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Published Version

Mayer, C., Adler, L., Armbruster, W. S., Dafni, A., Eardley, C., Huang, S.-Q., Kevan, P.G., Ollerton, J., Packer, L., Ssymank, A., Stout, J. C. and Potts, S. ORCID: https://orcid.org/0000-0002-2045-980X (2011) Pollination ecology in the 21st century: key questions for future research. Journal of Pollination Ecology, 3. pp. 8-23. ISSN 1920-7603 Available at https://centaur.reading.ac.uk/24986/

Published version at: http://www.pollinationecology.org/index.php?journal=jpe&page=article&op=view&path[]=103

Publisher: Enviroquest Ltd

Journal of Pollination Ecology, 3(2), 2011, pp 8-23

POLLINATION ECOLOGY IN THE 21ST CENTURY: KEY QUESTIONS FOR FUTURE RESEARCH

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Abstract—To inspire new ideas in research on pollination ecology, we list the most important unanswered questions in the field. This list was drawn up by contacting 170 scientists from different areas of pollination ecology and asking them to contribute their opinion on the greatest knowledge gaps that need to be addressed. Almost 40% of them took part in our email poll and we received more than 650 questions and comments, which we classified into different categories representing various aspects of pollination research. The original questions were merged and synthesised, and a final vote and ranking led to the resultant list. The categories cover plant sexual reproduction, pollen and stigma biology, abiotic pollination, evolution of animal-mediated pollination, interactions of pollinators and floral antagonists, pollinator behaviour, taxonomy, plant-pollinator assemblages, geographical trends in diversity, drivers of pollinator loss, ecosystem services, management of pollination, and conservation issues such as the implementation of pollinator conservation. We focused on questions that were of a broad scope rather than case-specific; thus, addressing some questions may not be feasible within single research projects but constitute a general guide for future directions. With this compilation we hope to raise awareness of pollination-related topics not only among researchers but also among non-specialists including policy makers, funding agencies and the public at large.

Keywords: *angiosperms, conservation, evolution, ecosystem services, diversity, mutualism, species interactions*

INTRODUCTION

Since Sprengel (1793) published his famous findings on the interactions between flowers and insects that transport pollen grains to the stigmas of plants, demonstrating that they are essential for the production of seeds and fruit, our knowledge of pollination as an essential ecosystem process has vastly increased. The large majority of flowering plant species in almost all angiosperm-dominated communities studied so far interact with pollinators, ranging on average from 78% in temperate communities to 94% in tropical communities, equalling over 308,000 species or more than 87% of all angiosperms (Ollerton et al. 2011). Moreover, it has been suggested that over 300,000 animal species are directly dependent upon floral resources (Buchmann & Nabhan 1996).

Plant-pollinator interactions have always provided excellent model systems to test and develop new theories in ecology and evolution (Mitchell et al. 2009). Nevertheless, because of the huge breadth (for a few examples see Fig. 1), depth and scope of this discipline, there is no doubt that many issues remain unresolved or have not been fully explored. All of the questions that we present in this paper

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Received 19 November, accepted 10 March 2011

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have previously been addressed by researchers to some degree and we do not wish to give the impression that they have never been investigated. However, these are questions that, in the minds of a significant sample of researchers in the field, are not yet fully resolved. By defining the most urgent questions, we seek to identify knowledge gaps in pollination ecology to inspire future research. Today, we are facing a global decline of biodiversity, fuelled by the immense destruction and degradation of habitats and climate change through human activities, which also heavily affects and interrupts plant – pollinator relationships (Kevan & Baker 1983; Aizen & Feinsinger 1994; Kearns et al. 1998; Kevan 1999; Kremen et al. 2002; Biesmeijer et al. 2006; Winfree et al. 2007; Memmott et al. 2007). This spurs the need to define priorities for plant and pollinator conservation and to invoke responses from policy makers and stakeholders to seize the initiative for action.

Previous 'brainstorms' have been highly successful in informing researchers and decision makers (National Research Council 2006; Sutherland et al. 2006, 2009). Such overarching efforts can inspire lively discussions not only from scientists but also from conservationists, politicians and funders. Our aim is to organize our efforts into thematic approaches, to raise consciousness among non-specialists and to draw attention to research topics that are still largely outside public awareness. In this paper we are using the term "pollination ecology" in its broadest sense to cover a range of topics associated with plant reproduction and the role of pollinators (and other interacting species) in influencing that reproduction. Scientists must help to define priorities for plant and pollinator conservation in order to engage policy makers, conservation organisations and other stakeholders.

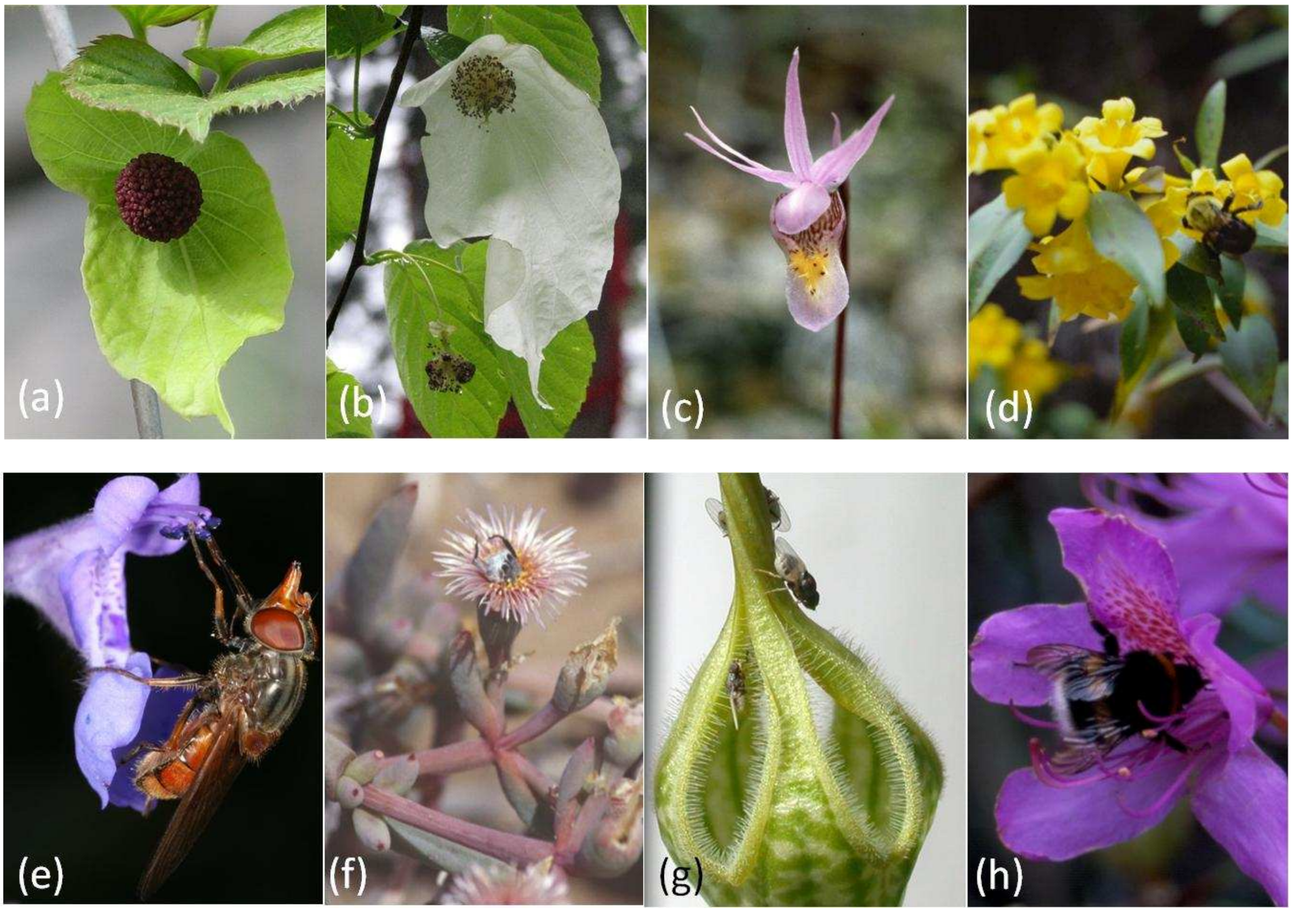

Figure 1. A few examples of the amazing breadth of pollination ecology: The dove tree (*Davidia involucrata*) has "naked" flowers that lack a perianth but are surrounded by two large bracts. These turn from green (a) to white (b) when flowers open which increases pollinator attraction (see Sun et al. 2008). *Calypso bulbosa* (c), a rewardless orchid, has evolved to deceive naïve bumblebees in the early spring to effect pollination without payment in nectar (see Ackerman 1981). The perennial vine, *Gelsemium sempervirens* (d), contains alkaloids in all plant parts including corollas and nectar which deter floral herbivores and nectar robbers but - in high concentrations - also pollinators (Adler & Irwin 2005). Hoverflies (e) visit flowers in a large range of habitats, they even pollinate cultivated plants. Though they are numerous, species-rich and wide-spread, their role as pollinators is often still neglected. (f) In the Succulent Karoo of South Africa, monkey beetles (Hopliini) are important pollinators of many plant species (Mayer et al. 2006). This one is diving into a flower of *Ruschia goodiae* (Aizoaceae) to reach nectar. (g) Flowers of *Ceropegia arabica* (Apocynaceae) are pollinated by small Diptera in common with all other members of the genus studied to date (Ollerton et al. 2009). Photograph by Sage Reynolds. *Rhododendron ponticum* (h) is a highly invasive plant in Ireland. Though it provides food resources for generalist bumblebees, effects on native plant pollinator interactions vary with intensity of invasion.

METHODS

The authors of this paper compiled a list of 170 researchers in pollination ecology around the world with whose work they were familiar and who had made (in their opinions) significant contributions to the field of pollination ecology over the last two decades. This was not meant to be an exhaustive polling but rather a representative sample, and the exclusion of any researchers from the process in no way implied that the authors did not value their work. In March 2010, these researchers were consulted by email and asked to formulate what they thought were the crucial questions in pollination ecology that should be explored within the coming decades. Most (>80%) of those polled are based in Europe or Northern America (Appendix I).

We asked for questions that should (a) address important knowledge gaps, (b) not be too case-specific or detailed, (c) be of interest to non-specialists, and (d) answerable in time and space under reasonable budgetary constraints. We proposed 17 preliminary broad thematic categories that were meant to assist in structuring one's opinion, but there was no demand for respondents to contribute to all of them. However, when compiling the final list we set value on the significance and scope of the questions rather than feasibility within the timeframes of single research projects.

From the 170 scientists contacted, 66 were able to respond (39 % of those asked). They provided a total of 663 queries and comments that were assigned to the categories (if not done so by the consultees themselves). Of the 17 preliminary categories, four were discarded since there were hardly any replies which could not be fitted into other topics (the discarded topics were: "Status and trends of global pollinators", "Pollinators and technological development", "Methodology in pollination" and "Environmental effects on pollination"). On the other hand, one new category was created ("Evolution of animal-mediated pollination") corresponding to the demand from several contributors. The questions were then merged and rephrased within categories, which were handled by different members of our team. This procedure narrowed the initial list to about 170 questions (Appendix II). The authors of this paper (who comprise most of the Editorial Board of the Journal of Pollination Ecology) then indicated their preferences by vote, either giving one credit to each of 100 questions or allocating more credits to fewer questions (to a total of 100 credits per voter). After voting, the questions were ranked according to preference (i.e. number of credits) and the first one hundred selected. Based upon feedback from the respondents and discussions among the authors and because of persisting overlap between the general topics of some questions after voting, we narrowed down the number of questions to a final list of 86. In October 2010 these questions were presented to delegates at the 24th Scandinavian Association for Pollination Ecology (SCAPE) meeting at Tovetorp, Sweden. The long and detailed discussion that followed was used as the basis for the final refinement of the list of questions. In this final list, we have not ranked nor ascribed an order of importance to the questions. The contributors are acknowledged at the end of this paper.

RESULTS

For each of the 14 categories of questions given below, we present a short piece of text to give the questions context and then list the questions themselves. The categories are sorted so as to begin with more basic aspects of plant sexual reproduction followed by topics on the interaction of plants and animals. Risks for plant-pollinator interactions are then addressed, leading to more applied fields of study such as management and conservation.

1. Plant sexual reproduction (Box 1)

Unlike most animals, many plants are capable of reproduction via sexual and asexual means. Since plants are sessile, in order to successfully reproduce sexually they have evolved specialised floral structures, many of which promote out-crossing, driven by the benefits associated with population level genetic diversity (such as the ability of a population to adapt in response to environmental change, improved resistance to disease, etc.; Barrett & Harder 1996). Despite this, self-fertilisation is possible, frequent and even promoted in some flowers (within and among individuals, populations and species; Uyenoyama et al. 1993; Redbotorstensson & Berg 1995; Culley 2002). However, it is not clear what drives plants to adopt autonomous pollination strategies, although possibilities include reproductive assurance in the face of pollen limitation, maintenance of locally-adapted genotypes and lack of requirement for a mate during colonisation of new habitats (Lloyd 1979; Kalisz & Vogler 2003).

Recent work suggests that floral traits are not just driven by the breeding strategy of the plant (whether its strategy is out-crossing or selfing), but are the result of selection by abiotic and biotic factors, which can in turn affect the breeding strategy of the plant. For example, water availability can inflict constraints on the evolution of floral size, which then influences the likelihood of selfing (Elle 2004); other abiotic factors, such as soil nutrients, light, and temperature, could play similar roles. Flower shapes may affect intrafloral temperature, or even function as pollen shelter to reduce rain damage (Mao & Huang 2009). The role of abiotic factors in floral evolution is largely underappreciated.

1. Why are some plant species capable of autonomous pollination – and what are the consequences regarding inbreeding depression and population viability?
2. Does pollen limitation affect breeding systems, genetic diversity and speciation rates and, if so, how?
3. What is the relative contribution of abiotic versus biotic factors in shaping the evolution of flowers?
4. Is male reproductive success more variable than female reproductive success?
5. Is there sexual selection in plants?
6. What is the role of hybridization in plant speciation?

Box 1: Questions on plant sexual reproduction

Since the majority of flowers are hermaphrodite, fitness can be determined as the result of female (seed set) and male (pollen dispersal) reproductive success. Male success can be more variable since, theoretically, a male (or male phase) flower can fertilize numerous female (or female phase) flowers. Although the importance of male function was emphasized by Bell (1985), tracking pollen movement, male success and fitness is technically difficult. Furthermore, variation in female fitness according to structural properties of flowers remains to be investigated. For example, we do not know whether apocarpous species with distinct, single-carpelled pistils are more likely to experience pollen limitation than syncarpous species with united carpels (Endress 1982; Armbruster et al. 2002). Or, whether there is a functional difference between polypetalous (separate petals) and sympetalous (united petals) flowers.

2. Pollen and stigma biology (Box 2)

Assessments of the duration of pollen viability and stigma receptivity are critical for many aspects of pollination biology (Dafni et al. 2005 and references therein), including: monitoring pollen and stigma life spans, the success of pollination at different stages in the flower life-cycle, the relative importance of various pollinators, the interference between male and female functions, the rate of competition through improper pollen transfer, the chances of gametophytic selection, and the assessment of pollination efficiency. Evaluation of pollen viability and stigma receptivity is the first step towards an evaluation of the chances of a given pollen grain to germinate. A pollen grain that fails to germinate on a conspecific and genetically appropriate receptive stigma, and later to fertilize an ovule, results in an unsuccessful pollination event.

7. How can we assess pollen viability and stigma receptivity under field conditions?
8. How often is "stigma clogging" (incompatible pollen physically blocking the stigma) an important effect in nature?
9. What influences the pollen availability of a population?
10. What proportion of pollen grains from a plant are viable?
11. How much viable pollen is transferred to flowers?
12. What is the lifespan of pollen grains?

Box 2: Questions on pollen and stigma biology

The pollen-stigma relationship depends on pollen viability, stigmatic receptivity, and genetic interaction of both partners as dictated by the incompatibility system and may vary according to environmental conditions such as relative humidity or temperature (Franchi et al. 2007; Douglas & Freyre 2010). Even a successful pollen germination event does not ensure later success. For example, pollen grains compete with each other or interact with style tissues which may interfere and block fertilization, as may late-acting incompatibility processes, post-zygotic abortion and pollen allelopathy. Any study on the quality and quantity of pollen grains, their fate and chances of pollination success in the context of environmental variation and pollinator performance should try to understand these components as a basic background (Ne'eman et al. 2010).

3. Abiotic pollination (Box 3)

About 20% of all angiosperm families contain plant species that do not rely on animal vectors for pollen transport, but use physical agents such as wind and water for pollen transfer (Ackerman 2000). Anemophily (wind pollination) has evolved many times and is quite common (estimated at about 10 to 13 % of all angiosperm species; Friedman & Barrett 2009; Ollerton et al. 2011). Hydrophily (water pollination) is mainly confined to monocotyledons and is found in only 2.7% of all angiosperm species (Ackerman 2000). Phylogenetic analyses propose that wind pollination evolves from insect pollination, but our knowledge about the underlying mechanisms or evolutionary pathways is still rudimentary (Culley et al. 2002; Friedman & Barrett 2009). However, a few cases exist suggesting some wind pollinated plants reverted to become insect pollinated (Norman et al. 1997; Peeters & Totland 1999).

Increasing records report anemophily in otherwise entomophilous families and species (Weller et al. 2006). Ambophily (both biotic and abiotic pollination occurring in the same flower) may occur under certain circumstances that favour either wind or insect pollination, providing an alternative to self-pollination to ensure successful reproduction (Culley et al. 2002). Ambophily may also be favoured where pollinator abundance varies and wind can transport supplementary pollen to pollinate otherwise unvisited flowers (Duan et al. 2009). One might hypothesise that pollen limitation is scarce among wind-pollinated plants if pollen transport by wind for some species serves as a reproductive assurance in the absence of pollinators (Friedman & Barrett 2009). However, apart from a few studies on species in fragmented habitats (e.g. Knapp et al. 2001; Eppley & Pannell 2009), investigations of pollen limitation or population densities and plant reproductive success in wind pollinated species are still lacking (see Friedman & Barrett 2009 and references therein).

13. How many animal-pollinated plant species have cryptic or partial wind pollination?
14. When, where and how did evolutionary shifts from biotic to abiotic pollination systems, and vice versa, occur?
15. How are biophysical mechanisms involved in abiotic pollination?
16. What are the relative proportions of biotic vs. abiotic pollination services in crop and wild plants?
17. How frequent is pollen limitation in wind pollinated plants?

Box 3: Questions on abiotic pollination

Early work concerning pollen release and dispersal described models of boundary-layer air flow around pollen grains and morphological structures of flowers adapted to direct microcurrents to deposit pollen on stigmas (Niklas 1985). Since high proportions of conspecific pollen can be found on stigmas (>40%, Linder & Midgley 1996), biophysical proportions such as settling speed may enhance filtering of pollen during pollen capture (Aylor et al. 2005; Friedman & Barrett 2009).

4. Evolution of animal-mediated pollination (Box 4)

Pollinators exert selective pressures on plants and their floral traits, and, similarly, plants may influence the evolution of pollinating animals. The evolution of floral traits has been proposed to be moulded by the most frequent and effective pollinators (Stebbins 1970; although see Aigner 2001). This can lead to co-evolution and co-adaptation resulting in varying degrees of specialisation, which can increase pollination accuracy and/or reduce heterospecific pollen interference. For example, mechanical fit between pollinators and flowers can partly explain the evolution of floral traits (such as spur length) and complementary animal traits (such as tongue length; Nilsson 1988; Whittall & Hodges 2007). However, it is increasingly recognised that the evolution of flowers is probably not so straightforward because many plants have more than one type of pollinator (Waser et al. 1996; Waser & Ollerton 2006) and floral evolution can be driven by conflicting selection by these pollinators, as well as by herbivores and other antagonists. The relative contributions of mutualists, antagonists (see topic 5) and abiotic factors in shaping the evolution of flowers is only beginning to be studied for most species.

18. What roles do pollinators play in the processes that lead to plant speciation?
19. What role does coevolution play in plant diversification?
20. How, and how frequently, do positive correlations emerge between floral specialisation and species diversity within a clade?
21. How and why does specialisation in pollination systems evolve and what are the driving factors?
22. Why does floral deception evolve?
23. How do plants avoid heterospecific pollen interference given that generalist pollinators visit other sympatric flowering plants?
24. How frequently do floral traits converge on traditional pollination syndromes?
25. What are the ultimate factors determining taxonomic diversity of visitors to a plant species?
26. How is floral diversity generated, or why are there so many kinds of flowers?

Box 4: Questions on evolution of animal-mediated pollination

Three methodological approaches and lines of enquiry have developed in the study of the evolution of plants, pollinators, and pollination systems: i) genetic and/or experimental research focusing on speciation and reproductive isolation, ii) genetic and/or experimental research focusing on microevolution, and iii) comparative research inferring evolutionary process from macroevolutionary patterns.

Traditionally, shifts between pollination systems or pollinators have been viewed in light of the establishment and maintenance of reproductive isolation and the speciation process (Grant 1949; Stebbins 1970). This perspective has enjoyed a renaissance with the advent of new molecular and analytical approaches (Bradshaw et al. 1995; Schemske & Bradshaw 1999; Ramsey et al. 2003; Kay & Schemske 2008). As the process of speciation is still poorly understood, it is critical that we understand the contributions of pollination ecology to the establishment and reinforcement of reproductive isolation and other speciation processes. At the same time, associations between specialised pollination and clade species richness (biodiversity) suggest that specialised pollination may increase speciation rates or reduce extinction rates (Sargent 2004; but see also Armbruster & Muchhala 2009).

Various aspects of specialisation in pollination ecology have been addressed in the past using ecological, microevolutionary, and comparative approaches, but there is still much debate and uncertainty about the broad applicability of the traditional pollination syndrome concept (in which the main pollinators can be predicted from flower colour, shape, scent and so forth) and the relative frequency and importance of specialised and generalised plant pollination ecologies (see Waser et al. 1996; Ollerton & Watts 2000; Fenster et al. 2004; Ollerton et al. 2009).

A final question concerns the evolutionary and ecological processes that have generated and maintained the diversity of flower types across species of angiosperms; this issue inspired a significant part of Darwin's research and contributed to his insights into natural selection and the origin of species. Comparative analysis in the context of phylogeny has been the main approach used to tackle this question, and the evolution of floral diversity remains a major theme in evolutionary research.

5. Interactions of plants, pollinators and floral antagonists (Box 5)

The evolution of floral traits is not only shaped by interactions with pollinators, but also with antagonists (Strauss & Whittall 2006; Adler 2007), and floral traits probably represent a compromise between selection by mutualists and antagonists (e.g. Gómez 2003). The outcome of interactions with pollinators and antagonists may depend on community context and vary geographically (e.g. Thompson & Cunningham 2002), but the extent to which this occurs is unknown for most systems. Furthermore, not much is known about how visits by one pollinator species affect floral interactions with other pollinators (Morris et al. 2007) or how floral antagonists affect interactions with other floral antagonists. Finally, compared to herbivores, the role of community context such as bottom-up (resource availability) and top down factors (predators or parasites Dukas 2001; Gegear et al. 2006; Otti & Schmid-Hempel 2008) on pollinator behaviour and population dynamics is relatively understudied.

27. What is the relative importance of selection on floral traits and mating systems by mutualists (pollinators) vs. antagonists (florivores, nectar robbers, pathogens, seed predators, pollinating herbivores)?
28. How does community context alter the outcome of floral interactions with pollinators and antagonists?
29. How do floral traits mediate interactions with pollinators and floral antagonists, and how do pollinators and floral antagonists alter these traits?
30. How do pathogens transmitted at flowers affect population dynamics and evolution of plants and pollinators?

Box 5: Questions on interactions of plants, pollinators and floral antagonists

Apart from floral cues and nectar rewards, floral volatiles and secondary compounds may also play important roles in pollinator behaviour (Adler 2000; Kessler & Baldwin 2007; Theis et al. 2007). However, the examination of how traits like scent, colour, morphology, floral longevity, and defence and reward traits (including chemical defences in both nectar and pollen) mediate interactions with floral mutualists and antagonists is in its infancy. Such traits can have synergistic effects on visitor behaviour (Raguso & Willis 2005), and can be induced or altered in response to leaf and floral damage (e.g. Adler et al. 2006; McCall & Karban 2006), but this has been examined in only a handful of systems.

Flowers have the potential to host and transmit a wide range of micro-organisms (Herrera et al. 2009) with consequent effects on both insect and plant hosts. For example, some of the most serious pathogens of bumble bees, such as *Crithidia*, are transmitted at flowers (Durrer & Schmid-Hempel 1994), as are major plant agricultural diseases such as fire blight in apples (Johnson et al. 2006). Bacterial wilt (*Erwinia tracheiphila*), a lethal disease of cucurbit crops, was thought to be transmitted only through leaf damage from a specialist beetle herbivore. However, beetles also consume cucurbit pollen, and recent work found that defecation in flowers can cause infection through nectaries (Sasu et al. 2010). More work is needed to examine how plant pathogens transmitted via flowers affect the evolution of mating systems and floral traits (Shykoff et al. 1997; Liu & Carlsson 2002; Hood et al. 2010).

6. *Pollinator behaviour (Box 6)*

To receive the service of pollen transfer, plants often offer rewards to flower visiting animals, such as nectar, oil, resin, pollen, breeding sites, etc. Flowers attract pollinators via various stimuli, whether they are olfactory or visual cues acting from a distance or tactile cues to guide pollinators to rewarding resources at close vicinity. Floral traits, resource distribution, and cognitive and learning abilities of pollinators influence their behaviour, which in turn is strongly linked to plant mating patterns and gene flow within and among plant populations (Goulson 1999; Karron et al. 2009). Interdisciplinary studies that combine all the different aspects of stimuli, pollination biology and genetics are still lacking (Whitehead & Peakall 2009).

31. What influences the pattern of movement of pollinators across landscapes?
32. How does pollinator behaviour affect pollen dispersal, gene flow, pollination, and plant reproductive success?
33. Are pollinator preferences mainly driven by learned or innate behaviour?
34. How and to what extent do pollinator species differ from one another in their cognitive abilities?
35. What factors determine the foraging choices of pollinators, and to what extent do these approximate optimal choices?
36. How and at which distances do floral traits influence foraging choices of pollinators?
37. How does competition for pollinator services influence patterns of gene dispersal?

Box 6: Questions on pollinator behaviour

Apart from social bees and birds (including work by Heinrich 1979; Pyke 1981; Chittka & Raine 2006), our knowledge about the different aspects of pollinator behaviour, such as foraging strategies or distances, cognitive or learning abilities, and flower constancy remain rudimentary (Weiss 2001; Riffell et al. 2008). We know that sensory perception of floral cues varies among taxa (Weiss 2001), but we have little knowledge about colour vision, smell or taste, their interaction, and or learning speed in individuals in space and time and how these affect the evolution of floral traits, mediated through behavioural differences. Innate colour preferences, for example, can be found over a broad taxonomic range of insect families but may differ between genera, species or even sexes (Weiss 2001; Kandori et al. 2009; Alarcón et al. 2010). Spatial processes, especially at large scales, and their consequences for pollen distribution in and between plant populations are even less well understood (Westrich 1996; Schulke & Waser 2001; Greenleaf et al. 2007; Beil et al. 2008).

Inter- and intraspecific competition among flower visiting animals can change the availability of resources and lead to changes in behaviour through enlargement of pollinator diets, though this can vary according to species, individuals and body size of pollinators (Inouye 1978; Walther-Hellwig et al. 2006; Fontaine et al. 2008). The consequences for plant reproductive success are still to be investigated (Dohzono & Yokoyama 2010).

7. *Taxonomy (Box 7)*

Pollinators do not need taxonomy but communicating scientific results on pollination research does. Therefore, taxonomy is essential for people to understand the intricate interactions in nature and to appreciate the world around them. Taxonomy is also needed for more practical endeavours, like the study of biodiversity, conservation and improving agricultural production. This is because taxonomy does not only provide names; it provides a systematic framework to our understanding of the natural world. In addition, taxonomic revisions usually give a lot more information; they document colour and morphological variability, enable predictability (closely related species often have similar behaviour and ecology), give distribution patterns and phenological information, and document associated organisms, such as parasites and food plants.

38. How do we solve the taxonomic impediment?
39. Which molecular methods are useful to evaluate inter- and intraspecific diversity of pollinators?
40. What are the ecological, social and economic impacts resulting from an inability to identify and manage pollinators?
41. How many species of pollinators have been described and how many undiscovered species remain to be described?

Box 7: Questions on taxonomy

However, enormous knowledge gaps still exist in our taxonomic system, and taxonomic expertise is in decline. Through the Convention on Biological Diversity (CBD), governments have acknowledged the existence of a "taxonomic impediment" in 1998 on the fourth Conference of the Parties and launched the Global Taxonomic Initiative (COP 4 Decision IV/1). Thereby it is hoped to help alleviate the problem of shortage of taxonomic workforce which hinders sound work and management on biodiversity. Identification guides that can be easily used by non-taxonomists are still rare, and available for relatively few taxonomic groups and geographic areas (e.g. Eardley et al. 2010). For bees, there exist fully-illustrated keys to family level (Packer & Ratti 2009, Fig. 2) and the monograph of Michener (2007) with keys to genera and subgenera, but for many important groups of pollinators like Diptera (see Ssymank et al. 2008), there remains a need for keys and catalogues. DNA barcoding has shown promise for the identification of bees and other pollinators (Packer et al. 2009). However, additional genetic markers may be required to obtain clearer patterns of species differentiation.

Figure 2. Detailed images taken from a user-friendly key to identify the bee families of the world (Packer and Ratti, 2009). Distinguishing characters (here: scopae on female hind legs) are described and highlighted. Further images show different forms of the character making correct identification much easier.

8. The breadth and depth of our current understanding of plant-pollinator assemblages (Box 8)

Plants and their pollinators do not exist in isolation, but rather in highly connected assemblages of interacting species (Memmott 1999; Jordano et al. 2003). These assemblages vary temporally within flowering seasons (requiring some matching between plant and pollinator activities) and between seasons, as pollinator populations fluctuate. There is also spatial variation, with similar plant communities having rather different groups of pollinators which may vary in their relative effectiveness. Spatial and temporal variation in a plant species' pollinators means that for many plants the terms "specialised" or "generalised" are relative ones, highly dependent upon assemblage/community context (Ollerton et al. 2007).

42. To what extent are local plant communities dependent upon pollinators?
43. To what extent is functional replacement of different species of pollinators possible?
44. What is the relationship between pollinator diversity and plant diversity?
45. How do pollinator population fluctuations affect pollination?
46. What are the proximate, ecological determinants of pollination system specialisation or generalisation?
47. What ecological and evolutionary processes determine the structure of interactions in a network?
48. What proportion of pollination is undertaken by the different functional groups of pollinators in a community?
49. To what extent are pollinator life cycles synchronised to the phenologies of their forage plants?
50. What factors influence the composition of pollinator species at the community level?
51. How commonly do pollinators compete for floral resources?
52. How do plants of different species interact through competition or facilitation via common pollinators?

Box 8: Questions on plant-pollinator assemblages

How this variation in pollinators subsequently feeds into immediate effects on plant reproduction and longer term effects on plant diversity is only now being addressed experimentally, and even then, experiments are necessarily constrained and may not represent the true ecological situation (e.g. Fontaine et al. 2006).

Although the advent of sophisticated network analytical techniques has allowed us to probe these assemblages at levels not anticipated even 20 years ago, there are significant gaps in our knowledge of how such assemblages come about over ecological and evolutionary time scales. For instance, we know little about how increases in plant diversity result in greater species richness of pollinators, although recent research shows that they may be correlated (e.g. Ebeling et al. 2008; Fründ et al. 2010).

Finally, the interactions of plants and pollinators within their respective groups, via competition for resources (nectar, pollen or pollinator services) or facilitation is an area currently under-studied in community pollination ecology but where novel approaches are revealing some interesting results regarding the frequency of positive versus negative effects, both within and between species (Hegland et al. 2009).

9. Geographical trends in pollinator diversity (Box 9)

A glance at the history of pollination ecology shows us that research within Europe and North America dominated the field from the 18th to the first half of the 20th centuries (work by Sprengel, Delpino, Darwin, Müller, Robertson, etc., with notable exceptions such as Burkill's work in India and some of the early research in Southern Africa and South America, see Faegri & Pijl 1979; Proctor et al. 1996). This has resulted in a rather Euro-American view of the diversity of plant-pollinator interactions that has only begun to be challenged in the last two decades (Johnson and Steiner 2000). Even now, our understanding about geographical patterns of the diversity of pollinators and pollination systems in large parts of the world is virtually non-existent or at most patchy.

53. How does the diversity of pollinators vary geographically at the level of species and functional groups?
54. How and why do plant and pollinator specialisation, ecological redundancy, and other network characteristics vary geographically?
55. What are the geographic units of functional relevance to pollinator diversity, e.g. local, landscape, regional, or continental?
56. How common are geographical mosaics of plant-pollinator interactions?
57. What is the scale of the biotic homogenisation of pollinators, as observed in Europe?

Box 9: Questions on geographical trends of pollinator diversity

Research in such areas each year bring accounts of pollination by taxa previously considered unlikely to be pollinators of specialised plants, for example crickets (Micheneau et al. 2010), spider hunting wasps, fruit chafers (Ollerton et al. 2003) and cockroaches (Nagamitsu & Inoue 1997). In some instances, these taxa are dominant pollinators within communities, not simply marginal curiosities of natural history, and there is the need to more fully understand the roles played by the full complement of pollinators.

Questions also remain on processes and their ultimate consequences. For example, we strongly suspect that the ecological isolation of oceanic islands reduces the diversity of pollinators that can reach such islands (Woodell 1979), resulting in the evolution of "unusual" pollination systems such as lizard pollination (e.g. Hansen & Müller 2009). We do not know what the consequences are of habitat loss and species extinctions for such isolated biota. Such interaction networks could either be more fragile than those on the continents, because there are fewer species which can act as substitute pollinators for the plants, or they might be relatively robust because the more brittle interactions are already lost. The latter idea is backed up by work showing that "super-generalist" plants and pollinators may be common on islands, increasing the robustness of island interaction networks (Olesen et al. 2002).

Geographic patterns, however, occur at all spatial scales and adjacent regions may harbour distinctly different groups of pollinators, though this is little studied (but see Galen et al. 1987; Armbruster & Guinn 1989). Consequently, a significant concern of pollination ecologists is that in highly agro-industrialised parts of the world, the removal of natural habitats, the extinction of rare species and the introduction of non-native pollinators is resulting in the biological homogenisation of regional pollinator faunas (see also topic 10).

10. Drivers of pollinator loss (Box 10)

Pollinator decline and loss of pollination services have become issues of political, media and scientific focus worldwide. Many studies have identified relationships between various human activities and changes in pollinator behaviour, population structure, overall abundance, richness and diversity (Biesmeijer et al. 2006; Winfree et al. 2007), their interactions with plants and pollination services (Ricketts et al. 2008; Carvalheiro et al. 2010). However, although some social bees have been widely studied (e.g. Williams & Osborne 2009), the extent to which other taxa are declining, and geographical variations in the decline, are not as widely understood (Kevan & Fonseca 2002).

As with biodiversity losses in other taxa, key drivers of decline are identified as: (1) habitat destruction, degradation and fragmentation (resulting in a loss of foraging, mating and nesting sites - particularly driven by changes in agricultural management practices; Kearns et al. 1998; Taki et al. 2008; Brown & Paxton 2009), (2) pollution (in particular by agri-chemicals including neonicotinoids; Kevan 1999; Brittain et al. 2010), (3) invasive alien species (including introduced plants, pollinators, pests and diseases; Stout & Morales 2009; Dafni et al. 2010), and (4) climate change (which affects the spatio-temporal dynamics of plant-pollinator interactions; Memmott et al. 2007; Hegland et al. 2009). In the future, new drivers of decline may emerge, either as a result of the introduction of novel species into the environment (such as bioenergy crops and genetically modified organisms) or other technological and social changes (associated with renewable energy generation, electromagnetic fields, urbanisation or other factors).

However, many questions remain, and it is likely that drivers are spatio-temporally variable, differ among species and/or functional groups, and interact synergistically (Schweiger et al., 2010). One feature that is of particular relevance to bee declines is that the genetic load caused by their unusual sex determining mechanism makes them particularly susceptible to environmental impacts that reduce population sizes (Zayed & Packer 2005; Packer 2010).

Furthermore, many studies are limited to field-scale, pair-wise interactions, and it may be difficult to assess impacts on entire ecological systems at the landscape scale (Taki et al. 2007) or to determine how resilient pollinators (from individuals, populations and species to communities) are to change (Kevan & LaBerge 1979). For a meta-analysis of the ecological traits of bees that make different groups susceptible to different environmental impacts, see Williams et al. (2010).

58. Besides habitat destruction, pollution, invasive species, and climate change – how can we best identify future risks to plant-pollinator interactions?
59. Which pollinator taxa and functional groups are in decline?
60. What are the geographical patterns of decline?
61. What are the rates of decline?
62. What is the relative importance of the various drivers of pollinator decline?
63. How do drivers of loss interact, and how do they vary in space and time?
64. Do drivers of pollinator decline also drive loss of pollination services and, if so, what is the rate and shape of change?
65. How do we quantify drivers of decline experimentally and at the landscape scale?
66. What features of the life histories of pollinators (e.g. haplodiploidy in bees, or specialist larval food plants in Lepidoptera) make them more susceptible to extirpation?

Box 10: Questions on drivers of pollinator loss

11. Pollination as an ecosystem service (Box 11)

The Millennium Ecosystem Assessment (MEA 2005) characterises pollination as a regulating service which underpins the reproduction of the most flowering plant species and the productivity of many of the world's crops. Despite many decades of study, there is still a fundamental gap in our understanding of which animals are the primary pollinators of wild flowers and crops. Although some landmark agriculturally-focussed publications (e.g. Free 1993; Klein et al. 2007) explore these relationships, there remains an outstanding challenge to compile a systematic catalogue including variation with location, plant variety, season, and time of day.

Reviews estimate that 62-73% of wild plant species are pollen limited (e.g. Burd 1994; Ashman et al. 2004), however, for most wild plants and for many crops this basic information is still missing.

Globally it is estimated that the value of pollinators for crop production was €153 billion per year in 2005 (Gallai et al. 2009). Although this figure provides a useful initial overview, the calculation does not include all of the world's pollinator-dependent crops and also excludes subsistence farming, the value of non-cultivated plant products (e.g. wild harvested fruits and berries), and indirect values of livestock reliant on pollination products such as clover or alfalfa. The aesthetic and cultural values of pollination, e.g. by providing florally rich environments for pleasure and recreation, are also of high scientific and policy relevance (Eardley et al. 2006).

Most of the world's staple crops (e.g. rice, wheat, maize and sorghum) are abiotically pollinated. However, most fruits and vegetables benefit from biotic pollination (Roubik 1995; Klein et al. 2007). They provide many of the micronutrients (e.g. vitamins and minerals) essential for healthy diets (Johns 2007). There is, therefore, an increasing demand for pollination services for world agriculture, as the area planted with these crops expands (Aizen & Harder 2009). This suggests an increasing divergence in the demand and supply of pollination services. Future challenges will centre on ways of ensuring sufficient and reliable pollination services for food production and security.

Wild plant communities themselves also contribute to a suite of other essential ecosystem services such as water filtration, maintenance of soil quality, fertility and structure, carbon balance and oxygen production. Plants also provide habitats and resources for much of terrestrial biodiversity. The role of pollination in supporting other ecosystem services has already begun to be valued by initiatives such as TEEB (The Economics of Ecosystems and Biodiversity, TEEB 2010). Still, how these ecosystem services may be threatened by pollinator loss is not well understood. This knowledge gap must be bridged if we are to manage ecosystems for human livelihoods and biodiversity conservation (Kevan & Phillips 2001; Potts et al. 2010).

67. What are the most important pollinators of crops and wild plants?
68. How widespread are pollination deficits in crops and wild plants?
69. What is the economic value of pollination services?
70. How will we supply the growing demand from agriculture for pollination services?
71. What is the role of pollination in global food security?
72. What other ecosystem services would be affected by the loss of pollinators?

Box 11: Questions on pollination as an ecosystem service

12. Managing pollination services (Box 12)

Whenever 'free' naturally provided pollination services are insufficient in magnitude and reliability, pollination needs to be managed through: (i) managing habitats, including agro-ecosystems, to support wild pollinators; and/or (ii) introducing domesticated pollinators. In order to best match pollinators and crops, detailed studies of pollinator behaviour, morphology and physiology and the availability of crop forage rewards, breeding system and pollination requirements are needed (Delaplane & Mayer 2000). For example, Sheffield et al. (2008) have shown that alternative food sources can help maintain pollinator populations outside of crop flowering time, but this needs further investigation.

Honey bees (*Apis* spp.) are the most widely used managed pollinators across the globe. However, other bee species are also being managed for crop pollination (Delaplane & Mayer 2000; Mader et al. 2010), including some stingless bees (Meliponini), bumblebees (*Bombus* spp.), mason bees (*Osmia* spp.), leafcutter bees (e.g. *Megachile rotundata*) and ground nesting solitary bees (e.g. *Nomia melanderi*). Many of these are more efficient pollinators than honey bees on specific crops but are generally not managed on the same scale (Free 1993). Undoubtedly other wild species could be developed for crop pollination, but the species requirements and techniques for managing them need to be underpinned by fundamental research into their ecology and behaviour.

Large-scale commercial beekeeping is well established in the USA (NRC 2006), and some other developed countries, whereby growers pay directly for hive rental and benefit from the enhanced service. However, throughout much of the rest of the world beekeepers often place hives in cultivated areas and only derive indirect benefits through honey production, unconscious of the value of the service they provide to agriculture. The challenge is to quantify the value of pollination services and develop fiscal mechanisms whereby service providers can be compensated for the real value of the service provided. The development of Payment for Ecosystem Services (PES, Jack et al. 2008) for pollination is a key future research and policy need that could be extended to other parts of the world, not just the USA.

73. How do we match the right pollinators to individual crops?
74. When do we need to use managed pollinators?
75. What alternative species of pollinators can we manage for pollination services?
76. How can beekeepers, and providers of other pollinators, be paid for delivering pollination services?
77. How can the potentially conflicting demands for pollinator diversity conservation and crop pollination be reconciled?

Box 12: Questions on managing pollination services

There are demands on our landscapes to provide multiple functions simultaneously and some of these demands may be in conflict. For food production, the objective may be to maximise productivity and profit, while conservation of pollinators may require more extensive farming practices (Tscharntke et al. 2005). There is a need for research to identify and test other management practices which can produce win-win options where both productivity and pollinators co-benefit.

13. Conservation (Box 13)

Plants and pollinators may have very close links and examples show that the loss of pollinators lead to the decline of their associated plants, as recently reported by Anderson et al. (2011) for a New Zealand shrub species (see also Biesmeijer et al. 2006). Thus, also the conservation of plants and pollinators is strongly associated, and so strategies to promote pollinator conservation will have knock on benefits for plant conservation and *vice versa*. Classic conservation measures involve site protection in national parks and nature conservation areas, but these alone cannot stop plant or pollinator decline over broader landscapes. Strict species protection regimes have been set up in several countries for some plants, butterflies and bees. These may be useful for reducing direct threats such as collection and trade but are of minor help for most biodiversity since they do not prevent general major threats such as habitat destruction, degradation and fragmentation. Plants often suffer from inbreeding depression when population size becomes too small (Honnay et al. 2005; Aguilar et al. 2006). Most pollinating insects are dependent on a habitat mosaic to fulfil different needs (for example, nest sites as well as floral resources for bees, and larval food plants as well as the flowers required for adult feeding for butterflies and moths). Therefore, a "Green Infrastructure" with habitat connectivity is needed for conservation of plants and their pollinators (Benedict & McMahon 2006). Stepping stones, corridors, buffers or nodes at different spatial scales offer possibilities to connect fragmented habitats (Dover & Settele 2008). Agri-environment schemes are good examples where potential conflicts between economic profit and conservation can be resolved; non-cultivated areas, such as flower-rich field margins provide pollinator habitat, which in turn may enhance local pollination services for plants, and farmers receive financial support for establishing the margins (Carvell et al. 2007; Potts et al. 2009). Migratory species, such as some butterflies, bats, hoverflies, and hummingbirds, especially need nectar corridors for conservation (see the Migratory Pollinators Program of the Arizona-Sonora Desert Museum, http://www.desertmuseum.org/pollination).

Comprehensive monitoring of the pollinator status and the threats and pressures on plants and pollinators is indispensible to develop conservation measures. Red Data books are a possibility, but a shortage of resources and expertise may result in smaller or taxonomically difficult groups being ignored. Targeted species action plans for plants or pollinators are still rare, and general monitoring schemes are missing (except for honey bees and other managed bee species in some countries).

78. What conservation laws, policy requirements and adaptation of existing agri-environmental funding schemes are needed to sustainably conserve pollination services, as well as plant and pollinator diversity?
79. How can we best monitor and document the status, threats and pressures on pollinators including effects on plants and biodiversity as a whole?
80. What essential modifications in land use management and practices are needed to halt and reverse plant and pollinator declines?
81. How can we ensure adequate prioritisation, sufficient action and implementation?

Box 13: Questions on conservation

The 2010 target of reducing the loss of biodiversity could not be reached worldwide under the Convention on Biological Diversity (CDB) nor within the EU, despite the latter's common nature conservation law such as the Habitats Directive (i.e. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora). To achieve the goal of stemming the loss of plant and pollinator biodiversity, major questions for research must focus on monitoring their status, and designing effective laws, policies and financial incentives as well as the necessary adaptations in land use.

14. Implementation of plant-pollinator interaction conservation (Box 14)

The first political steps to acknowledge the importance of pollinators and their interactions with plants and to raise awareness were undertaken within the CBD on the 5th Conference of Parties (in 2000) with the "Sao Paulo Declaration on Pollinators" (International Pollinator Initiative 1999). An action plan (decision VI/5) was developed, and an International Pollinator Initiative was formed under the leadership of the Food and Agriculture Organisation (FAO). Several regional initiatives in Europe, North America, Canada, Africa, Brazil and Oceania have been established since then (Ssymank et al. 2009). FAO's rapid assessment of pollinator status (FAO 2008) gave an important input for politics. Recently the International Risk Governance Council in Geneva addressed the policy needs in pollination services (IRGC 2009), pointing out risks related to the loss of pollination services, regulatory and governance shortcomings and knowledge deficits. The ALARM project of the EU (Assessing LArge-scale environmental Risks for biodiversity with tested Methods) included projects on diversity of plants and pollinators and follow-up projects under the EU research programme will be started. Further, the United Nations Environment Programme (UNEP), Global Environment Facility (GEF) and FAO have launched a Global Pollination Project on "Conservation and Management of Pollinators for Sustainable Agriculture, through an Ecosystem Approach" for almost $27 million.

82. How can we promote strategic networking on pollination issues in a broad, integrated, and interdisciplinary approach?
83. How can we effectively raise awareness among society about plants, pollinators and pollination services?
84. What kinds of training, education and capacities are needed to protect the diversity of pollinators and their food plants?
85. How can we better employ plants and their pollinators as educational tools for public awareness?
86. How can pollination ecologists learn from other fields to communicate effectively about pollinators with policy makers and the general public?

Box 14: Questions on implementation of plant-pollinator interaction conservation

Despite these efforts, more education, capacity building and networking for the implementation of plant and pollinator management are desperately needed. Taxonomists, plant and pollination ecologists, training for students, materials, and identification keys are missing for many pollinator groups (Packer et al. 2009). Museum and research capacities as well as capacities for practical implementation and management are still low and neglected. The main questions are therefore expressing the concern on raising awareness, capacity building and closing the enormous knowledge gaps on pollination services in a systematic way including all major pollinator groups over all major terrestrial ecosystems worldwide. This will be beneficial not only for plant diversity and agriculture, but also for forestry, gardening, medicine and human health.

DISCUSSION

We conclude that sufficient unanswered questions remain to feed research for several generations to come. This exercise has some shortcomings as does every scientific study: only a limited number of consultees were contacted and only a fraction of them (<40%) responded. However, there was substantial overlap in the more than 650 contributions we received, and the themes of the most urgent subjects were easily identified. We found it much more difficult to select from the mass of good questions which might have been too case-specific to be included in a publication also intended for non-specialists. We decided to focus on a broader level, which makes it difficult to answer single questions with single projects. Nevertheless, many of the questions can be split or broken down into digestible parts and offer objectives for studies within a defined time frame. On the other hand, it may be argued that 86 questions are too many to represent the "key" issues, but the final number of questions reflects the breadth of the topic and the current debates within the field. Pollination ecology is a complex area and despite more than 200 years of study, many topics are not yet fully understood, whilst all the time new questions arise as our environment changes and novel mechanisms for investigation and interpretation appear.

We do not claim our list to be comprehensive nor to have dealt with the various thematic areas with exhaustive profundity. There may be other good ways to categorize the questions; we chose the thematic groupings that made the most sense to us. Reviews or special issues can provide much more detailed and specific information about research needs in a particular topic (e.g. Raguso 2009; Friedman & Barrett 2009). We are also aware that we have focussed primarily on the angiosperms, though many of these questions would also apply to wind and biotic pollination in the gymnosperms. Still, we hope that we can inspire new tracks in research on pollination, thereby offering politicians, stakeholders, and donors insight into research and conservation priorities with the goal of conserving plant and pollinator biodiversity and preserving an ecosystem service essential for our well-being. An understanding of patterns and processes is necessary if we are to fully comprehend the rich ecological and evolutionary interplay between pollinators and the plants they service, and how these interactions can be conserved in an anthropogenically changing world.

ACKNOWLEDGEMENTS

We would like to express our sincere thanks to all of the pollination scientists who freely and generously shared their ideas with us by taking part in our poll:

Josef Ackerman, Canada; Klaus Amman, Switzerland; Bruce Anderson, RSA; Jordi Bascompte, Spain; Peter Bernhardt, USA; Andrew Bourke, UK; Mark Brown, UK; Stefanie Christmann, Germany; Richard Corlett, Singapore; James Cresswell, UK; Saul Cunningham, Australia; Ben Darvill, UK; Robin Dean, UK; Antonio Felicioli, Italy; Charles Fenster, USA; Una Fitzpatrick, Ireland; Ted Fleming, USA; Vera Fonseca, Brazil; Francis Gilbert, UK; José María Gómez , Spain; Dave Goulson, UK; Melanie Hagen, Germany; Andre Hamm, Germany; Carlos Herrera, Spain; David Inouye, USA; Rebecca Irwin, USA; Anne-Laure Jaquemart, Belgium; Steve Johnson, RSA; Jeffrey Karron, USA; Makoto Kato, Japan; Danny Kessler, Germany; Vicky Kindemba, UK; Michael Kuhlmann, UK; Peter Kwapong, Ghana; John Manning, RSA; Maria Angeles Marcos García, Spain; Dino Martins, USA/Kenya; Andrew McCall, USA; Jane Memmott, UK; Denis Michez, Belgium; Pierre Mineau, Canada; Randall Mitchell, USA; Carolina Morales, Argentina; Linda Newstrom-Lloyd, NZ; Kazuharu Ohashi, Japan; Anton Pauw, RSA; Robert Paxton, UK; Theodora Petanidou, Greece; Marino Quaranta, Italy; Robert Raguso, USA; Nelson Ramirez, Venezuela; T'ai H. Roulston, USA; Lauren Ruane, USA; Chris Saure, Germany; Florian Schiestl, Switzerland; Josef Settele, Germany; Matt Shardlow, UK; Andrew Stephenson, USA; Juergen Tautz, Germany; John Thompson, USA; James D. Thomson, Canada; Teja Tscharntke, Germany; Diego Vázquez, Argentina; Nick Waser, USA; Dieter Wittmann, Germany; Lorne Wolfe, USA.

We further thank the participants of the SCAPE meeting at Tovetorp (Sweden), 2010, for their highly appreciated comments on the questions. Thanks go also to Koos Biesmeijer and two anonymous reviewers for helping us to improve earlier versions of the manuscript.

APPENDICES

Additional supporting information may be found in the online version of this article:

Appendix I. Number of researchers who were contacted and who replied in the different regions of the world.

Appendix II. List of questions after first compression.

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