystem structures that control fluxes of information, energy, and matter through the ecosystem (Cardinale & al. 2012).
Ecosystem Services	The benefits to human well-being provided by ecosystems, which may or may not have a distinct monetary value (Mace & al. 2012).
Ecosystem Services Supply	The capacity of an ecosystem to supply a service regardless of the perception, use, or outcomes to human populations (Assis & al. 2023).
Ecosystem Services Demand	The demand for ecosystem services from human populations, regardless of their acknowledgement of it (Assis & al. 2023).
Ecosystem Service Flow	Service-specific flow of matter or organisms that connects the areas of service supply and demand (Metzger & al. 2021, Assis & al. 2023).
Final Ecosystem Service	An ecosystem service that directly underpins or provides a good (Mace & al. 2012).
Goods	The benefits or products derived from final ecosystem services. Typically involves human mobilisation (Spangenberg & al. 2014).
Human Well-being	It includes the basic requirements for satisfactory living conditions, freedom of choice, health, good social relations, and security (Millennium Ecosystem Assessment 2005)
Nature's Contribution to People (NCP)	All the contributions, both positive and negative, of living nature (i.e., all organisms, ecosystems, and their associated ecological and evolutionary processes) to people's quality of life (Díaz & al. 2018, IPBES 2019). Divided into regulation of environmental processes, and material and non-material contributions, each contributing to different aspects of people's well-being.
Scale	Scale is the intrinsic characteristic of a pattern, process or ecological entity being studied, defined in three main components: i) spatial; ii) temporal; and iii) organizational (Levin 1992).

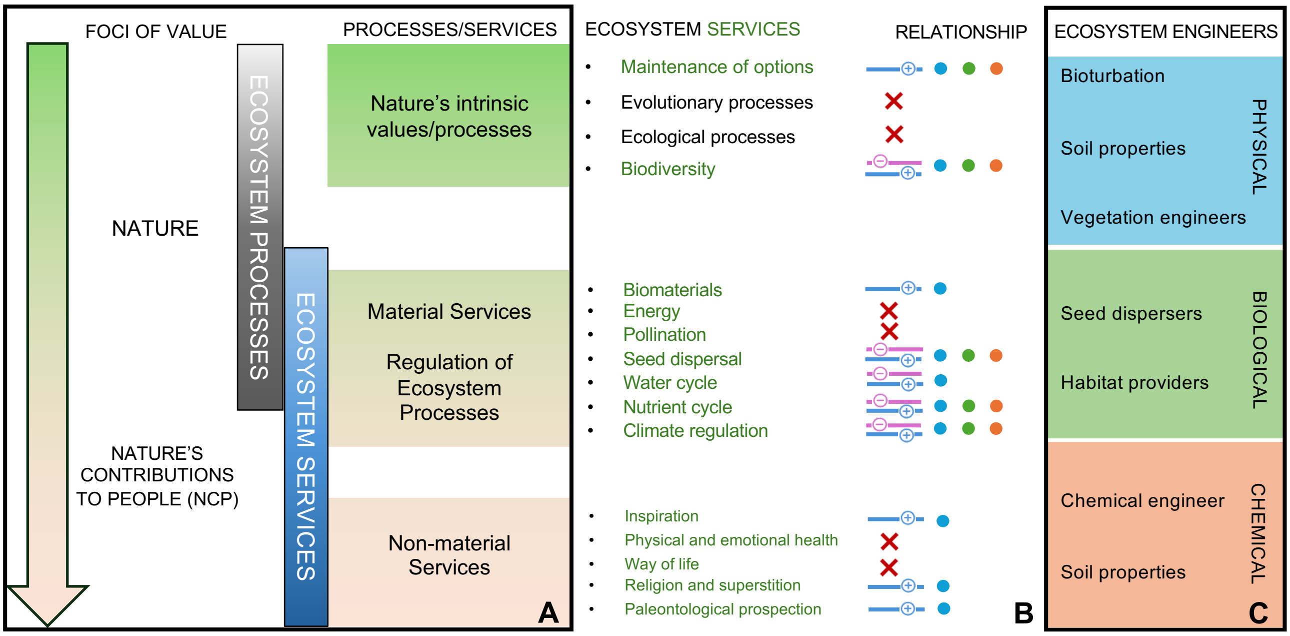

Fig. 1: Summary of the relationship between ecosystem processes, services and engineering. In A), the ecosystem processes and services (including its categories) are related according to their main foci of value, either nature or nature's contributions to people (NCP). From there, in B), examples of ecosystem processes (in black) and services (in green) are given and their relationship with ant engineering is shown. No relationship between service and engineering is represented with a red cross, positive relationship is represented in blue, and negative in pink. Then, the blue, green, and orange dots represent the ecosystem engineering type that is related to the listed service. In C), examples of the different engineering activities of ants are listed according to their classification in physical, biological, or chemical. Ants with large, durable colonies and nests tend to be the most impactful ecosystem engineers, this includes leafcutter ants, harvester ants, *Formica* spp., for example (Farjí-Brener & Werenkraut 2015, Viles & al. 2021, Uhey & Hofstetter 2022). This figure is modified from the framework presented in Figure 2 of Pascual & al. (2017) and Figure SPM 1 of the IPBES report (IPBES 2019).

provide multiple ES or serve as indicators for other services will enable us to optimize conservation outcomes within the extant framework of limited time and funding (Caro 2010). Ecosystem engineers are uniquely positioned to contribute to this effort as their alteration of the physical, chemical, and biological aspects of their environments play a critical role in this regard. Ultimately, their activities can induce profound and widespread effects on the surrounding community (Jones & al. 1994) and thus be of prime importance for ecosystem maintenance and conservation.

The relationship between ES and ecosystem engineering is well-documented in certain taxonomic groups. For instance, beavers (*Castor* spp.) are renowned for their construction of natural dams, which modulate water flow and mitigate extreme flooding events, yielding an estimated annual savings of approximately $32 million in the northern hemisphere (Thompson & al. 2021). While mammals certainly play important roles in providing services through ecosystem engineering, invertebrates typically have stronger impacts, yet most lack quantitative assessment (Romero & al. 2015, Coggan & al. 2018). Terrestrial invertebrates, especially, are instrumental engineers. Their activities, such as soil modification, burrowing, and leaf-structuring, alter the environment around them creating habitats and regulating a wide array of ecosystem functions (Lavelle & al. 2016).

Considering the high abundance and biomass of ants in most biomes and habitats of the world (Schultheiss & al. 2022), it is not surprising that their roles within ecosystems may surpass or equal those of many other organisms. For instance, ants are second only to earthworms in bioturbation but are, however, likely more important in absolute terms due to their wider distribution and diverse range of engineering activities (Folgarait 1998). Through their sophisticated colony structures and efficient labor division, ants adeptly build nests, clear soil from vegetation, and concentrate nutrients, thus facilitating vital ecosystem processes (Leal & al. 2014, Farjí-Brener & Werenkraut 2017). Moreover, ants contribute to ES across all the categories delineated by both the Millenium Ecosystem Assessment (MA) and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Service (IPBES) frameworks (Fig. 1); the IPBES frames them as Nature's Contribution to People (Del Toro & al. 2012, IPBES 2019, Elizalde & al. 2020). Despite their critical role in terrestrial ecosystems, the study of service provision and engineering activities of ants has often been conducted independently.

Here, we explore the relationship between ES and engineering in ants, and the study of these roles, to answer the following questions: Are they linked? How are they linked? Can these two different roles of ants in ecosystems be interchangeably studied, meaning they are the same phenomenon of a system? Or only by combining both approaches we can reach a better understanding of these organisms' roles in the environment, meaning they are complementary or contrasting within a system? The goal of this review is to synthesize results on ant ecosystem engineering and examine the processes it affects, then to evaluate how these engineering activities relate to well-established ES (reviews on these topics alone are presented in Tab. 1) and, finally, to determine what are these links and how are they linked.

First, we review the roles of ants as multifaceted ecosystem engineers, to then discuss ant functional traits related to engineering and how engineer's traits and diversity are connected to ecosystem functions and service provision. Following this introduction on ant engineering, we highlight how it relates to service provision of all types, including the services provided by ant communities – a topic still hardly discussed – and disservices. Then, using extensive information on both topics, we address the posed question through a comparison of conceptual, historical, and methodological differences. Finally, we identify and emphasize areas where information is currently limited, concluding with directions that can significantly improve our understanding of the potential cascading effects of biodiversity loss on ecosystems and human well-being within the field of myrmecology. Throughout this review, we use the terminology of the IPBES and the MA.

Tab. 1: A non-exhaustive list of meta-analyses and reviews on the topic of ants (or social insects) as ecosystem engineers and service providers. Studies are presented in a chronological order.

Article Type	Scope	Gaps and Future Directions	References
Ecosystem Engineers			
Review	The review focuses on the effects of ant nests in the physical and chemical environment around it. Further, the role of ant populations in controlling other taxa and ants themselves is explored.	The author suggests that ants are a good model to study adaptations to greatly modified environments.	Pętal (1978)
Review	Role of ants in ecosystems, mainly from the perspective of the effects of ground-dwelling ants on soil processes and functions, emphasizing their role as ecosystem engineers.	Studies are needed on ants' resistance and resilience to disturbance and if all species are equally relevant to overall ecosystem functioning. Furthermore, if their engineering role is dependent on abundance.	Folgarait (1998)
Review	To discuss the relevance and boundaries of different soil engineer classifications, like the extended phenotype engineering type of ants, and how the engineering effects have feedback on the engineers' fitness.	Research is needed on the ecological requirements and responses of soil engineers to the environment and environmental changes, particularly in agroecosystems where their presence has direct effects on humans. Further, interactions between soil engineers should be further studied.	Jouquet & al. (2006)
Review	An overview of the impact of soil-dwelling ants on fine scale soil properties with emphasis on physical, chemical and biological aspects, and the possible effects of ants on soil properties on landscape scale.	More information is needed on the spatial distribution, size and density of ant nests and foraging holes at different scales.	Cammeraat & Risch (2008)
Review	A review on the main mechanisms by which ants affect the soil environment and soil processes.	Some future directions include testing hypothesis on the mechanisms through which ants affect soil properties, testing the effects on various spatiotemporal scales of the ecosystem, and testing the effects of other interactions (e.g., predation, myrmecochory, etc) on soil properties.	Frouz & Jilková (2008)
Review	An overview of leaf cutting ants' (LCAs) mechanisms that modify soil structure and fertility and how these changes affect plant assemblages and landscape structure.	NA	Farji-Brener & Tadey (2009)

Article Type	Scope	Gaps and Future Directions	References
Review	A review on the Ant Garden (AGs) interactions around the world with discussion on the outcomes for the partners and the extended community interacting with it.	More information is needed on the ecology of AGs from ant and plant perspectives, as well as the chemical components of this interaction which are key to its success.	Orivel & Leroy (2011)
Review	Synthesis on the non-trophic interactions of LCAs with plants and their habitats to elucidate the outcomes in local and landscape levels with discussion on disturbance regimes and management.	Test hypotheses on the patterns found with cross-taxa and cross-ecosystem comparison, establish the traits that make LCAs successful around disturbance. Further, study the ecosystem-level effects promoted by LCAs activities, and inactive nests, on soil structure and function which end up affecting the vegetation too.	Leal & al. (2014)
Meta-analysis	A quantitative determination of the effects of leaf-cutting ants (LCAs) on soil fertility and plant performance moderated by variables of interest (substrate, location of refuse pile, genus, and latitude).	Studies on internal refuse piles of *Acromyrmex* to establish a full comparison between the two LCA genera. Further, to test the effects of LCAs in regional level.	Farji-Brener & Werenkraut (2015)
Meta-analysis	A quantitative determination of ants nests' effects on soil fertility and plant performance moderated by variables of interest (feeding type, latitude, soil sampled, etc).	Additional data on nest size, nest density, and the rate of refuse production are needed from a wide range of ant groups and habitats.	Farji-Brener & Werenkraut (2017)
Review	The roles of ants in north temperate grasslands are reviewed, focusing on aspects of conservation and provision of ecosystem services.	The authors suggest that the impact of ants on microbial communities and soil processes are further explored, based on ant activity, diversity, and identity of species or functional groups. Moreover, that consequences of climate change on ants should be explored.	Wills & Landis (2018)
Review and Meta-analysis	A review on the mechanisms ants use to keep themselves and their nest clean of pathogens, and whether their hygiene measures extend to their surrounding environment, especially plants.	Studies are needed in non-symbiotic plants and temperate latitudes to confirm the generality of ants' hygienic effects. Further, experiments on the mechanisms behind ant-plant-pathogen protection are needed.	Offenberg & Damgaard (2019)
Review	The review aims to identify the current knowledge and gaps on the effects of LCAs in ecosystems through engineering and to develop a framework to quantify these effects.	The main gaps and areas for future exploration are nest attributes and physical alterations, nest inputs and outputs, carbon and nutrient transformation within nests, transport of organic matter, and the spatiotemporal heterogeneity of nest dynamics.	Swanson & al. (2019)
Review	The review goals are to identify, quantify and map globally the importance of ants on Earth's geomorphology.	Field experiments to assess the roles of ants in soil processes relative to other soil engineers, like earthworms and termites, and in more complex processes too, like their importance for sedimentation, erosion, and weathering.	Viles & al. (2021)
Review	The review focuses on harvester ants (common name for species of three ant genera: *Pogonomyrmex, Messor,* and *Veromessor* sp.), especially their effects on ecosystem and the different situations they are seen as important keystone species and pests.	More studies on less-studied harvester ant species, as well as their interactions with plants, like invasive grasses, and their capacity for habitat restoration.	Uhey & Hofstetter (2022)
Review	A review on the ecological aspects of leafcutter ants that have implications on geomorphological processes.	More detailed studies on soil turnover and weathering rates are needed to get a better picture of their roles on soil and geomorphological development.	Nascimento & al. (2024)

Article Type	Scope	Gaps and Future Directions	References
Ecosystem Services Providers			
Review	The author reviews studies on ant provisioning services, including food and pharmaceutical usage of ants.	The author suggests more investigation on ants' nutritional composition, immune defence, and the pharmacological properties of different ant species and castes.	Rastogi (2011)
Review	A major review on the ecosystem services provided by ants framed in the Millennium Ecosystem Assessment; the first review on the topic since the introduction of it by Folgarait (1998).	The authors suggest a few avenues for future research, including expanding our knowledge about ant biodiversity within and across ecosystems, exploring their roles as engineers, quantifying and valuating their services, and quantifying the impacts of anthropogenic changes in service provision.	Del Toro & al. (2012)
Review	The author reviews the importance of the weaver ant to sustainable crop production and pest control and the possibility of other ants being able to deliver the same services.	Several directions are identified by the author, including the identification of the best ant-crop matches based on outcomes of interactions, finding proper Integrated Pest Management techniques to broaden ants' efficacy in different contexts, quantifying the repelling properties of ant pheromones and the indirect advantages for plants of disease protection.	Offenberg (2015)
Review	The roles of ants in agroecosystems is reviewed with focus on biological control and weaver ants.	More studies are needed on the net outcomes of the interactions observed in cropping systems between ants and herbivores, predators and parasitoids.	Diamé & al. (2017)
Review	SEE ABOVE	SEE ABOVE	Wills & Landis (2018)
Meta-analysis	The authors analyse the effects of weaver ants on pests and crop yield. Case studies are also presented to deepen the understanding of their services versus disservices.	In general, research is needed on the interactions between weaver ants and other arthropods on crops, to understand the outcomes of possible interactions observed. Further, to investigate plant material feeding and nutrient cycling on the tree.	Thurman & al. (2019)
Review	The authors analyse the traits of social insects that make them good suppliers of ecosystem services. Further, they compile and assess conservation management strategies in order to improve and preserve the services provided.	The authors identify the need to standardize methodologies for the quantification of service provision, as well as developing sustainable ways to manage and use social insects as service providers.	Elizalde & al. (2020)
Meta-analysis	The review analyses the impacts of ants in biological control in agroecosystems by balancing their services and disservices to crop yield.	The authors point out to other factors that can affect the role of ants on pest control and need to be studied, such as landscape composition, climate change and ant invasive status.	Anjos & al. (2022)
Review and Meta-analysis	The objective was to search for chemicals originating from ants or their cuticle microbiome that are harmful to phytopathogens and quantify their effects.	The main gap for future studies is to test the effects of the chemicals found, antibiotics and growth inhibitors, *in vivo*.	Offenberg & al. (2022)
Review	The ecosystem services or disservices provided by ants in the context of urban ecology and expected impacts of climate change to the ant communities.	The authors identify the need to gather more information on the effects of climate change and landscape characteristics on the provision of ecosystem services. Further, investigating the services provisioned in specific urban habitats.	Perfecto & Philpott (2023)

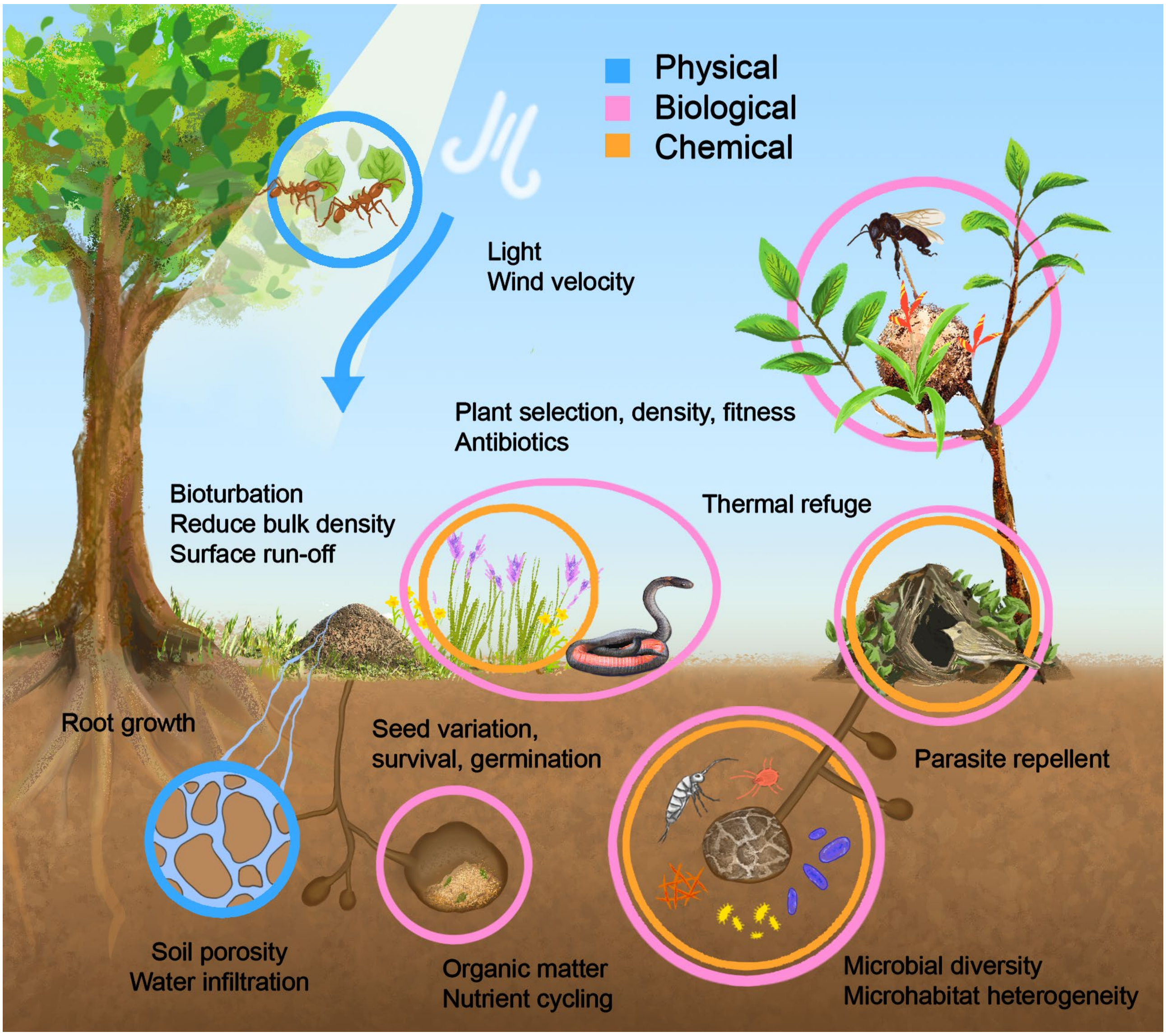

Fig. 2: A visual representation of the different ant-mediated engineering activities, including physical, biological, and chemical changes to the environment, in blue, pink, and orange, respectively.

Ants as ecosystem engineers

Ants have emerged as the archetypal model of terrestrial ecosystem engineers, distinguished from other known engineers, like earthworms, due to their remarkable blend of collective organization and behavioral plasticity (Hölldobler & Wilson 1990). Through interactions with their environment, ants modify the physical, chemical, and biological properties of ecosystems, thereby modifying the conditions in which other species and themselves thrive (Fig. 2). In the following section, we synthesize the current knowledge and evidence of ants acting as ecosystem engineers, highlighting the connections to ecosystem processes. Although our classification was devised to streamline and emphasize the varied engineering activities, they often happen concurrently. Furthermore, this review does not include trophic interactions in the definition of ecosystem engineering (Box 1), including the cases where structural changes to the ecosystem are a result of trophic interactions. For example, the ant *Anoplolepis gracilipes* (Smith, 1857) affected the forest structure on Christmas Island by decimating the land crab *Gecarcoidea natalis* and establishing mutualistic interactions with invasive scale bugs (O'Dowd & al. 2003). However, we acknowledge that the co-occurrence of trophic / non-trophic interactions is interconnected and may be difficult to discern in some cases (Jones & al. 1994).

Physical engineering

Soil physical properties

To date, much of the literature has focused on physical engineering, defined as the alteration of environments through mechanical activities (Lavelle & al. 2016), with changes in soil characteristics receiving the most attention. Several studies have documented the impact of ants on soil properties through two primary mechanisms: 1) the nest building process itself, and 2) the collection and transport of food and other materials to the nest from the surrounding environment (Jouquet & al. 2006, Frouz & Jilková 2008, Del Toro & al. 2012, Tuma & al. 2022). Bioturbation is typically a byproduct of nest construction where, through excavation of the intricate network of tunnels and galleries associated with ground nesting ants, soil is exchanged between the surface and lower depths (de Bruyn & Conacher 1990, Decaëns & al. 2002, Frouz & Jilková 2008). It is estimated that ants provide an average bioturbation rate of 1.5 t ha^{-1} yr^{-1}, with some values higher than 60 t ha^{-1} yr^{-1} (Viles & al. 2021). As a result, soil texture surrounding nests may change due to the redistribution of clay, silt, and sand content (Tschinkel 2015), which can impact the structural stability of the soil (Cammeraat & Risch 2008, De Almeida & al. 2020a). Furthermore, when workers excavate, they bring smaller particles to the surface, creating nest soils with higher macro-porosity and lower micro-porosity compared with non-nest soils (Moutinho & al. 2003). Such alterations can enhance water drainage and infiltration rates, facilitating the horizontal movement of water (Cherret 1989, Leite & al. 2018). Other effects include higher soil water content, decreased surface run-off, increased soil sediment loss from loose aggregates, and alterations of preferential flow due to turret-shaped mounds (Li & al. 2019). Ant nest architecture, however, can have species-specific effects on soil microtopography, increasing water infiltration depending on vertical soil biopore depth and pore size (Farji-Brener 2010, Li & al. 2019), with reduction in bulk density dependent on nesting materials used (Carlson & Whitford 1991). Consequently, ant nest activity on freshly excavated soil can increase run-off and soil loss, water infiltration, soil organic matter, and porosity, while reducing bulk density (Cerdà & Jurgensen 2008, Drager & al. 2016). The effect of ant engineering on soil erosion remains controversial, with evidence for both positive and negative roles and context dependency (Viles & al. 2021). Therefore, more studies and a meta-analysis including variations in climate and soils on the topic should help to settle it.

Finally, another common change to soil physical properties is in the temperature within nest space, which is usually different from the surrounding external temperature. This is a result of the passive and / or active thermoregulation of ants, which is responsible for keeping the environment within the physiological limits of ants (Jones & Oldroyd 2006). Although this is of great advantage to the ants, it can benefit other organisms that utilize their nest space as dealt in the next subsection.

Ants as habitat producers and providers

The biogenic structure of the nest itself can act as potential habitat for secondary inhabitants during ant occupancy and post-occupancy. Ant nests, galleries, foraging trails, and many other constructions near or distant from the main nest provide shelters, access, and resources for a wide range of other organisms, including insects, mites, springtails, and fungi (Anderson & McShea 2001, Hölldobler & Kwapich 2022). Numerous other examples exist, including obligatory associations seen in certain stingless bees with *Crematogaster* nests (Sakagami & al. 1989), mutualistic / parasitic relationships that range from being obligatory to facultative between Lycaenidae and ants (Pierce & al. 2002), or purely facultative such as reptiles laying eggs in ant nests (Nagy & al. 2017). At a microscopic scale, refuse piles can contain high diversity of bacteria and fungi (Farji-Brener 2010). These, and other microhabitats, promote diversification of microbial communities (Boots & al. 2012, Boots & Clipson 2013, Travanty & al. 2022), which can also influence soil fertility (Ginzburg & al. 2008). At larger scales, ant nests provide warmer temperatures in proximity to the mound, providing thermal refugee for reptiles, as is the case in Canada where the persistence of the snake *Storeria occipitomaculata* in northern climates is likely reliant on such nests (Cairns & al. 2018). Alternatively, songbirds may lay their eggs in ant nests to protect them against predators and ectoparasites (Maziarz & al. 2021). More often, ant nests may be re-used by other ant species (Assis & al. 2017), which may be accompanied with their own suite of myrmecophiles (see also Kistner 1982). Diversity in nests can be quite remarkable, for instance, the *Formica rufa* group Linnaeus, 1761 has up to 125 myrmecophiles species (Päivinen & al. 2004, Parmentier & al. 2014); ponerines, which have small nests, can host up to 43 different species (Rocha & al. 2020), army ants from the genus *Eciton* have as much as 62 species of myrmecophiles (von Beeren & al. 2021). The use of biogenic structures can enhance biodiversity by creating living spaces and providing protection from unfavorable environmental conditions or biotic interactions (Berke 2010, Romero & al. 2015).

Within the tree canopy, ant gardens promote diversity and modify the distribution of specific epiphytes by incorporating them into their nests (Morales-Linares & al. 2018), to the point that some epiphytes have evolved obligate species-specific relationship with ants and depend on them from dispersal to growth (Campbell & al. 2023). This mutualistic relationship allows the epiphytes to benefit from the nutrient-rich environment within ant nests (Céréghino & al. 2010, Orivel & al. 2011, Gonçalves & al. 2016) and effectively creates habitat islands for arthropods (Rodgers & Kitching 2011). Different ant species may select specific epiphytes for their nests, which indirectly modify the invertebrate diversity found within bromeliad phytotelmata (Céréghino & al. 2010).

Other physical engineering

Beyond physical changes to soil and tree epiphytes, species such as *Atta* spp. shape the understory / canopy structure, effectively becoming light engineers. In fact, 95% of *Atta cephalotes* (Linnaeus, 1758) colonies make small to medium forest gaps near their nest in the Atlantic Forest (Corrêa & al. 2016). Leaf-cutting ants' removal of leaves can lead to stem death and occasional tree falls, enabling the preservation of light-rich areas in the tropical forest (Corrêa & al. 2016, Knoechelmann &

al. 2020), as well as increased wind velocity within open patches (MEYER & al. 2011). Light and wind complexity increases the heterogeneity of the environment, creating microhabitats (TINYA & ÓDOR 2016, SWANSON & al. 2019) and supporting light-dependent plant species in tropical forests (CORRÊA & al. 2016). Although several arboreal ants can build conspicuous structures on tree branches (i.e., *Camponotus, Crematogaster, Dolichoderus, Oecophylla, Polyrhachis*, etc.; MORALES-LINARES & al. 2018), it does not appear to influence light configuration in ecosystems. This might occur because, as is the case in *Oecophylla longinoda* (LATREILLE, 1802), they tend to choose shaded nest sites (WIJNGAARDEN & al. 2007), or because they are not big enough to cause an important change (ORIVEL & LEROY 2011). Further, ant gardens and their associated vascular plants (from ferns to flowering plants; CAMPBELL & al. 2023) are another study system that should be explored for their possible light engineering. To the best of our knowledge no current studies have focused on these physical changes. In conclusion, although the aforementioned examples may not be responsible for measurable differences in light penetrating the canopy, they act as habitat for numerous other arthropod associates which will be further discussed below (PÉREZ-LACHAUD & LACHAUD 2014).

Biological and Chemical Engineering

Aside from physical engineering, ant activity can alter the surrounding soil and community, benefiting other organisms by nutrient redistribution, seed dispersal, and chemical protection. These effects are heterogeneous depending on the species and their associated traits, nest architecture, environmental conditions, and the community involved.

Soil chemical properties

Through foraging activities, ants acquire substantial quantities of sugars, proteins, and lipids from external sources such as litter, plant tissue, honeydew, seeds, resin from distant trees, invertebrate prey (BLÜTHGEN & FELDHAAR 2010), or vertebrate carrion (EUBANKS & al. 2019), which influence nutrient content of ant nest soil contributing to soil fertility. Ant mounds are characterized by higher concentrations of specific nutrients (such as N, Ca, P, Mg, K, Na, S, Zn, and Cu) compared with the surrounding soil (FROUZ & al. 1997, LENOIR & al. 2001, RISCH & al. 2005, OHASHI & al. 2007), with a positive effect size range (nutrients 95% highest posterior density interval, HPD: 1.14 - 1.89, cations 95% HPD: 0.05 - 1.64) as evaluated by meta-analysis (FARJÍ-BRENER & WERENKRAUT 2017). Overall, no effect on pH (effect size range 95% HPD: -1.11 - 0.53) could be detected through a meta-analysis (FARJÍ-BRENER & WERENKRAUT 2017). However, some studies might show differences in soil pH between nest mound and the surrounding soil (BLOMQVIST & al. 2000). Organic material is incorporated into the soil through decomposition, with the fertility effect varying depending on the type of food ants consume and where they store the food and detritus (BRIESE 1982). Ants that create refuse piles on the soil surface promote nutrient enrichment in the topsoil layer, while refuse stored in nest chambers enrich the soil layer within the nest itself, promoting shallow or deeper root growth, respectively (FARJI-BRENER & WERENKRAUT 2017). Such enrichment effects can range between 40 and 100-fold between nest and non-nest soils (MOUTINHO & al. 2003, TADEY & FARJI-BRENER 2007). Although ant-nest soil is higher in nutrients, the benefits experienced by plants typically occur with long-lasting nests with few nest relocations, and if soil turnover and plant-clearing rate is low (HIGASHI & al. 1989, CARLSON & WHITFORD 1991, HUGHES 1991, FARJÍ-BRENER & WERENKRAUT 2015). It is worth mentioning that most studies deal with soil-nesting ants, while leaf-litter-nesting and army ants' middens could also represent an important share of nutrient input to the soil and should be better investigated (ROBLES LÓPEZ & al. 2024). Further, there is still a largely unexplored role of foliar uptake of nutrients from ant defecation (PINKALSKI & al. 2018), expanding this discussion from roots to tips.

Refuse piles also create favorable microenvironments that enhance seed survival and germination rates (RISSING 1986, LEVEY & BYRNE 1993). Both physical and chemical changes to soil can extend beyond the nest mound proximity, positively benefiting plant growth (NKEM & al. 2000, FARJI-BRENER & WERENKRAUT 2017). Apart from these direct effects, the fertile ant soil may also affect plant fitness indirectly. For instance, research by HANSEN & al. (2023) suggests that ant mounds can extend the duration of plant phenology events and enhance flowering success, potentially increasing the resilience of plant-insect interactions in the face of climate change. However, not all ant nests will enrich soil nutrient content (FARJI-BRENER & WERENKRAUT 2017). In some areas with low intrinsic soil nutrient content, certain ant species with large colonies, such as leaf-cutting ants in Neotropical regions, will deplete soil nutrient content (MEYER & al. 2013). These ants remove most plant material in their vicinity, resulting in reduced nutrients transfer from litter into the soil. This effect is particularly notable in forested habitats where soil has limited nutrient reserves and depends on continuous recycling of decomposed organic matter (RICHARDS 1996).

Seed dispersers

At least 255 ant species have been classified as seed dispersers of an estimated ~11,000 plant species in various ecosystems (LENGYEL & al. 2010), having a direct impact on the local plant community composition and on the granivores by mediating the seed bank and germination within and around their nest soil and by modifying the distribution and abundance of seeds in the landscape, respectively (BEATTIE 1985, GILADI 2006, WILLS & LANDIS 2018, DE ALMEIDA & al. 2020a). Overall, seed dispersal is an interesting case of ecosystem engineering because through an interaction with plant propagules, either failed seed consumption, or elaiosome consumption, ants physically alter seed distribution in the landscape. This alters the conditions for the propagules (i.e., distinct physical and chemical properties of the nest soil) and the resources for granivores (Sanders & Frago 2024), resulting in changes of fitness and composition of these organisms in an ecosystem.

The conditional mutualism of myrmecochory supports the directed dispersal hypothesis where seeds reach suitable micro-habitats for germination, as well as elaiosome removal which further increases germination success (Handel & Beattie 1990, Leal & al. 2007). For example, *Messor barbarus* (Linnaeus, 1767), although a granivorous species, will store seeds in their refuse piles in Mediterranean grasslands, providing advantageous microsites with protection from abiotic and biotic conditions (Rissing 1986, Levey & Byrne 1993, Azcárate & Peco 2007), increasing plant species richness and seed density (Bulot & al. 2016). Further, there is evidence that harvester ants, in general, affect seed dispersal and survival beyond their consumption. One study showed that seedling survival rates are similar within the nest as compared with outside, however, density increased for the seedling species selected by the ant (Anjos & al. 2020). Furthermore, seeds are sometimes transported to the refuse pile, in which 41.3% of the 1% selected were found to germinate (Retana & al. 2004). It has also been suggested that aardvark-ant interaction in South Africa increases seed transport to nutrient-rich sites and the viability of these seeds (Dean & Yeaton 1992). Varying preferences for seed species by ants lead to non-random seed selection. As a result, the seed composition within ant nest soil may differ from that of the surrounding soil (Farji-Brener & Medina 2000, Schütz & al. 2008, Zhao & al. 2020). Nonetheless, selected plant species tend to be more abundant in the nest soil than in the surrounding soil (Schütz & al. 2008), driving seed bank variation at ant nests and creating a mosaic of plant species.

Chemical repertoire of ants and their symbionts

Sociality in ants is a key evolutionary feature, yet it is not without risks. Frequent worker interaction enhances the quick dissemination of pathogens creating a need for a strict hygiene protocol (Schmid-Hempel 1998). Although certain mechanical practices such as grooming and refuse pile placement can mitigate some of the risks, the use of chemicals have also appeared in some species (Schmid-Hempel 1995, Offenberg & Damgaard 2019). Multiple chemicals are already produced by ants, ranging from use in communication to defense against competitors or predators (Attygalle & Morgan 1984). Passive application of antibiotics (terpenoids, mullein and myrmicacin) obtained while foraging can extend to plants, decreasing plant disease incidence (Akino & al. 1995, Offenberg & Damgaard 2019). Interestingly, there are also examples of ectosymbionts present on the ant cuticle biofilm that provide chemicals as a defense against pathogens (Samuels & al. 2013, Gao & al. 2014), and this might extend to the leaf microbiota, for example, due to the interaction with the forager microbiota (Bitar & al. 2021). The genera *Acromyrmex, Allomerus, Oecophylla, Pseudomyrmex, Tetraponera,* and possibly others (leaf-cutting ants having a vast literature themselves; see Samuels & al. 2013), have antibiotic-producing ectosymbionts in their cuticle (i.e., bacteria of the genus *Bacillus* and *Lactococcus*). Anti-pathogenic compounds are passively transferred to foraging areas including plants, reducing the pathogen-inflicted leaf damage and the epiphytic bacterial abundance (Samuels & al. 2013).

The presence of ants might in many cases increase the chances of success of plants, but typically only if evolutionary mutualistic interactions are shared (Ness & al. 2010, González-Teuber & al. 2014). Within some ant-plant mutualisms, ant chemical compounds are actively responsible for plant dominance. For example, in *Myrmelachista schumanni* Emery, 1890 and *Duroia hirsuta* mutualism, non-host plants are sprayed with formic acid by *M. schumanni* allowing extensive areas to be dominated by *D. hirsuta* (see Frederickson & al. 2005). Other organisms might also use ant compounds for their benefits. Songbirds have been observed to apply ants on their feathers (anting), mainly from Formicinae species. There are a few potential reasons for this behavior, including the usage of their compounds produced for their anti-parasitic, bactericidal, and fungicidal properties (Revis & Waller 2004, Bush & Clayton 2018). However, compelling evidence for any of the hypotheses coined are still missing (Morozov 2015). Ants have a large and undiscovered pharmacological potential that can be efficiently explored with new technological developments (Agarwal & al. 2022).

With all these examples of ant engineering in mind, we turn our attention now to the functional aspect of ant diversity, which is important to consider when discussing their contribution to ecosystem processes, and finally, to service provision.

Engineer's functional traits

A functional trait approach adds a dimension to biodiversity measurements facilitating a more mechanistic understanding of ecological phenomena (Wong & al. 2019). A functional trait is a phenotypic entity measured on an individual organism that has a demonstrable link to its fitness (McGill & al. 2006, Violle & al. 2007) or its ability to regulate ecosystem functioning (Mlambo 2014, Schmitz & al. 2015). The traits of ecosystem engineers can have important implications for their contribution to ecosystem processes and service provision, relating to the magnitude and efficiency, or the consistency and stability of these processes (De Almeida & al. 2020a, Elizalde & al. 2020). Ants play a unique role as ecosystem engineers in this regard as their eusociality confers an extended phenotype on the nest itself, allowing for the consideration of traits at both the individual and colony levels (Hölldobler & Wilson 1990, Arnan & al. 2014). Within ant functional ecology, morphological traits have had the most attention due to the relative ease at which one can measure them. In addition to morphology (body size, pilosity, etc.), other factors have been identified as important to consider when studying terrestrial invertebrates, including physiology (temperature tolerance, relative growth rate, etc.), behavior (activity time, locomotion speed, etc.), ecology (ingestion rate, feeding guild, etc.), and life history traits (life span, ontogeny, etc.) (Moretti & al. 2017). Specifically, traits measured at the colony level, especially those associated with nest construction and structure, may be more indicative of effectiveness of an ant species as ecosystem engineers. Here we highlight specific traits of interest, both at the individual and colony levels, that have been either demonstrated or theorized to impact engineer ability or efficiency.

In relation to bioturbation, body size is likely to be a key functional trait related to the excavation process, determining size and shape of tunnels (Espinoza & Santamarina 2010). As physical engineers, larger bodied individuals tend to have the most impact on soil displacement and movement (Lehmann & al. 2017) with larger burrows increasing soil porosity and water infiltration (Lee & Foster 1991, Auclerc & al. 2022). Along with body size, traits such as mandible length restrict the choices available by limiting the size and mass of particles being carried (Dostál & al. 2005, Oliveras & al. 2005, De Almeida & al. 2020b), while other measurable modifications to mandible morphology may relate to specialized functions such as leaf cutting or digging (Hölldobler & Wilson 1990). Such constraints have consequences for other aspects of engineering, such as seed dispersal or nutrient cycling, where the size and mass of the particle being carried likely alters the local seed bank, the nutrient concentration in the soil, or the dispersal distance (Kaspari 1996, Wills & Landis 2018). Furthermore, some species of ants are known to exhibit varying levels of polymorphism, where the breadth of a trait can add heterogeneity to engineering activities (Wills & al. 2018). However, within a polymorphic species (*Solenopsis invicta* Buren, 1972), there is evidence that topological features of the tunnel network are conserved among individuals of different sizes, with nest area and length being correlated with the number of active workers instead (Gravish & al. 2012).

Colony size is positively correlated with the nest volume (Buhl & al. 2005, Tschinkel 2011), with larger colonies containing more chambers and tunnels (Tschinkel 2021, Miller & al. 2022), allowing for more potential microhabitats for myrmecophiles (Parmentier & al. 2014). Additionally, the connectivity and modularity of the nests can influence collective behavior, with higher connectivity increasing the speed of resource transportation (Pinter-Wollman 2015). Nest architecture is an important trait that can vary greatly from relatively shallow nests to up to 7 m in depth (Hölldobler & Wilson 1990, Moreira & al. 2004, Guimarães & al. 2018). Construction is often responsive to environmental conditions, so physiological traits such as critical thermal limit or desiccation resistance may determine certain nest characteristics. For example, workers of *Formica podzolica* Francoeur, 1973 that experience higher temperatures excavate deeper nests (Sankovitz & Purcell 2021), while *Temnothorax rugatulus* (Emery, 1895) built thicker nest walls in higher humidity (DiRienzo & Dornhaus 2017). While individual morphological traits may act as constraints in the rate of excavation, physiological and colony properties likely mediate the overall impacts in ecosystems. Trait acquisition and inclusion in studies of ant engineering and service provision is a promising venue to connect different axes of diversity to the provision of ES. In the next section, we explore the connection between biodiversity and ecosystem functions and services.

Engineer diversity and ecosystem functions and services

The functioning and stability of ecosystems are critically dependent on biological diversity (Hooper & al. 2005, Cardinale & al. 2012, Tilman & al. 2014). Animal engineering activities generally have a positive effect on species richness (Romero & al. 2015), thereby supporting the ecological processes they provide. Nonetheless, the diversity of the engineering species themselves may play a significant role in maintaining ecosystem stability (Yeakel & al. 2020). It is important to note, however, that most studies have primarily focused on single dominant ant species with large nest footprints, while species with relatively smaller nests have received less attention.

Ant nest building, in particular, creates "fertility islands" by increasing surrounding soil organic matter and biota diversity. This results in enhanced nutrient availability and cation concentrations, which in turn promotes plant biomass and fitness. Yet, this does not necessarily result in higher density and or plant species richness (Boulton & Amberman 2006, Farji-Brener 2010, Farji-Brener & Werenkraut 2017). It is also evident that there is species-specific variation which influences the contribution to ecosystem functioning. The fertility associated with these islands depend on ant diet, with herbivorous ants increasing nest cation content more than omnivorous ants, thus promoting greater primary production (Farji-Brener & Werenkraut 2017). However, while the degree of influence exerted by ants on a given community is correlated with their diet and functional traits (Elizalde & al. 2020, Auclerc & al. 2022), the modulation of environmental modification is contingent on soil types and topographical factors (James & al. 2008). Arid environments benefit substantially more as ants have a greater impact on fertility due to the lack of surface vegetation or water (Briese 1982, Carlson & Whitford 1991, Dostál & al. 2005, Cerdà & Jurgensen 2008, Farji-Brener 2010, De Almeida & al. 2020a). For example, redistributing water to create moisture-rich patches in semi-arid environments contributes to small-scale landscape heterogeneity, further amplified with their impacts on soil chemistry (Richards 1996).

Heterogeneity evidently emerges as a significant attribute of ecosystem engineering, potentially enhancing community diversity on broader scales and governing larger ecosystem processes (Romero & al. 2015, Farji-Brener & Werenkraut 2017). Engineers' impacts on the physical environment operate through altering abiotic conditions, modifying consumable resources, and / or influencing nontrophic resources (i.e., living spaces) (Sanders & al. 2014, Sanders & Frago 2024). Communities of engineers in a habitat create mosaics of different soil structures as well as varying concentrations of organic matter and nutrients (Boulton & Amberman 2006, Lavelle & al. 2016). Such small-scale impacts can accumulate into the landscape as long-term effects, with downstream consequences for ecosystem functioning and services being dependent on diversity effects (Nkem & al. 2000, Lavelle & al. 2006, Feng & al. 2022). Particularly, if a single dominant species (or trait) is linked to an ecosystem function, then the abundance or biomass of that species (or traits) in a community will be more important in predicting that function (mass ratio hypothesis; Grime 1998). Alternatively, functions may be dependent on contributions from many different individuals (or traits) to be fully realized (complementarity hypothesis; Díaz & Cabido 2001, Tilman & al. 2001). For example, the diversity of nest construction strategies may not mitigate erosion as effectively as having high density of larger compact nests in an area (which last longer and offer overall better resistance) (Paton & al. 1995). Alternatively, ant-derived variability in nutrient concentration can indirectly increase soil resilience towards erosion by increasing its heterogeneity, preventing plant invasions and structural homogenization (Lavelle & al. 2006). Subsequent research should transit from concentrating on local-scale mechanisms to encompassing community-scale dynamics to adequately comprehend and address the impact of engineering on the delivery of ES (Mace & al. 2012, Lavelle & al. 2016).

Ecosystem services are essentially what human societies obtain, in terms of direct or indirect goods or well-being, from ecosystems functioning. There is extensive research that causally connects biodiversity with functioning, thus with service provision (Balvanera & al. 2006), elucidating the potential connecting mechanisms (Srivastava & Vellend 2005). The supply of services, measured as ecosystem functioning, is usually the only component considered in service provision studies in the natural sciences (Metzger & al. 2021). For example, taxonomic and functionally diverse communities of insects can deliver a greater number of services than less diverse communities (fruit yield: Klein & al. 2003, nutrient cycling: Beynon & al. 2012). In fact, biodiversity showed to be a key factor for stable service provision in the short- and long-term through different mechanisms (Beynon & al. 2012). There is also a growing trend to evaluate the multifunctionality of ecosystems, or their capacity to provide more than one function or service at the same time (Hector & Bagchi 2007, Lefcheck & al. 2015). The connection between biodiversity and multifunctionality is even stronger, thus diverse communities and landscapes better fulfill multiple functions and services (Hector & Bagchi 2007, Gamfeldt & al. 2013). For instance, in an experimental mesocosm, functionally diverse dung beetle treatments were more important to provide higher levels of three ES (Manning & al. 2016). At the landscape scale, efficient and diverse service provision is better guaranteed by higher beta diversity and diverse local communities (Van Der Plas & al. 2016, Brockerhoff & al. 2017, Van Der Plas & al. 2018). Practically, the connection between biodiversity and ES is complex and can be approached in various ways (Mace & al. 2012); for ants and ant engineering, most of the examples given here connect their diversity with the regulation of ecosystem processes, therefore, providing services directly and indirectly.

Engineers as ecosystem service providers

Several ecosystem services are known to be directly or indirectly provisioned by ants (Del Toro & al. 2012, Perfecto & Philpott 2023), some being the result of their diverse engineering activities detailed previously (Fig. 1). Instead of listing engineering as a supporting service itself, in this review, however, we prefer to classify engineering activity as an ecological process mediated by ants' individual- and colony-level traits, which accumulate in the landscape leading to the provision of regulation of environmental processes. Such distinction avoids confusion in understanding the relationship between biodiversity and ES (Mace & al. 2012). Further, the end product of these engineering activities – in most cases the nest – is itself contributing with material and non-material services to people, thus being an indirect link between both roles.

In general, studies only refer to the connection of ecosystem functions and services without quantification or valuation efforts. In this section, we provide an overview of these studies on engineering-related ES and disservices, mostly from the perspective of service supply.

Material services

Typically, the material services attributed to ants are derived from their bodies, as many ant species are used for food (Rastogi 2011), and not their built structures. However, a few examples exist where the construction materials used in nest building, the end product of the engineering process, are potential goods for humans. In the case of *Oecophylla* spp., the final-instar larvae produce silk used in stitching leaves together to form a nest (Crozier & al. 2010), these natural nanofiber membranes possess unique features that makes them suitable for potential medical applications (Reddy & al. 2011). Additionally, *Oecophylla* spp. silk may be utilized as biomaterial, such as a cell matrix (Siri & Maensiri 2010) with application in various biotechnological fields including tissue culture, drug loading, biosensoring, biodegradable solar cells, and artificial nerve tubes (Prajwal & al. 2015). In Africa, nest extract from *Oecophylla longinoda* was also used as treatment for asthma or severe coughing (Van Huis 2003). Similarly, the Paniyan tribe of Southern India would treat scabies with the mud found in ant nests (Wilsanand & al. 2007). While such practices may be rooted in tradition, potentially serving as part of cultural identity, there is a significant chance that medically novel and important products can arise from such practices (Seabrooks & Hu 2017). Finally, *Rhytidoponera mayri* (Emery, 1883) nests in Australia showed to be potential indicators for geochemical explorations and prospecting of gold, copper, and zinc (Stewart & Anand 2014).

Regulation of environmental processes

Ants' engineering activities give support and regulate many ecosystem processes that can be advantageous to humans, including regulation of freshwater flow through the soil (Li & al. 2014, 2017, Leite & al. 2018), erosion and runoff (Cerdà & Jurgensen 2008, Cerdà & al. 2009, Li & al. 2017), regulation of climate (Wu & al. 2013), regulation of nutrient cycles (Lavelle & al. 2006), and formation and decontamination of soils (Lei 2000, Swanson & al. 2019, Viles & al. 2021). The magnitude of their effects can vary according to their traits and is usually uncoupled from human demand, except in agroecosystems.

Multiple regulating services are provisioned by ants due to their engineered changes to soil physical and chemical properties. An experiment found that farmland with ants and termites showed an increase in crop yield by 36% due to improved water infiltration (Evans & al. 2011). Another study showed that plots with active ant nests had, on average, 60% higher water infiltration rate in an orange orchard, where soil properties get altered under intensive herbicide application and machinery use (Cerdà & Jurgensen 2008). Moreover, habitat and ecosystem restoration are other possible benefits; ant nests promote water infiltration and retention of deep-rooted plants, which eventually reduces vegetation loss in desert areas that have been revegetated (Li & al. 2014). Further, the reintroduction of *Camponotus japonicus* Mayr, 1866 in the Loess Plateau (China) improved water infiltration and lowered water evaporation around the nest, potentially contributing to revegetate that area (Li & al. 2017).

Ants have been extensively studied as important bioindicators. Ant species richness, density, diversity, and even identity have all provided insight into the soil quality in mine sites and agricultural lands (Majer 1983, Peck & al. 1998, Venuste & al. 2018, Kavehei & al. 2021). Soil cycling and bioaccumulation of heavy metals in ant workers highlight how important ants can be for the restoration of sites and the positive consequences for human well-being (Grześ 2010). Concentrations of several heavy metals have been detected in harvester ants (*Pogonomyrmex rugosus* Emery, 1895) residing near an inactive copper and lead smelter (Del Toro & al. 2010), and wood ants (*Formica lugubris* Zetterstedt, 1838) which accumulate high levels of heavy metals in proximity to a cobalt smelter in Finland (Skaldina & al. 2018). Above findings suggest that ants can serve as reliable surrogates for assessing heavy metal contamination. In coal mines, two ant species, *Cataglyphis longipedem* (Eichwald, 1841) and *Camponotus compressus* (Fabricius, 1787), consistently demonstrated bioaccumulation of heavy metals in levels greater than grasshoppers; moreover, *C. longipedem* exhibited higher levels of zinc and manganese due to their excavation activities, while *C. compressus* showed elevated iron content attributed to their consumption of plant-derived liquids (Khan & al. 2017, Khan & al. 2023).

Non-material services

Non-material services provided by ant engineers are relatively uncommon, primarily manifested through their remarkable nest-building activities. Here too, the results of the engineering process, by being a physical, objective part of a landscape, provide non-material services to humans in an indirect pathway between engineering and services. The intricate underground ant colony nests have inspired civil engineers and architects in terms of ant mound bionics, structures, and materials (Garcia-Holguera & al. 2016, Yang & al. 2022, Belachew & al. 2024). Indeed, leaf-cutting ants provide such inspiration for engineering application by showcasing their ability to control their nest microclimate. In a nest of *Acromyrmex heyeri* (Forel, 1899), workers maintain a stable nest temperature by actively modifying the nest structures (Bollazzi & Roces 2010), and similarly, workers of *Atta vollenweideri* Forel, 1893 design the nest openings with turrets to facilitate the wind-induced nest ventilation (Kleineidam & al. 2001). As a result of nest excavation, some species (e.g., *Messor barbarus*) have potential use in paleontological prospection (Martín-Perea & al. 2019).

Ant nests also play an important role in religious rituals and superstition. For instance, in sub-Saharan Africa, people make offerings on the ant nest as a means of expelling demons (in Mali and Niger), as these nests are often associated with spiritual beliefs, and it is believed that rainbow snakes emerge from ant nests to stop the rain in Niger and Sudan (van Huis 2021). It is important to note that the relevant ant species involved in these rituals are not mentioned by the author. More interestingly, anthills are occasionally referenced in literature, as an indicator of, for example, "potential regeneration" (Opata 2003) or "an indictment" (Wozniuk 2008). To clarify, termite mounds, with conspicuous aboveground structures, are sometimes mistakenly referred to as anthills. Hence, when anthills are documented as a bionic object of the underground city of Cappadocia in Turkey (Yang & al. 2022) or a venue where locals conduct ritualized worships in many parts of India (Shulman 1978, Irwin 1982), they are constructed by termite workers rather than ants.

Services provided by communities of engineering ants

The nest building and central foraging traits of ants make them all potential contributors, though to different degrees (e.g., see Nooten & al. 2022, Bogar & al. 2024), to the same ecosystem processes. More interestingly, however, is to utilize the effects of their species-specific traits that potentially create a mosaic of outcomes to a service in question. Ant-engineering effects to ecosystem processes and services at community- and landscape- levels are less studied and remain speculative, as well as the accuracy of scaling up the well-studied effects of some species. Therefore, we present some examples and directions for future studies in this area.

Services provided by ant communities

As mentioned previously, researching ant assemblages can give us a more realistic understanding of their impact on functioning and services provision (and multifunctionality) by including potential interactions and the net effect of their diverse life histories. The net outcomes of local and regional processes and supply of services are contingent, among other factors, on the components of the respective ant fauna (Perfecto & Philpott 2023), including its functional components (Cadotte & al. 2011, Wong & al. 2019). Functional diversity is high among soil-nesting ants, related to their nest building and foraging activities, creating a true mosaic of conditions and resources for other organisms by increasing soil-nutrient-profile heterogeneity (Farjí-Brener & Werenkraut 2017, Viles & al. 2021), which differentially affects plant and microbial communities by influencing their fitness (Boots & al. 2012, Farjí-Brener & Werenkraut 2017), and reflects on landscape-level heterogeneity (Cammeraat & Risch 2008). This might be especially true for those regions containing, among other ants, species that are recognized as important ecosystem engineers, like leafcutter ants, harvester ants, *Formica* spp., and others.

The direct contribution of ant engineering to the water cycle and soil maintenance, plus the promotion of diverse soil microbiome and plant root growth (Gyssels & al. 2005, Boots & al. 2012, Hao & al. 2021), which affect the carbon cycle, are all expected to have important outcomes to climate regulation, a service that is of utmost importance considering the effects of anthropogenic climate change. Wu & al. (2013), in a well-rounded experiment, quantified the contribution of the three most abundant ant species in a marsh to the production of important atmospheric gasses, as well as the net ecosystem production based on nest densities and total area studied (a landscape-scale outcome). Ant nests acted as sources of carbon dioxide but sinks of methane. Therefore, they bring essential information to properly quantify the role of ant engineering in marshlands, directly or indirectly through microorganisms, to the balance of greenhouse gasses and nutrient cycles, and ultimately, to the supply of climate regulation services, or potentially disservices.

The contribution to soil-based ES is part of what ant engineering does, as they further contribute to structuring of local plant communities and their fitness by promoting seed dispersal, creation of ant gardens, clearings in forests, and above- and belowground growth (Farjí-Brener & Werenkraut 2017). All these processes contribute at some level to primary production and community heterogeneity (Rissing 1986, Nkem & al. 2000, Romero & al. 2015, Hansen & al. 2023). Even though ant engineering does not promote plant diversity according to the meta-analysis of Farjí-Brener & Werenkraut (2017), we argue that community-level studies are necessary to answer this question fully as the mosaic of conditions created by ant communities cannot be properly captured by the synthesis of distinct population-level studies, the primary source for this article. One good example of ant community engineering that results in provisioning service comes from Zhong & al. (2021). In this article, they demonstrate how ants' improvement of soil bulk density, together with grazers' improvement of soil N levels, facilitate plant biomass accumulation that offsets negative grazing effects. This system provides carbon uptake and primary production (regulating), meat production in agroecosystems (provisioning), and other grassland-related services (Dauber & al. 2006, De Almeida & al. 2020a,b).

Finally, ant engineering promotes habitat creation and maintenance for a variety of organisms that use nests or ant gardens in some way (myrmecophiles) (Hölldobler & Kwapich 2022, Campbell & al. 2023), but they also promote biodiversity and maintenance of options with their capacity to diversify conditions (e.g., microhabitats) and modulate resources to other organisms (Jones & al. 1994, Romero & al. 2015). Maintenance of options is a fourth category of services recently identified by the IPBES that is important for human well-being as we walk towards a future with greater consequences of anthropogenic climate change (IPBES 2019).

Disservices provided by engineering ants

Ant engineering can also contribute in negative ways to an ecosystem process, production of goods (plants and agriculture crops), or even human infrastructure; all of which are termed ecosystem disservices to humans. Many of these disservices, however, typically involve invasive ant species or ant populations that become a problem by being overabundant (Holway & al. 2002). Leafcutter ants, which have been extensively studied, are known for the potential disservices they provide by building immense nests. The first concern comes from their disturbances to the soil structure, altering soil aeration and temperature, thus affecting microbial and organic matter decomposition in the soil (Swanson & al. 2019). These changes may reduce soil fertility and water retention, which can affect vegetation growth and promote the establishment of invasive plants, and the invasive plants may further affect the soil environment (Farjí-Brener & al. 2010, Xu & al. 2022). In another aspect, leafcutter ants can promote soil subsidence due to the sheer volumes of soil they move, causing potential accidents by weakening the structures that support buildings (Montoya-Lerma & al. 2012). Another ant that can damage human-made structures is *Solenopsis invicta,* their excavation and removal of soil can damage roads, walkways, farming machinery, electrical equipment, and other public facilities (Vinson 2013). Ants can also become pathogen vectors in foraged plants, which lead to increased pathogen and infection load and impacts on plant health and agricultural productivity (El-Hamalawi & Menge 1996, Moyo & al. 2014, Bisseleua & al. 2017). This can be the case of *Phillidris* sp. that has been reported to transmit the spores of *Phytophthora palmivora* in tropical agroecosystems (Wielgoss & al. 2014).

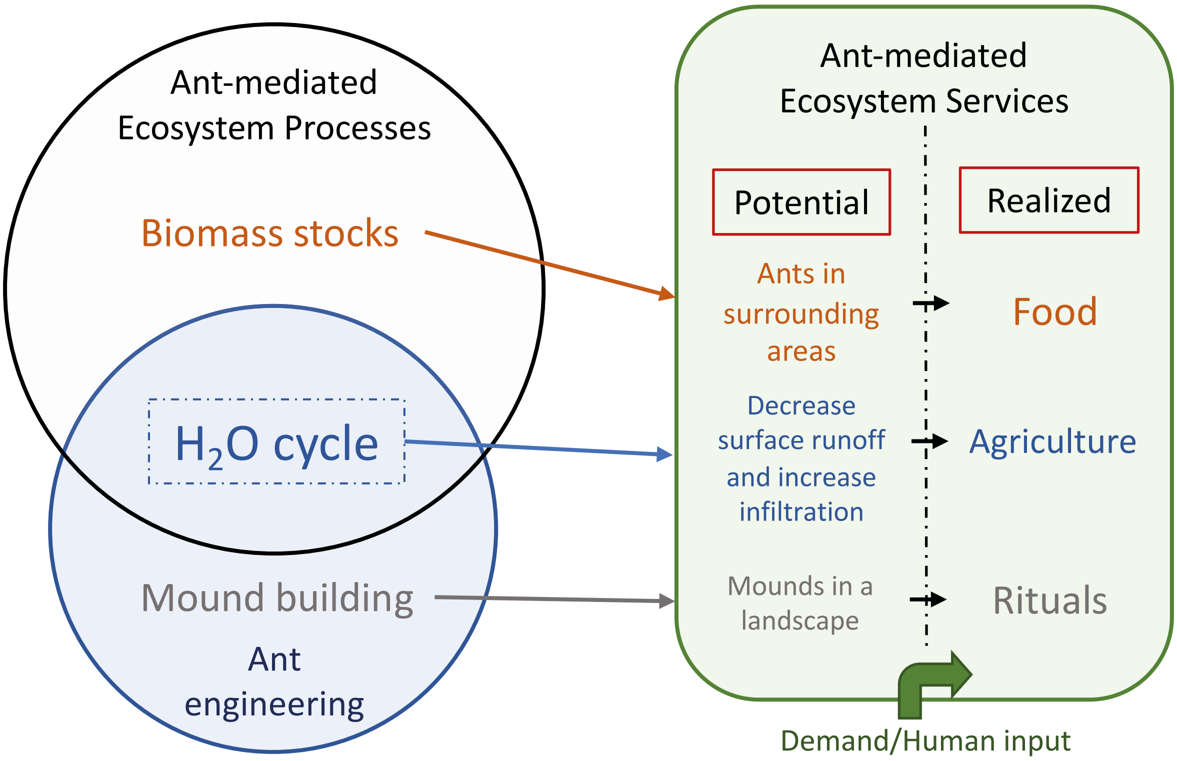

Fig. 3: A diagram showing the relationship between ant-mediated ecosystem processes and ES, mediated or not through ant engineering. Examples are given for each subcategory including the process, the potential service, and the realized service – in case there is demand and / or human input (green arrow).

Soil-nesting invasive ants, such as *Pheidole megacephala* (Fabricius, 1793), can negatively affect the surrounding plants by constructing underground nests near plant roots. This activity can directly reduce carbon fixation and storage in screenhouse-reared *Acacia drepanolobium* saplings (Milligan & al. 2022). Moreover, many invasive ants can harm agricultural crops through excavation around their roots (Holway & al. 2002). The yellow crazy ant, *Anoplolepis gracilipes*, has been documented to undermine the roots of several agricultural plants (Haines & Haines 1978, Lee & Yang 2022), and this can weaken the plants' root systems and thus, ultimately reduce crop yield. The disservices promoted by invasive species in most cases underscore the importance of managing and controlling them to reduce potential long-term impacts of their presence on human well-being.

Other aspects of ants' disservices were not included in this review because they are not directly linked to ant engineering, like native species displacement, "Invasional meltdown", and distress caused by home invasions, to name a few. These can be found, for example, in Del Toro & al. (2012).

Links between ant ecosystem engineering and ecosystem services

The rapid growth of population and urban centers based on an economical and technological model of predatory exploration of ecosystems has taken us to a point of accelerated environmental degradation (IPBES 2019, Wagner & al. 2021). However, it has also led to raised global awareness of our impacts and the intrinsic importance of nature to all processes responsible for sustaining life and human well-being (IPBES 2019). Therefore, considering the importance of ecological processes to life and human well-being, and the important contribution of ants to those processes, we believed it was time to review and compare their roles to answer the following questions: Can these two different roles of ants in ecosystems be interchangeably studied, meaning they are the same phenomenon of a system? Or only by combining both approaches we can reach a better understanding of these organisms' roles in the environment, meaning they are complementary or contrasting within a system? Throughout this review, we highlighted the nature and aspects of ants as ecosystem engineers and providers of ES through engineering, and now we lay our conclusions.

Conceptually, a connection between fields exists because the provisioning of ES is derived from ecosystem processes, of which engineering is a part of (see Box 1 for definitions of the relevant concepts above). From the definition itself it is possible, however, to separate what is the process (engineering), the material results of the process (in most cases the nest), and its outputs to humans (services). While logically, all engineering processes and their material results are potential services, not all potential services are derived from engineering processes and not all potential services will turn into realized services (Fig. 3).

Furthermore, both phenomena can be described by their actors, recipients, processes, measurable properties, and results. In the case of ants, ecosystem engineering and the potential service "Regulation of environmental processes" are directly linked by the same actor – ants, through the same processes and measurable properties, therefore, they can be considered the same phenomenon. Further, the result of engineering, the nest or nest space, is directly linked to potential "Material" and "Non-material" services. However, not being derived from the engineering process itself, provision of potential "Material" and "Non-material" services has an indirect link with ant engineering and cannot be described as the same phenomenon, as they do not share the same actor, processes, and measurable properties.

Now, in terms of the study of both phenomena, they were and still are often studied separately because of their conceptual and methodological differences, a consequence of the historical construction of both fields and of their focus (Berke 2010, Pesche & al. 2013). Historically, ES is a concept that slowly grew in importance and acceptance since the 70s in science and economy circles, reaching common acceptance in the late 90s. Its roots come from the need to bring the attention of policy makers to the threats posed to ecosystems by humans (Pesche & al. 2013). The "ecosystem engineering" concept, however, was coined by Jones & al. (1994), although the idea is present for many years in ecological studies. Since then, it is a topic of debate between ecologists, evolutionists, and philosophers on its validity and breadth (see Berke 2010 for a review on the topic).

From this historical construction, we observe the use of two distinct methodologies. While studies of ecosystem engineering use ecological methods to understand ecosystem processes, studies of ES utilize both ecological and socio-economical approaches to understand the supply, demand, and flow of services (see Box 1) (Metzger & al. 2021). The latter is also a field with extensive synthesis and a "distributed research, assessment, and decision support system" (Pesche & al. 2013) that bridges the developments of the field with policy makers and stakeholders. Finally, these two concepts have different perspectives on the same process. Engineering is concerned with the organismic / ecosystem-centric measure and output of processes, while ES is concerned with the human / society-centric measure and output and the bridge between function and service, the demand and flow. To sum up, while engineering may support a variety of services directly or indirectly, it is not a one-to-one comparison, and for services to be met, there must be human demand and input (Spangenberg & al. 2014; Fig. 3).

Considering the relevance of ants to the environment as extensively shown in the previous sections and their widespread presence and abundance (Schultheiss & al. 2022), it is time to combine the study of these roles and directly quantify ants' importance to the sustenance of humans' well-being on Earth. The extensive literature and literature synthesis on ant engineering should facilitate research development on ant-mediated ES, from identification, to mapping and quantification (Romero & al. 2015, Farjí-Brener & Werenkraut 2017), because these studies have mapped important engineering guilds and ecosystems affected that can be a starting point for research on the demand and flow of service provision. Additionally, ant engineering researchers could garner valuable attention to their research if clearer connections and quantifications were done regarding the impacts of ant engineering to human well-being. Adding humans to the equation better captures the reality of today's ecosystems. It could potentially bring important investments for conservation and management of areas and populations of ants, either native or exotic, especially those that have stronger impacts on ecological processes or services.

Scale

Beyond the differences already presented, it is also worth mentioning the relevant scales concerning each concept. For studies on ant-mediated services, relevant spatiotemporal scales range from the size or duration of a single nest to a whole landscape and its existence through time, dealing with individual colonies, to populations and communities (Lavelle & al. 2006). The scope for engineering is slightly smaller; as ecological studies require replication, a single nest does not typically serve as the sole research source. This often leads to investigations at larger spatiotemporal scales. The study of both roles of ants is limited, though, by the capacity of researchers to collect relevant data, especially at larger scales. Furthermore, there is a lack of cross-scale studies in these disciplines that hinders predictions on the impacts of processes in other scales, referred to as scalability (Wheatley & Johnson 2009). This is important because fine-scale local processes have impacts on larger spatiotemporal scales (Lavelle & al. 2006, Cammeraat & Risch 2008). For instance, most soil-based ES are perceived at the landscape scale, yet the structures that affect these services' delivery are built by individual engineer units, so that modifying soil structure in a local scale can influence services such as water supply or erosion prevention (detailed in Lavelle & al. 2016).

Ant engineering studies typically focus on describing the impacts of species, the engineers, at the population level (Farjí-Brener & Werenkraut 2017); however, we already stressed the importance of community-level studies to understand these processes in other scales. The scale at which an ecosystem service is relevant depends on the scale that an ecosystem process operates and on the demand size. Whether it is ant colonies in a hillslope or colonies in a garden, it is important to know that for each specific service different supplier units of interest are relevant (Andersson & al. 2015, Malinga & al. 2015). Thus, the scales at which "ecosystem services" can be analyzed are broader than for ecosystem engineering, in a similar fashion to Figure 3. Wheatley & Johnson (2009) provide a good review of the common pitfalls and solutions to design multi- and cross-scalar studies in ecology, the key being to vary the grain or extent in the study while keeping the other factors fixed.

Future Directions

The study of ants as ecosystem engineers and mediators / providers of ES is a prolific field of myrmecological research. From the time that Del Toro and collaborators (2012) wrote their review on the topic, ecosystem service research has continued to grow in importance (Tab. 1 for a list on the topic). Here, we delineate a few topics that have great potential to bridge the topics approached in this review, further contributing to understand ants and their contribution to ecosystem processes and human well-being worldwide.

Ant communities

Larger ants, or ant species with big colonies, are responsible for big engineering impacts on the ecosystem, and consequently, service provision. However, to fully understand how service provision happens in different contexts, it is important to study not only key species, but whole ant communities. For instance, if the engineering effect of a single species does not promote plant diversity (Farjí-Brener & Werenkraut 2017), the accumulation of many species may promote overall nutrient heterogeneity (or homogeneity) across the landscape, shaping community structure (Jouquet & al. 2007). Furthermore, the significance of complementarity becomes more evident when viewed through the lens of multifunctionality (Van Der Plas & al. 2016), where different members of the myrmecofauna contribute asymmetrically to different ecosystem processes (Jouquet & al. 2007, Lu & al. 2019).

To effectively analyze the impact of ant engineering communities on ecosystem function and service provision, it is crucial to know their community composition, nesting habits, and nest density (Cammeraat & Risch 2008, Viles & al. 2021). Despite being hard to quantify those variables, studies like De Almeida & al. (2020a) and Wu & al. (2013) had success; both quantified ant nest density and different biotic and abiotic variables to explore the influence of ant engineering on diverse ecosystem processes and their ability for restoration. The difficulties can be partially solved by doing experiments in amenable conditions where more variables are controlled (e.g., total diversity, and more desirably, the total density), and then interesting metrics can be assessed with more ease. This is achievable in human-made environments, like orchards, agroecosystems, and greenhouses, but also in certain simple biomes like deserts, characterized by lower structural complexity and diversity. To give an example of a service outside of engineering scope, Bisseleua & al. (2017) opted for a cocoa agroforestry system to examine the impact of ant communities and individual dominant ant species (*Crematogaster* sp. and *Oecophylla longinoda*) on cocoa tree yield. In their design, they measured the net outcome between pest predation and disease spread (by walking on the leaves), thus accounting not only for individual and community effects but also for the balance between services and disservices, concluding that ant diversity had a net positive effect on cocoa yield. Similarly, the incorporation of individual and community effects into ant engineering and ecosystem service provision is likely to yield fresh insights in both fields.

Understudied biomes and locations

The supply of services by ants may be more prominent in certain landscapes, biomes, or regions due to pedological / geological (landscape structure, type of soil, elevation, rugosity, slope), evolutionary (coevolution), ecological (density, interactions, community composition), and anthropogenic (demand, coupling, flow, disturbances) variables. For example, leafcutter ants and their effects are restricted to the southern Nearctic and Neotropical regions. Moreover, myrmecochory is more important in Mediterranean biomes (Lengyel & al. 2010, Luo & al. 2023), and finally, soil nutrition in consequence of ant engineering seems to be more important in arid and semi-arid regions, because their baseline is lower than in other regions (Farji-Brener & Werenkraut 2017). Thus, analyzing Farji-Brener & Werenkrauts' (2017) meta-analysis according to countries and biomes included, we found that studies on Temperate Broadleaf & Mixed Forests and Temperate Grasslands, Savannas & Shrublands were the most abundant, with 19 and 15 studies, respectively, mainly from Europe and the Americas (Fig. S1, as digital supplementary material to this article, at the journal's web pages). However, there were no studies or only a few in other grassland biomes of the world (Montane, Flooded Grasslands, Tropical Grasslands) which could also have ants contributing significantly to ecosystem functions and services (Tab. S1, Supplementary Material). Considering the high abundance of ants in tropical forests and savannah (Schultheiss & al. 2022), future focus on these biomes may be particularly promising. Overall, this highlights the uneven distribution of studies on ant engineering and service provision in different biomes and provides guidance for future research locations.

Invasive ants: aiding or disrupting services?

The escalating proliferation of invasive ant species has persistently posed risks to both ecosystem and human well-being (Angulo & al. 2022, Wong & al. 2023). Exotic species have the capacity to modify ecosystem processes through their trophic and non-trophic interactions, which can subsequently propagate through other processes (Cameron & al. 2016, Rilov & al. 2024). Alternatively, through engineering activity, they may influence the size and accessibility of specific resource pools (Ehrenfeld 2010), altering community structure and service provision. An example of this is their effects on soil structure and chemical composition. *Linepithema humile* (Mayr, 1868), the Argentine ant, have short-lived, shallower nests than native species, with a lower contribution to soil turnover and accumulation of nutrients and organic matter in invaded plots (Suarez & al. 1998, Holway & al. 2002). This can affect the accessibility to resources for plants and microfauna in invasion fronts. However, more research is needed on this topic to ascertain their contribution compared with native ants (Lach & Hooper-Bùi 2010).

Apart from posing a significant threat to human health through antagonistic interactions, invasive engineering activity near humans can cause significant damage to critical infrastructure (Luo 2005, Zhao & al. 2008, Siddiqui & al. 2021). Conversely, evidence suggests that invasive species provide certain services by themselves, including increasing the soil nitrogen (Rilov & al. 2024), fertility (Lafleur & al. 2005), or promoting biological control (Eubanks 2001). Because the knowledge about these positive impacts on processes is still shy compared with their negative impacts, and because of the increasing risk of invasions globally, it is important to explore the role of invasive ecosystem engineers to the services or disservices they provide, in order to develop effective management strategies to mitigate disservices and promote the services offered by them.

Ants as ecological engineers

Using biological means to assist in habitat restoration, such as planting nitrogen-fixing plants to improve soil nutrient levels (Macedo & al. 2008) or inoculating earthworms to modify soil physical properties (Blouin & al. 2013), has a long history in restoration ecology. As reviewed in this paper, ants play a crucial role in regulating soil bio-physicochemical properties and act as soil engineers. However, harnessing their services and applying them in restoration programs is still in its early stages, despite their potential to actively participate in and promote soil restoration processes (De Almeida & al. 2023). For instance, a study by De Almeida & al. (2020a) highlights the role of *Messor barbarus* in accelerating the restoration of Mediterranean grasslands through its soil modification capacities.

Nevertheless, to harness the soil modification services provided by ants, a key question arises: How can we introduce the "right" species and the appropriate number of individuals or nests that will effectively perform the desired service? Furthermore, when considering the introduction of ants, restoration managers must also decide on the approach to be used. This could involve direct inoculation, where ant species with the desired traits are stocked into the degraded area, or indirect methods, where the area is modified to facilitate colonization by suitable ant species from nearby areas, thus achieving the goal of soil modification (e.g., De Almeida & al. 2020a). Both approaches present challenges and gaps that need to be overcome. This is the case for species of the *Formica rufa* group, intentionally introduced previously for biological control purposes in Italy (Apennines in the 1950s) and Canada (Valcartier, Quebec in the 1970s) (Storer & al. 2008, Seifert 2016, Frizzi & al. 2018). The consequences of these introductions to local soil processes or their capacity to be used in restoration programs are unknown to this point. Furthermore, the continuous surveillance of these ants, which did not happen, is an example of what should not be done in any attempted restoration. Unpredictable consequences can arise from introducing any new species to an ecosystem, even if closely related to some of the ants already found locally, which was the case in these two regions (Storer & al. 2008, Frizzi & al. 2018).

The direct approach may face challenges related to the availability of local ant species that are suitable for the intended purpose, as they may not be commercially available. Additionally, for indirect methods, the degraded habitat may not initially be suitable for the target ant species to establish a presence, requiring further habitat modification. Moreover, this method also does not provide full control over the species and the extent of the engineering function they can perform. Implementing either approach necessitates a comprehensive understanding of ant ecology and the ability to determine the appropriate number of colonies or fertilized queens needed for a particular area to achieve the desired restoration outcome. However, compared with plants, earthworms, and termites, which have long been recognized as ecological engineers (Jouquet & al. 2014), information on ant species engineering properties and function may not be readily available.

Therefore, further research is needed to investigate which ant species would be suitable candidates for restoration efforts and to determine their contribution during this process. A functional trait-based approach would be effective for development in this regard (Auclerc & al. 2022, Merchant & al. 2023). It is important to note that ant species composition is influenced not only by habitat types but also by geographic regions. Understanding which species possess the potential to act as ecological engineers in one location may have limited application in restoration programs elsewhere. Therefore, by identifying functional traits that are linked to specific modifications in soil properties, we can generalize the findings and apply them more broadly. With the rapid development of trait-based ecology and the application of nature-based solutions, we believe this will foster more studies and experiments involving the use of ants as ecological engineers in the field of restoration ecology.

Valuation of engineering services

Human society demands the valuation (monetarily) of goods and services to raise interest (Villamagna & al. 2013). However, ES were not included in this valuation for most of our modern history; and to make matters worse, they have been quantified without consensus on the method, going from market-based to science-based ones (Sagoff 2011, Tallis & al. 2012). In addition, ES demand is, in many studies, lacking in numerical values (Schägner & al. 2013). In contrast, disservices are better evaluated and quantified. For example, major invasive species data related to direct and indirect (i.e., administrative, agricultural, health-related, etc.) costs are available through InvaCost database (Diagne & al. 2020). This database is not exhaustive, yet it is the most complete to date (Angulo & al. 2022, Hulme & al. 2024). Most of ants' engineering-related services are harder to assess in terms of financial benefits to humans considering their uncoupled, complex nature. Therefore, to better valuate these uncoupled services, at least the supply offered by ant communities must be quantified. The demand and flow should be considered together and in context, and the progress in the field can be observed with new methods and their proposed metrics (Serna-Chavez & al. 2014, Wolff & al. 2015). Moreover, non-material services are usually difficult to value, yet there are studies available, such as Plieninger & al. (2013), which combined land cover and structured surveys to assess and quantify different non-material services to the land use type, of which myrmecologists could base their assessments of ant non-material services on.

In recent years, ES valuation is expanding in the number of studies, geographical extension, and methodology of analysis (de Groot & al. 2012, Brander & al. 2024). Brander & al. (2024) created the Ecosystem Services Valuation Database (ESVD), analyzing 1300 studies worldwide. During their review, they acknowledged some of the gaps and limitations, such as the importance to increase data collection in underrepresented biomes, as well as to account for unbalanced region representation, which is also valid for ants. Further, some ES might have trade-off effects among them that should be accounted for to obtain trustable values. Like for other taxa, we need to develop valuation methods that embrace the particularities of services derived from ant engineering, especially regulatory services, which originate mainly from soil-based processes and are usually physically disconnected from the regions that seek and benefit from such services (i.e., human populated regions).

Conclusions

As important ecological engineers in nature, ants have far-reaching impacts on the physical properties, chemical composition, and biodiversity of soils through the construction of complex nest structures from the soil to the canopy, extensive food collection and distribution, and multiple symbiotic relationships with other organisms. All these activities contribute to the well-being of human societies in direct or indirect ways. Only by studying them together we can improve our understanding of the connection between their activities and our life quality. In sum, enhancing our comprehension of ants as ecosystem engineers and service providers requires a comprehensive research approach that joins empirical studies, theoretical modeling, and applied conservation efforts, paving the way for biodiversity promotion, ecosystem resilience enhancement, sustainable natural resource management, and promotion of healthy ecosystems and human societies.

Acknowledgments

We would like to thank the other members of the Insect Biodiversity and Biogeography Laboratory for their initial contribution to this project. In addition, the authors would like to thank the funding sources and more specifically for FPR funded by a HKU Presidential PhD Scholar Programme (2021/22), AIW funded by GRF17121922, JH & SAK funded GRF17117020, ML & SAK funded by NSFC/GRF N_HKU792/22 and YLN funded by Lantau Conservation Fund RE-2021-14. Finally, the authors would like to thank the reviewers and editor for their constructive and valuable comments on an earlier version of the manuscript.

Declaration on use of generative artificial intelligence tools

The authors declare that they did not utilize generative artificial intelligence tools in any part of the composition of this manuscript.

References

Abson, D.J. & Termansen, M. 2010: Valuing ecosystem services in terms of ecological risks and returns: economic valuation of ecosystem services. – Conservation Biology 25: 250-258.

Agarwal, S., Sharma, G., Verma, K., Latha, N. & Mathur, V. 2022: Pharmacological potential of ants and their symbionts – a review. – Entomologia Experimentalis et Applicata 170: 1032-1048.

Akino, T., Turushima, T. & Yamaoka, R. 1995: 3-formyl-7, 11-dimethyl-(2E, 6Z, 10)-dodecatrienal: antifungal compound in the mandibular gland of the ant, *Lasius fuliginosus* Latreille. – Journal of the Agricultural Chemical Society of Japan 69: 1581-1586.

Anderson, C. & McShea, D.W. 2001: Intermediate-level parts in insect societies: adaptive structures that ants build away from the nest. – Insectes Sociaux 48: 291-301.

Andersson, E., McPhearson, T., Kremer, P., Gomez-Baggethun, E., Haase, D., Tuvendal, M. & Wurster, D. 2015: Scale and context dependence of ecosystem service providing units. – Ecosystem Services 12: 157-164.

Angulo, E., Hoffmann, B.D., Ballesteros-Mejia, L., Taheri, A., Balzani, P., Bang, A., Renault, D., Cordonnier, M., Bellard, C., Diagne, C., Ahmed, D.A., Watari, Y. & Courchamp, F. 2022: Economic costs of invasive alien ants worldwide. – Biological Invasions 24: 2041-2060.

Anjos, D.V., Andersen, A.N., Carvalho, R.L., Sousa, R.M.F. & Del-Claro, K. 2020: Switching roles from antagonist to mutualist: a harvester ant as a key seed disperser of a myrmecochorous plant. – Ecological Entomology 45: 1063-1070.

Anjos, D.V., Tena, A., Viana-Junior, A.B., Carvalho, R.L., Torezan-Silingardi, H., Del-Claro, K. & Perfecto, I. 2022: The effects of ants on pest control: A meta-analysis. – Proceedings of the Royal Society B-Biological Sciences 289: art. 20221316.

Arnan, X., Cerdá, X. & Retana, J. 2014: Ant functional responses along environmental gradients. – Journal of Animal Ecology 83: 1398-1408.

Assis, D.S., Morris, S. & Nascimento, F.S. 2017: "Empty spaces 'Where' we are living for" – first record of *Dinoponera quadriceps* reusing nests of *Atta sexdens*. – Sociobiology 64: 130-132.

Assis, J.C., Hohlenwerger, C., Metzger, J.P., Rhodes, J.R., Duarte, G.T., Da Silva, R.A., Boesing, A.L., Prist, P.R. & Ribeiro, M.C. 2023: Linking landscape structure and ecosystem service flow. – Ecosystem Services 62: art. 101535.

Attygalle, A.B. & Morgan, E.D. 1984: Chemicals from the glands of ants. – Chemical Society Reviews 13: 245-278.

Auclerc, A., Beaumelle, L., Barantal, S., Chauvat, M., Cortet, J., De Almeida, T., Dulaurent, A.-M., Dutoit, T., Joimel, S., Séré, G. & Blight, O. 2022: Fostering the use of soil invertebrate traits to restore ecosystem functioning. – Geoderma 424: art. 116019.

Azcárate, F.M. & Peco, B. 2007: Harvester ants (*Messor barbarus*) as disturbance agents in Mediterranean grasslands. – Journal of Vegetation Science 18: 103-110.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D. & Schmid, B. 2006: Quantifying the evidence for biodiversity effects on ecosystem functioning and services. – Ecology Letters 9: 1146-1156.

Beattie, A.J. 1985: The evolutionary ecology of ant-plant mutualisms. – Cambridge University Press, New York, NY, 196 pp.

Belachew, M., Yamamoto, K., Nichols, E., Zhang, D., Frost, J.D. & Arson, C. 2024: Ant nest geometry, stability, and excavation – inspiration for tunneling. – Acta Geotechnica 19: 1295-1313.

Berke, S.K. 2010: Functional groups of ecosystem engineers: a proposed classification with comments on current issues. – Integrative and Comparative Biology 50: 147-157.

Beynon, S.A., Mann, D.J., Slade, E.M. & Lewis, O.T. 2012: Species-rich dung beetle communities buffer ecosystem services in perturbed agro-ecosystems. – Journal of Applied Ecology 49: 1365-1372.

Birkhofer, K., Diehl, E., Andersson, J., Ekroos, J., Früh-Müller, A., Machnikowski, F., Mader, V.L., Nilsson, L., Sasaki, K., Rundlöf, M., Wolters, V. & Smith, H.G. 2015: Ecosystem services – current challenges and opportunities for ecological research. – Frontiers in Ecology and Evolution 2: art. 87.

Bisseleua, D.H.B., Begoude, D., Tonnang, H. & Vidal, S. 2017: Ant-mediated ecosystem services and disservices on marketable yield in cocoa agroforestry systems. – Agriculture, Ecosystems & Environment 247: 409-417.

Bitar, M.R., Pinto, V.D., Moreira, L.M. & Ribeiro, S.P. 2021: Gram-negative bacteria associated with a dominant arboreal ant species outcompete phyllosphere-associated bacteria species in a tropical canopy. – Oecologia 195: 959-970.

Blomqvist, M.M., Olff, H., Blaauw, M.B., Bongers, T. & Van Der Putten, W.H. 2000: Interactions between above- and belowground biota: importance for small-scale vegetation mosaics in a grassland ecosystem. – Oikos 90: 582-598.

Blouin, M., Hodson, M.E., Delgado, E.A., Baker, G., Brussaard, L., Butt, K.R., Dai, J., Dendooven, L., Peres, G., Tondoh, J.E., Cluzeau, D. & Brun, J.-J. 2013: A review of earthworm impact on soil function and ecosystem services. – European Journal of Soil Science 64: 161-182.

Blüthgen, N. & Feldhaar, H. 2010: Food and shelter: how resources influence ant ecology. In: Lach, L., Parr, C.L. & Abbott, K.L. (Eds.): Ant Ecology. – Oxford University Press, New York, NY, pp. 115-136.

Bogar, T.A., Nooten, S.S. & Guénard, B. 2024: Development of a new apparatus to partition ant body size reveals their respective functional role within ant communities. – Basic and Applied Ecology 74: 90-97.

Bollazzi, M. & Roces, F. 2010: Control of nest water losses through building behavior in leaf-cutting ants (*Acromyrmex heyeri*). – Insectes Sociaux 57: 267-273.

Boots, B. & Clipson, N. 2013: Linking ecosystem modification by the yellow meadow ant (*Lasius flavus*) to microbial assemblages in different soil environments. – European Journal of Soil Biology 55: 100-106.

Boots, B., Keith, A.M., Niechoj, R., Breen, J., Schmidt, O. & Clipson, N. 2012: Unique soil microbial assemblages associated with grassland ant species with different nesting and foraging strategies. – Pedobiologia 55: 33-40.

Boulton, A.M. & Amberman, K.D. 2006: How ant nests increase soil biota richness and abundance: a field experiment. – Biodiversity and Conservation 15: 55-68.

Brander, L.M., De Groot, R., Schägner, J.P., Guisado-Goñi, V., Van't Hoff, V., Solomonides, S., McVittie, A., Eppink, F., Sposato, M., Do, L., Ghermandi, A., Sinclair, M. & Thomas, R. 2024: Economic values for ecosystem services: a global synthesis and way forward. – Ecosystem Services 66: art. 101606.

Briese, D.T. 1982: The effect of ants on the soil of a semi-arid saltbush habitat. – Insectes Sociaux 29: 375-386.

Brockerhoff, E.G., Barbaro, L., Castagneyrol, B., Forrester, D.I., Gardiner, B., González-Olabarria, J.R., Lyver, P.O., Meurisse, N., Oxbrough, A., Taki, H., Thompson, I.D., Van Der Plas, F. & Jactel, H. 2017: Forest biodiversity, ecosystem functioning and the provision of ecosystem services. – Biodiversity and Conservation 26: 3005-3035.

Buhl, J., Deneubourg, J.L., Grimal, A. & Theraulaz, G. 2005: Self-organized digging activity in ant colonies. – Behavioral Ecology and Sociobiology 58: 9-17.

Bulot, A., Provost, E. & Dutoit, T. 2016: Refuse pile turnover by harvester ants (Hymenoptera: Formicidae) increases seed density and seedling species richness in dry grasslands. – Myrmecological News 23: 91-100.

Bush, S.E. & Clayton, D.H. 2018: Anti-parasite behaviour of birds. – Philosophical Transactions of the Royal Society B-Biological Sciences 373: art. 20170196.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. 2011: Beyond species: functional diversity and the maintenance of ecological processes and services. – Journal of Applied Ecology 48: 1079-1087.

Cairns, N.A., Rutherford, P.L. & Hoysak, D.J. 2018: Morphology, reproduction, habitat use, and hibernation of Red-bellied Snake (*Storeria occipitomaculata*) near its northern range limit. – The Canadian Field-Naturalist 132: 150-162.

Cameron, E.K., Vilà, M. & Cabeza, M. 2016: Global meta-analysis of the impacts of terrestrial invertebrate invaders on species, communities and ecosystems. – Global Ecology and Biogeography 25: 596-606.

Cammeraat, E.L.H. & Risch, A.C. 2008: The impact of ants on mineral soil properties and processes at different spatial scales. – Journal of Applied Entomology 132: 285-294.

Campbell, L.C.E., Kiers, E.T. & Chomicki, G. 2023: The evolution of plant cultivation by ants. – Trends in Plant Science 28: 271-282.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. 2012: Biodiversity loss and its impact on humanity. – Nature 486: 59-67.

Carlson, S.R. & Whitford, W.G. 1991: Ant mound influence on vegetation and soils in a semiarid mountain ecosystem. – The American Midland Naturalist 126: 125-139.

Caro, T. 2010: Conservation by proxy: Indicator, umbrella, keystone, flagship, and other surrogate species. – Island Press, Washington, D.C., 374 pp.

Cerdà, A. & Jurgensen, M.F. 2008: The influence of ants on soil and water losses from an orange orchard in eastern Spain. – Journal of Applied Entomology 132: 306-314.

Cerdà, A., Jurgensen, M.F. & Bodi, M.B. 2009: Effects of ants on water and soil losses from organically managed citrus orchards in eastern Spain. – Biologia 64: 527-531.

Céréghino, R., Leroy, C., Dejean, A. & Corbara, B. 2010: Ants mediate the structure of phytotelm communities in an ant-garden bromeliad. – Ecology 91: 1549-1556.

Cherret, J.M. 1989: Leaf-cutting ants, biogeographical and ecological studies. In: Lieth, H. & Werger, M.J.A. (Eds.): Tropical rain forest ecosystems. Biogeographical and ecological studies. Ecosystems of the world 14B. – Elsevier, New York, NY, pp. 473-488.

Coggan, N.V., Hayward, M.W. & Gibb, H. 2018: A global database and "state of the field" review of research into ecosystem engineering by land animals. – Journal of Animal Ecology 87: 974-994.

Corrêa, M.M., Silva, P.S.D., Wirth, R., Tabarelli, M. & Leal, I.R. 2016: Foraging activity of leaf-cutting ants changes light availability and plant assemblage in Atlantic Forest. – Ecological Entomology 41: 442-450.

Crozier, R.H., Newey, P.S., Schlüns, E.A. & Robson, S.K.A. 2010: A masterpiece of evolution – *Oecophylla* weaver ants (Hymenoptera: Formicidae). – Myrmecological News 13: 57-71.

Dauber, J., Bengtsson, J. & Lenoir, L. 2006: Evaluating effects of habitat loss and land-use continuity on ant species richness in seminatural grassland remnants. – Conservation Biology 20: 1150-1160.

De Almeida, T., Arnan, X., Capowiez, Y., Hedde, M., Mesléard, F., Dutoit, T. & Blight, O. 2023: Ants in restoration ecology: why, what's and the way forward. – Land Degradation & Development 35: 1284-1295.

De Almeida, T., Blight, O., Mesléard, F., Bulot, A., Provost, E. & Dutoit, T. 2020a: Harvester ants as ecological engineers for Mediterranean grassland restoration: impacts on soil and vegetation. – Biological Conservation 245: art. 108547.

De Almeida, T., Mesléard, F., Santonja, M., Gros, R., Dutoit, T. & Blight, O. 2020b: Above- and below-ground effects of an ecosystem engineer ant in Mediterranean dry grasslands. – Proceedings of the Royal Society B-Biological Sciences 287: art. 20201840.

De Bruyn, L.A.L. & Conacher, A.J. 1990: The role of termites and ants in soil modification - a review. – Australian Journal of Soil Research 28: 55-93.

De Groot, R., Brander, L., Van Der Ploeg, S., Costanza, R., Bernard, F., Braat, L., Christie, M., Crossman, N., Ghermandi, A., Hein, L., Hussain, S., Kumar, P., McVittie, A., Portela, R., Rodriguez, L.C., Ten Brink, P. & Van Beukering, P. 2012: Global estimates of the value of ecosystems and their services in monetary units. – Ecosystem Services 1: 50-61.

Dean, W.R.J. & Yeaton, R.I. 1992: The importance of harvester ant *Messor capensis* nest-mounds as germination sites in the southern Karoo, South Africa. – African Journal of Ecology 30: 335-345.

Decaëns, T., Asakawa, N., Galvis, J.H., Thomas, R.J. & Amézqita, E. 2002: Surface activity of soil ecosystem engineers and soil structure in contrasted land use systems of Colombia. – European Journal of Soil Biology 38: 267-271.

Del Toro, I., Floyd, K., Gardea-Torresdey, J. & Borrok, D. 2010: Heavy metal distribution and bioaccumulation in Chihuahuan Desert Rough Harvester ant (*Pogonomyrmex rugosus*) populations. – Environmental Pollution 158: 1281-1287.

Del Toro, I., Ribbons, R.R. & Pelini, S.L. 2012: The little things that run the world revisited: a review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). – Myrmecological News 17: 133-146.

Diagne, C., Leroy, B., Gozlan, R.E., Vaissière, A.-C., Assailly, C., Nuninger, L., Roiz, D., Jourdain, F., Jarić, I. & Courchamp, F. 2020: InvaCost, a public database of the economic costs of biological invasions worldwide. – Scientific Data 7: art. 277.

Diamé, L., Rey, J.-Y., Vayssières, J.-F., Grechi, I., Chailleux, A. & Diarra, K. 2018: Ants: major functional elements in fruit agro-ecosystems and biological control agents. – Sustainability 10: art. 23.

Díaz, S. & Cabido, M. 2001: Vive la différence: plant functional diversity matters to ecosystem processes. – Trends in Ecology & Evolution 16: 646-655.

Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R.T., Molnár, Z., Hill, R., Chan, K.M.A., Baste, I.A., Brauman, K.A., Polasky, S., Church, A., Lonsdale, M., Larigauderie, A., Leadley, P.W., van Oudenhoven, A.P.E., van der Plaat, F., Schröter, M., Lavorel, S., Aumeerud-dy-Thomas, Y., Bukvareva, E., Davies, K., Demissew, S., Erpul, G., Failler, P., Guerra, C.A., Hewitt, C.L., Keune, H., Lindley, S. & Shirayama, Y. 2018: Assessing nature's contributions to people. – Science 359: 270-272.

DiRienzo, N. & Dornhaus, A. 2017: *Temnothorax rugatulus* ant colonies consistently vary in nest structure across time and context. – Public Library of Science One 12: art. e0177598.

Dostál, P., Březnová, M., Kozlíčková, V., Herben, T. & Kovář, P. 2005: Ant-induced soil modification and its effect on plant below-ground biomass. – Pedobiologia 49: 127-137.

Drager, K.I., Hirmas, D.R., Hasiotis, S.T. & Bents, T.C. 2016: Effects of ant (*Formica subsericea*) nest development on physical and hydrological properties in a coarse-textured soil. – Soil Science 181: 166-174.

Ehrenfeld, J.G. 2010: Ecosystem consequences of biological invasions. – Annual Review of Ecology, Evolution, and Systematics 41: 59-80.

El-Hamalawi, Z.A. & Menge, J.A. 1996: The role of snails and ants in transmitting the avocado stem canker pathogen, *Phytophthora citricola*. – Journal of the American Society for Horticultural Science 121: 973-977.

Elizalde, L., Arbetman, M., Arnan, X., Eggleton, P., Leal, I.R., Lescano, M.N., Saez, A., Werenkraut, V. & Pirk, G.I. 2020: The ecosystem services provided by social insects: traits, management tools and knowledge gaps. – Biological Reviews 95: 1418-1441.

Espinoza, D.N. & Santamarina, J.C. 2010: Ant tunneling – a granular media perspective. – Granular Matter 12: 607-616.

Eubanks, M.D. 2001: Estimates of the direct and indirect effects of red imported fire ants on biological control in field crops. – Biological Control 21: 35-43.

Eubanks, M.D., Lin, C. & Tarone, A.M. 2019: The role of ants in vertebrate carrion decomposition. – Food Webs 18: art. e00109.

Evans, T.A., Dawes, T.Z., Ward, P.R. & Lo, N. 2011: Ants and termites increase crop yield in a dry climate. – Nature Communications 2: art. 262.

Farji-Brener, A.G. 2010: Leaf-cutting ant nests and soil biota abundance in a semi-arid steppe of Northwestern Patagonia. – Sociobiology 56: 549-557.

Farji-Brener, A.G., Lescano, N. & Ghermandi, L. 2010: Ecological engineering by a native leaf-cutting ant increases the performance of exotic plant species. – Oecologia 163: 163-169.

Farji-Brener, A.G. & Medina, C.A. 2000: The importance of where to dump the refuse: seed banks and fine roots in nests of the leaf-cutting ants *Atta cephalotes* and *A. colombica*. – Biotropica 32: 120-126.

Farjí-Brener, A.G. & Tadey, M. 2009: Contributions of leaf-cutting ants to soil fertility: causes and consequences. In: Lucero, D.P. & Boggs, J.E. (Eds.): Soil Fertility. – Nova Science Publishers, Inc., Hauppauge, NY, pp. 81-91.

Farjí-Brener, A.G. & Werenkraut, V. 2015: A meta-analysis of leaf-cutting ant nest effects on soil fertility and plant performance. – Ecological Entomology 40: 150-158.

Farjí-Brener, A.G. & Werenkraut, V. 2017: The effects of ant nests on soil fertility and plant performance: a meta-analysis. – Journal of Animal Ecology 86: 866-877.

Feng, Y., Wang, Y., Lin, Y., Zhao, W., Gao, J. & Liu, J. 2022: Effects of ant nest microhabitats on the diversity of soil macrofauna in Gobi ecosystems. – Biodiversity Science 30: art. 22282.

Fisher, B. & Turner, R.K. 2008: Ecosystem services: classification for valuation. – Biological Conservation 141: 1167-1169.

Folgarait, P.J. 1998: Ant biodiversity and its relationship to ecosystem functioning: a review. – Biodiversity and Conservation 7: 1221-1244.

Frederickson, M.E., Greene, M.J. & Gordon, D.M. 2005: "Devil's gardens" bedeviled by ants. – Nature 437: 495-496.

Frizzi, F., Masoni, A., Quilghini, G., Ciampelli, P. & Santini, G. 2018: Chronicle of an impact foretold: the fate and effect of the introduced *Formica paralugubris* ant. – Biological Invasions 20: 3575-3589.

Frouz, J. & Jilková, V. 2008: The effect of ants on soil properties and processes (Hymenoptera: Formicidae). – Myrmecological News 11: 191-199.

Frouz, J., Šantrůčková, H. & Kalčík, J. 1997: The effect of wood ants (*Formica polyctena* Foerst.) on the transformation of phosphorus in a spruce plantation. – Pedobiologia 41: 437-447.

Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Fröberg, M., Stendahl, J., Philipson, C.D., Mikusiński, G., Andersson, E., Westerlund, B., Andrén, H., Moberg, F., Moen, J. & Bengtsson, J. 2013: Higher levels of multiple ecosystem services are found in forests with more tree species. – Nature Communications 4: art. 1340.

Gao, H., Grüschow, S., Barke, J., Seipke, R.F., Hill, L.M., Orivel, J., Yu, D.W., Hutchings, M. & Goss, R.J.M. 2014: Filipins: the first antifungal "weed killers" identified from bacteria isolated from the trap-ant. – RSC Advances 4: 57267-57270.

Garcia-Holguera, M., Zisa, A. & Clark, O.G. 2016: An ecomimetic case study: Building retrofit inspired from the ecosystem of leaf-cutting ants. – Proceedings of the CIB World Building Congress 2016 2: 36-50.

Giladi, I. 2006: Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory. – Oikos 112: 481-492.

Ginzburg, O., Whitford, W.G. & Steinberger, Y. 2008: Effects of harvester ant (*Messor* spp.) activity on soil properties and microbial communities in a Negev Desert ecosystem. – Biology and Fertility of Soils 45: 165-173.

Goncalves, A.Z., Oliveira, R.S., Oliveira, P.S. & Romero, G.Q. 2016: Species-specific effects of ant inhabitants on bromeliad nutrition. – Public Library of Science One 11: art. e0152113.

González-Teuber, M., Kaltenpoth, M. & Boland, W. 2014: Mutualistic ants as an indirect defence against leaf pathogens. – New Phytologist 202: 640-650.

Gravish, N., Garcia, M., Mazouchova, N., Levy, L., Umbanhowar, P.B., Goodisman, M.A.D. & Goldman, D.I. 2012: Effects of worker size on the dynamics of fire ant tunnel construction. – Journal of the Royal Society Interface 9: 3312-3322.

Grime, J.P. 1998: Benefits of plant diversity to ecosystems: immediate, filter and founder effects. – Journal of Ecology 86: 902-910.

Grześ, I.M. 2010: Ants and heavy metal pollution – a review. – European Journal of Soil Biology 46: 350-355.

Guimarães, I.D.C., Pereira, M.C., Batista, N.R., Rodrigues, C.A.P. & Antonialli Jr, W.F. 2018: The complex nest architecture of the ponerinae ant *Odontomachus chelifer*. – Public Library of Science One 13: art. e0189896.

Gyssels, G., Poesen, J., Bochet, E. & Li, Y. 2005: Impact of plant roots on the resistance of soils to erosion by water: a review. – Progress in Physical Geography 29: 189-217.

Haines, I.H. & Haines, J.B. 1978: Colony structure, seasonality and food requirements of the crazy ant, *Anoplolepis longipes* (Jerd.), in the Seychelles. – Ecological Entomology 3: 109-118.

Handel, S.N. & Beattie, A.J. 1990: Seed dispersal by ants. – Scientific American 263: 76-83.

Hansen, R.R., Nielsen, K.E., Byriel, D.B., Damgaard, C., Strandberg, M.T., Schmidt, I.K. & Offenberg, J. 2023: Ant mounds extend the duration of plant phenology events and enhance flowering success. – Arthropod-Plant Interactions 17: 205-216.

Hao, H.-X., Qin, J.-H., Sun, Z.-X., Guo, Z.-L. & Wang, J.-G. 2021: Erosion-reducing effects of plant roots during concentrated flow under contrasting textured soils. – CATENA 203: art. 105378.

Hector, A. & Bagchi, R. 2007: Biodiversity and ecosystem multifunctionality. – Nature 448: 188-190.

Higashi, S., Tsuyuzaki, S., Ohara, M. & Ito, F. 1989: Adaptive advantages of ant-dispersed seeds in the myrmecochorous plant *Trillium tschonoskii* (Liliaceae). – Oikos 54: 389-394.

Holway, D.A., Lach, L., Suarez, A.V., Tsutsui, N.D. & Case, T.J. 2002: The causes and consequences of ant invasions. – Annual Review of Ecology and Systematics 33: 181-233.

Hooper, D.U., Chapin III, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. 2005: Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. – Ecological Monographs 75: 3-35.

Hölldobler, B. & Kwapich, C.L. 2022: The guests of ants: how myrmecophiles interact with their hosts. – Harvard University Press, Cambridge, MA, 576 pp.

Hölldobler, B. & Wilson, E.O. 1990: The ants. – Harvard University Press, Cambridge, MA, 732 pp.

Hughes, L. 1991: The relocation of ant nest entrances: potential consequences for ant-dispersed seeds. – Australian Journal of Ecology 16: 207-214.

Hulme, P.E., Ahmed, D.A., Haubrock, P.J., Kaiser, B.A., Kourantidou, M., Leroy, B. & McDermott, S.M. 2024: Widespread imprecision in estimates of the economic costs of invasive alien species worldwide. – Science of the Total Environment 909: art. 167997.

Ipbes 2019: Global assessment report of the intergovernmental science-policy platform on biodiversity and ecosystem services. Brondízio, E.S., Settele, J., Díaz, S. & Ngo, H.T. (Eds.). – IPBES Secretariat, Bonn, 1144 pp.

Irwin, J.C. 1982: The sacred anthill and the cult of the primordial mound. – History of Religions 21: 339-360.

James, A.I., Eldridge, D.J., Koen, T.B. & Whitford, W.G. 2008: Landscape position moderates how ant nests affect hydrology and soil chemistry across a Chihuahuan Desert watershed. – Landscape Ecology 23: 961-975.

Jones, J.C. & Oldroyd, B.P. 2006: Nest thermoregulation in social insects. – Advances in Insect Physiology 33: 153-191.

Jones, C.G., Lawton, J.H. & Shachak, M. 1994: Organisms as ecosystem engineers. – Oikos 69: 373-386.

Jones, C.G., Lawton, J.H. & Shachak, M. 1997: Positive and negative effects of organisms as physical ecosystem engineers. – Ecology 78: 1946-1957.

Jouquet, P., Blanchart, E. & Capowiez, Y. 2014: Utilization of earthworms and termites for the restoration of ecosystem functioning. – Applied Soil Ecology 73: 34-40.

Jouquet, P., Dauber, J., Lagerlöf, J., Lavelle, P. & Lepage, M. 2006: Soil invertebrates as ecosystem engineers: Intended and accidental effects on soil and feedback loops. – Applied Soil Ecology 32: 153-164.

Jouquet, P., Mathieu, J., Barot, S. & Choosai, C. 2007: Soil engineers as ecosystem heterogeneity drivers. In: Muñoz, S.I. (Ed.): Ecology research progress. – Nova Science Publishers, New York, NY, pp. 187-199.

Kaspari, M. 1996: Worker size and seed size selection by harvester ants in a Neotropical forest. – Oecologia 105: 397-404.

Kavehei, A., Gore, D.B., Wilson, S.P., Hosseini, M. & Hose, G.C. 2021: Assessment of legacy mine metal contamination using ants as indicators of contamination. – Environmental Pollution 274: art. 116537.

Khan, S.R., Rastogi, N. & Singh, S.K. 2023: Bio-transfer and bioaccumulation patterns of heavy metals in mine site-inhabiting ants and grasshoppers, across mine site restoration chronosequence. – Ecotoxicology 32: 683-698.

Khan, S.R., Singh, S.K. & Rastogi, N. 2017: Heavy metal accumulation and ecosystem engineering by two common mine site-nesting ant species: implications for pollution-level assessment and bioremediation of coal mine soil. – Environmental Monitoring and Assessment 189: art. 195.

Kistner, D.H. 1982: The social insects' bestiary. In: Social insects. – Academic Press, New York, NY, 244 pp.

Klein, A., Steffan-Dewenter, I. & Tscharntke, T. 2003: Fruit set of highland coffee increases with the diversity of pollinating bees. – Proceedings of the Royal Society B-Biological Sciences 270: 955-961.

Kleineidam, C., Ernst, R. & Roces, F. 2001: Wind-induced ventilation of the giant nests of the leaf-cutting ant *Atta vollenweideri*. – Naturwissenschaften 88: 301-305.

Knoechelmann, C.M., Oliveira, F.M.P., Siqueira, F.F.S., Wirth, R., Tabarelli, M. & Leal, I.R. 2020: Leaf-cutting ants negatively impact the regeneration of the Caatinga dry forest across abandoned pastures. – Biotropica 52: 686-696.

Lach, L. & Hooper-Bùi, L.M. 2010: Consequences of ant invasions. In: Lach, L., Parr, C.L. & Abbott, K.L. (Eds.): Ant Ecology. – Oxford University Press, Oxford, UK, pp. 261-286.

Lafleur, B., Hooper-Bùi, L.M., Mumma, E.P. & Geaghan, J.P. 2005: Soil fertility and plant growth in soils from pine forests and plantations: Effect of invasive red imported fire ants *Solenopsis invicta* (Buren). – Pedobiologia 49: 415-423.

Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P. & Rossi, J.-P. 2006: Soil invertebrates and ecosystem services. – European Journal of Soil Biology 42: S3-S15.

Lavelle, P., Spain, A., Blouin, M., Brown, G., Decaëns, T., Grimaldi, M., Jiménez, J.J., McKey, D., Mathieu, J., Velasquez, E. & Zangerlé, A. 2016: Ecosystem engineers in a self-organized soil: a review of concepts and future research questions. – Soil Science 181: 91-109.

Leal, I.R., Wirth, R. & Tabarelli, M. 2007: Seed dispersal by ants in the semi-arid Caatinga of Northeast Brazil. – Annals of Botany 99: 885-894.

Leal, I.R., Wirth, R. & Tabarelli, M. 2014: The multiple impacts of leaf-cutting ants and their novel ecological role in human-modified neotropical forests. – Biotropica 46: 516-528.

Lee, C.-Y. & Yang, C.-C.S. 2022: Biology, ecology, and management of the invasive longlegged ant, *Anoplolepis gracilipes*. – Annual Review of Entomology 67: 43-63.

Lee, K.E. & Foster, R.C. 1991: Soil fauna and soil structure. – Australian Journal of Soil Research 29: 745-775.

Lefcheck, J.S., Byrnes, J.E.K., Isbell, F., Gamfeldt, L., Griffin, J.N., Eisenhauer, N., Hensel, M.J.S., Hector, A., Cardinale, B.J. & Duffy, J.E. 2015: Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. – Nature Communications 6: art. 6936.

Lehmann, A., Zheng, W. & Rillig, M.C. 2017: Soil biota contributions to soil aggregation. – Nature Ecology and Evolution 1: 1828-1835.

Lei, S.A. 2000: Ecological impacts of seed-harvester ants on soil attributes in a *Larrea*-dominated shrubland. – Western North American Naturalist 60: 439-444.

Leite, P.A.M., Carvalho, M.C. & Wilcox, B.P. 2018: Good ant, bad ant? Soil engineering by ants in the Brazilian Caatinga differs by species. – Geoderma 323: 65-73.

Lengyel, S., Gove, A.D., Latimer, A.M., Majer, J.D. & Dunn, R.R. 2010: Convergent evolution of seed dispersal by ants, and phylogeny and biogeography in flowering plants: A global survey. – Perspectives in Plant Ecology, Evolution and Systematics 12: 43-55.

Lenoir, L., Bengtsson, J. & Persson, T. 2001: Wood ant nests as potential hot spots for carbon and nitrogen mineralisation. – Biology of Fertility of Soils 34: 235-240.

Levey, D.J. & Byrne, M.M. 1993: Complex ant-plant interactions: rainforest ants as secondary dispersers and post-dispersal seed predators. – Ecology 74: 1802-1812.

Levin, S.A. 1992: The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. – Ecology 73: 1943-1967.

Li, T., Shao, M. & Jia, Y. 2017: Effects of activities of ants (*Camponotus japonicus*) on soil moisture cannot be neglected in the northern Loess Plateau. – Agriculture, Ecosystems & Environment 239: 182-187.

Li, T.C., Shao, M.A., Jia, Y.H., Jia, X.X., Huang, L.M. & Gan, M. 2019: Small-scale observation on the effects of burrowing activities of ants on soil hydraulic processes. – European Journal of Soil Science 70: 236-244.

Li, X.R., Gao, Y.H., Su, J.Q., Jia, R.L. & Zhang, Z.S. 2014: Ants mediate soil water in arid desert ecosystems: mitigating rainfall interception induced by biological soil crusts? – Applied Soil Ecology 78: 57-64.

Lu, M., Wang, S., Zhang, Z., Chen, M., Li, S., Cao, R., Cao, Q., Zuo, Q. & Wang, P. 2019: Modifying effect of ant colonization on soil heterogeneity along a chronosequence of tropical forest restoration on slash-burn lands. – Soil & Tillage Research 194: art. 104329.

Luo, Y., Taylor, A., Weigelt, P., Guénard, B., Economo, E.P., Nowak, A., Inderjit & Kreft, H. 2023: Climate and ant diversity explain the global distribution of ant-plant mutualisms. – Ecography 2023: art. e06841.

Luo, Z.-D. 2005: Harm of red imported fire ants to power facilities and their control. – Guangdong Electric Power 18: 1-3.

Mace, G.M., Norris, K. & Fitter, A.H. 2012: Biodiversity and ecosystem services: a multilayered relationship. – Trends in Ecology & Evolution 27: 19-26.

Macedo, M.O., Resende, A.S., Garcia, P.C., Boddey, R.M., Jantalia, C.P., Urquiaga, S., Campello, E.F.C. & Franco, A.A. 2008: changes in soil C and N stocks and nutrient dynamics 13 years after recovery of degraded land using leguminous nitrogen-fixing trees. – Forest Ecology and Management 255: 1516-1524.

Majer, J.D. 1983: Ants: bio-indicators of mine site rehabilitation, land-use, and land conservation. – Environmental Management 7: 375-383.

Malinga, R., Gordon, L.J., Jewitt, G. & Lindborg, R. 2015: Mapping ecosystem services across scales and continents – a review. – Ecosystem Services 13: 57-63.

Manning, P., Slade, E.M., Beynon, S.A. & Lewis, O.T. 2016: Functionally rich dung beetle assemblages are required to provide multiple ecosystem services. – Agriculture, Ecosystems & Environment 218: 87-94.

Martín-Perea, D., Fesharaki, O., Domingo, M.S., Gamboa, S. & Hernández Fernández, M. 2019: *Messor barbarus* ants as soil bioturbators: implications for granulometry, mineralogical composition and fossil remains extraction in Somosaguas site (Madrid basin, Spain). – CATENA 172: 664-677.

Maziarz, M., Broughton, R.K., Casacci, L.P., Hebda, G., Maák, I., Trigos-Peral, G. & Witek, M. 2021: Interspecific attraction between ground-nesting songbirds and ants: the role of nest-site selection. – Frontiers in Zoology 18: art. 43.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. 2006: Rebuilding community ecology from functional traits. – Trends in Ecology & Evolution 21: 178-185.

Merchant, T.K., Henn, J.J., De Silva, I., Van Cleemput, E. & Suding, K.N. 2023: Four reasons why functional traits are not being used in restoration practice. – Restoration Ecology 31: art. e13788.

Metzger, J.P., Villarreal-Rosas, J., Suárez-Castro, A.F., López-Cubillos, S., González-Chaves, A., Runting, R.K., Hohlenwerger, C. & Rhodes, J.R. 2021: Considering landscape-level processes in ecosystem service assessments. – Science of the Total Environment 796: art. 149028.

Meyer, S.T., Leal, I.R., Tabarelli, M. & Wirth, R. 2011: Ecosystem engineering by leaf-cutting ants: Nests of *Atta cephalotes* drastically alter forest structure and microclimate. – Ecological Entomology 36: 14-24.

Meyer, S.T., Neubauer, M., Sayer, E.J., Leal, I.R., Tabarelli, M. & Wirth, R. 2013: Leaf-cutting ants as ecosystem engineers: Topsoil and litter perturbations around *Atta cephalotes* nests reduce nutrient availability. – Ecological Entomology 38: 497-504.

Millennium Ecosystem Assessment 2005: Ecosystems and human well-being: synthesis. – Island Press, Washington, DC, 137 pp.

Miller, J.S., Wan, E., O'Fallon, S. & Pinter-Wollman, N. 2022: Modularity and connectivity of nest structure scale with colony size. – Evolution 76: 101-113.

Milligan, P.D., Martin, T.A., Pringle, E.G., Riginos, C., Mizell, G.M. & Palmer, T.M. 2022: A soil-nesting invasive ant disrupts carbon dynamics in saplings of a foundational ant-plant. – Journal of Ecology 110: 359-373.

Mlambo, M. 2014: Not all traits are "functional": insights from taxonomy and biodiversity-ecosystem functioning research. – Biodiversity and Conservation 23: 781-790.

Montoya-Lerma, J., Giraldo-Echeverri, C., Armbrecht, I., Farji-Brener, A. & Calle, Z. 2012: Leaf-cutting ants revisited: towards rational management and control. – International Journal of Pest Management 58: 225-247.

Morales-Linares, J., Garcí-Franco, J.G., Flores-Palacios, A., Valenzuela-González, J.E., Mata-Rosas, M. & Díaz-Castelazo, C. 2018: Orchid seed removal by ants in Neotropical ant-gardens. – Plant Biology 20: 525-530.

Moreira, A.A., Forti, L.C., Andrade, A.P.P., Boaretto, M.A.C. & Lopes, J.F.S. 2004: Nest architecture of *Atta laevigata* (F. Smith, 1858) (Hymenoptera: Formicidae). – Studies on Neotropical Fauna and Environment 39: 109-116.

Moretti, M., Dias, A.T.C., de Bello, F., Altermatt, F., Chown, S.L., Azcárate, F.M., Bell, J.R., Fournier, B., Hedde, M., Hortal, J., Ibanez, S., Öckinger, E., Sousa, J.P., Ellers, J. & Berg, M.P. 2017: Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. – Functional Ecology 31: 558-567.

Morozov, N.S. 2015: Why do birds practice anting? – Biology Bulletin Reviews 5: 353-365.

Moutinho, P., Nepstad, D.C. & Davidson, E.A. 2003: Influence of leaf-cutting ant nests on secondary forest growth and soil properties in Amazonia. – Ecology 84: 1265-1276.

Moyo, P., Allsopp, E., Roets, F., Mostert, L. & Halleen, F. 2014: Arthropods vector grapevine trunk disease pathogens. – Phytopathology 104: 1063-1069.

Nagy, Z.T., Dekoninck, W., De Block, F., Yeo, K., Silue, K.S. & Delsinne, T. 2017: Oviposition of the snake *Thelotornis kirtlandii* in a parabiotic ant nest. – Salamandra 53: 167-170.

Nascimento, D.L., Chiapini, M., Vidal-Torrado, P., Phillips, J.D., Ladeira, F.S.B., Machado, D.F.T., Da Silva Camargo, R. & Valezio, E.V. 2024: The underestimated role of leaf-cutting ants in soil and geomorphological development in neotropical America. – Earth-Science Reviews 248: art. 104650.

Ness, J., Mooney, K. & Lach, L. 2010: Ants as mutualists. In: Lach, L., Parr, C.L. & Abbott, K.L. (Eds.): Ant ecology. – Oxford University Press, New York, NY, pp. 97-114.

Nkem, J.N., De Bruyn, L.A.L., Grant, C.D. & Hulugalle, N.R. 2000: The impact of ant bioturbation and foraging activities on surrounding soil properties. – Pedobiologia 44: 609-621.

Nooten, S.S., Chan, K.H., Schultheiss, P., Bogar, T.A. & Guénard, B. 2022: Ant body size mediates functional performance and species interactions in carrion decomposer communities. – Functional Ecology 36: 1279-1291.

O'Dowd, D.J., Green, P.T. & Lake, P.S. 2003: Invasional "meltdown" on an oceanic island. – Ecology Letters 6: 812-817.

Offenberg, J. 2015: Ants as tools in sustainable agriculture. – Journal of Applied Ecology 52: 1197-1205.

Offenberg, J. & Damgaard, C. 2019: Ants suppressing plant pathogens: a review. – Oikos 128: 1691-1703.

Offenberg, J., Jensen, I.C. & Hansen, R.R. 2022: Combatting plant diseases with ant chemicals: a review and meta-analysis. – Journal of Applied Ecology 59: 25-38.

Ohashi, M., Kilpeläinen, J., Finér, L., Risch, A.C., Domisch, T., Neuvonen, S. & Niemelä, P. 2007: The effect of red wood ant (*Formica rufa* group) mounds on root biomass, density, and nutrient concentrations in boreal managed forests. – The Japanese Forest Society 12: 113-119.

Oliveras, J., Bas, J.M. & Gómez, C. 2005: Reduction of the ant mandible gap range after biotic homogenization caused by an ant invasion (Hymenoptera: Formicidae). – Sociobiology 45: 829-838.

Opata, D.U. 2003: The metaphor of "anthills of the savannah" in Chinua Achebe's anthills of the savannah. – Journal of Comparative Literature and Aesthetics 26: 59-64.

Orivel, J., Lambs, L., Malé, P.-J.G., Leroy, C., Otto, T., Quilichini, A. & Dejean, A. 2011: Dynamics of the association between a long-lived understory myrmecophyte and its specific associated ants. – Oecologia 165: 369-376.

Orivel, J. & Leroy, C. 2011: The diversity and ecology of ant gardens (Hymenoptera: Formicidae; Spermatophyta: Angiospermae). – Myrmecological News 14: 73-85.

Päivinen, J., Ahlroth, P., Kaitala, V. & Suhonen, J. 2004: Species richness, abundance and distribution of myrmecophilous beetles in nests of *Formica aquilonia* ants. – Annales Zoologici Fennici 41: 447-454.

Parmentier, T., Dekoninck, W. & Wenseleers, T. 2014: A highly diverse microcosm in a hostile world: a review on the associates of red wood ants (*Formica rufa* group). – Insectes Sociaux 61: 229-237.

Pascual, U., Balvanera, P., Díaz, S., Pataki, G., Roth, E., Stenseke, M., Watson, R.T., Başak Dessane, E., Islar, M., Kelemen, E., Maris, V., Quaas, M., Subramanian, S.M., Wittmer, H., Adlan, A., Ahn, S., Al-Hafedh, Y.S., Amankwah, E., Asah, S.T., Berry, P., Bilgin, A., Breslow, S.J., Bullock, C., Cáceres, D., Daly-Hassen, H., Figueroa, E., Golden, C.D., Gómez-Baggethun, E., González-Jiménez, D., Houdet, J., Keune, H., Kumar, R., Ma, K., May, P.H., Mead, A., O'Farrell, P., Pandit, R., Pengue, W., Pichis-Madruga, R., Popa, F., Preston, S., Pacheco-Balanza, D., Saarikoski, H., Strassburg, B.B., Van den belt, M., Verma, M., Wickson, F. & Yagi, N. 2017: Valuing nature's contributions to people: the IPBES approach. – Current Opinion in Environmental Sustainability 26-27: 7-16.

Paton, T.R., Humphreys, G.S. & Mitchel, P.B. 1995: Soils: a new global view. UCL Press, London, UK, 213 pp.

Peck, S.L., Mcquaid, B. & Campbell, C.L. 1998: Using ant species (Hymenoptera: Formicidae) as a biological indicator of agroecosystem condition. – Environmental Entomology 27: 1102-1110.

Pérez-Lachaud, G. & Lachaud, J. 2014: Arboreal ant colonies as "Hot-Points" of cryptic diversity for myrmecophiles: the weaver ant *Camponotus* sp. aff. *textor* and its interaction network with its associates. – Public Library of Science One 9: art. e100155.

Perfecto, I. & Philpott, S.M. 2023: Ants (Hymenoptera: Formicidae) and ecosystem functions and services in urban areas: a reflection on a diverse literature. – Myrmecological News 33: 103-122.

Pesche, D., Méral, P., Hrabanski, M. & Bonnin, M. 2013: Ecosystem services and payments for environmental services: two sides of the same coin? In: Muradian, R. & Rival, L. (Eds.): Governing the provision of ecosystem services. – Studies in Ecological Economics, Springer Netherlands, Dordrecht, pp. 67-86.

Pętal, J. 1978: The role of ants in ecosystems. In: Production ecology of ants and termites. – International Biological Programme, Cambridge University Press, Cambridge, UK, pp. 293-325.

Pierce, N.E., Braby, M.F., Heath, A., Lohman, D.J., Mathew, J., Rand, D.B., Travassos, M.A. & Al, P.E.T. 2002: The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). – Annual Review of Entomology 47: 733-771.

Pinkalski, C., Jensen, K.-M.V., Damgaard, C. & Offenberg, J. 2018: Foliar uptake of nitrogen from ant faecal droplets: an overlooked service to ant-plants. – Journal of Ecology 106: 289-295.

Pinter-Wollman, N. 2015: Nest architecture shapes the collective behaviour of harvester ants. – Biology Letters 11: art. 20150695.

Plieninger, T., Dijks, S., Oteros-Rozas, E. & Bieling, C. 2013: Assessing, mapping, and quantifying cultural ecosystem services at community level. – Land Use Policy 33: 118-129.

Prajwal, M., Sangamesha, M.A. & Pushpalatha, K. 2015: Ant larvae silk fibres mat. – Current Science 108: 1544-1547.

Rastogi, N. 2011: Provisioning services from ants: food and pharmaceuticals. – Asian Myrmecology 4: 103-120.

Reddy, N., Xu, H. & Yang, Y. 2011: Unique natural-protein hollow-nanofiber membranes produced by weaver ants for medical applications. – Biotechnology and Bioengineering 108: 1726-1733.

Retana, J., Xavier Picó, F. & Rodrigo, A. 2004: Dual role of harvesting ants as seed predators and dispersers of a non-myrmechorous Mediterranean perennial herb. – Oikos 105: 377-385.

Revis, H.C. & Waller, D.A. 2004: Bactericidal and fungicidal activity of ant chemicals on feather parasites: an evaluation of anting behavior as a method of self-medication in songbirds. – The Auk 121: 1262-1268.

Richards, P.W. 1996: The tropical rain forest. 2nd edition. – Cambridge University Press, Cambrige, UK, 600 pp.

Rilov, G., Canning-Clode, J. & Guy-Haim, T. 2024: Ecological impacts of invasive ecosystem engineers: a global perspective across terrestrial and aquatic systems. – Functional Ecology 38: 37-51.

Risch, A.C., Jurgensen, M.F., Schütz, M. & Page-Dumroese, D.S. 2005: The contribution of red wood ants to soil C and N pools and CO_2 emissions in subalpine forests. – Ecology 86: 419-430.

Rissing, S.W. 1986: Indirect effects of granivory by harvester ants: Plant species composition and reproductive increase near ant nests. – Oecologia 68: 231-234.

Robles López, K.Y., Sosa-Calvo, J., Calixto, J.M., Zoppas de Albuquerque, E. & Baudier, K.M. 2024: One ant's trash is another ant's treasure: Army ant middens provide resources for diverse ant assemblages. – Biotropica 56: 58-70.

Rocha, F.H., Lachaud, J. & Pérez-lachaud, G. 2020: Myrmecophilous organisms associated with colonies of the ponerine ant *Neoponera villosa* (Hymenoptera: Formicidae) nesting in *Aechmea bracteata* bromeliads: a biodiversity hotspot. – Myrmecological News 30: 73-92.

Rodgers, D.J. & Kitching, R.L. 2011: Rainforest Collembola (Hexapoda: Collembola) and the insularity of epiphyte microhabitats. – Insect Conservation and Diversity 4: 99-106.

Romero, G.Q., Gonçalves-Souza, T., Vieira, C. & Koricheva, J. 2015: Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis. – Biological Reviews 90: 877-890.

Sagoff, M. 2011: The quantification and valuation of ecosystem services. – Ecological Economics 70: 497-502.

Sakagami, S.F., Inoue, T., Yamane, S. & Salmah, S. 1989: Nests of the myrmecophilous stingless bee, *Trigona moorei*: How do bees initiate their nest within an arboreal ant nest? – Biotropica 21: 265-274.

Samuels, R.I., Mattoso, T.C. & Moreira, D.D.O. 2013: Chemical warfare: Leaf-cutting ants defend themselves and their gardens against parasite attack by deploying antibiotic secreting bacteria. – Communicative & Integrative Biology 6: art. e23095.

Sanders, D. & Frago, E. 2024: Ecosystem engineers shape ecological network structure and stability: a framework and literature review. – Functional Ecology 38: 1683-1696.

Sanders, D., Jones, C.G., Thébault, E., Bouma, T.J., van der Heide, T., van Belzen, J. & Barot, S. 2014: Integrating ecosystem engineering and food webs. – Oikos 123: 513-524.

Sankovitz, M. & Purcell, J. 2021: Ant nest architecture is shaped by local adaptation and plastic response to temperature. – Scientific Reports 11: art. 23053.

Schägner, J.P., Brander, L., Maes, J. & Hartje, V. 2013: Mapping ecosystem services' values: current practice and future prospects. – Ecosystem Services 4: 33-46.

Schmid-Hempel, P. 1995: Parasites and social insects. – Apidologie 26: 255-271.

Schmid-Hempel, P. 1998: Parasites in social insects. – Princeton University Press, Princeton, NJ, 392 pp.

Schmitz, O.J., Buchkowski, R.W., Burghardt, K.T. & Donihue, C.M. 2015: Functional traits and trait-mediated interactions. In: Pawar, S., Woodward, G. & Dell, A.I. (Eds.): Advances in ecological research. – Academic Press, Elsevier, Oxford, UK, pp. 319-343.

Schultheiss, P., Nooten, S.S., Wang, R., Wong, M.K.L., Brassard, F. & Guénard, B. 2022: The abundance, biomass, and distribution of ants on Earth. – Proceedings of the National Academy of Sciences of the United States of America 119: art. e2201550119.

Schütz, M., Kretz, C., Dekoninck, L., Iravani, M. & Risch, A.C. 2008: Impact of *Formica exsecta* Nyl. on seed bank and vegetation patterns in a subalpine grassland ecosystem. – Journal of Applied Entomology 132: 295-305.

Seabrooks, L. & Hu, L. 2017: Insects: an underrepresented resource for the discovery of biologically active natural products. – Acta Pharmaceutica Sinica B 7: 409-426.

Seifert, B. 2016: The supercolonial European wood ant *Formica paralugubris* Seifert, 1996 (Hymenoptera: Formicidae) introduced to Canada and its predicted role in Nearctic forests. – Myrmecological News 22: 11-20.

Seipke, R.F., Barke, J., Heavens, D., Yu, D.W. & Hutchings, M.I. 2013: Analysis of the bacterial communities associated with two ant–plant symbioses. – MicrobiologyOpen 2: 276-283.

Serna-Chavez, H.M., Schulp, C.J.E., Van Bodegom, P.M., Bouten, W., Verburg, P.H. & Davidson, M.D. 2014: A quantitative framework for assessing spatial flows of ecosystem services. – Ecological Indicators 39: 24-33.

Shulman, D. 1978: The serpent and the sacrifice: an anthill myth from Tiruvārūr. – History of Religions 18: 107-137.

Siddiqui, J.A., Bamisile, B.S., Khan, M.M., Islam, W., Hafeez, M., Bodlah, I. & Xu, Y. 2021: Impact of invasive ant species on native fauna across similar habitats under global environmental changes. – Environmental Science and Pollution Research International 28: 54362-54382.

Siri, S. & Maensiri, S. 2010: Alternative biomaterials: natural, non-woven, fibroin-based silk nanofibers of weaver ants (*Oecophylla smaragdina*). – International Journal of Biological Macromolecules 46: 529-534.

Skaldina, O., Peräniemi, S. & Sorvari, J. 2018: Ants and their nests as indicators for industrial heavy metal contamination. – Environmental Pollution 240: 574-581.

Spangenberg, J.H., Görg, C., Truong, D.T., Tekken, V., Bustamante, J.V. & Settele, J. 2014: Provision of ecosystem services is determined by human agency, not ecosystem functions. Four case studies. – International Journal of Biodiversity Science, Ecosystem Services & Management 10: 40-53.

Srivastava, D.S. & Vellend, M. 2005: Biodiversity-ecosystem function research: is it relevant to conservation? – Annual Review of Ecology, Evolution, and Systematics 36: 267-294.

Sterner, T. & Persson, U.M. 2008: An even Sterner review: introducing relative prices into the discounting debate. – Review of Environmental Economics and Policy 2: 61-76.

Stewart, A.D. & Anand, R.R. 2014: Anomalies in insect nest structures at the Garden Well gold deposit: investigation of mound-forming termites, subterranean termites and ants. – Journal of Geochemical Exploration 140: 77-86.

Storer, A.J., Jurgensen, M.F., Risch, A.C., Delisle, J. & Hyslop, M.D. 2008: The fate of an intentional introduction of *Formica lugubris* to North America from Europe. – Journal of Applied Entomology 132: 276-280.

Suarez, A.V., Bolger, D.T. & Case, T.J. 1998: Effects of fragmentation and invasion on native ant communities in coastal southern California. – Ecology 79: 2041-2056.

Swanson, A.C., Schwendenmann, L., Allen, M.F., Aronson, E.L., Artavia-León, A., Dierick, D., Fernandez-Bou, A.S., Harmon, T.C., Murillo-Cruz, C., Oberbauer, S.F., Pinto-Tomás, A.A., Rundel, P.W. & Zelikova, T.J. 2019: Welcome to the *Atta* world: a framework for understanding the effects of leaf-cutter ants on ecosystem functions. – Functional Ecology 33: 1386-1399.

Tadey, M. & Farji-Brener, A.G. 2007: Indirect effects of exotic grazers: Livestock decreases the nutrient content of refuse dumps of leaf-cutting ants through vegetation impoverishment. – Journal of Applied Ecology 44: 1209-1218.

Tallis, H., Mooney, H., Andelman, S., Balvanera, P., Cramer, W., Karp, D., Polasky, S., Reyers, B., Ricketts, T., Running, S., Thonicke, K., Tietjen, B. & Walz, A. 2012: A global system for monitoring ecosystem service change. – BioScience 62: 977-986.

Thompson, S., Vehkaoja, M., Pellikka, J. & Nummi, P. 2021: Ecosystem services provided by beavers *Castor* spp. – Mammal Review 51: 25-39.

Thurman, J.H., Northfield, T.D. & Snyder, W.E. 2019: Weaver ants provide ecosystem services to tropical tree crops. – Frontiers in Ecology and Evolution 7: art. 120.

Tilman, D., Isbell, F. & Cowles, J.M. 2014: Biodiversity and ecosystem functioning. – Annual Review of Ecology, Evolution, and Systematics 45: 471-493.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. & Lehman, C. 2001: Diversity and productivity in a long-term grassland experiment. – Science 294: 843-845.

Tinya, F. & Ódor, P. 2016: Congruence of the spatial pattern of light and understory vegetation in an old-growth, temperate mixed forest. – Forest Ecology and Management 381: 84-92.

Travanty, N.V., Vargo, E.L., Schal, C., Apperson, C.S. & Ponnusamy, L. 2022: Bacterial isolates derived from nest soil affect the attraction and digging behavior of workers of the red imported fire ant, *Solenopsis invicta* Buren. – Insects 13: art. 444.

Tschinkel, W.R. 2011: The nest architecture of three species of North Florida *Aphaenogaster* ants. – Journal of Insect Science 11: art. 105.

Tschinkel, W.R. 2015: Biomantling and bioturbation by colonies of the Florida harvester ant, *Pogonomyrmex badius*. – Public Library of Science One 10: art. e0120407.

Tschinkel, W.R. 2021: Ant architecture: the wonder, beauty, and science of underground nests. – Princeton University Press, Princeton, NJ, 227 pp.

Tuma, J., Frouz, J., Veselá, H., Křivohlavý, F. & Fayle, T.M. 2022: The impacts of tropical mound-building social insects on soil properties vary between taxa and with anthropogenic habitat change. – Applied Soil Ecology 179: art. 104576.

Uhey, D.A. & Hofstetter, R.W. 2022: From pests to keystone species: Ecosystem influences and human perceptions of harvester ants (*Pogonomyrmex*, *Veromessor*, and *Messor* spp.) – Annals of the Entomological Society of America 115: 127-140.

Van Der Plas, F., Manning, P., Allan, E., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala, M.A., Hector, A., Ampoorter, E., Baeten, L., Barbaro, L., Bauhus, J., Benavides, R., Benneter, A., Berthold, F., Bonal, D., Bouriaud, O., Bruelheide, H., Bussotti, F., Carnol, M., Castagneyrol, B., Charbonnier, Y., Coomes, D., Coppi, A., Bastias, C.C., Dawud, S.M., De Wandeler, H., Domisch, T., Finér, L., Gessler, A., Granier, A., Grossiord, C., Guyot, V., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F.-X., Jucker, T., Koricheva, J., Milligan, H., Müller, S., Muys, B., Nguyen, D., Pollastrini, M., Raulund-Rasmussen, K., Selvi, F., Stenlid, J., Valladares, F., Vesterdal, L., Zielínski, D. & Fischer, M. 2016: Jack-of-all-trades effects drive biodiversity-ecosystem multifunctionality relationships in European forests. – Nature Communications 7: art. 11109.

Van Der Plas, F., Ratcliffe, S., Ruiz-Benito, P., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala, M.A., Ampoorter, E., Baeten, L., Barbaro, L., Bastias, C.C., Bauhus, J., Benavides, R., Benneter, A., Bonal, D., Bouriaud, O., Bruelheide, H., Bussotti, F., Carnol, M., Castagneyrol, B., Charbonnier, Y., Cornelissen, J.H.C., Dahlgren, J., Checko, E., Coppi, A., Dawud, S.M., Deconchat, M., De Smedt, P., De Wandeler, H., Domisch, T., Finér, L., Fotelli, M., Gessler, A., Granier, A., Grossiord, C., Guyot, V., Haase, J., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F.-X., Jucker, T., Kambach, S., Kaendler, G., Kattge, J., Koricheva, J., Kunstler, G., Lehtonen, A., Liebergesell, M., Manning, P., Milligan, H., Müller, S., Muys, B., Nguyen, D., Nock, C., Ohse, B., Paquette, A., Peñuelas, J., Pollastrini, M., Radoglou, K., Raulund-Rasmussen, K., Roger, F., Seidl, R., Selvi, F., Stenlid, J., Valladares, F., Van Keer, J., Vesterdal, L., Fischer, M., Gamfeldt, L. & Allan, E. 2018: Continental mapping of forest ecosystem functions reveals a high but unrealised potential for forest multifunctionality. – Ecology Letters 21: 31-42.

Van Huis, A. 2003: Medical and stimulating properties ascribed to arthropods and their products in sub-Saharan Africa. In: Motte-Florac, É. & Thomas, J.M.C. (Eds.): "Insects" in oral literature and traditions. – Peeters, Leuven, Paris & Dudley, MA, pp. 367-382.

Van Huis, A. 2021: Cultural aspects of ants, bees and wasps, and their products in sub-Saharan Africa. – International Journal of Tropical Insect Science 41: 2223-2235.

Van Wijngaarden, P.M., Van Kessel, M. & Van Huis, A. 2007: *Oecophylla longinoda* (Hymenoptera: Formicidae) as a biological control agent for cocoa capsids (Hemiptera: Miridae). – Proceedings of the Netherlands Entomological Society Meeting 18: 21-30.

Venuste, N., Beth, K.A., Frederic, F., Lombart, K.M.M., Wouter, D. & Donat, N. 2018: Use of soil and litter ants (Hymenoptera: Formicidae) as biological indicators of soil quality under different land uses in Southern Rwanda. – Environmental Entomology 47: 1394-1401.

Viles, H.A., Goudie, A.S. & Goudie, A.M. 2021: Ants as geomorphological agents: a global assessment. – Earth-Science Reviews 213: art. 103469.

Villamagna, A.M., Angermeier, P.L. & Bennett, E.M. 2013: Capacity, pressure, demand, and flow: a conceptual framework for analyzing ecosystem service provision and delivery. – Ecological Complexity 15: 114-121.

Vinson, S.B. 2013: Impact of the invasion of the imported fire ant. – Insect Science 20: 439-455.

Violle, C., Navas, M., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. 2007: Let the concept of trait be functional! – Oikos 116: 882-892.

von Beeren, C., Blüthgen, N., Hoenle, P.O., Pohl, S., Brückner, A., Tishechkin, A.K., Maruyama, M., Brown, B.V., Hash, J.M., Hall, W.E. & Kronauer, D.J.C. 2021: A remarkable legion of guests: diversity and host specificity of army ant symbionts. – Molecular Ecology 30: 5229-5246.

Wagner, D.L., Grames, E.M., Forister, M.L., Berenbaum, M.R. & Stopak, D. 2021: Insect decline in the Anthropocene: death by a thousand cuts. – Proceedings of the National Academy of Sciences 118: art. e2023989118.

Wheatley, M. & Johnson, C. 2009: Factors limiting our understanding of ecological scale. – Ecological Complexity 6: 150-159.

Wielgoss, A., Tscharntke, T., Rumede, A., Fiala, B., Seidel, H., Shahabuddin, S. & Clough, Y. 2014: Interaction complexity matters: disentangling services and disservices of ant communities driving yield in tropical agroecosystems. – Proceedings of the Royal Society B-Biological Sciences 281: art. 20132144.

Wills, B.D. & Landis, D.A. 2018: The role of ants in north temperate grasslands: a review. – Oecologia 186: 323-338.

Wills, B.D., Powell, S., Rivera, M.D. & Suarez, A.V. 2018: Correlates and consequences of worker polymorphism in ants. – Annual Review of Entomology 63: 575-598.

Wilsanand, V., Varghese, P.V.P. & Rajitha, P. 2007: Therapeutics of insects and insect products in South Indian traditional medicine. – Indian Journal of Traditional Knowledge 6: 563-568.

Wolff, S., Schulp, C.J.E. & Verburg, P.H. 2015: Mapping ecosystem services demand: a review of current research and future perspectives. – Ecological Indicators 55: 159-171.

Wong, M.K.L., Economo, E.P. & Guénard, B. 2023: The global spread and invasion capacities of alien ants. – Current Biology 33: 566-571.

Wong, M.K.L., Guénard, B. & Lewis, O.T. 2019: Trait-based ecology of terrestrial arthropods. – Biological Reviews 94: 999-1022.

Wozniuk, V. 2008: In the shadow of the anthill: religious faith, individual freedom, and the common good in the thought of V.S. Solovev. – The Russian Review 67: 622-637.

WU, H., LU, X., WU, D., SONG, L., YAN, X. & LIU, J. 2013: Ant mounds alter spatial and temporal patterns of CO_2, CH_4 and N_2O emissions from a marsh soil. – Soil Biology and Biochemistry 57: 884-891.

XU, H., LIU, Q., WANG, S., YANG, G. & XUE, S. 2022: A global meta-analysis of the impacts of exotic plant species invasion on plant diversity and soil properties. – Science of the Total Environment 810: art. 152286.

YANG, G., ZHOU, W., QU, W., YAO, W., ZHU, P. & XU, J. 2022: A review of ant nests and their implications for architecture. – Buildings 12: art. 2225.

YEAKEL, J.D., PIRES, M.M., AGUIAR, M.A.M. DE, O'DONNELL, J.L., GUIMARÃES, P.R., GRAVEL, D. & GROSS, T. 2020: Diverse interactions and ecosystem engineering can stabilize community assembly. – Nature Communications 11: art. 3307.

ZHAO, J., ZHONG, P.-S., ZHANG, S.-S. & SONG, X.-X. 2008: Control effect of *Solenopsis invicta* BUREN in transformer substations. – Chinese Journal of Hygienic Insecticides & Equipment 14: 267-269.

ZHAO, Y., LIU, Z. & WU, J. 2020: Grassland ecosystem services: a systematic review of research advances and future directions. – Landscape Ecology 35: 793-814.

ZHONG, Z., LI, X., SANDERS, D., LIU, Y., WANG, L., ORTEGA, Y.K., PEARSON, D.E. & WANG, D. 2021: Soil engineering by ants facilitates plant compensation for large herbivore removal of aboveground biomass. – Ecology 102: art. e03312.

ZUCCHI, T.D., GUIDOLIN, A.S. & CÔNSOLI, F.L. 2011: Isolation and characterization of Actinobacteria ectosymbionts from *Acromyrmex subterraneus brunneus* (Hymenoptera, Formicidae). – Microbiological Research 166: 68-76.