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Pollinator Diversity: Distribution, Ecological Function, and Conservation

Jeff Ollerton

Faculty of Arts, Science and Technology, University of Northampton, Northampton NN2 6JD, United Kingdom; email: jeff.ollerton@northampton.ac.uk

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Abstract

By facilitating plant reproduction, pollinators perform a crucial ecological function that supports the majority of the world's plant diversity, and associated organisms, and a significant fraction of global agriculture. Thus, pollinators are simultaneously vital to supporting both natural ecosystems and human food security, which is a unique position for such a diverse group of organisms. The past two decades have seen unprecedented interest in pollinators and pollination ecology, stimulated in part by concerns about the decline of pollinator abundance and diversity in some parts of the world. This review synthesizes what is currently understood about the taxonomic diversity of organisms that are known to act as pollinators; their distribution in both deep time and present space; the importance of their diversity for ecological function (including agro-ecology); changes to diversity and abundance over more recent timescales, including introduction of non-native species; and a discussion of arguments for conserving their diversity.

1. INTRODUCTION

Pollinators have a high profile in both the scientific literature and the public consciousness. This is driven in part by well-meaning media campaigns aimed at "Saving the Bees" and by a recognition that plant–pollinator relationships are an inherently fascinating class of interactions: They are both ecologically and agriculturally important and are at the core of a great deal of evolutionary innovation. Indeed, they are arguably one of the most important classes of ecological interactions in terrestrial ecosystems, responsible for most plant reproduction by seeds and driving significant levels of evolutionary diversification in both those plants and the pollinators that service them. By their nature plants are static organisms that cannot move to find mates. Instead they must either self-pollinate (a strategy that has long-term risks of inbreeding and loss of genetic diversity) or rely on external vectors to carry their male gametes (contained within pollen) from one flower to another. These vectors are wind, water, and animals (both vertebrates and invertebrates). This review focuses on animal pollination. However, note that mixed pollination systems involving wind plus animals, termed ambophily, are known for some plants. This is almost certainly an under-recorded strategy that deserves further attention (e.g., Rios et al. 2014).

Most flowering plants are pollinated by animals. A recent global estimate suggests that 87.5% of angiosperms utilize invertebrates or vertebrates in this way (Ollerton et al. 2011), and a significant fraction of gymnosperms are likewise biotically pollinated (e.g., Kato et al. 1995). However, it is clear that considerable media bias, and journalistic misrepresentation, has been given to the diversity and relative importance of pollinators, with honeybees receiving attention that is disproportionate to both their importance and their need for conservation (Ollerton et al. 2012, Smith & Saunders 2016). The main aims of this review, therefore, are to highlight how taxonomically diverse pollinators actually are, how this diversity has evolved and become distributed globally, and why conserving this diversity is so important.

2. POLLINATOR DIVERSITY OVER TIME

The first appearance of the flowering plants (angiosperms or Magnoliophyta), possibly as early as the mid-Jurassic approximately 170 million years ago (Gang et al. 2016), set the scene for one of the iconic stories of evolutionary biology, in which supposedly primitive wind pollination by gymnosperms was replaced by evermore complex animal pollination in flowering plants, leading to the diversification and dominance of angiosperms. It is a story that has been repeated in many textbooks and documentaries even up to recent times. The problem is that it is incorrect: The earliest angiosperms evolved in a biotically complex milieu that included many insect-pollinated gymnosperms, and insect pollination is the most likely ancestral state for flowering plants. The evidence for biotic pollination of early gymnosperms has been discussed since at least the 1970s (Crepet 1979), but only in recent times has the true diversity and importance of insect pollination in pre-angiosperm floras become apparent. Fossil insects from China, Spain, and Russia have revealed ancient groups of insects that appear, on the basis of interpretations of their mouthparts and associated pollen grains, to have been pollinators; examples include mid-Mesozoic thrips (Thysanoptera), flies (Diptera), lacewings (Neuroptera), scorpion flies (Mecoptera), and beetles (Coleoptera) (Labandeira 2010; Labandeira et al. 2007, 2016; Peñalver et al. 2012, 2015; Peris et al. 2017; Ren 1998; Ren et al. 2009). Notably, lacewings and scorpion flies are no longer significant pollinators (in terms of diversity) compared with groups such as the bees (Hymenoptera) and butterflies and moths (Lepidoptera) that have replaced them over time (see Section 2.1).

The eventual radiation and dominance of the flowering plants from the mid-Cretaceous (approximately 100 million years ago) onward seem to correlate with the diversification of some

modern groups of pollinators. For example, Cardinal & Danforth (2013) estimated that the main extant clades of bees also originated during the mid- to late Cretaceous. This estimation was made on the basis of a dated molecular phylogeny of the major groups of bees calibrated by fossils such as those in early Cretaceous amber (Poinar & Danforth 2006).

Such amber inclusions and molecular phylogenetics are also providing important insights into the more recent deep history of plant–pollinator interactions, for example, by showing that relationships between orchids and their bee pollinators are at least 15 million years old and the orchids themselves probably originated approximately 80 million years ago (Ramírez et al. 2007). Likewise, the recent description of an asclepiad (Apocynaceae: Asclepiadoideae) flower from Dominican amber together with its termite pollinator, is both a paleontological first and a tantalizing glimpse into a vanished world of unpredicted interactions (Poinar 2017). The fossil record no doubt will yield many further exciting discoveries in the coming years.

2.1. The Current Diversity of Pollinators

At the present time we do not have an accurate estimate of the diversity of multicellular life on Earth to even an order of magnitude, with published figures ranging from 2 to 100 million, though lower estimates are probably more realistic (Costello et al. 2013). The majority of these species are insects, which are of course the main groups of pollinators; therefore, trying to estimate the current diversity of pollinators is clearly problematic and subject to many caveats. However, we can provide more accurate estimates for some groups (particularly birds and mammals and probably bees), and so working toward a full account of the overall phylogenetic diversity, and the number of species involved, becomes incrementally possible (Ollerton 1999, Regan et al. 2015, Wardhaugh 2015). **Table 1** brings together recent estimates of described pollinator diversity for some well-studied groups on the basis of the cited reviews plus recent studies such as that by van Tussenbroek et al. (2016). For the arthropods, Wardhaugh (2015) is the most up-to-date review of flower visitors (rather than just pollinators per se), but his estimates include taxa such as predatory crab spiders and mantids that are almost certainly not regular pollinating species. I have therefore excluded them from **Table 1**.

The most diverse group of pollinators, by a large margin, is the Lepidoptera (and in particular the moths), with more than 140,000 species that are expected to visit flowers, based on 90% of species with functional mouthparts as adults, following Wardhaugh (2015), though some butterflies feed on plant and animal exudates rather than flowers. This is more than twice as many as the next most diverse groups, the Coleoptera and the Hymenoptera. Diptera is the least diverse of these four main orders of pollinating insects, though that may change in the future as more work is done and the true diversity of flies as pollinators is revealed (Larson et al. 2001; Ollerton et al. 2009, 2017; Orford et al. 2015). The remaining groups are all rather low in diversity in overall terms, although they are no doubt ecologically important in certain regions and for particular plants. These figures will certainly change in the future because most insects are not yet described. For example, Kristensen et al. (2007) suggest there may be approximately half a million extant species of Lepidoptera, most of them moths and most with coiled mouthparts (clade Glossata), though adult feeding has been lost in some groups. This begs the question of why moth pollination is not more prevalent in the literature, and the probable reason is because few people study it (Hahn & Brühl 2016). When moth communities are studied in detail, it is clear that a significant proportion of the species can act as pollinators (Devoto et al. 2011, Haber & Frankie 1989).

The vertebrate pollinating groups also have relatively low diversity. Birds, with more than 1,000 species, are the most diverse. Nocturnal rodents are likely more important than we realize, especially in tropical forests, but have not been as well studied as birds or even bats. The same is

Table 1 The estimated described species richness of the major groups of pollinators

Taxon	Estimated number of pollinating species in the major groups	Diversity of significant subgroups	Source(s)
Lepidoptera (butterflies and moths)	141,600		Wardhaugh (2015)
Moths (Heterocera)		123,100	
Butterflies (Rhopalocera)		18,500	
Coleoptera (beetles)	77,300		Wardhaugh (2015)
Flower chafers (Cetoniinae)		4,000	Sakai & Nagai (1998)
Hymenoptera (bees, wasps, ants)	70,000		Wardhaugh (2015)
Bees (Anthophila)		17,000	Danforth et al. (2006), Michener (2007)
Spider wasps (Pompilidae)		5,000	Pitts et al. (2005)
Social wasps (Vespoidea)		5,000	
Diptera (flies)	55,000		Wardhaugh (2015)
Hoverflies (Syrphidae)		6,000	
Bee flies (Bombyliidae)		4,500	
Thysanoptera (thrips)	1,500		Wardhaugh (2015)
Aves (birds)	1,089		Regan et al. (2015)
Hummingbirds (Trochilidae)		365	
Honeyeaters (Meliphagidae)		177	
Sunbirds (Nectariniidae)		124	
White eyes (Zosteropidae)		100	
Parrots (Psittacidae)		93	
Hemiptera (bugs)	1,000		Wardhaugh (2015)
Collembola (springtails)	400		Wardhaugh (2015)
Blattodea (termites and cockroaches)	360		Wardhaugh (2015)
Mammalia (mammals)	344		Regan et al. (2015)
Bats (Chiroptera)		236	
Nonflying mammals (various)		108	
Neuroptera (lacewings)	293		Wardhaugh (2015)
Trichoptera (caddis flies)	144		Wardhaugh (2015)
Orthoptera (crickets)	100		Wardhaugh (2015); possibly an overestimate, as only one species has been confirmed as pollinator (Micheneau et al. 2010)
Mecoptera (scorpion flies)	76		Wardhaugh (2015)
Psocoptera (bark flies)	57		Wardhaugh (2015)
Plecoptera (stone flies)	37		Wardhaugh (2015)
Lacertilia (lizards)	37		Olesen & Valido (2003)
Dermaptera (earwigs)	20		Wardhaugh (2015)
Crustacea (mainly Isopoda)	11		Ollerton (1999), van Tussenbroek et al. (2016)
Polychaeta (marine worms)	3		van Tussenbroek et al. (2016)
Total for the major groups:	349,368		

probably true for the lizards, particularly on oceanic islands (Olesen & Valido 2003) where plants have a tendency to evolve interactions with pollinators that are rather different than their mainland relatives (e.g., Shrestha et al. 2016). Although fish pollination was suggested to be a possibility some time ago (Ollerton 1999), it has yet to be observed; however, the recent experimental confirmation of animal pollination in a seagrass (van Tussenbroek et al. 2016) perhaps makes it more likely.

In total we might expect there to be approximately 350,000 known species of pollinators servicing the approximately 352,000 species of flowering plants (Paton et al. 2008), an interesting (though purely coincidental) symmetry, as flowering plant diversity could be as high as 400,000, whereas the estimates of insect pollinator diversity in **Table 1** are certainly too low. If the best estimate of total eukaryotic diversity of 5 million (range 2 to 8 million) species by Costello et al. (2013) is reasonably accurate, and given that at least 1 million of these species are fungi, algae, plants, and protists (i.e., not animals) and that a significant fraction of the remaining animals are aquatic, then as many as 1 in 10 terrestrial animals on the planet are pollinators.

All of these animals have the potential to be effective pollinators of at least some of the flowers that they visit. However, the relative effectiveness of different groups of pollinators varies in relation to three components: the abundance of the animal in a community; the propensity for that animal to touch anthers, carry pollen, and contact stigmas; and whether or not the animal will move to a flower of the same species and the distance it travels to do so (Herrera 1987, Rodriguez-Rodriguez et al. 2013). The first of these is generally considered a quantity measure of pollination; the second and third relate to the quality of the pollinator, though all measures are quantitative and can be combined to produce indices of pollinator importance for a given plant (e.g., Watts et al. 2012, reviewed in Ne'eman et al. 2009). Measuring pollinator importance is time consuming and technically difficult to do at a whole community level, never mind assessing it from a global perspective, though it is beginning to be done (Ballantyne et al. 2015, 2017). There is also the added complication of intraspecific variation in pollination ability—for example, large *Bombus terrestris* individuals deposit more pollen on stigmas per visit, and are also active for longer in the day, than smaller conspecifics (Willmer & Finlayson 2014).

Another way to gain a broader view of the relative importance of different pollinators is to consider the plant's perspective. **Figure 1** summarizes the relative average frequency of plants that possess different pollination systems in 32 plant communities across the world (see **Supplemental Materials**). These data contain a mix of arctic, temperate, subtropical, and tropical sites. Clearly, biogeographic differences exist between regions (see Section 3.1), as represented by the high standard deviations associated with these mean values, but we are not in a position to be able to deal with these in such a small data set (which represents most of the data currently available in this format). In relation to **Figure 1**, the single most dominant pollinating taxon is the bees, closely followed by the flies. Other groups of insects tend to be of lesser importance as specialized categories of pollinators, though they no doubt contribute as pollinators to the single largest group of plants, the insect generalists. Butterflies and moths are apparently of lesser importance, but that may be because nocturnal moths, at least, are less well studied (see comments above). That the results in **Figure 1** do not correlate with the values for species richness shown in **Table 1** tells us a lot about the effectiveness of these different groups as pollinators: Bees and flies are less diverse than Lepidoptera, but they can be relatively large and hairy and show the kinds of behaviors that make them good pollinators. In addition, bees are the only group more or less totally reliant on floral resources as both adults and larvae.

The cataloguing of biodiversity is a key component of global efforts to conserve ecosystems, and it has long been recognized that an understanding of how an ecosystem functions is required before we can make decisions about its preservation. Plant–pollinator interactions cut across these two aspects of conservation biology inasmuch as species diversity of pollinators is crucial to how
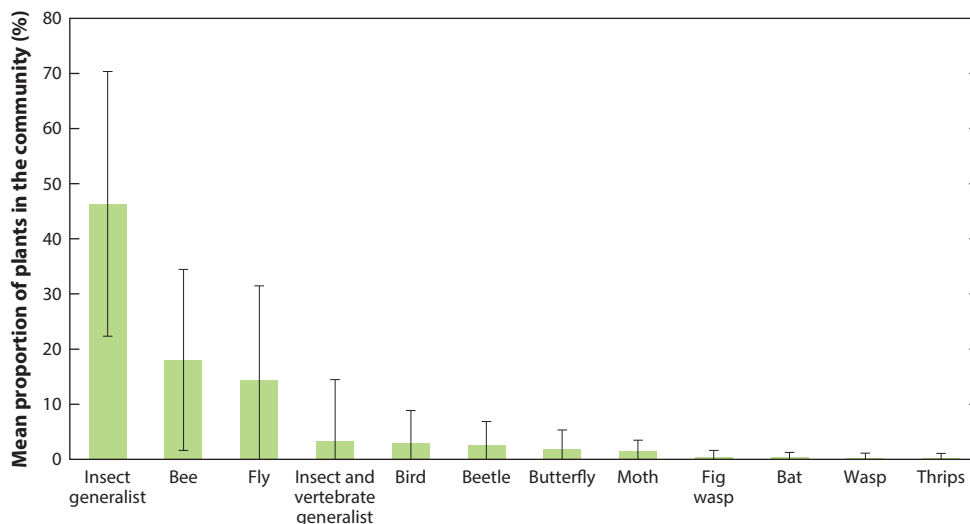
▶ Supplemental Material

Figure 1

The mean ($\pm$SD) proportions of plant species from 32 communities that have been classified into 12 broad pollination systems by the original authors of these studies. Note that wind pollination has been excluded from this graph but averages 17.5% (SD = 20.5) across the communities. Full details of the studies are provided in the **Supplemental Materials Appendix 1**.

most plants reproduce and therefore how many terrestrial ecosystems function in the long term. The preceding sections should give a sense of the diversity of animals that act as pollinators and the number and proportion of plants that require these flower visitors as pollen vectors, whereas in Section 4 we explore the implications of this diversity, and its loss, for ecosystem function. However, the diversity of the interactions between plants and their pollinators is still far from fully explored and researchers continue to discover novel pollination systems at a rate that does not seem to be declining. Even as recently as 2016 a previously undocumented pollination system, involving marine seagrasses and flower-visiting crustaceans and polychaete worms, was described (van Tussenbroek et al. 2016).

Although it can be rather neglected in biodiversity assessments, studying what we might currently term the biodiversity of species interactions has a long and venerable history. Plant–pollinator interactions, in particular, have held the attention of serious researchers since at least the eighteenth century and include important scientists such as Joseph Gottlieb Koelreuter, Christian Konrad Sprengel, Charles Darwin, and Hermann Müller (Waser 2006). An important question is whether, over that time period, we have discovered the full range of the diversity of plant–pollinator interactions or we are still in a phase of discovering and cataloguing, as well as understanding. Global taxonomic species accumulation curves are beginning to level off for some taxa but not for others (Costello et al. 2013). Despite 200 years of studying plant–pollinator interactions, our understanding of the global patterns of these interactions, and the players involved, is not yet mature.

Expectations of what constitutes normal pollinators have historically been dominated by a northern temperate viewpoint that sees bees, butterflies, and hoverflies as proper pollinators. Pollination systems that involve unusual or unexpected taxa, such as flower chafers, spider hunting wasps, lizards, or rodents, are still considered exceptional despite the fact that such oddities can be locally dominant (Johnson 2004, Olesen & Valido 2003, Ollerton et al. 2003, Shuttleworth & Johnson 2009) and may in fact be much more widespread than we realize—they are not just

Supplemental Material

tropical novelties. This then begs the question of just how different plant–pollinator interactions are in the tropics compared with higher latitudes, a topic that has received growing interest in the past few years and which I explore in Section 3.

3. POLLINATOR DIVERSITY IN SPACE

Pollinator diversity is not evenly distributed in space: Considerable biogeographic structure exists for both the numbers of pollinators in different parts of the world and their taxonomic identities. In particular, the biodiversity of pollinators changes with both latitude and continent, reflecting the varied evolutionary histories of different parts of our planet. However, significant geographical bias currently affects our understanding of the relative importance of different groups of pollinators, and many parts of the world remain largely unstudied (Rech et al. 2016). There is also much that we do not understand about the potential effects of pollinators that have been introduced to parts of the world in which they are not native.

3.1. Biogeographic Patterns of Pollinator Diversity and Distribution

In general terms, pollinator diversity follows the expected pattern of increasing species richness with latitude: The tropics have more pollinators, which is not unexpected as tropical communities (with some exceptions) generally possess a richer flora and the two are correlated (see Section 6.2). However, it has long been known that the diversity of bees, one of the major groups of pollinators, peaks not in the tropics but rather in dry, subtropical, Mediterranean-type communities (see **Figure 2**) (Michener 2007, Ollerton et al. 2006). More complete bee diversity lists for tropical sites need to be collated to assess the robustness of this pattern (Michener 2007). In contrast, other groups of pollinators conform to the normal pattern of greatest diversity occurring in the tropics; for example, Lepidoptera species in the Neotropics are approximately five times more diverse (in terms of species per unit area) than those in the Nearctic, as are Indo-Australian faunas compared with those in the Palaearctic, though Afrotropical Lepidoptera diversity is only approximately twice that of the Palaearctic (Kristensen et al. 2007).

In some parts of the world, such as southern Africa (Johnson 2004), bee diversity is much lower than one might expect. This seems to have resulted in the evolution of plants exploiting unusual (from a northern temperate perspective) pollinators such as groups of beetles, wasps, and rodents that rarely act as specialized pollinators elsewhere in the world (Johnson 2004; Ollerton et al. 2003, 2006; Shuttleworth & Johnson 2009). Similarly, Australian plants have evolved pollinator relationships with a wide diversity of what may be considered nonstandard pollinators (Armstrong 1979). In the Arctic, flies are the dominant pollinators (Tiusanen et al. 2016), whereas the genus *Bombus* is rather dominant as a pollinator across much of the rest of the Northern Hemisphere and into South America. The absence of the genus from sub-Saharan Africa, despite the fact that some species appear to be excellent dispersers (see Section 3.4), is rather a conundrum.

Another notable biogeographic pattern of pollinator distribution is the rarity of bird pollination of native plants across much of Europe, with some exceptions in the Mediterranean (Ortega-Olivencia et al. 2005), whereas other parts of the world contain different clades of flower-visiting birds (e.g., hummingbirds in the Americas; sunbirds in Africa, Asia, and Australasia; and honeyeaters in Australia; Cronk & Ojeda 2008). The relative absence of specialized bird pollination in Europe is a mystery given the historical presence of hummingbirds during the Oligocene (see Section 3.4). However, a range of nonspecialist passerines visit flowers and carry a diversity of pollen from both native and introduced plants (da Silva et al. 2014), so it may be more common than we realize yet relatively unrecorded.
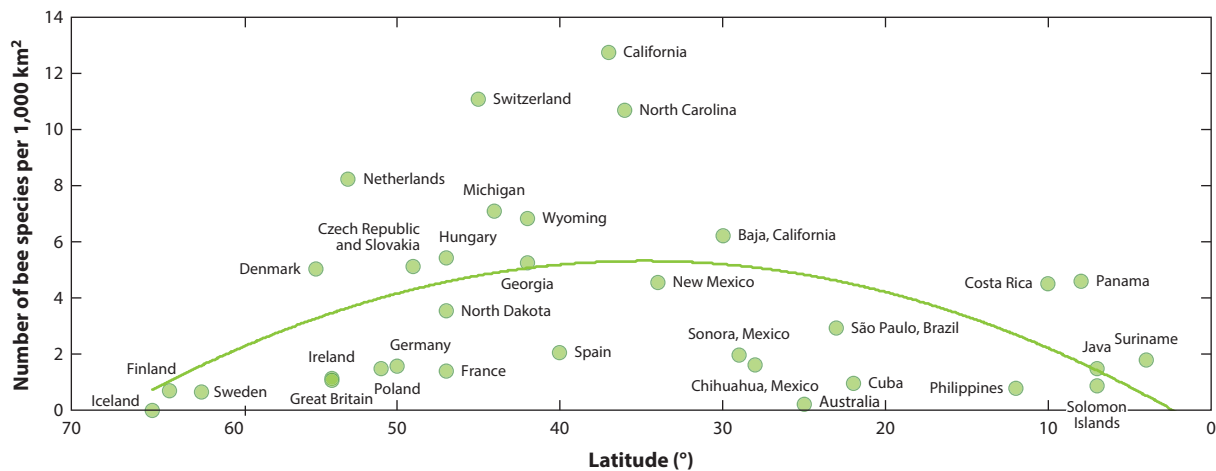
Figure 2

Regional- and country-level bee species richness in relation to latitude. Data are from Michener (2007) and Kirkitadze & Japoshvili (2015), corrected for area of the country or region concerned.

3.2. How Different Are Plant–Pollinator Interactions in the Tropics?

The trend of increasing species richness from polar to tropical regions has been recognized since at least the eighteenth century (Hillebrand 2004). Greater species richness implies that tropical taxa may more frequently be specialized in their interactions with other taxa because competition for resources (including the species with which they interact) ought to have resulted in the evolution of narrower niche breadths (but see Moles & Ollerton 2016, Vázquez & Stevens 2004). It is certainly true that tropical communities possess, on average, a greater diversity of functionally specialized plant–pollinator interactions (Ollerton et al. 2006), possibly because of the relatively low bee diversity in the tropics (**Figure 2**; see also my comments in Section 3.1 about subtropical southern Africa). However, the hypothesis that tropical plant–pollinator interactions are more specialized has rarely been tested, and those tests have resulted in mixed findings (e.g., Olesen & Jordano 2002, Ollerton & Cranmer 2002). Recently, Schleuning et al. (2012) showed that networks of plants and their flower visitors actually tended to be ecologically less specialized in the tropics, whereas Pauw & Stanway (2015) presented evidence suggesting there may be a trend of increasing specialization toward the tropics in the Southern (but not the Northern) Hemisphere. They attributed this to climatic stability in the Southern Hemisphere over a long timescale that may have allowed specialized interactions to persist (see also Dalsgaard et al. 2011).

One implication of our current state of knowledge is that biotic pollination as an ecological function may be more likely to be disrupted in certain parts of the world, such as northern temperate and Southern Hemisphere communities, rather than just tropical areas as a whole, in other words, that sensitivity to perturbation is geographically complex rather than predictable from latitude alone (Vizentin-Bugoni et al. 2017).

3.3. The Introduction of Non-Native Pollinators

The diversity of pollinating insects has been artificially increased in some parts of the world by the introduction of non-native species, particularly bees (Goulson 2003, Russo 2016), either purposefully to enhance crop pollination or accidentally. In some oceanic islands, introduced

species can outnumber native pollinators; for example, a recently published checklist of the bees of the Azores showed that of 19 recorded species (including managed hives of honeybees) only 4 were likely to be native (Weissmann et al. 2017). Although such a high proportion of non-native species is exceptional, the number of introduced pollinators being found in surveys is no doubt increasing, and oceanic islands seem to be especially susceptible to invasion (Olesen et al. 2002).

The ecological effects of these introductions range from harmful to positive, depending upon the species, the context in which it was introduced, and (in particular) the local density of the pollinator (Russo 2016). The most abundant and impactful of these introductions has been the Western honeybee (*Apis mellifera*), managed colonies of which are used to support agricultural pollination in parts of the world far outside its native range. A number of studies have shown that honeybees can outcompete native bees and other flower visitors, although this seems to depend upon whether the landscapes are simple and homogenous or complex and heterogeneous in their structure, with regard to the amount of seminatural habitat available for bee foraging (see Herbertsson et al. 2016). Studies have also shown that honeybees can become well integrated into local pollination webs and have no obvious negative effects, at least at low density (Watts et al. 2016).

Other introduced bees include *B. terrestris*, which is now widely considered to be an invasive alien in regions where it is non-native (Dafni et al. 2010) and has been implicated in the regional loss of native *Bombus* species (Morales et al. 2013). Conservationists are concerned about not only the direct effects of competition but also the diseases that introduced bees can bring that may pass on to native species (e.g., Arbetman et al. 2013).

There are some positive aspects to pollinator introductions, however, with a number of case studies indicating that non-native pollinators are facilitating reproduction in threatened plants in areas where the native pollinators are rare or absent. For example, in the 1980s Cox (1983) determined that pollination of a Hawaiian vine (*Freycinetia arborea*) was now being carried out by an introduced bird, the Japanese white-eye (*Zosterops japonica*), following the extinction of its native bird pollinators. A decade later, Lord (1991) showed that an introduced possum (*Trichosurus vulpecula*) had replaced two native bats (one very rare, the other possibly extinct) as the pollinator of another species in the same genus (*Freycinetia baueriana*) in New Zealand. More recently Fox et al. (2013) showed that, over nine years of study, the most consistent pollinator found in populations of the threatened Western prairie fringed orchid (*Platanthera praeclara*) in North America was a Eurasian hawkmoth (*Hyles euphorbiae*), originally introduced as a control agent of invasive plants. However, this introduced moth could possibly have outcompeted the native pollinators of the orchid.

The outcomes of pollinator introduction are clearly contingent on local circumstances, but those circumstances can change over time, such that currently benign introductions of species may in the future become ecologically problematical. For this reason, proposals to maintain a ban on the introduction of non-native bumblebees to mainland Australia for pollination of greenhouse crops are probably a wise move given their impact in Tasmania (Hingston 2007) and the fact that such commercial crop pollination can be carried out by native bees (Hogendoorn et al. 2006).

3.4. Natural Range Expansions and Contractions by Pollinators

In addition to direct anthropogenic changes in the distribution of species, we also expect some natural changes to occur due to the expansion and contraction of ranges by species in response to processes such as variations in resource availability, weather, opportunistic dispersal, and so forth (some of which can also be anthropogenic of course). Such natural changes have occurred since the start of the new millennium in Britain, where a number of previously unrecorded bee

species have become established and flourished. The best documented of these are the ivy bee (*Colletes hederae*) and the tree bumblebee (*Bombus hypnorum*), which both arrived in 2001 (Goulson & Williams 2001, Roberts & Vereecken 2010) and have been tracked by the Bees, Wasps, and Ants Recording Society (BWARS). According to Rasmont et al. (2015), the expansion of *B. hypnorum* into Britain was just the next step in an ongoing increase in this Eurasian-wide species that has even made it to Iceland. This is not the only example: Rasmont et al. (2015) also showed that the Asian *Bombus schrencki* has expanded westward as far as Poland and Finland, López-Uribe & Cane (2016) documented the expansion of a specialist squash bee (*Peponapis pruinosa*) in parallel with crop domestication, and Russo (2016) cited other North American examples.

Such expansions in range should not surprise us because it has long been known that queen bumblebees and wasps can engage in long-distance dispersal events across tens of kilometers of open water (Mikkola 1984). In contrast, natural range contractions are more rarely considered, in part because of a hubristic tendency to assume that any local decline of a species must have an anthropogenic cause, which is clearly nonsensical: The fossil record tells us that species come and go across whole regions at a range of timescales. But untangling the natural from the anthropogenic in human-dominated landscapes is probably impossible. Of the 23 species of British bees and flower-visiting wasps that are known to have gone extinct since the 1850s, it is almost certain that one or more was lost naturally (Ollerton et al. 2014). Indeed, during the long revision period for that article, one species was rediscovered and had almost certainly naturally recolonized Britain from the continent. The fossil record documents examples of taxa that were previously found in parts of the world where they no longer exist and where their ancient presence comes as a complete surprise. In recent years it has been shown that hummingbirds, an important group of pollinators long thought to be found only in the New World, were present in Europe in the early Oligocene, approximately 30 million years ago (Louchart et al. 2008, Mayr 2004). Such findings reinforce the view that there is much that we currently do not understand about the biogeography and biodiversity of interactions between pollinators and the plants that they service.

4. DECLINES IN POLLINATOR DIVERSITY AT GLOBAL, REGIONAL, AND LOCAL LEVELS

Perhaps more important, and certainly more urgent, than assessing the current diversity of pollinators in space and time is understanding the rate of loss of diversity at local, regional, and global geographic scales and what this loss of diversity might mean for pollination as an ecological function and as an ecosystem service. In this section, and in Section 5, I try to address these questions.

4.1. How Good Is the Evidence Base for Pollinator Declines?

The loss of pollinator diversity and abundance has been discussed in a number of influential primary studies and reviews, for example, Biesmeijer et al. (2006), Potts et al. (2010a), and Lebuhn et al. (2013). However, disagreements have emerged as to the accuracy of these assessments and whether the decline of pollinators (and particularly bees) has been overplayed in the literature and by the media (Ghazoul 2005). Recently, Goulson and colleagues (2015a) reviewed the evidence for drivers of bee declines, which resulted in some correspondence questioning their conclusions from a number of perspectives but particularly criticizing the paucity of the evidence base for pollinator declines (Ghazoul 2015), eliciting a rejoinder from the authors (Goulson et al. 2015b). In some respects this was an unsatisfactory exchange, as the focus was largely on agricultural pollinators rather than on pollinators of all plants (including the majority, noncultivated species) and on bees. Looking more broadly across pollinator species, the evidence is much more clear-cut: Pollinators are declining at local, regional, and global scales, in both diversity and abundance.

The most striking statement in Ghazoul (2015) was that the "evidence for pollinator declines is almost entirely confined to honeybees and bumblebees in Europe and North America" (p. 981). Underlying this statement is the suggestion that global concerns about declining pollinator biodiversity is underpinned by a taxonomically and geographically thin evidence base. This is clearly not the case, as the following summary of the current evidence shows. This summary is not meant to be a full review, by any means, but rather to give a flavor of the taxonomic and geographical breadth and depth of the evidence as it currently stands.

4.1.1. Wild bees (including bumblebees and solitary and primitively eusocial bees). A significant reduction of abundance and diversity of these species at local, regional, and country levels has been documented in Britain and continental Europe (Biesmeijer et al. 2006, Nieto et al. 2014, Ollerton et al. 2014); South America (Morales et al. 2013); Asia (Williams et al. 2009); South Africa (Pauw 2007); and North America (Burkle et al. 2013, Cameron et al. 2011). In the United States, authorities have recently added all seven of Hawaii's native bees to the Endangered Species Act, the first time this has occurred for bees in the United States.

4.1.2. Honeybees. Colony declines have been documented in North America and in parts of Europe, though hive numbers have remained stable or increased in other parts (see Potts et al. 2010b). Globally, the number of managed hives is increasing, but there is evidence that demand for honeybee pollination services is outstripping supply (Aizen & Harder 2009).

4.1.3. Hoverflies. Declines in diversity have been documented in the Netherlands and Britain (Biesmeijer et al. 2006). However, the situation in other parts of the world is unclear, as hoverflies are chronically understudied outside Europe.

4.1.4. Butterflies and moths. Diversity and abundance of Lepidoptera species have declined in the United Kingdom (Fox 2013, Thomas et al. 2004). In North America, almost 60 species are Red Listed by the Xerces Society as Vulnerable, Imperiled or Critically Imperiled, and there is particular concern about the iconic monarch butterfly. Likewise, conservationists are concerned about a significant fraction of butterflies in other parts of the world (e.g., southern Africa, Australia, and Europe).

4.1.5. Flower-visiting wasps. A reduction in country-level diversity in Britain has been observed for aculeate wasps (Ollerton et al. 2014). However, for the rest of the world there is little or no published information for this group, which remains poorly studied despite being significant pollinators in some parts of the world (Ollerton et al. 2003). Concerns have also been raised about the effects of climate change on fig wasps (Jevanandam et al. 2013).

4.1.6. Birds and mammals. The major vertebrate pollinators have recently been assessed at a global level by Regan et al. (2015) using IUCN Red List criteria. The authors concluded that, over the past few decades, each year 2.5 species (on average) have shifted one Red List category closer to extinction. Extinctions have already been reported for pollinating birds on islands such as Hawaii, and of two native bat species thought to act as pollinators in New Zealand, one (greater short-tailed bat, *Mystacina robusta*) may have gone extinct in the 1960s and the other (lesser short-tailed bat, *Mystacina tuberculata*) has declined greatly.

Of course, a number of the studies cited above have shown that some species are doing better than others and a proportion of the taxa they have assessed are stable or even increasing in abundance (including managed honeybee colonies in some parts of the world). Additionally, evidence

of a slowdown in the loss of pollinators across northwest Europe has also been shown (Carvalheiro et al. 2013; but see Ollerton et al. 2014). But overall, the current evidence base points toward significant declines in pollinator abundance and diversity for a wide range of taxa at multiple spatial scales across all regions that have thus far been assessed with any rigor.

The causes of these declines continue to be widely discussed, but loss of habitat from transformation of land use and changes in land management following agricultural intensification are the most likely reasons (Bartomeus et al. 2013, Goulson et al. 2015a, Ollerton et al. 2014, Potts et al. 2010a). However, recent assessments of the impact of climate change on pollinator diversity indicate that declines and range shifts will continue into the future, as I show in the next section.

4.2. Climate Change and Pollinator Diversity

Flower-visiting insects have been the subject of climate change species distribution modeling approaches for some time, beginning with butterflies in the 1990s (Parmesan et al. 1999, Settele et al. 2008), largely because more data were available for that group of insects than for any other rather than because of their importance as pollinators. More recently, bees have been studied including the bumblebees (*Bombus* spp. Apidae), arguably the most important single genus of pollinators of plants in northern temperate regions. This genus has been the subject of detailed scenario modeling in the "Climatic Risk and Distribution Atlas of European Bumblebees" (Rasmont et al. 2015). Bumblebees mainly show adaptations to colder climates, notably their thick body hair, which is incidentally also one of the reasons that they are such good pollinators. Given this, we might expect them to be particularly vulnerable to climate change (though other bees may benefit as some areas become warmer and drier; see **Figure 2**). Rasmont and colleagues (2015) applied a range of climate change scenarios to 56 European bumblebees and showed that as many as 36% of the species are at high climatic risk (defined as losing more than 80% of their current range), whereas 41% are at risk (losing 50% to 80%). Just over 5% (three species) were projected to increase their range across Europe. Overall, climatic conditions suitable for bumblebees were likely to decrease for 34–52 species in the period leading up to 2050, and for 49–55 species in the period leading up to 2100. This loss of suitable climate is likely to be most notable in southern Europe, an area that already has few bumblebee species. Regions in Spain and Portugal may be left with just one bumblebee species by 2050, potentially creating subsequent problems for fruit and seed set of wild and cultivated plants.

Polar regions are predicted to experience the earliest, and initially most extreme, ecological effects of anthropogenic climate change. In this regard, the observations that, between 1996 and 2009, arctic flowering seasons became shorter and flower visitors less abundant are concerning (Høye et al. 2013), particularly as one of the most affected groups (species of the Diptera family Muscidae) are the main pollinators of *Dryas*, one of the key nectar and pollen sources in this region (Tiusanen et al. 2016). However, tropical species may have narrow thermal tolerances and therefore be vulnerable to direct effects of global warming (Jevanandam et al. 2013).

Forecasts of how well pollinators may respond to climate change are very dependent upon the ability of species to adapt to the warmer climate and/or to disperse and colonize new suitable areas. Conservation programs to future proof (sensu Samways 2015) pollinators should include strategies that enable species to move through a landscape to areas that have been suitably restored or managed for pollinators, principles that are enshrined at a national and international government level in national pollinator strategies developed by the United Kingdom, United States, Ireland, and other countries and by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services *Assessment of Pollinators, Pollination and Food Production* (IPBES 2016). At a local and regional level, a lot of practical conservation monitoring and proof-of-concept work is taking place to restore, manage, and assess habitats as diverse as temperate heathlands (Forup et al. 2008),

boreal pinewoods (Devoto et al. 2012), capped landfill sites (Tarrant et al. 2013), urban centers (Baldock et al. 2015, Sirohi et al. 2015), and tropical island inselbergs (Kaiser-Bunbury et al. 2017). National initiatives by nongovernmental organizations such as Buglife's B-Lines project in the United Kingdom and work by the Xerces Society in the United States are also ongoing. However, such strategies may not be feasible in high alpine and arctic regions where pollinators are limited by where they can actually move to.

5. WHY IS CONSERVING POLLINATOR DIVERSITY IMPORTANT?

Arguments for the importance of conserving pollinator diversity usually invoke three main factors that are practical, theoretical, or abstract in their point of view. First, the ecological and agricultural function of diverse, as opposed to depauperate, pollinator assemblages is claimed to be superior. Second, diverse assemblages provide us with future ecological insurance if particular key pollinators decline or go extinct. Finally, species diversity per se is seen as being part of the bio-cultural heritage of humanity and, ultimately, of the planet. These are not mutually exclusive arguments, but they do reflect inherent tensions in the ways in which conservation is perceived and presented to wider society by ecologists and conservationists. These three arguments, in turn, can be presented within a natural capital and ecosystem services (NC-ES) framework that has gained wide acceptance over the past 20 years or so (Mace et al. 2012). However, one unresolved issue is that NC-ES arguments about agricultural services do not always reflect the ecological reality of biological communities in which species rarity and specialization are a significant part of the ecological complexes in which these species are embedded.

5.1. The Specialization–Generalization Continuum

A considerable amount of research has been conducted, and dissimilar views expressed, over the past 30 years concerning the specialization–generalization continuum in plant–pollinator interactions (Brosi 2016, Fenster et al. 2004, Johnson & Steiner 2000, Jordano 1987, Waser et al. 1996). This work has recently been reviewed and discussed by Armbruster (2016), who describes it as "central to our thinking, not just about the ecology of plant–pollinator interactions and pollinator services, but also about reproductive isolation, speciation, extinction and assembly of communities" (p. 88). Clearly, these discussions must also therefore be central to our thinking about why we need to conserve pollinators.

At one pole of this continuum are highly specialized, one-to-one relationships between a plant and its pollen vectors. These are thought to include some mutually dependent brood site pollination systems such as between some figs and fig wasps, leafflowers and leafflower moths, and yuccas and yucca moths that have evolved from seed parasite relationships, though not all of these relationships are mutually exclusive (Hembry & Althoff 2016). Others are also not mutually dependent when they involve deception of insects that would not normally visit flowers, such as the relationship between *Ceropegia* spp. (Apocynaceae) and their Diptera pollinators (Ollerton et al. 2009, 2017). The other pole of the continuum contains highly generalized relationships between flowers and the wide range of pollinators that they attract. For example, some North American *Asclepias* species are known to be pollinated by more than 100 different types of insects (Ollerton & Liede 1997), and pollinators such as bees in the genera *Bombus* and *Apis* that can visit and pollinate a high proportion of plants within a community, or super generalist pollinators on islands (Olesen et al. 2002).

Categorizing a plant or pollinator, and placing it on this continuum, depends upon the spatial and temporal scale at which we observe the interactions. Widespread species can be rather special-ized in their immediate locality but much more generalized when considered across their whole

range (e.g., Gómez et al. 2013, Herrera 1988, Ollerton et al. 2009). Likewise, relationships between flowers and pollinators can vary year to year, depending upon the relative abundance of species.

This space and time aspect to understanding how specialized or generalized a species is in its interactions encompasses issues around ecological sampling efforts: How do we know that we have put enough time into understanding a study system? Undersampling can lead to spurious conclusions regarding the level of specialization of a plant or pollinator, whereas it is hardly possible to oversample except insofar as interactions will reach an asymptote sooner or later (Ollerton & Cranmer 2002), though this may take some time.

Most plants and pollinators lie somewhere in the middle of the specialization–generalization continuum and more toward the generalist than specialist pole at least in terms of ecological specialization (i.e., the number of other species with which a given species interacts). This means that (in theory at least) there is some degree of redundancy within the ecologies of most plants and pollinators, such that a particular pollinator can gain resources from a range of different types of flowers, whereas a specific plant can be pollinated by any of a number of flower visitors. The importance of this redundancy in relation to local loss of pollinator diversity is beginning to be studied in detail using pollinator exclusion experiments, with mixed results (see Section 5.2).

A commonly voiced criticism of assessments of so-called pollinator diversity of plants is that the "pollinators" surveyed are usually flower visitors rather than actual pollinators. This criticism has been particularly aimed at network studies of plant–flower visitor assemblages, and there is some validity in that criticism (though it is worth noting that flower visitation itself, regardless of the outcome for the plant, is usually a positive interaction from the visitor's perspective). Unfortunately, few data are available with which to assess the correspondence between flower visitors and pollinators for plant species, in order to understand what fraction of the visitors are indeed effective pollen vectors. This is an important question, however, given that non-bees are often neglected in surveys of pollinators on the assumption that it is the bees that are the most important for pollination (Rader et al. 2015).

The asclepiads (Apocynaceae: Asclepiadoideae) can give very useful insight into this question because they disperse their pollen as discrete units (pollinia) that mechanically clip on to an animal, making the identification of effective pollinators much easier than is the case with most other plant groups (Ollerton & Liede 1997). **Figure 3a** shows the relationship between the number of insects observed visiting flowers of 18 species of asclepiad in the grasslands of KwaZulu-Natal in South Africa and the number of proven pollinators. Clearly, the more specialized species with only one or two flower visitors are pollinated by all or most of their flower visitors and lie close to the 1:1 line that would show the relationship if all visitors were pollinators. As species become progressively more generalized, however, a lower proportion of flower visitors act as pollinators. Indeed, for the most generalist of plants, fewer than one third of the visitors are effective pollinators (**Figure 3b**), although this must be considered a conservative value as some of those insects that were recorded as not carrying pollinaria almost certainly do but have not yet been observed owing to low visitation frequency or limited sampling. Note that few of the visitors to these flowers are actually bees: Wasps, beetles, and flies are much more common (see Ollerton et al. 2003, Shuttleworth & Johnson 2009, and comments regarding southern Africa in Section 3.1).

Species redundancy is possible only if species diversity is maintained: In communities where species have been extirpated, the absence of some species in particular years may mean the collapse of a plant population if pollinators are missing or a pollinator population if a vital flower is lost. This is seen in its most extreme expression in monoculture agro-ecosystems where the loss of native vegetation and its associated flowers and pollinators leads to a situation in which either managed pollinators must be imported (e.g., honeybees to almond orchards) or a loss of crop yield endured. The potential outcomes of loss of pollinators are explored in more detail in the following section.
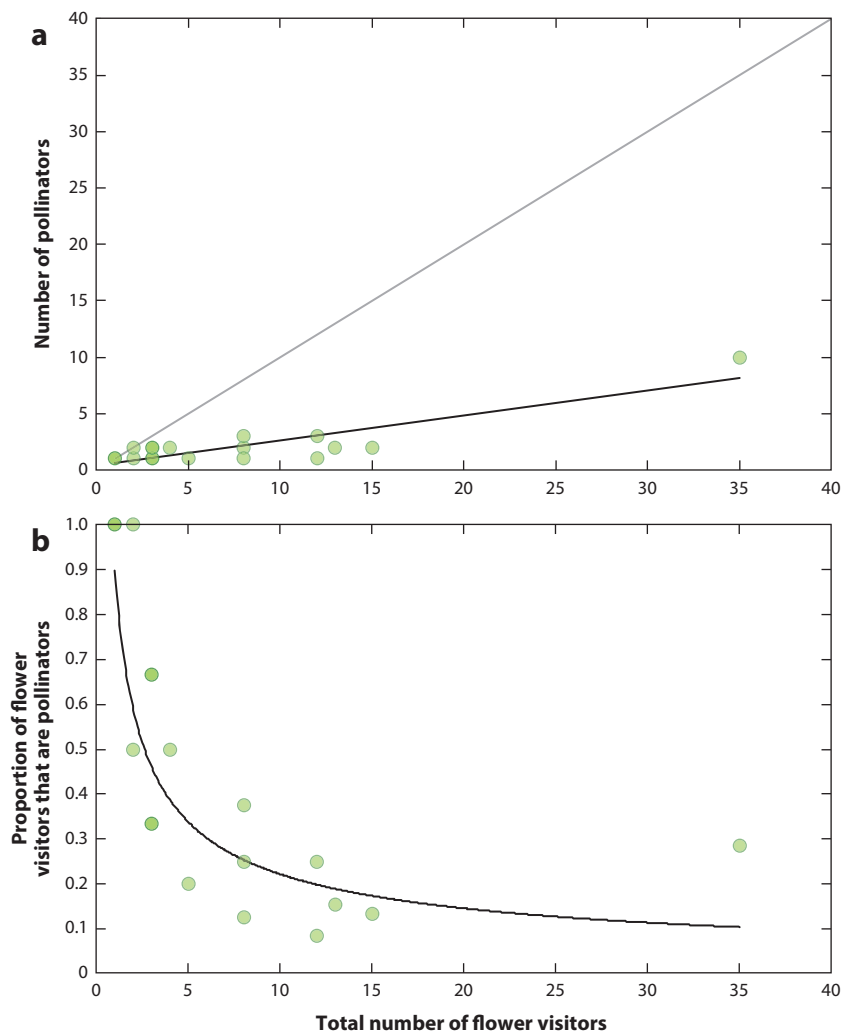
Figure 3

Apparent plant generalization and actual pollinators for a sample of plants in South Africa. Panel *a* shows the relationship between the number of observed flower visitors and the number of proven pollinators for 18 grassland asclepiad species (Apocynaceae: Asclepiadoideae) in the grasslands of KwaZulu-Natal. The gray line is the 1:1 relationship expected if all visitors were pollinators. The black line is the regression line for this relationship ($R^2 = 0.75$). Panel *b* shows the relationship between the number of flower visitors and the proportion of flower visitors that act as pollinators. Data from Ollerton et al. (2003) and Shuttleworth & Johnson (2009).

5.2. The Outcomes of Pollinator Decline: Pollinator Diversity, Plant Diversity, and Seed Set Are Intrinsically Linked

Loss of plant diversity through land use change has been proposed to be one of the major drivers of loss of pollinator diversity, notwithstanding other considerations such as pesticides, climate change, disease, and so forth (Goulson et al. 2015a, Ollerton et al. 2014, Potts et al. 2010a). It
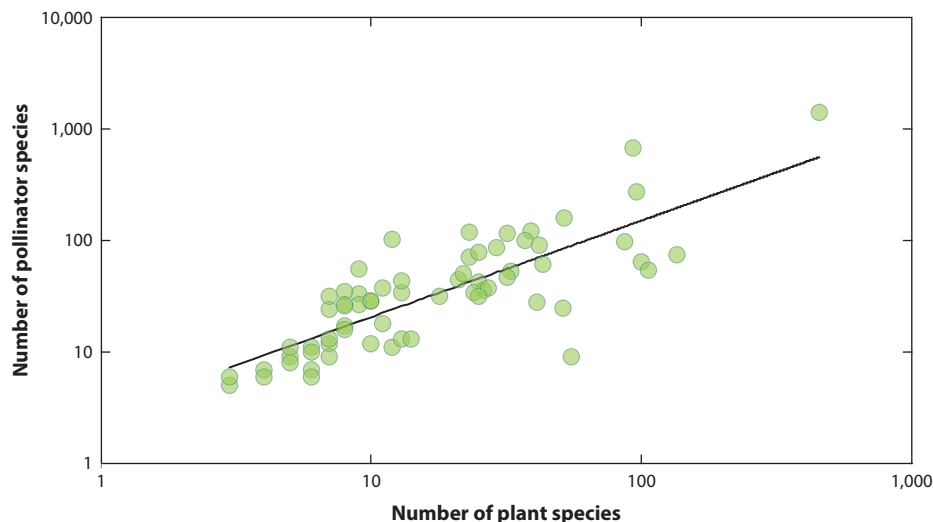
Figure 4

The relationship between plant species richness and pollinator species richness across 65 sites. Note the log scale on each axis. Sources of data are in the **Supplemental Materials Appendix 2**.

is not surprising, though certainly not trivial, to note that there is a strong positive correlation between the number of plant species found in a community and the number of associated flower visitors (**Figure 4**). Usually there are more pollinators than plants, such that the mean ratio of pollinators to plants in this data set is 2.4 (SD = 1.5)—in other words, on average every plant in a community brings with it an additional one or two pollinators, though sometimes more. The relationship between plant diversity and pollinator diversity is thus intrinsically linked: The more animal-pollinated plants we add to a community, in a restoration project for example, the greater the number of pollinators we can expect to find. This relationship has important implications for pollinator conservation and is at the center of "planting for pollinators" initiatives and agricultural stewardship policies worldwide but is certainly not the only factor that needs to be taken into account, as pollinators also require breeding sites and supplementary resources, including food other than nectar and pollen.

Perhaps because this relationship between plant and pollinator diversity is so obvious, it has been rather little explored. As so often in ecology, patterns that we see are scale dependent; for example, Hegland & Boeke (2006), using plots of 1.5×1.5 m, found no correlation between overall plant and pollinator richness. In contrast, Ebeling et al. (2008) studied this relationship in rather larger (20×20 m) grassland plots in Germany. They discovered that pollinator species richness in relation to plant diversity at a plot level reached an asymptote at approximately 10 insect species, whereas Steffan-Dewenter & Tscharntke (2001) found a strong positive relationship between bee and flowering plant species richness across a successional gradient in an agricultural landscape in the same country. The strong positive relationship in **Figure 4** can be considered a global expression of relationships between regional and local diversity that are happening at smaller spatial scales.

Declines in abundance and diversity of pollinators have stimulated some researchers to consider the implications of pollinator loss: Does it result in greater pollen limitation and reduced seed set and subsequently influence plant recruitment to populations and therefore community

structure? Pollen limitation can have many causes (Knight et al. 2005), and lower pollinator diversity in some populations of a species is certainly one of them, as Gómez et al. (2010) showed in the generalist *Erysimum mediohispanicum*. Related to this, Biesmeijer et al. (2006) observed that there have been correlated declines in pollinators and insect-pollinated plants across Britain and the Netherlands, which may indicate cause and effect: lower pollinator diversity reducing seed production and subsequently affecting population recruitment over a longer period. However, research using an experimental approach shows mixed support for this idea. For example, removal of bumblebees (*Bombus* spp.) from patches of *Asclepias verticillata* (Apocynaceae) had no significant effect on the reproduction of those plants because the role of the bumblebees was taken up by *Polistes* wasps that were just as effective as pollinators (Hallett et al. 2017)—an example of ecological redundancy within the system (see Section 5.1). In contrast, Brosi & Briggs (2013) found that removing a single bumblebee species from localized patches reduced the reproductive success of *Delphinium barbeyi* (Ranunculaceae), even though alternative pollinators were present. Clearly the outcomes of local pollinator loss are idiosyncratic according to both the species involved and the community context. Using a different approach, Albrecht et al. (2012) showed that increased pollinator functional group richness resulted in greater fruit and seed set in a model plant, *Raphanus sativus*. At a larger ecological scale, Lundgren et al. (2016) reduced pollinator availability at the community level over 4 years and assessed how this affected recruitment of seedlings in 10 perennial hay meadow herbs in Norway. The results were complex and to some extent dependent upon the plant being studied, but overall the loss of pollinators resulted in a decline in the diversity and abundance of seedlings. To date, this is the only study to show a direct causal relationship between pollinator declines and a loss of plant species richness and individual abundance.

The yield, and therefore commercial, implications of pollinator loss for crop plants are easier to assess, especially if the species have separate-sex flowers or are otherwise highly dependent upon pollinators for outcrossing (Klein et al. 2007). There are numerous examples of crops that have an increased and/or better quality yield when pollinator diversity is high—for example, coffee (Klein et al. 2003), cherries (Holzschuh et al. 2012), apples (Blitzer et al. 2016, Garratt et al. 2014a), and holly and mistletoe (Ollerton et al. 2016).

However, few good examples of pollinator deficits affecting crop yields have been found (Aizen et al. 2008), although UK apple production may be one emerging example (Garratt et al. 2014b). But clearly maintenance of pollinator abundance and diversity is critically important for both agricultural services and ecological function: It would be foolish to wait until pollinator declines reach the level of affecting crop production before acting to conserve them. Although animal-pollinated crops represent only a minority of total agricultural production, they are responsible for a disproportionate amount of both essential minor nutrients in the human diet and economic value (IPBES 2016). One case study example serves to illustrate the scale of the dependence of modern human society on animal pollination. Coffee is pollinated by a range of wild insects (mainly bees) and managed honeybees (Ngo et al. 2007), is second only to oil in terms of its value as a commodity, and supports millions of subsistence farmers. Global coffee production in 2016 amounted to 151.624 million bags, each weighing 60 kg (Int. Coffee Org. 2017). One coffee bean is the product of a single fertilization event following the deposition of at least one pollen grain on a flower's stigma. The mean weight of a single coffee bean is approximately 0.1 g, which means there are approximately 600,000 beans in a 60-kg bag. The total number of coffee beans produced in 2016 is therefore 151.624 million bags multiplied by 600,000 beans per bag, which equals 90,974,400,000,000, or more than 90 trillion coffee beans. However, coffee is on average 50% self-pollinating (Klein et al. 2003), and a single bee visit may deposit enough pollen to fertilize both ovules in each coffee flower, so we can divide that figure by four. Nonetheless, global coffee

production requires at least 22 trillion pollinator visits to flowers. Clearly, the global coffee market is supported by many billions of bees that require seminatural habitats as well as coffee plantations to survive.

6. CONCLUSION

Pollinators have serviced the plants that they visit for at least 170 million years, since the mid-Mesozoic, and conceivably for far longer. Over that period the relative importance of different groups of pollinators has waxed and waned, while overall diversity has increased in parallel with flowering plants until, at the present time, there could be as many as 350,000 described species of pollinators (and many more awaiting scientific discovery). The relative importance of different taxonomic groups (from the levels of genus to order) varies biogeographically, but overall it is clear that diversity is important and loss of species (at whatever geographical scale) should be avoided. At the same time, we should not expect current patterns to be fixed, and the loss or gain of species regionally and nationally could be part of natural fluctuations in biodiversity irrespective of anthropogenic processes.

Current understanding of global patterns of pollinator diversity and importance and the role of different modes of pollination (specifically wind versus animal pollination) has been significantly advanced, but much still needs to be learned. Only in the last 20 years or so have scientists interested in these questions begun to assemble global data sets that address questions such as how wind and animal pollination varies across the globe, how different groups of animals are important as pollinators, what the patterns of pollen limitation are, and how these patterns relate to plant sexual and mating systems.

Understanding the diversity of pollinators, the evolution of the pollination systems in which they play a role, and ecology of the networks in which they are embedded (and how all of this can be conserved as a vital aspect of the biodiversity of the planet) requires even more observational and experimental data, monitoring, and detailed surveys to build a robust picture of pollinator diversity and declines. Contemporary pollinator diversity is the result of millions of years of tight and diffuse coevolution with gymnosperms and angiosperms. As well as being directly key to the continuation of this plant diversity, pollinators also provide enormous added value by indirectly supporting a vast array of other organisms, including yeasts and other microbes in nectar, fungal diseases of flowers, cleptoparasitic insect species and other parasites, specialist predators and herbivores, fruit- and seed-eating animals, and so forth. Losing any of this diversity is a tragic loss for the biological heritage of planet Earth.

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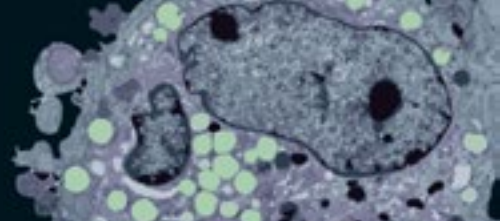
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