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Pollinator diversity: distribution, ecological function, and conservation

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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 couple of decades have seen unprecedented interest in pollinators and pollination ecology, stimulated in part by concerns over 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.

KEYWORDS: bees, biodiversity, biogeography, conservation, mutualism, pollination

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 it is arguable that they are 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 will focus on animal pollination, though noting that mixed pollination systems involving wind plus animals are known for some plants; termed “ambophily” 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 the gymnosperms is likewise biotically pollinated (e.g. Kato et al. 1995). However, although there has been limited research on the topic, it is clear that there is considerable media bias, and journalistic misrepresentation, of the diversity and relative importance of pollinators, with honey bees receiving attention that is disproportionate to both their importance and their need for conservation (Ollerton et al. 2012, Smith and Saunders 2016). One of the main aims of this review, therefore, is 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 some 170 million years ago (Gang et al. 2016), set the scene for one of the iconic stories of evolutionary biology, in which “primitive wind pollination” by gymnosperms is replaced by ever-more complex animal pollination in the flowering plants, leading to the diversification and dominance seen for the angiosperms. It’s a story that has been repeated in many textbooks and documentaries even up to recent times (e.g. Willmer 2011). The problem is that it is incorrect: the earliest angiosperms evolved in a biotically complex milieu that included many (perhaps the majority) 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 it is only in recent times that the true diversity and importance of insect pollination in pre-angiosperm floras has become apparent. Fossil insects from China, Spain and Russia have revealed ancient groups of insects that appear, based on interpretations of their mouthparts and associated pollen grains, to have been pollinators; examples include mid-Mesozoic thrips (Thysanoptera), flies (Diptera), lacewings (Neuroptera), scorpionflies (Mecoptera) and beetles (Coleoptera) (Ren 1998; Ren et al. 2009; Labandeira 2010; Labandeira et al., 2007, 2016; Peñalver et al. 2012, 2015; Peris et al. in press). It is notable that lacewings and scorpionflies are no longer significant pollinators (in terms of diversity) compared to 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 (c. 100 million years) onwards seems to correlate with the diversification of some modern groups of pollinators. For example Cardinal and Danforth (2013) estimated that the main extant clades of bees also have their origins in during the mid to late Cretaceous, based on a dated molecular phylogeny of the major groups of bees, calibrated by fossils such as those in early Cretaceous amber (Poinar and 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 showing that relationships between orchids and their bee pollinators are at least 15 million years old, and the orchids themselves probably originated around 80 million years ago (Ramirez 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 tantalising 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 accurate (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 problematical 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 towards a full account of the overall phylogenetic diversity, and the number of species involved, becomes incrementally possible (Ollerton 1999, Wardhaugh 2015, Regan et al. 2015). Table 1 brings

together recent estimates of described pollinator diversity for some well-studied groups, based on these reviews, plus recent studies such as 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). 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, Orford et al. 2015). The remaining groups are all rather low diversity in overall terms though they are no doubt ecologically important in certain regions and for particular plants. These figures will no doubt change in the future because most insects are not yet described. For example Kristensen et al. (2007) suggest that there may be around 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. When moth communities are studied in detail it is clear that a significant proportion of the species can act as pollinators (Haber and Frankie 1989, Devoto et al. 2011).

The vertebrate pollinating groups are also of relatively low diversity, of which the birds, with over 1000 species, are the most diverse. Nocturnal rodents are likely to be more important than we realize, especially in tropical forests, but have not been as well studied as

birds, or even bats. The same is probably true for the lizards, particularly on oceanic islands (Olesen and Valido 2003) where plants have a tendency to evolve interactions with pollinators that are rather different to 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, though the recent experimental confirmation of animal pollination in a seagrass (Tussenbroek et al. 2016) perhaps makes it more likely.

In total we might expect there to be around 350,000 known species of pollinator servicing the c. 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, whilst the estimates of insect pollinator diversity in Table 1 are certainly too low. If the best estimate of total eukaryotic diversity of 5 (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 in order 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 they can be combined to produce indices of pollinator importance for a given plant (e.g. Watts et al. 2012, reviewed by Ne’eman et al. 2009). This 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 for low diversity communities (Ballantyne et al. 2015). There is also the added complication of intra-specific variation in pollination ability, e.g. large *Bombus terrestris* individuals deposit more pollen on stigmas per visit, and are also active for longer in the day, than smaller conspecifics (Willmer and 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 summarises the relative average frequency of plants that possess different pollination systems in 32 plant communities across the world (see Supplementary Information). These contain a mix of arctic, temperate, subtropical and tropical sites; clearly there will be biogeographic differences between regions (see section 3.1) and this is represented by the high standard deviations associated with these mean value, 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 that's 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 behaviours that make them good pollinators. In addition the bees are the only group that are 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 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, whilst in section 4 we will 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 class of pollination system, involving marine seagrasses and flower-visiting crustaceans and polychaete worms was described (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 18th century, and include important scientists such as Koelreuter, Sprengel, Darwin, and Muller (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 whether 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) but, despite 200 years of studying plant-pollinator interactions, our understanding of 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 north-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 (Ollerton et al. 2003, Shuttleworth and Johnson 2009, Olesen and Valido 2003, Johnson 2004) and may in fact be much more widespread than we realise – they are not just “tropical novelties”. This then begs the question of just how “different” plant-pollinator interactions are in the tropics compared to 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 fixed in space: there is considerable biogeographic structure to both the numbers of pollinators in different parts of the world, and their taxonomic identity. In particular the biodiversity of pollinators changes with both latitude and continent, reflecting the varied evolutionary histories of different parts of our planet. However there is currently significant geographical bias that affects our understanding of the relative importance of different groups of pollinators, and many parts of the world remain largely unstudied (Rech et al. 2015). 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 (Ollerton et al. 2006, Michener 2007) – see Figure 2. However 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 in the Neotropics are around five times more diverse (in terms of species per unit area) than those in the Nearctic, as are Indo-Australian faunas compared to those in the Palaeartic, though Afrotropical Lepidoptera diversity is only about twice that of the Palaeartic (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 north-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 and Johnson 2009). Similarly, Australian plants have evolved pollinator relationships with a wide diversity of “non-standard” pollinators (Armstrong 1979). In the Arctic flies are the dominant pollinators (Tiusanen et al. 2016), whilst 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.

Other notable biogeographic patterns of pollinator distribution include the fact that bird pollination of native plants is rare 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, honeyeaters in Australia (Cronk and Ojeda 2008). The relative absence of specialised bird pollination in Europe is a mystery given the historical presence of hummingbirds during the Oligocene (see section 3.4). However a range of non-specialist

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 realise, but relatively unrecorded.

3.2 How “different” are plant-pollinator interactions in the tropics?

The trend of increasing species richness from polar to tropical regions has been recognised since at least the 18th 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 Vázquez and Stevens 2004, Moles and Ollerton 2016). 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 noted above (see also my comments about sub-tropical 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 and Jordano 2002, Ollerton and 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, whilst Pauw & Stanway (2015) presented evidence that suggested there may be a trend of increasing specialisation towards the tropics in the southern (but not the northern) hemisphere, which they attributed to climatic stability in the southern hemisphere over a long time scale, which 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 north temperate and southern hemisphere communities, rather than just tropical areas as a

whole, i.e. that sensitivity to perturbation is geographically complex rather than predictable just from latitude (Bugoni et al. in press).

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 species recorded (including managed hives of honey bees) only 4 were likely to be native (Weissmann et al. 2017). This is exceptional but nonetheless 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 honey bee (*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 honey bees can out-compete native bees and other flower visitors though this does seem to depend upon whether the landscapes are simple and homogenous or complex and heterogeneous in their structure, with regard to the amount of semi-natural habitat available for bee foraging (see Herbertsson et al. 2016). Studies have also shown that honey bees 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 *Bombus terrestris* which is now widely considered to be an invasive alien in regions where it is non-native (Dafni et al. 2010), and implicated in the regional loss of native *Bombus* species (Morales et al. 2013). It is not just the direct effects of competition that concerns conservationists, 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 where the native pollinators are rare or absent. For example in the 1980s Paul Alan Cox 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 (Cox 1983). 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 (*F. 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 an invasive plants. However there is also the possibility that this introduced moth has 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 what are 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

As well as human-induced changes in the distribution of species, we would also expect there to be some natural changes occurring due to the expansion and contraction of ranges by species in response to processes such as changes in resource availability, weather, opportunistic dispersal, and so forth. This has been well documented in Britain since the start of the new millennium, where a number of bee species new to the British Isles have become established and flourished. The best documented of these are the Ivy Bee (*Colletes hederæ*) and the Tree Bumblebee (*Bombus hypnorum*), that both arrived in 2001 (Goulson and Williams 2001, Roberts and Vereecken 2010) and have been tracked by the Bees, Wasps and Ants Recording Society (BWARS). According to Rasmont et al. (2015), the expansion of *Bombus hypnorum* into Britain was just the next step in an on going increase in this Eurasian-wide species that has even made it to Iceland. This is not the only example: the Asian *Bombus schrencki* has expanded westwards as far as Poland and Finland (Rasmont et al. 2015), whilst López-Urbe and Cane (2016) have documented the expansion of a specialist squash bee (*Peponapis pruinosa*) in parallel with crop domestication, and Russo (2016) cites 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 kilometres 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 will have been lost naturally (Ollerton et al. 2014). Indeed during the long revision period for that paper, one species was rediscovered and had almost certainly naturally re-colonised 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 documented 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, some 30 million years ago (Mayr 2004, Louchart et al. 2008). 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 will 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. (2010), Lebnh et al. (2013). However disagreements have emerged as to how accurate these assessments are, and whether the decline of pollinators (and particularly bees) has been overplayed in the literature and by the media (Ghazoul 2005). Recently Dave Goulson and colleagues reviewed the evidence for drivers of bee declines (Goulson et al. 2015a), which

resulted in some correspondence criticising their conclusions from a number of perspectives, but particularly 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 pollinators of all plants (including the majority non-cultivated species) and on bees. Looking more broadly across the pollinators 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”. Underlying this statement is the suggestion that global concerns about declining pollinator biodiversity is underpinned by a taxonomically and geographically thin evidence base. However this is clearly not the case as the following summary of the current evidence shows; it’s not meant to be a full review, by any means, but rather to give a flavour of the taxonomic and geographical breadth and depth of the evidence as it currently stands:

Wild bees (including bumblebees, and solitary and primitively eusocial bees) – significant reduction of abundance and diversity at local, regional and country-levels documented in Britain and the Continent (Biesmeijer et al. 2006, Ollerton et al. 2014, Nieto et al 2014); South America (Morales et al. 2013); Asia (Williams et al. 2009); South Africa (Pauw 2007); and North America (Cameron et al. 2011, Burkle et al. 2013) where 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.

Honey bees – colony declines documented in Europe and North America (see Potts et al. 2010) and evidence that global demand for honey bee pollination services is outstripping supply (Aizen and Harder 2009).

Hoverflies – diversity declines documented in Holland and Britain (Biesmeijer et al. 2006).

Butterflies and moths – diversity and abundance of Lepidoptera has declined in the UK (Fox 2013), whilst in North America some 50 species are IUCN criteria Red Listed and there is particular concern about the iconic Monarch butterfly. Likewise a significant fraction of butterflies in other parts of the world are of conservation concern, e.g. southern Africa, Australia, and Europe.

Flower-visiting wasps – reduction in country-level diversity in Britain (Ollerton et al. 2014).

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. They 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, whilst 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 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 honey bee colonies in some parts of the world). There is also evidence of a slow down in the loss of pollinators across north-west Europe (Carvalho et al. 2013 – but see Ollerton et al. 2014). But over all the current evidence base points towards significant declines in pollinator abundance and diversity at multiple spatial scales across all regions that have so-far been assessed with any rigour, for a wide range of taxa.

The causes of these declines continue to be widely discussed, but changes in land use and management following agricultural intensification are the most likely reasons (Potts et al 2010, Ollerton et al. 2014, Goulson et al. 2015a, Bartomeus et al. 2013). 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 modelling approaches for some time, beginning with butterflies in the 1990s (Parmesan et al. 1999) 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 the bees have been studied including the bumblebees (*Bombus* spp. Apidae), arguably the most important single genus of pollinators of plants in north temperate regions. This genus has been the subject of detailed scenario modelling 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 (by the by) 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 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 over 80% of their current range), whilst 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 between 34 and 52 species in the period up to 2050, and for 49 to 55 species in the period 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, with regions in Spain and Portugal being left with just one

bumblebee species by 2050, with potential knock-on 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 observation that, between 1996–2009, arctic flowering seasons became shorter and flower visitors less abundant is of concern (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).

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 colonise new suitable areas. Conservation programmes 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 UK, USA, Ireland and other countries, and 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 centres (Baldock et al. 2014, Sirohi et al. 2014) and tropical island inselbergs (Kaiser-Bunbury et al. 2017), as well as national initiative by NGOs such as (in the UK) Buglife’s B-Lines project and work by the Xerces Society in the USA. However such strategies may not be feasible in high alpine and arctic regions that are limited in terms of where pollinators 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 varyingly practical, theoretical or abstract in their point of view. First of all, the ecological and agricultural function of diverse, as opposed to depauperate, pollinator assemblages is claimed to be superior. Secondly, 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 (Jordano 1987; Waser et al. 1996; Fenster et al. 2004, Brosi 2016) and 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”. 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 and Althoff 2016). Others are also not mutually dependent where 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). The other pole of the continuum contains highly generalized relationships between flowers that attract a wide range of pollinators, for example some North American *Asclepias* species that are known to be pollinated by more than one hundred different types of insects (Ollerton & Liede 1996), 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).

Categorising a plant or pollinator, and placing it upon this continuum, depends upon the spatial and temporal scale at which we observe the interactions. Widespread species can be rather specialized in their immediate locality but much more generalized when considered across their whole range, for example Herrera 1988, Ollerton et al. 2009, Gómez et al. 2013. Likewise, relationships between flowers and pollinators can vary between years 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 effort: how do we know that we have put enough time into understanding a study system? Under-sampling can lead to spurious conclusions regarding the level of specialization of a plant or pollinator, whilst it is

hardly possible to over-sample 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 towards 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, whilst 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, however with mixed results (see section 5.2).

A commonly voiced criticism of assessments of “pollinator” diversity of plants is that the “pollinators” surveyed are usually flower visitors rather than actual pollinators. This is a criticism that has been particularly aimed at network studies of plant-flower visitor assemblages, and there is some validity in that criticism (though it’s worth noting that flower visitation itself, regardless of the outcome for the plant, is a positive interaction from the visitor’s perspective). Unfortunately there are rather few data 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. However this is an important question 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 (Radar et al. 2016). The asclepiads (Apocynaceae: Asclepiadoideae) can give us a very useful an 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 and Liede 1997). Figure 3 shows the relationship

between the number of insects observed visiting flowers of 18 species of asclepiad in the grasslands of KwaZulu-Natal (South Africa) and 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. However as species become progressively more generalized, a lower proportion of flower visitors act as pollinators. Indeed for the most generalist plants fewer than one third of the visitors are effective pollinators. However this must be considered a conservative value as some of those insects that were recorded as not carrying pollinaria almost certainly do, though the insects have not yet been observed due 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), Johnson and Shuttleworth (2009), and comments regarding southern Africa above.

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 where either managed pollinators must be imported (for example honey bees to almond orchards) or a loss of crop yield endured. This is explored in more detail in the following section.

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, etc. (Potts et al. 2010, Ollerton et al. 2014, Goulson et al.

2015a). It 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 has important implications for pollinator conservation and is at the centre 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 and Boeke (2006), using plots of 1.5 m x 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 m x 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 about 10 insect species, whereas Steffan-Dewenter and Tschardtke (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,

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 there is mixed support for this idea coming from research that has used an experimental approach. 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 and Briggs (2013) found that removing a single bumblebee species from localised 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 four 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 over all 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 loss of pollinators for crop plants is 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 (Garratt et al. 2014a, Blitzer et al. 2016), and holly and mistletoe (Ollerton et al. 2016).

There are, however, few good examples of pollinator deficits affecting crop yields (Aizen et al. 2008) though 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 both disproportionate amount of essential minor nutrients in the human diet, and economic value (IPBES 2016). One case study example will serve 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. 2011), 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 60kg (International Coffee Organisation 2017). One coffee bean is the product of a single fertilisation event following the deposition of at least one pollen grain on a flower's stigma. The mean weight of a single coffee bean is about 0.1g which means there are approximately 600,000 beans in a 60kg 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 >90 trillion coffee beans. However coffee is on average 50% self pollinating (Klein et al. 2003) and a single bee visit

may pollinate 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 semi-natural habitat as well as coffee plantations in order 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 the that period the relative importance of different groups of pollinators has waxed and waned, whilst overall diversity has increased in parallel with the 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 (at levels from 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 made significant progress, but there is still a lot to learn. It is only in the last twenty years or so that scientists interested in these questions have begun to assemble global data sets that address questions such as: how does wind and animal pollination vary across the globe; how important are different groups of animals as pollinators; what are the patterns of pollen limitation, and how do they 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 ever more

observational and experimental data, and monitoring and detailed surveys to build a robust picture of pollinator diversity and declines. Contemporary pollinator diversity is the result of millions years of tight and diffuse co-evolution 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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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 appendix 1.

Figure 2: Regional and country-level bee species richness in relation to latitude. Data are from Michener 2007 and Kirkitadze and Japoshvili (2015), corrected for area of the country/region concerned.

Figure 3: (a) The relationship between number of observed flower visitors and number of proven pollinators for 18 species of grassland asclepiad (Apocynaceae: Asclepiadoideae) in the South African grasslands of KwaZulu-Natal. The grey line is the 1:1 relationship expected if all visitors were pollinators; (b) the relationship between number of flower visitors and the proportion of flower visitors that act as pollinators. Data from Ollerton et al. (2003) and Shuttleworth and Johnson (2009).

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 appendix 2.

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 sub-groups	Sources
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)		5000	Pitt et al. 2005
Social wasps (Vespoidea)		5000	
Diptera (flies)	55,000		Wardhaugh (2015)
Hoverflies (Syrphidae)		6,000	
Bee flies (Bombyliidae)		4,500	

Thysanoptera (thrips)	1,500	Wardhaugh (2015)
Aves (birds)	1089	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
Non-flying mammals (various)		108
Neuroptera (lacewings)	293	Wardhaugh (2015)

Trichoptera (caddisflies)	144	Wardhaugh (2015)
Orthoptera (crickets)	100	Wardhaugh (2015) - possibly an over-estimate, as only one species confirmed as pollinator (Micheneau et al. 2010)
Mecoptera (scorpionflies)	76	Wardhaugh (2015)
Psocoptera (barkflies)	57	Wardhaugh (2015)
Plecoptera (stoneflies)	37	Wardhaugh (2015)
Lacertilia (lizards)	37	Olesen & Valido (2003)
Dermaptera (earwigs)	20	Wardhaugh (2015)
Crustacea (mainly Isopoda)	11	Ollerton 1999, Tussenbroek et al. (2016)
Polychaeta (marine worms)	3	Tussenbroek et al. (2016)
Total	349,368	

Figure 1:

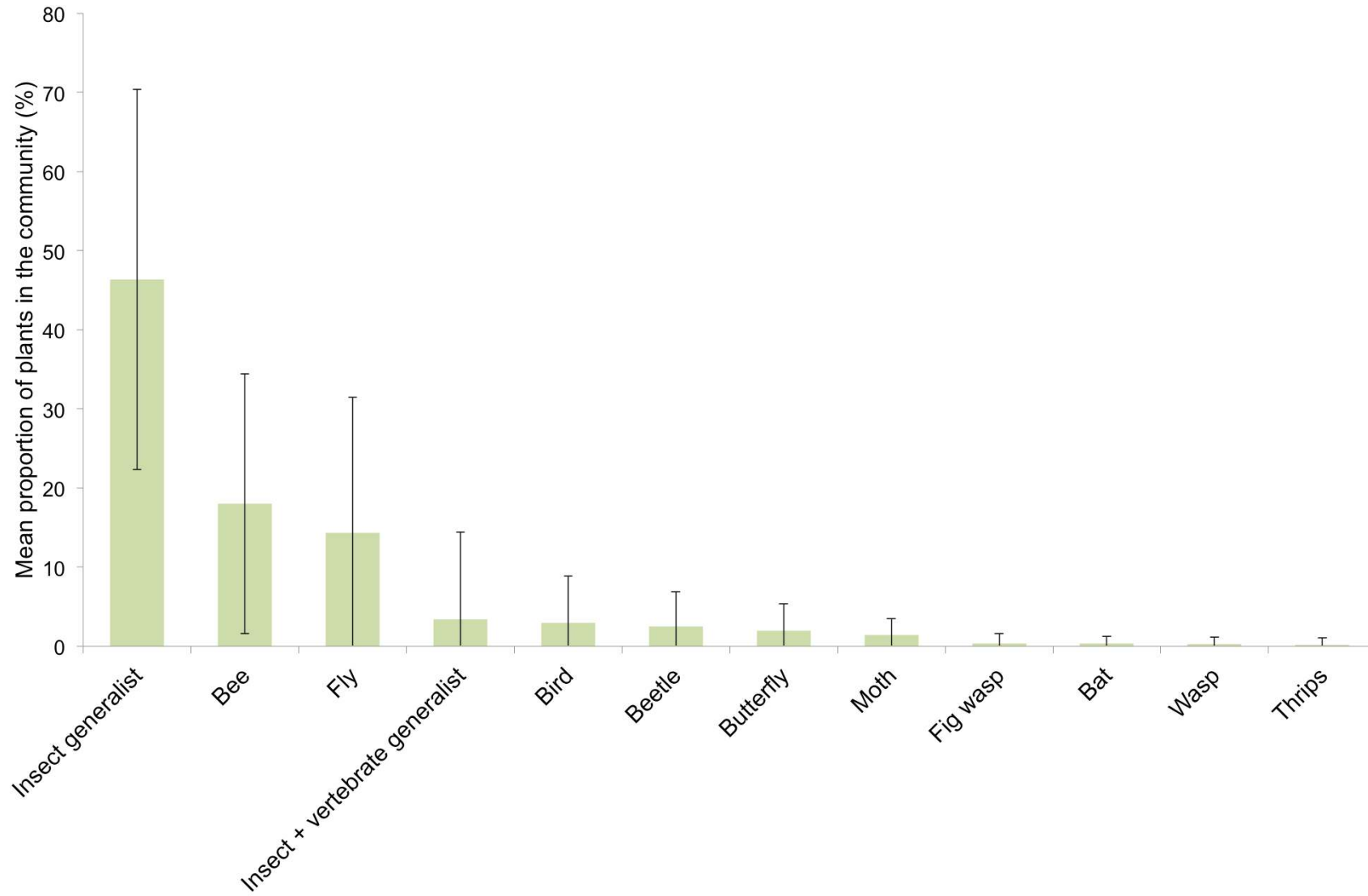


Figure 2:

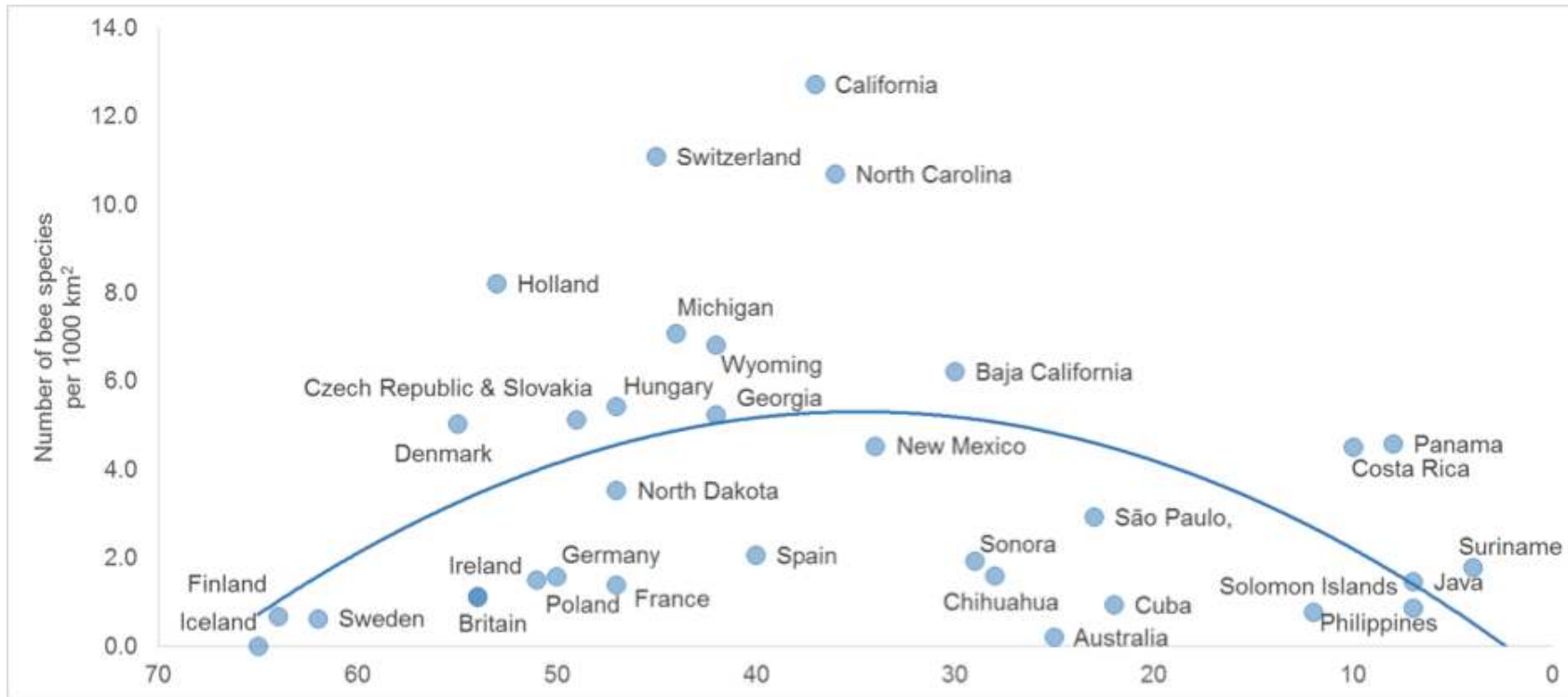


Figure 3:

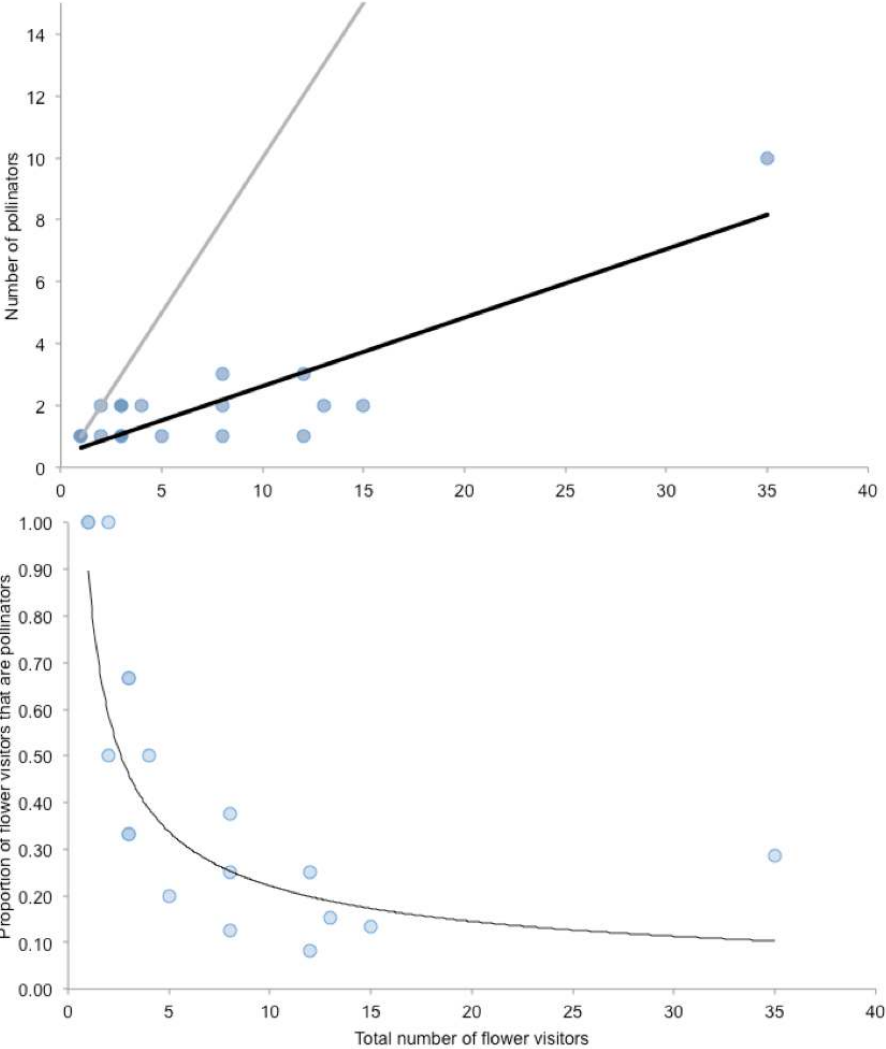
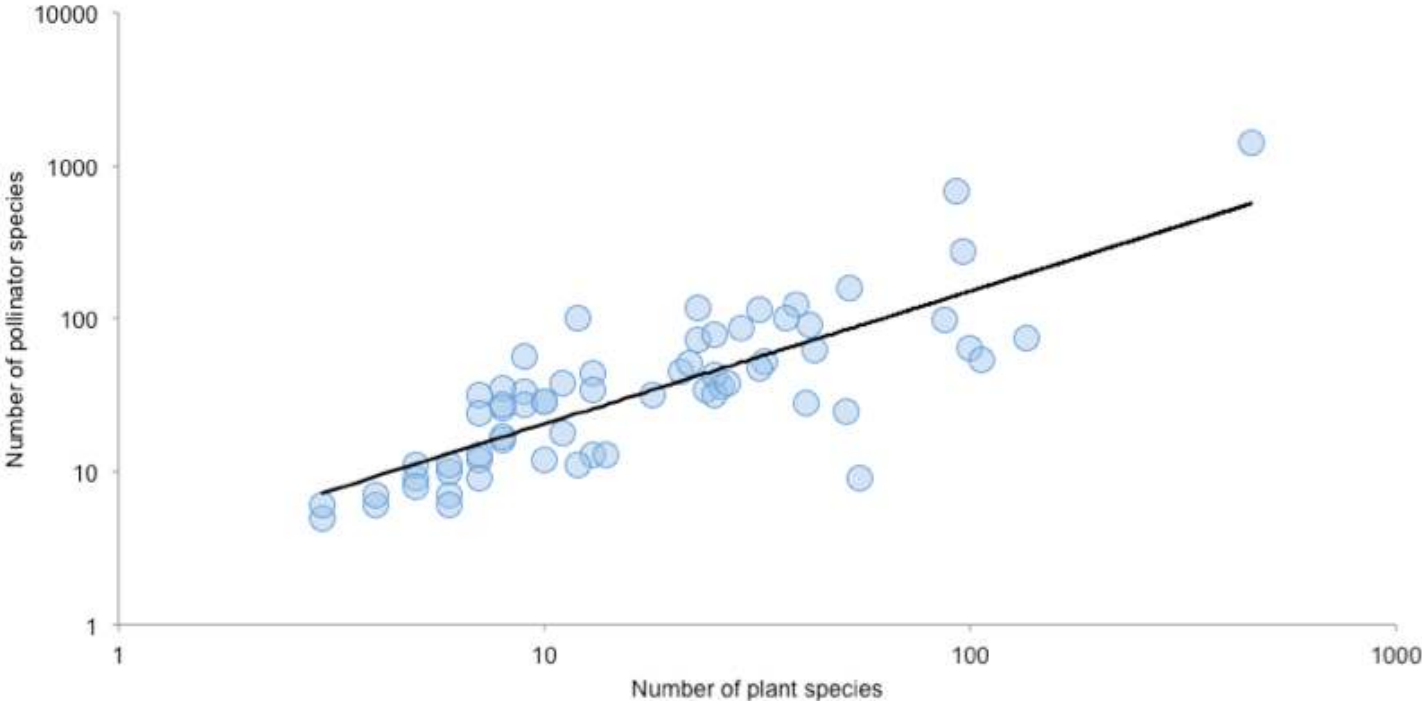


Figure 4:



Appendix 1:

Percentages of total number of plants in community assigned to pollination systems

Reference	Study site	Moth	Bee	Butterfly	Wasp	Fig wasp	Beetle	Fly	Thrips	Insect		Insect + vertebrate		Wind	
										generalist	Bird	generalist	Bat		
Anderson et al. (2001)	Juan Fernandez Islands, Chile	?	0.0	0.0	0.0	0.0	2.4	4.8	0.0	9.5	26.2	2.4	0.0	54.8	SUBTRO
Arroyo et al. (1982)	Andes, Chile		0.0	11.4	0.0	0.0	0.0	0.0	25.7	0.0	62.9	0.0	0.0	0.0	SUBTRO
Barrett & Helenurm (1987)	Boreal forest, New Brunswick, Canada		0.0	0.0	0.0	0.0	12.5	12.5	0.0	75.0	0.0	0.0	0.0	0.0	TEMP
Bosch et al. (1997)	Savannah grassland, NE Spain	?		5.9	0.0	0.0	0.0	5.9	0.0	88.2	0.0	0.0	?	?	TEMP
Burkill (1895)	Coastal scrub, UK		0.0	18.9	0.0	0.0	0.0	18.9	0.0	37.8	0.0	0.0	0.0	24.3	TEMP
Clements & Long (1923)	Alpine grassland, Pike's Peak		1.1	39.4	2.1	0.0	0.0	1.1	4.3	46.8	0.0	5.3	0.0	?	TEMP
Corlett (2001)	Degraded tropical scrub/secondary forest		1.2	34.9	2.4	1.2	0.0	1.2	0.0	55.4	0.0	3.6	0.0	0.0	TROP
Eberling & Olesen (1999)	subarctic alpine, North Sweden		0.0	0.0	0.0	0.0	0.0	47.4	0.0	52.6	0.0	0.0	0.0	?	ARCT
Herrera (1988)	Spain		0.0	0.0	0.0	0.0	0.0	0.0	0.0	80.8	0.0	0.0	0.0	19.2	SUBTRO
Hingston & McQuillan (2000)	Tasmania, Australia	?		1.6	0.0	0.0	0.0	0.0	0.0	85.2	0.0	13.1	?	?	TEMP
Hocking (1968)	Arctic tundra		0.0	16.0	0.0	0.0	0.0	32.0	0.0	44.0	0.0	0.0	0.0	8.0	ARCT
Inoue et al. (1990)	Kibune, temperate deciduous forest	?		11.4	0.0	0.0	0.0	1.1	6.8	0.0	80.7	?	?	?	TEMP
Inouye & Pyke (1988)	Snowy Mts, NSW, Australia		3.1	3.1	0.0	0.0	0.0	40.6	0.0	53.1	0.0	0.0	0.0	?	SUBTRO
Kato et al. (1990)	Ashu, Japan	?		29.4	0.0	0.0	0.0	1.5	8.8	0.0	60.3	?	?	?	TEMP
Kress & Beach (1994)	La Selva, Costa Rica		7.5	38.3	2.5	0.0	2.5	12.3	1.8	0.4	13.0	16.2	0.0	2.9	2.5
Medan et al. (2002)	Andean lower altitude	?		39.1	8.7	0.0	0.0	8.7	0.0	34.8	8.7	0.0	0.0	?	SUBTRO
Medan et al. (2002)	Andean higher altitude	?		28.6	0.0	4.8	0.0	4.8	4.8	52.4	0.0	0.0	0.0	?	SUBTRO
Momose et al. (1998)	Rainforest, Malaysia		0.8	50.4	3.9	0.8	0.0	17.1	3.9	1.6	10.9	8.5	0.0	2.3	0.0
Mosquin & Martin (1967)	Arctic tundra		0.0	0.0	0.0	0.0	0.0	75.0	0.0	25.0	0.0	0.0	0.0	?	ARCT
O'Brien (1980)	Alpine pavement plain, California		0.0	6.7	0.0	0.0	0.0	20.0	0.0	53.3	6.7	0.0	0.0	13.3	SUBTRO
Percival (1974)	Jamaica	?		0.0	10.0	0.0	0.0	0.0	0.0	30.0	0.0	60.0	?	?	TROP
Pojar (1974)	Salt marsh, Canada		0.0	5.6	0.0	0.0	0.0	11.1	0.0	16.7	0.0	0.0	0.0	66.7	TEMP
Pojar (1974)	Sphagnum bog, Canada		0.0	17.6	0.0	0.0	0.0	26.5	0.0	11.8	0.0	2.9	0.0	41.2	TEMP
Pojar (1974)	Subalpine meadow, Canada		2.2	15.6	0.0	0.0	0.0	6.7	0.0	46.7	2.2	2.2	0.0	24.4	TEMP
Primack (1983)	New Zealand montane		3.4	1.7	0.0	0.0	0.0	32.2	0.0	62.7	0.0	0.0	0.0	?	TEMP
Ramirez & Brito (1992)	Palm swamp, Venezuela	?		45.5	9.1	0.0	0.0	3.0	3.0	0.0	18.2	6.1	0.0	0.0	15.2
Robertson (1928)	Prairie, Illinois		0.3	13.3	0.3	0.0	0.0	1.3	0.0	73.7	0.8	6.6	0.0	3.8	TEMP
Small (1976)	Peat bog, Canada		0.0	7.7	0.0	0.0	0.0	15.4	0.0	76.9	0.0	0.0	0.0	?	TEMP
Struck (1995)	Semi-arid plain, South Africa		5.7	37.1	11.4	0.0	0.0	5.7	8.6	0.0	31.4	0.0	0.0	?	SUBTRO
van Dulmen (2001)	Upland rainforest, Colombia		2.3	41.9	3.5	1.2	3.5	7.0	0.0	29.1	7.0	3.5	1.2	0.0	TROP
van Dulmen (2001)	Flooded rainforest, Colombia		4.0	38.6	6.9	0.0	5.9	5.9	0.0	19.8	5.9	2.0	3.0	2.0	TROP
Willis & Burkill (1895-1908)	Lower alpine, Scotland		0.7	17.5	0.7	0.0	0.0	31.5	0.0	44.8	0.0	0.0	0.0	4.9	TEMP

	Moth	Bee	Butterfly	Wasp	Fig wasp	Beetle	Fly	Thrips	Insect ge	Bird	Insect + vertebr:	Bat	Wind
Mean	1.4	18.6	2.0	0.3	0.4	2.5	14.7	0.2	47.5	2.1	3.4	0.4	15.0
SD	2.1	16.4	3.5	0.9	1.3	4.4	17.3	0.9	23.4	4.0	11.3	0.9	18.6

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