Research trends in ecosystem services provided by insects

Article *in* Basic and Applied Ecology · September 2017

DOI: 10.1016/j.baae.2017.09.006

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Authors: Jorge Ari Noriega, Joaquín Hortal, Francisco M. Azcárate, Matty P. Berg, Núria Bonada, Maria J.I. Briones, Israel Del Toro, Dave Goulson, Sébastien Ibanez, Douglas A. Landis, Marco Moretti, Simon G. Potts, Eleanor M. Slade, Jane C. Stout, Michael D. Ulyshen, Felix L. Wackers, Ben A. Woodcock, Ana M.C. Santos

PII: S1439-1791(17)30084-1
DOI: http://dx.doi.org/10.1016/j.baae.2017.09.006
Reference: BAAE 51059

To appear in:

Received date: 3-3-2017
Revised date: 29-7-2017
Accepted date: 4-9-2017

Please cite this article as: {http://dx.doi.org/

REVIEW

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

Jorge Ari Noriega[a, *], Joaquín Hortal[a, b], Francisco M. Azcárate[c], Matty P. Berg[d, e], Núria Bonada[f], Maria J. I. Briones[g], Israel Del Toro[h], Dave Goulson[i], Sébastien Ibanez[j], Douglas A. Landis[k], Marco Moretti[l], Simon G. Potts[m], Eleanor M. Slade[n, o], Jane C. Stout[p], Michael D. Ulyshen[q], Felix L. Wackers[r], Ben A. Woodcock[s] & Ana M.C. Santos[t, u]

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

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

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

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

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

[f] *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.*

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

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

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

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

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

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

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

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

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

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

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

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

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

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

[u] *Centre for Ecology, Evolution and Environmental Changes (cE3c)/Azorean Biodiversity Group, University of the Azores, Angra do Heroísmo and Ponta Delgada, Azores, Portugal.*

*Corresponding author. Jorge A. Noriega

E-mail address: *jnorieg@hotmail.com*

Running title: Insect ecosystem services research

Word count: 5,683 words (main text), 300 words (abstract)

129 references

5 Figures

2 Tables

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 examined publication trends in the research on ES provided by insects, ascertaining which ES and taxa have been more intensively investigated, and which methodologies have been used, with particular emphasis on experimental approaches. We first 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 each 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, 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 density, species richness, diversity indices, or the number of functional groups. Pollinators, predators, parasitoids, herbivores, and decomposers are the most commonly 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 show 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, community ecology, and biodiversity conservation under current global changes.

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, Díaz et al. 2013). Ecosystem services 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, Díaz et al. 2015). These services are critical for human welfare (Daily et al. 2000), since they include, amongst others, the provision of food, fiber, 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, 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, Spangenberg et al. 2014), and this concept is often confounded with related terms such as "ecosystem functions" and "ecosystem goods" (Millennium Ecosystem Assessment 2003, 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, or benefit, for humans (Spangenberg et al. 2014). While ecosystem goods correspond to the products of ecosystem services that can be traded by humans through either perception, expectations, experience, utilitarian use, or consumption (Díaz et al. 2015).

Insects (Arthropoda: Insecta) are the largest and most diverse group within the animal kingdom. They are key components in the provision, regulation, and dynamics of many ecosystem services (referred to as insect ES herein; Weisser & Siemann 2004, 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 magnitude and directionality of ecosystem processes; and (iv) cultural services, that do not provide material benefits but have an educational, spiritual and/or aesthetic value (GEO4 2007, Prather et al. 2013). Previous efforts to assign monetary values to several ES provided by insects usually underestimated the value of these animals to our economies and quality of life (Beynon et al. 2015). Nevertheless, 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 than other organisms such as plants (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, Boerema et al. 2017), their main focus is on a subset of either functional or iconic 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 relationships are often simply assumed (e.g. Philpott & Armbrecht 2006, Allsopp et al. 2008). Thus, assessment of insect ES includes a wide variety of approaches such as field observations, expert opinions or estimates, assumptions or inferences made from proxies of several aspects of biodiversity (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 relevance 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, 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 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 ES 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) Which methodological approaches have been used to study these ES? (iii) Which functional and taxonomic groups of insects have been investigated in this context? (iv) Which ecosystems have been monitored experimentally for examining insect ES?

Materials and methods

We performed a literature search using different online platforms to identify articles dealing with insect ES published during the last six decades (1956–2016, time interval preselected by default by many 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 separately and thereafter discarded those references that were not clearly related to any insect 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 that provided ES estimates.

The following information was collected from each selected publication: author(s); year of publication; journal; method used for quantifying each ES according to 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 we considered when analyzing the data and interpreting the results. First, the search may miss some relevant papers, simply because either the title, the abstract or the keywords did not contain the focal keywords. 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. Second, the approach we used might have overlooked publications that refer to a particular ES 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 (see Prather et al. 2013). Third, the term "ecosystem service" is fairly recent, and its use was not common prior to the 1990s, so some older publications addressing some kind of 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 limitations, 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 ES 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 other services, some of them not previously detected by 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), and 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 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 pollination, biological control, 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 quantify the actual level or extent of the ES studied: categories not quantified and proxies together comprise 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). Interestingly, most of them perform 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 lesser extent, ecological diversity indices such as Simpson or Shannon (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, and some functional traits (e.g. body size/biomass, behavioral traits, colony density, etc.) and associated measures of functional diversity, community mean trait value, species composition, beta diversity, niche overlap or endemicity, amongst others. Very few studies corroborated the existence of a direct link between the investigated proxy and the functional aspect that it 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, 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 most studied services 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). A great amount of experimental evidence on insect ES comes from the 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 include a large number 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 much lesser extent, forests, savannas, wetlands, or lakes have also received some 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 change scenarios 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 efforts, 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, and 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 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 merely 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, 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 each specific ES (e.g. Slade et al. 2007, de Bello et al. 2010, Ibanez et al. 2013). A better understanding of the links between insect diversity, insect behavior, and interaction with organisms from different trophic levels in providing ES is also needed (Schmitz 2008, 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 hamper the assessment of global change effects, preventing us from identifying and/or quantifying the impacts of environmental changes on ES, and therefore making it difficult to develop adequate actions to mitigate them.

From proxies to experiments

Further analyses are required to evaluate and 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, 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 quality of life (see Nallakumar 2003, Choosai et al. 2009). Quantifying the value of a number of ES, such as the spatial redistribution and accumulation of soil nutrients, seed dispersal and germination, or soil aeration, presents important methodological difficulties (see Folgarait 1998, Pringle et al. 2010, Wu et al. 2010). One big challenge to ES field experimentation is excluding a particular taxon (i.e. the insect-exclusion treatment) to measure the effects of individual taxa on the ES of interest, without having unintentional effects on other organisms. For example, methods to experimentally exclude insects can sometimes alter microbial activity due to changes in microclimate. 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, Slade & Roslin 2016).

The most commonly used proxies for insect ES are species richness and species abundance. However, these two metrics could only 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, Klein et al. 2015). Studies addressing the importance of insects for wood decomposition, for example, have shown termites to consume much 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 to improve 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, Wood et al. 2015).

Metrics related to functional diversity, functional identity or attributes (i.e. traits) that affect an ES (sensu Violle et al. 2007, Díaz et al. 2013) may be more informative than those related to total abundance or taxonomic richness and permit to investigate the interactions among organisms from different trophic levels as one of the potentially most important mechanisms behind key ES (e.g. Lavorel et al. 2013, Gagic et al. 2015). 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' functions leading to non-additive effects of the process in focus (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 can be 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, 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 to the studied service

can provide a mechanistic understanding of the role of insects in ES provision, and will ultimately have the greatest potential to infer ES delivery (e.g. Woodcock et al. 2013, Griffiths et al. 2016b). However, often the traits used for ES analyses are chosen based on either readily-available trait data, or on traits used in previous studies, rather than on functional hypotheses linking traits, ecosystem functions, and their associated services. This can result in a consistent bias towards using small subsets of traits, some of which may have little value for particular functions or services. Even in those few studies where the traits were genuinely related to the ES studied, the data was typically limited to a handful of species, and their measurement was 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. (2017)– are key for further advances on insect ES research.

Functional and taxonomic biases

The biases in insect ES research are both functional and taxonomic: Not only are some services studied more intensively than others, some groups are also more often investigated than others. 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 most studied using experimental approaches, together with nutrient cycling. A good example of why biases are often functional rather than taxonomic can be found by looking at the high

proportion of papers that have focused on 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, 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 organisms of different trophic levels, the resulting ES and 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, 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, Stanley & Stout 2013). However, very few studies have analyzed the possible range of interactions (from synergies to antagonisms or trade-offs) between two or more ES within a specific network or for the whole ecosystem (e.g. multitrophic relationships; see Perovic et al. 2017). 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). Current knowledge indicates that these regulatory relationships usually affect the 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, prevents us from resolving whether these groups are underrepresented in ES research, or if they actually provide few ES of minor importance, or whether the lack of general knowledge on their ecology and systematics is the main cause of their misrepresentation. However, the key ecological roles played by some of them in freshwater ecosystems (e.g. litter decomposition) suggest 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 only 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 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, Eckberg et al. 2014). Herbivores also influence nutrient cycles and can contribute to soil fertility and enhance primary production (Belovsky & Slade 2000). Similarly, 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, 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, Dale & Frank 2014); (ii) damage to wood plantations by xylophagous insects (e.g. DeSantis et al. 2013, Reich et al. 2014); and (iii) harmful effects on human health by hematophagous insects (e.g. Sommerfeld & Kroeger 2013, 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 ES provided by insects is relatively scarce and biased. This occurs despite their numerical abundance, the ecological functions they perform for the maintenance of ecosystem functioning, and their links to human well-being. Part of the reason behind this poor knowledge on insect ES is partly due to the traditional view of considering insects to be mainly providers of 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 exceed those harmful effects and disservices they cause, even when considering some specific areas such as crop production. Indeed, the value of many 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 future research on them – through increasing financial support and societal engagement.

It is therefore essential to achieve a better understanding of the role played by insects in ES delivery. This requires combining the efforts of ES researchers (including ecologists, entomologists, economists, and social scientists) to identify direct links between insect species and the ES they provide, ideally through field observations and experiments. A good map of

our current knowledge could help define further needs in insect ES research. Our work provides an insightful 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 have characterized 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 different components of biodiversity, the study of functions and the traits associated with them, and the quantification of the delivery of services can help to increase the research impact of insect ES 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 design and implement a combination of laboratory and field experiments, as well as the adoption of more mechanistic trait-based approaches that

allow to disentangle both the direct and indirect contribution of insect biodiversity mediated by traits and trait-matching between organisms of different trophic levels. While the use of controlled microcosms can provide accurate information, manipulative field experiments are more realistic since they take into account a whole range of the interacting environmental factors. Obtaining accurate and comprehensive information on the ES provided by insects therefore requires joint efforts among ES researchers in implementing such an ambitious research program that combines both empirical and experimental evidence.

Acknowledgements

We want to thank Teja Tscharntke and Timothy D. Schowalter for encouraging us to carry 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). EMS was supported by NERC HMTF grant (NE/K016261/1). 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.

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FIGURES AND TABLES

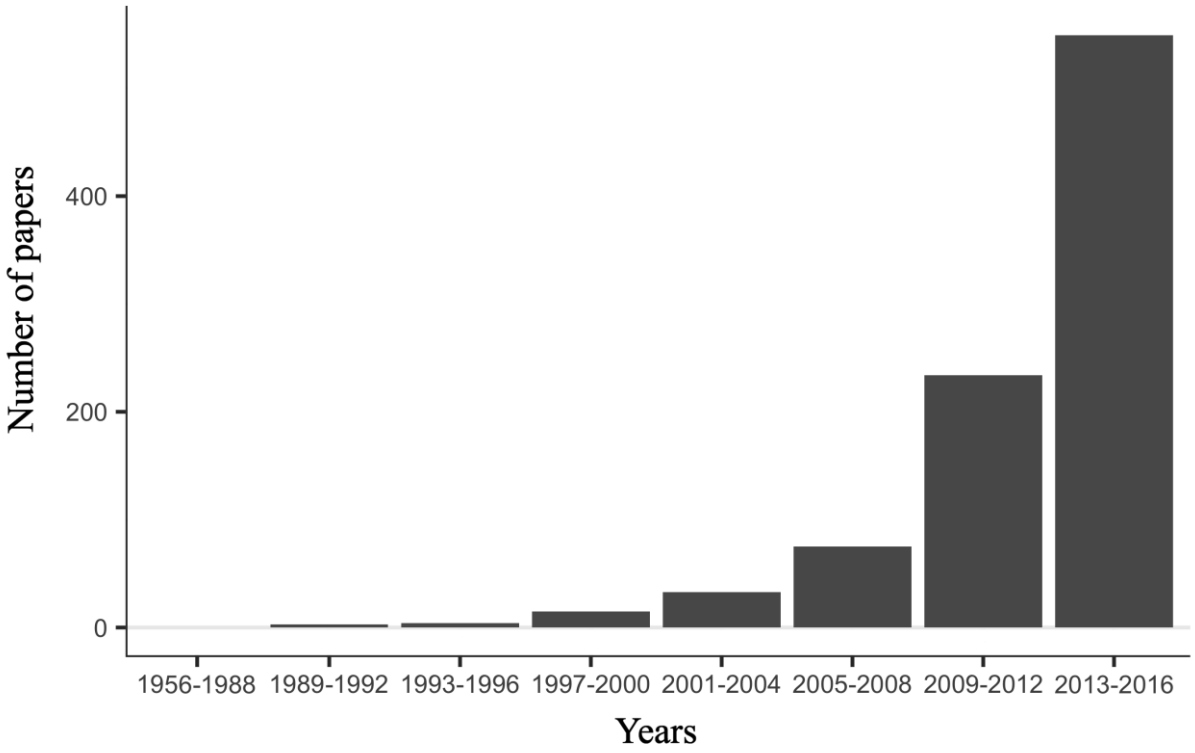

Fig. 1. Temporal trends in the number of published articles dealing with ecosystem services provided by insects across all the literature analyzed from 1956 to 2016 using two search engines (ISI Web of Knowledge and Scopus) and two academic social networks (ResearchGate and ACADEMIA). See methods section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

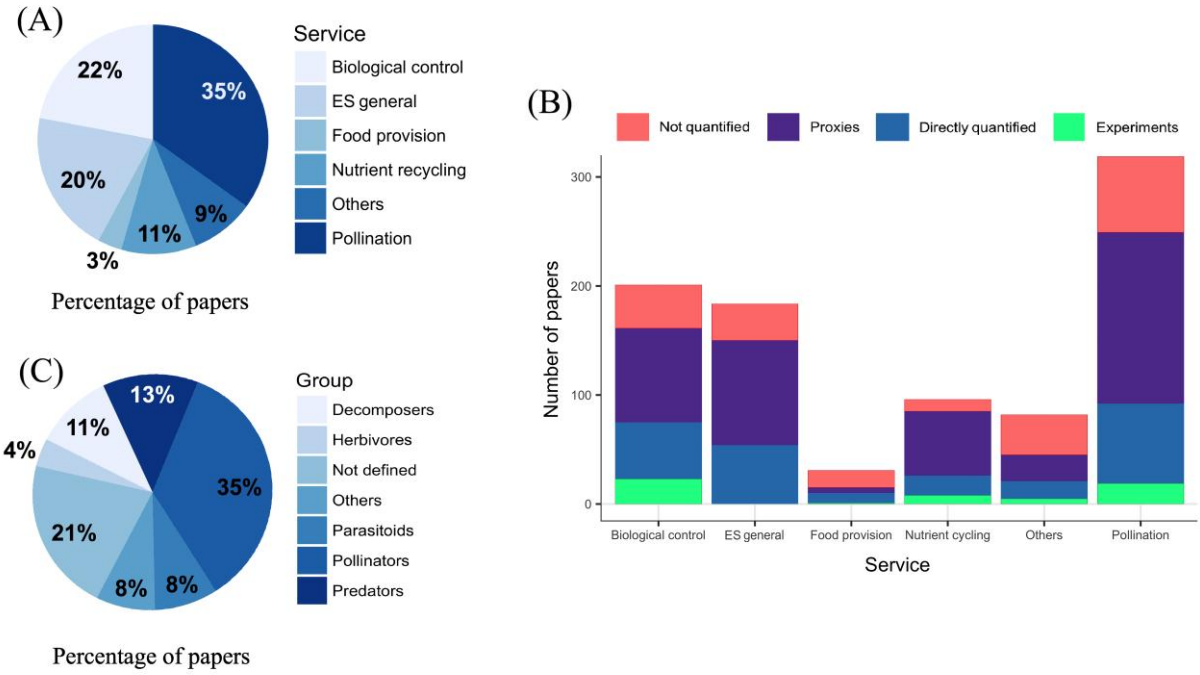

Fig. 2. Percentages and numbers of articles found in the literature search on ecosystem services provided by insects (1956-2016), examined at three levels: (A) main ecosystem service categories; (B) cumulative number of articles devoted to studying each of these services in relation to the the four main 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 investigated. See main text for more details.

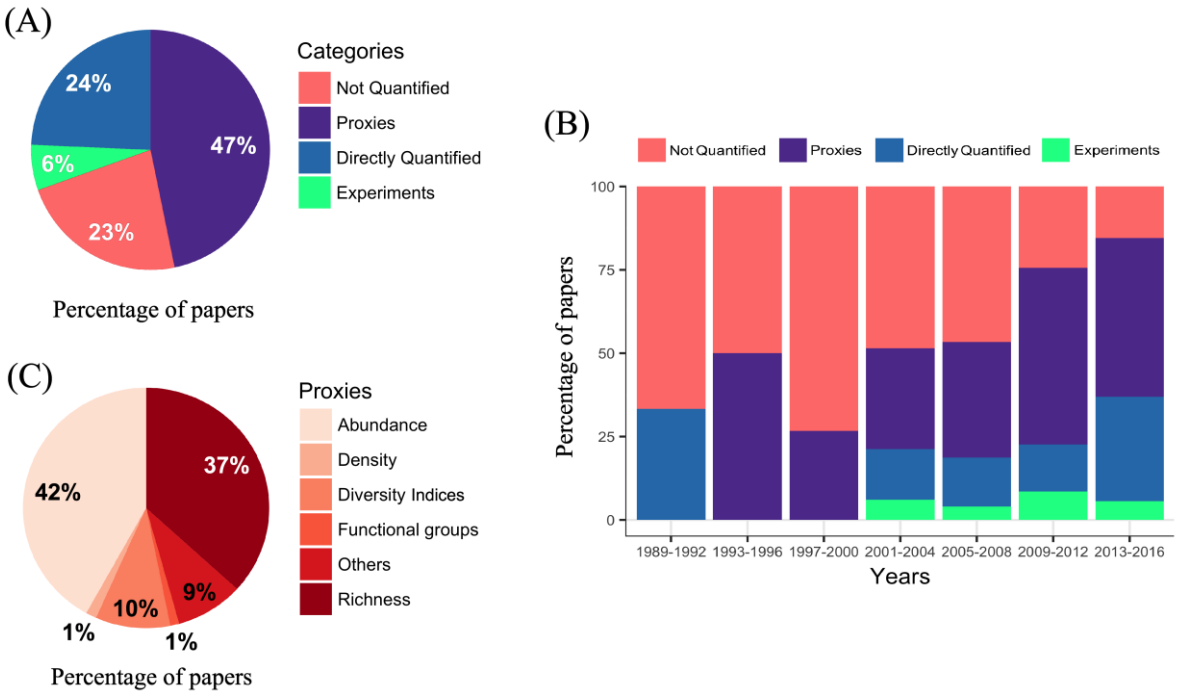

Fig. 3. Percentages of articles retrieved in our literature review on the ecosystem services provided by insects (1956-2016), examined at three levels: (A) type of approach used to quantify the ecosystem services provided by insects; (B) cumulative percentage of articles over time in relation to the 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.

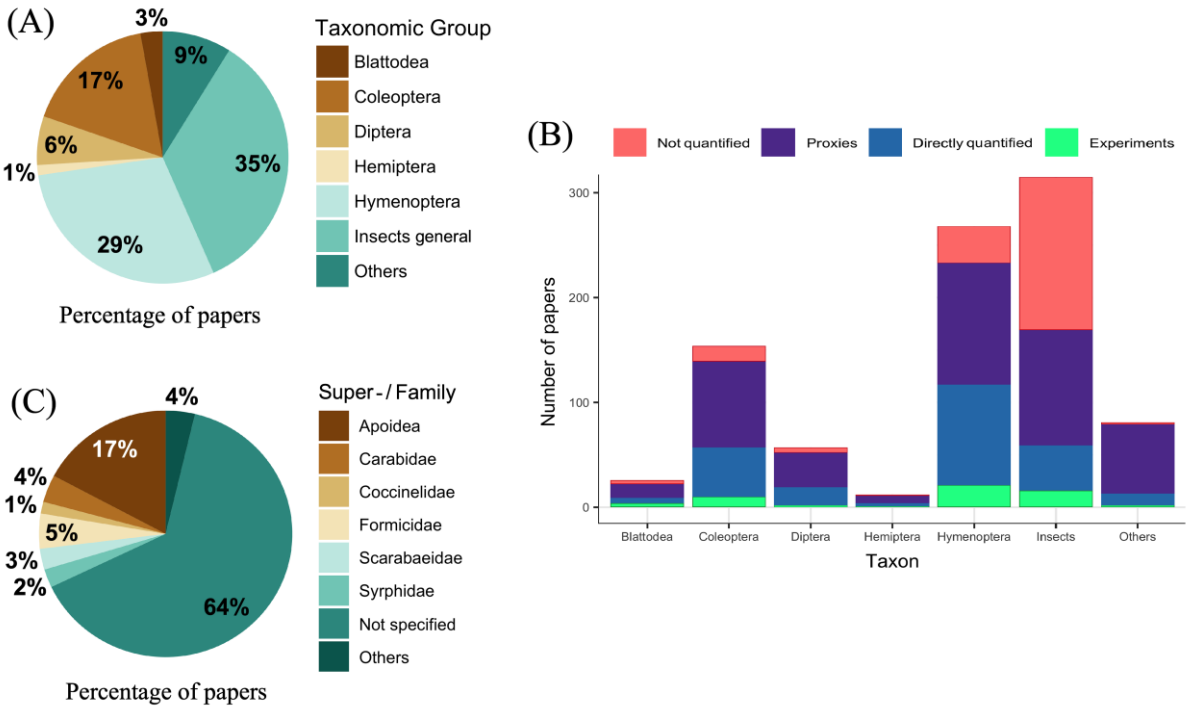

Fig. 4. Percentages and numbers of articles retrieved in our literature review on ecosystem services provided by insects (1956-2016), examined at three levels: (A) higher-level taxonomic groups (i.e. orders); (B) cumulative number of articles studying these groups in relation to the the four main categories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

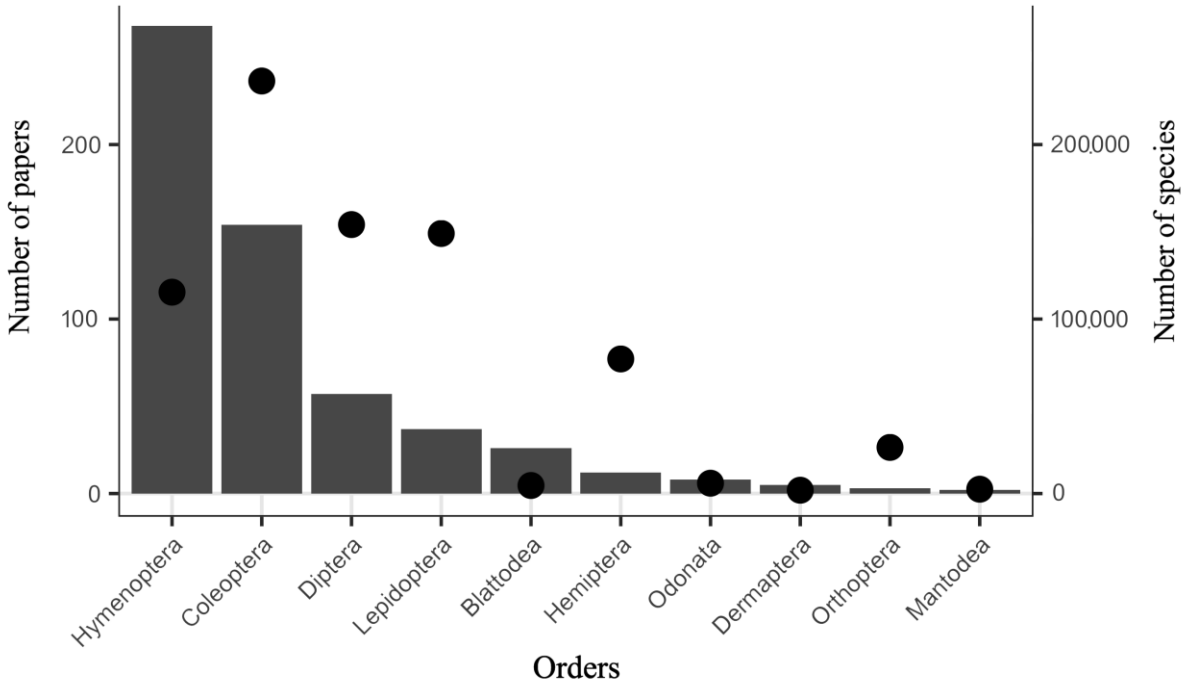

Fig. 5. Comparison of the total number of papers on ecosystem services provided by insects (1956-2016) in each major insect order (grey bars) and the number of described species in these major orders (black dots).

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.	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 the 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
Fungus 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