The ecosystem services provided by social insects: traits, management tools and knowledge gaps

Luciana Elizalde[1]* ⓘ, Marina Arbetman[2], Xavier Arnan[3,†], Paul Eggleton[4], Inara R. Leal[5], María Natalia Lescano[1] ⓘ, Agustín Saez[2], Victoria Werenkraut[1] and Gabriela I. Pirk[1]

[1]*LIHo - Laboratorio Ecotono, INIBIOMA-CONICET-Universidad Nacional del Comahue, Pasaje Gutiérrez 1125, Bariloche, 8400, Argentina*
[2]*Ecopol, INIBIOMA-CONICET – Universidad Nacional del Comahue, Pasaje Gutiérrez 1125, Bariloche, 8400, Argentina*
[3]*CREAF, Cerdanyola del Vallès, Catalunya, Barcelona, E-08193, Spain*
[4]*Life Sciences Department, The Natural History Museum, London, SW7 5BD, U.K.*

[5]*Departamento de Botânica, Universidade Federal de Pernambuco, Av. Prof. Moraes Rego, 1235 - Cidade Universitária, Recife, 50670-901, Brazil*

ABSTRACT

Social insects, i.e. ants, bees, wasps and termites, are key components of ecological communities, and are important ecosystem services (ESs) providers. Here, we review the literature in order to (*i*) analyse the particular traits of social insects that make them good suppliers of ESs; (*ii*) compile and assess management strategies that improve the services provided by social insects; and (*iii*) detect gaps in our knowledge about the services that social insects provide. Social insects provide at least 10 ESs; however, many of them are poorly understood or valued. Relevant traits of social insects include high biomass and numerical abundance, a diversity of mutualistic associations, the ability to build important biogenic structures, versatile production of chemical defences, the simultaneous delivery of several ESs, the presence of castes and division of labour, efficient communication and cooperation, the capacity to store food, and a long lifespan. All these characteristics enhance social insects as ES providers, highlighting their potential, constancy and efficiency as suppliers of these services. In turn, many of these traits make social insects stress tolerant and easy to manage, so increasing the ESs they provide. We emphasise the need for a conservation approach to the management of the services, as well as the potential use of social insects to help restore habitats degraded by human activities. In addition, we stress the need to evaluate both services and disservices in an integrated way, because some species of social insects are among the most problematic invasive species and native pests. Finally, we propose two areas of research that will lead to a greater and more efficient use of social insects as ES providers, and to a greater appreciation of them by producers and decision-makers.

Key words: ants, bees, environmental variables, eusociality, human well-being, quantification, termites, traits, valuation, wasps

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* Author for correspondence (Tel: +54 294 4579693; E-mail: luelizalde@gmail.com).
  †Present address: Department of Biological Sciences, University of Pernambuco, Rua Capitão Pedro Rodrigues, 105, 55290-000 , Garanhuns, Brazil

I. INTRODUCTION

Insects, one of the most taxonomically and functionally diverse group of organisms on Earth, are the main component of 'the little things that run the world' (Wilson, 1987). Indeed, they provide ecosystem services (ESs) within all categories proposed by The Millennium Ecosystem Assessment (regulating, supporting, provisioning, and cultural) as well as within all categories of the recently proposed Nature Contribution to People concept proposed by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) (Díaz et al., 2018). Regulating services, those that regulate ecosystem processes, are among the most recognised services that insects provide to humans, and include pollination, pest control and seed dispersal (e.g. Losey & Vaughan, 2006; Kremen & Chaplin-Kramer, 2007). Insects also provide fundamental supporting services, which relate to ecosystem processes that are necessary to produce all other services, like soil formation, bioturbation, nutrient cycling, and decomposition (Losey & Vaughan, 2006; Farji-Brener & Werenkraut, 2017). Regarding provisioning services, which are the products obtained from ecosystems by humans, insects provide food and are used as therapeutic resources. About 2000 species of insects are consumed by humans (Ramos-Elorduy, 2009) and entomophagy is starting to be accepted by reticent populations such as Western Europeans (Caparros Megido et al., 2014). Since ancient times, many insects have been used for therapeutic purposes (Costa Neto & Ramos-Elorduy, 2006). Insect chemical compounds are also an actual or potential source of therapeutic

drugs (Dossey, 2010; Ratcliffe et al., 2011). Finally, insects provide cultural services, as they are part of human culture and religion. Insects are frequently used in the Western film industry, and images of charismatic insects, such as butterflies and ladybirds, are often found in art, as well as on clothing and other consumer goods. Among insects, social insects show behavioural, physical, physiological and life-history traits that make them particularly relevant for supplying ESs.

Within social insects, eusocial insects have the highest level of social organisation. They form colonies of genetically related individuals, within which there are various castes. These facilitate the division of labour, which leads to cooperative behaviours to meet challenges faced by the colony including food gathering, defence from predators and competitors, reproduction, dispersal and the avoidance of abiotic stress (Wilson, 1975). This review considers only eusocial insects, which we will refer to throughout as 'social insects' for simplicity. The majority of the known social insects belong to the order Hymenoptera (ants, bees, and wasps; Snelling, 1981) or to the order Blattodea (termites and cockroaches). The ants, encompassing some 16240 described species (Bolton, 2019), represent by far the largest group of social organisms, and the remaining social Hymenoptera are scattered among some wasp families (Vespidae, Sphecidae; Sumner, Law & Cini, 2018) and bees (Halictidae, Anthophoridae and Apidae; Snelling, 1981). The termites have >2600 species (Kambhampati & Eggleton, 2000). Social Hymenoptera are cosmopolitan (Snelling, 1981; Hölldobler & Wilson, 1990; Chapman & Bourke, 2001), while termites are globally distributed in tropical and sub-tropical regions, with only a few species

in temperate environments. Ants and termites dominate soil and leaf litter arthropod assemblages (Hölldobler & Wilson, 1990; Aanen & Eggleton, 2005; King, Warren & Bradford, 2013b), while social bees are among the most important pollinators worldwide (Steffan-Dewenter, Potts & Packer, 2005; Velthuis & van Doorn, 2006; Klein *et al.*, 2007), and social wasps are keystone predators (Richter, 2000). The apparent high diversity of social insects is misleading; in fact, they are only 2% of total insect species in the world. However, they are likely to represent more than half of the terrestrial animal biomass (Hölldobler & Wilson, 2009). This, together with their widespread distribution, make them key providers of ESs. In this review we do not include the eusocial ambrosia beetles (Curculionidae: Coleoptera), aphids (family Aphididae), and thrips (order Thysanoptera) because in contrast to the other eusocial insect groups, they include few eusocial species that have limited distribution and narrow niches (Crespi, 1996; Kirkendall, Biedermann & Jordal, 2015).

Our aims in this review are: (*i*) to analyse the traits of social insects that make them good suppliers of ESs; (*ii*) to compile and assess conservation management strategies in order to improve the services provided by social insects and preserve them; and (*iii*) to detect gaps in our knowledge about the services that social insects provide. We do not provide an exhaustive review on the ESs provided by social insects, since there are several recent studies dealing with particular taxa and their services (e.g. Del Toro, Ribbons & Pelini, 2012; Hanley *et al.*, 2015; Matias *et al.*, 2017; Govorushko, 2019; Prezoto *et al.*, 2019; see online Supporting information, Appendix S1 for a summary). Instead, we highlight the role of social insects as dominant organisms in terms of biomass and other relevant traits for the provision and management of ESs, analyse how these traits translate into the provisioning of ESs, and develop a conceptual framework, which we hope will be helpful in identifying knowledge gaps.

II. OVERVIEW AND VALUE OF ECOSYSTEM SERVICES PROVIDED BY SOCIAL INSECTS

The definition and classification of ESs remains the subject of ongoing discussion and research (Díaz *et al.*, 2018; Peterson *et al.*, 2018). Recently, research on the ESs provided by insects was integrated in an attempt to identify solutions for sustainable development goals (Prather & Laws, 2018; Dangles & Casas, 2019). We include the classification systems established by both the Millennium Assessment and IPBES in Table 1, but use only the former in our discussion below.

Social insects provide ESs in all categories (Table 1). Among the provisioning services, social insects provide pharmaceuticals and medicines, food, and other goods such as silk or wax, as well as contributing to biofuel production (Table 1). The traditional knowledge of local people is fundamental to quantifying and valuing these ESs. For example, social insects represent the majority of all insects used in traditional medicine; in Latin America, 61% of invertebrate species used are social insects (Alves & Alves, 2011). Social insect larvae and reproductive female castes are consumed by humans in several parts of the world, and honey from several bees and wasps is used broadly (Table 1, Appendix S1). Regarding regulating services, social insects provide pollination, biological control and seed dispersal (Table 1, Appendix S1). It is in agroecosystems, which make up approximately 40% of terrestrial Earth (Foley *et al.*, 2005), that these regulating services provided by social insects are best known and valued. Within the supporting ESs, social insects, especially termites and ants, provide bioturbation of soils, improving water infiltration and holding capacity, contribute to nutrient cycling and decomposition, and have an important role in carbon cycling through carbon mineralization (Table 1, Appendix S1). In addition, social insects are key to energy flow in both natural and human altered ecosystems (Appendix S1). Finally, social insects are important providers of cultural services and have inspired artists and spiritual beliefs since antiquity (Table 1, Appendix S1). The ability of social insects to function as biological indicators of habitat quality is being increasingly recognised (Table 1, Appendix S1).

Many of the ESs that social insects provide are not widely known or valued (Table 1). For example, the use of termite activity to reduce the risk of soil erosion has never been properly valued (Jouquet, Blanchart & Capowiez, 2014), and the remarkable potential that social insect biodiversity holds for commercial bio-prospecting and future nutritive and pharmaceutical benefits to humans is still little explored (Table 1). The same applies to seed dispersal services that social insects provide, in contrast to the same service provided by birds (Hougner, Colding & Söderqvist, 2006). However, for some ESs, such as pollination services provided by honeybees or some provisioning services in agroecosystems (Table 1, Appendix S1), the value of social insects has been explored in detail. Some ESs related to productive systems such as agroecosystems are relatively simple to value quantitatively and monetarily. This is important since farmers generally will modify agricultural practices if the cost–benefit analysis is favourable (de Buck *et al.*, 2001). Economic valuations including these ESs in yield equations highlight the services provided by social insects to producers and decision-makers. Non-market valuations of ESs can also be important. A recent study valuing pollination services illustrated that public support for conserving pollinators can exceed their market value derived from agricultural benefits (Mwebaze *et al.*, 2018). In fact, the strategy of basing nature conservation solely on appraisals of its economic value is debatable: nature can also be valued qualitatively and for its intrinsic value (Anderson, 2019).

Finally, in economic valuations of ESs, quantification of how species provide services is a prerequisite (Kontogianni, Luck & Skourtos, 2010). In so doing, it is important to consider the relevant variables to measure, and ideally to perform these measurements in a standardised way (e.g. Bartholomée & Lavorel, 2019). For instance, the level of pollination by bees has been quantified for many crops, however it is usually measured by proxies such as pollinator

Table 1. Ecosystem services (ESs) provided by social insects. Well-known taxa within each group of social insects are provided as examples, however, other taxa might also contribute to a particular ES (see Appendix S1 for further details and examples). When available, the most detailed category of quantification (*Q*) of the ES is indicated (*sensu* Noriega *et al.*, 2018) and the monetary valuation. Ecosystem services and categories are taken from the Millennium Ecosystem Assessment and IPBES (in parentheses). Many services fit into more than one of these four categories, e.g. food can be both a provisioning service and a cultural service. Key variables to measure for a valuation of each ecosystem service are also provided (see Appendix S2 for references)

Type	Ecosystem service	Taxa and details	Key variables to measure
Provisioning (Material)	Pharmaceuticals & medicines	•**Termites:** antibiotics identified from *Nasutitermes, Pseudacanthotermes, Reticulitermes*. *Q:* not quantified (Da Silva *et al.*, 2003; Coutinho *et al.*, 2009; de Figueirêdo *et al.*, 2015; Zeng, Hu & Suh, 2016). •**Ants:** antibiotics, anti-inflammatory, and venom therapies. *Q:* not quantified (Rastogi, 2011; Santos *et al.*, 2011). •**Bees:** venom therapies (anti-inflammatory, neuroactive compounds), antimicrobial peptides from propolis and royal jelly. *Q:* experiment, and monetary valuation for honeybees propolis and venom (Krell, 1996; Santos *et al.*, 2011; Silva *et al.*, 2015). •**Wasps:** antibiotics, venom anti-inflammatory and neuroactive therapies. *Q:* not quantified (Kroiss *et al.*, 2010; Santos *et al.*, 2011; Silva *et al.*, 2015).	•Identity of species •Secretion of antimicrobial agents (e.g. from metapleural gland of ants) •Mutualist antimicrobial properties
	Food	•**Termites:** *Macrotermes* and 'termite mushrooms' (*Termitomycesi*) in Africa, *Syntermes* in South America; around 43 termite species are used as food by humans or livestock. *Q:* not quantified (de Figueirêdo *et al.*, 2015). •**Ants:** leaf-cutting ant reproductives; honey pot ants used by aborigines in Australia and USA; *Oecophylla* weaver ants in Thailand. *Q:* direct quantification, and monetary valuation for a few species of *Oecophylla* (Rastogi, 2011). •**Bees:** *Apis* honeybees deliver about 1.2 million tonnes of commercial honey per year; the honey of *Melipona* and *Trigona* spp. is increasingly used worldwide. Honeybee larvae are consumed in Africa and Asia. *Q:* direct quantification, and monetary valuation for honey and honeybee larvae sold in local markets (Krell, 1996; Carreck & Williams, 1998; Cortopassi-Laurino *et al.*, 2006). •**Wasps:** larvae are used locally by some human cultures. *Q:* not quantified (Puwastien & Attig, 1997; Acuña *et al.*, 2011).	• Identity and biomass of species •Nutrient content
	Others	•**Termites:** biofuel production using cellulose-degrading species. *Q:* not quantified (Scharf & Boucias, 2010). •**Ants:** silk of *Oecophylla* ants. *Q:* not quantified (Siri & Maensiri, 2010). •**Bees:** wax of honeybees and meliponinid bees. *Q:* direct quantification, and monetary valuation for honeybee wax (Krell, 1996; Carreck & Williams, 1998; Cortopassi-Laurino *et al.*, 2006).	Highly variable
Regulating (Regulating)	Pollination	•**Ants:** at least 60 species (common genera: *Camponotus, Formica, Proformica, Lasius, Crematogaster, Iridomyrmex*) pollinate around 46 plants, mainly in natural habitats. *Q:* not quantified (Vega & Gómez, 2014). •**Bees:** *Lasioglossum, Halictus, Trigona* (Halictidae), *Bombus* and *Apis* (Apidae) are managed for pollination services. *Q:* experiment, and monetary valuation for honeybees and bumblebees (Southwick & Southwick, 1992; Carreck & Williams, 1998; Slaa *et al.*, 2006; Klein *et al.*, 2007).	• Identity and abundance of species •Trait match with crop of interest (e.g. prosboscis–corolla size) •Pollen transfer/deposition •Crop yields with *versus* without pollinator •Adequate densities to maximise crop yields

(Continues)

Table 1. *(Cont.)*

Type	Ecosystem service	Taxa and details	Key variables to measure
	Biological control	•**Wasps:** one example in an avocado plantation, and few others in natural habitats. **Q:** direct quantification (Perez-Balam *et al.*, 2012). •**Ants:** predatory *Oecophylla* and *Azteca* arboreal ants are important in tree plantations and forestry; *Formica* and *Solenopsis* as terrestrial genera for annual crops; other genera are less known. Seed-harvesting ants used for weed control to increase crop production. **Q:** experiment, and quantification of yield increase of 27% in cocoa (Baraibar *et al.*, 2009; Offenberg & Wiwatwitaya, 2010; Drummond & Choate, 2011; Wielgoss *et al.*, 2014). •**Bees:** honeybees and bumblebees are vectors of bacterial biocontrol agents of crop pests. **Q:** not quantified (Kovach, Petzoldt & Harman, 2000; Dedej, Delaplane & Scherm, 2004). •**Wasps:** control of pest caterpillars on crops. Control of flies and mosquitoes in urban settings, including disease vectors. **Q:** direct quantification (Prezoto *et al.*, 2019).	• Identity and abundance of species •Trait match with pest of interest (e.g. prey–predator size) •Pest reduction by active predation •Crop yields with *versus* without predator
	Seed dispersal	•**Termites (termitochory):** one anecdotal report of grass seeds in termite food chambers germinating only if a termitophagous mammal damages the termite nest. **Q:** not quantified (Jolivet, 1986). •**Ants (myrmecochory):** at least 11,000 angiosperm species (4.5% of total) from 334 genera and 77 families are dispersed by ants. **Q:** not quantified (Lengyel *et al.*, 2009). •**Bees (melitochory):** stingless bees disperse three plant species. **Q:** not quantified (Wallace & Trueman, 1995; Bacelar-Lima *et al.*, 2006; Wallace, Howell & Lee, 2008). •**Wasps (vespichory):** yellow jackets remove seed from one myrmecochorous plant species and interact with ants removing the seeds. **Q:** not quantified (Jules, 1996; Bale *et al.*, 2003).	• Identity and abundance of species •Trait match with seed of interest (e.g. seed–disperser sizes) •Removal, transport distance and fate of seeds
Supporting (Regulating)	Bioturbation	•**Termites:** soil movement due to nest and gallery construction, increases soil porosity for water drainage, facilitates soil formation and contributes to soil heterogeneity; mainly in the subfamily Macrotermitinae (e.g. *Macrotermes*, *Pseudacanthotermes*) and genera *Trinervitermes* and *Cubitermes*. **Q:** direct quantification (Jouquet *et al.*, 2011; Tuma *et al.*, 2019). •**Ants:** soil movement due to nest and gallery construction in several species, increases water-holding capacity and favours soil formation and heterogeneity; with *Formica*, *Lasius*, *Camponotus*, and *Atta* among the most important genera. **Q:** not quantified (Folgarait, 1998; Frouz & Jilková, 2008).	• Identity and abundance of species •Traits related to nest construction (e.g. deep and profuse nest galleries) •Amount of soil removed •Soil porosity with *versus* without the species of interest
	Nutrient cycling & decomposition	•**Termites:** soil nutrients and pH increased by activities of several species nesting in and on soils and trees. **Q:** direct quantification (Jouquet *et al.*, 2011). •**Ants:** soil nutrients and pH increased by activities of several species nesting on soils and trees. **Q:** direct quantification (Cammeraat & Risch, 2008; Farji-Brener & Werenkraut, 2017).	• Identity and abundance of species •Traits related to high organic matter accumulation (e.g. diet, external refuse) •Nutrient, organic matter content and micro-organism activity in soil from nest *versus* nearby soil •Decomposition measured by mass loss of leaf litter in bags with and without social insect entry

Table 1.   *(Cont.)*

Type	Ecosystem service	Taxa and details	Key variables to measure
	Carbon cycling (C mineralization)	•**Termites:** fungus-growing termite genera. ***Q:*** experiment (Griffiths *et al.*, 2019). •**Ants:** some *Camponotus* spp. ***Q:*** not quantified (King *et al.*, 2018).	• Identity of species, abundance and nest distribution on logs with varying levels of decay •Mass loss of standard wood blocks within bags with and without social insect entry
	Energy flow	•**Termites:** used as food by many vertebrate and invertebrate species. ***Q:*** not quantified (Redford & Dorea, 2009). •**Ants:** used as food by many vertebrate and invertebrate species; remove more than half of food resources from rainforest floors. ***Q:*** not quantified (Hölldobler & Wilson, 1990; Redford & Dorea, 2009; Griffiths *et al.*, 2018).	•Identity and biomass of species •Number of species that use social insects as resource •Biomass of social insects consumed by other species
Cultural (Non-material)	Biological indicators	•**Termites:** one example of termite community as bioindicator of habitat quality (Alves *et al.*, 2011). •**Ants:** different species used for evaluation of habitat restoration, land management practices, heavy metal contamination (Andersen, 1997; Skaldina, Peräniemi & Sorvari, 2018). •**Bees:** honeybees used as bioindicators of pollution (Celli & Maccagnani, 2003). •**Wasps:** one example of use of vespids as a bioindicator of habitat conservation status (de Souza *et al.*, 2010).	• Identity of species •Responses of species to stimuli of interest (e.g. fire, pollution, etc.)
	Literature & arts	•**Ants:** films: *The Naked Jungle* (1954), *Antz* (1998), *Ant-Man* (2015); various novels and fables inspired by ants (Sleigh, 2003). •**Bees:** *Bee Movie* (2007); various novels and fables inspired by honeybees (Preston, 2006). •**Wasps:** *Green Hornet* (2010) and *Ant-Man and the Wasp* (2018) movies (https://www.marvel.com)	•Market prices of movies, books, and art pieces •Preference and aesthetic values
	Cultural traditions & religion	•**Termites:** used in ritual practices Southeast Asia (Neoh, 2013). •**Ants:** tucandeira's (*Dinoponera* sp.) ritual in Amazonian aborigines; mentioned in religious stories (e.g. *The Bible*) (Sleigh, 2003; Botelho & Weigel, 2011). •**Bees:** mentioned in religious stories, *Bombus dahlbomii* in Mapuche culture (Preston, 2006; Smith-Ramírez *et al.*, 2018).	•Interviews with people to estimate use and importance

abundance or resulting crop yield, rather than by direct measurement of pollen transfer, visitation rates or plant fitness (King, Ballantyne & Willmer, 2013a). In one attempt to value qualitatively ant-provided ESs in response to urban disturbance, ant species were grouped according to the main ESs they provided (i.e. decomposers, soil bioturbators, and species relevant to nutrient cycling). The highest ant diversity and abundance was found at intermediate disturbance levels (Sanford, Manley & Murphy, 2009). However, this study only considered species richness and abundance, but no other relevant measures for these ES provisions (see Table 1). Despite calls for adequate quantification of ESs, there has been no attempt to standardise the methodology used to value ESs. Standardised methods currently only exist to value pollination (Mburu *et al.*, 2006; King, Ballantyne & Willmer, 2013a; Hanley *et al.*, 2015; Bartholomée & Lavorel, 2019). Thus, as a first attempt towards providing a standardised methodology, we provide a list of relevant variables to measure in the field or in the laboratory (Table 1, Appendix S2).

III. SOCIAL INSECT TRAITS AND THEIR RELEVANCE TO ECOSYSTEM SERVICE PROVISION

Social insects can have large effects on other species and on the structure and functioning of ecological communities (Wilson & Kinne, 1990). This seems to be due to a combination of unique characteristics that are relevant when considering social insects as providers of ESs and for the management of these services. We highlight here the particular traits that sociality confers on these insects that make

them outstanding ES providers, either because these traits relate directly to the provision of the service, to its magnitude and efficiency, or to its constancy/stability (Fig. 1). In addition, many of these traits make social insects easy to manipulate (see Section V) and stress tolerant. Stress-tolerant and disturbance-tolerant social insects can survive in agroecosystems, urban areas, and other human-modified areas, providing ESs in these harsh environments (Straub *et al.*, 2015). Although the classification of traits used herein is useful for conceptualisation and generalisation, it is neither rigid nor static; thus, traits might be categorised differently when considering other ESs or other species.

(1) Traits related to provision of services and their magnitude

(a) High biomass and numerical abundance

Social insects represent, relative to vertebrates and other arthropods, a very high proportion in terms of numbers of individuals and biomass within terrestrial ecosystems (Fig. 1A, B; Wilson & Kinne, 1990). The high biomass of social insects is key for provisioning services, and they represent a significant seasonal food in some local indigenous communities (Chen & Akre, 1994; Kinyuru *et al.*, 2013). In temperate hardwood forests, termites and ants are the dominant (in terms of both abundance and biomass) macroinvertebrates in dead wood, and ants are key components in litter and soil ecosystems (King, Warren & Bradford, 2013*b*), making them important in nutrient cycling and bioturbation processes. For several ESs, the high number of workers per colony is especially important, for example, bees and ants are the dominant providers of pollination or biological control, respectively, in natural and agricultural landscapes (Winfree *et al.*, 2015; Gill *et al.*, 2016; Nielsen, Nielsen & Offenberg, 2018).

(b) Mutualisms

Social insects are at the centre of a series of unique mutualisms with a wide array of organisms, including bacteria, protists, fungi, plants, and other arthropods. Mutualistic associations with plants are key for pollination (Aizen *et al.*, 2014). These mutualisms allow social insects to provide a great variety of ESs. For instance, the digestive symbionts of termites, which are primary decomposers that consume a broad array of litter types with high assimilation efficiencies, allow termites to use organic matter that otherwise would be unavailable to them (Bignell, 2000), and contribute to carbon cycling. The mutualistic fungus cultivated by leaf-cutting ants and macrotermitine termites as their main food source enables these taxa to provide ESs related to nutrient cycling and decomposition due to the high concentrations of organic matter in their nests (Bignell & Eggleton, 2000; Farji-Brener & Werenkraut, 2017).

In addition, social insects associate with many antibiotic-producing bacteria that allow them to maintain pathogen-free colonies. Examples include actinobacteria in the cuticles of leaf-cutting ants that combat specific infections in their fungus gardens (Fig. 1D; Heine *et al.*, 2018) and in the heads of other ants (Liu *et al.*, 2018). Actinobacteria are also present in the bodies of stingless bees (Rodríguez-Hernández *et al.*, 2019), wasps (Madden *et al.*, 2013) and termites (Sujada, Sungthong & Lumyong, 2014; Chouvenc *et al.*, 2018; Krishanti *et al.*, 2018), which produce antimicrobial secretions. Microbial natural products represent an important source for the discovery of potential new antibiotics, with actinomycetes being one of the most prolific groups that produce bioactive compounds (Genilloud, 2018; Niu, 2018). These sources of natural antibiotics are increasingly of interest in bioprospecting for drugs to combat multi-drug resistant pathogens and emerging infections (Genilloud, 2018; Niu, 2018).

Another highly studied mutualistic association, which might be important in supporting biodiversity and providing biological control services (see Appendix S1), is mutualisms of ants with trophobionts (aphids, mealybugs, cicadellids, etc.). Many ant species tend trophobionts, from which they harvest honeydew, sometimes as a main food source (Styrsky & Eubanks, 2010). In exchange for this, ants protect trophobionts, possibly increasing their density and diversity. Such ants exhibit increased aggressiveness towards other non-sap-sucking herbivores (e.g. Floate & Whitham, 1994; Styrsky & Eubanks, 2010), and many ant species important in biological control are dependent on trophobionts (Clough, Philpott & Tscharntke, 2017). Such trophobiosis can be an ecosystem disservice if ants promote high trophobiont densities, thus harming plants of commercial value, or if trophobiotic interactions promote the establishment of invasive ants (see e.g. Wilder *et al.*, 2011).

(c) Building capacity

The social insect nest is the extended phenotype (i.e. effects that genes have on the environment both inside and outside the body of the individual organism) of eusociality, and organises the colony social structure, including the division of labour and protection of the colony members. The nest may also act as a thermoregulatory device that buffers against temperature and moisture extremes (Tschinkel, 2015). Thus, the activity of nest building, by changing the local environmental conditions due to the building activity itself or due to the effect that the nest has on the local environment, make social insects unique providers of ESs. In addition, since the size of these nests in some species is incredibly large, the magnitude of the ESs is also important. For example, termite colonies can cover thousands of square metres, and a single colony's tunnel network can extend 50 m from the nest (Traniello & Leuthold, 2000). Mound-building termites produce the largest non-human terrestrial structures: *Nasutitermes triodiae*, for example, builds a 'cathedral mound' up to 5 m tall; while in the Brazilian caatinga, *Syntermes* spp. mounds cover an area roughly the size of Great

Britain (Martin *et al.*, 2018). Ant nests may vary in depth from a few centimetres in tropical and temperate systems to up to 4 m in deserts (Fig. 1E; Tschinkel, 2003), and some leaf-cutting ant nests are composed of up to 8000 subterranean interconnected chambers reaching as deep as 8 m underground (Moreira *et al.*, 2004). By constructing nests, termites and ants move nearly 10 t/ha/year of subterranean soil in moist subtropical and temperate ecosystems (Paton, Humphreys & Mitchell, 1995). Their foraging trails may extend more than 250 m from the nest (Hölldobler & Wilson, 2009), with a foraging area covering more than 1 ha (Urbas *et al.*, 2007). The large nest mounds and excavations of ants and termites, their extensive subterranean tunnel networks, and networks of soil sheeting above the ground all contribute to their bioturbation role in soil ecosystems (Lobry de Bruyn & Conacher, 1990; Folgarait, 1998; Tuma *et al.*, 2019), as well as their contribution to soil water balance, nutrient cycling and decomposition (Table 1, Appendix S1).

Other social insects also build structures that impact ES provision. Social bee nests vary strongly in their structure and placement (e.g. soil, trees, etc.) among species. Honeybees (*Apis mellifera*) preferentially use tree cavities to build their nests, producing beeswax and propolis, important goods to humans (Table 1, Appendix S1), for use as building materials (Seeley & Morse, 1978). Social wasps can have up to a million cells packed in stacked combs, the largest being built by highly social species (Wenzel, 1991; Theraulaz, Bonabeau & Deneubourg, 1998). Wasps use diverse substrates of plant origin in the construction of their nests (Wenzel, 1991), and may thus have an effect on local concentrations of nutrients, but there have been no studies that assessed this to date. Finally, some ant gardens provide ESs by increasing biodiversity and concentrating nutrients: some species of ants plant a variety of epiphytic plants and then live in their root systems. By so doing, they enhance local biodiversity and create habitats for other organisms (e.g. microorganisms in phytotelmata) that in turn are colonised by an array of other organisms (Céréghino *et al.*, 2010; Orivel & Leroy, 2011).

(d) Chemical production

Several species of social insects produce a huge variety of chemicals, which are used mainly for defensive functions. The wide variety of venoms that ants, bees and wasps produce (Schmidt, 1990; Touchard *et al.*, 2016) is popularly known. These substances are increasingly of interest in bioprospecting studies for pharmaceutical or medical purposes (e.g. Touchard *et al.*, 2016; see Appendix S1). Termites produce a vast array of defensive salivary secretions, as well as peculiar secretions that are released when bitten (Prestwich, 1984; Šobotník, Jirošová & Hanus, 2010). Hymenopteran venoms as well as some termite secretions are known to have fungistatic activity (Schmidt, 1990; Rosengaus *et al.*, 2004). However, we are not aware of their application in human cultures, with the exception of some hymenopteran venoms (see Appendix S1).

(e) Provision of multiple services

Several social insect species provide more than one ES at the same time. For instance, some bee species simultaneously provide honey and propolis (provisioning services) and pollination (regulating service); some ant species accumulate nutrients in their nests on soils (supporting service) and provide biological control of pests or are good seed dispersers (regulating services); and termites are important soil bioturbators and involved in nutrient cycling and decomposition (supporting services). Although wasps are likely to provide several services, they have been poorly studied compared with other social insect groups (Sumner, Law & Cini, 2018). The provision of multiple services is important in ecosystems that social insects inhabit since the manipulation of one species will affect several ESs at the same time. We expand on this in Sections IV and V, while also considering the disservices that they provide.

(2) Traits contributing to the efficiency of ecosystem service delivery

(a) Castes and division of labour

Division of labour is a key characteristic of social insects, and refers to the specialisation of colony members for different tasks. Sometimes, task specialisation is accompanied by polymorphism, with the most obvious differentiation often related to reproductive tasks (Fig. 1C). Such division of labour can result in a more efficient provision of particular ESs. For instance, reproductive females accumulate fat and proteins, making them a nutrient-rich food source for other animals, including humans (Table 1, Appendix S1). Some social insect colonies only have one egg-laying queen, but others have multiple queens (polygyny; e.g. some ant and bee species), facilitating their management, and the services they provide. For example, polygyny enables single colonies to be split into multiple queenright fragments (Nielsen, Nielsen & Offenberg, 2018), simplifying the management of their populations (see Section V). Polygyny also makes colonies less vulnerable to queen death, this being key to colony resilience (Straub *et al.*, 2015) and allowing these species to inhabit human-modified areas.

Non-reproductive castes may be specialised in defence, foraging, nest building, or brood care (Wilson, 1971; Hart, Anderson & Ratnieks, 2002; Ballari, Farji-Brener & Tadey, 2007). Little is known about how differences in non-reproductive castes might affect the provision of ESs. However, in some termites foragers play a more important role in N_2 fixation than soldiers (Curtis & Waller, 1998) whereas the opposite occurs in other species (Prestwich, Bentley & Carpenter, 1980). For ESs such as pollination and biological control, foragers provide most of the service. Some termite species nest and feed in dead wood (about 15%, around 500 described species), and do not leave the nest to forage (Korb, 2007), and thus they will have less important roles in the provision of some ESs, such as bioturbation, than other species. There is a clear need to study in
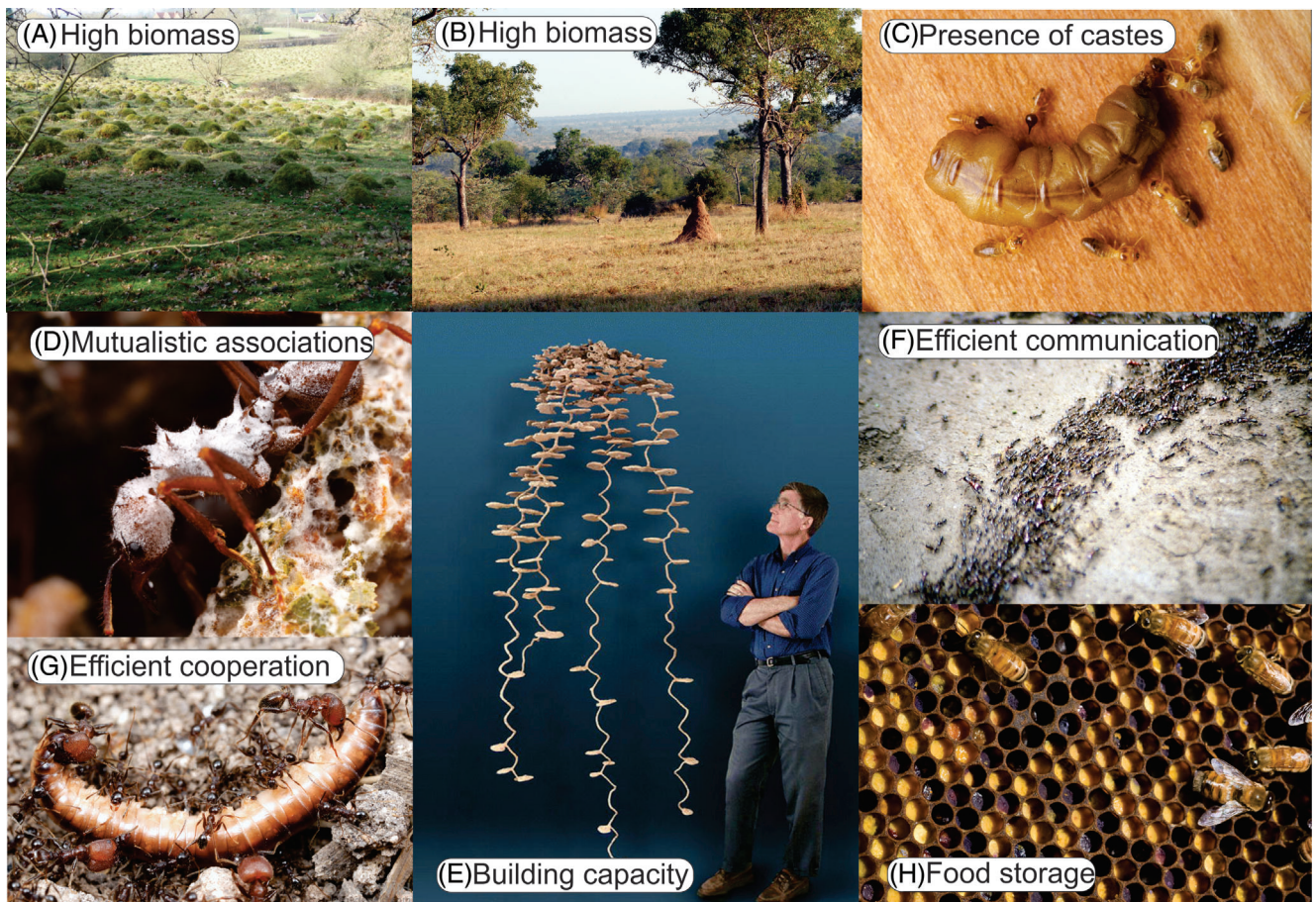
Fig 1. Relevant traits of social insects for the provision and management of ecosystem services. (A, B) High biomass and abundance, as shown for example by (A) anthills of the yellow meadow ant (*Lasius flavus*) in pastures in Britain (Richard Greenwood/Anthills/CC BY-SA 2.0), or the (B) termite mounds in the Kruger National Park (Harvey Barrison/CC BY-SA 2.0). (C) The presence of castes and division of labour, e.g. a mature queen *Nasutitermes exitiosus* termite surrounded by both workers and soldiers (Forestry and Forest Products, CSIRO/CC BY-SA 3.0). (D) Diverse mutualistic associations, e.g. this leaf-cutting ant covered with white *Actinomyces* bacteria (Alex Wild). (E) The impressive infrastructure of their nests and foraging trails, as shown by the nest architecture of the Florida harvester ant, *Pogonomyrmex badius* (Shaners Becker/CC BY-SA 2.0). (F, G) Their ability to communicate and cooperate, e.g. Safari ants (*Dorylus* sp.; F) that forage following pheromone trails (Mehmet Karatay/CC BY-SA 3.0), or *Pheidole* sp. ants (G) cooperating to subdue a millipede (Alex Wild). (H) A long lifespan and the ability to store food, e.g. in honeybees (*Apis mellifera*) storing pollen (Nick Pitsas, CSIRO/CC BY-SA 3.0).

more detail how different species, and different castes within species, are involved in the provision of particular ESs.

(b) Efficient communication and cooperation

Social insects owe their ecological success in part to cooperation within their sophisticated social systems (Hölldobler & Wilson, 1990; Bignell, 2000). The 'waggle dance language' of honeybees and 'sound signals' in stingless bees are well-understood processes of communication. In the case of honeybees, the dancer provides the coordinates of new food resources to other foragers (Dyer, 2002). This communication increases the efficiency by which the colony 'superorganism' can utilise food sources (Dornhaus & Chittka, 2004), and is fundamental for the ESs they provide (Dyer, 2002;

Díaz *et al.*, 2013). Social insects also communicate by the use of pheromones, which can be manipulated in order to control their effects (e.g. Sunamura, 2018). Trail pheromones in ants (Fig. 1F), termites, and some bees are important in the recruitment of foragers to a food source (Reinhard & Kaib, 2001; Morgan, 2009), thus, enhancing the efficiency of ESs related to foraging activities (e.g. biological control, pollination).

Cooperative transport of resources, or the movement of an object by two or more individuals, is a common behaviour in many ant species (McCreery & Breed, 2014). This cooperation allows ants to retrieve arthropod prey much larger than the size of individual foragers (Fig. 1G), as well as adjusting the number of foragers according to prey size, and also requires information transfer among workers (McCreery &

Breed, 2014). Seed-harvesting and leaf-cutting ants partition tasks according to the size of the load they need to carry to their nests, with implications for nutrient cycling and seed dispersal ESs (Wetterer, 1994; Arnan *et al.*, 2011).

(3) Traits related to constancy and stability of service provision

(a) Food storage capacity

Social insects are able to store food in the crops of some members of the colony, in what has been termed the 'social stomach' (Eisner & Brown, 1958). This task is mainly carried out by workers and brood, with the huge gasters of honeypot ants being the most remarkable example (Hölldobler & Wilson, 1990). It has been shown that queens in colonies with many workers survive harsh seasons better (Kaspari & Vargo, 1995), allowing increased stress tolerance. Besides food storage within their bodies, some species of social insects store food outside their bodies. In fungus-growing termites, the fungus comb serves as a food store that meets seasonal peaks in colony nutrient and energy requirements, and can be used to sustain the colony when adverse conditions impede foraging (Bignell & Eggleton, 2000). A similar process of food storage occurs in leaf-cutting ants that cultivate a fungus inside their nests (Hölldobler & Wilson, 1990), harvester ants that store seeds in inner chambers of their nests called 'granaries' (Reyes-López & Fernandez Haeger, 2002), and in some species of bees, like honeybees (Fig. 1H), bumblebees and stingless bees that store honey and pollen inside their nests (Fewell & Winston, 1996; Slaa *et al.*, 2006). Their ability to store food makes social insects able to tolerate periods of food shortage, and thus might make their contribution to ESs more constant, stable and predictable that those provided by other organisms. This prediction requires further study.

(b) Long lifespan

Many social insect colonies are perennial and survive for decades. Most individuals, except for the queen (in ants, bees and termites) or the king (only in termites), live for short periods, but the colonies can survive for several years depending on the queen and/or king lifespan. Termite queens can live as long as two decades (Elsner, Meusemann & Korb, 2018) and adult ant queens can live for 14 years (Hölldobler & Wilson, 1990), whereas most solitary insects only live for a few weeks (Simpson & Raubenheimer, 2009). When a queen dies, workers of some species may be able to replace it. One stingless bee nest remained active for more than 50 years in a protected log hive, although it is not known how many swarms issued during its lifetime, nor how many queens were involved (Slaa *et al.*, 2006). Furthermore, colonies with many queens may be considered immortal, since a new queen can replace the dead one (e.g. Sanetra & Crozier, 2002). Such colony longevity allows constancy in the provision of ESs, and might help in maintaining a particular colony density to provide a desired level of ESs. Although social insect colonies can move (e.g. by relocating to other nest sites), most colonies remain in a fixed position for long periods (McGlynn, 2012). This makes them reliable ES providers, with low temporal fluctuations.

IV. INTEGRATIVE EVALUATION OF ECOSYSTEM SERVICES AND DISSERVICES

Some species of social insects are among the most problematic invasive species and native pests. For example, while leaf-cutting ants make ES contributions as soil engineers and soil fertilisers, these may be irrelevant to farmers when these ants invade their crops, as they are important native pests in the Neotropics (Della Lucia, Gandra & Guedes, 2014). Termites that colonise wood structures can cause huge problems in their native range (Su & Scheffrahn, 2000), and introduced pollinators can have detrimental effects on fruit production or on native pollinators (Morales *et al.*, 2013; Aizen *et al.*, 2014). Here, we discuss the importance of an integrated view of the benefits (services) or damage (disservices) that social insects bring to ecosystems.

The accidental or intentional introduction of social insects may result in them becoming invasive. Seven social insect species are included among the 100 worst invasive species globally (five ants, one wasp and one termite species; Global Invasive Species Database http://www.issg.org/database). The Argentine ant *Linepithema humile* has become a structural pest in urban areas around the world generating important economic losses through its control (Wetterer *et al.*, 2009). In addition, this species disrupts natural ant seed dispersal (Gómez, Pons & Bas, 2003), and biological control of pests in vineyards (Phillips & Sherk, 1991) and orchards (Haney, Luck & Moreno, 1987) outside its native area. Some species of vespid wasps (e.g. *Vespula vulgaris*, *V. germanica* and *V. velutina*), accidentally introduced into New Zealand, Australia, South and North America, and Europe, affect biodiversity through direct predation or competition for food or space, and ecosystem function. They also disrupt human activities outdoors due to their painful stings (Chauzat & Martin, 2009; Beggs *et al.*, 2011). Finally, the introduction of commercial pollinators for crop pollination services in many regions of the world has resulted in major negative events (Dafni *et al.*, 2010), even disrupting the capacity of ecosystems to deliver services (Traveset & Richardson, 2006; Schweiger *et al.*, 2010). For example, *Bombus terrestris* colonies were introduced in Chile for crop pollination services, and a few years later they spread into the Patagonian region, including the neighbouring Argentinean area (Torretta, Medan & Abrahamovich, 2006). Its invasion not only generated the near extinction of the native bumblebee *Bombus dahlbomii*,

apparently by transmission of pathogens (Arbetman *et al.*, 2013), but also negatively affected the reproduction of native and cultivated plant species through flower damage (Morales *et al.*, 2013; Aizen *et al.*, 2014).

These few species that are agricultural pests or cause significant nuisance to humans, generate a negative perception of social insects by society and might hinder opportunities to adopt the beneficial ESs they provide (e.g. Sumner, Law & Cini, 2018). For example, farmers generally perceive termites as pests of several agricultural crops and apply various indigenous control practices (Yêyinou Loko *et al.*, 2017). However, these farmers also use some termite species as food and medicinal resources, highlighting the need for a more sophisticated approach to termite control in order to assure the conservation of non-pest termite species (Yêyinou Loko *et al.*, 2017). While some farmers can identify several termite species on their farms using their indigenous names, many others lack this knowledge (Yêyinou Loko *et al.*, 2017). Such indigenous taxonomic skills are vital for communication between researchers, extension agents, educators, and farmers for social insect management programmes (Orikiriza, Nyeko & Sekamatte, 2012).

Given that some social insects are multiple service providers, an integrated evaluation of these services is fundamental. One example of an ecologically dominant social insect that provides multiple benefits is the arboreal ants *Oecophylla* spp. These ants provide pest suppression (Van Mele, 2008), and by feeding on pests they provide a protein-rich food for humans that use the ants as a food source (Table 1; Offenberg & Wiwatwitaya, 2010; Rastogi, 2011), produce substances that are used in local medicines (Oudhia, 2002), and constitute a source of income from sale as food in local markets (Sribandit *et al.*, 2008). Foliar uptake of nutrients from ants may have implications for agricultural production as an ES provided by ants (Pinkalski *et al.*, 2016, 2018), in addition to the pest control service that ants provide (Perfecto, Vandermeer & Philpott, 2014; Offenberg, 2015). However, few studies integrate the value of both the services and disservices that social insects provide. One exception is a study in a tropical cacao plantation, where the overall benefits of ants in crop yields were estimated, including biological control of herbivores (measured as reduced leaf herbivory and fruit pest damage) and pollination facilitation, and weighed against disservices such as increased mealybug density, phytopathogen dissemination and indirect pest-damage enhancement (Wielgoss *et al.*, 2014). Another example of multiple service valuation identified hotspots for honeybee pollination and honey production ESs (Affek, 2018), highlighting the need for a multiservice spatial analysis of social-insect-provided ESs.

In summary, further research considering all the services and disservices that social insects provide is necessary before implementing management practices that increase social insect abundance for the provision of a particular service. The challenge will be to find management techniques and tools that allow services to be enhanced and disservices to be reduced in order to obtain the maximum benefit from native or already introduced social insects.

V. MANAGEMENT OF SOCIAL INSECTS TO ENHANCE ECOSYSTEM SERVICES AND REDUCE DISSERVICES

In order to enhance ESs provided by social insects as well as to increase the use of social insects as tools for restoring degraded habitats (Losey & Vaughan, 2006; Schowalter, 2013; Prather & Laws, 2018) it will be necessary to develop and optimise management tools. This can be achieved by directly managing social insect populations or their environment, in a conservation-led approach, in order to make sustainable use of the services that they provide. Because of negative effects of some social insects when they become invasive, management techniques that increase the abundance of native species are recommended.

(1) Management of populations

There are several management methods that can be used to increase population sizes to provide the desired level of ESs, or where social insect populations have been reduced by anthropogenic habitat modification. These methods include transplantation of colonies in some form. Although many species are difficult to maintain under laboratory conditions, some can be directly implanted. Possibly the best example of management of social insect populations is apiculture, using the honeybee (*Apis mellifera*). This bee has been managed since ancient times, initially for honey production, and later for pollination services to crops; it is the most important managed pollinator in agroecosystems worldwide (Southwick & Southwick, 1992; Klein *et al.*, 2007). More recently (~30 years ago), several species of bumblebee (*Bombus* spp.) were reared in captivity and sold commercially, especially for crop pollination services (Velthuis & van Doorn, 2006). The domestication of bees has allowed humans to exploit (and overexploit) their pollination services by transporting colonies in artificial hives to sites with high pollination demand (Velthuis & van Doorn, 2006; Potts *et al.*, 2010; Breeze *et al.*, 2011; but see Section IV for negative effects following introduction of bumblebees). Besides these well-known examples, traditional knowledge of indigenous people was fundamental in the development of modern methods of management of stingless bees for honey production (Cortopassi-Laurino *et al.*, 2006; Slaa *et al.*, 2006).

For ants, there are several methods of rearing them in the laboratory, which can be adapted to suit different species (Bhatkar & Whitcomb, 1970; Czechowski & Pisarski, 1992; Wardlaw, Elmes & Thomas, 1998). Ants can be transplanted into areas in the form of colonies or as founding queens. Transplantation of colonies was successfully used to control oil palm disease, reducing economic damage and avoiding the use of insecticides (Aldana de la Torre,

Calvache & Arias, 2000). Colony transplantation has potentially negative aspects, as the extraction of colonies from one habitat to transport to another involves damage to the soil as well as the removal of an already established colony (Bulot *et al.*, 2014). By contrast, transplanting inseminated alate females after nuptial flights may not affect the source colony or local population due to the high numbers of females that are released per colony (Bulot *et al.*, 2014).

The management of ants to enhance pest control has a long tradition, and colonies of weaver ants (*Oecophylla* spp.) have been managed since 304 CE in China (Van Mele, 2008). Ants have been managed to control pest insects in orchards (coconut, cocoa, fruit and nut crops) in Africa, Asia and Australia (Van Mele, 2008; Vandermeer, Perfecto & Philpott, 2010; Offenberg, 2015). As long as 175 years ago, recommendations were made in Germany to encourage the use and multiplication of ant nests as desirable measures against forest pests (Gosswald, 1951). This potential for Palearctic mound-building wood ants (*Formica paralugubris*) to protect forests from pest insects led to extensive artificial introduction programs in Germany, Poland, European Russia, Italy and Canada during the last century, particularly during the 1950s and 1960s (Pavan, 1976; Otto, 2005; Seifert, 2016; Frizzi *et al.*, 2018). These introductions were successful, but they were highly controversial. While no hard data on their effectiveness as biological control agents was gathered, there is scientific evidence of non-target effects on local fauna (Seifert, 2016; Frizzi *et al.*, 2018). There is no doubt that wood ants are important stabilising elements of their native temperate and boreo-montane woodland ecosystems due to their control of populations of herbivorous insects (Sorvari, 2016).

Termites can also be reared in the laboratory (Becker, 1969), however we are not aware of any reports of direct implantation in order to increase or restore their populations for the provision of ESs. African traditional management of termites to increase soil fertility, aeration and water-holding capacity uses the creation of mulched pits to encourage colony formation (Mando & Miedema, 1997; Jouquet, Chaudhary & Kumar, 2018).

ESs can also be enhanced by slowing down the negative impacts of ants on ecosystems. For example, the populations of leaf-cutting ants can be managed when they become pests, usually through chemical control, to reduce herbivory rates and thus to enhance crop productivity (Della Lucia, Gandra & Guedes, 2014). Similarly, we can manage the populations of invasive ants to restore the invaded communities and their associated ESs (Buczkowski, Mothapo & Wossler, 2018; Ujiyama & Tsuji, 2018).

(2) Management of environments

There are several environmental management techniques that favour populations of social insects (both in terms of number of individuals per colony as well as number of colonies). These methods include habitat management to increase connectivity, reducing the use of pesticides, increasing the quantity and quality of available resources such as food or nesting materials, providing artificial nesting sites, reducing predators, and limiting the activity of competitors (Offenberg, 2015; Sorvari, 2016). Habitat management in agroecosystems involves reducing soil erosion by changes to tillage (Van Mele, 2008; Jouquet, Blanchart & Capowiez, 2014; Offenberg, 2015), avoiding burning practices that damage soil-nesting social insects (Araújo *et al.*, 2005), reducing mowing (Heuss *et al.*, 2019; Seibold *et al.*, 2019), retaining or restoring native hedgerows around agricultural fields to promote pollination (Kleijn *et al.*, 2006; Morandin & Kremen, 2013; M'Gonigle *et al.*, 2015) and the use of biological control (Aldana de la Torre, Calvache & Arias, 2000; Isaacs *et al.*, 2009). Managing a habitat for one ES provided by social insects might also promote other important functions and services provided by other organisms (Wratten *et al.*, 2012; Morandin & Kremen, 2013; Blaauw & Isaacs, 2014; Lundin, Ward & Williams, 2019). For instance, native people in Brazil, apparently aware of the prominent role of stingless bees as crop pollinators, used to plant species that attract bees near to their crops in order to increase bee abundance (Slaa *et al.*, 2006). A similar approach is nowadays advocated in Western agriculture (Kleijn *et al.*, 2006; Morandin & Kremen, 2013; M'Gonigle *et al.*, 2015).

Excessive use of pesticides in agriculture is one of the main causes of the pollinator crisis (Steffan-Dewenter, Potts & Packer, 2005) and negatively affects biological control (Vandermeer, Perfecto & Philpott, 2010). Biomagnification, i.e. the increasing concentration of pesticides in the tissues of organisms at higher levels in the food chain, leads to higher pesticide content in edible insects harvested from pesticide-sprayed agroecosystems (Houbraken *et al.*, 2016), which might pose a risk for human cultures collecting social insects for food or medicine, as well as all other animals that eat social insects. Besides agricultural landscapes, urban and suburban areas can be important habitats for maintaining pollinators (Baldock *et al.*, 2015), biological control agents (Yadav, Duckworth & Grewal, 2012), and possibly other social insects that provide ESs. Chemicals with negative impacts on social insects are widely used in such areas, so a large-scale reduction in chemical use in ever-growing urban and suburban areas could have significant positive effects (Muratet & Fontaine, 2015; Gill *et al.*, 2016).

Techniques that use increases in quantity of required resources in order to improve populations of soil-nesting social insects include the application of mulch, soil organic components, lime, or the establishment of plant cover (Van Mele, 2008; Jouquet *et al.*, 2011; Wynhoff *et al.*, 2011; Offenberg, 2015; Sorvari, 2016). By selecting the appropriate types of organic resources, responses by target species can be obtained. Food supplementation is another simple and economic technique that can be used to increase social insect local abundance. For example, termite alate production increased dramatically with experimental food supplementation (Korb & Linsenmair, 2001), and similar results were obtained for ants (Wade, Zalucki & Robinson, 2008). In

addition, the use of sugar supplementation shows promise in avoiding increases in aphid populations in response to ant-tending aphids, allowing ants to focus instead on predation of pest insects (Nagy, Cross & Markó, 2015; Wäckers *et al.*, 2017).

The use of artificial nests or shelters in order to provide nesting sites may improve the habitat for social insects. For example, the addition of pebbles to the soil seems to enhance natural colonization by ant queens (Bulot *et al.*, 2014), and the addition of shelters for native bees seems to improve local populations of pollinators (Gill *et al.*, 2016). A variety of artificial shelters have been developed to manage colonies of social wasps in order to target their biocontrol services to the crop of interest (Turillazzi, 1980; Elisei *et al.*, 2012).

(3) Conservation management

The populations of many social insects are decreasing in size, and part of this decrease might result from human activities. There are at least 200 species of social insects categorised as Critically Endangered, Endangered, Vulnerable, or Near-Threatened by the IUCN Red List (www.iucnredlist.org), mainly ants. Some social bees are relatively unresponsive to agricultural intensification and wide-scale insecticide application (e.g. *Halictus* spp. and *Lasioglossum* spp.), whereas others (e.g. *Bombus* spp.) are more sensitive (Larsen, Williams & Kremen, 2005; Rundlöf *et al.*, 2015; Potts *et al.*, 2016). Stingless bees might be affected by logging practices and by the destruction of trees for the extraction of living bee colonies (Slaa *et al.*, 2006). Thus, management techniques for ES provision should also consider the preservation of social insect populations. For instance, the commercialization of native bees should be allowed only if produced from propagation of colonies in artificial hives, rather than colonies taken from the wild, in order to avoid negatively impacting the bee population (Slaa *et al.*, 2006). In addition, indiscriminate harvesting for food or medicine of particular social insect species might put them in danger. Traditional collectors harvest social insects for individual/family consumption, using a prudent strategy of harvesting only colony fragments, ensuring sustainability (Sribandit *et al.*, 2008). However, careless overharvesting of naturally occurring colonies for commercial purposes by untrained collectors has led to a decline in populations of edible/medically important species (Wang, Chen & Lu, 2001; Ramos-Elorduy, 2006; Sribandit *et al.*, 2008).

(4) Managing social insects for the restoration of degraded habitats

Native social insects can be used to restore human-degraded habitats. Particularly in ants, many species are tolerant to anthropogenic disturbance (Arnan, Rodrigo & Retana, 2006; Arnan *et al.*, 2013, 2018; Shukla, Singh & Rastogi, 2017; Andersen, 2019) or are relatively resistant to heavy metal pollution (Grześ, 2010). Ant species that tolerate soil pollution by sequestering heavy metals in their cuticles might contribute to reductions in concentration of total and available heavy metals in contaminated soils, highlighting their potential as agents of bioremediation (Khan, Singh & Rastogi, 2017). The high concentration of organic matter accumulated by ants makes their nests unique microhabitats for microorganisms (Dauber, Schroeter & Wolters, 2001; Amador & Görres, 2007; Ginzburg, Whitford & Steinberger, 2008; Boots *et al.*, 2012; Dymova *et al.*, 2016) and mycorrhizal fungi (Dauber *et al.*, 2008), which are known to be useful in bioremediation of heavy metals from the soil (Lloyd & Lovley, 2001). Ants might have a role in improving the pH of highly acidic soils, both natural or created by anthropogenic activities such as coal mines (Maiti & Ghose, 2005), since the high microbial activity in their enriched nests may neutralise soil pH (Frouz & Jilková, 2008). Finally, ants might be a valuable tool in the bioremediation of phthalates, a common environmental contaminant used in the plastic industry, since the ant cuticle rapidly adsorbs phthalates (Lenoir *et al.*, 2012, 2014).

Ants can also be used to contribute to the restoration of disturbed areas, since, for example, seed-harvesting ants both disperse seeds and improve soil fertility and plant performance around their nests (Table 1, Appendix S1), thus playing a key role in post-disturbance successional dynamics (Wolff & Debussche, 1999; Olivier Blight, personal communication). Ants have been used successfully to enhance biodiversity in habitats altered by human activity; by creating favourable habitats for the ants *Myrmica* spp., and unfavourable for their competitors, reintroduction and expansion of endangered populations of obligate myrmecophilic butterfly species (*Maculinea* sp.) was facilitated (Wynhoff *et al.*, 2011).

Termites are employed by traditional African farmers for the remediation of compacted and crusted soils. They increase native termite activity by the application of mulch or organic matter on or into the soil, with termite mounds improving water infiltration and retention for their crops, thus making agriculture possible in these otherwise infertile soils (Mando & Miedema, 1997; Léonard & Rajot, 2001).

VI. INTERACTION OF SERVICES PROVIDED BY SOCIAL INSECTS WITH ENVIRONMENTAL VARIABLES

Besides human management, delivery of ESs will be modulated by environmental variables. Precipitation and temperature gradients are some of the most influential environmental variables for biodiversity and the ESs provided (Douglass, Duffy & Bruno, 2008; Dunn *et al.*, 2009; Philpott, Pardee & Gonthier, 2012; Wilby & Orwin, 2013). For instance, in arid agricultural fields, where earthworms are rare or absent, improvement of water infiltration and nitrogen concentration by ants and termites resulted in an increase of 36% in crop yield in a drought year (Evans *et al.*, 2011). In fact, the effects of ant and termite nests as

'fertility islands' are greater in arid lands, possibly because fertility is intrinsically lower in such habitats (Davies *et al.*, 2014; Farji-Brener & Werenkraut, 2017). The effects of termites on soil fertility increase along gradients of increasing aridity, and in Africa and Asia fungus-growing termites in particular are more dominant in drier areas (Bignell & Eggleton, 2000). During a drought period, termites increased in activity and abundance, resulting in accelerated litter decomposition, elevated soil moisture, soil nutrient heterogeneity, and seedling survival rates, thus enhancing ecosystem resistance to drought (Ashton *et al.*, 2019). Fungus-growing termites mediate about 2% of all carbon mineralization in rainforests, but in dry habitats of Africa, especially in the dry season, they can mediate up to 20%, consuming 1500 kg/ha of dry litter/year (Bignell & Eggleton, 2000). These drought-tolerant ESs are important given that predicted changes in temperature and precipitation suggest that many areas of the world will be more arid in the future.

Climate change is likely to affect most key ecosystem processes and services mediated by invertebrates (e.g. nutrient cycling, decomposition and habitat formation; Prather *et al.*, 2013). A microcosm experiment designed to evaluate the effect of climate warming on ESs provided by ants suggests that they might move more soil and build deeper nests to escape increasing temperatures, but warming may also influence their direct and indirect effects on soil ecosystem processes (Del Toro, Ribbons & Ellison, 2015). In addition, shifts in temperature decouple the phenology of flowering and insect emergence, potentially reducing pollination services (Memmott *et al.*, 2007). Increased atmospheric CO_2 concentrations, which could affect the C:nutrient ratios of many plant species (Zvereva & Kozlov, 2006), may also affect social insects. The predicted higher C:nutrient ratios of plant tissues may affect the quality of sugar-rich secretions of the trophobionts on which many ants forage, consequently increasing the proportion of C in ant diets. Since ants have selective foraging behaviour for nutrient balance, this may result in a shift towards foraging on other invertebrates richer in N and P (Kay *et al.*, 2004; Bujan & Kaspari, 2017). This might be relevant for the biological control services that they provide (Passos & Leal, 2019).

The effectiveness and quality of ESs provided by social insects along environmental gradients may depend on the spatial scale considered. For instance, the anti-herbivory protective service provided by ants globally is more effective in arid environments (Leal & Peixoto, 2017), probably due to an increase in attendance by behaviourally dominant ants on extrafloral-nectar-bearing plants. However, at a regional spatial scale in the Brazilian Caatinga dry forest, the specialisation (Câmara *et al.*, 2018), temporal stability (Câmara *et al.*, 2019), and effectiveness (Oliveira, Camara, Durval, Arnan, Andersen, Ribeiro & Leal, personal communication) of ant-mediated protection of nectar-bearing plants markedly declined with increasing aridity.

Finally, it has been shown that several ESs provided by social insects are enhanced by higher biodiversity. For example, the biological control service provided by ants depends on the number of species both of pests and ant predators (Philpott, Pardee & Gonthier, 2012; Wielgoss *et al.*, 2014; Gonthier, Kuesel & Perfecto, 2015). While species richness does not necessarily affect the diversity of ESs performed by social insects, it can increase ES magnitude, stability, and resilience to future disturbances (Houadria *et al.*, 2016; Arnan, Molowny-Horas & Blüthgen, 2019). In an artificial predator community with three ant species, pest suppression was higher than in a community with only one predator ant species; additionally, pest diversity reduced the efficiency of a single predator species at suppressing pest damage but did not limit multiple-predator communities (Gonthier, Kuesel & Perfecto, 2015). Ants reduced damage caused by coffee pests in landscapes with high forest cover within a 2 km radius, where biodiversity is higher (Aristizábal & Metzger, 2019). Also in coffee farms, the fruit set increases with the diversity of pollinating bees, and this diversity is mediated by the distance to tropical forest (Klein *et al.*, 2002). A similar pattern of crop-pollination services declining with distance from natural and semi-natural habitats has been shown for different systems worldwide (Garibaldi *et al.*, 2011; Kennedy *et al.*, 2013). These examples highlight the need to consider biodiversity when designing and implementing ESs provided by social insects.

VII. KNOWLEDGE GAPS AND FUTURE DIRECTIONS

We provide a conceptual model in Fig. 2 to summarise the available information for ESs provided by social insects and to detect knowledge gaps. We propose two areas of research that will eventually lead to a greater and more efficient use of social insects as ES providers. First, more research is needed on the value of the ESs that social insects provide. Second, improved management tools are needed.

(1) The value of ecosystem services

More research on value of the value of ESs provided by social insects will allow us to understand better what they can offer to humans and may be key to conserving social insect populations. The main research areas include: (*i*) increasing our knowledge of the biology and ecology of social species in order to enable ES valuation; (*ii*) quantifying the abundance and biomass of the social insect provider of the ES of interest; (*iii*) studying how social insect species richness influences the ESs performed by them; and (*iv*) standardising the assessment and quantification of the services. Even for better-known ESs, such as pollination, there remains a need for standardised evaluation, since knowledge on pollination is mostly restricted to *Apis mellifera* and some commercially reared *Bombus* spp. (e.g. *B. terrestris* and *B. impatiens*). Many native social bees are excellent pollinators (Kremen, Williams & Thorp, 2002; Morandin & Kremen, 2013), and their use would avoid potential threats of introducing exotic/invasive species. In addition,
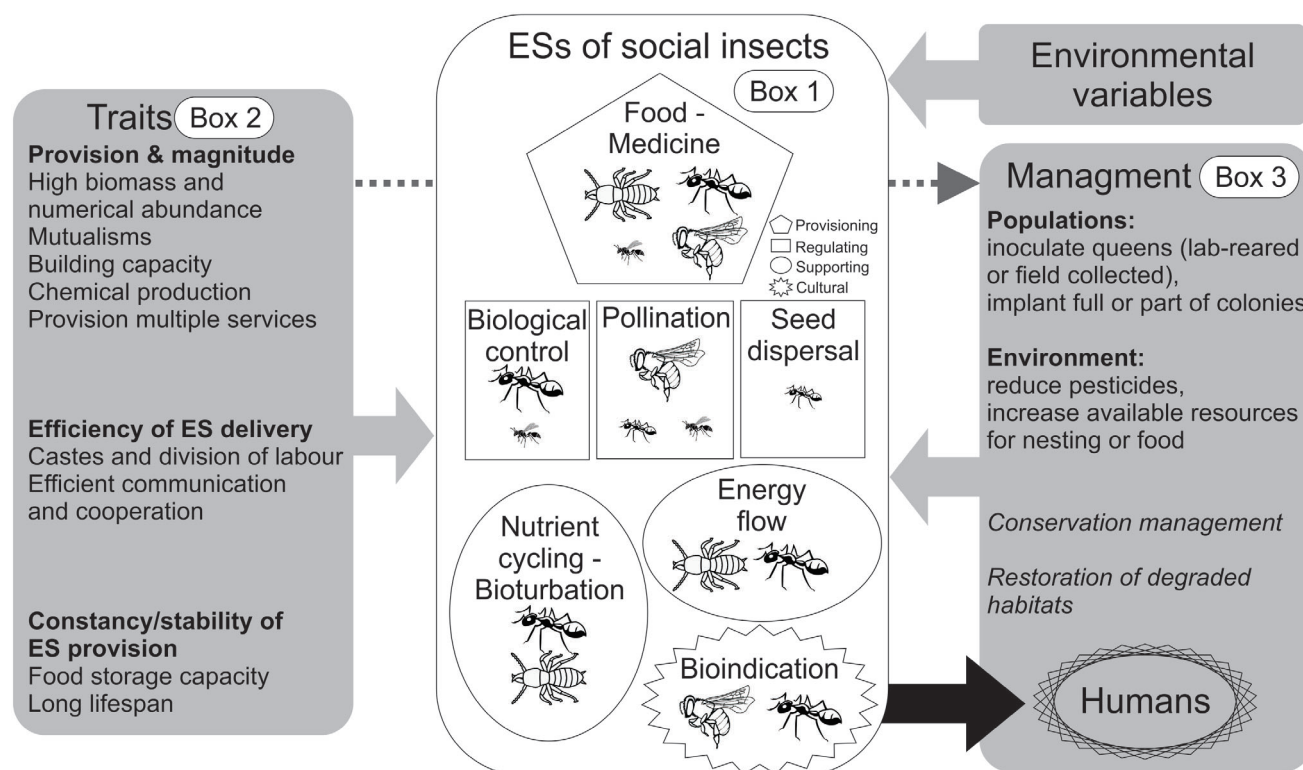
Fig 2. Conceptual model of ecosystem services (ESs) provided by social insects. Different types of ES provided by social insects are represented in box 1, with larger insect sizes indicating more knowledge of that particular service (in terms of numbers of publications for that service from different species). Relevant traits of social insects for different aspects of provision of ESs to humans are represented in box 2, with some (such as the presence of castes and division of labour, efficient communication and cooperation, food storage capacity, and long lifespan) being important for management of social insects by humans (dotted line connecting box 2 with box 3). Management strategies for social insects are shown in box 3, and can be used to improve the ES (by population or environmental management), but also in conservation and for the restoration of degraded areas. In addition, environmental variables (mainly drought and temperature, both of which are severely affected by climate change) will influence ES provision.

even when quantification of the ecosystem function exists, quantification as an ES is mostly absent (Table 1).

To increase knowledge on the biology of the species of interest, good taxonomic identification is a necessary step: closely related species might show differences in the ESs they provide (Davies *et al.*, 2003; Leite, Carvalho & Wilcox, 2018). The widespread use of molecular techniques should help to fill such knowledge gaps (Eggleton, 1999; Scharf, 2015; Turčinavičienė *et al.*, 2016; Oberprieler *et al.*, 2018; Sonet *et al.*, 2018). To quantify the abundance and biomass of the social insect provider of an ES is also important since the ESs that social insects provide depend on their abundance or biomass. However, abundance data tend to be lacking, in many cases, together with adequate species identification (King, Warren & Bradford, 2013*b*; Gill *et al.*, 2016). In addition, research on the association between social insect species richness and the performance of the ES they provide could emphasise the importance of conserving species richness to stakeholders and decision makers. Some studies have shown that a higher species richness of social insects provides more stability and resilience to ESs [e.g. predation and scavenging by

ants (Houadria & Menzel, 2017; Arnan, Molowny-Horas & Blüthgen, 2019); pollination by bees (Matias *et al.*, 2017)]. Thus, in order to provide incentives for the conservation of biodiversity, it is not only the importance of certain species of social insects as ES providers that should be considered, but also social insect diversity should be emphasised and quantified.

Standardised tools for the assessment and valuation of ESs provided by social insects are not yet available, with a few exceptions (e.g. *Apis* and *Bombus* beekeeping). Standardising will allow comparison of information from different studies around the world, and for different species (Maes *et al.*, 2013). There has been recent progress in attempts to standardise sampling methods for social insects [ants (Agosti *et al.*, 2000); bees (Prado *et al.*, 2017); termites (Jones & Eggleton, 2000; Davies *et al.*, 2013); wasps (De Souza *et al.*, 2011)], and for valuation of some services (King *et al.*, 2013*a*; Hanley *et al.*, 2015). However, there are still no unified methods to study most of the ESs that social insects provide, such as nutrient cycling, bioturbation, or biological control. Our list of relevant variables to measure for each ES in Table 1 is a first step to standardising the methodology.

(2) The improvement of management techniques

Management of social insects in order to enhance the ESs that they provide will be improved mainly by (*i*) increasing our knowledge on the biology of these species in order to allow conservation and management; (*ii*) standardising tools and methods for the assessment and provision of ESs; (*iii*) selecting species with traits that allow humans to manage their social behaviour; and (*iv*) including traditional local knowledge in management techniques.

Conservation management of social insect species in many cases still awaits a basic knowledge of their ecology, behaviour, demography, and distribution, as well as a real estimation of the potential effect of large-scale harvesting activities for food, medicine or other provisioning ESs. Researchers and practitioners are now turning to management of local pollinators, a goal that requires careful studies of their, generally poorly known, biologies (e.g. Slaa *et al.*, 2006). Since social insects are often key functional regulators of ecosystem processes, unlimited extractive strategies could jeopardise these ecosystem functions. It will also be important to coordinate regulation policies at a regional or country level (e.g. Aizen *et al.*, 2019).

It will be important to select species with traits that allow humans to manage their social behaviour. As described in Section III, social insects have many traits that may facilitate their management. In particular, their communication allows them respond to changes in the type and abundance of food sources *via* recruitment systems that amplify and enhance functional responses. From waggle-dance robots that can stimulate bees to forage (Landgraf *et al.*, 2018) to manipulations of pheromone communication that have been used successfully to control social insects as pests (Westermann *et al.*, 2016; Sunamura, 2018), tools are available with great potential to be used to manage social insects. For example, ant pheromones have potential uses as herbivore repellents (Offenberg *et al.*, 2004), while the use of pheromones to enhance the provision of ESs has not yet been studied.

Finally, the inclusion of traditional and local knowledge regarding social insect management will help to improve their use as ES providers. For example, at least 33 species of stingless bees are managed in Mexico, Costa Rica, Venezuela, Brazil, Peru, Paraguay and Australia, potentially allowing a change in paradigm to encompass the empowerment of local markets, an increase in local knowledge, and enhanced respect for the environment (Cortopassi-Laurino *et al.*, 2006). In return, making accurate information available to farmers and local stakeholders will also be important. For instance, informing farmers about the role of wild bees (which include many social as well as solitary species) as pollinators and of forest pollination services could play a major role in the conservation of wild bees and their natural nesting habitats. Some species of stingless bees, especially from the genus *Trigona*, have toothed mandibles and are known to damage fruits, leaves and flower buds (Wille, Orozco & Raabe, 1983). Some farmers consider these species as pests and destroy their nests without realising that they are losing valuable pollinators.

VIII. CONCLUSIONS

(1) Social insects provide important ecosystem services to humans, both in terms of the diverse array of service types, the magnitude of these services, often their simplicity of management, and the multiple services provided by some species, making a significant contribution to human society.

(2) However, much work remains in order to improve our knowledge of these services and their quantification for different species, and in developing a standardised methodology. There is also a need for the development of management techniques that allow sustainable use of the services provided by social insects. This lack of knowledge hinders an accurate valuation of the impact of social insects on human economy and culture. The challenge will be to enhance the provision of services by native social insect species with effective conservation management that can be adapted to local requirements.

(3) In order to improve conservation of social insects, which is urgently needed as for most other insects (Hochkirch, 2016), it is important that the general public values them appropriately. The examples of ecosystem services that they provide included herein will hopefully help to boost the public image of social insects other than bees, i.e. of termites, wasps and ants that are not yet appreciated for their vital importance in natural and human-modified ecosystems.

IX. ACKNOWLEDGEMENTS

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XI. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Detailed review of the ecosystem services provided by social insects.

Appendix S2. References used to derive the 'Key variables to measure' listed in Table 1.