

PLANT–POLLINATOR INTERACTIONS FROM FLOWER TO LANDSCAPE

Landscape impacts on pollinator communities in temperate systems: evidence and knowledge gaps

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Summary

1. This review assesses current knowledge about the interplay between landscape and pollinator communities. Our primary aim is to provide an evidence base, identify key gaps in knowledge and highlight initiatives that will help develop and improve strategies for pollinator conservation.
2. Human-dominated landscapes (such as arable land and urban environments) can have detrimental impacts on pollinator communities but these negative effects can be ameliorated by proximity to semi-natural habitat and habitat corridors. There is also evidence to suggest that increased landscape heterogeneity and landscape configuration can play an important role in the maintenance of diverse pollinator communities.
3. Landscape characteristics have direct impacts on pollinator communities, but can also influence abundance and richness through interaction with other drivers such as changing climate or increased chemical inputs in land management.
4. The majority of existing literature focuses on specific hymenopteran groups, but there is a lack of information on the impact of landscape changes on non-bee taxa. Research is also needed on the effectiveness of management interventions for pollinators and multiple year observations are required for both urban and rural initiatives.
5. Current policies and monitoring schemes could contribute data that will plug gaps in knowledge, thus enabling greater understanding of relationships between landscapes and pollinator populations. This would in turn help design mitigation and adaptation strategies for pollinator conservation.

Key-words: agri-environment, habitat characteristics, policy, pollinator conservation, spatial scales, species abundance, species richness

Introduction

Pollinators provide a crucial ecosystem service by improving quality or stabilising yields of approximately 75% of crop-plant species globally (Kleijn *et al.* 2015). They are also intricately linked to wider biodiversity as they are essential for the reproduction of many wild plant species (Ollerton, Winfree & Tarrant 2011) and involved in indirect ecological interactions with taxa from other trophic guilds, including predators and parasitoids (Senapathi *et al.* 2015a). Pollinators are facing pressures from multiple

drivers leading to their declines with potentially serious implications for human food security and health, as well as ecosystem functions (Vanbergen *et al.* 2013). Concern over pollinator declines has sparked a remarkable increase in studies assessing threats to pollinators and quantifying the impact of their decline on pollination services. Landscape changes, including conversion of natural habitats to anthropogenic land-use and agricultural intensification, have been identified as one of the major drivers of pollinator declines (Kennedy *et al.* 2013; Vanbergen *et al.* 2013) and with an ever-increasing human population, indications are that land-use changes will further intensify. Understanding the effects of landscape change on pollinators is

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crucial for the prevention of further pollinator loss and to help design strategies to protect pollinators in human-dominated landscapes (Viana *et al.* 2012). Assessing our current knowledge about the interplay between landscape and pollinator communities, as well as identifying and addressing knowledge gaps will help develop effective mitigation strategies.

A number of national and international initiatives have been developed to improve understanding of the risks posed to pollinators (Gill *et al.* 2016) such as the first thematic assessment of the Intergovernmental Platform on Biodiversity and Ecosystem Services, which is focused on pollinators, pollination and food production (IPBES 2016). Some of these initiatives have facilitated research projects that explore the impact of landscape on pollinator communities. To date, the majority of landscape-scale studies has come from Europe and North America where researchers have used well-established methods for assessing the impacts of landscape drivers on pollinator communities. This review therefore predominantly focuses on research in temperate regions but includes studies that have carried out global meta-analyses.

We assess information within the existing literature in three main sections: we first examine how landscape-level impacts on pollinators are assessed (section Assessing landscape-level impacts on pollinators); then explore which landscape characteristics affect pollinators (section Landscape–pollinator interactions). Finally, we consider the evidence for conserving pollinators at the landscape scale and the importance of policy in landscape-scale management (section Enhancing landscapes for pollinators). Viana *et al.* (2012) addressed the question of how well we understand landscape effects on pollinator and pollination services, but in the intervening years more than 250 studies have been published on interactions between landscapes and pollinators, requiring an updated review of this topic. Studies included in our review focus on pollinators rather than pollination services (with a few exceptions) and cover the impacts of both natural landscapes (land cover) and anthropogenic landscapes (land use) at regional, national and continental scales. Our main aims are to provide an evidence base, identify key gaps in knowledge and also highlight recent policy and monitoring schemes that will help develop and improve strategies for pollinator conservation.

Assessing landscape-level impacts on pollinators

SPATIAL VERSUS TEMPORAL STUDIES

Most previous studies have employed one of two main approaches to assess the impacts of various landscape-level variables on pollinator densities and/or distributions. The commonest is effectively a “spatial” approach to assessing these relationships, with studies examining the response of pollinator richness, abundance and composition to

landscape structure and spatial heterogeneity (e.g. Meyer, Jauker & Steffan-Dewenter 2009) and the influence of local and landscape-level effects of agroecosystems on wild pollinators (e.g. Kennedy *et al.* 2013). Studies assessing the impact of landscape-level changes over time are less common, probably due to the rarity and difficulty of access to long-term data on pollinator communities and landscape changes. However, few studies have employed this “temporal” approach by resampling sites across multiple habitat and land cover types and comparing findings to historical data sets (Burkle, Marlin & Knight 2013; Aguirre-Gutiérrez *et al.* 2015; Senapathi *et al.* 2015b; Aguirre-Gutiérrez *et al.* 2016). Others have focussed on changes in single land-use types over time and the resulting impact on pollinator extinctions. Studies combining both spatial and temporal approaches are rare, although Carvalheiro *et al.* (2013) employed a spatio-temporal design to examine changes in pollinator richness and abundance over time in European landscapes.

To date, the majority of studies has focused on single landscape types e.g. agricultural (for e.g. Brosi *et al.* 2009; Le Feon *et al.* 2010; Garibaldi *et al.* 2011), or urban habitats (Matteson, Grace & Minor 2013), but comparison of pollinator communities between multiple land-use types is becoming more common (Kennedy *et al.* 2013; Verboven *et al.* 2014; Baldock *et al.* 2015). These approaches enable a better understanding of how pollinators use and respond to changes in different landscapes.

SPATIAL SCALES

The scale of the studies examining the impact of landscape on pollinator communities varies considerably, from local to global scales. Several recent meta-analyses have combined findings from multiple studies to assess landscape-level effects at a global scale. For example, Garibaldi *et al.* (2011) conducted a global synthesis of studies from six continents examining landscape scale effects on flower-visitor richness and pollination services in crop fields from contrasting biomes. A number of studies have combined data from multiple locations on the same continent, particularly in Europe. For example, Carre *et al.* (2009) explored the impact of landscape on bee diversity in European annual crops; Clough *et al.* (2014) explored the effect of intensively managed landscapes on bee abundance and diversity in semi-natural grasslands at 239 sites from five countries and Le Feon *et al.* (2010) compared the response of wild bee communities to agricultural intensification in four European countries. More common are studies testing the effects of habitat area, quality and connectivity as well as landscape composition and configuration on managed and wild pollinators within countries, including Germany (Meyer, Jauker & Steffan-Dewenter 2009; Hopfenmueller, Steffan-Dewenter & Holzschuh 2014; Steckel *et al.* 2014), Sweden (Andersson *et al.* 2013; Jonsson *et al.* 2015) and the UK (Baldock *et al.* 2015; Senapathi *et al.* 2015b) or regional studies from the US (Jha & Kremen 2013a;

Bennett & Isaacs 2014; Connelly, Poveda & Loeb 2015). While the studies above explore spatial context from an anthropogenic viewpoint (i.e. the geographical dispersion of sites) this may not align with a pollinator's perception of landscape. Further studies on how pollinator species respond to land-use change at different scales are therefore required to better inform conservation schemes.

Landscape–pollinator interactions

Landscape-level changes have the potential to affect pollinator species in a number of ways. There is evidence to suggest that landscape characteristics affect pollinator richness, abundance and composition of communities (Kennedy *et al.* 2013; Aguirre-Gutierrez *et al.* 2015) and that response diversity (differential response to environmental variables among species), density-compensation (negative co-variance among species' abundances) and cross-scale resilience (response to the same environmental variable at different scales by different species of pollinators) can be affected by landscape disturbance (Winfree & Kremen 2009). In this section, we review the evidence for and against specific hypotheses regarding the impact of landscape characteristics on pollinator communities.

AGRICULTURAL INTENSIFICATION HAS A DETRIMENTAL IMPACT ON POLLINATOR COMMUNITIES

The proportion and intensity of agricultural land in the landscape tends to be negatively related to pollinator abundance and species richness (Marini *et al.* 2014; Steckel *et al.* 2014; Connelly, Poveda & Loeb 2015; Scheper *et al.* 2015). However, the type of agriculture can make a difference; for example, apple-dominated landscapes exhibit drastically reduced wild bee species richness and abundance compared to landscapes dominated by either grassland or forest (Marini *et al.* 2014). In another study, Brittain *et al.* (2010) found that the species richness of wild bees declined in vine fields where the insecticide was applied, but did not decline in maize or uncultivated fields. Interestingly, Le Feon *et al.* (2013) found that species richness, abundance and diversity of wild bees were greater in sites with arable land compared to those under intensive animal husbandry. Mass flowering crops may be one aspect of agricultural landscapes that benefit pollinators (see section Mass flowering crops), but the limited flowering season does not provide longevity of resources (Holzschuh *et al.* 2013).

Bee functional diversity can be lower in agricultural landscapes compared to natural habitats. Forrest *et al.* (2015) found that bee assemblages in Californian farmland were functionally depauperate compared to those in nearby natural communities with farmland communities dominated by social, polylectic ground-nesting species with long flight seasons and natural areas dominated by bees that had shorter but later flight seasons. A study that collated data for 257 bee species from multiple studies across

Europe (De Palma *et al.* 2015) found that smaller-bodied species and those with shorter flight seasons were less likely to be present in areas of intensive agriculture. Smaller bee species may be more sensitive to intensive agriculture as larger species can forage greater distances (Greenleaf *et al.* 2007). However, Forrest *et al.* (2015) found no difference in bee body size between farmed and natural habitats and Rader *et al.* (2014) found that larger-bodied insect pollinators in New Zealand were more sensitive to intensive land use than smaller species.

RESPONSE TO URBANISATION VARIES AMONG DIFFERENT POLLINATOR TAXA

Urban land cover is increasing globally (Seto, Guneralp & Hutrya 2012) and the resultant habitat loss and fragmentation is an important driver of plant–pollinator interactions (Harrison & Winfree 2015). Pollinator abundance and richness tends to decrease with increasing urbanisation (e.g. Ahrne, Bengtsson & Elmquist 2009; Bates *et al.* 2011), but studies comparing pollinator communities in urban and non-urban landscapes have revealed that towns and cities can support higher species richness of bees compared to agricultural land (Baldock *et al.* 2015) and even nature reserves (Sirohi *et al.* 2015). Reproductive performance may also be enhanced in urban areas; colony growth rate and nest density of bumblebees in domestic gardens can exceed that found in rural and agricultural habitats (e.g. Osborne *et al.* 2008), with diverse urban bee communities also providing a benefit by pollinating urban crops and garden plants (e.g. Lowenstein, Matteson & Minor 2015).

The response to urbanisation also varies among taxa with different functional groups of pollinators dominating in different urban landscapes (Threlfall *et al.* 2015). Specialist bees are rare in cities (Hernandez, Frankie & Thorp 2009; Tonietto *et al.* 2011) whilst other studies have shown a positive effect of urbanisation on bumblebees (Carre *et al.* 2009), cavity-nesting bees (Cane *et al.* 2006) and later-season small-bodied bees (Wray, Neame & Elle 2014). De Palma *et al.* (2015) found that overall European bee species were less likely to be present in urban areas, although cavity-nesting species were unaffected by land use. Those present in urban areas tended to be generalist short-tongued species. Several studies show that hoverflies seem to be more negatively affected by urban development than bees (Verboven *et al.* 2014; Baldock *et al.* 2015) but in general the effect of urbanisation on non-bee pollinators has been under-researched and further information is required to augment urban habitat management.

INCREASED LANDSCAPE HETEROGENEITY ENHANCES POLLINATOR RICHNESS AND ABUNDANCE

Increased landscape heterogeneity and the amount of high-quality (natural and semi-natural) habitat typically enhances species richness and abundance (Kennedy *et al.*

2013; Steckel *et al.* 2014; Aguirre-Gutierrez *et al.* 2015; Senapathi *et al.* 2015b) with species richness affected by factors related to resource heterogeneity, including richness of flowering plants, area and landscape diversity (Meyer, Jauker & Steffan-Dewenter 2009). Andersson *et al.* (2013) found that pollinator richness generally declined with decreasing landscape heterogeneity, but taxonomic breadth only declined with landscape heterogeneity on conventionally managed farms. While the majority of studies was conducted in agricultural landscapes, they also considered the impact of semi-natural habitats. For example, solitary bee abundance was positively influenced by the presence of temporary grasslands in cereal rotations (Le Feon *et al.* 2013) and bee species richness in wildflower strips on arable land increased with the amount of semi-natural habitats in the landscape (Scheper *et al.* 2015) (see also section Agri-environment schemes). Proximity to natural habitat can be important for wild pollinators, with pollinator species richness, visitation, and overall stabilisation of pollination services found to decrease with isolation from natural areas (Ricketts *et al.* 2008; Garibaldi *et al.* 2011; Kennedy *et al.* 2013).

LANDSCAPE CONFIGURATION SIGNIFICANTLY INFLUENCES POLLINATOR DIVERSITY

Landscape configuration can play an important role in the maintenance of diverse pollinator communities. Decreased patch size, loss of habitat area and reduced connectivity have all been identified as important drivers of species richness declines (Marini *et al.* 2014). Harrison & Winfree's (2015) review of urban drivers of plant–pollinator interactions shows how habitat loss and fragmentation can change flower visitation rates and pollination success through changes in pollinator foraging behaviour or through population-level effects on pollinators. Hopfenmueller, Steffan-Dewenter & Holzschuh (2014) found that wild bee richness and community functional trait diversity in calcareous grasslands in Germany increased with complex landscape configuration, habitat area and habitat quality. The findings suggest a strong dependence of habitat specialists on local habitat characteristics such as habitat area and quality, whereas cuckoo bees and bumblebees are more likely affected by the surrounding landscape. Jha & Kremen (2013a) found that the foraging distance of bees can also be influenced by landscape composition; *Bombus vosneskii* foraged further in pursuit of species-rich floral patches in landscapes with lower resource diversity. An experimental study set within calcareous grasslands and intensive agricultural landscapes found that increasing isolation of small habitat islands resulted in both decreased abundance and species richness of flower-visiting bees and that wildflower seed set was positively correlated with bee visitor abundance, suggesting that fragmented habitats can negatively affect both pollinators and pollination services (Steffan-Dewenter & Tschardtke 1999). Increasing wildflower patch size can lead to increases in wild bee density

and result in greater seed set in wild flowers within agricultural landscapes (Bennett & Isaacs 2014). In addition, Van Geert, Van Rossum & Triest (2010) demonstrated how existing linear landscape elements in intensively used farmland may act as functional biological corridors facilitating pollen dispersal through pollinator movements. Thus a combination of large high-quality patches and heterogeneous landscapes may help to maintain high bee species richness and communities with diverse trait composition, which might stabilize pollination services provided to crops and wild plants on local and landscape scales.

LANDSCAPE CHANGES INTERACT WITH OTHER DRIVERS OF CHANGE TO INFLUENCE POLLINATOR COMMUNITIES

Landscape effects do not occur in isolation and can interact with other drivers to impact pollinator and pollination (González-Varo *et al.* 2013). One synthesis paper demonstrated how pollinator persistence depends both on the maintenance of high-quality habitats around farms and on local management practices (Kennedy *et al.* 2013). For example Brittain *et al.* (2010) revealed how bee responses to insecticide application varied depending on crop type and spatial scale. Park *et al.* (2015) also found that while bee abundance and species richness decreased linearly with increasing pesticide use in apple orchards 1 year after application, the pesticide effects on wild bees were buffered by increasing proportion of natural habitat in the surrounding landscape.

There is also increasing evidence that an interaction between future climate change and landscape and habitat configuration could pose challenges to pollinators (Kerr *et al.* 2015). For instance, the potential for pollinator species at their current climatic limits to migrate to newly suitable areas may depend on the amount and spatial connectivity of habitats, and habitat loss and fragmentation arising from land-use changes in response to changing climate could limit compensatory species migrations (Warren *et al.* 2001; Forister *et al.* 2010). Differing rates of dispersal (Warren *et al.* 2001) could also lead to spatial dislocation of plants and their specialist pollinators, and lower connectivity between habitat remnants combined with future climate shifts may reduce population sizes and increase extinction likelihood of pollinators especially those of poor dispersers or habitat specialist (Warren *et al.* 2001; Burkle, Marlin & Knight 2013). While there are increasing studies in this area, further rapid investigation into interactions between multiple drivers and their combined effects is crucial in order to enable mitigation measures to counteract future threats to pollinators.

Enhancing landscapes for pollinators

In this section we review the existing evidence for how pollinator populations and communities can be enhanced at the landscape scale through management in both urban

and rural landscapes. We also highlight some of the underlying policies and monitoring schemes for incentivising this management, illustrating the importance of establishing long-term, national-scale monitoring schemes for pollinators.

LANDSCAPE MANAGEMENT

Habitats can be enhanced for pollinators using a variety of approaches, but most management tends to focus on increasing the abundance or diversity of floral resources (i.e. nectar and pollen). In addition to floral food sources, wild pollinators depend on a range of other resources, for example, the majority of Hymenoptera requires nest sites, whilst Diptera and Lepidoptera require larval host habitat, which is often species-specific. However few studies examine the availability of non-floral resources (such as host plant preference) in relation to landscape factors. To date, the majority of initiatives to improve habitat for pollinators has focused on adding floral resources in agricultural landscapes where pollinators perform an economically important crop pollination service. However, evidence is growing as to the importance of urban areas for pollinator conservation (Baldoek *et al.* 2015; Sirohi *et al.* 2015), and maintaining biodiversity in urban green spaces is likely to benefit human well-being as well as wildlife (e.g. Fuller *et al.* 2007).

Agri-environment schemes

Agri-environment schemes (AES) are financial incentives offered to land managers to compensate for a loss of yield when they set aside part of their land for wildlife conservation. AES are widely used to support biodiversity of multiple taxa in agricultural landscapes, but they remain controversial due to their high cost and variable success (Batary *et al.* 2015). AES appear to be important tools for providing flowers and other resources that lead to increased abundance and diversity of pollinators at local to landscape scales (e.g. Jonsson *et al.* 2015). Recent work has also demonstrated enhanced bumblebee reproductive capacity (Carvell *et al.* 2015) and nest density (Wood, Holland & Goulson 2015b) associated with flower-rich AES. However, the ability of AES to enhance the reproduction of non-bumblebee taxa is unknown and it appears that AES are most beneficial to generalist pollinators such as bumblebees and honeybees (Wood, Holland & Goulson 2015).

At local scales, the performance of AES are influenced by their management, with wild pollinators benefitting from uncut refugia in extensively managed hay meadows (Buri, Humbert & Arlettaz 2014) and cutting regimes that extend the flowering season in sown flower patches (Pywell *et al.* 2011). At larger scales, the effectiveness of AES is moderated by landscape context. For instance, a Europe-wide meta-analysis suggested that AES deliver greater benefits to pollinators in relatively simple (but not intensively

managed) landscapes where they offer greater 'ecological contrast' compared to more complex landscapes with substantial areas of natural habitat (Scheper *et al.* 2013).

Despite the efficacy of AES for increasing pollinator diversity and reproductive capacity, there remains a dearth of evidence that AES can increase pollinator populations over time at the landscape scale. In order to demonstrate a population response rather than a spatio-temporal behavioural response, AES need to be monitored for a minimum of 2 years as the number of individuals of univoltine bee species in a given year depends on the foraging resources available to females in the previous year and population growth in bumblebees depends on the number of colonies founded by queens the previous year. Experiments therefore need to be run for multiple years to test whether floral resources attract more pollinators in second and subsequent years (behavioural + population effects) than they do when first presented (behavioural effects alone). In an experiment across four European countries, Scheper *et al.* (2015) compared the effectiveness of wild-flower strips for enhancing bee abundance and richness and were unable to detect a population response in the second year of monitoring. They suggest that the creation of larger flower patches and longer-term monitoring would help to pick up population-level changes. The larger scale impact of AES is also dependent on their uptake as evidenced by a recent study showing that AES flower strips make a negligible contribution to resources for pollinators at national or regional scales in the UK due to low uptake by farmers (Baude *et al.* 2016).

Mass flowering crops

Although agricultural intensification is a driver of pollinator declines worldwide (Vanbergen *et al.* 2013), mass flowering crops (MFCs) such as oilseed rape (*Brassica napus*) and field bean (*Vicia faba*) can provide a reliable, albeit short-lived, 'resource pulse' for pollinators in agricultural landscapes. For example, oilseed rape improves colony growth in bumblebees (Westphal, Steffan-Dewenter & Tscharnkte 2009 and references therein) and also has a positive effect on the abundance (Holzschuh *et al.* 2013) and species richness of cavity-nesting bees and wasps (Diekötter *et al.* 2014). It appears that MFCs such as oilseed rape may be particularly important for population growth in early-season solitary bees that are able to produce sexuals during the mass-flowering period (Jauker *et al.* 2012). Bumblebees, in contrast, do not produce males and queens until after the flowering period of oilseed rape and therefore appear less able to respond to MFCs in a reproductive capacity (Westphal, Steffan-Dewenter & Tscharnkte 2009; Riedinger *et al.* 2015). However, late season MFCs, such as red clover (*Trifolium pratense*), can increase the reproductive capacity of bumblebees (Rundlöf *et al.* 2014).

Mass flowering crops can influence plant–pollinator interactions in non-crop habitat through facilitation (i.e.

'pollinator spillover') or competition (i.e. a 'dilution effect') and these effects may vary with spatial and temporal scale (Hanley *et al.* 2011; Kovács-Hostyánszki *et al.* 2013). MFCs can also cause shifts in pollinator community composition, for example, by being disproportionately beneficial to short-tongued bumblebees at the expense of more specialised longer tongued species (Diekötter *et al.* 2010). A further limitation of MFCs is that they are often treated with systemic pesticides, such as neonicotinoids, which appear to play a significant role in the decline of bees (Goulson *et al.* 2015) and impair pollination services (Stanley *et al.* 2015). A ban on neonicotinoids use on MFC across Europe was brought into effect in the winter of 2013, but this policy is currently under review and conclusive evidence on the effectiveness of the ban for pollinators is yet to be obtained.

Urban habitat management

A positive association between pollinator diversity and the extent of floral resources has been demonstrated for a range of individual habitats in urban areas, including domestic and community gardens (Smith *et al.* 2006; Matteson & Langelotto 2010), green roofs (Tonietto *et al.* 2011), urban forests (Carper *et al.* 2014) and parks and cemeteries (Matteson, Grace & Minor 2013). However, systematic studies that compare the value of different urban habitats for pollinators in multiple cities are lacking. The importance of floral resources may also vary with geographic context and taxon. For example, honeybees in green spaces of Melbourne, Australia, were positively associated with the diversity of flowering plants, whilst cavity and ground nesting floral specialist bee species appeared to depend more on the availability of nesting habitat (Threlfall *et al.* 2015).

These findings and those detailed in section Response to urbanisation varies among different pollinator taxa, lend credence to initiatives that seek to maintain and enhance the value of urban green spaces for pollinators. Gardeners can now make evidence-based decisions on best plant species to attract pollinators (e.g. Garbuzov & Ratnieks 2014; Salisbury *et al.* 2015) and confirmation that creation of wildflower areas (Blackmore & Goulson 2014) and reduced mowing regimes (Garbuzov, Fensome & Ratnieks 2015) provide important floral resources for pollinators is useful for green space managers. Novel urban habitats, such as green roofs and walls, offer considerable potential for supporting pollinators but at present, data are available from only small-scale studies from which it is hard to generalise (e.g. MacIvor, Ruttan & Salehi 2015). Pollinators may also be nest-site limited in cities (Threlfall *et al.* 2015; but see Wray & Elle 2015) and 'bee hotels' and bumblebee nest boxes are widely promoted solutions despite a lack of evidence from urban studies regarding their effectiveness in supporting cavity nesting bees (MacIvor & Packer 2015) or bumblebees (Gaston *et al.* 2005). As habitat configuration has been shown to affect highly mobile pollinators in

cities (Sattler *et al.* 2010), remnants of natural habitats and other green areas in urban areas could act as natural corridors thereby enhancing habitat connectivity and preserving biodiversity. In general, however, much more research is needed on the effectiveness of management interventions for pollinators in urban areas, especially with respect to how networks of habitats facilitate the dispersal of pollinators across cities at the landscape scale and subsequent effects on population dynamics.

Landscape-scale habitat creation schemes

As outlined in section Agricultural intensification has a detrimental impact on pollinator communities, pollinators, especially the larger Hymenoptera (as well as Syrphids), can forage over considerable distances and therefore often respond to the composition and configuration of habitat at the landscape scale. Molecular ecology studies have also shown that habitat connectivity, in the form of corridors or networks of habitat patches, promotes increased dispersal and gene flow (e.g. Jha & Kremen 2013b). In response to this evidence, and concerns about biodiversity declines more widely, a number of multi-partner conservation initiatives and NGO campaigns are aiming to create corridors of pollinator-friendly habitat across both urban and agricultural landscapes. For instance, England has a series of large-scale ecological connectivity initiatives across the country known as Nature Improvement Areas (NIAs) (Defra 2014) and some of these NIAs are working with partners to improve the transport network for pollinators (<https://www.gov.uk/government/news/greener-transport-network-to-provide-highways-for-wildlife>). Similarly, the 'B-Lines' project, led by the UK invertebrate conservation charity Buglife, seeks to create and restore a network of at least 150 000 ha of flower-rich habitat corridors and stepping stones across rural and urban Britain (<https://www.buglife.org.uk/campaigns-and-our-work/habitat-at-projects/b-lines>). Buglife are also working in eight UK cities to promote urban habitat creation and connectivity for pollinators (<https://www.buglife.org.uk/urban-buzz>), with similar projects emerging across Europe, e.g. Pollinator Passage in Oslo, Norway (<http://www.pollinatorpassa.sjen.no>). However, many of these schemes have been established only recently; the extent to which they have enhanced pollinator populations at the landscape scale is currently unknown, and inferences may well be hindered by a lack of baseline data and suitable control landscapes with which to compare.

Given appropriate management, roadside verges provide important habitat for pollinators and could facilitate dispersal (e.g. Hanley & Wilkins 2015). In the UK, the plant conservation charity Plantlife campaigns for sympathetic management of road verges (<http://www.plantlife.org.uk/roadvergecampaign>). However, enhancing roadside habitats for pollinators could create an ecological trap, due to direct mortality from roads (Baxter-Gilbert *et al.* 2015) or from reduced navigational abilities due to diesel

Table 1. National level pollinator strategies or action plans and key recommendations relevant to landscape-level pollinator conservation

Strategy/Plan	Year published	Country	Co-ordinating organisation	Key recommendations relevant to landscape-level conservation for pollinators
Action Plan for Pollinators in Wales <i>Welsh Government (2013) The Action Plan for Pollinators in Wales. Welsh Government Publication, Aberystwyth, Wales</i>	2013	Wales, UK	Welsh Government	One of the agreed outcomes of the Plan is for Wales to provide diverse and connected flower rich habitats to support pollinators in Wales which will be achieved by: <ol style="list-style-type: none"> Promoting, creating and enhancing beneficial flower rich habitats at a landscape scale, and also at smaller scales Promoting and supporting opportunities for habitat creation and enhancement for pollinators on farmland across protected areas and the wider countryside, and in urban and developed areas One of the Strategy's outcomes is "More, bigger, better, joined-up, diverse and high-quality flower-rich habitats (including nesting places and shelter) supporting our pollinators across the country" DEFRA plan to bring farmers and other land managers together to promote action at a landscape scale. Two of the Strategy's five key areas are as follows: <ol style="list-style-type: none"> Supporting pollinators on farmland Supporting pollinators across towns, cities and the countryside <ol style="list-style-type: none"> The strategy's actions are guided by Lawton's (2010) review "Making Space for Nature" which proposes to increase the size of wildlife sites, improve their quality and enhance connections between sites A number of targets and actions in the Plan will address or examine pollinators at a landscape scale: 1.1.1 Increase the area of farmland that is farmed in a pollinator friendly way 1.1.2 Create a network of meadows and other flower-rich habitats to serve as pollinator havens 1.2.1 Increase the area of public & semi-state land that is managed in a pollinator friendly way 1.2.2 Create linking areas of flower-rich habitat along transport routes 1.3.1 Increase the number of gardens across Ireland that are pollinator friendly A39. Encourage business properties to make their outdoor spaces more pollinator friendly (including country hotels, golf courses, quarries, retail carparks) A66. Integrate plant and land-cover data to generate floral resource heat-maps for Ireland showing which areas can provide adequate nutrition for pollinators and have the potential to provide pollination services for adjacent insect-pollinated crops A67. Develop predictive models to determine the economic impacts of land-use changes on pollinators and pollination services
National Pollinator Strategy for England <i>Defra (2014) The National Pollinator Strategy: for bees and other pollinators in England. DEFRA publication, York, UK. Pb14221</i>	2014	England, UK	UK Government (DEFRA)	
All Ireland Pollinator Plan <i>National Biodiversity Data Centre (2015) All-Ireland Pollinator Plan 2015-2020 National Biodiversity Data Centre Series No. 3, Waterford, Ireland</i>	2015	Northern Ireland, UK & Ireland	National Biodiversity Data Centre for Ireland	

(continued)

Table 1 (continued)

Strategy/Plan	Year published	Country	Co-ordinating organisation	Key recommendations relevant to landscape-level conservation for pollinators
French National Action Plan <i>France, Terre de Pollinisateurs (2015) Ministère de L'Ecologie du Développement Durable et de l'Energie, France</i>	2015	France	Ministère de L'Ecologie du Développement Durable et de l'Energie	A69. Determine how pollinators and pollination services vary according to the surrounding landscape at a range of scales 5.2 Monitor changes in the abundance and distribution of wild pollinators across Ireland A76. Develop an publicly available online system to map locations where pollinator friendly actions have been taken with a view towards creating an integrated network of pollinator habitat across the landscape This 10-point action plan includes the following: 1. Promote favourable management of roadside verges for pollinators 2. Recommendation of a monitoring programme to measure pollinator populations
National strategy to promote the health of honeybees and other pollinators <i>Pollinator Health Task Force (2015) National strategy to promote the health of honeybees and other pollinators. The White House, Washington, USA</i>	2015	USA	White House Pollinator Health Task Force	One of the Strategy's three overarching goals is to restore or enhance 7 million acres of land for pollinators over 5 years. 'Increasing and improving pollinator habitat' is one of four themes in the Strategy. The Strategy does not specifically discuss enhancing pollinator habitat at a landscape scale, although many of the activities outlined in the Strategy will promote action at a landscape-scale. The Strategy identifies the importance of utilising land adjacent to highways, railways and power transmission lines to provide corridors of favourable habitat that will connect pollinator habitat at a large scale

exhaust pollution (Girling *et al.* 2013) and research is needed to ascertain whether roadside verges can sustain pollinator populations over time.

POLICY DRIVERS

Land management for pollinators at regional and national scales relies on multiple land managers implementing pollinator-friendly practices. To best harness the beneficial practices of these multiple managers in a holistic and coordinated way requires political intervention. Several national governments have recognised the economic and ecological importance of pollinators by developing national strategies or action plans to promote activities to benefit pollinators (Table 1). Since they all promote action at a national scale, they are supporting the concept of landscape-scale habitat enhancement for pollinators, however some are more explicit than others in recognising the importance of landscape-scale factors for pollinators (see Table 1). For example, not all mention habitat connectivity, although the majority mentions the need to improve transport networks (e.g. road verges) for pollinators. Whilst the development of government-supported pollinator-specific national plans is encouraging news for pollinator conservation, the actions promoted by such plans are rarely mandated and therefore require support through other policies. For example, the National Pollinator Strategy for England does not include any new legislation that will enforce particular practices, but instead refers to other policies that may indirectly impact pollinators, such as the creation of NIAs (section Landscape-scale habitat creation schemes).

At broader scales, regional policy such as the EU Common Agricultural Policy (CAP) will have wide-ranging impacts on pollinator populations at national and even continental scales. In response to CAP reform, a new AES was recently developed for England, Countryside Stewardship, and this includes a Wild Pollinator and Farmland Wildlife Package of which the pollinator elements were informed by the latest ecological evidence (Dicks *et al.* 2015). The importance of pollinator conservation has also been recognised at an international level, with the first deliverable of the recently-formed Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) being a thematic assessment of pollinators, pollination and food production. The assessment aims to identify policy-relevant findings for decision-making in government, the private sector and civil society. Incorporating actions to help landscape-scale conservation for pollinators into policy will be essential for regional and national success.

MONITORING

Much of the evidence for pollinator declines has been derived from analyses of haphazardly collected species records (e.g. Carvalheiro *et al.* 2013) and therefore does not allow detailed analyses of population trends and

abundance patterns, which are important for policy making. As a result, programmes to understand the impact of the wider landscape on pollinators and to establish long-term monitoring are underway at national (e.g. National Pollinator and Pollination Monitoring Framework for England) and continental scales (e.g. EU LIBERATION project, <http://www.fp7liberation.eu/>). The success of national monitoring programmes will hinge on the choice of sampling methods, the spatial and environmental distribution of sites and the frequency of sampling (Lebuhn *et al.* 2013).

Conclusion

The main aims of our review were to provide an evidence base, identify key gaps in knowledge and help develop and improve strategies for pollinator conservation. We have covered a broad range of research pertaining to landscape-level impacts on pollinators, how these are assessed and quantified and what policy and schemes are currently in place to further enhance our understanding. However, there is still much we do not know about how landscape level impacts pollinator communities: The majority of studies focus on bee taxa and whilst bees are an important pollinator group, we need to understand how the other pollinator communities are affected by landscape level factors. Given that increases in land use intensity are likely to affect the pollinator species present it is important that future research should investigate how pollinator communities might respond to land-use change, particularly in the face of future climate change which is itself likely to affect the composition of pollinator communities (Kerr *et al.* 2015). The policies and monitoring schemes highlighted in our review, if executed properly, should provide some of the required data. This would allow for further examination and better understanding of relationships between landscapes and pollinator populations which in turn would help mitigation and adaptation strategies for pollinator conservation.

Acknowledgements

DS was funded by the Insect Pollinators Initiative (grant code BB/I000216/1). KCRB was funded by a NERC Knowledge Exchange Fellowship (grant code NE/M006956/1).

Data accessibility

This manuscript does not use data.

References

- Aguirre-Gutierrez, J., Biesmeijer, J.C., van Loon, E.E., Reemer, M., WallisDeVries, M.F. & Carvalheiro, L.G. (2015) Susceptibility of pollinators to ongoing landscape changes depends on landscape history. *Diversity and Distributions*, **21**, 1129–1140.
- Aguirre-Gutiérrez, J., Kissling, W.D., Carvalheiro, L.G., WallisDeVries, M.F., Franzén, M. & Biesmeijer, J.C. (2016) Functional traits help to

- explain half-century long shifts in pollinator distributions. *Scientific Reports*, **6**, 24451.
- Ahrne, K., Bengtsson, J. & Elmquist, T. (2009) Bumble bees (*Bombus* spp.) along a gradient of increasing urbanization. *PLoS ONE*, **4**, e5574.
- Andersson, G.K.S., Birkhofer, K., Rundlof, M. & Smith, H.G. (2013) Landscape heterogeneity and farming practice alter the species composition and taxonomic breadth of pollinator communities. *Basic and Applied Ecology*, **14**, 540–546.
- Ballock, K., Goddard, M., Hicks, D. et al. (2015) Where is the UK's pollinator biodiversity? Comparing flower-visitor communities between cities, farmland and nature reserves using visitation networks. *Proceedings of the Royal Society B-Biological Sciences*, **282**, 20142849.
- Batary, P., Dicks, L.V., Kleijn, D. & Sutherland, W.J. (2015) The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, **29**, 1006–1016.
- Bates, A.J., Sadler, J.P., Fairbrass, A.J., Falk, S.J., Hale, J.D. & Matthews, T.J. (2011) Changing bee and hoverfly pollinator assemblages along an urban-rural gradient. *PLoS ONE*, **6**, e23459.
- Baude, M., Kunin, W.E., Boatman, N.D., Conyers, S., Davies, N., Gillespie, M.A.K., Morton, R.D., Smart, S.M. & Memmott, J. (2016) Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature*, **530**, 85–88.
- Baxter-Gilbert, J., Riley, J., Neufeld, C.H., Litzgus, J. & Lesbarrères, D. (2015) Road mortality potentially responsible for billions of pollinating insect deaths annually. *Journal of Insect Conservation*, **19**, 1029–1035.
- Bennett, A.B. & Isaacs, R. (2014) Landscape composition influences pollinators and pollination services in perennial biofuel plantings. *Agriculture Ecosystems & Environment*, **193**, 1–8.
- Blackmore, L.M. & Goulson, D. (2014) Evaluating the effectiveness of wildflower seed mixes for boosting floral diversity and bumblebee and hoverfly abundance in urban areas. *Insect Conservation and Diversity*, **7**, 480–484.
- Brittain, C.A., Vighi, M., Bommarco, R., Settele, J. & Potts, S.G. (2010) Impacts of a pesticide on pollinator species richness at different spatial scales. *Basic and Applied Ecology*, **11**, 106–115.
- Brosi, B.J., Daily, G.C., Chamberlain, C.P. & Mills, M. (2009) Detecting changes in habitat-scale bee foraging in a tropical fragmented landscape using stable isotopes. *Forest Ecology and Management*, **258**, 1846–1855.
- Buri, P., Humbert, J.-Y. & Arlettaz, R. (2014) Promoting pollinating insects in intensive agricultural matrices: field-scale experimental manipulation of hay-meadow mowing regimes and its effects on bees. *PLoS ONE*, **9**, e85635.
- Burkle, L.A., Marlin, J.C. & Knight, T.M. (2013) Plant–pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science*, **339**, 1611–1615.
- Cane, J.H., Minckley, R.L., Kervin, L.J., Roulston, T.H. & Williams, N.M. (2006) Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecological Applications*, **16**, 632–644.
- Carper, A.L., Adler, L.S., Warren, P.S. & Irwin, R.E. (2014) Effects of suburbanization on forest bee communities. *Environmental Entomology*, **43**, 253–262.
- Carre, G., Roche, P., Chifflet, R. et al. (2009) Landscape context and habitat type as drivers of bee diversity in European annual crops. *Agriculture Ecosystems & Environment*, **133**, 40–47.
- Carvalho, L.G., Kunin, W.E., Keil, P. et al. (2013) Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants. *Ecology Letters*, **16**, 870–878.
- Carvell, C., Bourke, A.F.G., Osborne, J.L. & Heard, M.S. (2015) Effects of an agri-environment scheme on bumblebee reproduction at local and landscape scales. *Basic and Applied Ecology*, **16**, 519–530.
- Clough, Y., Ekroos, J., Báldi, A. et al. (2014) Density of insect-pollinated grassland plants decreases with increasing surrounding land-use intensity. *Ecology Letters*, **17**, 1168–1177.
- Connelly, H., Poveda, K. & Loeb, G. (2015) Landscape simplification decreases wild bee pollination services to strawberry. *Agriculture Ecosystems & Environment*, **211**, 51–56.
- De Palma, A., Kuhlmann, M., Roberts, S.P.M., Potts, S.G., Börger, L., Hudson, L.N., Lysenko, I., Newbold, T. & Purvis, A. (2015) Ecological traits affect the sensitivity of bees to land-use pressures in European agricultural landscapes. *Journal of Applied Ecology*, **52**, 1567–1577.
- Defra. (2014) *The National Pollinator Strategy: for Bees and Other Pollinators in England*. The Department for Environment, Food and Rural Affairs, Bristol, UK.
- Dicks, L.V., Baude, M., Roberts, S.P.M., Phillips, J., Green, M. & Carvell, C. (2015) How much flower-rich habitat is enough for wild pollinators? Answering a key policy question with incomplete knowledge. *Ecological Entomology*, **40**, 22–35.
- Diekötter, T., Kadoya, T., Peter, F., Wolters, V. & Jauker, F. (2010) Oilseed rape crops distort plant–pollinator interactions. *Journal of Applied Ecology*, **47**, 209–214.
- Diekötter, T., Peter, F., Jauker, B., Wolters, V. & Jauker, F. (2014) Mass-flowering crops increase richness of cavity-nesting bees and wasps in modern agro-ecosystems. *GCB Bioenergy*, **6**, 219–226.
- Forister, M.L., McCall, A.C., Sanders, N.J., Fordyce, J.A., Thorne, J.H., O'Brien, J., Waetjen, D.P. & Shapiro, A.M. (2010) Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. *Proceedings of the National Academy of Sciences*, **107**, 2088–2092.
- Forrest, J.R.K., Thorp, R.W., Kremen, C. & Williams, N.M. (2015) Contrasting patterns in species and functional-trait diversity of bees in an agricultural landscape. *Journal of Applied Ecology*, **52**, 706–715.
- France, Terre de Pollinisateurs (2015) *Un plan national d'actions*. Ministère de l'Ecologie du Développement Durable et de l'Énergie, Puteaux, France.
- Fuller, R.A., Irvine, K.N., Devine-Wright, P., Warren, P.H. & Gaston, K.J. (2007) Psychological benefits of greenspace increase with biodiversity. *Biology Letters*, **3**, 390–394.
- Garbuzov, M., Fensome, K.A. & Ratnieks, F.L.W. (2015) Public approval plus more wildlife: twin benefits of reduced mowing of amenity grass in a suburban public park in Saltdean, UK. *Insect Conservation and Diversity*, **8**, 107–119.
- Garbuzov, M. & Ratnieks, F.L.W. (2014) Quantifying variation among garden plants in attractiveness to bees and other flower-visiting insects. *Functional Ecology*, **28**, 364–374.
- Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C. et al. (2011) Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecology Letters*, **14**, 1062–1072.
- Gaston, K.J., Smith, R.M., Thompson, K. & Warren, P.H. (2005) Urban domestic gardens (II): experimental tests of methods for increasing biodiversity. *Biodiversity and Conservation*, **14**, 395–413.
- Gill, R.J., Ballock, K.C.R., Brown, M.J.F. et al. (2016) Protecting an ecosystem service: approaches to understanding and mitigating threats to wild insect pollinators. *Advances in Ecological Research*, **53**, 22.
- Girling, R.D., Lusebrink, I., Farthing, E., Newman, T.A. & Poppy, G.M. (2013) Diesel exhaust rapidly degrades floral odours used by honeybees. *Scientific Reports*, **3**, 2779.
- González-Varo, J.P., Biesmeijer, J.C., Bommarco, R. et al. (2013) Combined effects of global change pressures on animal-mediated pollination. *Trends in Ecology & Evolution*, **28**, 524–530.
- Goulson, D., Nicholls, E., Botias, C. & Rotheray, E.L. (2015) Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, **347**, 1255957.
- Greenleaf, S.S., Williams, N.M., Winfree, R. & Kremen, C. (2007) Bee foraging ranges and their relationship to body size. *Oecologia*, **153**, 589–596.
- Hanley, M. & Wilkins, J. (2015) On the verge? Preferential use of road-facing hedgerow margins by bumblebees in agro-ecosystems. *Journal of Insect Conservation*, **19**, 67–74.
- Hanley, M.E., Franco, M., Dean, C.E. et al. (2011) Increased bumblebee abundance along the margins of a mass flowering crop: evidence for pollinator spill-over. *Oikos*, **120**, 1618–1624.
- Harrison, T. & Winfree, R. (2015) Urban drivers of plant-pollinator interactions. *Functional Ecology*, **29**, 879–888.
- Hernandez, J.L., Frankie, G.W. & Thorp, R.W. (2009) Ecology of urban bees: a review of current knowledge and directions for future study. *Cities and the Environment*, **2**, 3.
- Holzschuh, A., Dormann, C., Tscharntke, T. & Steffan-Dewenter, I. (2013) Mass-flowering crops enhance wild bee abundance. *Oecologia*, **172**, 477–484.
- Hopfenmueller, S., Steffan-Dewenter, I. & Holzschuh, A. (2014) Trait-specific responses of wild bee communities to landscape composition, configuration and local factors. *PLoS ONE*, **9**, e104439.
- IPBES. (2016). *Summary for Policymakers of the Assessment Report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on Pollinators, Pollination and Food Production*. Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany.
- Jauker, F., Peter, F., Wolters, V. & Diekötter, T. (2012) Early reproductive benefits of mass-flowering crops to the solitary bee *Osmia rufa* outweigh post-flowering disadvantages. *Basic and Applied Ecology*, **13**, 268–276.

- Jha, S. & Kremen, C. (2013a) Resource diversity and landscape-level homogeneity drive native bee foraging. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 555–558.
- Jha, S. & Kremen, C. (2013b) Urban land use limits regional bumble bee gene flow. *Molecular Ecology*, **22**, 2483–2495.
- Jonsson, A.M., Ekroos, J., Danhardt, J., Andersson, G.K.S., Olsson, O. & Smith, H.G. (2015) Sown flower strips in southern Sweden increase abundances of wild bees and hoverflies in the wider landscape. *Biological Conservation*, **184**, 51–58.
- Kennedy, C.M., Lonsdorf, E., Neel, M.C. *et al.* (2013) A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters*, **16**, 584–599.
- Kerr, J.T., Pindar, A., Galpern, P. *et al.* (2015) Climate change impacts on bumblebees converge across continents. *Science*, **349**, 177–180.
- Kleijn, D., Winfree, R., Bartomeus, I. *et al.* (2015) Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications*, **6**, 7414.
- Kovács-Hostyánszki, A., Haenke, S., Batáry, P., Jauker, B., Báldi, A., Tscharntke, T. & Holzschuh, A. (2013) Contrasting effects of mass-flowering crops on bee pollination of hedge plants at different spatial and temporal scales. *Ecological Applications*, **23**, 1938–1946.
- Lawton, J.H., Brotherton, P.N.M., Brown, V.K. *et al.* (2010) *Making Space for Nature: A Review of England's Wildlife Sites and Ecological Network*. Defra, London, UK.
- Le Feon, V., Schermann-Legionnet, A., Delettre, Y., Aviron, S., Billeter, R., Bugter, R., Hendrickx, F. & Burel, F. (2010) Intensification of agriculture, landscape composition and wild bee communities: a large scale study in four European countries. *Agriculture Ecosystems & Environment*, **137**, 143–150.
- Le Feon, V., Burel, F., Chifflet, R., Henry, M., Ricroch, A., Vaissiere, B.E. & Baudry, J. (2013) Solitary bee abundance and species richness in dynamic agricultural landscapes. *Agriculture Ecosystems & Environment*, **166**, 94–101.
- Lebuhn, G., Droege, S., Connor, E.F. *et al.* (2013) Detecting insect pollinator declines on regional and global scales. *Conservation Biology*, **27**, 113–120.
- Lowenstein, D., Matteson, K. & Minor, E. (2015) Diversity of wild bees supports pollination services in an urbanized landscape. *Oecologia*, **179**, 811–821.
- MacIvor, J.S. & Packer, L. (2015) 'Bee Hotels' as tools for native pollinator conservation: a premature verdict? *PLoS ONE*, **10**, e0122126.
- MacIvor, J.S., Ruttan, A. & Salehi, B. (2015) Exotics on exotics: pollen analysis of urban bees visiting *Sedum* on a green roof. *Urban Ecosystems*, **18**, 419–430.
- Marini, L., Ockinger, E., Bergman, K.-O. *et al.* (2014) Contrasting effects of habitat area and connectivity on evenness of pollinator communities. *Ecography*, **37**, 544–551.
- Matteson, K.C., Grace, J.B. & Minor, E.S. (2013) Direct and indirect effects of land use on floral resources and flower-visiting insects across an urban landscape. *Oikos*, **122**, 682–694.
- Matteson, K. & Langellotto, G. (2010) Determinates of inner city butterfly and bee species richness. *Urban Ecosystems*, **13**, 333–347.
- Meyer, B., Jauker, F. & Steffan-Dewenter, I. (2009) Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic and Applied Ecology*, **10**, 178–186.
- National Biodiversity Data Centre (2015) *All-Ireland Pollinator Plan 2015–2020*. National Biodiversity Data Centre Series No. 3, Waterford, Ireland.
- Ollerton, J., Winfree, R. & Tarrant, S. (2011) How many flowering plants are pollinated by animals? *Oikos*, **120**, 321–326.
- Osborne, J.L., Martin, A.P., Shortall, C.R., Todd, A.D., Goulson, D., Knight, M.E., Hale, R.J. & Sanderson, R.A. (2008) Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. *Journal of Applied Ecology*, **45**, 784–792.
- Park, M.G., Blitzer, E.J., Gibbs, J., Losey, J.E. & Danforth, B.N. (2015) Negative effects of pesticides on wild bee communities can be buffered by landscape context. *Proceedings of the Royal Society B-Biological Sciences*, **282**, 20150299.
- Pollinator Health Task Force (2015) *National Strategy to Promote the Health of Honey Bees and Other Pollinators*. The White House, Washington, DC, USA.
- Pywell, R.F., Meek, W.R., Hulmes, L., Hulmes, S., James, K.L., Nowakowski, M. & Carvell, C. (2011) Management to enhance pollen and nectar resources for bumblebees and butterflies within intensively farmed landscapes. *Journal of Insect Conservation*, **15**, 853–864.
- Rader, R., Bartomeus, I., Tylianakis, J.M. & Laliberte, E. (2014) The winners and losers of land use intensification: pollinator community disassembly is non-random and alters functional diversity. *Diversity and Distributions*, **20**, 908–917.
- Ricketts, T.H., Regetz, J., Steffan-Dewenter, I. *et al.* (2008) Landscape effects on crop pollination services: are there general patterns? *Ecology Letters*, **11**, 499–515.
- Riedinger, V., Mitesser, O., Hovestadt, T., Steffan-Dewenter, I. & Holzschuh, A. (2015) Annual dynamics of wild bee densities: attractiveness and productivity effects of oilseed rape. *Ecology*, **96**, 1351–1360.
- Rundlöf, M., Persson, A.S., Smith, H.G. & Bommarco, R. (2014) Late-season mass-flowering red clover increases bumble bee queen and male densities. *Biological Conservation*, **172**, 138–145.
- Salisbury, A., Armitage, J., Bostock, H., Perry, J., Tatchell, M. & Thompson, K. (2015) Enhancing gardens as habitats for flower-visiting aerial insects (pollinators): should we plant native or exotic species? *Journal of Applied Ecology*, **52**, 1156–1164.
- Sattler, T., Duelli, P., Obrist, M.K., Arlettaz, R. & Moretti, M. (2010) Response of arthropod species richness and functional groups to urban habitat structure and management. *Landscape Ecology*, **25**, 941–954.
- Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G. & Kleijn, D. (2013) Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss – a meta-analysis. *Ecology Letters*, **16**, 912–920.
- Scheper, J., Bommarco, R., Holzschuh, A. *et al.* (2015) Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. *Journal of Applied Ecology*, **52**, 1165–1175.
- Senapathi, D., Biesmeijer, J.C., Breeze, T.D., Kleijn, D., Potts, S.G. & Carvalheiro, L.G. (2015a) Pollinator conservation — the difference between managing for pollination services and preserving pollinator diversity. *Current Opinion in Insect Science*, **12**, 93–101.
- Senapathi, D., Carvalheiro, L.G., Biesmeijer, J.C. *et al.* (2015b) The impact of over 80 years of land cover changes on bee and wasp pollinator communities in England. *Proceedings Biological Sciences*, **282**, 20150294.
- Seto, K.C., Guneralp, B. & Hutyra, L.R. (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences*, **109**, 16083–16088.
- Sirohi, M., Jackson, J., Edwards, M. & Ollerton, J. (2015) Diversity and abundance of solitary and primitively eusocial bees in an urban centre: a case study from Northampton (England). *Journal of Insect Conservation*, **19**, 487–500.
- Smith, R.M., Warren, P.H., Thompson, K. & Gaston, K.J. (2006) Urban domestic gardens (VI): environmental correlates of invertebrate species richness. *Biodiversity and Conservation*, **15**, 2415–2438.
- Stanley, D.A., Garratt, M.P.D., Wickens, J.B., Wickens, V.J., Potts, S.G. & Raine, N.E. (2015) Neonicotinoid pesticide exposure impairs crop pollination services provided by bumblebees. *Nature*, **528**, 548–550.
- Steckel, J., Westphal, C., Peters, M.K., Bellach, M., Rothenwoehrer, C., Erasmí, S., Scherber, C., Tscharntke, T. & Steffan-Dewenter, I. (2014) Landscape composition and configuration differently affect trap-nesting bees, wasps and their antagonists. *Biological Conservation*, **172**, 56–64.
- Steffan-Dewenter, I. & Tscharntke, T. (1999) Effects of habitat isolation on pollinator communities and seed set. *Oecologia*, **121**, 432–440.
- Threlfall, C.G., Walker, K., Williams, N.S.G., Hahs, A.K., Mata, L., Stork, N. & Livesley, S.J. (2015) The conservation value of urban green space habitats for Australian native bee communities. *Biological Conservation*, **187**, 240–248.
- Tonietto, R., Fant, J., Ascher, J., Ellis, K. & Larkin, D. (2011) A comparison of bee communities of Chicago green roofs, parks and prairies. *Landscape and Urban Planning*, **103**, 102–108.
- Van Geert, A., Van Rossum, F. & Triest, L. (2010) Do linear landscape elements in farmland act as biological corridors for pollen dispersal? *Journal of Ecology*, **98**, 178–187.
- Vanbergen, A.J., Baude, M., Biesmeijer, J.C. *et al.* (2013) Threats to an ecosystem service: pressures on pollinators. *Frontiers in Ecology and the Environment*, **11**, 251–259.
- Verboven, H.A.F., Uytendbroeck, R., Brys, R. & Hermy, M. (2014) Different responses of bees and hoverflies to land use in an urban–rural gradient show the importance of the nature of the rural land use. *Landscape and Urban Planning*, **126**, 31–41.
- Viana, B.F., Boscolo, D., Neto, E.M., Lopes, L.E., Lopes, A.V., Ferreira, P.A., Pigozzo, C.M. & Primo, L.M. (2012) How well do we understand landscape effects on pollinators and pollination services? *Journal of Pollination Ecology*, **7**, 31–41.

- Warren, M.S., Hill, J.K., Thomas, J.A. *et al.* (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.
- Westphal, C., Steffan-Dewenter, I. & Tscharntke, T. (2009) Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *Journal of Applied Ecology*, **46**, 187–193.
- Welsh Government (2013) *The Action Plan for Pollinators in Wales*. Welsh Government Publication, Aberystwyth, UK.
- Winfree, R. & Kremen, C. (2009) Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proceedings of the Royal Society of London B: Biological Sciences*, **276**, 229–237.
- Wood, T.J., Holland, J.M. & Goulson, D. (2015) Pollinator-friendly management does not increase the diversity of farmland bees and wasps. *Biological Conservation*, **187**, 120–126.
- Wray, J. & Elle, E. (2015) Flowering phenology and nesting resources influence pollinator community composition in a fragmented ecosystem. *Landscape Ecology*, **30**, 261–272.
- Wray, J.C., Neame, L.A. & Elle, E. (2014) Floral resources, body size, and surrounding landscape influence bee community assemblages in oak-savannah fragments. *Ecological Entomology*, **39**, 83–93.

Received 31 March 2016; accepted 25 October 2016

Handling Editor: Geraldine Wright