Research trends in ecosystem services provided by insects

Submitted to *Basic and Applied Ecology*

Title: **Research trends in ecosystem services provided by insects**

Jorge Ari Noriega[1, *], Joaquín Hortal[1, 2], Francisco M. Azcárate[3], Matty P. Berg[4, 5], Núria Bonada[6], Maria J. I. Briones[7], Israel Del Toro[8], Dave Goulson[9], Sébastien Ibanez[10], Douglas A. Landis[11], Marco Moretti[12], Simon G. Potts[13], Eleanor M. Slade[14, 15], Jane C. Stout[16], Michael D. Ulyshen[17], Felix L. Wackers[18], Ben A. Woodcock[19] & Ana M.C. Santos[20]

[1] *Department of Biogeography and Global Change, Museo Nacional de Ciencias Naturales (MNCN-CSIC), C/José Gutiérrez Abascal 2, 28006 Madrid, Spain.*

[2] *cE3c – Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências da Universidade de Lisboa, 1749-016 Lisboa, Portugal.*

[3] *Terrestrial Ecology Group, Department of Ecology, Universidad Autónoma de Madrid, 28049 Madrid, Spain.*

[4] *Department of Ecological Science, Section Animal Ecology, Vrije Universiteit Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands.*

[5] *Groningen Institute for Evolutionary Life Sciences, Community and Conservation Ecology Group, Nijenborgh 7, 9747 AG, Groningen, The Netherlands.*

[6] *Grup de Recerca Freshwater Ecology and Management (FEM), Department de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, 08028 Barcelona, Spain.*

[7] *Departamento de Ecología y Biología Animal, Universidad de Vigo, 36310 Vigo, Spain.*

[8] *Biology Department, Lawrence University, Appleton, Wisconsin, USA.*

[9] *School of Life Sciences, University of Sussex, Falmer, Brighton, BN1 9QG, UK.*

[10] *Laboratoire d'Écologie Alpine (LECA), UMR 5553, CNRS/Université Savoie Mont Blanc, Chambéry, France.*

[11] *Department of Entomology, Michigan State University, East Lansing, Michigan, USA.*

[12] *Swiss Federal Research Institute, Biodiversity and Conservation Biology, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland.*

[13] *Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, Reading University, Reading, RG6 6AR, UK.*

[14] *Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, UK.*

[15] *Lancaster Environment Centre, University of Lancaster, Lancaster, UK.*

[16] *School of Natural Sciences, Trinity College Dublin, Dublin 2, Republic of Ireland.*

[17] *USDA Forest Service, Southern Research Station, Athens, Georgia, USA.*

[18] *Lancaster Environment Centre, Lancaster University, Lancaster, UK.*

[19] *NERC Centre for Ecology & Hydrology, Crowmarsh Gifford, Wallingford, OX10 8BB, UK.*

[20] *Forest Ecology and Restoration Group, Department of Life Sciences, University of Alcalá, 28805 Alcalá de Henares, Madrid, Spain.*

*Corresponding author: Jorge A. Noriega

E-mail address: jnorieg@hotmail.com

Running title: Insect ecosystem services research

Word count: 5,512 words (main text), 292 words (abstract)

127 references

2 Tables

5 Figures

2 Supplementary Appendices

Abstract

Insects play a key role in the regulation and dynamics of many ecosystem services (ES). However, this role is often assumed, with limited or no experimental quantification of its real value. We examine publication trends in the research on ES provided by insects, ascertaining which ES and taxa were more intensively investigated, and with which methodological approaches, with particular emphasis on experimental approaches. We performed a systematic literature search to identify which ES have been attributed to insects. Then we classified the references retrieved according to the ES, taxonomic group and ecosystem studied, as well as to the method applied to quantify the ES (in four categories: no quantification, proxies, direct quantification and experiments). Pollination, biological control, food provisioning and recycling organic matter are the most studied ES. However, the majority of papers do not specify the ES under consideration, and from those that do it, most do not quantify the ES provided. From the rest, a large number of publications use proxies as indicators for ES, assuming or inferring their provision through indirect measurements such as species abundances, species richness, diversity indices, species density or the number of functional groups. Pollinators, predators, parasitoids, herbivores and decomposers are the most studied functional groups, while Hymenoptera, Coleoptera and Diptera are the most studied taxa. Experimental studies are relatively scarce and they mainly focus on biological control, pollination, and decomposition performed in agroecosystems. These results suggest that our current knowledge on the ES provided by insects is relatively scarce and biased, and shows obvious gaps in the least-studied functional and taxonomic groups. An ambitious research agenda to improve the empirical and experimental evidence of the role played by insects in ES provision is essential to fully assess synergies between functional ecology and biodiversity conservation.

Keywords: Biological control; Coleoptera; Decomposition; Ecosystem functions; Experimental research; Hymenoptera; Insecta; Nutrient cycling; Pest regulation; Pollination.

Introduction

Understanding, valuing, quantifying and ensuring the provision of ecosystem services (ES) under current global changes have become increasingly important during the last two decades (Turner et al., 2007, Seppelt et al., 2011 and Díaz et al., 2013). ES can be defined as the beneficial functions and goods that humans obtain from ecosystems, that support directly or indirectly their quality of life (Harrington et al., 2010 and Díaz et al., 2015). These services are critical for human welfare (Daily et al., 2000), since they include, amongst others, the provision of food and water, the regulation of floods, diseases and climate, the control of organic matter decomposition and nutrient cycling, the suppression of pests, and the cultural services associated with recreation or education (Millennium Ecosystem Assessment, 2003 and Díaz et al., 2015). The definition and interpretation of ES has varied considerably in the literature over the years (De Groot et al., 2002, Harrington et al., 2010 and Spangenberg et al., 2014), and this concept is often confounded with related terms such as "ecosystem functions" and "ecosystem goods" (Millennium Ecosystem Assessment, 2003 and Díaz et al., 2015). Ecosystem functions refer to all biogeochemical characteristics of ecosystems (including the structures and processes that may arise as emergent properties), regardless of whether they have a value for, or benefit, humans (Spangenberg et al., 2014). Whereas ecosystem goods correspond to the products of ecosystem services that can be traded by humans through either perception, expectations, experience, use or consumption (Díaz et al., 2015).

Insects are the largest and most diverse group in the animal kingdom. They are key

components in the provision, regulation and dynamics of many ecosystem services (referred as insect ES herein; Weisser & Siemann, 2004 and Schowalter, 2013). Insects are potentially involved in the four broad types of services defined by the Millennium Ecosystem Assessment (2003): (i) provisioning services, that correspond to material or energy outputs from the ecosystems; (ii) supporting services, that allow the maintenance of other ES; (iii) regulating services, that regulate the processes and structure of ecosystems; and iv) cultural services, that do not provide material benefits but have an educational, spiritual and/or aesthetic value (GEO4, 2007 and Prather et al., 2013). Previous efforts to assign monetary values to several ES provided by insects usually understimated the value of these animals to our economies and quality of life (Beynon et al., 2015). Still, insects provide ES worth at least $57 billion per year in the United States alone (Losey & Vaughan, 2006), and insect pollination may have an economic value of $235 to 577 billion per year worldwide (IPBES, 2016).

A realistic assessment of the contribution of natural resources and biodiversity for the delivery and maintenance of ES depends on having accurate information and a clear understanding of the processes involved in the provision of those services (Haines-Young & Potschin, 2010). There is a general lack of knowledge on the functional roles played by most species in nature (i.e. the so-called Raunkiaeran Shortfall; Hortal et al., 2015). This is particularly important when assessing the value of insect ES. Despite their enormous diversity, insects are often under-represented in ecosystem studies, so their contribution to ecosystem functioning has been comparatively less investigated (Schowalter, 2016). As a consequence, we often lack a comprehensive understanding of the role of insects in many ecosystem processes that underlie ES. Although many efforts to quantify insect ES have been developed in the last decade (e.g. Prather et al., 2013 and Boerema et al., 2017), they

particularly focused on a subset of either functional or taxonomic groups, such as pollinating bees or dung beetles.

Current knowledge on the ES provided by insects has usually been obtained from a variety of methodological approaches, ranging from field observations to manipulative controlled experiments, even though such relationship is often simply assumed (e.g. Philpott & Armbrecht, 2006 and Allsopp et al., 2008). Thus, assessment of insect ES includes a wide variety of approaches such as opportunistic field observations, expert opinions or estimates, assumptions or inferences made from proxies (e.g. species richness, total abundance, morphological traits), estimates inferred from trait values and empirical data obtained from field and/or microcosm experiments that may or may not have been specifically designed to quantify the real ES provision in the first place. These approaches also differ widely in their replicability, accuracy, and applicability of their outputs, direct relevancy to the ES itself, as well as in their costs in terms of time and resources. Further, while they may allow inferring which insects provide which ES, proxies might not be approriate to reveal the mechanisms linking specific traits to particular ecosystem functions or services. A better quantification of the specific relationship between ES and specific traits provides a potentially useful link to the wide-scale prediction of ES (de Bello et al., 2010), although this information is limited to a few groups and ecosystems (see Hortal et al., 2015). This contrasts with greenhouse and cage experiments performed on individual species or simple communities, which enable either maintaining a tighter control of the environmental conditions or subjecting the object of study to well-defined treatments, or both (Lähteenmäki et al., 2015). This allows establishing –and measuring– direct links between given ES and particular individual(s), trait values, and functional compontents of biodiversity (e.g. Dias et al., 2013 and Bílá et al., 2014), while revealing mechanisms behind the relationship between biodiversity and ES. However, these

types of studies present several disadvantages, as they can be expensive and laborious. Further, synergies and/or antagonistic effects are difficult to control, and their findings might not be relevant or realistic when up-scaling to real-world conditions and/or when they are extrapolated to a different taxa from the model species

We examine the general trends in published research on ES provided by insects, to provide an overview of the overall quality and extent of the current state-of-the-art on this topic. To do this, we conduct a systematic literature search, identifying which specific services have been attributed to insects, which methodological approaches have been applied to describe and quantify these ES over time, and whether there are any important gaps in current knowledge. In particular, we seek to answer the following questions: (i) Which insect ES have been studied? (ii) What type of methodological approaches have been used for their study of these ES? (iii) Which functional and taxonomic groups of insects have been investigated in this context? and, (iv) Which ecosystems have been monitored experimentally for insect ES?

Materials and methods

We performed a literature search using different online platforms to identify articles dealing with insect ES that were published during the last six decades (1956–2016, time interval preselected by default by some of the online platforms). Firstly, we conducted bibliographic queries in the ISI Web of Knowledge (WOK) and Scopus using the keyword string "(ecosystem* service* OR ecosystem* function* AND insect*)", looking for matches in the title, abstract and/or keywords. In addition, we used the same keywords to retrieve articles from the group associated with "ecosystem services and insects" in ResearchGate (www.researchgate.net, one group: ecosystem service insects) and ACADEMIA

(www.academia.edu, three groups: ecosystem services, ecosystem service and ecosystem functions). Since the terms "ecosystem services" and "ecosystem functions" are often used very loosely in the literature, we widened our search by using both terms and thereafter discarded those references that were not clearly related to any ES. Therefore, from the initial search (updated on 30th December 2016) we retrieved 8,424 records (WOK: 2,348, Scopus: 2,859, ResearchGate: 200, Academia: 3,017). We then eliminated conference papers, articles in press, duplicate records (i.e. articles that appeared more than once in the different search engines, or in the same platform due to typographical errors) and finally, all those references not related to any ES or insect group. The finally selected records included 913 papers papers that provided ES estimates.

The following information was retrieved from each selected publication: author(s); year of publication; journal; method used for quantifying each ES in four categories: not quantified, proxies, directly quantified, and experiments (Table 1); trophic group(s); taxonomic group(s) (order and superfamily or family); ES studied (specific ES or ES in general); and any relevant additional observation as notes. To keep consistency with the literature, we used the term 'biological control' to refer to the most-adequate term "pest and pathogen suppression" (that includes both human-controlled and 'natural' regulation of pest populations). In addition, the type of ecosystem investigated and the location of the study were recorded for the experimental studies.

This type of literature search has several limitations that were considered when analyzing the data and interpreting the results. Firstly, the search may miss some relevant papers, simply because the title, abstract or keywords did not contain the keywords searched. In fact, our literature search was biased towards publications specifically referring to insect groups (i.e. studies that included the word 'insects' only), which could result in missing some

papers that focus on particular species (e.g. *Apis mellifera*), functional groups (e.g. pollinators) or larger groups of invertebrates that also include insects. Secondly, the approach used here might have overlooked publications that refer to a particular ecosystem service by its name (e.g. pollination) without quoting the words "ecosystem services" *per se* in their abstract or keywords. These limitations have been previously identified by other authors using similar search approaches (e.g. Prather et al., 2013). Thirdly, the term "ecosystem service" is fairly recent, and its use was not common prior to the 1990s, so some older publications addressing insect ES may not have been detected by our search. Finally, we may have failed to include some works that were not indexed by the platforms used here. However, and despite these problems, we believe that the data retrieved gives us enough relevant information to examine general trends in insect ES research and to identify knowledge gaps on the topic that could help us to develop future research strategies to better evaluate the ES provided by insects.

Results

Our search retrieved 913 articles, published from 1989 to 2016, with relevant information on the ecosystem services provided by insects (see Appendix A). There were no papers before 1989 with the specific keyword string used for our search. These articles show an exponentially increasing trend in the number of insect ES studies over time (Fig. 1). Pollination, biological control, food provisioning, and recycling organic matter are the most well studied ES (Fig. 2A), although the role of insects has been investigated for many others, including a number of services that were not included in former reviews on insect ES (Table 2). Remarkably, 20% of the publications (N=184) mention ES in general without referring to any specific service (Fig. 2A), without clarifying the role that the investigated insect groups or

species performed to deliver these services. ES of high socio-economic relevancy, such as pollination and biological control in agricultural ecosystems, are both the most commonly studied and those with the highest proportion of experimental data supporting the link between the studied insects and the service provided (Fig. 2B). Indeed, there is a remarkable similarity between the proportions of studies focused on these two ES and nutrient cycling, and the functional groups performing these services (i.e., pollinators, predators and parasitoids, and decomposers, respectively; compare Figs. 2A and 2C).

The majority of insect ES literature does not include a quantification of the actual level or extent of the ES studied: categories not quantified and proxies sum up 69.6% of all papers (N=635; Fig. 3A). These studies are not restricted to those not specifying the ES under consideration, but rather extend to all types of services (Fig. 2B). Strikingly, almost half of the publications retrieved by our search used proxies as indicators for ES (46.8%, N=427; Fig. 3A), particularly for pollination and non-specified biological control services (Fig. 2B). Less than a third of studies actually quantify insect ES either directly or through experiments (N=278, 30.4%), although the proportion of these two kinds of studies together has increased steadily during the last 15 years (Fig. 3B). Strikingly, most of them make direct measures without any experimental manipulation (N=222, 24.3% of all papers), whereas experimental studies undertaken either in the laboratory or in the field represented only 6.1% (N=56) of the total number of publications (Fig. 3A; see Appendix B). Pollination, biological control and nutrient cycling were the ES most studied using experiments (Fig. 2B).

As identified above, insect ES are most commonly studied through proxies. These proxies are typically species abundance, species richness and, to a less extent, ecological diversity indices such as Simpson or Shannon, among others (sometimes referred to as alpha diversity, but see Magurran, 2004) (Fig. 3C). However, many other proxies have been used in

the literature, including species density, the number of functional groups, visitation rates, network complexity and modularity, functional traits (e.g. body size/biomass, behavioral traits, colony density and health, etc.) and associated measures of functional diversity, species composition, beta diversity, niche overlap or endemicity, among others. Very few studies corroborated the existence of a direct link between the proxy and the functional aspect that was intended to represent, at the studied geographical scales and/or for a specific taxonomic or trophic group (exceptions being, e.g., Arnan et al., 2013 and Rader et al., 2014).

Pollinators, predators of pests, parasitoids, herbivores and decomposers (especially dung beetles) were the most studied functional groups (Fig. 2C), together with some charismatic and/or easy to identify groups such as ground beetles or bumblebees. The order Hymenoptera –that includes many pollinators (particularly bees), parasitoids (commonly used for biological control), predators and decomposers (such as ants)– has been the most studied taxonomic group, followed by Coleoptera and Diptera (Fig. 4A). In fact, hymenopterans have been comparatively overstudied if we take into account the total number of described species (Fig. 5). At a finer taxonomic level, several superfamilies or families also emerge as being highly studied subjects, including Apoidea (particularly Apidae), Formicidae and Braconidae belonging to Hymenoptera; Carabidae, Coccinellidae and Scarabaeidae within Coleoptera; Syrphidae among Diptera and several families of termites from Blattodea (Fig. 4C).

The services most studied using experimental approaches are biological control, pollination and decomposition (see Appendix B). Thus, the links with ES have been more often quantified in experimental studies for Hymenoptera and Coleoptera (Fig. 4B). Most experimental evidence on insect ES comes from USA and Europe – in particular Switzerland, Germany and Sweden, although a few studies have also been performed in developing countries such as Costa Rica, Mexico, Philippines, Tanzania, Indonesia, Kenya and Argentina

(see Appendix B). The ecosystems most commonly studied experimentally were agroecosytems, which included a long list of different types of crops (e.g. almonds, cabbage, cacao, cereals, coffee, rice, potato, wheat, etc.). The services provided by insects in grasslands and, to a lesser extent, forests, savannas, wetlands or lakes have also received some (though much less) attention (see Appendix B).

Discussion

Research interest on the ecosystem services provided by insects grew during the last decade (Stout & Finn, 2015, and references therein). The increase in the number of papers published on this topic mirrors the pattern described by Hallouin et al. (2016) for ES in general, and reflects the expanding significance of identifying, analyzing, conserving, and managing ES under the global changes that characterize the Anthropocene. This general interest has reached entomological research, resulting in a clear increase in the number of studies focusing on insect ES (compare our Table 2 with the list provided by GEO4, 2007 or Turner et al., 2007). Despite such recent work, the services provided by insects still remain relatively understudied compared to other groups. Insects comprise 49.9% of the 1'656,025 accepted species currently included in the Catalogue of Life (accessed on 23rd December 2016; Roskov et al., 2017). However, a quick search in Scopus (using "ecosystem service*" AND [insect* OR coleop* OR hymenop* OR lepidop* OR dipter* OR bees OR beetle*], 26th January 2017) produced 1,102 documents on insect ES out of 16,476 for ES in general. That is, about 6.7% of the total research output on ES is devoted to these invertebrates making up half of known diversity, containing species and trophic groups with unique roles in ES provision. This comparatively low level of knowledge arises despite the fact that, in many cases, it is likely that the majority of particular ES are supported by a relatively small number

of invertebrate species (e.g. for pollination, Klein et al., 2015).

Remarkably, the majority of the studies on insect ES published so far are descriptive, either making no quantification of the ES or using proxies to indirectly link species and/or groups to particular ES, even for the better-studied groups such as bees (e.g. Eardley, 2000, Morandin et al., 2007 and Kimoto et al., 2012). Experimental studies and direct ES quantifications have become more common in recent years, but still account for a small proportion of published studies. Experiments are therefore needed to ascertain in detail which species or functional groups provide a particular service, and which mechanisms and aspects of biodiversity are behind the provision of specific ES (e.g. Slade et al., 2007, de Bello et al., 2010 and Ibanez et al., 2013). A better understanding of the links between insect diversity, insect behavior, and ES provisioning is also needed (Schmitz, 2008 and Brosi & Briggs, 2013). Considering that most information on insect ES comes from studies using proxies rather than direct quantifications or experiments, it is likely that most current knowledge on these services holds a high degree of uncertainty, for it is based only on estimates rather than quantitative assessments (Boerema et al., 2017). This lack of robust quantitative data can indeed hamper the assessment of global change effects, preventing us from identifying and/or quantifying the impacts of environmental changes on ES, and therefore making difficult to design adequate actions to mitigate them.

From proxies to experiments

Further analysis is required to determine why proxies are preferred to direct service quantifications and/or experiments in ES research, both in general and in the particular case of insects. Some ES, such as nutrient cycling or soil nutrient regulation, are difficult to quantify and/or require laborious, expensive and time-consuming work, making the use of proxies

more attractive (e.g. Hoffman et al., 1996 and Palin et al., 2011). In fact, there are no well-established standardized ways of quantifying the value for some ES, such as provision of nursery habitats, cultural, educational and pharmaceutical services, tourism, and urban quality of life (see Nallakumar, 2003 and Choosai et al., 2009). Quantifying the value of a number of ES presents important methodological difficulties, such as the spatial redistribution and accumulation of soil nutrients, seed dispersal and germination, or soil removal (see Folgarait, 1998, Pringle et al., 2010 and Wu et al., 2010). One big challenge to ES field experimentation is excluding a particular taxon from the system to measure the effects of different taxa on the ES of interest. This has strained efforts to accurately quantify the contribution of insects to the decomposition of both litter (Kampichler & Bruckner, 2009) and wood (Ulyshen & Wagner, 2013), and to nitrogen cycling in grasslands (Risch et al., 2015). Some success has been, however, achieved with dung beetles (e.g. Slade et al., 2007, Beynon et al., 2012, Griffiths et al., 2015, Lähteenmäki et al., 2015 and Slade & Roslin 2016).

The most commonly used proxies for ES are species richness and species abundance. However, these two metrics could provide limited information on service delivery if they do not adequately capture the uneven contributions of different taxa to an ES (e.g. Klein et al., 2015). The relationship between taxonomic diversity and ecosystem function is often context-dependent (Tylianakis et al., 2008), and it is not uncommon for the effects of a single taxon on a particular service to eclipse those of all other species in a community (e.g. Straub & Snyder, 2006 and Klein et al., 2015). Studies addressing the importance of insects for wood decomposition, for example, have shown termites to consume by far more wood than all other insects combined (Ulyshen et al., 2014). Indeed, an increasing number of studies show the importance of considering functional aspects of biodiversity in improving our understanding of the relationships between proxies and ES (Díaz et al., 2013, Lavorel et al., 2013, Moretti et

al., 2013, Harrison et al., 2014 and Wood et al., 2015).

Metrics related to functional diversity or attributes (i.e. traits) that affect an ES (sensu Violle et al., 2007 and Díaz et al., 2013) may be more informative than those related to total abundance or taxonomic richness (Lavorel et al., 2013). Trait-based metrics can take into consideration that different species (and individuals) have different effects on the ecosystem, and assume that there may also exist some complementarity among species' functioning (Hoehn et al., 2008). Indeed, it has been argued that trait diversity at the community level is one of the key factors governing ecosystem properties (Hooper et al., 2005), sometimes exceeding species richness in importance (Hoehn et al., 2008). However, a proper use of traits to link diversity and ES requires good knowledge on which traits are associated with a particular ecosystem function and/or service, the intraspecific variability of these traits, under what environmental conditions are those functional traits more important, and which component of the distribution of trait values within communities is most appropriate to account for service provision (i.e. mean or variance; e.g. Ricotta & Moretti, 2011, Dias et al., 2013 and Griffiths et al., 2016a).

Unfortunately, data on traits and knowledge on how these traits translate into ES are limited (Hortal et al., 2015), at least at the spatial scales relevant to the study of ES. This shortfall is even more acute in insects and other soil invertebrates (but see e.g. Ibanez, 2012 or Martins et al., 2015). An adequate selection of traits genuinely related with the studied service could provide a mechanistic understanding of the role of insects in ES provision, and will nonetheless have the greatest potential to infer ES delivery (e.g. Woodcock et al., 2013 and Griffiths et al., 2016b). However, many times, the traits used for ES analyses are chosen based on either readily-available trait data, or on traits used by former studies, rather than on a functional hypothesis linking traits, ecosystem functions, and their associated services. This

can result in a consistent bias towards using small subsets of traits, some of which could have little value for particular functions or services. Even in those few cases where the traits genuinely related with the studied service have been identified, their data are typically limited to a handful of species, as their measurement is often labour intensive. Therefore to improve the use of trait-based proxies for insect ES research further work is needed to provide experimental evidence on the relationship between trait variation and service provision. Initiatives to provide standardized measures of traits across terrestrial invertebrates and their effect on ecological functioning –such as the invertebrate trait handbook proposed by Moretti et al. (2016)– are key for the advance of insect ES research.

Functional and taxonomic biases

The biases in insect ES research are both functional and taxonomic; not only some services are more studied than others, but also some groups are more studied than others. Indeed, the most-studied ecosystems are croplands and consequently, the focus is placed on those ES that have a larger impact on the goods we receive from these managed ecosystems such as pollination and biological control, two services with high economic impacts (Losey & Vaughan, 2006). These two services are also the ones that have been more studied using experimental approaches, together with nutrient cycling. Hence, a good example of why biases are often functional rather than taxonomic is the high proportion of papers that have studied pollination. These often analyze more than one insect group or the whole community of pollinators, including Hymenoptera (predominantly Apoidea and some additional families), Diptera (Syrphidae) and Lepidoptera (e.g. Gardiner et al., 2010, and Lundin et al., 2013). This contrasts with the research on many ES of less obvious and/or indirect economic importance, such as dung removal, seed dispersal, soil aeration, pest control or soil water infiltration.

These studies are typically constrained to a single trophic group and/or a single taxonomic group, hence providing very little information on the whole-community responses and/or the interactions between ecosystem services, functional and/or taxonomic groups. In addition, there is an evident bias in the literature we reviewed towards those groups that can be easily studied (e.g. towards above- vs. below-ground organisms), have larger body sizes (e.g. butterflies vs. flies), are readily identifiable (e.g. Carabidae are more often studied than the taxonomically complex Staphylinidae), or are more charismatic (e.g. bumblebees compared with flies).

The publications that study multiple ES rarely focus on a single group of insects (e.g. Klein et al., 2006 and Campbell et al., 2012; but see Slade & Roslin, 2016). In fact, many recent articles considering several taxonomic groups have investigated how their combined responses to different stressors interact with service provision, such as biological control or pollination (e.g. Mody et al., 2011, Caballero-Lopez et al., 2012 and Stanley & Stout, 2013). However, very few studies have analyzed the possible range of interactions (from synergies to antagonistic or trade-offs) between two or more ES within a specific network or for the whole ecosystem. A significant exception to this lack of knowledge are those studies investigating the interaction between different groups of pollinators and those describing the regulating services provided by other elements of the ecological network, such as pest control provided by predators and parasitoids, or the effects of herbivores on the pollinated plants (e.g. Morandin et al., 2007, Hegland et al., 2010, and). Indeed, current knowledge indicates that these regulatory relationships usually affect network dynamics and hence, the supporting ES provided by insects in a negative way (Badano & Vergara, 2011).

There are few quantitative assessments of the ES provided by several functional and taxonomic groups, either from experiments or from indirect quantifications. Our bibliographic

search failed to find any information for several key functional groups, such as rhyzophagous insects, some decomposers and many symbionts and kleptoparasites. Similarly, very few studies were found concerning several small insect Orders, such as Ephemeroptera, Plecoptera or Neuroptera. Therefore, the design of our review, which focused on describing publication trends rather than assessing knowledge gaps in a conceptual map, might have prevented us from resolving whether these groups are underrepresented in ES research, if they actually provide few services of minor importance, or whether the lack of general knowledge on their ecology and systematics is the main cause of their misrepresentation. The key ecological roles played by some of them in freshwater ecosystems (e.g. litter decomposition) suggests that many of these groups are likely to have a very significant role in the provision of many ES (Macadam & Stockan, 2015). Our bibliographic survey also pinpoints other biases that are common in biodiversity knowledge, such as the lack of data for many geographical areas and ecosystem types. Knowledge on all aspects of biodiversity is typically concentrated in northern temperate regions, particularly Europe and North America (Hortal et al., 2015). This widespread bias is also evident in the published work on insect ES; very little is known about the services provided by insects in agroecosystems outside these two regions, with the exception of some limited work in tropical plantations (mostly coffee and trees) or savannas. However, the sheer lack of knowledge on insect ES throughout most of the world's ecosystems makes more developed analyses on geographical and ecological biases premature.

A cautionary note on insect disservices

It is important to highlight that we did not include in our analysis papers studying disservices by insects for two main reasons. First, the goal of this paper was to characterize the trends in insect ES research and, in particular, how much current information comes from

experimental evidence. Second, the study of insect disservices is a vast topic that would not be easy to embrace using literature searches, and that definitively requires a separate analysis. However, the line that separates an ES from a disservice is sometimes very thin. In fact, in some cases, the same ecological function can be qualified as service or disservice depending on the perspective. While the effects of many foliage or root feeders might often be considered as disservices, they do provide regulating services by controlling the populations of both weeds and certain pests through herbivory and/or competitive exclusion, respectively or by helping to maintain populations of generalist predators and parasitoids (e.g. Martin et al., 2010, Evans et al., 2011 and Eckberg et al., 2014). Herbivores also influence nutrient cycles and can contribute to soil fertility and enhance primary production (Belovsky & Slade, 2000). Also, bark and wood boring insects, create suitable habitats for other insects (e.g. Zuo et al., 2016) and have been shown to facilitate colonization by fungi, thus indirectly accelerating the decomposition of woody debris (Strid et al., 2014 and Ulyshen et al., 2016). It is therefore important to understand which ecological functions performed by herbivores can in fact result in regulating services, and how they interact with supporting and provisioning services.

As a consequence of this, during our bibliographic search we found some articles that evaluated or studied ecosystem disservices, related to three main topics: (i) damage of agricultural crops by herbivores (e.g. Hiltpold et al., 2013 and Dale & Frank, 2014); (ii) damage to wood plantations by xylophagous insects (e.g. DeSantis et al., 2013 and Reich et al., 2014); and (iii) harmful effects on human health by hematophagous insects (e.g. Sommerfeld & Kroeger, 2013 and Muturi et al., 2014). Some of these studies were not discarded from our final list because they refer to ecological functions that can be classified either as services or disservices.

Concluding remarks

Knowledge on the ecosystem services provided by insects is relatively scarce and biased. This occurs despite the fundamental importance of the ecological functions they perform for the maintenance of ecosystem functioning and their links to human well-being. Part of the reason behind the poor knowledge on insect ES comes from the tradition of considering insects as providing mainly disservices to humanity, through pest and parasite outbreaks. However, given the sheer diversity of insects and their key ecological role in all terrestrial and freshwater ecosystems, it is extremely likely that the economic and non-economic benefits provided by this group through many ES may be much larger than the damage and disservices they provide even in some specific areas such as crop production. Indeed, the value of some ES provided by insects, such as pollination, is widely accepted in financial, food security and health terms. Valuing these services can therefore be a good way to stimulate and promote research into them – through increasing financial support and societal engagement.

It is therefore key to gain an increased understanding of the role played by insects in ES delivery. This requires combining the efforts of ES researchers (including ecologists, entomologists, economist and social scientists) to identify direct links between insect species and the ES they provide, either through field observations or experiments. A good map of our current knowledge could help defining further needs in insect ES research. Our work provides a review of current knowledge in the area and identifies obvious gaps in the less-studied functional and taxonomic groups. Moreover, we also highlight the existence of knowledge gaps in the research of some ES that either have a lower direct economic value, or their study poses important methodological challenges. However, the nature of our analyses prevents us

from obtaining a complete overview of what is actually known and a full distribution of the knowledge gaps, since we characterize publication trends rather than the level of completeness, accuracy and usefulness of the knowledge on each ES, ecosystem and/or insect group.

A clear shortfall in current knowledge is the lack of high-quality quantifications of ES delivery (Boerema et al., 2017), either directly in the field or through experiments. Ideally, such information should be obtained by adopting a robust and cohesive common framework for insect ES research, which clearly separates ES from ecological functions, which have been more commonly studied for insects. Many studies use the term ES very loosely; actually, some consider ecological functions of non-human value as services too. A conceptual and methodological framework that clearly links the study of functions with the quantification of the delivery of services can help to increase the research impact of ES for insects in general, and for many seldom-studied groups in particular. This framework should consider the interactions and trade-offs among the services provided by different insect groups, allowing us to also identify and measure the services provided by less diverse insect orders. A first step in the implementation of such framework is certainly to quantify insect ES provision in the field, but in the mean time, it is necessary to implement a combination of laboratory and field experiments. While the use of controlled microcosms can provide accurate information, manipulative field experiments are more realistic since they take into account the interacting environmental factors. Obtaining accurate and comprehensive information on the ES provided by insects therefore requires joining efforts in implementing such an ambitious research program that combines empirical and experimental evidence.

Acknowledgements

We want to thank Teja Tscharntke and Timothy D. Schowalter for encouraging us to carrying forward our initial bibliographic survey into this review, and for inviting us to submit this manuscript to the special issue on insect ecosystem services. JAN has been supported by a Colombian COLCIENCIAS PhD scholarship. DAL was supported by the NSF Long-term Ecological Research Program (DEB 1027253) at the Kellogg Biological Station and by Michigan State University AgBioResearch. SGP was supported by the European Community's Seventh Framework Programme under grant agreement no 311781, LIBERATION Project (www.fp7liberation.eu). BAW was supported by the NERC/BBSRC funded ASSIST project (NE/N018125/1). AMCS by a Juan de la Cierva Fellowship (IJCI-2014-19502) funded by the Spanish 'Ministerio de Economía y Competitividad'.

Author contributions: JAN, JH and AMCS designed research; JAN performed research; all authors discussed the results; JAN, JH and AMCS wrote the paper, with all authors; all authors approved the last version of the manuscript.

Appendix A and B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at XXXXX.

References

Allsopp, M. H., de Lange, W. J., & Veldtman, R. (2008). Valuing insect pollination services with cost of replacement. *PLoS ONE*, *3*, e3128.

Aluja, M., Sivinski, J., Van Driesche, R., Anzures-Dadda, A., & Guillén, L. (2014). Pest management through tropical tree conservation. *Biodiversity and Conservation*, *23*, 831-853.

Arnan, X., Cerda, X., Rodrigo, A., & Retana, J. (2013). Response of ant functional composition to fire. *Ecography*, *36*, 1182-1192.

Ayieko, M. A., & Oriaro, V. (2008). Consumption, indigeneous knowledge and cultural values of the lakefly species within the Lake Victoria region. *African Journal of Environmental Science and Technology*, *2*, 282-286.

Badano, E. I., & Vergara, C. H. (2011). Potential negative effects of exotic honey bees on the diversity of native pollinators and yield of highland coffee plantations. *Agricultural and Forest Entomology*, *13*, 365-372.

Baron, G. L., Raine, N. E., & Brown, M. J. F. (2014). Impact of chronic exposure to a pyrethroid pesticide on bumblebees and interactions with a trypanosome parasite. *Journal of Applied Ecology*, *51*, 460-469.

Belovsky, G. E., & Slade, J. B. (2000). Insect herbivory accelerates nutrient cycling and increases plant production. *Proceedings of the National Academy of Sciences USA*, *97*, 14412-14417.

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

Beynon, S. A., Wainwright, W. A., & Christie, M. (2015). The application of an ecosystem services framework to estimate the economic value of dung beetles to the UK cattle industry. *Ecological Entomology*, *40*, 124-135.

Bílá, K., Moretti, M., Dias, A. T. C., de Bello, F., van Oosten, R., & Berg, M. P. (2014). Disentangling community functional components in a litter-macrodetritivore model system reveals the predominance of the mass ratio hypothesis. *Ecology & Evolution*, *4*, 408-416.

Bloor, J. M. G., Jay-Robert, P., Le Morvan, A., & Fleurance, G. (2012). Dung of domestic grazing animals: characteristics and role for grassland function. *Inra Productions Animales*, *25*, 45-55.

Boerema, A., Rebelo, A. J., Bodi, M. B., Esler, K. J., & Meire, P. (2017) Are ecosystem services adequately quantified? *Journal of Applied Ecology*, *54*, 358-370.

Brittain, C., Bommarco, R., Vighi, M., Settele, J., & Potts, S. G. (2010). Organic farming in isolated landscapes does not benefit flower-visiting insects and pollination. *Biological Conservation*, *143*, 1860-1867.

Brosi, B. J., & Briggs, H. M. (2013). Single pollinator species losses reduce floral fidelity and plant reproductive function. *Proceedings of the National Academy of Sciences USA*, *110*, 13044-13048.

Brown, J., Scholtz, C. H., Janeau, J. L., Grellier, S., & Podwojewski, P. (2010). Dung beetles (Coleoptera: Scarabaeidae) can improve soil hydrological properties. *Applied Soil Ecology*, *46*, 9-16.

Caballero-Lopez, B., Bommarco, R., Blanco-Moreno, J. M., Sans, F. X., Pujade-Villar, J., Rundlof, M., & Smith, H. G. (2012). Aphids and their natural enemies are differently affected by habitat features at local and landscape scales. *Biological Control*, *63*, 222-229.

Campbell, A. J., Biesmeijer, J. C., Varma, V., & Wackers, F. L. (2012). Realising multiple ecosystem services based on the response of three beneficial insect groups to floral traits and trait diversity. *Basic and Applied Ecology*, *13*, 363-370.

Choosai, C., Mathieu, J., Hanboonsong, Y., & Jouquet, P. (2009). Termite mounds and dykes are biodiversity refuges in paddy fields in north-eastern Thailand. *Environmental Conservation*, *36*, 71-79.

Corbet, S. A. (1997). Role of pollinators in species preservation, conservation, ecosystem stability and

genetic diversity. *Acta Horticulturae*, *437*, 219-229.

Daily, G.C., Söderqvist, T., Aniyar, S., Arrow, K., Dasgupta, P., Ehrlich, P. R., Folke, C., Jansson, A., Jansson, B.-O., Kautsky, N., Levin, S., Lubchenco, J., Mäler, K.-G., Simpson, D., Starrett, D., Tilman, D., & Walker, B. (2000). The value of nature and the nature of value. *Science*, *289*, 395-396.

Dale, A. G., & Frank, S. D. (2014). The effects of urban warming on herbivore abundance and street tree condition. *PLoS ONE*, *9*, e102996.

de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J. H. C., Bardgett, R. D., Berg, M. P., Cipriotti, P., Feld, C. K., Hering, D., Martins da Silva, P., Potts, S. G., Sandin, L., Sousa, J. P., Storkey, J., Wardle, D. A., & Harrison, P. A. (2010). Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation*, *19*, 2873-2893.

De Groot, R. S., Wilson, M. A., & Boumans, R. M. (2002). A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecological Economics*, *41*, 393-408.

DeSantis, R. D., Moser, W. K., Huggett, R. J., Ruhong, L., Wear, D. N., & Miles, P. D (2013). Modeling the effects of emerald ash borer on forest composition in the Midwest and Northeast United States. *US Forest Service General Technical Report NRS*, *112*, 2-23.

Dzerefos, C. M., & Witkowski, E. T. F. (2014). The potential of entomophagy and the use of the stinkbug, *Encosternum delegorguei* Spinola (Hemipera: Tessaratomidae), in sub-Saharan Africa. *African Entomology*, *22*, 461-472.

Dias A. T. C., Berg, M. P., de Bello, F., Van Oosten, R. A., Bílá, K., & Moretti, M. (2013). An experimental framework to identify community functional components driving ecosystem processes and services delivery. *Journal of Ecology*, *101*, 29-37.

Díaz, S., Purvis, A., Cornelissen, J. H. C., Mace, G. M., Donoghue, M. J., Ewers, R. M., Jordano, P., & Pearse, W. D. (2013). Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution*, *3*, 2958-2975.

Díaz, S., Demissew, S., Carabias, J., Joly, C., Lonsdale, M., Ash, N., Larigauderie, A., Adhikari, J. R., Arico, S., Báldi, A., Bartuska, A., Baste, I. A., Bilgin, A., Brondizio, E., Chan, K. M. A., Figueroa, V. E., Duraiappah, A., Fischer, M., Hill, R., Koetz, T., Leadley, P., Lyver, P., Mace, G. M., Martin-Lopez, B., Okumura, M., Pacheco, D., Pascual, U., Pérez, E.S., Reyers, B., Roth, E., Saito, O., Scholes, R. J., Sharma, N., Tallis, H., Thaman, R., Watson, R., Yahara, T., Hamid, Z. A., Akosim, C., Al-Hafedh, Y., Allahverdiyev, R., Amankwah, E., Asah, S. T., Asfaw, Z., Bartus, G., Brooks, L. A., Caillaux, J., Dalle, G., Darnaedi, D., Driver, A., Erpul, G., Escobar-Eyzaguirre, P., Failler, P., Fouda, A. M. M., Fu, B., Gundimeda, H., Hashimoto, S., Homer, F., Lavorel, S., Lichtenstein, G., Mala, W. A., Mandivenyi, W., Matczak, P., Mbizvo, C., Mehrdadi, M., Metzger, J. P., Mikissa, J. B., Moller, H., Mooney, H. A., Mumby, P., Nagendra, H., Nesshover, C., Oteng-Yeboah, A. A., Pataki, G., Roué, M., Rubis, J., Schultz, M., Smith, P., Sumaila, R., Takeuchi, K., Thomas, S., Verma, M., Yeo-Chang, Y., & Zlatanova, D. (2015). The IPBES conceptual framework — connecting nature and people. *Current Opinion in Environmental Sustainability*, *14*, 1-16.

Eardley, C. (2000). Apoidea (Hymenoptera). *Cimbebasia Memoir*, *9*, 365-370.

Eckberg, J. O., Tenhumberg, B., & Louda, S. M. (2014). Native insect herbivory limits population growth rate of a non-native thistle. *Oecologia*, *175*, 129-138.

Evans, D. M., Pocock, M. J. O., Brooks, J., & Memmott, J. (2011). Seeds in farmland food-webs:

Resource importance, distribution and the impacts of farm management. *Biological Conservation*, *144*, 2941-2950.

Folgarait, P. J. (1998). Ant biodiversity and its relationship to ecosystem functioning: A review. *Biodiversity and Conservation*, *7*, 1221-1244.

Frank, S. D., Shrewsbury, P. M., & Esiekpe, O. (2008). Spatial and temporal variation in natural enemy assemblages on Maryland native plant species. *Environmental Entomology*, *37*, 478-486.

Ganade G., & Brown, V. K (1997). Effects of below-ground insects, mycorrhizal fungi and soil fertility on the establishment of *Vicia* in grassland communities. *Oecologia, 109*, 374-81.

Gardiner, M. A., Tuell, J. K., Isaacs, R., Gibbs, J., Ascher, J. S., & Landis, D. A. (2010). Implications of three biofuel crops for beneficial arthropods in agricultural landscapes. *Bioenergy Research*, *3*, 6-19.

GEO4. (2007). United Nations Environmental Program, Global Environment Outlook: Environment for Development. http://www.unep.org/geo/assessments/global-assessments

Giraldo, C., Escobar, F., Chara, J. D., & Calle, Z. (2011). The adoption of silvopastoral systems promotes the recovery of ecological processes regulated by dung beetles in the Colombian Andes. *Insect Conservation and Diversity*, *4*, 115-122.

Gray, C. L., Slade, E. M., Mann, D. J., & Lewis, O. T. (2014). Do riparian reserves support dung beetle biodiversity and ecosystem services in oil palm-dominated tropical landscapes? *Ecology and Evolution*, *4*, 1049-1060.

Griffiths, H. M., Louzada, J., Bardgett, R. D., Beiroz, W., França, F., Tregidgo, D., & Barlow, J. (2015). Biodiversity and environmental context predict dung beetle-mediated seed dispersal in a tropical forest field experiment. *Ecology, 96*, 1607-1619.

Griffiths, H. M., Louzada, J., Bardgett, R. D., & Barlow, J. (2016a). Assessing the importance of intraspecific variability in dung beetle functional traits. *PLoS ONE*, *11*, e0145598.

Griffiths, H. M., Bardgett, R. D., Louzada, J., & Barlow, J. (2016b). The value of trophic interactions for ecosystem function: dung beetle communities influence seed burial and seedling recruitment in tropical forests. *Proceedings of the Royal Society B*, 283, 20161634.

Haines-Young, R. H., & Potschin, M. (2010). The links between biodiversity, ecosystem services and human well-being. D. Raffaelli, C. Frid (Eds.), Ecosystem ecology: A new synthesis. BES Ecological Reviews Series, Cambridge University Press, Cambridge, pp. 110-139.

Hallouin, T., Bruen, M., Kelly-Quinn, M., Christie, M., Bullock, C., Kelly, F., & Freeley, H. B. (2016). Multi-criteria decisión analysis and ecosystem services: knowledge gaps and challenges for policy and decisión-making. Sanchez-Perez, J. M., & Rizzoli, A. (eds.) 8th International Congress on Environmental Modelling and Software, iEMSs, Toulouse, France.

Hammer, T. J., Fierer, N., Hardwick, B., Simojoki, A., Slade, E., Taponen, J., Viljanen, H., & Roslin, T. (2016). Treating cattle with antibiotics affects greenhouse gas emissions, and microbiota in dung and dung beetles. *Proceedings of the Royal Society B*, *283*, 20160150.

Harrington, R., Anton, C., Dawson, T. P., de Bello, F., Feld, C. K., Haslett, J. R., Kluvánkova-Oravská, T., Kontogianni, A., Lavorel, S., Luck, G. W., Rounsevell, M. D. A., Samways, M. J., Settele, J., Skourtos, M., Spangenberg, J. H., Vandewalle, M., Zobel, M., & Harrison, P. A. (2010). Ecosystem services and biodiversity conservation: concepts and a glossary. *Biodiversity and Conservation*, *19*, 2773-2790.

Harrison, P. A., Berry, P. M., Simpson, G., Haslett, J. R., Blicharska, M., Bucur, M., Dunford, R., Egoh, B., Garcia-Llorente, M. & Geamănă, N. (2014). Linkages between biodiversity

attributes and ecosystem services: A systematic review. *Ecosystem Services, 9*, 191-203.

Hegland, S. J., Dunne, J., Nielsen, A., & Memmott, J. (2010). How to monitor ecological communities cost-efficiently: The example of plant-pollinator networks. *Biological Conservation, 143*, 2092-2101.

Hiltpold, I., Bernklau, E., Bjostad, L. B., Alvarez, N., Miller-Struttmann, N. E., Lundgren, J. G., & Hibbard, B. E. (2013). Nature, evolution and characterisation of rhizospheric chemical exudates affecting root herbivores. *Advances in Insect Physiology*, *45*, 97-157.

Hoehn, P., Tscharntke, T., Tylianakis, J. M., & Steffan-Dewenter, I. (2008). Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society B*, *275*, 2283-2291.

Hoffman, R. L., Liss, W. J., Larson, G. L., Deimling, E. K., & Lomnicky, G. A. (1996). Distribution of nearshore macroinvertebrates in lakes of the Northern Cascade Mountains, Washington, USA. *Archiv Fur Hydrobiologie, 136*, 363-389.

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

Hope, P. R., Bohmann, K., Gilbert, M. T. P., Zepeda-Mendoza, M. L., Razgour, O., & Jones, G. (2014). Second generation sequencing and morphological faecal analysis reveal unexpected foraging behaviour by *Myotis nattereri* (Chiroptera, Vespertilionidae) in Winter. *Frontiers in Zoology*, *11*, 39.

Hortal, J., de Bello, F., Diniz-Filho, J. A. F., Lewinsohn, T. M., Lobo, J. M., & Ladle, R. J. (2015). Seven shortfalls that beset large-scale knowledge of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *46*, 523-549.

Ibanez, S. (2012). Optimizing size thresholds in a plant–pollinator interaction web: Towards a mechanistic understanding of ecological networks. *Oecologia*, *170*, 233-242.

Ibanez, S., Bernard, L., Coq, S., Moretti, M., Lavorel, S., & Gallet, C. (2013). Herbivory differentially alters litter dynamics of two functionally contrasted grasses. *Functional Ecology*, *27*, 1064-1074.

IPBES. (2016). The assessment report of the Intergovernmental Science-Policy Platform on biodiversity and ecosystem services on pollinators, pollination and food production. Potts, S. G., Imperatriz-Fonseca, V. L., & Ngo, H. T. (eds). Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany.

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

Jouquet, P., Traore, S., Choosai, C., Hartmann, C., & Bignell, D. (2011). Influence of termites on ecosystem functioning. Ecosystem services provided by termites. *European Journal of Soil Biology*, *47*, 215-222.

Kampichler, C., & Bruckner, A. (2009). The role of microarthropods in terrestrial decomposition: A meta-analysis of 40 years of litterbag studies. *Biological Reviews, 84*, 375-389.

Kimoto, C., De Bano, S. J., Thorp, R.W., Rao, S., & William, S. P. (2012). Investigating temporal patterns of a native bee community in a remnant North American bunchgrass prairie using blue vane traps. *Journal of Insect Science*, *12*, 1-23.

Klein, A. M., Hendrix, S. D., Clough, Y., Scofield, A., & Kremen, C. (2015). Interacting effects of pollination, water and nutrients on fruit tree performance. *Plant Biology*, *17*, 201-208.

Klein, A., Steffan-Dewenter, I., & Tscharntke, T. (2006). Rain forest promotes trophic interactions and diversity of trap-nesting Hymenoptera in adjacent agroforestry. *Journal of Animal Ecology, 75*, 315-323.

Lähteenmäki, S., Slade, E. M., Hardwick, B., Schiffler, G., Louzada, J., Barlow, J., & Roslin, T. (2015). MESOCLOSURES – increasing realism in mesocosm studies of ecosystem functioning. *Methods in Ecology and Evolution, 6*, 916-924.

Lavorel, S., Storkey, J., Bardgett, R. D., de Bello, F., Berg, M. P., Le Roux, X., Moretti, M., Mulder, C., Pakeman, R. J., Díaz, S., & Harrington, R. (2013). A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *Journal of Vegetation Science, 24,* 942-948.

Leal, L. C., Andersen, A. N., & Leal, I. R. (2014). Anthropogenic disturbance reduces seed-dispersal services for myrmecochorous plants in the Brazilian Caatinga. *Oecologia, 174*, 173-181.

Losey, J. E., & Vaughan, M. (2006). The economic value of ecological services provided by insects. *Bioscience, 56*, 331-323.

Lundin, O., Smith, H. G., Rundlöf, M., & Bommarco, R. (2013). When ecosystem services interact: crop pollination benefits depend on the level of pest control. *Proceedings of the Royal Society B, 280,* 20122243.

Macadam, C. R., & Stockan, J. A. (2015). More than just fish food: Ecosystem services provided by freshwater insects. *Ecological Entomology, 40*, 113-123.

Magurran, A.E. (2004). Measuring biological diversity. Blackwell Publishing, Oxford. 256 p.

Maleque, M. A., Maeto, K., & Ishii, H. T. (2009). Arthropods as bioindicators of sustainable forest management, with a focus on plantation forests. *Applied Entomology and Zoology, 44*, 1-11.

Martin, M. R., Tipping, P. W., Reddy, K. R., Daroub, S. H., & Roberts, K. M. (2010). Interactions of biological and herbicidal management of *Melaleuca quinquenervia* with fire: Consequences for ecosystem services. *Biological Control, 54*, 307-315.

Martins, K. T., Gonzalez, A., & Lechowicz, M. J. (2015). Pollination services are mediated by bee functional diversity and landscape context. *Agriculture, Ecosystems & Environment, 200*, 12-20.

Metcalfe, D. B., Asner, G. P., Martin, R. E., Espejo, J. E. S., Huasco, W. H., Amezquita, F. F. F., Carranza-Jimenez, L., Cabrera, D. F. G., Baca, L. D., Sinca, F., Quispe, L. P. H., Taype, I. A., Mora, L. E., Dávila, A. R., Solórzano, M. M., Vilca, B. L. P., Román, J. M. L., Bustios, P. C. G., Revilla, N. S., Tupayachi, R., Girardin, C. A. J., Doughty, C. E., & Malhi, Y. (2014). Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests. *Ecology Letters, 17*, 324-332.

Midega, C. A. O., Bruce, T. J. A., Pickett, J. A., & Khan, Z. R. (2015). Ecological management of cereal stemborers in African smallholder agricultura through behavioural manipulation. *Ecological Entomology, 40*, 70-81.

Millennium Ecosystem Assessment. (2003). Ecosystems and human well-being; a framework for assessment. Island Press, Washington, D.C., USA. 266 p.

Mitchell, R. J., Liu, Y., O'Brien, J. J., Elliott, K. J., Starr, G., Miniat, C. F., & Hiers, J. K. (2014). Future climate and fire interactions in the southeastern region of the United States. *Forest Ecology and Management, 327*, 316-326.

Mody, K., Spoerndli, C., & Dorn, S. (2011). Within-orchard variability of the ecosystem service

'parasitism': Effects of cultivars, ants and tree location. *Basic and Applied Ecology, 12*, 456-465.

Morandin, L. A., Winston, M. L., Abbott, V. A., & Franklin, M. T. (2007). Can pastureland increase wild bee abundance in agriculturally intense areas? *Basic and Applied Ecology*, *8*, 117-12.

Moretti, M., de Bello, F., Ibanez, S., Fontana, S., Pezzatti, G. B., Dziock, F., Rixen, C. & Lavorel, S. (2013). Linking traits between plants and invertebrate herbivores to track functional effects of land-use changes. *Journal of Vegetation Science*, *24*, 949-962.

Moretti, M., Dias, A. T. C., de Bello, F., Altermatt, F., Chown, S. L., Azcárate, F. M., Bell, J. R., Fournier, B., Hedde, M., Hortal, J., Ibanez, S., Öckinger, E., Sousa, J. P., Ellers, J., & Berg, M. P. (2016). Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Functional Ecology*, *31*, 558-567.

Morley, E. L., Jones, G., & Radford, A. N. (2014). The importance of invertebrates when considering the impacts of anthropogenic noise. *Proceedings of the Royal Society B*, *281*, 20132683.

Muturi, E. J., Spencer, J. L., & Allan, B. F. (2014). Influence of biofuel crops on mosquito production and oviposition site selection. *Global Change Biology Bioenergy*, *6*, 61-66.

Nallakumar, K. (2003). The synchronously flashing aggregative fireflies of Peninsular Malaysia. *Biodiversity*, *4*, 11-16.

Palin, O. F., Eggleton, P., Malhi, Y., Girardin, C. A. J., Rozas-Davila, A., & Parr, C. L. (2011). Termite diversity along an Amazon-Andes elevation gradient, Peru. *Biotropica*, *43*, 100-107.

Philpott, S. M., & Armbrecht, I. (2006). Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. *Ecological Entomology*, *31*, 369-377.

Prather, C. M., Pelini, S. L., Laws, A., Rivest, E., Woltz, M., Bloch, C. P., Del Toro, I., Ho, C.-K., Kominoski, J., Newbold, T. A. S., Parsons, S., & Joern, A. (2013). Invertebrates, ecosystem services and climate change. *Biological Reviews*, *88*, 327-348.

Premalatha, M., Abbasi, T., Abbasi, T., & Abbasi, S. A. (2011). Energy efficient food production to reduce global warming and ecodegradation: The use of edible insects. *Renewable and Sustainable Energy Reviews*, *15*, 4357-4360.

Pringle, R. M., Doak, D. F., Brody, A. K., Jocque, R., & Palmer, T. M. (2010). Spatial pattern enhances ecosystem functioning in an African savanna. *Plos Biology*, *8*, e1000377.

Rader, R., Bartomeus, I., Tylianakis, J. M., & Laliberté, E. (2014). The winners and losers of land use intensification: Pollinator community disassembly is non-random and alters functional diversity. *Diversity and Distributions*, *20*, 908-917.

Reich, R. M., Lundquist, J. E., & Acciavatti, R. E. (2014). Influence of climatic conditions and elevation the spatial distribution and abundance of *Trypodendron* ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) in Alaska. *Forest Science*, *60*, 308-316.

Ricotta, C., & Moretti, M. (2011). CWM and Rao's quadratic diversity: A unified framework for functional ecology. *Oecologia*, *167*, 181-188.

Risch, A. C., Schutz, M., Vandegehuchte, M. L., van der Putten, W. H., Duyts, H., Raschein, U., Gwiazdowicz, D. J., Busse, M. D., Page-Dumroese, D. S., & Zimmerman, S. (2015). Aboveground vertebrate and invertebrate herbivore impacts on net N mineralization in subalpine grasslands. *Ecology*, *96*, 3312-3322.

Rodriguez, L. C., U. Pascual, & H. M. Niemeyer. (2006). Local identification and valuation of ecosystem goods and services from *Opuntia* scrublands of Ayacucho, Peru. *Ecological Economics*, *57*, 30-44.

Roskov, Y., Abucay, L., Orrell, T., Nicolson, D., Bailly, N., Kirk, P., Bourgoin, T., DeWalt, R. E., Decock, W., De Wever, A., & Nieukerken, E. van, eds. (2017). Species 2000 & ITIS Catalogue of Life, 23rd December 2016. Digital resource at: www.catalogueoflife.org/col. Species 2000, Naturalis, Leiden, the Netherlands.

Ryan, U., Yang, R., Gordon, C., & Doube, B. (2011). Effect of dung burial by the dung beetle *Bubas bison* on numbers and viability of *Cryptosporidium* oocysts in cattle dung. *Experimental Parasitology*, *129*, 1-4.

Sands, B., & Wall, R. (2016). Dung beetles reduce livestock gastrointestinal parasite availability on pasture. *Journal of Applied Ecology*, doi:10.1111/1365-2664.12821.

Schmitz, O. J. (2008). Effects of predator hunting mode on grassland ecosystem function. *Science, 319*, 952-954.

Schowalter, T. D. (2013). Insects and sustainability of ecosystem services. Social environmental sustainability series. CRC Press/Taylor & Francis Group, Boca Raton, FL. USA. 362 p.

Schowalter, T. D. (2016). Insect ecology: An ecosystem approach. 4rd Ed. Academic Press. 774 p.

Schrader, S., Wolfarth, F., & Oldenburg, E. (2013). Biological control of soil-borne phytopathogenic Fungi and their mycotoxins by soil fauna a review. *Bulletin of University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca. Agriculture, 70*, 291-298.

Sehnal, F., & Sutherland, T. D. (2008). Silks produced by insect labial glands. *Prion, 2*, 145-153.

Seppelt, R., Dormann, C. F., Eppink, F. V., Lautenbach, S., & Schmidt, S. (2011). A quantitative review of ecosystem service studies: Approaches, shortcomings and the road ahead. *Journal of Applied Ecology*, *48*, 630-636.

Shi, E., & Shofler, D. (2014). Maggot debridement therapy: A systematic review. *British Journal of Community Nursing*, *19*, 14-20.

Shukla, R. K., Singh, H., Rastogi, N., & Agarwal, V. M. (2013). Impact of abundant *Pheidole* ant species on soil nutrients in relation to the food biology of the species. *Applied Soil Ecology, 71*, 15-23.

Slade, E. M., Mann, D. J., Villanueva, J. F., & Lewis, O. T. (2007). Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. *Journal of Animal Ecology, 76*, 1094-1104.

Slade, E. M., Riutta, T., Roslin, T., & Tuomisto, H. L. (2016). The role of dung beetles in reducing greenhouse gas emissions from cattle farming. *Scientific Reports, 6*, 18140.

Slade, E.M., & Roslin, T. (2016). Dung beetle species interactions and multifunctionality are affected by an experimentally warmed climate. *Oikos*, *125*, 1607-1616.

Sommerfeld, J., & Kroeger, A. (2013). Eco-bio-social research on dengue in Asia: A multicountry study on ecosystem and community-based approaches for the control of dengue vectors in urban and peri-urban Asia. *Pathogens and Global Health*, *106*, 428-435.

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

Stanley, D. A., & Stout, J. C. (2013). Quantifying the impacts of bioenergy crops on pollinating insect abundance and diversity: A field-scale evaluation reveals taxon-specific responses. *Journal of Applied Ecology, 50*, 335-344.

Stout, J., & Finn, J. A. (2015). Recognizing the value of insects in providing ecosystem services.

Ecological Entomology, 40, 1-2.

Straub, C. S., & Snyder, W. E. (2006). Species identity dominates the relationship between predator biodiversity and herbivore suppression. *Ecology, 87*, 277-282.

Strid, Y., Schroeder, M., Lindahl, B., Ihrmark, K., & Stenlid, J. (2014). Bark beetles have a decisive impact on fungal communities in Norway spruce stem sections. *Fungal Ecology, 7*, 47-58.

Thies, C., Roschewitz, I., & Tscharntke, T. (2005). The landscape context of cereal aphid–parasitoid interactions. *Proceedings of the Royal Society of London B, 272*, 203-210.

Turner, W. R., Brandon, K., Brooks, T. M., Costanza, R., da Fonseca G. A. B., & Portela, R. (2007). Global conservation of biodiversity and ecosystem services. *BioScience, 57*, 868-873.

Tylianakis, J. M., Rand, T. A., Kahmen, A., Klein, A. M., Buchmann, N., Perner, J., & Tscharntke, T. (2008). Resource heterogeneity moderates the biodiversity-function relationship in real world ecosystems. *PLoS Biology, 6*, e122.

Ulyshen, M. D., & Wagner, T. L. (2013). Quantifying arthropod contributions to wood decay. *Methods in Ecology and Evolution, 4*, 345-352.

Ulyshen, M. D., Wagner, T. L., & Mulrooney, J. E. (2014). Contrasting effects of insect exclusion on wood loss in a temperate forest. *Ecosphere, 5*, 47.

Ulyshen, M. D., Muller, J., & Seibold, S. (2016). Bark coverage and insects influence wood decomposition: Direct and indirect effects. *Applied Soil Ecology, 105*, 25-30.

Vidal, O., López-García, J., & Rendón-Salinas, E. (2014). Trends in deforestation and forest degradation after a decade of monitoring in the Monarch Butterfly Biosphere Reserve in Mexico. *Conservation Biology, 28*, 177-186.

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

Weisser, W. W., & Siemann, E. (eds.) (2004). Insects and ecosystem function. Springer-Verlag, Berlin, Germany. 415 p.

Wood, S. A., Karp, D. S., DeClerck, F., Kremen, C., Naeem, S., & Palm, C. A. (2015). Functional traits in agriculture: Agrobiodiversity and ecosystem services. *Trends in Ecology and Evolution, 30*, 531-539.

Woodcock, B. A., Edwards, M., Redhead, J., Meek, W. R., Nuttall, P., Falk, S., & Pywell, R. F. (2013). Crop flower visitation by honeybees, bumblebees and solitary bees: Behavioural differences and diversity responses to landscape. *Agriculture, Ecosystems & Environment, 171*, 1-8.

Woodger, M. (2011). Insects in the art and mythology of ancient Mesoamerica (Part 1). *Antenna, 35*, 97-101.

Wu, H. T., Lu, X. G., Wu, D. H., & Yin, X. M. (2010). Biogenic structures of two ant species *Formica sanguinea* and *Lasius flavus* altered soil C, N and P distribution in a meadow wetland of the Sanjiang Plain, China. *Applied Soil Ecology, 46*, 321-328.

Zuo, J., Cornelissen, J. H. C., Hefting, M. M., Sass-Klaassen, U., van Logtestijn, R. S. P., van Hal, J., Goudzwaard, L., Liu, J. C., & Berg, M. P. (2016). The (w)hole story: Facilitation of dead wood fauna by bark beetles? *Soil Biology and Biochemistry, 95*, 70-77.

FIGURES AND TABLES

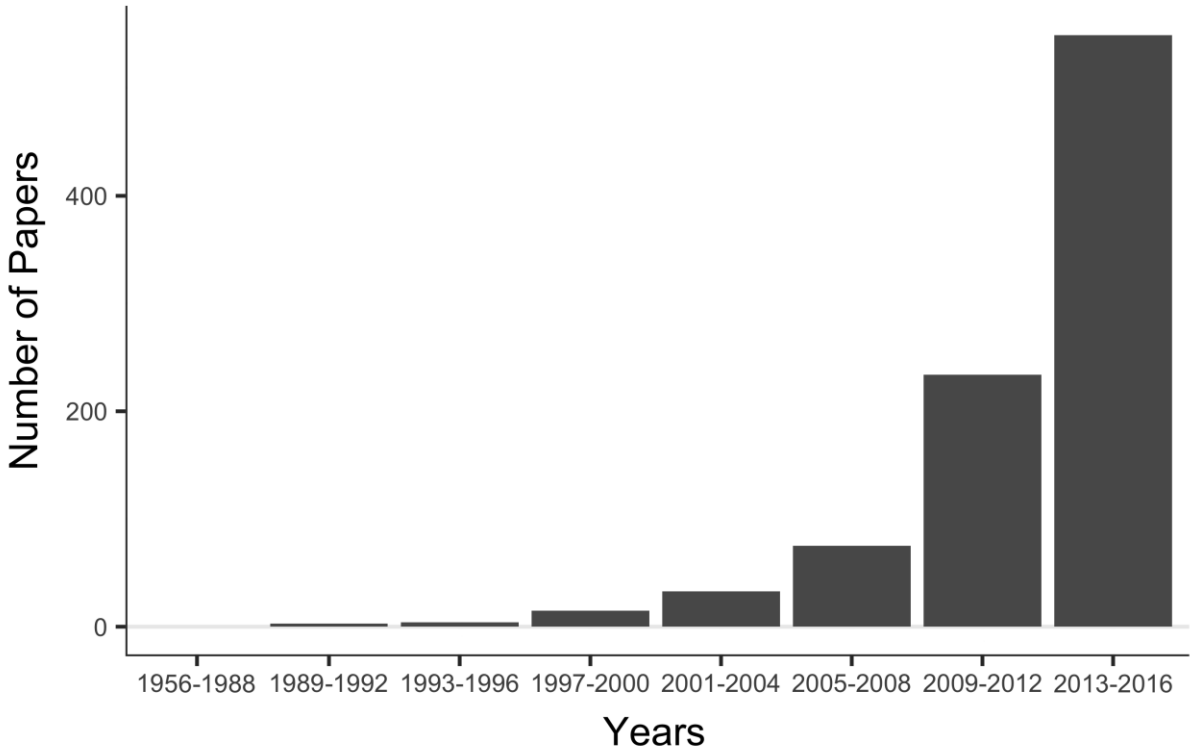

Fig. 1. Temporal trends in the number of published articles dealing with ecosystem services provided by insects across all the literature analyzed from 1956 to 2016 using two search engines (ISI Web of Knowledge and Scopus) and two academic social networks (ResearchGate and ACADEMIA). See methods section for the keyword strings used in this search. Note that no article published before 1989 was retrieved using these search strings.

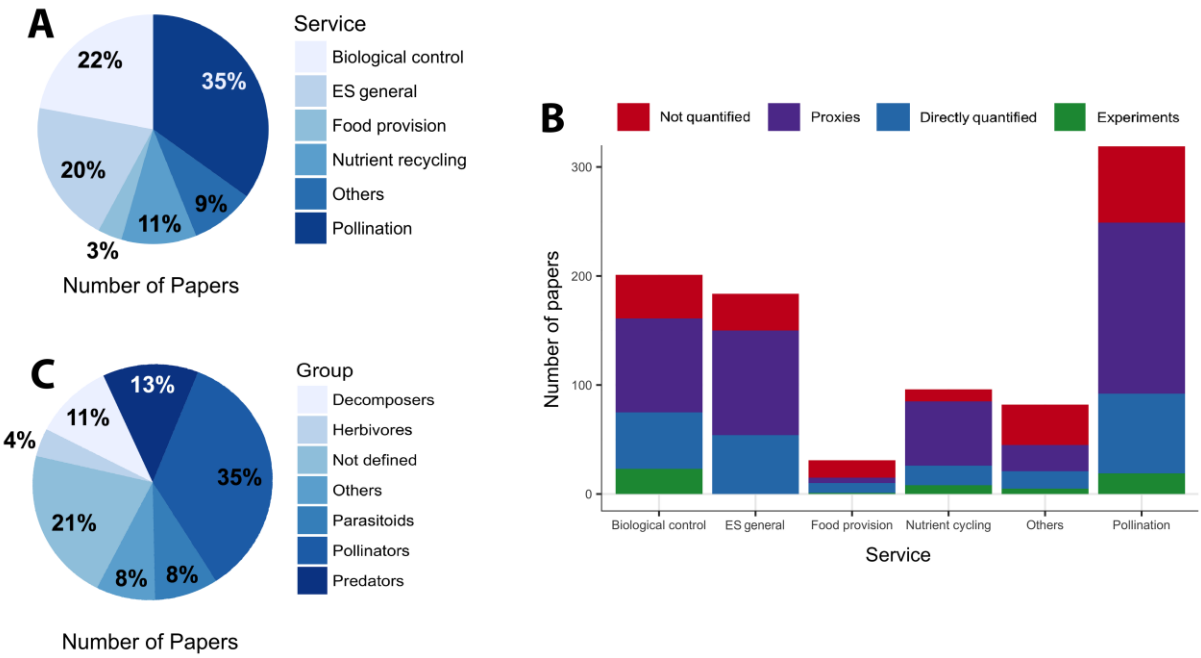

Fig. 2. Percentage and number of articles found in the literature search on ecosystem services provided by insects (1956-2016), examined at three levels: A) main ecosystem service categories; B) cumulative number of articles devoted to study each one of these services in relation with the four main categories of quantification (not quantified, proxies, directly quantified and experiments) and, C) main functional insect groups studied (trophic groups). ES general refers to ecosystem services in general, with no specification of which type of services were studied. See main text for more details.

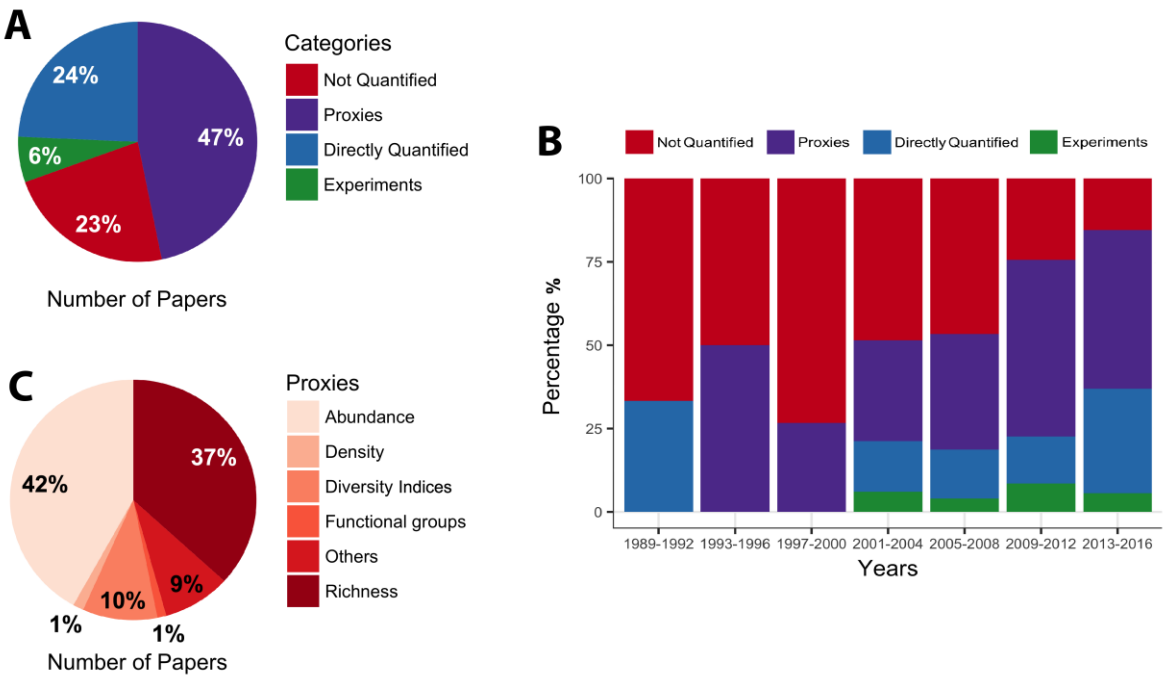

Fig. 3. Percentage of articles retrieved in our literature review on the ecosystem services provided by insects (1956-2016), examined at three levels: A) type of approach used to quantify the ecosystem services provided by insects; B) cumulative percentage of articles over time in relation to the four main categories of quantification (not quantified, proxies, directly quantified and experiments) and, C) main proxies used in the papers that do not quantify directly an ecosystem service.

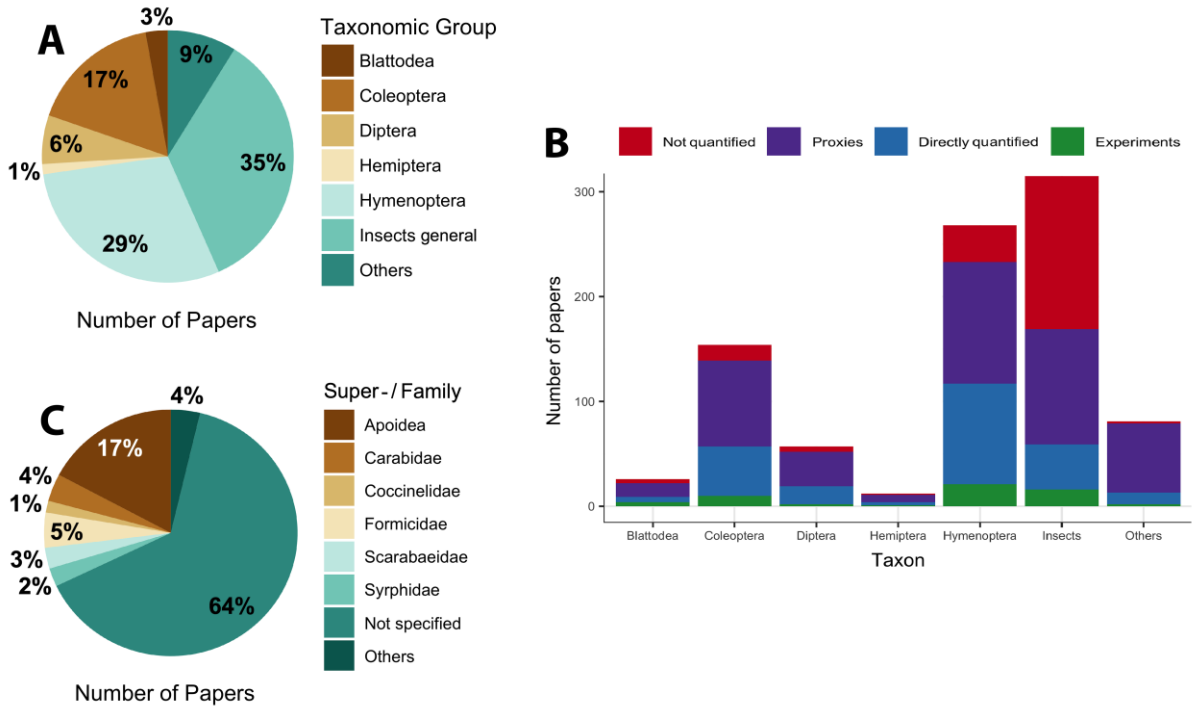

Fig. 4. Percentage and number of articles retrieved in our literature review on ecosystem services provided by insects (1956-2016), examined at three levels: A) higher-level taxonomic groups (i.e. orders); B) cumulative number of articles studying these groups in relation with the four main categories of quantification (not quantified, proxies, directly quantified and experiments); and, C) most studied taxonomic groups at superfamily/family level.

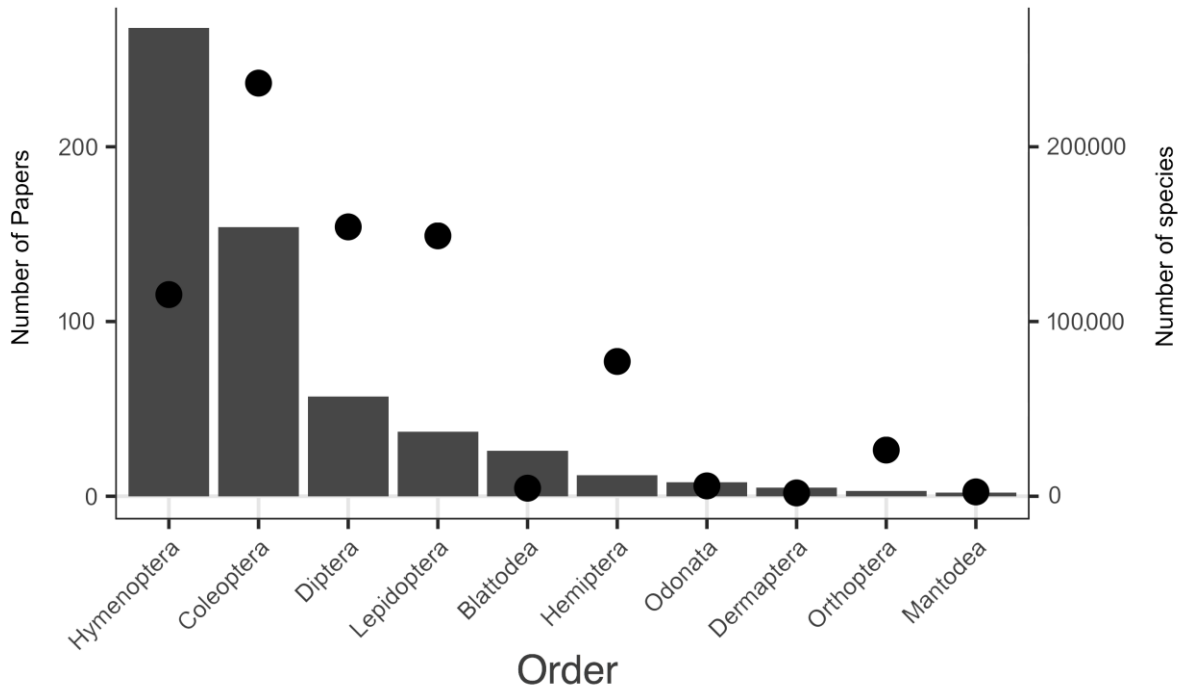

Fig. 5. Comparison of the total number of papers investigating ecosystem services provided by insects (1956-20016) in each major insect order (grey bars) and the number of described species in these major orders (black dots).

Table 1. Categories of quantification of the ecosystem services (ES) provided by insects used to classify the studies retrieved by our literature review.

Quantification category	Description	Example
Not quantified	Assume the relationship between ES and the studied taxonomic or functional group following the criteria of experts. There is no attempt to measure the service, neither directly nor indirectly.	Philpott and Armbrecht (2006) discuss the costs and benefits of promoting ants in agroecosystems from their functional role as predators and the known impacts of intensive agriculture practices on their diversity. No direct or indirect quantification of service delivery is either made or inferred.
Proxies	Use of biodiversity aspects –such as species richness or abudance– as proxies for ES provision, instead of quantifying the relationship between ES and insects.	Frank et al. (2008) assess the potential benefits of promoting certain native plants in croplands, assuming that the richness and abundance of natural enemies inhabiting these plants are a good proxy for their effectiveness for biological control.
Direct quantification	Direct quantification in the field of the ES provided by insects, without following any experimental design.	Thies et al. (2005) quantify the increase in aphid mortality by parasitoids in different landscape conditions, as a direct measure of his latter group on biological control.
Experiments	Quantification of the ES through laboratory or field experiments, with one or more environmental and/or biotic factors being controlled for.	Brittain et al. (2010) measure pollinator abundance and richness, flower visitation rates, pollination of experimental potted plants and seed production to quantify pollination in their analysis of the benefits of organic farming in different landscape contexts.

Table 2. List of ecosystem services provided by insects across our literature review (1956-2016) with selected examples of each one.

Ecosystem services	Selected reference
Provisioning services	
Alternative nutrition source	Dzerefos and Witkowski, 2014
Economic services	Rodriguez et al., 2006
Food chain supplementation	Macadam and Stockan, 2015
Industrial production	Sehnal and Sutherland, 2008
Medicine services	Shi and Shofler, 2014
Regulating services	
Below-ground exchange	Folgarait, 1998
Carbon absorption	Metcalfe et al., 2014
Climate regulation	Hammer et al., 2016
Control and suppression of pathogens	Ryan et al., 2011
Counteract climate change	Premalatha et al., 2011
Fungi control	Schrader et al., 2013
Gastrointestinal parasite control	Sands and Wall, 2016
Greenhouse gas emissions	Slade et al., 2016
Habitat genetic diversity	Corbet, 1997
Network services	Hope et al., 2014
Pest control	Aluja et al., 2014
Pollination	Baron et al., 2014
Population regulation	Midega et al., 2015
Soil fertility regulation	Jouquet et al., 2011
Soil nutrient regulation	Shukla et al., 2013
Soil nutrients spatial variability	Wu et al., 2010
Soil erosion prevention	Ganade and Brown, 1997
Supporting services	
Biodiversity protection	Choosai et al., 2009
Decomposition	Mitchel et al., 2014
Dung removal	Gray et al., 2014
Hydrological soil properties	Brown et al., 2010
Mineralization	Palin et al., 2011
Nutrient accumulation	Pringle et al., 2010
Nutrient flow	Bloor et al., 2012
Recycling of matter	Ulyshen et al., 2014
Seed dispersal	Leal et al., 2014
Soil removal	Giraldo et al., 2011
Soil structure	Jouquet et al., 2014
Soil water infiltration	Evans et al., 2011
Cultural services	
Bioindicators tool	Maleque et al., 2009
Conservation tool	Stout and Finn, 2015
Cultural heritage	Vidal et al., 2014
Education	Macadam and Stockan, 2015
Recreation services	Woodger, 2011
Religion and spiritual values	Ayieko and Oriaro, 2008
Tourism services	Nallakumar, 2003
Urban quality life	Morley et al., 2014