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The little things that run the world revisited: a review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae)

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Abstract

Ants are important for the maintenance and functioning of many ecosystems and provide a variety of ecosystem services and disservices.This review summarizes information on ecosystem services provided by ants in a framework modeled after the Millennium Ecosystem Assessment. In this framework, ecosystem services are divided into provisioning, regulating, cultural, and supporting services, and we show that ants provide services in each of these categories. We also present a review of some of the major disservices mediated by ants (i.e., the roles of ants that have negative consequences on human and environmental health, and societal well-being). Our review does not exhaustively review any single ecosystem service or disservice, but rather pieces together the many ways in which ants are influential in our changing planet and society. We conclude by describing future areas of research that will help better understand the impact of ants on ecosystems and society.

Key words: Ants, ecosystem function, provisioning services, regulating services, cultural services, supporting services, Millennium Ecosystem Assessment, biodiversity conservation, climate change, meta-analysis.

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Introduction

The anthropogenic footprint on ecosystems and biodiversity is more notable now than at any other point in history. On a changing planet, the impacts of biodiversity loss must be carefully considered. Of particular interest are organisms that provide one or more ecosystem services, which are defined as any service that benefits human society and supports well-being (WRI 2005, CHAN & al. 2006). The Millennium Ecosystem Assessment (MA) provides a general framework for classifying the various forms of ecosystem services provided by organisms these are: (1) provisioning services: goods provided directly by an organism that directly influence human well-being; (2) regulating services: services that regulate ecosystem processes, or the intrinsic ecosystem characteristics whereby an ecosystem maintains its integrity; (3) supporting services: services required to maintain the other forms of ecosystem services which include ecosystem functions; and (4) cultural services: nonmaterial benefits obtained from ecosystems. The concept of "human well-being" is simplified by categorizing it into five main components (even though more do exist and are likely influenced by ecosystem services provided by organisms): (1) having the basic material needs for a good life; (2) health; (3) having good social relations; (4) security; and (5) freedom of choice and action (WRI 2005). In this review we show that ants provide multiple ecosystem services that can be placed within each of the categories of the MA framework but also deliver important and costly disservices that may detract from the services they do provide.

Ants are the most diverse group of social insects: more than 12,500 species have been formally described, and there may be as many as another 12,500 unknown species (BOLTON & al. 2007, WARD 2009). Current phylogenetic analyses group ants into 21 extant subfamilies and estimate that ants originated in the Cretaceous, approximately 120 million years ago (BRADY & al. 2006, MOREAU & al. 2006). Since their origin, ants have occupied almost every continent and have become a dominant taxon of the terrestrial arthropod fauna. Species discovery and an improved understanding of phylogenetic relationships of ants will continue to expand our understanding of their true diversity. Ants are also extremely abundant in most terrestrial ecosystems and can account for large percentages of the total animal biomass in many environments (WILSON 1987, HÖLLDOBLER & WILSON 1990). Of the thousands of known species only a handful have been extensively studied beyond their taxonomy (frequently in the context of "disservices" of pest and invasive species), and so our understanding of the major ecosystem services provided by ants is still very limited. That said, myrmecological research on ecosystem services mediated by ants has increased over the past twenty years (Fig. 1), but further species discoveries can potentially uncover even more ant-mediated services that are currently unknown to us.

Even before the MA, ants were recognized as having major ecological roles in most terrestrial ecosystems (including mediating ecosystem functions, reviewed by FOLGARAIT 1998). Additional reviews since then have also synthesized the knowledge of the influence of ant-mediated ecosystem functions and services for different environmental and ecological scenarios (e.g., habitat fragmentation, CRIST 2009, and use of ants as indicators of environmental change ANDERSEN & MAJER 2004, ELLISON 2012). We use the MA as a framework to expand and facilitate our understanding of the important roles that ants play in terrestrial ecosystems. Many of the examples presented here are of studies conducted at local or regional scales, and should not be considered the general rules for all ant communities globally.

In this review we synthesize how ant biodiversity influences ecosystem services and functions and how this line of research has developed in the 13 years since the last major review of this topic (FOLGARAIT 1998); we note that many of the topics discussed herein merit their own exhaustive analysis (and some have been recently reviewed). We also show that ant biodiversity plays an important role in all four categories of ecosystem services defined in the MA. We emphasize the role of ants in soil processes and seed dispersal, two areas for which there is a growing body of literature linking ants, ecosystem services and ecosystem functions. We further expand our review by addressing some of the major ecosystem "disservices" that are associated with ants. We conclude by highlighting research needs that may advance our understanding of ant-mediated ecosystem services and functions.

Ant biodiversity and provisioning, regulating and cultural ecosystem services

Provisioning services: Provisioning services are goods or services provided by organisms that directly improve human well-being; examples include the provisioning of food, timber, and fiber (WRI 2005). Here we describe two ways in which ants provide a product or service which directly promotes human well-being by providing material goods, and sustaining health and security: (I) the use of ants as food resources, and (II) the use of ants in medical and pharmaceutical applications.

Entomophagy, or the use of insects as food, is a provisioning ecosystem service frequently overlooked, most likely due to the taboo in many western cultures on the traditional practices of having insects as potential sources of protein and other essential nutrients in various regions of the world (DEFOLIART 1999). Due to their abundance and global distribution, ants are frequently consumed as part of traditional dishes in multiple cultures, especially in tropical and subtropical countries (SRIVASTAVA & al. 2009). In North America, larvae of *Liometopum apiculatum* MAYR, 1870, are increasingly being consumed as a delicacy, but are also a significant protein source (approximately 58% of their mass is protein) (RAMOS ELORDUY 1977). Recent work

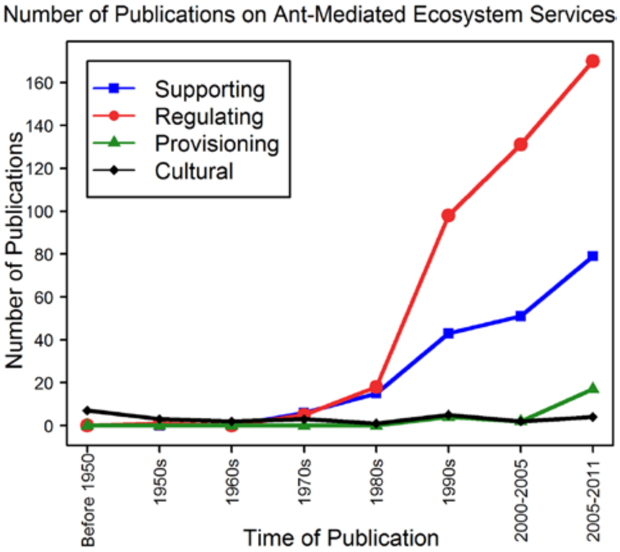

Fig. 1: Number of publications on ant-mediated ecosystem services categorized into the four MA Ecosystem Service categories; additional graphs subdivided by keyword searches are presented in Appendix 1.

has considered the potential for management and harvesting of this valuable resource in northern Mexico (ESPARZA-FRAUSTO & al. 2008). In Central and South America, reproductive females of the genus *Atta* are consumed by indigenous populations (DEFOLIART 1997) and are considered a valuable source of protein and minerals (RUDDLE 1973, DUFOUR 1987, ARAUJO & BESERRA 2007). In Africa and Southeast Asia, workers and larvae of the genera *Oecophylla* and *Polyrhachis* are rich in protein, lipids, and carbohydrates (CROZIER & al. 2010, RAKSAKANTONG & al. 2010). The provisioning of food from ants and other insects, while important, is still underreported for many countries (DEFOLIART 1997), and further exploration of nutritional value of ants and the possibility of using ants in a sustainable manner which contributes to society is necessary.

Ants are also providers of biomedical services arising from biotechnological developments and pharmaceutical products. Recent developments of treatments for the potentially deadly anaphylactic reactions that sometimes result from ant stings ironically are derived from the ant venom itself, a treatment known as immunotherapy, in which the patient's immune response is enhanced by small dosage exposure to the ant venom. This has been particularly well explored and experimentally tested with *Solenopsis invicta* BUREN, 1972, in the U.S.A. and *Myrmecia pilosula* SMITH, 1858, in Australia (DUPLANTIER & al. 1998, BROWN & al. 2003, BROWN & al. 2004). Although initial results are encouraging (with patients showing increased resistance to anaphylactic reactions), the authors suggested that further exploration of ant venom immunotherapy is required before widespread application. A recent synthesis of the applications of many insects, including ants, in pharmaceutical biochemical exploration highlights the important chemical properties of various ant species' venoms and their potential for pharmacological development (DOSSEY 2010). Finally, products like the fine silk produced by the weaver ant *Oecophylla smaragdina* (FABRICIUS, 1775) larvae are

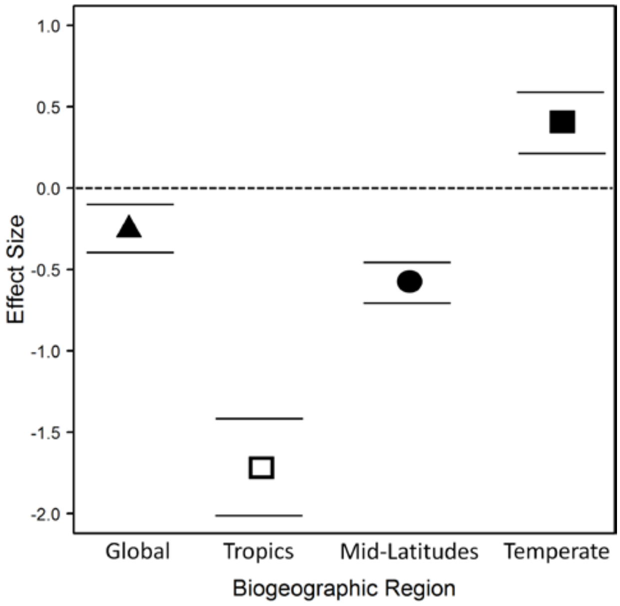

Fig. 2: Standard effect sizes of percentage of seeds moved by ants versus rodents during various experiments globally and across three global biogeographic regions (Appendix 2). Solid horizontal lines indicate the upper and lower bounds of the 95% confidence intervals about the mean standard effect sizes. Total Global n = 29; Tropics n = 6, Mid-Latitudes n = 13, Temperate Forests n = 10. A negative effect size indicates that rodents moved a greater percentage of seeds than ants, and a positive response indicates that ants moved a greater percentage of seeds than rodents.

being considered as nanofibers to be used in pharmaceutical and biotechnological development (REDDY & al. 2011).

Regulating services: Regulating services (along with cultural and supporting services discussed in subsequent sections) are often harder to recognize and quantify, because direct links from them to human well-being are not as obvious as they are for provisioning services. However, regulating and supporting services are necessary to maintain life on Earth, and in some cases promote provisioning services (WRI 2005). Here we explore some of the published literature on four regulating services that ants are often associated with: seed dispersal, pollination, regulation of animal community structure, and the use of ants as biological control agents. These four examples of regulating services are frequently mentioned in the ant literature but rarely considered as valuable ecosystem services that are essential for maintaining much of the plant and animal biodiversity across terrestrial ecosystems.

Seed dispersal in ants is well documented and is the most widely studied regulating ecosystem service provided by ants. In our literature review we encountered approximately 350 publications, the earliest from the 1970s, that either documented or examined ant-mediated seed dispersal or myrmecochory (Appendix 1, as digital supplementary material to this article, at the journal's web pages). Myrmecochory is the result of a co-evolutionary, mutualistic relationship in which the seed provides ants with a lipid-rich nutritional resource, called an elaiosome, in return for which the ant collects and disperses the seed (BEATTIE 1985, GILADI 2006). This relationship has been documented for at least 11,000 plant species, is a geographically widespread phenomenon, and is hypothesized to have evolved multiple times (BEATTIE 1985, WESTOBY & al. 1991, LENGYEL & al. 2010). The large number of myrmecochorous plant species and the multiple evolutionary origins of this mutualism suggest that this trait is important in the maintenance of global plant biodiversity. Thus, it meets the definition of a regulating service mediated by ants. Myrmecochory has evolved in every continent where ants occur but is most evident in eastern North America, southern Europe and most of Australia (LENGYEL & al. 2010), which suggests that it may have more of an influence on community structure in temperate latitudes. In fact, ants disperse 40% of all herbaceous plants in some temperate woodlands (BEATTIE 1985).

We completed a meta-analysis to quantify the relative contribution of ants and rodents (another major seed disperser) as seed dispersers across broad geographic scales (tropics, mid-latitudes, and temperate ecosystems). On January 5, 2012, we searched Web of Science for publications using the following search terms: "Ants" AND "Rodents" AND "Seed Dispersal" OR "Myrmecochory" AND "Experiment". This search resulted in 111 citations which met the search criteria, but we selected only publications which had completed experiments using exclosures of both ants and rodents and that quantified which seed disperser had the greatest impact. In all the selected studies we used the percentage of seeds moved throughout the duration of the experiment as the response variable. This narrowed our total number of studies to ten (Appendix 2, as digital supplementary material to this article, at the journal's web pages), but we note that several of the studies analyzed seeds from multiple plant species or had additional experimental treatments. We treated each plant species as the unit of replication and so our final number of plant species considered in the meta-analysis was 29.

We calculated the effect size of ants and rodents on seed movement as the log-response ratio (ln *R*) following the methods used in RODRIGUEZ-CABAL & al. (2009). A negative effect size indicates that rodents moved a greater percentage of seeds than ants, and a positive response indicates that ants moved a greater percentage of seeds than rodents. Our meta-analysis used a random-effects model and calculated the effect size and 95% confidence interval for ants and rodents using MetaWin 2 (ROSENBERG & al. 2000). Our meta-analysis results suggest that globally, rodents tend to have a greater impact on seed movement than ants (Fig. 2). This is also true for tropical and mid-latitude (typically arid and semi-arid) biogeographic zones. In contrast, ants have a greater impact than rodents on seed movement in temperate forests, supporting the notion that ants may be important seed dispersers in temperate ecosystems (BEATTIE 1985 and LENGYEL & al. 2010). We used "seed removal" as a metric of seed dispersal, but this metric will be improved as more studies with standardized data on seed viability become available. Seed viability may be more informative of the impact of seed dispersers on eventual plant community composition and some studies suggest that, at least for myrmecochorous plants, seeds dispersed by ants tend to be more viable than seeds consumed by rodent predators (CHRISTIAN & STANTON 2004). We used this meta-analytic approach as an example of how to quantify the impacts of ants on major ecosystem services across broad geographic scales.

Tab. 1: Key examples and major reviews of ecosystem services provided or mediated by ants. Note that the studies presented in this table are only a minor subset of the literature available for each example. * indicates review articles on the given examples.

Service	Example	Direct / Indirect benefit	References
Provisioning services			
Food	*Liometopum apiculatum* larvae consumed in Mexico and Western U.S.	Direct	RAMOS ELORDUY (1977)
	Alates of *Atta* species consumed in Central and South America	Direct	DEFOLIART (1997, 1999)
	Larvae of *Oecophylla* species consumed in southeast Asia	Direct	SRIBANDIT & al. (2008), RAKSAKANTONG & al. (2010)
Biomedical / Pharmaceutical	Venoms of *Solenopsis invicta* and *Myrmecia pilosula* used in immunotherapy treatment against anaphylaxis	Direct	DUPLANTIER & al. (1998), BROWN & al. (2003), BROWN & al. (2004)
	Nanofibers from *Oecophylla* silk used in biomedical technology development	Direct	REDDY & al. (2011)
Regulating services			
Seed dispersal	Geographically widespread, and evolved multiple times in as many as 11,000 plant species	Indirect	LENGYEL & al. (2010)
Pollination	Pollination via pseudocopulation of orchids	Indirect	PEAKALL (1989)
	May be important pollinators of plants which occur in high local densities, produce little nectar, and have flowers easily accessible to ants.	Indirect	ROSTÁS & TAUTZ (2011)*
Animal community regulation	Regulation of ant community structure by behaviorally dominant ants	Indirect	ANDERSEN & PATEL (1994)
	Regulation of invertebrate community structure by army ant species	Indirect	KASPARI & al. (2011)
	Influence of avian community structure by army ants	Indirect	HARPER (1989)
Biological control	Use of ants to regulate pest populations in coffee and cacao agroecosystems	Direct	PHILPOTT & ARMBRECHT (2006)*
	Use of *Oecophylla* species to regulate pests in nuts, fruit and timber in Old World and Australian tropics	Direct	VAN MELE (2008)
	Use of *Dolichoderus thoracicus* in pest regulation in sapodilla production	Direct	VAN MELE & CUC (2001)
Cultural services			
Ancient religion / Symbology	Various examples from religious texts	Indirect	SLEIGH (2004)*
Literature	Various examples for classical and contemporary literature	Indirect	SLEIGH (2004)*
New world traditions	*Paraponera clavata* used in *Tucandeira* practices of several South American indigenous peoples	Direct	BOTELHO & WEIGEL (2011)
Western culture	Various examples from film industry	Indirect	SLEIGH (2004)*, MARIÑO-PÉREZ (2006)*
Supporting services			
Nutrient cycling	Nest soil pH is moderated by ant activities	Indirect	LAVELLE & al. (2006)
	Ants enrich soil around nest with nitrogen	Indirect	WAGNER & JONES (2006)
	Ants track nutrients like sodium	Indirect	KASPARI & al. (2010)
Soil movement	Soil movement due to nest and gallery construction increases soil porosity	Indirect	FROUZ & JILKOVA (2008)
Decomposition	*Camponotus punctulatus* nests regulate soil organisms and decomposition	Indirect	PARIS & al. (2008)
	Ant nests promote microbes which lead to enhanced decomposition	Indirect	KASPARI & YANOVIAK (2009)
	Messor spp. ant nests enhance soil nutrients via increased microbial biomass	Indirect	GINZBURG & al. (2008)
Ecosystem engineering	*Lasius flavus* nests increase soil nutrients and facilitate plant succession	Indirect	VLASAKOVA & al. 2009
	Nest soil chemistry is enhanced compared with surrounding soils due to ant presence	Indirect	VELE & al. (2010)
Carbon cycling	*Formica rufa* nests are net producers of carbon compared with soils without nests	Indirect	RISCH & al. (2005a)
Biological indicators	Use of ants in estimating the environmental impacts on biodiversity from mining	Direct	ANDERSEN & MAJER (2004)*
	Use of ants in measurement of bioaccumulated heavy metals resulting from copper smelting	Direct	DEL TORO & al. (2010)
	Use of ants to estimate impacts on biodiversity from natural fire disturbances	Direct	PARR & al. (2004)

Pollination mediated by ants can occur under certain ecological and evolutionary situations (ROSTÁS & TAUTZ 2011) and be considered necessary for the maintenance of plant community structure. However, pollination by ants usually is treated as unimportant because ants are frequently thought to be ineffective pollinators (e.g., metapleural gland secretions can adversely impact *Brassica* and *Acacia* pollen; BEATTIE & al. 1985) and even more frequently are viewed as nectar thieves (GALEN & BUTCHART 2003). Even though the frequency of occurrence of plant pollination is much lower than seed dispersal by ants, it could still be considered a valuable ecosystem service. Many of the reported cases of successful ant pollination occur in the family Orchidaceae. For example, *Myrmecia urens* LOWNE, 1865, males are attracted and attempt to mate with the orchid *Leporella fimbriata*, resulting in crosspollination of multiple orchids as the male ant visits multiple flowers (PEAKALL 1989). These interactions are poorly studied, and experimental tests to evaluate the efficiency of ant facilitated pollination are limited (ROSTÁS & TAUTZ 2011). Ants could potentially be effective pollinators of flowering plants that occur in high local densities, produce little nectar, and have flowers easily accessible to ants (HICKMAN 1974, ROSTÁS & TAUTZ 2011), a topic that requires further experimentation.

Ants also can regulate the community structure of both ants and other animals. Behaviorally and ecologically dominant ant species have a strong influence on ant community structure mostly due to interference competition and competitive exclusion (ANDERSEN & PATEL 1994, PARR 2008). Meat ants (*Iridiomyrmex* species) are dominant ants in many of Australia's ecosystems. In a series of exclosure experiments, meat ant exclusion resulted in increased abundances of other, behaviorally subdominant, ant species (ANDERSEN & PATEL 1994). Additionally, the presence of competitively dominant ant species can decrease the abundances of co-occurring predatory spiders (HALAJ & al. 1997). Ants are also highly efficient and mobile predators of other invertebrate taxa, leading to top-down regulation effect of invertebrate communities (KASPARI & al. 2011). In temperate regions of Europe, the wood ant *Formica rufa* LINNAEUS, 1761 has been documented to decrease abundances and species richness of carabid beetles, and could be better predictors of ground beetle abundances than vegetation cover (HAWES & al. 2002). In the tropics, massive and aggressive colonies of army ants (particularly those in the genera *Eciton* and *Labidus*) can influence the abundance of other invertebrates that play important roles in other ecosystem services (KASPARI & al. 2011). Finally, the influence of army ants expands beyond their impact on invertebrate communities to avian ones. Ant-birds have evolved behavioral traits that involve tracking army ant colonies as they move through the forest floor and capitalize on the vulnerable invertebrates driven out by the raiding ants, generally benefiting the bird community (WILLSON 2004, WREGE & al. 2005). In cases where army ants have been extirpated, frequently as a result of habitat loss or fragmentation, ant-bird communities have also suffered, suggesting that army ants are essential in structuring tropical avian communities of ant-birds (HARPER 1989).

The use of ants as biological control agents is a growing topic of research and has been discussed in the literature since the 1950s (WAY 1953) (Appendix 1). Predatory and territorial ant species are used for management and control of pest species and diseases in various agroecosystems (see reviews by WAY & KHOO 1992, PHILPOTT & ARMBRECHT 2006). Weaver ants are commonly used in biological control of pests of fruits, nuts and timber resources of Asia, Africa and Australia (reviewed in VAN MELE 2008). The African ant *Myrmicaria opaciventris* EMERY, 1893 has predatory life history traits that may be beneficial in controlling pest termite population in sugar cane plantations (KENNE & al. 2000), but further research should consider it as a viable candidate biological control agent of termites. In Vietnam, *Dolichoderus thoracicus* (SMITH, 1860) is an effective biological control agent of various pests of sapodilla (*Manilkara zapota*), an important economic crop, and presence of *D. thoracicus* has been accepted by many of the farmers surveyed (VAN MELE & CUC 2001). In some cases, even non-native, invasive ants like *Solenopsis invicta* control pest populations in cotton and sugarcane agroecosystems (REAGAN 1986). In agroecosystems worldwide maintenance of predatory ant diversity improves agricultural practices by controlling pest and fungal outbreaks; therefore ants' roles as biological control agents provide multiple ecosystem services (PHILPOTT & ARMBRECHT 2006).

Cultural services: Cultural services are essential to human well-being by stimulating cultural and spiritual identity but they can be difficult to understand and quantify (WRI 2005). Ants provide cultural services to various communities across the world (SLEIGH 2004). One of the oldest and best documented uses of ants in symbology, culture, and myth is characterized in Homer's Iliad, in which there is a description of a unique legion of men called the "Myrmedons" or "Ant People". The Myrmedons were an elite group of warriors, said to have been created from ants by Zeus on Aegina. Perhaps their most notable mention is in the battle of Troy, where the Myrmedons were commanded by Achilles into battle (SEARS 2010). Additionally, ants are mentioned in several cultural and spiritual texts (e.g., The Talmud, The Bible, and The Quran). Ants are also mentioned in some well-known contemporary works of literature (e.g., "Walden" by H.D. THOREAU 1854, "Empire of the ants" by H.G. WELLS 1905, "Leiningen versus the ants" by C. STEPHENSON 1938, and "Anthill" by E.O. WILSON 2010), and if we consider literature to be an important component in structuring cultural development, we argue that ants too, are part of this cultural service.

Perhaps a more direct link between ants and cultural traditions and spiritual rituals comes from the use of bullet ants, *Paraponera clavata* (FABRICIUS, 1775), in the ceremonial use of several New World indigenous tribes. The ceremony frequently referred to as the "Tucandeira" is a traditional rite of passage of young boys into manhood and involves the stinging by several bullet ants as ceremonial dances and prayers are completed (LIEBRECHT 1886, BOTELHO & WEIGEL 2011). Other Native American cultures also attached value to ants in social and spiritual rituals and art (CAPINERA 1993, CHERRY 1993). In Western cultures, ants have also become a topic of interest; their influence can be seen in the film industry with at least six major films using ants as the focal point of the plot (e.g., Them! 1954, Warner Brothers, Naked Jungle 1954, Paramount Pictures, Phase IV 1974, Paramount Pictures, Empire of the Ants 1977, Cinema 77, Ants: It happened at Lakewood Manor 1977, Alan Landsburg Productions, Antz 1998, Dreamworks SKG; MARIÑO-PÉREZ 2006). In an exhaustive review, SLEIGH (2004) explored the influence ants have on humanity and the important role that ants play in influencing cultural and scientific development.

Ant biodiversity and supporting ecosystem services and ecosystem function: Ants provide a variety of supporting services that support regulating, provisioning, and cultural ecosystem services. Examples of ant-mediated supporting services include common ecosystem processes such as nutrient cycling, formation of soil structure, decomposition, provisioning of habitat, carbon flux, and the use of ants as biological indicators of environmental change. Some of these services have received attention in the scientific literature, but the mechanistic or functional roles of ants in these services are not well understood.

Ants act as ecosystem engineers, and influence ecosystem structure and function through processes that provide habitat for other species or modulate other ecosystem functions (LAVELLE & al. 1997, FROUZ & JILKOVA 2008). Ants create habitat for other organisms by increasing nutrients in a localized area around ant nests, facilitating a more favorable growing environment for plant species (WAGNER & al. 1997, WAGNER & JONES 2004, 2006). Ants influence the trajectory of succession of ecosystems and alter vegetation cover types via changes in soil chemistry. For example, VLASAKOVA & al. (2009) found that the soil around *Lasius flavus* (FABRICIUS, 1782) anthills in Slovakian grasslands was more productive and resulted in spruce seedlings germinating at a higher rate compared with surrounding soils. The presence of ants in these grasslands led to an acceleration of succession away from grassland vegetation to a spruce forest by increasing the abundance of spruce seedlings (VLASAKOVA & al. 2009). Ants can also directly influence plant community structure or successional trajectories by manipulating the seed bank via preferential seed dispersal of myrmecochorous plant species (see also Regulating services section, along with BROWN & HUMAN 1997, REY & MANZANEDA 2007, SERVIGNE & DETRAIN 2010, ZELIKOVA & al. 2011). In an experiment conducted in a semiarid live oak savannah, *Pogonomyrmex barbatus* (SMITH, 1858) ant nests served as the chief seed source and refugia for grass species recolonizing following a five-year drought that exhausted the seed bank, with effects ranging up to 30 m from the nest (NICOLAI & al. 2010).

Nutrient cycling: Ants create nutrient rich oases around nests, which are more productive than surrounding points in the same environment (LAVELLE & al. 2006). This is the result of ants adding organic matter to their nests (frequently used to support their nest structures) that also influences nutrient retention via organic inputs (LAVELLE & al. 1997, JOUQUET & al. 2006). The presence of ant nests can significantly alter nutrient concentrations and nutrient cycling dynamics relative to surrounding soils (WAGNER & JONES 2004, 2006).

A variety of ant mutualisms exist between ants and plants, fungi, or other organisms that enhance nutrient cycling (STRADLING & WHITFORD 1978, CURRIE & al. 1999b, MUELLER & al. 2001, OHGUSHI 2008, WAGNER & NICKLEN 2010, DEFOSSEZ & al. 2011, MUELLER & al. 2011). Fungal-ant associations have been well documented between Attines and fungal communities (QUINLAN & CHERRETT 1979, WILSON 1980, CURRIE & al. 1999a, b, MUELLER & al. 2001) as well as symbiotic mutualisms between various ant species and plant domatia (DEFOSSEZ & al. 2011). In their study of the ant *Petalomyrmex phylax* SNELLING, 1979 and a plant mutualist *Leonardoxa africana*, DEFOSSEZ & al. (2011) traced enriched forms of carbon and nitrogen originating from ant food sources throughout the plant and fungal associates. In the isotope pulse-chase experiment, they observed that ants transferred nitrogen to host plants as quickly as four days after the ants were given N-enriched foods. Furthermore, this enriched nitrogen remained in parts of the plant and fungal associates for almost two years after the initial experiment.

Nest soil chemistry can differ significantly from surrounding environments (VELE & al. 2010) because of alterations in nutrient concentrations and soil pH, which ants tend to shift towards neutral values (FROUZ & JILKOVA 2008). For example, some ant nests contain greater concentrations of several macronutrients like phosphorus (FROUZ & al. 1997, WAGNER & al. 1997, FROUZ & al. 2005, WAGNER & JONES 2006, KILPELAINEN & al. 2007). Two examples of the impact of macronutrients on ant colonies include the various studies on *Pogonomyrmex rugosus* EMERY, 1895 (WAGNER & al. 1997, WAGNER & JONES 2004, 2006) and *Lasius niger* (LINNAEUS, 1758) (FROUZ & al. 1997, 2005, FROUZ & JILKOVA 2008). WAGNER & NICKLEN (2010) hypothesized that extrafloral nectaries produced by plants enhance plant nutrition because ant activities altered soil nutrients, and significantly influenced vegetation growth.

Carbon cycling: Ant nests produce trace amounts of greenhouse gases including methane (BENDER & WOOD 2003, GOLICHENKOV & al. 2009), and the presence of ant nests can lead to increased soil respiration compared with surrounding soil (ants increase carbon / soil respiration) (PEAKIN & JOSENS 1978, OHASHI & al. 2005, RISCH & al. 2005a, OHASHI & al. 2007, JURGENSEN & al. 2008). In a recent experiment, we documented soil respiration in soils with and without *Formica subsericea* SAY, 1836, nests and found that this species may indirectly increase soil respiration rates over the growing season compared with soils without ants (I. Del Toro, unpubl.). Red wood ants in boreal forests can alter the composition of forest floor vegetation and have large influences on belowground properties and processes including altered decomposition rates, microbial biomass and activity, and carbon and nitrogen loss from the environment (WARDLE & al. 2011). A wide body of research exists on the impact of European *Formica rufa* group ants on soil carbon dynamics (OHASHI & al. 2005, RISCH & al. 2005a, RISCH & al. 2005b, DOMISCH & al. 2006, KILPELAINEN & al. 2007, OHASHI & al. 2007, JURGENSEN & al. 2008). These studies suggest that ant nests produce more carbon than surrounding environments. Although studies have only examined these patterns at local scales, future research should study them at regional and landscape scales, to better understand how carbon and other nutrient dynamics change across large spatial scales and entire species ranges.

Soil formation, structure, and nutrient retention: Ants play important roles in shaping soil physical properties, such as soil structure and porosity, through construction and maintenance of nests, accumulation of organic matter, and interactions with other soil fauna. The effects of ants on soils were recently reviewed with an emphasis on the changes in physical properties associated with ant presence (FROUZ & JILKOVA 2008). Ant activities lead to increased soil aggregate formation and increased soil porosity (LAVELLE & al. 2006). These activities have localized influences on the hydrology of an area, and depending on nest density, can have larger-scale influences on ecosystem hydrology (RISCH & JURGENSEN 2008). Decreases in soil compaction and increases in porosity can lead to increased soil water retention, healthier plant root growth, and enhanced primary productivity. Ants alter microclimates within and around nests, modifying the environment of other organisms including myrmecophiles that live inside the nests. Thus, ants and ant activities (e.g., nest construction) could lead to more productive soils based on changes in physical soil properties.

Decomposition: Decomposition is a key process that connects aboveground inputs with belowground activities (MEGIAS & al. 2011). Ants play important roles in nutrient cycling via decomposition in many environments (KRISTIANSEN & AMELUNG 2001, MCINTYRE & al. 2001, HUNTER & al. 2003, DOMISCH & al. 2005, WAGNER & JONES 2006, GINZBURG & al. 2008, PARIS & al. 2008, WHITFORD & al. 2008, SHIK & KASPARI 2010, ZELIKOVA & al. 2011). Ants alter decomposition via direct pathways (such as the removal by attines of vegetation for fungal gardens) and indirect pathways (such as altering microbial community composition, which can control decomposition rate). Vegetation type influences ant-mediated decomposition, as plants with higher lignin content are harder to decompose, and ants can preferentially select more palatable vegetation (SILVA & VASCONCELOS 2011). Vegetation richness may also influence the diversity and abundance of ant decomposers in some environments (DONOSO & al. 2010). Many ant species are limited by access to nutrients such as phosphorous and nitrogen, which in turn limits decomposition rates (MILTON & KASPARI 2007). A variety of ant exclusion experiments have been established (LENOIR & al. 2007, ELLISON & al. 2010, ROMEU-DALMAU & al. 2010, PIOVIA-SCOTT 2011, PIÑOL & al. 2012), and some have shown that the removal of ants from environments increase decomposition rates (WARDLE & al. 2011).

Ecosystem structure and function: Ants may influence soil nutrient concentrations by changing germination rates of some vegetation (REY & MANZANEDA 2007) and altering composition of soil-dwelling animals within ant nests (BOULTON & AMBERMAN 2006) and within larger food webs. SANDERS & VAN VEEN (2011) found that ant presence directly shapes grassland communities through altering the densities of decomposers, herbivores and higher trophic levels. They determined this relationship to be dependent on increased nest density which led to greater predation on decomposers (SANDERS & VAN VEEN 2011).

Bioindicators: Since ants are so responsive to environmental change, it is no surprise that ants are often used as biological indicators. The use of ants as indicators of environmental change is the most heavily documented example of a supporting service provided by ants, with at least 65 articles published on the topic and most published during the last decade (Appendix 1). These studies frequently highlight the usefulness of ants in evaluating remediation efforts and disturbance intensities of mining and smelting activities, and the bioaccumulation of toxins and pollutants across multiple linked trophic levels (ANDERSEN & MAJER 2004, MAJER & al. 2007, DEL TORO & al. 2010). Ants can also be used to evaluate the impact of natural disturbance events like fire (PARR & al. 2004) and changes in temperature associated with climate change (PELINI & al. 2011). Additionally the use of ants in evaluating the impacts of habitat fragmentation on community composition is a useful tool in landscape management and restoration (CRIST 2009). The growing body of literature that uses ants as bioindicators of environmental change suggests that this is an ecosystem service with multiple benefits for environmental monitoring and management.

Linking ant-mediated ecosystem processes and services

Though the structure of this review follows the MA categorization of ecosystem services, MACE & al. (2012) developed a conceptual framework that builds on the MA and distinguishes between ecosystem processes and services and their consequent benefits for people. For example, ecosystem processes like trophic and competitive interactions result in the regulation of plant and animal communities (an ecosystem service) and ultimately influence the maintenance of biodiversity and stable ecosystems (a good valued by people). One area that remains unexplored, however, is the quantification of the resulting goods of ant-mediated services and processes.

Here we implement the framework developed by MACE & al. (2012) for a subset of ant species that play important roles in ecosystem processes and ecosystem services and provide beneficial products and goods to people (Fig. 3). Some of these include: leaf-cutter ants (Fig. 3A), which move vast amounts of soil, decompose organic matter, and influence nutrient cycling; harvester ants (Fig. 3B), important seed dispersers and an indicator species; and weaver ants (Fig. 3C), which provide food for people, and help maintain healthy ecosystems and manage agricultural pests.

Ant-mediated ecosystem disservices

Most ant-mediated disservices arise when ants live in close proximity to humans, when ants are introduced into new areas (and become invasive), or when new interactions, such as those involving invasive plants, are formed with native ants. A disproportionate number of disservices involve invasive ant species. Because ant introductions are, in many cases, facilitated by humans, invasive ant species are often found in human-dominated landscapes but their adverse effects span urban, agricultural, and "natural" settings. Once introduced into new areas, ants' successes as invaders are attributed to their ability to spread rapidly and because they are efficient breeders, competitors, and predators (CHAPMAN & BOURKE 2001). Five out of the fourteen insect species listed as the worst alien species in the IUCN Global Invasive Species Database and Early Warning System are ants (CHAPMAN & BOURKE 2001, GISP 2012).

Ants have a variety of perceived negative impacts on human well-being. The invasive fire ant, *Solenopsis invicta*, is referred to as "Public Enemy Number One" in the southern US because it frequently colonizes electrical equipment and other urban settings and has adverse effects on livestock, wildlife, and recreation activities (MYERS & al. 1998), damages that incur $1 billion annually in the U.S. (PIMENTEL & al. 2005). Invasive (e.g., *Monomorium pharaonis* (LINNAEUS, 1758)) and native ants (e.g., *Camponotus* spp.) alike also can be nuisance pests when they enter homes or businesses, commandeer food, or cause structural damage (KLOTZ & al. 1995, WETTERER & al. 2010). In some areas ants dominate commercial pest control complaints, and the insecticides used to treat those ants can have toxic effects when they leech into local aquatic systems (GREENBERG & al. 2010). Ant baits purchased by homeowners sometimes contain arsenic trioxide, a chemical that is toxic when accidentally consumed by people (YARRIS & al. 2008).

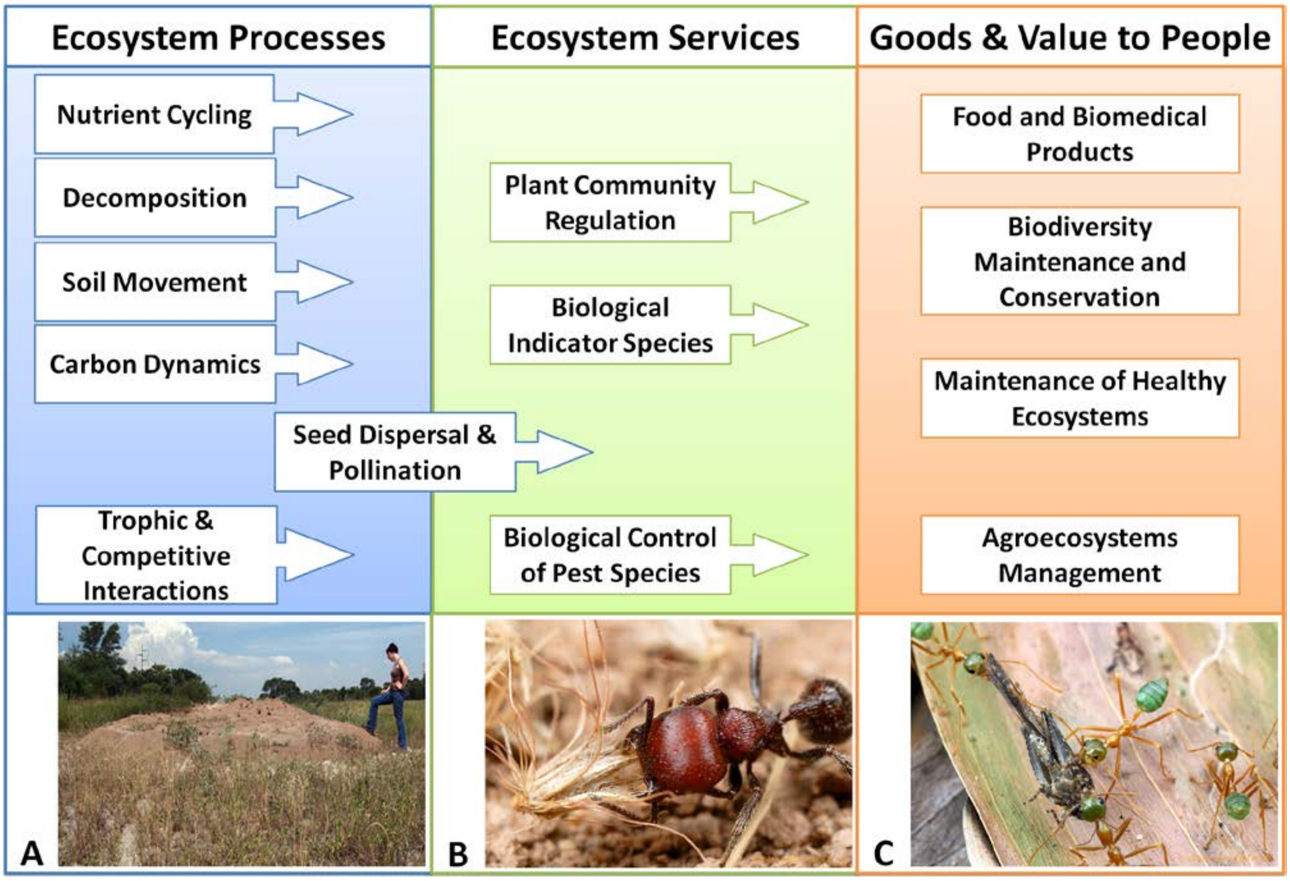

Fig. 3: Concept map linking ecosystem processes and services to the products and goods valued by people. Modeled from MACE & al. (2012) to include examples of ant-mediated ecosystem processes and services. (A) Leaf-cutter ant nest mound; (B) harvester ant transporting grass seed; (C) weaver ants attacking a grasshopper. Photo credits: Alexander Wild <myrmecos.net>

Ant stings also have negative impacts on human health. While stings of native ant species, e.g., the Jack-jumper ant (*Myrmecia pilosula*) in Australia, can cause anaphylactic reactions in humans (BROWN & al. 2003, BROWN & al. 2004), stings of *Solenopsis invicta* are expected by health professionals to cause more frequent anaphylactic reactions in humans because of their unusual venom and ability to establish large, aggressive supercolonies in human-dominated areas (SOLLEY & al. 2002). Other invasive ants, such as *Pachycondyla chinensis* (EMERY, 1895), are public health concerns because of their stings (NELDER & al. 2006), and stings of *Wasmannia auropunctata* (ROGER, 1863), an invasive ant species in the tropics, can cause blindness in mammals (WETTERER & PORTER 2003). *Monomorium pharaonis*, because of its small size and habit of colonizing urban environments, disturbs equipment and patients, thereby spreading disease in hospitals (KLOTZ & al. 1995).

In addition to directly affecting humans, invasive ants impact native fauna via competition with, and predation of, native ants and other taxa in their introduced ranges. Invasive ants have driven compositional changes in native ant assemblages in a variety of ecosystems (HOLWAY & al. 2002, GUÉNARD & DUNN 2010). Invasions by *Solenopsis invicta* and *Linepithema humile* (MAYR, 1868) are linked to declines in other arthropods, birds, reptiles, amphibians, and mammals (KENIS & al. 2009, WETTERER & al. 2009). Invasive ants also cause damage to agricultural crops and other plants through herbivory and excavation around roots (HOLWAY & al. 2002). Invasive ants can be beneficial to growers because they do prey on agricultural herbivore pests, and also are negatively associated with other natural enemies of those pests (EUBANKS 2001).

The changes in native fauna driven by ant invasions can have cascading consequences on plants and the ecosystem services they provide. For example, in New Caledonia, the invasive ant *Wasmannia auropunctata* is threatening populations of geckos that pollinate and disperse several plant species (TRAVESET & RICHARDSON 2006). Displacement of native ants by the Argentine ant, *Linepithema humile*, led to the disruption of seed dispersal, primarily of large seeded-plants, thereby causing changes in plant community composition. Using a meta-analysis, RODRIGUEZ-CABAL & al. (2009), provide strong evidence that Argentine ants can reduce the diversity of native ant seed dispersers by up to 92%, reducing overall seed dispersal and seedling establishment in invaded sites.

Disrupted seed dispersal also has been associated with invasions by *Solenopsis invicta* in the U.S. and *Pheidole megacephala* (FABRICIUS, 1793) in Australia (HOLWAY & al. 2002). Invasive ant species are also effective tenders of honeydew-producing herbivores, causing increases in their abundance and subsequent damage to crops and other plants (HOLWAY & al. 2002, WETTERER & PORTER 2003, NESS & BRONSTEIN 2004). The Yellow crazy ant, *Anoplolepis* *gracilipes* (SMITH, 1857), is associated with shifts in the vegetation on Christmas Island, where this ant displaced the primary crab consumers; in other places, associations between *A. gracilipes* and scale insects were linked with increased tree mortality (KENIS & al. 2009). Native ants also can negatively affect plant communities when they defend or disperse seeds of invasive plant species (JENSEN & SIX 2006, ALBA-LYNN & HENK 2010, LACH & al. 2010). For example, in Brazil, leaf cutter ants (*Acromyrmex niger* (SMITH, 1858)) disperse seeds of *Murraya paniculata*, an invasive plant that hosts the bacterium that causes greening disease in citrus trees (PIKART & al. 2011).

Invasive ant activities also can change physical and chemical soil properties. For example, displacement of deep-nesting harvester ants (*Messor* and *Pogonomyrmex*) in the western U.S. by shallow-nesting *Linepithema humile* changes soil turnover and decomposition rates, thereby altering nutrient cycles (MACMAHON & al. 2000). Invasions by *Wasmannia auropunctata*, *Solenopsis invicta*, and *Linepithema humile* are coupled with changes in detritivore communities, ultimately changing decomposition rates and nutrient cycles that can have consequences on soil as well as plant properties (DUNHAM & MIKHEYEV 2010, and references therein). However, LAFLEUR & al. (2005) found that *Solenopsis invicta* nesting and foraging activities increased the availability of nitrogen and therefore enhanced plant growth in longleaf pine plantations in the southern U.S.

Research needs

Myrmecological research of ecosystem services mediated and regulated by ants has increased dramatically during the last 20 years (Fig. 1, Appendix 1). Several ecosystem services have been extremely well studied and reviewed in recent years (e.g., ant-mediated seed dispersal; the use of ants as biological indicators of environmental change), yet several important areas remain largely unexplored. From this synthesis, it is clear that ants are fundamentally important in many terrestrial ecosystems at local scales, but just how important they can be under different environmental conditions and across larger spatial scales remains unclear. FOLGARAIT (1998) presented a list of five major research areas that have been increasingly studied during the last 13 years: evaluations of the importance of ants using ant removal experiments; evaluations of the importance of ants using ant addition experiments; understanding the roles of native and invasive ants in disturbed environments; the use of long-term research sites to evaluate impacts of ants on ecosystems through time; and studies of ants at larger biogeographic spatial scales. Here we present a list of another five lines of research that will improve our understanding of how important ants are to ecosystem functioning and mediating ecosystem services.

(1) Explore the biodiversity of ants. By increasing our understanding of ant species diversity we have the potential to discover new applications and mechanisms mediated by ants which may prove to be valuable to ecosystems and society. If the diversity estimates are correct (BOLTON & al. 2007, WARD 2009), then approximately half of the species of ants are not yet known to science, meaning that there is a good chance that some of these species may be playing fundamental roles in terrestrial ecosystem functioning and structure. It is also important to identify species that are key ecosystem service providers and determine what environmental variables (e.g., temperature, competition, geographic location) affect their capacity to mediate processes and provide services (KREMEN & OSTFELD 2005). These species are likely to be widely distributed, abundant, and ecologically dominant in their respective biomes; thus, investigating their respective roles across ecosystems will be a major undertaking which links biodiversity exploration with ecological studies.

(2) Quantify the value and importance of ant-mediated ecosystem services. This has been done for some of the disservices of ants (e.g., invasive species eradication). Moving forward, quantifying the value of ecosystem service providers like ants is an area of research which has many obstacles to overcome, yet is necessary to promote management and conservation of biodiversity. Research in this area should be the result of cross-collaborations with social scientists, economists, policy makers, and biodiversity researchers, who together must explore the socioeconomic and environmental benefits of conservation of organism-mediated ecosystem services (KREMEN &OSTFELD 2005, LUCK & al. 2009). LUCK & al. (2009) present a conceptual framework for completing work of this magnitude and heavily emphasize that more research is required in understanding the key functional traits of a taxon that provides a key ecosystem service, a crucial research need in myrmecology.

(3) Explore the variability in the importance of ants across ecosystems. Ecosystem services provided by organisms are not the same across the entire planet. Services are influenced by landscape structure, habitat type, and geographical variables (NELSON & al. 2009). We suggest that future research should quantify the effects of ants relative to those of other ecosystem engineers and mediators of ecosystem services (e.g., earthworms and termite roles in soil formation; rodents and birds in seed dispersal). This comparative approach also should extend to larger ecosystem and biogeographic scales as well as longer temporal scales. Comparative studies of this nature should also consider the roles and impacts of ants across different habitats and ecoregions, which vary in degrees of disturbance across the world. One approach would be to analyze these ecosystem effects using a meta-analysis framework to quantify the overall impact of ants on ecosystems and their benefits to ecosystems and society.

Our analysis of effect sizes of ant and rodent-mediated seed dispersal in the regulating services section of this review (Fig. 2), quantitatively synthesized the results of multiple seed dispersal experiments to derive large scale conclusions about the effect of ants relative to rodents on seed dispersal, but finding high quality, comparable data was very difficult because methods are not standardized across myrmecological experiments. For example, our literature search for the meta-analysis yielded 111 publications of seed dispersal experiments on ants and rodents. However, of those 111 publications only ten studies had the necessary standardized methods and valid controls required to complete a meta-analysis. We suggest that future experiments not only standardize their methods across studies but also make their raw data and results (e.g., means, number of replicates, and measures of variation) more easily accessible for use in large-scale comparative studies which will ultimately inform us about the relative importance of ants in mediating ecosystem services. We were unable to find sufficient comparable data for the other ecosystem services we reviewed to allow for additional meta-analyses, and this suggestion will also allow future researchers to identify the significance of ecosystem services thought to be provided by ants.

(4) Explore the mechanistic basis of ants as ecosystem engineers. Further research is needed to determine the mechanistic basis for ant functional contributions to ecosystem processes. It is widely recognized that ants alter ecosystem processes in important ways, but there are few studies that quantitatively evaluate these contributions. Ant species exclusion, removal, addition, and long-term experiments are parts of the framework suggested by FOLGARAIT (1998). Using this framework would be especially helpful for exploring questions about supporting and regulating services provided by ants. It is also important to understand how ants influence ecosystem processes and functions in light of management for future environmental conditions. Here we suggest that combining the experimental framework proposed by FOLGARAIT (1998) with experimental manipulations of predicted environmental change using standardized methods will yield informative predictions of how ant mediated ecosystem processes may respond to a changing planet.

(5) Quantify the influence of anthropogenic climate change and land use change on provisioning, regulating, and supporting ecosystem services and disservices of ants. Ecosystem services and disservices provided by ants are likely to be impacted by anthropogenic alterations of the environment. In response to these changes, ant diversity and abundances, including those of invasive species, are likely to change as the environment changes, which ultimately can result in changes to the ecosystem services mediated by ants and the organisms they interact with. We propose that future research should make use of modeling approaches parameterized by field experiments to predict how ant-mediated services and processes will respond in a changing planet.

Discussion and conclusion

"Ants are everywhere, but only occasionally noticed. They run much of the terrestrial world as premier soil turners, channelers of energy and dominatrices of the insect fauna – yet receive only passing attention in text books on ecology." (HÖLLDOBLER & WILSON 1990).

A growing body of literature continues to suggest that ants are amongst "the little things that run the world" (WILSON 1987). Ants provide important ecosystem services that promote human well-being and can be categorized using the MA framework (i.e., provisioning, regulating, cultural and supporting ecosystem services) and new frameworks that distinguish between services and processes mediated by ants (e.g., MACE & al. 2012). Ants are culturally valued, can be managed to become important nutritional resources, and have the potential to provide important fibers and biochemical compounds to be used in pharmaceutical products. Ants are important regulators of plant and animal community structure and act as biological control agents in major agroecosystems across the world. Ants also play important roles in supporting ecosystem processes, which include nutrient and carbon cycling, soil movement and formation and decomposition of organic matter, and the use of ants as biological indicators of environmental change. HÖLLDOBLER & WILSON (1990) recognized the importance of ants in terrestrial ecosystems and the value of the conservation of these keystone invertebrates is exemplified many times by WILSON (1987). Our review has shown that both our understanding of the roles of ants in ecosystems and the list of benefits to society that ants can provide continue to grow.

Yet ants also deliver disservices that have consequences on the functioning of ecosystems and human well-being. Ants are nuisance pests when they enter and damage human-modified landscapes. As stinging insects, ants also can affect human health. Invasive ants or ants that are introduced into new areas can have adverse effects on humans, livestock, and native fauna, causing changes in biodiversity and a variety of regulating and supporting services, such as plant productivity and nutrient cycling. Altogether, these disservices have cost many billions of (US) dollars every year. Less frequently, invasive ants provide positive ecosystem services such as soil turnover and control of plant pests, but the net effects of invasive ants have not yet been quantified.

On our changing planet, the importance of invertebrate-mediated ecosystem services cannot be underappreciated. Ants are a highly diverse group of insects that provide or mediate many important ecosystem services. The services mediated and provided by ants across the planet are likely to be affected by increasing anthropogenic impacts, whether it be land-use or climate change, environmental degradation or the mismanagement of natural resources. Our review highlights fields of research that will improve our understanding of ant-mediated ecosystem services as interpreted by the MA. We conclude that conservation efforts for "the little things that run the world" should be a center of research focus as promoted by WILSON (1987) and we suggest that by increasing our research efforts in the areas highlighted in this synthesis, society and ecosystems can continue to maximize and understand the benefits provided by the rich biodiversity of ants.

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