# *Pollinator conservation: the difference between managing for pollination services and preserving pollinator diversity*

Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Insect Science

# Pollinator conservation — the difference between managing for pollination services and preserving pollinator diversity

Deepa Senapathi[1], Jacobus C Biesmeijer[2], Thomas D Breeze[1], David Kleijn[3], Simon G Potts[1] and Luísa G Carvalheiro[4,5]

Our review looks at pollinator conservation and highlights the differences in approach between managing for pollination services and preserving pollinator diversity. We argue that ecosystem service management does not equal biodiversity conservation, and that maintaining species diversity is crucial in providing ecosystem resilience in the face of future environmental change. Management and policy measures therefore need to focus on species not just in human dominated landscapes but need to benefit wider diversity of species including those in specialised habitats. We argue that only by adopting a holistic ecosystem approach we can ensure the conservation and sustainable use of biodiversity and ecosystem services in the long-term.

**Addresses**
[1] Centre for Agri-Environmental Research, School of Agriculture, Policy & Development, University of Reading, Reading RG6 6AR, UK
[2] Naturalis Biodiversity Centre, 2333 CR Leiden, The Netherlands
[3] Plant Ecology and Nature Conservation Group, Wageningen University, Droevendaalsesteeg 3a, 6708 PB Wageningen, The Netherlands
[4] Departamento de Ecologia, Universidade de Brasília, Campus Universitário Darcy Ribeiro, Brasília - DF 70910-900, Brazil
[5] Centre for Ecology, Evolution and Environmental Changes (CE3C), Faculdade de Ciencias da Universidade de Lisboa, 1749-016 Lisboa, Portugal

Corresponding author: Senapathi, Deepa (g.d.senapathi@reading.ac.uk)

**Current Opinion in Insect Science** 2015, **12**:93–101

This review comes from a themed issue on **Insect conservation**

Edited by **Jeff Harvey**

http://dx.doi.org/10.1016/j.cois.2015.11.002



## Introduction

Society requires ecosystems to be managed for many purposes with priorities varying depending on location, historical use, local and international demands, regulations and governance. There is, however, a long history of conflict between wildlife conservation and food production, as historically these were often viewed as incompatible goals of land management. Over recent decades there has been a strong move to try and reconcile these goals, coupled with a better understanding that landscapes can be multifunctional in their in uses. The establishment and development of ecosystem service frameworks (e.g. MEA, IPBES [1,2]) have helped conceptualise and operationalise approaches to managing ecosystems to meet different societal needs [1,2]. These frameworks recognise that biodiversity underpins all ecosystem services and that food production and biodiversity conservation are individual services in their own right, and specifically include conservation as an explicit cultural services which recognises the intrinsic value of biodiversity *per se*.

The ecosystem approach developed by the Convention on Biological Diversity is a strategy for the integrated management of land, water and living resources that promotes conservation and sustainable use in an equitable way [3]. Applying the ecosystem approach in its full sense can readily reconcile potential conflicts between conservation and other human activities. However, a recent trend by policymakers and researchers of using ecosystem services as a (partial) surrogate for biodiversity conservation (e.g. EU Biodiversity strategy to 2020 [4]) poses potentially serious problems for conservation if these services are provided by small suites of relatively resilient species. Therefore managing for services alone may only benefit widespread, common species which are usually not of great concern to conservation.

Here we use pollinators and pollination services to illustrate the risks of naively substituting ecosystem service management for biodiversity conservation, and argue that adopting a holistic ecosystem approach, is a more viable strategy for ensuring the conservation and sustainable use of biodiversity and ecosystem services in the long-term. Using real world examples, we highlight the different pathways to achieving resilient ecosystems which integrate both biodiversity conservation and ecosystem services.

## Few pollinator species have an obvious importance for the delivery of pollination services

Several studies demonstrate that wild pollinator diversity (particularly in bees) has declined globally over recent decades [5,6,7••]. Concerns over these declines however seem to mainly focus on how reduction in pollinator abundance limits crop yield and its implications for global food security [8]. A recent study has shown that approximately

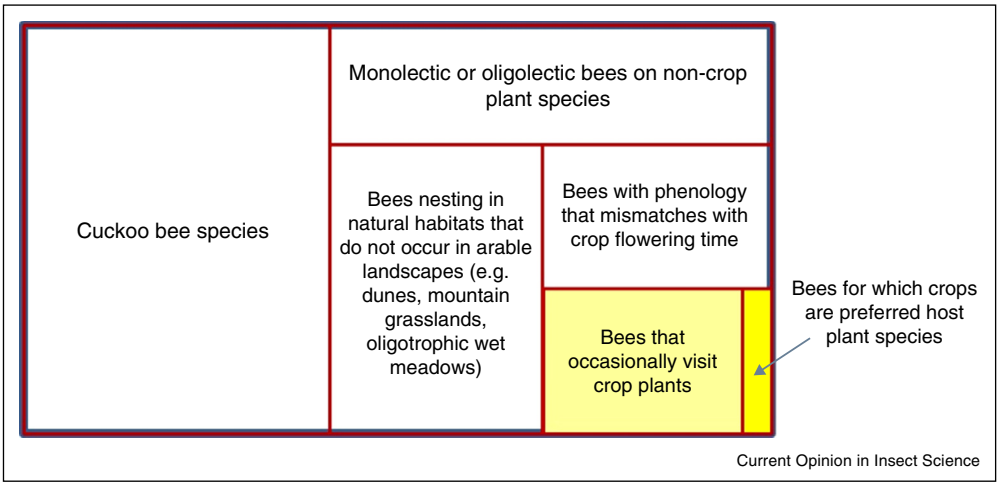
80% of global pollination services are carried out by around 2% of pollinator species [9••]. Even when considering all species visiting crop flowers, however infrequently, these only make up a small proportion of the more than 20 000 species of bees that exist worldwide [9••,10] and the vast majority of bee species currently have no direct economic importance (Figure 1). This is not really surprising because of spatio-temporal mismatches between the foraging range of many bee species and the location or flowering time of the crop. Furthermore although a majority of crop species benefit from pollination services [11], these plants represent only a small fraction of flowering plant biodiversity and are thus unlikely to cover the foraging needs of many pollinator species (Figure 1). While a number of species with no direct importance for pollination are needed to sustain nesting and alternative flower resources of crop pollinators (see following sections), many other species are unlikely to have any direct or indirect role on ecosystem service provision. An extreme but illustrative example that combines all these traits, is the bumblebee species *Bombus gerstaeckeri*, which forages exclusively on monkshoods (*Aconitum* spp.) in the subalpine zone of European mountain ranges [12], playing no direct role in crop pollination. Furthermore, a significant proportion of all bees are brood parasites on other bees, that is, cleptoparasitic or cuckoo bees [13–15]. Because these bees lay their eggs in brood cells produced by other bee species, they do not collect pollen themselves, do not store nectar, and are therefore rarely observed on crops (but see [16]). The rate of parasitism within agricultural landscapes can be quite high (e.g. 79–92%, see [17]), with many species recognised as important for crop pollination being parasitised (e.g. *B. terrestris*). Studies comparing the foraging behaviour of host species with and without the presence of a parasitic bee species are lacking (but see [18]) but are necessary to understand the impact of parasites on pollination services.

## Pollinators connect crop plants to natural ecosystems

Pollinator species rarely rely solely on a single plant species for both food and nesting resources; neither are all flower visitors effective pollinators. All crop pollinators (dominant or not) depend on diverse plant species often provided by (semi-) natural habitats, and few species are found in abundance far away from natural habitat [19,20]. One of the main reasons for such dependence on diverse natural habitat is the provision of the diverse set of nesting resources (e.g. shrubs and trees, bare soil free from pesticides), which are typically unavailable within intensively managed crop fields [21•]. Since the flowering period of a single plant species is often short in comparison to the activity period of pollinators [22], pollinators depend on a range of plants which are more readily provided in (semi-) natural habitats than in intensively managed landscapes.

Pollinators both influence and are influenced by a range of other domesticated and wild species. Species that do not pollinate crops may play critical roles in natural ecosystems by ensuring seed and fruit set thus sustaining diversity of plants and higher trophic levels. For example, in Brazil *Xylocopa ordinaria*, an important pollinator of passionflowers has a wild native plant of the savannas of South America (the dioucious *Pera glabrata*) as main nest resource [23]. In another important bioma from South America, the Caatinga, other *Xylocopa* species (which pollinate passionflowers, blueberries, greenhouse tomatoes and melons) depend on *Commiphora leptophloeos*, a key species for the conservation of a vast number of native bees, for nesting [24], and on many other native plant

**Figure 1**




An illustration of the proportional distribution of different groups of bee species (based on existing knowledge — references in text) with respect to their usefulness for crop pollination. The outer rectangle indicates the total regional bee species pool. Species groups highlighted in yellow contribute to crop pollination.

species for pollen and nectar when passionflowers are not blossoming [25].

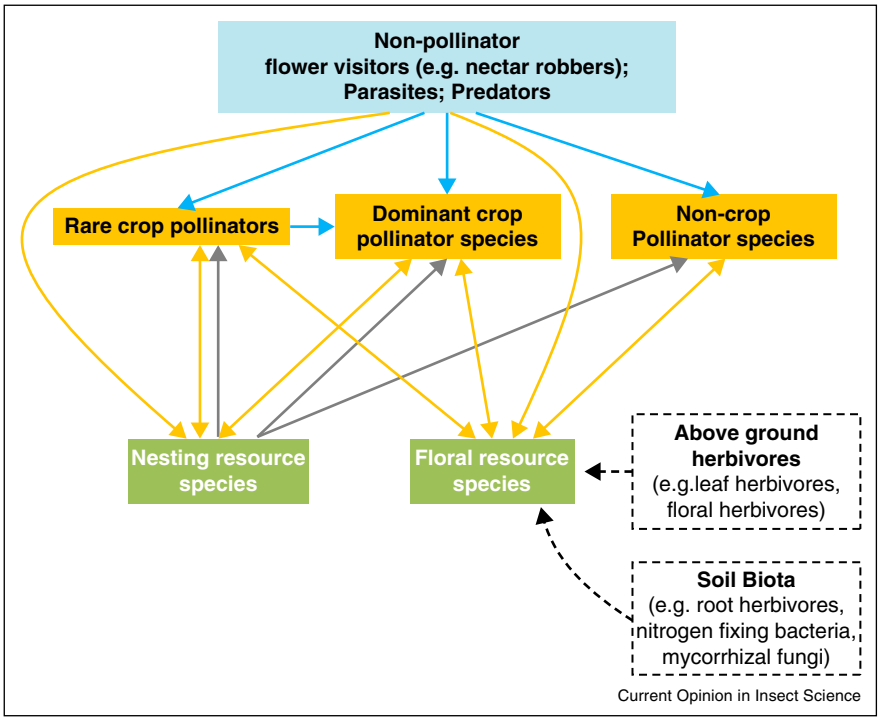
Some bee species engage in nectar and pollen robbing behaviour, leading to perceived negative impacts on crop pollination and plant reproduction. For example, a few species of stingless bees have frequently been reported to damage crops in South and Central America including cutting flower buds and flowers and scarring fruit, with potential negative effects on yield (e.g. [26]), thereby rendering the ecosystem service argument insufficient for their preservation. However, in most cases nectar robbers remove nectar by piercing or biting into the corolla of a flower, or even without damaging the flower (nectar thieves, *sensu* [27]). Moreover, recent evidence suggests that nectar robbing may sometimes be beneficial to plant reproduction, as after visiting a flower with less nectar, pollinators usually fly greater distances between flowers [28–30]. This behaviour can decrease self-pollination and increase pollen flow [31,32] leading to higher outcrossing, and consequently, to greater seed set [33].

In addition to the above interactions, pollinators' abundance and behaviour may be affected by indirect ecological interactions with many non-pollinator species from different trophic guilds, such as predators and parasitoids (Figure 2); as well as leaf herbivores and soil fungi and bacteria that affect plant biomass, architecture and physiology (e.g. [34]). In summary, crop and natural systems can influence each other in multiple indirect ways, many of which remain understudied.

## Species diversity and its implications for resilience to environmental change

There is increasing evidence that several species and groups of pollinators and the plants they pollinate are negatively affected by environmental change in many locations in the world. These pressures include climate change [35,36], agricultural intensification [37,38,39••], diseases, pests and pathogens [40] and invasive species [41,42]. Management strategies therefore need to focus not just on current issues but consider the response and resilience of these systems to future environmental conditions including possible ecological shocks. Response diversity, defined as the range of reactions to environmental change among species contributing to the same ecosystem function, is critical to resilience, particularly during periods of ecosystem reorganisation and recovery after disturbance [43]. Low response diversity can cause whole functional groups to go extinct or make systems ecologically insignificant as a result of environmental change [43]. Biological diversity appears to enhance

**Figure 2**




Ecological interactions that can influence the efficiency of dominant species as crop pollinators. Pollinators are represented in yellow boxes; animals that may interfere with pollinator behaviour are represented in blue boxes; plant resources are represented by green boxes; other biota that can lead to indirect interactions are represented by white boxes. Trophic and mutualistic interactions are represented by yellow arrows; behavioural interactions are represented by blue arrows; interactions related to nesting are represented by grey arrows, and indirect interactions mediated by changes in plant biomass or physiology are represented with dashed-black arrows.

the resilience of desirable ecosystem states [44]: Greater diversity of species can cause functional redundancy, where several species can contribute in a similar way to ecosystem function [45], and loss of some dominant species can be ameliorated by the presence of other rare species. While as yet this concept remains understudied in pollinator communities, studies in other ecological systems [45,46] strengthen the argument that diversity is required for functional redundancy and resilience to change.

Not all species of pollinators respond equally to environmental stresses, with both winners (mostly species that are generalist in their habitat or food needs) as well as losers (often specialists) emerging from environmental changes [47]. For example a study in the highly endemic cape floristic region of South Africa showed that climate change-induced impacts on species ranges varied from range expansions of 5–50% for two species of bees, to substantial range contractions, between 32% and 99%, in another six species [48]. Seasonal shifts within [49] and across species [50,51] have also been detected in regions with distinct seasons and may simulate species turnover when local climatic conditions change. While the loss of specialist species due to environmental change may not have direct impacts on crop pollinator community, it entails lower rates of ecosystem processes, and some functions performed by specialists may not be carried out at all [43], potentially leading to greater biodiversity loss and ecosystem instability in the long run.

## The non-economic value of pollinators and the services they provide

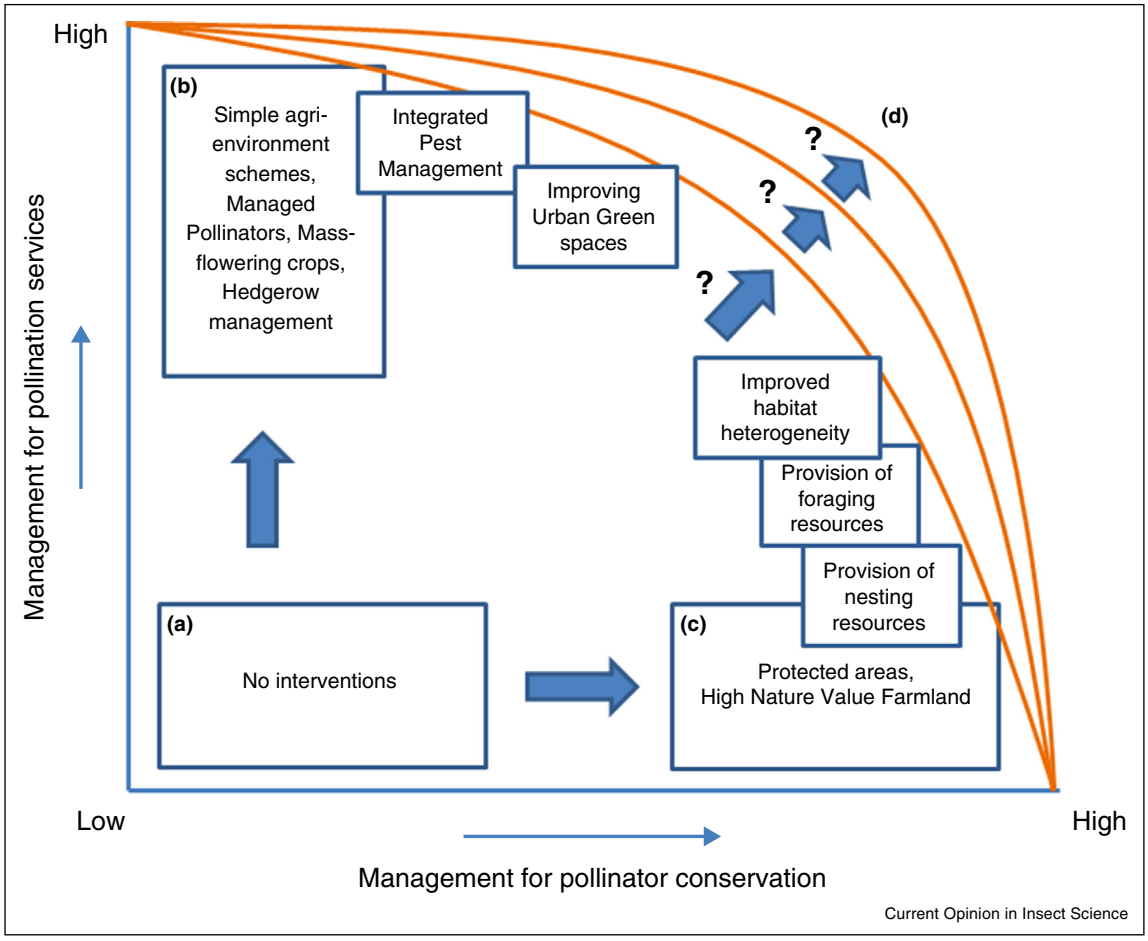
As mentioned above, pollinator species that do not visit crops may play critical roles in natural ecosystems by ensuring wild plant seed and fruit set, thus sustaining wider biodiversity throughout trophic webs. Eighty-seven per cent of all flowering plants are animal pollinated [52], with bees being considered the most important group of pollinators. While the economic value of crop pollination and other ecosystem services is undisputed, the importance of the wider diversity of pollinators that provide resilience to ecosystems via indirect services cannot be quantified in solely economic terms. Humans have also placed cultural importance on biodiversity for thousands of years and current research indicates that biodiversity and human health are intricately linked via cultural pathways [53]. Therefore, non-economic and moral arguments can be strongly made for the conservation of wider diversity. That this can be an effective approach is illustrated by the growing sales of seed mixtures for bees and civilian initiatives to plant wildflowers in towns and cities in north-western Europe (anecdotal evidence) as well as increased media and public awareness on the plight of pollinators. The general public buying or supporting these pollinator enhancement instruments do so because of cultural values and moral arguments that nature has intrinsic value and needs to be protected and conserved.

## Minimising trade-offs between pollination and conservation

As shown in previous sections, the most widespread generalist pollinator species (amongst which are many crop pollinators) are connected to a large range of other species. This means that if the quality/composition of the surrounding environment declines this will affect the abundance of pollinators and pollination. Therefore, managing systems for conservation of pollination services alone, will target fewer species and have very different outcomes when compared to managing for conservation of pollinator diversity. Whilst having no intervention measures may result in having low pollinator diversity as well as low services (Figure 3A); measures targeted at enhancing services (such as utilising managed pollinators to overcome pollination deficit, simple agri-environment schemes like hedgerow management and flower rich margins, and utilisation of mass flowering crops [21•]), only benefit a small suite of species, resulting in low pollinator diversity (Figure 3B). Evidence from biodiversity-ecosystem functioning studies [54] suggests that measures that succeed in boosting pollinator diversity (Figure 3C) automatically enhance delivery of pollination service. Nevertheless there is a trade-off between managing for pollinator conservation and pollination services because most measures targeting pollinator diversity compete for space with the cultivation of insect-pollinated crops. Modest increases in mostly common species can often be obtained by extensifying agricultural management [55]. High pollinator diversity or conservation of threatened species generally requires measures such as establishment of diverse wildflower strips, maintenance or enhancement of species-rich grasslands or cultivation of economically non-profitable crops (in Europe for example, red clover *Trifolium pratense* or sainfoin *Onobrychis viciifolia*). Threatened pollinator species can effectively be conserved even in intensively managed farmland [56] but this is most likely limited to species foraging on host plants that can persist under the conditions prevailing in contemporary agricultural landscapes and/or that use nest sites that are available in such landscapes. This suggests that the more adapted pollinator species are to non-agricultural habitats, the stronger conservation measures will compete for space with insect-pollinated crops.

The exact nature of the trade-off between delivery of pollination services on one hand and conservation of threatened species or high pollinator diversity on the other hand is unknown, but it probably follows a typical production–possibility frontier as shown in orange in Figure 3. Different measures may enhance pollination and conservation to different extents in different ways. For example, simple agri-environment schemes that extensify farm management enhance dominant pollinators

**Figure 3**




Schematic showing examples of trade-offs between management for pollination services versus management for pollinator conservation. A, B, C and D represent low diversity–low services (loss–loss), low diversity–high service (loss–win), high diversity–low service (win–loss) and high diversity–high service (win–win) scenarios respectively. The arrows depict pathways and management measures by which we can move from one scenario to another and these are explained further in the text.

but not threatened species [9••] and benefits will therefore be primarily restricted to pollination service delivery, although concrete evidence for that is mostly lacking. There is also increased awareness of the positive effect of habitat heterogeneity on pollinator numbers and diversity [57•] (such as those brought about by application of agri-environmental schemes), which could improve pollination services to a number of economically important crops while simultaneously enhancing local biodiversity [58–61]. However, such win-win situations might be restricted to highly transformed landscapes (e.g. intensively managed northwest European landscapes). In such landscapes, the decline of the pollen host plants of species has been identified as the key driver of population decline of bee species [62] suggesting that more emphasis on provisioning of specific foraging and nesting resources might go a long way in enhancing pollinator biodiversity, including even threatened species. Recently, there has also been a focus on the role played by urban landscapes to support higher diversity of pollinator species [63•] with examples of positive impacts on pollinators found in a several cities across the World, including those in USA [64], Brazil [65,66], South Africa [67] and Europe [68]. The overall challenge, however, is to design and incentivise measures that optimise both pollination service delivery and enhance biodiversity conservation (Figure 3D) and that would remain stable not just under current conditions but could withstand future environmental perturbations.

In any case, more attention should be given to measures to conserve rare or endemic species that might occur in more natural landscapes or specialised habitats such as dunes or mountain grasslands. Most existing initiatives to enhance pollinators and the studies supporting them, only focus on landscapes of high anthropogenic use. Strategies are needed to make sure that also in the future people can appreciate the beauty and fascinating life history of species such as the aforementioned *B. gerstaeckeri*. In

addition, actions aiming to conserve solely dominant pollinators should not ignore the wider diversity and landscapes which sustains these species: The focus needs to include conservation of plants that, while not economically important, are required to conserve biodiversity in its entirety. This is likely to have benefits for many other ecosystem services that are affected by biodiversity, as well as sustaining species that have solely cultural/spiritual/moral values (i.e. actions that consider the concept of ecosystem service as whole). This would guarantee a win–win situation, by conserving wider biodiversity whilst providing a suite of species capable of crop pollination in vast regions today and for the future.

## Pathways to delivering sustainability for pollinators and pollination services

Systems to actively deliver sustainable conservation for both pollinators and pollination services are presently lacking. Although farmers increasingly recognise the benefits of pollination services, national and regional government policy designed to support pollinator diversity provides limited incentives for them to support pollinators that do not provide services [69]. In the absence of specific incentives, farmers have little motivation to provide interventions on land that is not adjacent to fields that will benefit from pollination services [23] or to support non-crop pollinating species. Furthermore, many on-farm agri-environment measures support pollinators as a beneficial side-effect more than an overt, targeted objective [70]. These shortcomings highlight the potentially pivotal role in more classical conservation actions such as protected areas and dedicated species-specific conservation action that are often focused on more intrinsic goals. However, these measures, even in areas far from agricultural habitats, may still be affected, positively or negatively, by broader policies such as water quality management or land development regulations. Indeed many policies that affect pollinators and wider

**Figure 4**

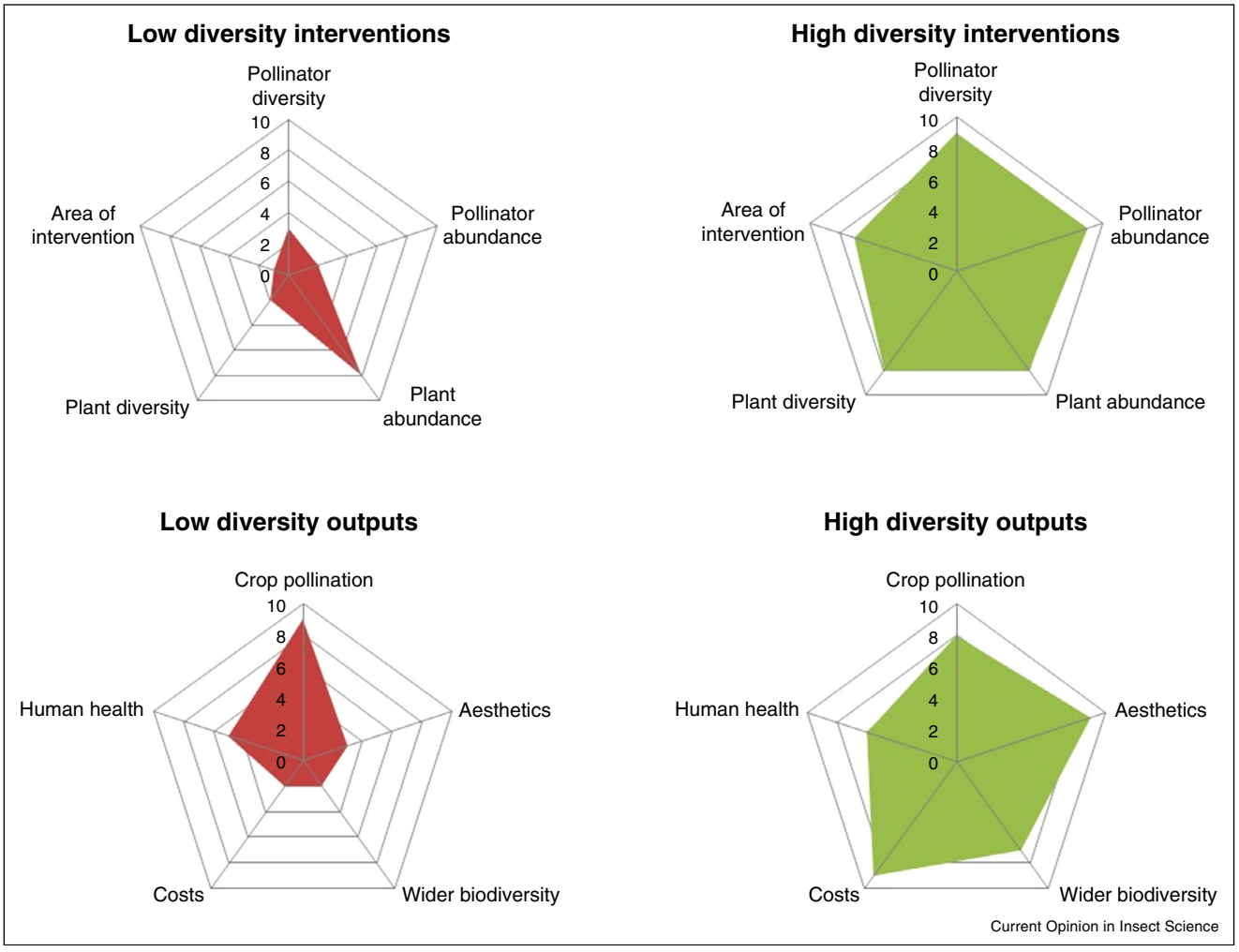



Illustration of a hypothetical comparison between interventions focussed on high and low diversity showing the resulting trade-offs and outputs.

biodiversity do not explicitly acknowledge them, focusing instead on food security, public health or development targets [69].

Reconciling these varied objectives within existing policy will likely benefit from a more targeted approach that optimises the placement and duration of measures to support wider pollinator diversity. This is likely to be expensive and complex to administer under current systems which are not designed around an ecosystems approach. An alternative system could be payments for ecosystem services (PES) schemes that paid producers based upon the measurable production of pollinators and pollination services. However, both pollinators and pollination services can be difficult and costly to monitor [71•]. Perhaps the most comprehensive solution would be to consider trade-offs in multiple dimensions (environmental, economic and social) using multi-criteria cost–benefit analyses that use different dimensional indexes [72] rather than focusing solely on economic benefit. Weighting within these indices can be used to emphasise certain objectives (benefits to endangered species, economic benefits to low income areas, among others) within each dimension. Using this framework, policy developed to explicitly consider and monitor trade-offs, may not necessarily maximise any one objective but could provide sustainable benefits to a number of objectives simultaneously, resulting in more desirable, win–win activities. This paradigm is illustrated in Figure 4. In order to fully achieve this framework, it will be essential that policy makers and scientists take a more holistic view of the issues surrounding biodiversity conservation rather than simply reframing an ecological issue as an economic one.

## Conclusion

- Only few species of pollinators have a direct and easily recognised economic importance. However, it is possible that pollinator species richness may create resilience to losses of current dominant species
- The vast numbers of pollinator species with no economic value are essential to guarantee the optimal functioning of ecosystems.
- The economic argument is inadequate as a sole reason for implementing management measures and we need to consider the biological, cultural and moral arguments for the conservation of wider diversity.
- Practices aimed at conserving only a limited number of species need to consider the vast number of ecological partners that sustain such species presence and influence their efficiency as pollinators.
- Management and policy measures need to focus on species not just in human dominated landscapes but need to benefit wider diversity of species including those in specialised habitats.
- Specific practices targeted at endangered and rare species are needed to not just guarantee the habitat requirements of a wider diversity of species, but for intrinsic biodiversity value.
- A more holistic approach to management, which recognises and measures biodiversity, economic and social impacts, will be required if policy is to provide true win–win situations

## Acknowledgments

DS was funded by NERC Knowledge Exchange Impact Accelerator Award and the Insect Pollinators Initiative (grant BB/I000364/1) S.G.P. was supported by European Union (EU) FP7 projects LIBERATION (grant 311781) and STEP (grant 244090). LGC was funded by the National Council for Scientific and Technological Development of Brazil, CNPq (grant AJT 300005/2015-6).

## References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Díaz S, Demissew S, Joly C, Lonsdale W, Ash N *et al.*: **The IPBES Conceptual Framework — 232 connecting nature and people**. *Curr Opin Environ Sustain* 2015:14 http://dx.doi.org/10.1016/j.cosust.2014.11.002.

2. MEA: *Millennium Ecosystem Assessment — Ecosystems and Human well-being: Synthesis*. Island Press; 2005.

3. COP. 2000 Decision V/6: Ecosystem approach. www.cbd.int/decision/cop/default.shtml?id=7148.

4. COM_244_final. 2011 Communication from the Commission to the European parliament, the Council, the Economic and Social Committee and the Committee of the regions. Our life insurance, our natural capital: an EU biodiversity strategy to 2020. http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:52011DC0244.

5. Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA, Baillie JEM, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM *et al.*: **Global biodiversity: indicators of recent declines**. *Science* 2010, **328**:1164-1168 http://dx.doi.org/10.1126/science.1187512.

6. Lebuhn G, Droege S, Connor EF, Gemmill-Herren B, Potts SG, Minckley RL, Griswold T, Jean R, Kula E, Roubik DW, Cane J, Wright KW *et al.*: **Detecting insect pollinator declines on regional and global scales**. *Conserv Biol* 2013, **27**:113-120 http://dx.doi.org/10.1111/j.1523-1739.2012.01962.x.

7. •• Carvalheiro LG, Kunin WE, Keil P, Aguirre-Gutierrez J, Ellis WN, Fox R, Groom Q, Hennekens S, Van Landuyt W, Maes D, Van de Meutter F, Michez D *et al.*: **Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants**. *Ecol Lett* 2013, **16**:870-878 http://dx.doi.org/10.1111/ele.12121.

Study evaluating the rates of biodiversity change in three European countries (Great Britain, Netherlands and Belgium) for plants and flower visiting insects. Results highlight the potential to maintain or even restore current species assemblages with appropriate land management.

8. Garibaldi LA, Aizen MA, Cunningham SA, Klein AM: **Pollinator shortage and global crop yield. Looking at the whole spectrum of pollinator dependency**. *Commun Integr Biol* 2009, **2**:37-39 http://dx.doi.org/10.4161/cib.2.1.7425.

9. •• Kleijn D, Winfree R, Bartomeus I, Carvalheiro LG, Henry M, Isaacs R, Klein A-M, Kremen C, M'Gonigle LK, Rader R, Ricketts TH, Williams NM *et al.*: **Delivery of crop pollination services is an insufficient argument for wild pollinator conservation**. *Nat Commun* 2015, **6**:7414 http://dx.doi.org/10.1038/ncomms8414.

Seminal paper providing evidence that while the contribution of wild bees to crop production is significant, service delivery is restricted to a limited subset of all known bee species. The authors show that conserving the biological diversity of bees requires more than just ecosystem-service-based arguments.

10. Gauld ID, Bolton B: *The Hymenoptera*. Oxford University Press; 1988.

11. Klein A-M, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T: **Importance of pollinators in changing landscapes for world crops**. *Proc Roy Soc B: Biol Sci* 2007, **274**:303-313 http://dx.doi.org/10.1098/rspb.2006.3721.

12. Ponchau O, Iserbyt S, Verhaeghe J-C, Rasmont P: **Is the caste-ratio of the oligolectic bumblebee *Bombus gerstaeckeri* Morawitz (Hymenoptera: Apidae) biased to queens?** *Ann Soc Entomol Fr* 2006, **42**:207-214.

13. Sheffield C, Pindar A, Packer L, Kevan P: **The potential of cleptoparasitic bees as indicator taxa for assessing bee communities**. *Apidologie* 2013, **44**:501-510 http://dx.doi.org/10.1007/s13592-013-0200-2.

14. Cardinal S, Straka J, Danforth BN: **Comprehensive phylogeny of apid bees reveals the evolutionary origins and antiquity of cleptoparasitism**. *Proc Natl Acad Sci* 2010, **107**:16207-16211 http://dx.doi.org/10.1073/pnas.1006299107.

15. Schwarz M, Gusenleitner F, Westrich P, Dathe HH: **Katalog der Bienen Österreichs, Deutschlands und der Schweiz (Hymenoptera, Apidae)**. *Entomofauna* 1996, **8**:1-398 http://dx.doi.org/10.1002/mmnd.19970440109.

16. Bouseman JK: **Coelioxys bisoncornua Hill in Illinois: a sunflower-associated cleptoparasitic bee new to the Eastern United States (Hymenoptera: Apoidea)**. *J Kansas Entomol Soc* 1982, **55**:406-407.

17. Carvell C, Rothery P, Pywell RF, Heard MS: **Effects of resource availability and social parasite invasion on field colonies of Bombus terrestris**. *Ecol Entomol* 2008, **33**:321-327 http://dx.doi.org/10.1111/j.1365-2311.2007.00961.x.

18. Lienhard A, Mirwald L, Hötzl T, Kranner I, Kastberger G: **Trade-off between foraging activity and infestation by nest parasites in the primitively eusocial bee *Halictus scabiosae***. *Psyche* 2009, **2010** http://dx.doi.org/10.1155/2010/707501 Article ID 707501.

19. Garibaldi LA, Steffan-Dewenter I, Kremen C, Morales JM, Bommarco R, Cunningham SA, Carvalheiro LG, Chacoff NP, Dudenhoffer JH, Greenleaf SS, Holzschuh A, Isaacs R *et al.*: **Stability of pollination services decreases with isolation from natural areas despite honey bee visits**. *Ecol Lett* 2011, **14**:1062-1072 http://dx.doi.org/10.1111/j.1461-0248.2011.01669.x.

20. Ricketts TH, Regetz J, Steffan-Dewenter I, Cunningham SA, Kremen C, Bogdanski A, Gemmill-Herren B, Greenleaf SS, Klein AM, Mayfield MM, Morandin LA, Ochieng A *et al.*: **Landscape effects on crop pollination services: are there general patterns?** *Ecol Lett* 2008, **11**:499-515 http://dx.doi.org/10.1111/j.1461-0248.2008.01157.x.

21. • Garibaldi LA, Carvalheiro LG, Leonhardt SD, Aizen MA, Blaauw BR, Isaacs R, Kuhlmann M, Kleijn D, Klein AM, Kremen C, Morandin L, Scheper J *et al.*: **From research to action: enhancing crop yield through wild pollinators**. *Front Ecol Environ* 2014, **12**:439-447 http://dx.doi.org/10.1890/130330.

Study providing a general framework and examples of approaches for enhancing pollinator richness and abundance, crop yield, and farmers' profit, including some benefits detected only through long-term monitoring.

22. Bluethgen N, Klein AM: **Functional complementarity and specialisation: the role of biodiversity in plant–pollinator interactions**. *Basic Appl Ecol* 2011, **12**:282-291 http://dx.doi.org/10.1016/j.baae.2010.11.001.

23. Bernardino AS, Gaglianone MC: **Nest distribution and nesting habits of *Xylocopa ordinaria* Smith (Hymenoptera, Apidae) in a restinga area in the northern Rio de Janeiro State, Brazil**. *Rev Bras Entomol* 2008, **52**:434-440 http://dx.doi.org/10.1590/s0085-56262008000300017.

24. Martins CF, Cortopassi-Laurino M, Koedam D, Imperatriz-Fonseca VL: **Espécies arbóreas utilizadas para nidificação por abelhas sem ferrão na caatinga (Seridó, PB; João Câmara, RN)**. *Biota Neotropica* 2004, **4**:n2.

25. Gianninia TC, Acostac AL, Silva CI, Oliveirae d, PEAM d, Imperatriz-Fonsecac VL, Saraivaa AM: **Identifying the areas to preserve passion fruit pollination service in Brazilian Tropical Savannas under climate change**. *Agric Ecosyst Environ* 2013, **171**:39-46 http://dx.doi.org/10.1016/j.agee.2013.03.003.

26. Buddenhagen IW, Elsasser TA: **An insect spread bacterial wilt epiphytotic of bluggoe banana**. *Nature* 1962:194 http://dx.doi.org/10.1038/194164a0.

27. Inouye DW: **The terminology of floral larceny**. *Ecology* 1980, **61**:1251-1253 http://dx.doi.org/10.2307/1936841.

28. Maloof JE: **The effects of a bumble bee nectar robber on plant reproductive success and pollinator behavior**. *Am J Bot* 2001, **88**:1960-1965.

29. Maloof JE, Inouye DW: **Are nectar robbers cheaters or mutualists?** *Ecology* 2000, **81**:2651-2661.

30. Pyke GH: **Optimal foraging: movement patterns of bumblebees between inflorescences**. *Theorit Popul Biol* 1978, **13**:72-98.

31. Kadmon R, Shmida A: **Departure rules used by bees foraging for nectar: a field test**. *Evol Ecol* 1992, **6**:142-151.

32. Klinkhamer PG, de Jong TJ: **Attractiveness to pollinators: a plant's dilemma**. *Oikos* 1993, **66**:180-184.

33. Charlesworth D, Charlesworth B: **Inbreeding depression and its evolutionary consequences**. *Ann Rev Ecol Evolut Syst* 1987, **18**:237-268.

34. Barber NA, Gorden NLS: **How do belowground organisms influence plant–pollinator interactions?** *J Plant Ecol* 2015, **8**:1-11 http://dx.doi.org/10.1093/jpe/rtu012.

35. Hegland SJ, Nielsen A, Lázaro A, Bjerknes A-L, Totland Ø: **How does climate warming affect plant–pollinator interactions?** *Ecol Lett* 2009, **12**:184-195 http://dx.doi.org/10.1111/j.1461-0248.2008.01269.x.

36. Memmott J, Craze PG, Waser NM, Price MV: **Global warming and the disruption of plant–pollinator interactions**. *Ecol Lett* 2007, **10**:710-717 http://dx.doi.org/10.1111/j.1461-0248.2007.01061.x.

37. Kremen C, Williams NM, Thorp RW: **Crop pollination from native bees at risk from agricultural intensification**. *Proc Natl Acad Sci U S A* 2002, **99**:16812-16816 http://dx.doi.org/10.1073/pnas.262413599.

38. Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C: **Landscape perspectives on agricultural intensification and biodiversity — ecosystem service management**. *Ecol Lett* 2005, **8**:857-874 http://dx.doi.org/10.1111/j.1461-0248.2005.00782.x.

39. •• Kennedy CM, Lonsdorf E, Neel MC, Williams NM, Ricketts TH, Winfree R, Bommarco R, Brittain C, Burley AL, Cariveau D, Carvalheiro LG, Chacoff NP *et al.*: **A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems**. *Ecol Lett* 2013, **16**:584-599 http://dx.doi.org/10.1111/ele.12082.

Synthesis paper explaining how pollinator persistence will depend on both the maintenance of high-quality habitats around farms, and on local management practices that may offset impacts of intensive monoculture agriculture.

40. Cameron SA, Lozier JD, Strange JP, Koch JB, Cordes N, Solter LF, Griswold TL: **Patterns of widespread decline in North American bumble bees**. *Proc Natl Acad Sci U S A* 2011, **108**:662-667 http://dx.doi.org/10.1073/pnas.1014743108.

41. Abe T, Makino S, Okochi I: **Why have endemic pollinators declined on the Ogasawara Islands?** *Biodivers Conserv* 2008, **17**:1465-1473 http://dx.doi.org/10.1007/s10531-008-9355-y.

42. Moron D, Lenda M, Skorka P, Szentgyorgyi H, Settele J, Woyciechowski M: **Wild pollinator communities are negatively affected by invasion of alien goldenrods in grassland landscapes**. *Biol Conserv* 2009, **142**:1322-1332 http://dx.doi.org/10.1016/j.biocon.2008.12.036.

43. Elmqvist T, Folke C, Nyström M, Peterson G, Bengtsson J, Walker B, Norberg J: **Response diversity, ecosystem change, and resilience**. *Front Ecol Environ* 2003, **1**:488-494 http://dx.doi.org/10.1890/1540-9295(2003)001[0488:RDECAR]2.0.CO;2.

44. Peterson G, Allen CR, Holling CS: **Ecological resilience, biodiversity, and scale**. *Ecosystems* 1998, **1**:6-18.

45. Laliberté E, Wells JA, DeClerck F, Metcalfe DJ, Catterall CP, Queiroz C, Aubin I, Bonser SP, Ding Y, Fraterrigo JM,

McNamara S, Morgan JW *et al.*: **Land-use intensification reduces functional redundancy and response diversity in plant communities**. *Ecol Lett* 2010:76-86 http://dx.doi.org/10.1111/j.1461-0248.2009.01403.x.

46. Carpenter SR, Cole JJ, Hodgson JR, Kitchell JF, Pace ML, Bade D, Cottingham KL, Essington TE, Houser JN, Schindler DE: **Trophic cascades, nutrients, and lake productivity: whole-lake experiments**. *Ecol Monogr* 2001, **71**:163-186 http://dx.doi.org/10.1890/0012-9615.

47. DEFRA: *Bees and Other Pollinators: Their Value and Health in England Review of Policy & Evidence*. 2013:. (in publication number: PB13981).

48. Kuhlmann M, Guo D, Veldtman R, Donaldson J: **Consequences of warming up a hotspot: species range shifts within a centre of bee diversity**. *Divers Distrib* 2012, **18**:885-897 http://dx.doi.org/10.1111/j.1472-4642.2011.00877.x.

49. Stone GN, Loder PMJ, Blackburn TM: **Foraging and courtship behavior in males of the solitary bee *Anthophora plumipes* (hymenoptera, anthophoridae) — thermal physiology and the roles of body size**. *Ecol Entomol* 1995, **20**:169-183.

50. Potts SG, Vulliamy B, Dafni A, Ne'eman G, Willmer P: **Linking bees and flowers: how do floral communities structure pollinator communities?** *Ecology* 2003, **84**:2628-2642 http://dx.doi.org/10.1890/02-0136.

51. Potts SG, Vulliamy B, Dafni A, Ne'eman G, O'Toole C, Roberts SPW: **Response of plant–pollinator communities to fire: changes in diversity, abundance and floral reward structure**. *Oikos* 2003, **101**:103-112.

52. Ollerton J, Winfree R, Tarrant S: **How many flowering plants are pollinated by animals?** *Oikos* 2011, **120**:321-326 http://dx.doi.org/10.1111/j.1600-0706.2010.18644.x.

53. Clark NE, Lovell R, Wheeler BW, Higgins SL, Depledge MH, Norris K: **Biodiversity, cultural pathways, and human health: a framework**. *Trends Ecol Evol* 2014, **29**:198-204 http://dx.doi.org/10.1016/j.tree.2014.01.009.

54. Hooper DU III, Ewel FSC, Hector JJ, Inchausti A, Lavorel P, Lawton S, Lodge JH, Loreau DM, Naeem M, Schmid S, Setala BH *et al.*: **Effects of biodiversity on ecosystem functioning: a consensus of current knowledge**. *Ecol Monogr* 2005, **75**:3-35.

55. Scheper J, Holzschuh A, Kuussaari M, Potts SG, Rundlöf M, Smith HG, Kleijn D: **Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss — a meta-analysis**. *Ecol Lett* 2013, **16**:912-920 http://dx.doi.org/10.1111/ele.12128.

56. Carvell C, Meek WR, Pywell RF, Goulson D, Nowakowski M: **Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins**. *J Appl Ecol* 2007, **44**:29-40 http://dx.doi.org/10.1111/j.1365-2664.2006.01249.x.

57. • Senapathi D, Carvalheiro LG, Biesmeijer JC, Dodson C-A, Evans RL, McKerchar M, Morton RD, Moss ED, Roberts SPM, Kunin WE, Potts SG: **The impact of over 80 years of land cover changes on bee and wasp pollinator communities in England**. *Proc Roy Soc B: Biol Sci* 2015, **282**:20150294 http://dx.doi.org/10.1098/rspb.2015.0294.
First paper to explore the relationship between historic land-use change and shifts in pollinator communities that shows that single habitat types and monocultures have led to greater loss of species when compared to diverse, heterogenous habitats that are essential for maintaining species richness and diversity.

58. McKenzie AJ, Emery SB, Franks JR, Whittingham MJ: **Landscape-scale conservation: collaborative agri-environment schemes could benefit both biodiversity and ecosystem services, but will farmers be willing to participate?** *J Appl Ecol* 2013, **50**:1274-1280 http://dx.doi.org/10.1111/1365-2664.12122.

59. Bartomeus I, Potts SG, Steffan-Dewenter I, Vaissiere BE, Woyciechowski M, Krewenka KM, Tscheulin T, Roberts SPM, Szentgyorgyi H, Westphal C, Bommarco R: **Contribution of insect pollinators to crop yield and quality varies with agricultural intensification**. *PeerJ* 2014, **2** http://dx.doi.org/10.7717/peerj.328 e328-e328.

60. Osgathorpe LM, Park K, Goulson D: **The use of off-farm habitats by foraging bumblebees in agricultural landscapes: implications for conservation management**. *Apidologie* 2012, **43**:113-127 http://dx.doi.org/10.1007/s13592-011-0083-z.

61. Schueepp C, Herzog F, Entling MH: **Disentangling multiple drivers of pollination in a landscape-scale experiment**. *Proc Roy Soc B-Biol Sci* 2014, **281** http://dx.doi.org/10.1098/rspb.2013.2667.

62. Scheper J, Reemer M, Van Kats R, Ozinga WA, Van der Linden GTJ, Schaminée JHJ, Siepel H, Kleijn D: **Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in the Netherlands**. *Proc Natl Acad Sci* 2014, **111**:17552-17557 http://dx.doi.org/10.1073/pnas.1412973111.

63. • Baldock K, Goddard M, Hicks D, Kunin WE, Mitschunas N, Osgathorpe LM, Potts SG, Robertson K, Scott A, Stone GN, Vaughan I, Memmott J: **Where is the UK's pollinator biodiversity? Comparing flower-visitor communities between cities, farmland and nature reserves using visitation networks**. *Proc Roy Soc B-Biol Sci* 2015, **282**:20142849 http://dx.doi.org/10.1098/rspb.2014.2849.
A study comparing pollinator communities in three different landscapes in Britain — urban, farmland and nature reserves showing that bee species richness was higher in urban areas than farmland and urban pollinator assemblages were more homogeneous across space than those in farmland or nature reserves.

64. Fetridge ED, Ascher JS, Langellotto GA: **The bee fauna of residential gardens in a suburb of New York City (Hymenoptera: Apoidea)**. *Ann Entomol Soc Am* 2008, **101**:1067-1077 http://dx.doi.org/10.1603/0013-8746-101.6.1067.

65. Zanette LRS, Martins RP, Ribeiro SP: **Effects of urbanization on Neotropical wasp and bee assemblages in a Brazilian metropolis**. *Landsc Urban Plann* 2005, **71**:105-121 http://dx.doi.org/10.1016/j.landurbplan.2004.02.003.

66. Aleixo KP, de Faria LB, Garófalo CAVLI-F, Silva CI: **Pollen collected and foraging activities of *Frieseomelitta varia* (Lepeletier) (Hymenoptera: Apidae) in an urban landscape**. *Sociobiology* 2013, **60**:266-276.

67. Anderson PML, Avlonitis G, Ernstson H: **Ecological outcomes of civic and expert-led urban greening projects using indigenous plant species in Cape Town, South Africa**. *Landsc Urban Plann* 2014, **127**:104-113 http://dx.doi.org/10.1016/j.landurbplan.2014.03.007.

68. Goddard MA, Dougill AJ, Benton TG: **Scaling up from gardens: biodiversity conservation in urban environments**. *Trends Ecol Evol* 2010, **25**:90-98 http://dx.doi.org/10.1016/j.tree.2009.07.016.

69. Ratamäki O, Jokinen P, Sorensen P, Breeze TD, Potts SG: **Multi-level analysis of misfit and interplay between pollination-related policies and practices**. *Ecosystem Serv* 2015, **14**:133-143 http://dx.doi.org/10.1016/j.ecoser.2015.01.002.

70. Blake RJ, Potts S, Westbury DB, Woodcock BA, Sutton P: **New tools to boost butterfly habitat quality in existing grass buffer strips**. *J Insect Conserv* 2011, **15**:221-232 http://dx.doi.org/10.1007/s10841-010-9339-6.

71. • Breeze TD, Bailey AP, Balcombe KG, Potts SG: **Costing conservation: an expert appraisal of the pollinator habitat benefits of England's entry level stewardship**. *Biodivers Conserv* 2014, **23**:1193-1214 http://dx.doi.org/10.1007/s10531-014-0660-3.
A study using novel expert survey methods to determine the costs of establishing and maintaining Entry level Agri environmental schemes. The study opened the debate on the costs and benefits of specific entry level stewardship management options and how these can be enhanced to benefit both participants and biodiversity more equitably.

72. Sijtsma FJ, van der Heide CM, van Hinsberg A: **Beyond monetary measurement: how to evaluate projects and policies using the ecosystem services framework**. *Environ Sci Pol* 2013, **32**:14-25 http://dx.doi.org/10.1016/j.envsci.2012.06.016.