REVIEW

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Network modelling, citizen science and targeted interventions to predict, monitor and reverse bee decline

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Societal Impact Statement

The global decline in pollinating insect populations has rightly received widespread news coverage as it imperils ecosystem function and human food security. Reversing and addressing this decline is an urgent global priority. However, in many locations we do not know what species are present, how large or small species populations are, or what types of specific resources the populations require. By adopting novel network analyses approaches and by working with monitoring programs, such as Oxford Plan Bee, we may be able to dramatically improve our ability to predict species extinctions and facilitate targeted conservation action to maintain abundant, diverse and stable pollinator communities.

Summary

Pollination is fundamentally important to ecosystem function and human food security. Recent reports of dramatic insect declines, and pollinator decline in particular, have increased public awareness and political motivation to act to protect pollinators. This article maps commonly proposed management interventions onto known drivers of bee decline, and identifies forage and nest site provision as a tractable management intervention that can simultaneously address multiple drivers of decline. However, it is recognized that there are gaps in the knowledge of exactly how much and which types of forage resources are necessary to support wild pollinator populations. A novel network analysis approach based on quantified floral resources and pollination services is proposed, which would illuminate the types and quantities of floral resources and pollinators necessary to maintain a diverse and abundant plant–pollinator community. The approach would also facilitate the prediction of species extinctions in plant–pollinator communities and help target conservation interventions. Finally, Oxford Plan Bee is introduced as a new, citizen-science-based project to monitor solitary bee populations, and provide empirical data to validate predictions from the proposed network approach. The over-arching aim of the described network analysis approach and the Oxford Plan Bee project is to facilitate effective, evidence-based conservation action to protect pollinators and the plants they pollinate into the future.

1 | INTRODUCTION

Approximately one eighth of species on Earth are now threatened with extinction (Díaz, Settele, & Brondízio, 2019). In line with this trend, there have been dramatic declines in pollinator species over the last 50 years (Biesmeijer et al., 2006; FAO, 2019b; Hallmann et al., 2017; Lister & Garcia, 2018; Powney et al., 2019; Sánchez-Bayo & Wyckhuys, 2019). Pollinator decline threatens ecosystem function and human food security, because approximately 88% of angiosperms globally are animal, mainly insect, pollinated (Ollerton, Winfree, & Tarrant, 2011), and of the plants cultivated for human consumption, 75% benefit from insect pollination (Klein, Steffan-Dewenter, & Tscharntke, 2003). This means reversing pollinator decline is a global priority. The resources available for conservation and management interventions to reverse pollinator decline are limited, so it is necessary to ascertain the most important drivers of decline, develop practical tools to identify the species at highest risk of extinction, understand the ecosystem-wide implications of those species' extinctions, and identify the most effective conservation and management interventions to reduce those extinction risks.

Part 1 of this manuscript reviews the literature on known drivers of bee decline and the broad intervention types that are available to land managers to start reversing the trend, and identifies the interventions that are likely to be the most tractable and effective. The manuscript focuses on bees because 50% to 75% of insect pollinators visiting crops are bees, making them the most important crop pollinators globally (Rader et al., 2016). In addition, there is an extensive body of research on bee decline which can underpin a robust analysis of the opportunities to reverse the trend. There is also a strong emphasis in the manuscript on management of agro-ecological systems. This is because agriculture (including arable land, permanent crops and permanent pastures) covers 37% of the world's land area (FAO, 2019a), accounts for 70% of the freshwater withdrawals, mainly for irrigation (FAO, 2012), and 3%–8% of total energy demand (FAO, 2000). Moreover, approximately one billion people (1 in 3 of all workers) are employed in the agricultural sector (FAO, 2012). The sheer area of land and resources involved in agriculture makes it an important focus. In addition, agricultural workers have a vested interest in protecting and enhancing local pollinator communities to provide pollination services for food crops, and so can be powerful allies in the effort to protect pollinators globally.

Part 2 of the manuscript presents a novel approach for developing specific guidance for land managers to support pollinators. There is a recognized knowledge gap regarding the very basic question of exactly how much and which types of forage resources are necessary to support wild pollinator populations (Dicks et al., 2015). A novel approach to network analysis is proposed in this section, which would illuminate the types and quantities of floral resources necessary to maintain an abundant, diverse and stable pollinator community. The approach can also help identify which species are at greatest risk of extinction, and which of the available interventions are most likely to be effective in reducing those specific extinction risks. Finally, this approach offers a mechanism for local land managers to prioritise interventions, given that most land managers are not in a position to implement all of the possible interventions to protect and enhance local bee populations.

Part 3 describes Oxford Plan Bee, a new citizen science project. The project provides empirical data on bee identity, diversity and abundance in relation to local plant species identity, diversity and abundance, thus providing empirical data to test the predictions of the approach described in Part 2.

2 | BEE DECLINE

Wild bee species richness has declined over the last 50 years in North America and Europe (Goulson, Nicholls, Botías, & Rotheray, 2015), and localized pollinator declines or disrupted pollination systems have been reported on every continent except Antarctica (Biesmeijer et al., 2006; Díaz et al., 2019; FAO, 2019b; Hallmann et al., 2017; Kearns, Inouye, & Waser, 1998; Lister & Garcia, 2018; Ollerton, Erenler, Edwards, & Crockett, 2014; Potts et al., 2010; Powney et al., 2019; Sánchez-Bayo & Wyckhuys, 2019; Winfree, Aguilar, Vazquez, LeBuhn, & Aizen, 2009; Woodcock et al., 2016). Bee decline has been attributed to habitat loss and fragmentation, often linked to agricultural intensification (Biesmeijer et al., 2006; Goulson et al., 2015; Hallmann et al., 2017; Kremen & Ricketts, 2000; Kremen, Williams, & Thorp, 2002; Ollerton et al., 2014; Potts et al., 2016; Sánchez-Bayo & Wyckhuys, 2019; Vanbergen & The Insect Pollinators Initiative, 2013; Winfree et al., 2009), climate change (Díaz et al., 2019; Memmott, Craze, Waser, & Price, 2007; Potts et al., 2016), exposure to agricultural chemicals (Goulson et al., 2015; Ollerton et al., 2014; Potts et al., 2010, 2016; Woodcock et al., 2016), parasites and pathogens (Goulson et al., 2015; Potts et al., 2016) and alien species (Kremen & Ricketts, 2000; Moron et al., 2009; Potts et al., 2010, 2016). Potts et al. (2010) and other authors recognize that these drivers frequently do not act in isolation, and that pollinators exposed to interacting drivers may be at even greater risk.

There are seven broad categories of interventions frequently recommended for land managers attempting to protect and enhance bee populations under pressure from the main drivers of decline (Table 1). These interventions vary in whether they are implemented in the short-term or long-term, whether they function at the local (often farm-scale) or regional scale, and whether they are mainly manager-initiated or would be better supported through government policy. Showler, Dicks, and Sutherland (2010) provide a review

of the evidence for effectiveness of some of these interventions, but as far as I am aware there has not been a synthesis to identify the interventions that address multiple drivers. Given that the drivers are thought to act in concert (e.g. Potts et al., 2010), and that there are likely to be economic costs to implementation of the interventions (Gill et al., 2016), interventions that address multiple drivers may be expected to be both effective and economical, and therefore attractive to land managers.

Two of the broad categories of interventions, 'set aside or active provision of forage plants and nest sites' and 'diversification of land-uses', are shown in Table 1 to simultaneously address multiple drivers. There is a great deal of cross-over in how different authors have defined these two intervention categories, but in general 'set-asides' are at the very local scale, such as field margins or individual fields within a farm, whereas 'land-use diversification' involves converting multiple fields within a farm, or larger areas across a landscape, to different types of agriculture or entirely different land-use types. These two interventions most directly act to mitigate 'habitat loss', which encompasses total area of forage plants, forage plant species identity and diversity, forage plant seasonal and/or temporal span, and the availability of nesting sites (see Dicks et al., 2015). Provision of forage plants and creation of suitable nesting areas through these two interventions may also buffer pollinator populations against climate change by reducing phenological mismatch between pollinators and food sources and increasing pollinator abundance, diversity and functional redundancy (Potts et al., 2016; Vanbergen & The Insect Pollinators Initiative, 2013). Non-crop areas also provide refugia for pollinators, potentially directly reducing their exposure to agrochemicals and/or providing source populations that can re-establish in areas where populations have been negatively affected by agrochemicals (Vanbergen and The Insect Pollinators Initiative, 2013). There is also some evidence that pollinators foraging on the more diverse diets provided in set-aside areas, as compared to single species crop areas, are better able to detoxify pesticides and resist parasites and pathogens (Vanbergen and The Insect Pollinators Initiative, 2013). Although there is abundant literature on invasive species and agriculture (reviewed in Dicks et al., 2013), what specific affect farm set-asides and landscape diversification might have on the sub-set of alien species that directly affect pollinators appears to be an area open for research. Overall, the provision of diverse and abundant forage resources and nest sites has the potential to address at least four of the five main threats to bees. Three of the other interventions in Table 1, specifically 'changes to the use and testing methods for agrochemicals', 'improved regulation of trade in managed pollinators' and 'use of a wider variety of managed bee species', address specific and acute threats to wild pollinators, and their implementation would provide useful, complementary interventions to run in parallel with 'set aside or active provision of forage plants and nest sites' and 'diversification of land-uses'.

It is recognized that there are economic 'opportunity costs' to providing forage resources and nest sites by removing land from production, as well as the direct costs of establishing and maintaining set-aside areas (Gill et al., 2016). These immediate costs must be balanced against the potential future costs of pollination deficit in economically valuable crops, pollination deficit in wild plant communities which could have knock-on effects for water cycling and soil retention and quality, and the loss of pollinating insects as a food source for other animals such as birds (Hallmann et al., 2017; Møller, 2019).

To develop practical guidelines for land managers to protect pollinators using 'set aside or active provision of forage plants and nest sites' and 'diversification of land-uses', we need to know specifically how much and what type of floral resources are needed to support viable pollinator populations, how the interventions should be deployed spatially, and how much and what type of floral resources are supplied per hectare of farmland under different management regimes. Remarkably, these are still open questions (see Dicks et al., 2015). Part 2 of this manuscript therefore focuses on a novel approach to determining the types and quantities of floral resources necessary to maintain an abundant, diverse and stable pollinator community. Results from this approach would provide a robust foundation for intervention guidelines to help protect and enhance pollinator populations.

3 | HOW MUCH AND WHAT TYPE OF FLORAL RESOURCES ARE NECESSARY TO MAINTAIN AN ABUNDANT, DIVERSE AND STABLE POLLINATOR COMMUNITY?

Network analysis is a mathematical technique widely used for understanding relationships between actors. It has been used to study a diversity of phenomena, from the flow of goods and services between cities and information transfer in social networks, to the movement of nutrients within slimemolds and species interactions in plant–pollinator communities (see review Landi, Minoarivelo, Brännström, Hui, & Dieckmann, 2018). Network metrics can be used to quantify the importance of relationships between individual actors, the importance of individual actors in the system as a whole, and how the system as a whole responds to the loss of individual actors. Network analysis therefore offers a potentially valuable tool for understanding which species the other species in the network are dependent upon, how the loss or addition of species to the network affects the other species in the network, which species are at highest risk of extinction following network perturbation, and which interventions are most likely to reduce the risk of extinctions and extinction cascades (e.g. Memmott, Waser, & Price, 2004). However, the value of the approach for management recommendations is obviously dependent on the accuracy of the predictions that are generated. Recent studies of plant–pollinator communities have found that traditional network predictions showed little agreement with empirical data (see Brosi & Briggs, 2013; Timoteo, Ramos, Vaughan, & Memmott, 2016). There is therefore a recognized need to improve the predictive power of ecological network analyses if we are to maximize their potential as a tool for understanding ecological interactions,

TABLE 1 The matrix shows the five main drivers of bee decline ('Threats to bees') and the seven broad categories of land management interventions recommended for protecting and enhancing bee populations

Land management interventions to address the threats	Threats to bees				
	Habitat loss and fragmentation, often linked to agricultural intensification	Climate change	Exposure to agricultural chemicals	Parasites and pathogens	Alien species
Set aside or active provision of forage plants and nest sites	Kremen & Ricketts, 2000; Showler et al., 2010; Carvalheiro et al., 2013; Kennedy et al., 2013; Scheper et al., 2013; Vanbergen & The Insect Pollinators Initiative, 2013; Goulson et al., 2015; Holland, Smith, Storkey, Lutman, & Aebischer, 2015; Senapathi et al., 2015; Gill et al., 2016; Potts et al., 2016	Vanbergen & The Insect Pollinators Initiative, 2013; Potts et al., 2016	Reviewed in Vanbergen & The Insect Pollinators Initiative, 2013	Reviewed in Vanbergen & The Insect Pollinators Initiative, 2013	Research opportunity
Diversification of land-uses	Gill et al., 2016; Holland et al., 2015; Kennedy et al., 2013; Potts et al., 2016; Scheper et al., 2013; Senapathi et al., 2015; Senapathi, Goddard, Kunin, & Baldock, 2017; Showler et al., 2010	Anwar, Liu, Macadam, & Kelly, 2013; Kurukulasuriya & Rosenthal, 2003; Potts et al., 2016	Reviewed in Vanbergen and The Insect Pollinators Initiative, 2013	Research opportunity	Research opportunity
Changes to crop types or varieties	----	Anwar et al., 2013; Gylling & Abildtrup, 2001; Kurukulasuriya & Rosenthal, 2003	----	----	----
Changes to timing of agricultural interventions	----	Anwar et al., 2013; Gylling & Abildtrup, 2001; Kurukulasuriya & Rosenthal, 2003	----	----	----
Changes to agrochemical use and testing methods	Holzschuh, Steffan-Dewenter, & Tscharntke, 2008; Kennedy et al., 2013; Scheper et al., 2013	Kurukulasuriya & Rosenthal, 2003	Showler et al., 2010; Carvalheiro et al., 2013; Vanbergen & The Insect Pollinators Initiative, 2013; Goulson et al., 2015; Gill et al., 2016; Potts et al., 2016	----	----
Improved regulation of trade in managed pollinators	----	----	----	Goulson et al., 2015; Potts et al., 2016; Showler et al., 2010	Goulson et al., 2015; Potts et al., 2016; Showler et al., 2010
Use of a wider variety of managed bee species	----	----	----	Vanbergen and The Insect Pollinators Initiative, 2013	Vanbergen and The Insect Pollinators Initiative, 2013

Note: The references in each cell indicate publications where the specific intervention is recommended for mitigation of the specific driver. Where there appears to be a potential relationship, but no publications I am aware of, the cell is marked as 'Research opportunity'.

identifying species at risk of extinction and for developing and prioritising management and conservation interventions.

In network analysis, actors (species, guilds, individuals, etc.) are called *nodes*, and lines of connection between nodes, which represent interactions, are called *edges*. It is possible to have network edges that are *weighted* (representing the strength or importance of the interaction) or unweighted (present or absent). Edges can be *symmetric* (also called undirected; the two species affect each other equally), or asymmetric (also called directed; the two species affect each other differently), and positive or negative (Landi et al., 2018). When a node changes or adds to its interaction partner(s) this is termed *rewiring*. If, following species loss, the network model does not allow for nodes to rewire, this is termed *static partner choice*. Network *stability* is defined as the ability of the network to return to a stable pattern of function following disturbance. *Resilience* is defined as the ability of the network to resist the effects of disturbances, such as species loss or species invasion, spreading and amplifying (propagating) through the network (Ludwig, Walker, & Holling, 1997). When analysing networks, the weights and symmetry assigned to edges, inclusion of dynamic rewiring versus static partner choice, and the basis on which rewiring choices are made, have profound impacts on predictions of network stability and resilience (CaraDonna et al., 2017; Tylianakis & Morris, 2017).

One of the great strengths of network analysis is the capacity to investigate the movement of actual material (e.g. energy, nutrients, currency, pathogens, etc.) along edges between nodes. Plant-pollinator network analyses have largely not taken advantage of this potential, instead using network edges to represent binary or qualitative node-node interactions, or proxy quantitative values such as interaction frequency which have been shown not to accurately represent the importance of interactions (e.g. Ballantyne, Baldock, Rendell, & Willmer, 2017). This trend can be explained by the fact that acquiring plant–pollinator interaction data is labour-intensive, published data on per-pollinator pollination efficiency and per-plant nectar and pollen volume is scarce, and published data on the nutritional quality of pollen and nectar is even rarer. There is a need for novel, empirically based, approaches to defining interaction (link) weights and symmetry in plant–pollinator networks to provide robust predictions of species' responses and network stability and resilience across space and through time. Networks that provide those robust predictions could be used to determine how much and what type of floral resources are necessary to maintain an abundant, diverse and stable pollinator community.

3.1 | 'Service provision' – based estimates of network links

I propose that link weights and symmetry should be defined in terms of 'service provision'. Specifically, both *pollination services to plants*: the quantity and quality of the pollen that the pollinator provides to the plant, and *resource rewards to pollinators*: the quantity and

nutritional quality of the rewards the plant provides to the pollinator. These specific physical values have been chosen because they play a direct role in reproductive success for the plant or affect pollinator nutritional status, which affects offspring quantity and quality (Vaudo, Tooker, Grozinger, & Patch, 2015). Although collection of the necessary data, as described below, will be an ambitious undertaking, I propose that quantified network interaction weights and symmetry based on pollination services and resource rewards would provide a more robust foundation for prediction of plant–pollinator network stability, resilience and extinction probabilities for individual species than any that has so far been used.

Pollination services can be calculated as the combination of visitation frequency in field observations, pollen export capacity and the ability to deposit viable pollen on conspecific stigmas. It has been suggested that pollen export capacity can be estimated as insect face hairiness calculated using image entropy analysis (Stavert et al., 2016). The ability to deposit viable pollen can also be estimated in single visit pollen deposition (SVD) experiments which measure the number of pollen grains deposited in a single visit on a virgin stigma. Here I propose to use all three measures: visitation frequency, pollen export capacity and single-visit pollen deposition, to provide more accurate data on interaction specialization and pollinator importance for individual plant species than interaction frequency alone (Ballantyne et al., 2017).

Resource rewards have typically been estimated using nectar and pollen volume per flower (e.g. Baude et al., 2016; Hicks et al., 2016). However, pollen of different plant species varies in protein content, amino acid composition, lipid, starch and vitamin and mineral content. Pollen crude protein content can range from 2.5% to 61% of dry mass, and protein-bound amino acids can range from 3.5% to 24.9% (Vanderplanck, Leroy, Wathelet, Wattiez, & Michez, 2014). Nectar also varies in both amino acid content and sugar concentration. Nectar sugar concentration can range from 7% to 70% w/w (7 to 70 g per 100 g of nectar; Power, Stabler, Borland, Barnes, & Wright, 2018). Pollen quality and diversity has been shown to have direct impacts on honeybee health (see references in Goulson et al., 2015), growth, development, immuno-competence, longevity, body size, ovary development and larval growth (Vanderplanck et al., 2017). Although little is known about the impact of pollen or nectar amino acid content on wild bees (Goulson et al., 2015), based on Dynamic Energy Budget Theory (Sousa, Domingos, & Kooijman, 2008) we expect a direct relationship between energy and nutrient uptake and reproductive output. Despite increasing calls for the integration of foraging behaviour studies with network analysis (e.g. Beckerman, Petchey, & Morin, 2010), network studies to date have not incorporated variation in pollen or nectar nutritional quality, which is expected to directly impact foraging behaviour and reproductive output. I propose that nectar quantity should be estimated as mean sugar mass/floral-unit/day and pollen quantity as: [(total number of pollen grains/floral unit) × (mean volume per pollen grain)]/ per day (Hicks et al., 2016). Nectar nutritional quality can be estimated as sugar concentration plus amino acid content (e.g. Corbet, 2003), and nectar and pollen amino acid content can be quantified using gas

chromatography–mass spectrometry (GC-MS) or liquid chromatography techniques (Power et al., 2018). Using these empirical data on plant resource reward quantity and quality for pollinators, and pollination service rewards for plants, it would be possible to develop empirically based edge weights and symmetry estimates for plant–pollinator networks. The stability and resilience analysis of the network in this case would focus on how the loss of a given species impacts the population growth rate of the species to which it was connected, and whether the remaining species avoid extinction (e.g. Okuyama & Holland, 2008).

3.2 | 'Service provision' – based predictions of network rewiring

Early plant–pollinator network analyses did not account for interaction rewiring (Abrams, 2010). However, because most plant–pollinator relationships are not strictly specialist (not exclusive; Menz et al., 2011; Vázquez & Aizen, 2004), field data show that species often interact with alternative partners in the absence of, or in addition to, favoured partners and loss of a species does not inevitably mean extinction for its partners (Carstensen, Sabatino, Trøjelsgaard, & Morellato, 2014; Trøjelsgaard, Jordano, Carstensen, & Olesen, 2015; Tylianakis & Morris, 2017). Moreover, modelling studies have found large differences in network stability and resilience when nodes are allowed to dynamically rewire (CaraDonna et al., 2017; Gilljam, Curtsdotter, & Ebenman, 2015). Given the wide variation in quality, quantity and availability of resource rewards offered by plant species, and behavioural attributes and physiological requirements of pollinators, pollinators' choices of partners and alternative partners is unlikely to be random (Trøjelsgaard et al., 2015). In support of this idea, network modelling studies which include dynamic rewiring have found that even a small amount of behaviour-based direction in re-wiring choices dramatically improves model predictive ability compared to random re-wiring (Tylianakis & Morris, 2017).

Previous studies suggest that plant–pollinator network rewiring is, by necessity, likely to be based on plant and pollinator phenology and abundance (e.g. CaraDonna et al., 2017). I propose that the nutritional characteristics of plant species' pollen and nectar will also play an important role in partner choice. Specifically, quantitative data on resource rewards, combined with data on phenology and abundance, will improve the accuracy of prediction of (a) interaction partner choice: which plant species a pollinator visits; (b) interaction partner preference: of the plant species visited by a pollinator, which are visited most frequently; and (c) interaction rewiring: which alternative plant species are selected in the absence of favoured plant species. The ability of pollinators and plants to find or be found by potential interaction partners and expand their repertoire of partner species is likely to be influenced by the size and species composition of the local site, distance to neighbouring sites with potential mutualist partners, and the nature of the land between patches where potential partners are present. In addition, even if new interactions are formed, whether an individual plant or pollinator species' population is stabilized by this rewiring depends on the quality of the new partner(s).

3.3 | Plant–pollinator network boundaries

Networks can occupy a discrete spatial location and be studied in isolation; this is termed local network analysis. However local networks are likely to be linked by shared species and organism dispersal, in which case they may be analysed as a 'network of networks', a meta-network (Tylianakis & Morris, 2017). A meta-network is a set of spatially distributed local networks of the same type (e.g. plant–pollinator). In a meta-network mobile species can provide services to, or mediate interactions between, species in networks that are spatially or temporally separated. In theory, meta-network connections could decrease local network stability or resilience by allowing perturbations such as disease to propagate across the whole-meta-network. Alternatively, meta-network connections could increase local network stability or resilience, because local extirpation of a mobile species may not mean that that species, or the interactions in which it participated, will be lost from the local network because the species could re-establish via dispersal from neighbouring networks (source-sink dynamics). Similarly, local loss of one or more of a mobile species' requirements (e.g. nest sites, a particular food source) may not necessarily mean that the species will be locally extirpated, because the mobile species could access those resources at other sites. Meta-network approaches have provided useful insight when investigating ecological networks at habitat-type edges and interfaces, and when attempting to scale investigations up from the field-scale to the landscape-scale (Tylianakis & Morris, 2017).

Meta-network analyses to date have created edges between local networks based on species or interaction overlap (the presence of the same species or interaction pair in separate networks), weighted by species abundance per site, with symmetry based on abundance differences between the connected sites (e.g. Devoto, Bailey, & Memmott, 2014). Meta-network analyses could use empirical data on patch-to-patch organism movement to quantify network-to-network edges (Tylianakis & Morris, 2017). However, to date plant–pollinator network-to-network edge values have not been based on empirical dispersal data (Pilosof, Porter, Pascual, & Kéfi, 2017), largely because these data are lacking. The current lack of empirical data on site-to-site pollinator dispersal is due at least in part to the difficulty of tracking individual pollinator dispersal events (Nathan et al., 2008). Studies of pollinator movement have traditionally used (a) mark–recapture methods, (b) feeding station observation, (c) waggle dance analysis and (d) parentage analysis of plant progeny arrays. Mark–recapture methods are limited by the fact that marked insect pollinators are inherently difficult to find and recapture and researchers will only find marked individuals where the researchers are able or choose to look. This makes the method potentially suitable for finding out if pollinators visit a particular site of interest (e.g. Hagler, Mueller, Teuber, Machtley, & Deynze, 2011), but not for finding out more broadly where insects travel. Feeding station observation can provide information on how far pollinators are capable of travelling to exploit an extraordinarily rich resource (the feeding station), but this does not provide information on where the pollinators would normally forage. Honeybee researchers have

interpreted the spatial information in waggle dances to identify the foraging locations of laboratory populations of honeybees (e.g. Couvillon & Ratnieks, 2015). This method is, unfortunately, limited to honeybees. Parentage analysis of plant progeny arrays provides information on effective pollination by pollinators moving between adult individuals of a plant species of interest, and plant population genetic structure can provide insight into the quantity of pollen flow between sites (e.g. Lander, Bebber, Choy, Harris, & Boshier, 2011). This approach unfortunately does not provide information on which pollinator species are moving between the sites, unless the plant has a single specialist pollinator.

Individual bees have been tracked with harmonic radar since 1997 with a system developed at Rothamsted Research (Osborne et al., 1997). However, there are three main limitations to the Rothamsted system: (a) the tags are larger than most insects, ~1.5 cm, and their size disrupts normal behaviour (Osborne et al., 1999). The tags are also arranged vertically, which means they get tangled in vegetation and are unsuitable for ground-nesting insects; (b) current radar transmitter/receivers are expensive and large (approximately 1.5 m × 1.5 m × 4 m tall), and require transport on flatbed trucks, making them unsuitable for most field sites; (c) the low signal strength achieved by the equipment means the signal cannot penetrate vegetation and it is limited to use in low-growing herbaceous fields. As soon as the target insect travels over a hedge or beyond a line of trees, the system is not able to track it (Osborne et al., 1999). There is an open niche for a new approach to insect tracking that uses smaller, lighter tags, has a signal which penetrates vegetation, uses a more portable transmitter/receiver, and provides accurate geo-location of the tagged insect. A number of labs in the UK are developing new approaches to insect tracking which, to date are not published or field ready. When available these approaches will significantly improve the study of insect behaviour and foraging and make a step-change in our ability to analyse plant–pollinator meta-network connections.

In summary, the proposed network analysis approach would provide practical guidance on how much and what type of floral resources are needed to support diverse and abundant pollinator populations and how the interventions should be deployed spatially, give new insight into plant–pollinator community dynamics, and provide robust predictions of species-level extinction probabilities. However, it is reliant on empirical data for parameterization and prediction validation. In Part 3 I describe a new citizen science project to collect data on bee identity, diversity and abundance in relation to local plant species identity, diversity and abundance. The data collected can be used to validate predictions of the network approach described here.

4 | OXFORD PLAN BEE: CITIZEN SCIENCE TO DEVELOP PRACTICAL LAND MANAGEMENT GUIDANCE

Oxford Plan Bee (https://oxfordplanbee.web.ox.ac.uk/) is a citizen science project to collect empirical data which can be used

to test the predictions of the approach described in Part 2. Specifically, the project collects annual data on cavity-nesting solitary bee species identity, diversity and abundance in relation to local plant species identity, diversity and abundance, as well as other habitat characteristics, for a network of 135 bee nest-boxes across the city of Oxford and in Wytham Woods, Oxfordshire, UK (Figures 1 and 2). Members of the general public tend to be most familiar with eusocial honey bees and bumblebees, but ~85% of the ~20,000 bee species in the world are solitary bees (Figure 2) (Batra, 1984). The term 'solitary bees' is used as an all-encompassing term to include non-parasitic, non-corbiculate, non-Apis (honeybee) and non-Bombus (bumblebee) bees that do not live in large colonies (Wood, Holland, & Goulson, 2016). In a 'classic' solitary bee, each adult female builds a separate nest consisting of a series of chambers or cells, each containing a single egg plus a provision ball of nectar and pollen. The cells are separated by walls made of soil or plant material. Solitary bees can make nests in soil, masonry and even snail shells, and about 5% of all bee and wasp species nest in above-ground holes in dead wood or grass stems and can be expected to make nests in bee nest-boxes (Tscharntke, Gathmann, & Steffan-Dewenter, 1998). Although cavity-nesting bees are only a proportion of all bee species, they are ecologically important wild pollinators, and they have been shown to be useful bioindicators of habitat quality for a diversity of insects, including butterflies and other pollinator species, as well as bioindicators of dead wood habitat which is vital for numerous saproxylic species, and effective habitat connectivity (Tscharntke et al., 1998).

FIGURE 1 Oxford Plan Bee nest-box

FIGURE 2 An example of one of the species of solitary bee we expect to occupy the Oxford Plan Bee nest-boxes, the leaf cutter bee *Megachile willughbiella*. Photo credit: Steven Falk

In addition to providing data to validate predictions of the proposed network analyses, Oxford Plan Bee aims to collect data on year to year changes in solitary bee species' abundance and diversity, and capture population declines over time should they occur. Our understanding of the pattern and extent of bee decline is limited because even in places as well-studied as the UK, we know broadly where species are present, but in most cases we do not know how many individuals there are in a given area (Goulson et al., 2015). That means a species could decline from abundant to infrequent at a site, but as long as it is sighted during a field survey it could be considered 'present' and there would be no reported change in presence or range. Range shifts and species declines are generally only discovered when there are local extinctions or catastrophic population declines, meaning the window of opportunity for conservation action may have been missed (Goulson et al., 2015). The long-term species-level data collected by Oxford Plan Bee is expected to complement the data collected by other national pollinator monitoring programs such as the UK Pollinator Monitoring Scheme (https://www.ceh.ac.uk/our-science/projects/pollinator-monitoring), which collect data on a wider diversity of pollinator groups, but to a very low taxonomic resolution (citizen scientists are asked to group flower visitors into categories such as 'small insects under 3 mm long', 'bumblebees', 'hoverflies'). These programs, together with other initiatives, should help to identify local bee species declines while there is still an opportunity for intervention.

5 | CONCLUSIONS

Recent analyses showing dramatic declines in insects, and particularly pollinators (Powney et al., 2019; Sánchez-Bayo & Wyckhuys, 2019) received widespread news coverage. Against this apocalyptic background, predicting, monitoring and, most importantly, reversing insect decline is a global priority. However, in most places we do not know what species are present, or how many of them there are, or how much or what types of specific resources they need to stabilize their populations. Here I propose that monitoring programs such as Oxford Plan Bee, which collect data on bee species' presence, abundance and resource requirements, combined with service provision-based estimates of species' dependencies, would dramatically improve our ability to predict species extinctions and network-wide extinction cascades, and also facilitate targeted conservation action to establish the types and quantities of floral resources most likely to maintain an abundant, diverse and stable pollinator community.

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REFERENCES

Abrams, P. A. (2010). Implications of flexible foraging for interspecific interactions: Lessons from simple models. *Functional Ecology*, *24*, 7–17. https://doi.org/10.1111/j.1365-2435.2009.01621.x

Anwar, M. R., Liu, D. L., Macadam, I., & Kelly, G. (2013). Adapting agriculture to climate change: A review. *Theoretical and Applied Climatology*, *113*, 225–245. https://doi.org/10.1007/s00704-012-0780-1

Ballantyne, G., Baldock, K. C. R., Rendell, L., & Willmer, P. G. (2017). Pollinator importance networks illustrate the crucial value of bees in a highly speciose plant community. *Scientific Reports*, *7*, 8389. https://doi.org/10.1038/s41598-017-08798-x

Batra, S. W. T. (1984). Solitary bees. *Scientific American*, *250*, 120–127. https://doi.org/10.1038/scientificamerican0284-120

Baude, M., Kunin, W. E., Boatman, N. D., Conyers, S., Davies, N., Gillespie, M. A. K., ... Memmott, J. (2016). Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature*, *530*, 85–88. https://doi.org/10.1038/nature16532

Beckerman, A., Petchey, O. L., & Morin, P. J. (2010). Adaptive foragers and community ecology: Linking individuals to communities and ecosystems. *Functional Ecology*, *24*, 1–6. https://doi.org/10.1111/j.1365-2435.2009.01673.x

Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T., ... Kunin, W. E. (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, *313*, 351–354. https://doi.org/10.1126/science.1127863

Brosi, B. J., & Briggs, H. M. (2013). Single pollinator species losses reduce floral fidelity and plant reproductive function. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 13044–13048. https://doi.org/10.1073/pnas.1307438110

CaraDonna, P. J., Petry, W. K., Brennan, R. M., Cunningham, J. L., Bronstein, J. L., Waser, N. M., & Sanders, N. J. (2017). Interaction rewiring and the rapid turnover of plant–pollinator networks. *Ecology Letters*, *20*, 385–394. https://doi.org/10.1111/ele.12740

Carstensen, D. W., Sabatino, M., Trøjelsgaard, K., & Morellato, L. P. C. (2014). Beta diversity of plant–pollinator networks and the spatial turnover of pairwise interactions. *PLoS ONE*, https://doi.org/10.1371/journal.pone.0112903

Carvalheiro, L. G., Kunin, W. E., Keil, P., Aguirre-Gutiérrez, J., Ellis, W. N., Fox, R., … Biesmeijer, J. C. (2013). Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants. *Ecology Letters*, 16(7), 870–878. https://doi.org/10.1111/ele.12121

Corbet, S. A. (2003). Nectar sugar content: Estimating standing crop and secretion rate in the field. *Apidologie*, 34, 1–10. https://doi.org/10.1051/apido:2002049

Couvillon, M. J., & Ratnieks, F. L. W. (2015). Environmental consultancy: dancing bee bioindicators to evaluate landscape "health". *Frontiers in Ecology and Environment*, 3, Article 44. https://doi.org/10.3389/fevo.2015.00044

Devoto, M., Bailey, S., & Memmott, J. (2014). Ecological meta-networks integrate spatial and temporal dynamics of plant – Bumble bee interactions. *Oikos*, 123, 714–720. https://doi.org/10.1111/j.1600-0706.2013.01251.x

Díaz, S., Settele, J., & Brondízio, E. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services. Intergovernmental Science—Policy Platform on Biodiversity and Ecosystem Services. https://www.ipbes.net/global-assessment-report-biodiversity-ecosystem-services

Dicks, L. V., Ashpole, J. E., Dänhardt, J., James, K., Jönsson, A., Randall, N., … Sutherland, W. J. (2013). *Farmland conservation: Evidence for the effects of interventions in northern and western Europe.* Exeter, UK: Pelagic Publishing.

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. https://doi.org/10.1111/een.12226

FAO. (2000). *Environment and natural resources working paper no. 4.* Rome, Italy: Food and Agriculture Organization of the United Nations.

FAO. (2012). *FAO statistical year book.* Rome, Italy: Food and Agriculture Organization of the United Nations.

FAO. (2019a). FAOSTAT. Retrieved from http://faostat.fao.org/. Food and Agriculture Organization of the United Nations.

FAO. (2019b). *The state of the world's biodiversity for food and agriculture.* Rome, Italy: FAO Commission on Genetic Resources for Food and Agriculture Assessments.

Gill, R. J., Baldock, K. C. R., Brown, M. J. F., Cresswell, J. E., Dicks, L. V., Fountain, M. T., … Potts, S. G. (2016). Protecting an ecosystem service: Approaches to understanding and mitigating threats to wild insect pollinators. *Advances in Ecological Research*, 54, 135–206.

Gilljam, D., Curtsdotter, A., & Ebenman, B. (2015). Adaptive rewiring aggravates the effects of species loss in ecosystems. *Nature Communications*, 6, 8412. https://doi.org/10.1038/ncomms9412

Goulson, D., Nicholls, E., Botías, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, 347, 125–957. https://doi.org/10.1126/science.1255957

Gylling, M., & Abildtrup, J. (2001). Climate change and regulation of agricultural land use : A literature survey on adaptation options and policy measures. Danish Institute of Agricultural and Fisheries Economics, Farm Management and Production Systems Division.

Hagler, J. R., Mueller, S., Teuber, L. R., Machtley, S. A., & Deynze, A. V. (2011). Foraging range of honey bees, *Apis mellifera*, in alfalfa seed production fields. *Journal of Insect Science*, 11, https://doi.org/10.1673/1031.1011.14401

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., …de Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE*, 12(10), e0185809. https://doi.org/10.1371/journal.pone.0185809

Hicks, D. M., Ouvrard, P., Baldock, K. C. R., Baude, M., Goddard, M. A., Kunin, W. E., … Stone, G. N. (2016). Food for pollinators: Quantifying the nectar and pollen resources of urban flower meadows. *PLoS ONE*, 11, e0158117. https://doi.org/10.1371/journal.pone.0158117

Holland, J. M., Smith, B. M., Storkey, J., Lutman, P. J. W., & Aebischer, N. J. (2015). Managing habitats on English farmland for insect pollinator conservation. *Biological Conservation*, 182, 215–222. https://doi.org/10.1016/j.biocon.2014.12.009

Holzschuh, A., Steffan-Dewenter, I., & Tscharntke, T. (2008). Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos*, 117, 354–361. https://doi.org/10.1111/j.2007.0030-1299.16303.x

Kearns, C. A., Inouye, D. W., & Waser, N. M. (1998). Endangered mutualisms: The conservation of plant–pollinator interactions. *Annual Review of Ecology and Systematics*, 29, 83–112. https://doi.org/10.1146/annurev.ecolsys.29.1.83

Kennedy, C. M., Lonsdorf, E., Neel, M. C., Williams, N. M., Ricketts, T. H., Winfree, R., … Kremen, C. (2013). A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters*, 16, 584–599. https://doi.org/10.1111/ele.12082

Klein, A. M., Steffan-Dewenter, I., & Tscharntke, T. (2003). Fruit set of highland coffee increases with the diversity of pollinating bees. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 270, 955–961. https://doi.org/10.1098/rspb.2002.2306

Kremen, C., & Ricketts, T. (2000). Global perspectives on pollination disruptions. *Conservation Biology*, 14, 1226–1228. https://doi.org/10.1046/j.1523-1739.2000.00013.x

Kremen, C., Williams, N. M., & Thorp, R. W. (2002). Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 16812–16816. https://doi.org/10.1073/pnas.262413599

Kurukulasuriya, P., & Rosenthal, S. (2003). *Climate change and agriculture: A review of impacts and adaptations.* World Bank Environment Department and Agriculture and Rural Development Department.

Lander, T. A., Bebber, D. P., Choy, C. T. L., Harris, S. A., & Boshier, D. H. (2011). The circe principle explains how resource-rich land can waylay pollinators in fragmented landscapes. *Current Biology*, 21, 1302–1307. https://doi.org/10.1016/j.cub.2011.06.045

Landi, P., Minoarivelo, H. O., Brännström, Å., Hui, C., & Dieckmann, U. (2018). Complexity and stability of ecological networks: A review of the theory. *Population Ecology*, 60(4), 319–345. https://doi.org/10.1007/s10144-018-0628-3

Lister, B. C., & Garcia, A. (2018). Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proceedings of the National Academy of Sciences of the United States of America*, 115, E10397–E10406. https://doi.org/10.1073/pnas.1722477115

Ludwig, D., Walker, B., & Holling, C. S. (1997). Sustainability, stability, and resilience. *Conservation Ecology*, 1.

Memmott, J., Craze, P., Waser, N., & Price, M. (2007). Global warming and the disruption of plant–pollinator interactions. *Ecology Letters*, 10, 710–717. https://doi.org/10.1111/j.1461-0248.2007.01061.x

Memmott, J., Waser, N. M., & Price, M. V. (2004). Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society B-Biological Sciences*, 271, 2605–2611. https://doi.org/10.1098/rspb.2004.2909

Menz, M. H. M., Phillips, R. D., Winfree, R., Kremen, C., Aizen, M. A., Johnson, S. D., & Dixon, K. W. (2011). Reconnecting plants and pollinators: Challenges in the restoration of pollination mutualisms. *Trends in Plant Science*, 16, 4–12. https://doi.org/10.1016/j.tplants.2010.09.006

Møller, A. P. (2019). Parallel declines in abundance of insects and insectivorous birds in Denmark over 22 years. *Ecology and Evolution*, 9, 6581–6587. https://doi.org/10.1002/ece3.5236

Moron, D., Lenda, M., Skorka, P., Szentgyorgyi, H., Settele, J., & Woyciechowski, M. (2009). Wild pollinator communities are

negatively affected by invasion of alien goldenrods in grassland landscapes. *Biological Conservation*, 142, 1322–1332. https://doi.org/10.1016/j.biocon.2008.12.036

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 19052–19059. https://doi.org/10.1073/pnas.0800375105

Okuyama, T., & Holland, J. (2008). Network structural properties mediate the stability of mutualistic communities. *Ecology Letters*, 11, 208–216. https://doi.org/10.1111/j.1461-0248.2007.01137.x

Ollerton, J., Erenler, H., Edwards, M., & Crockett, R. (2014). Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. *Science*, 346, 1360–1362. https://doi.org/10.1126/science.1257259

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

Osborne, J. L., Clark, S. J., Morris, R. J., Williams, I. H., Riley, J. R., Smith, A. D., ... Edwards, A. S. (1999). A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *Journal of Applied Ecology*, 36, 519–533. https://doi.org/10.1046/j.1365-2664.1999.00428.x

Osborne, J. L., Williams, I. H., Carreck, N. L., Poppy, G. M., Riley, J. R., Smith, A. D., ... Edwards, A. S. (1997). Harmonic radar: A new technique for investigating bumblebee and honeybee foraging flight. *Acta Horticulturae*, 437, 159–163. https://doi.org/10.17660/ActaHortic.1997.437.15

Pilosof, S., Porter, M. A., Pascual, M., & Kéfi, S. (2017). The multilayer nature of ecological networks. *Nature Ecology & Evolution*, 1, 0101. https://doi.org/10.1038/s41559-017-0101

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution*, 25, 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., ... Vanbergen, A. J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, 540, 220–229. https://doi.org/10.1038/nature20588

Power, E. F., Stabler, D., Borland, A. M., Barnes, J., & Wright, G. A. (2018). Analysis of nectar from low-volume flowers: A comparison of collection methods for free amino acids. *Methods in Ecology and Evolution*, 9, 734–743. https://doi.org/10.1111/2041-210X.12928

Powney, G. D., Carvell, C., Edwards, M., Morris, R. K. A., Roy, H. E., Woodcock, B. A., & Isaac, N. J. B. (2019). Widespread losses of pollinating insects in Britain. *Nature Communications*, 10, 1018. https://doi.org/10.1038/s41467-019-08974-9

Rader, R., Bartomeus, I., Garibaldi, L. A., Garratt, M. P. D., Howlett, B. G., Winfree, R., ... Woyciechowski, M. (2016). Non-bee insects are important contributors to global crop pollination. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 146–151. https://doi.org/10.1073/pnas.1517092112

Sánchez-Bayo, F., & Wyckhuys, K. A. G. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation*, 232, 8–27. https://doi.org/10.1016/j.biocon.2019.01.020

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. https://doi.org/10.1111/ele.12128

Senapathi, D., Biesmeijer, J. C., Breeze, T. D., Kleijn, D., Potts, S. G., & Carvalheiro, L. G. (2015). Pollinator conservation — The difference between managing for pollination services and preserving pollinator diversity. *Current Opinion in Insect Science*, 12, 93–101. https://doi.org/10.1016/j.cois.2015.11.002

Senapathi, D., Goddard, M. A., Kunin, W. E., & Baldock, K. C. R. (2017). Landscape impacts on pollinator communities in temperate systems: Evidence and knowledge gaps. *Functional Ecology*, 31, 26–37.

Showler, D. A., Dicks, L. V., & Sutherland, W. J. (2010). *Bee conservation: Evidence for the effects of interventions*. Exeter, UK: Pelagic Publishing.

Sousa, T., Domingos, T., & Kooijman, S. A. L. M. (2008). From empirical patterns to theory: A formal metabolic theory of life. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 363, 2453–2464. https://doi.org/10.1098/rstb.2007.2230

Stavert, J. R., Liñán-Cembrano, G., Beggs, J. R., Howlett, B. G., Pattemore, D. E., & Bartomeus, I. (2016). Hairiness: The missing link between pollinators and pollination. *PeerJ*, 4, e2779. https://doi.org/10.7717/peerj.2779

Timoteo, S., Ramos, J. A., Vaughan, I. P., & Memmott, J. (2016). High resilience of seed dispersal webs highlighted by the experimental removal of the dominant disperser. *Current Biology*, 26, 910–915. https://doi.org/10.1016/j.cub.2016.01.046

Trøjelsgaard, K., Jordano, P., Carstensen, D., & Olesen, J. (2015). Geographical variation in mutualistic networks: Similarity, turnover and partner fidelity. *Proceedings of the Royal Society B*, 282, 20142925.

Tscharntke, T., Gathmann, A., & Steffan-Dewenter, I. (1998). Bioindication using trap-nesting bees and wasps and their natural enemies: Community structure and interactions. *Journal of Applied Ecology*, 35, 708–719. https://doi.org/10.1046/j.1365-2664.1998.355343.x

Tylianakis, J. M., & Morris, R. J. (2017). Ecological networks across environmental gradients. *Annual Review of Ecology, Evolution, and Systematics*, 48, 25–48. https://doi.org/10.1146/annurev-ecolsys-110316-022821

Vanbergen, A. J., & Initiative, T. I. P. (2013). Threats to an ecosystem service: Pressures on pollinators. *Frontiers in Ecology and Environment*, 11, 251–259. https://doi.org/10.1890/120126

Vanderplanck, M., Leroy, B., Wathelet, B., Wattiez, R., & Michez, D. (2014). Standardized protocol to evaluate pollen polypeptides as bee food source. *Apidologie*, 45, 192–204. https://doi.org/10.1007/s13592-013-0239-0

Vanderplanck, M., Vereecken, N. J., Grumiau, L., Esposito, F., Lognay, G., Wattiez, R., & Michez, D. (2017). The importance of pollen chemistry in evolutionary host shifts of bees. *Scientific Reports*, 7, 43058. https://doi.org/10.1038/srep43058

Vaudo, A. D., Tooker, J. F., Grozinger, C. M., & Patch, H. M. (2015). Bee nutrition and floral resource restoration. *Current Opinion in Insect Science*, 10, 133–141. https://doi.org/10.1016/j.cois.2015.05.008

Vázquez, D. P., & Aizen, M. A. (2004). Asymmetric specialization: A pervasive feature of plant–pollinator interactions. *Ecology*, 85, 1251–1257. https://doi.org/10.1890/03-3112

Winfree, R., Aguilar, R., Vazquez, D. P., LeBuhn, G., & Aizen, M. A. (2009). A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology*, 90, 2068–2076. https://doi.org/10.1890/08-1245.1

Wood, T. J., Holland, J. M., & Goulson, D. (2016). Diet characterisation of solitary bees on farmland: dietary specialisation predicts rarity. *Biodiversity and Conservation*, 25(13), 2655–2671. https://doi.org/10.1007/s10531-016-1191-x

Woodcock, B. A., Isaac, N. J. B., Bullock, J. M., Roy, D. B., Garthwaite, D. G., Crowe, A., & Pywell, R. F. (2016). Impacts of neonicotinoid use on long-term population changes in wild bees in England. *Nature Communications*, 7, 12459. https://doi.org/10.1038/ncomms12459