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RESEARCH ARTICLE

Flowering plant communities mediate the effects of habitat composition and configuration on wild pollinator communities

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Abstract

1. There is strong evidence that landscape-scale factors such as habitat diversity, composition and configuration are important drivers of declines in pollinators and pollination services. However, context and species-specific responses make it challenging to draw general conclusions about the most important components of landscapes that support diverse and abundant pollinator communities.

2. In this study, we took a functional-traits approach to community assembly and tested the hypothesis that landscape properties act most strongly on pollinators indirectly, through their influence on flowering plant communities. Using plant and pollinator data from 96 landscapes in Britain, we tested the associations between plant and pollinator communities and local environmental factors, such as habitat cover and configuration, using path analysis based on Mantel and partial Mantel statistics.

3. When all pollinators were considered, we found that the environmental factors had stronger links to the composition of flowering plant communities than to the composition of pollinator communities. Further, the flowering plant community was strongly linked to the pollinator community suggesting a mediating role between land use and pollinators. When separating the pollinator community into taxonomic groups, we found the same result for hoverflies, but wild bees were linked to both environmental factors and flowering plants.

4. We further explored these links with structural equation models using the response-effect trait framework as a guiding principle. We found strong evidence that land-use composition and configuration influence the trait distribution and functional diversity of the pollinator community via plant community composition.

5. These findings suggest that the indirect effect of land use on pollinators via flowering plants should be considered in informing the design of pollinator friendly landscapes and in future research of the effects of land use and management on wild pollinators.

KEYWORDS
community ordination, environmental filtering, floral resources, functional diversity, landscape ecology, pollinator community composition, traits

1 | INTRODUCTION

Pollinator abundance and diversity are declining worldwide (Wagner, 2020; Zattara & Aizen, 2021), threatening ecological functioning and crop production (Hooper et al., 2012; Kremen, 2018). These trends are partly driven by agricultural intensification (Gabriel et al., 2013; Holzschuh et al., 2008; Potts et al., 2016), which in turn is associated with several key environmental stressors. Insect pollinators are directly impacted by pesticides (Goulson et al., 2015), habitat loss and fragmentation (Delnevo et al., 2020; Garibaldi et al., 2011; Winfree et al., 2009), and changes in habitat composition at landscape scales (Coutinho et al., 2021; Jauker et al., 2013). Intensive management practices also tend to simplify habitat configuration, reducing the structural complexity and connectivity between patches (Gillespie et al., 2022; Kennedy et al., 2013), leading to declines in the abundance and diversity of native plants, upon which pollinators rely for food (Duflot et al., 2017; Liccari et al., 2022).

Despite well-established evidence about the impact of these landscape-scale drivers, there is a lack of consensus about the most important components of a pollinator-supporting landscape, because most responses are context and/or species specific (Hopfenmüller et al., 2014; Kennedy et al., 2013), and drivers may have complicated and interacting effects on biodiversity (Gillespie et al., 2022; Kennedy et al., 2013). Recent research has also shown that the response of flowering plant diversity to landscape-scale management can have important knock-on effects to pollination services and pollinator diversity (Bennett et al., 2014; Rotchés-Ribalta et al., 2018; Theodorou et al., 2020). These findings underline a key point of a review by Roulston and Goodell (2011), who highlight that pollinators are likely to be impacted by factors that relate to resource needs such as plant forage and nesting locations, as well as by broader factors that alter the availability of those resources, such as land-use change. Despite this understanding, the possible mediating effect of flowering plants is understudied at the landscape scale; more research is needed to understand how a combination of stressors impact pollinator communities both directly and indirectly. In this study, we investigated how landscape-scale drivers impacted the composition of pollinator communities both directly and indirectly through floral resource availability, using a functional trait-based approach.

The trait-based approach to pollination ecology is important in managed landscapes because functionally diverse pollinator communities, those comprising species with a varied range of dispersal and foraging traits, can include species that provide complementary pollination services (Forrest et al., 2015; Rader et al., 2014; Williams et al., 2010). However, there is a lack of consensus over the most functionally important pollinator and plant traits and their responses to land use (De Palma et al., 2015; Rader et al., 2014). This may be because we have not yet identified the most informative traits for many species, or because the pollinator traits may also respond indirectly to land use through impacts on their fundamental resources (Lavorel et al., 2013; Pakeman & Stockan, 2013). Such an indirect effect may suggest a mediating role of flowering plant traits on pollinator traits and has been formalised by the 'response-effect trait framework' put forward by Lavorel et al. (2013), which aims to predict the impact of environmental change on ecosystems via multitrophic relationships. Plant traits may be considered 'response' traits if they are associated with environmentally filtered membership of a community, and 'effect' traits if they are associated with ecosystem functions such as pollination. The framework has been applied to plant and pollinator communities with contrasting methods and varying levels of support (e.g. Pakeman & Stockan, 2013; Robleño et al., 2018; Solé-Senan et al., 2018), and additional research is required to advance its utility (Goulnik et al., 2021; Lavorel et al., 2013). With this in mind, we used the framework as a guiding principle to generate hypothesised structural equation models (SEM) that tested the mediating role of plant communities in British landscapes. In contrast to previous uses of the framework where separate analyses are used to identify traits that are 'ideal' for the study system, we used gradients of dominant plant and pollinator traits from loadings on principal component analysis (PCA) axes and found a potential future direction of study.

We used floral and pollinator abundance data across a network of 96 2×2 km field sites in Britain, to test the links between landscape-scale environmental factors and community assemblages (Objective 1). We expected that the plant community would be more responsive to environmental factors than the pollinator community, and that this would affect pollinator communities. We then explored the mechanisms that may lie behind these patterns, assessing how the mediating effect of plant communities could be explained in terms of response and effect trait distributions (Objective 2). In line with previous studies, we expected that flowering plants with ruderal response traits would be associated with intensive land use types (Goulnik et al., 2021; Lavorel & Grigulis, 2012), with consequences for floral traits that may in turn attract different functional groups of pollinators (Goulnik et al., 2021). In general, we expected that these more intensive land use types would have reduced functional diversity (Le Provost et al., 2021; Staton et al., 2022).

2 | METHODS

2.1 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Community	Landscape (2×2 km sites)	16 landscapes clustered in each of 6 regions

2.1.1 | Study sites

We used a network of 96 field sites (2×2 km) clustered in 6 regions of Great Britain (16 sites per region), which were selected in 2011 (previously described in Gillespie et al., 2017) and surveyed for flowers and pollinators in 2012 and 2013 (Gillespie et al., 2022). The 6 study regions (100×100 km) were selected to maximise representation of British broad habitat types (as mapped by the 2007 Land Cover Map, Morton et al., 2011) and bioclimate (using the Institute of Terrestrial Ecology (ITE) land classes; Bunce et al., 1996; Figure 1). The regions cover several counties of England and Scotland, hereafter referred as (1) Inverness-shire (north Scotland), (2) Ayrshire (south Scotland), (3) Yorkshire (north England), (4) Staffordshire (Midlands), (5) Wiltshire (south-west), (6) Cambridgeshire (south-east).

Within each region, 16 study landscapes (hereafter: 'sites') were selected to maximise the contrast in four variables we considered to be important landscape-scale drivers of pollinator populations: honeybee densities, insecticide loadings, floral resource availability, and habitat diversity. Full details of the derivation of these metrics can be found in Gillespie et al. (2017). The sites within each region were within 50 km of each other and met other selection criteria (low

cover of urban and open water land use types). They were also found to decrease the level of inter-correlation between the gradients of our four drivers of interest by correlation analysis of the variable scores (Gillespie et al., 2017).

2.1.2 | Additional landscape metrics

In addition to the four environmental factors listed above, we derived metrics to represent habitat composition and configuration using the Land Cover Map data described above (2007 map; Morton et al., 2014). The broad habitat types for the study sites were validated by ground-truthing over the 2 years of the study, and corrected maps were used as inputs to the software programme FRAGSTATS (v4.2.1.603; McGarigal et al., 2023) to calculate edge density and a connectivity index. Edge density describes the total length of borders between different habitat types per unit area and represents the structural complexity of the landscape (Martin et al., 2019), while connectivity (percentage of all possible 'connections' between all habitat patches of the same type within 250 m) accounts more for the proximity of different habitat patches and provides an alternative structural dimension (McGarigal et al., 2023).

We also simplified the broad habitat categories of the Land Cover Map to aid analysis of the effects of land cover types. Use of the original categories resulted in a large number of zeros for many habitats, but exploration of the habitat make-up of these sites revealed strong land-use gradients from sites that were composed mostly of intensively managed land (arable or improved grazing; categories 1 and 2 below) to those dominated by semi-natural habitats (SNH; woodland, heathland, rough grazing common land etc., categories 3 and 4). We further divided SNH between open (3) and woodland (4) habitats, because the pollinator and plant communities often differ greatly (Thomas et al., 2015). However, the 'woodland' category would include large conifer plantations, an intensive land use type unlikely to support diverse pollinator communities (Humphrey et al., 2002). We therefore only included conifer patches of less than 10% land cover in 'woodland SNH', and classed larger blocks of conifer as category 5: conifer plantations. Finally, 'Linear Features' (category 6) was included to investigate the importance of these ubiquitous features. The resulting simplified habitat categories were:

1. Arable crops.
2. Improved grassland.
3. Open semi-natural habitats ('open SNH'; rough low-productivity grassland, other grassland (acid, neutral and calcareous), heath, bog and hay meadows).
4. Woodland habitats ('woodland SNH'; deciduous, mixed, recently planted woodland and conifer where patches were less than 10% of the site area).
5. Conifer plantations.
6. Linear features (water edges, stone walls, fence lines and hedges), where all were assumed to be 2 m wide.
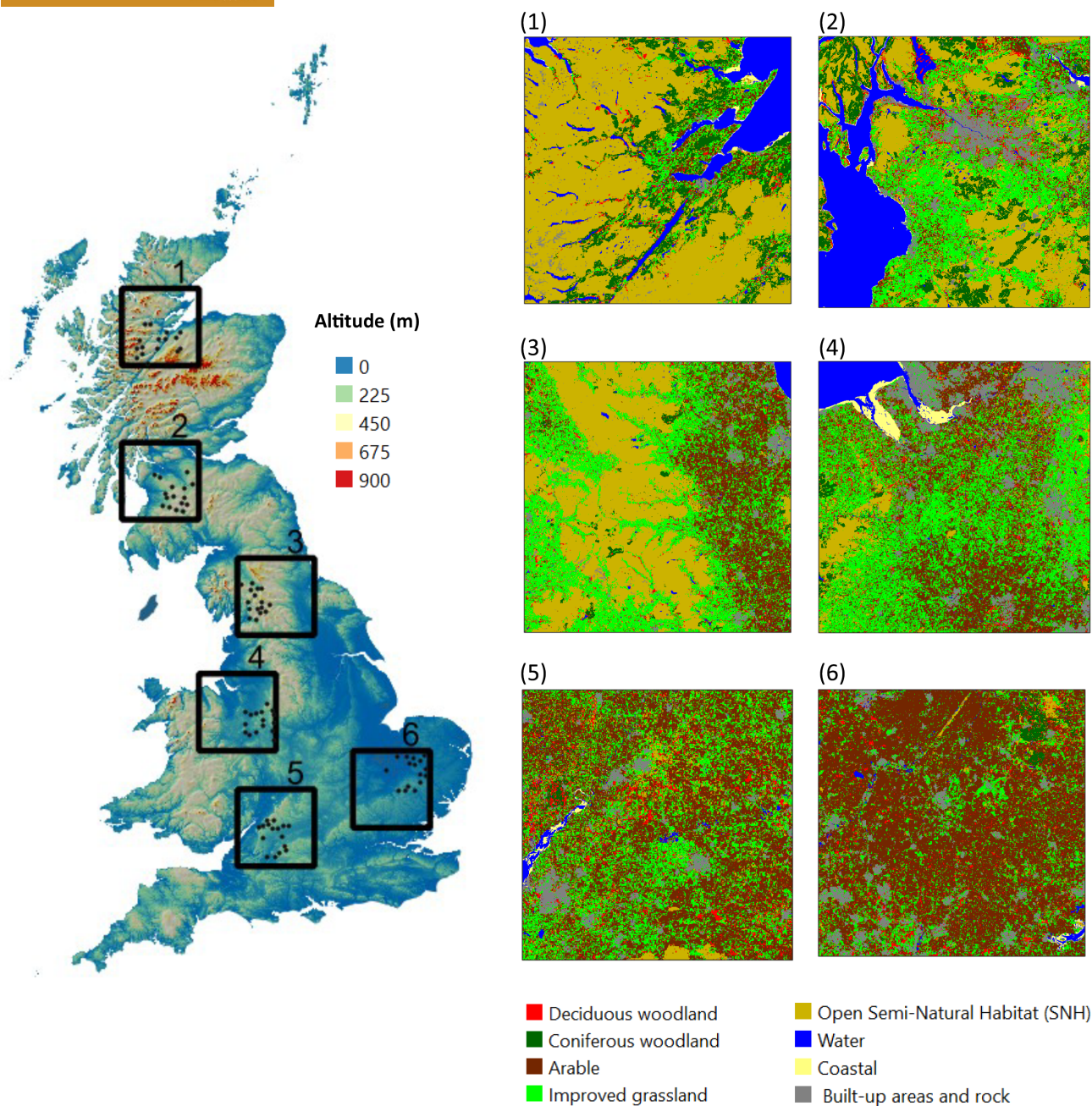
FIGURE 1 Map of the six study regions in Britain, indicating variation in terrain (left) and broad habitat composition of each region (right). The broad habitat categories correspond to a simplified topology used in this study (see section Additional landscape metrics). Region numbers: (1) Inverness-shire (north Scotland), (2) Ayrshire (south Scotland), (3) Yorkshire (north England), (4) Staffordshire (Midlands), (5) Wiltshire (south-west), (6) Cambridgeshire (south-east).

2.1.3 | Pollinator sampling

In this study, the term 'pollinators' is used to refer to all wild bee and hoverfly species. Pollinators were sampled in the spring and summer of 2012 and 2013 using five pan trap sets at each of the 96 field sites. The trap sets consisted of three bowls painted with UV-reflecting paint (blue, white, and yellow) and mounted to a wooden stake at the height of the ground vegetation within 1 m radius. Traps were located at least 100 m apart in the centre of each site in a regular pentagon where possible. However, traps were only set out in unshaded locations where they could not be disturbed by livestock or people, which required minor deviations from a regular formation in some sites. The traps were set up in three rounds per year (Round 1: April–May, Round 2: June–July, Round 3: August–September) during clear, dry conditions and were left in place for 24 h. Upon removal, insect material was stored in ethanol for later mounting and identification to species by Hymettus Ltd. Taxonomic resources included Stubbs and Falk ([2002](#)) for hoverflies, and test keys that formed the basis of Else and Edwards ([2018](#)) for bees and wasps.

2.1.4 | Flowering plant data collection

At each field site, we surveyed the flowering plant community using a quadrat and transects system in both 2012 and 2013 (see Gillespie et al., 2017 for full details). We surveyed 1000 m of transect at each site, divided proportionate to the broad habitats of the LCM, and added 40 m of transect per 'linear feature' type present for a total of 1100–1200 m per site. Each transect section was sub-divided into 10 m long segments, with each segment starting with a 1 m wide × 0.5 m quadrat followed by a 1 m × 9.5 m 'additional belt' to the next segment. In each quadrat, we counted the number of 'floral units' of each animal-pollinated plant species (a floral unit = the cluster of flowers over which a honeybee could walk, rather than fly, to reach all nectaries, e.g. capitulum, sub-umbel etc.). Any flowering plant species that occurred in the 9.5 m additional belt but not in the quadrat was also counted, but on an approximate logarithmic scale (i.e. 1, 2, 5, 10, 20, 50, 100, …). Flower counts were conducted three times during each season to coincide with the three pollinator survey rounds. As sampling usually required an entire day for one site, each site was surveyed on a different day and the order of surveys was randomised for each sampling round. We did not require licences or permits to carry out any of the fieldwork, and permission for land access was granted privately by landowners.

2.1.5 | Trait information

We used plant, bee and hoverfly traits commonly used in the literature (Table 1). We acknowledge that intraspecific variability may be important to many of these traits, but as our species database contained over 400 plant species and nearly 300 pollinator species, we opted for greater species coverage over individual measurements of a smaller subset of species. We selected 12 plant traits, six of which were categorised as 'response' traits (responsive to environmental variation), and six as 'effect' traits (likely to affect pollinator attraction). We limited the number of traits to ensure maximum coverage of the plant database (266 plant species), modelling accuracy and comparability to previous work.

The plant response traits covered a range of possible responses to management intensity, as traits such as life span (perennial, biennial or annual), specific leaf area (correlated with resource acquisition) and seed mass and number, can be related to varying levels of land-use intensity both in terms of disturbance and macronutrient availability (Díaz et al., 2016; Lavorel & Grigulis, 2012; Robleño et al., 2018). Similarly canopy height and date of first flowering have been related to competition and successional gradients (Lavorel & Grigulis, 2012; Storkey et al., 2013). The chosen effect traits covered factors likely to influence attractiveness to and associations with pollinator species, as different species tend to be attracted to different colours (in visual and UV spectra), flower shapes and reward levels (Goulnik et al., 2021; Lavorel et al., 2013).

Pollinator traits were selected to relate to aspects of species' mobility and foraging behaviour (Williams et al., 2010). For bees,

we used female inter-tegular distance (ITD) for body size, as well as tongue length guild, diet breadth and sociality, which are important determinants of forage resource needs (Williams et al., 2010). We used the phenological traits of month that activity begins and duration of activity in months as these can impact the availability of flowering plants on which bees forage (Woodcock et al., 2014). With bivoltine species, we treated activity duration as the difference between first activity month and the last activity month (i.e. ignoring any activity gaps), because trait database data were not detailed enough to determine precise durations. However, we included voltinism as a trait to attempt to account for this. For hoverflies, we used body size, the same phenological traits as for bees, as well as voltinism and the target floral reward of adults. We omitted traits relating to bee nesting and hoverfly larval needs as these are not directly related to floral traits and therefore not strictly conforming to the response-effect framework or relevant to understanding how the flowering plant community influences pollinator functional diversity. To ensure the largest dataset possible we included both resident and migrant species, and this resulted in a dataset of 112 bee species and 95 hoverfly species.

2.1.6 | Data analysis

All analyses were conducted in the R programming environment (version 4.2.2; R Core Team, 2023), and we used the *ade4* package (Thioulouse et al., 2018) for all multivariate analysis. Honeybees (*Apis mellifera*) were excluded from the pollinator dataset as they were used as a site selection variable and their presence is primarily driven by beekeeper decisions on apiary location. For initial exploration of the species abundance data, all species abundances were Hellinger transformed using the *vegan* package (Oksanen et al., 2019), as this method down weights the importance of rare species and extreme values, as well as double absences in the data table (Legendre & Gallagher, 2001). The pollinator and plant species data were arranged into species × site matrices by summing abundances across sampling rounds and years. We further separated the wild bee species and hoverfly species into their own data tables to analyse them separately. All four species tables (plants, all pollinators, wild bees and hoverflies) were then analysed by correspondence analysis (CA). Because our 96 sites are clearly clustered into six regions, we then applied a Between-class analysis (BCA) with region as the grouping factor to explore the differences in community composition. The site-level data on the four site selection criteria (honeybee density, insecticide loading, floral resource availability, habitat diversity), habitat composition (habitat cover variables) and habitat configuration (edge density and connectivity) were combined into an 'environmental matrix' and this was analysed by principal component analysis (PCA) to explore the regional gradients.

> Objective 1. The flowering plant community as mediator between environmental factors and the pollinator community composition.

TABLE 1 List of traits, the variable type and sources of information. See footnote for source definitions.

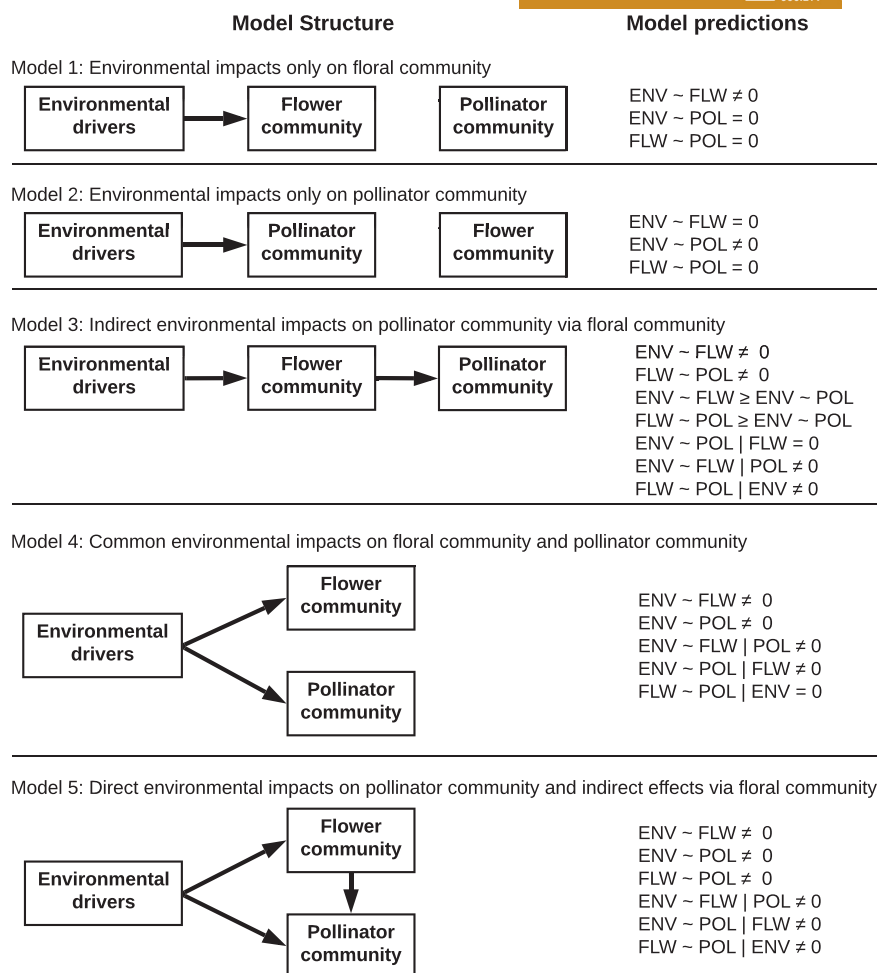| Species group	Trait	Variable type	Source
Plant response traits	First flower month	Numerical (month number)	1, 2, 3
	Canopy height	Numerical (m)	4
	Specific leaf area (SLA)	Numerical (mm^2/mg)	4
	Seed number	Numerical	4
	Seed mass	Numerical	4
	Life span	Categorical – converted to three binary variables (Annual, Biennial, Perennial)	1, 2, 3
Plant effect traits	Flower colour	Categorical (Blue/Violet, Red/Pink, White/Yellow, Green/Brown)	1, 3
	Flower type – a simplified classification of Müller's (1881) flower classes	Categorical – Fly (original classes F, FH, Fn, Ft, D, Dk, Ds, Dt), hidden nectar (B, B′, BD, BH), hymenoptera (H, Hb, Hh, Hi, Hw), open nectar (A, AD), part hidden nectar (AB), pollen (Po)	1, 3
	Flowering duration	Numerical (months)	1, 2, 3
	Nectar reward score	Ordinal – 0-3, based on BiolFlor scoring (0=nectar none, 1=nectar little, 2=nectar present, 3=nectar plenty)	1
	UV reflectance	Numerical – percentage light reflected as UV	3
	Insect pollination	Binary: 1=insect pollinated, 0=wind, apogamy or selfed	1, 3
Wild bee	Body size	Numerical (mean ITD of females)	5
	Sociality	Categorical (Cleptoparasitic, Social, Social parasite, Solitary)	5
	Diet	Categorical (None, Oligolectic, Polylectic)	5
	Active season start	Numerical (month)	5
	Duration of season	Numerical (months)	5
	Voltinism	Categorical, converted to three binary variables (Univoltine, Bivoltine, Multivoltine)	5
	Tongue length guild	Binary (0=short, 1=long)	5
Hoverfly	Body size (median body length)	Numerical	6
	Active season start	Numerical (month)	6
	Duration of season	Numerical (months)	6
	Diet	Binary (1=nectar only, 0=nectar and pollen)	6
	Voltinism	Binary (1=univoltine, 0=multivoltine)	6

Sources: 1=Biolflor: Klotz et al. (2002), 2=Ecoflora: Fitter and Peat (1994), 3=TRY database: Kattge et al. (2020), 4=LEDA: Kleyer et al. (2008), 5=unpublished database from University of Reading, 6=Syrph the Net: Speight et al. (2013).

To test the mediating role of the plant community, we used a method detailed by Frenette-Dussault et al. (2013), and adapted it to account for spatial autocorrelation in our sites. In that study, simple and partial Mantel correlations were used to test four path models of relationships between an environmental matrix, vegetation structure and ant communities. We tested similar hypotheses here (Models 1, and 3–5 in Figure 2), and an additional model (Model 2) to test the hypothesis that environmental drivers only impacted the pollinator community, which may have occurred if our environmental variables did not have strong impacts on the flowering community. We performed the Mantel tests on Bray–Curtis distance matrices of the Hellinger transformed pollinator and plant species data detailed above, and a Euclidean distance matrix of the

environmental matrix. To account for the spatial autocorrelation due to regional clustering of our study sites, we tested the Mantel statistics with Moran spectral randomisation (MSR) instead of standard permutation procedures (Crabot et al., 2019). This procedure is outlined in Appendix S1, but it essentially allows a spatially constrained permutation test of the Mantel statistics (r) that tests the null hypothesis: 'given the spatial structure in the original data, the distances in matrix X are not related to the distances in matrix Y' (Crabot et al., 2019).

Objective 2. The response and effect traits of plants as mediator between environmental factors and the pollinator functional traits.

FIGURE 2 Five plausible ecological models explaining pollinator community composition. Each model displays the hypothesised relationships between environmental drivers (ENV), the flowering plant community (FLW) and pollinator communities (POL). If a model is to be considered a plausible fit to the data, all model predictions should be met, as computed by Mantel tests. The notation of the model predictions in the form ENV~FLW, for example, represents the correlation between dissimilarity matrices for environmental drivers and the flowering plant community. Notation such as ENV~FLW|POL represents the partial correlation between dissimilarity matrices for ENV and FLW when statistically controlling for POL. Adapted from Frenette-Dussault et al. (2013).

Model Structure | Model predictions

Model 1: Environmental impacts only on floral community

Environmental drivers → Flower community   Pollinator community

ENV ~ FLW ≠ 0
ENV ~ POL = 0
FLW ~ POL = 0

Model 2: Environmental impacts only on pollinator community

Environmental drivers → Pollinator community   Flower community

ENV ~ FLW = 0
ENV ~ POL ≠ 0
FLW ~ POL = 0

Model 3: Indirect environmental impacts on pollinator community via floral community

Environmental drivers → Flower community → Pollinator community

ENV ~ FLW ≠ 0
FLW ~ POL ≠ 0
ENV ~ FLW ≥ ENV ~ POL
FLW ~ POL ≥ ENV ~ POL
ENV ~ POL | FLW = 0
ENV ~ FLW | POL ≠ 0
FLW ~ POL | ENV ≠ 0

Model 4: Common environmental impacts on floral community and pollinator community

Environmental drivers → Flower community; Environmental drivers → Pollinator community

ENV ~ FLW ≠ 0
ENV ~ POL ≠ 0
ENV ~ FLW | POL ≠ 0
ENV ~ POL | FLW ≠ 0
FLW ~ POL | ENV = 0

Model 5: Direct environmental impacts on pollinator community and indirect effects via floral community

Environmental drivers → Flower community → Pollinator community; Environmental drivers → Pollinator community

ENV ~ FLW ≠ 0
ENV ~ POL ≠ 0
FLW ~ POL ≠ 0
ENV ~ FLW | POL ≠ 0
ENV ~ POL | FLW ≠ 0
FLW ~ POL | ENV ≠ 0

Where plants were found to play a significant intermediary role between environment and pollinators (Model 3 or 5 in Figure 2), we further explored the nature of the relationships with piecewise structural equation models (SEM). We used the *piecewiseSEM* package (Lefcheck, 2016), as each 'piece' of the SEM can be constructed using linear mixed effects models, allowing us to account for the regional grouping as a random effect. In addition, this method identifies 'missing' links in the hypothesised model through tests of directed separation (Shipley, 2000). This enabled us to test the applicability of a path model built with the response-effect framework in mind, but to also identify any additional direct relationships between environmental drivers and pollinator communities. As inputs to the model, we reduced the six habitat cover variables to the first two axes of a PCA to avoid overfitting and collinearity. Similarly, the response traits of the 96 plant communities were first summarised by computing the community weighted mean (CWM) values of numerical traits, and proportions of categorical traits, and then reducing these variables to the first two axes of a PCA. This process was repeated for the effect traits and the bee and hoverfly traits. We limited the analysis to only the first two axes of each PCA in the interests of simplicity. We then fit these PCA axes, the habitat configuration metrics and the site selection criteria, to one of

two models depending on the results of the Mantel path analysis (Figure 3). Where Model 3 was the best fit, the SEM was structured according to the theory of the response-effect trait framework (Figure 3a). Where Model 5 was the best fit, the SEM had additional links between all environmental variables and the pollinator traits (Figure 3b).

The bee and hoverfly species data were further represented by the functional diversity metrics functional dispersion (FDis) and functional richness (FRic), computed using the *FD* package (Laliberté & Legendre, 2010), with the Cailliez correction for non-Euclidean distances due to the categorical trait variables included in the trait matrix. FDis is a metric that is mathematically independent of species richness, and accounts for the relative abundances of trait combinations (Laliberté & Legendre, 2010). We also used FRic as a measure of functional diversity that incorporates site differences in species richness. To test whether the response-effect framework could explain variation in these two metrics of pollinator functional diversity, we computed four separate SEMs replacing the pollinator trait gradients with (1) wild bee FDis, (2) wild bee FRic, (3) hoverfly FDis and (4) hoverfly FRic. Full details of the SEM fitting procedure are given in Appendix S1, but note that we omitted the insecticide loading variable from models as it was highly colinear with one of the habitat composition axes.
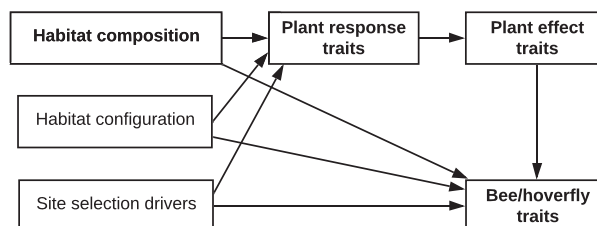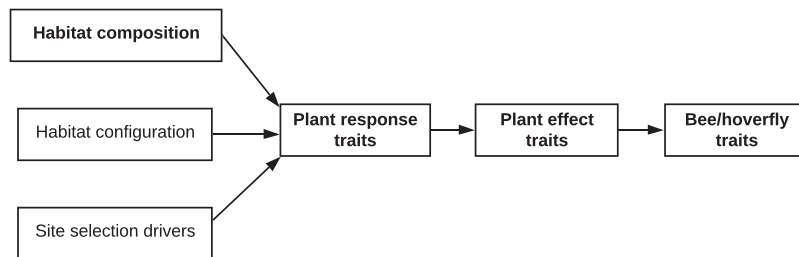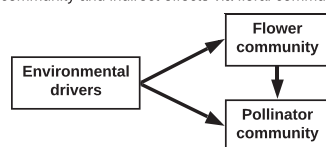
FIGURE 3 Hypothesised piecewise structural equation models on the right corresponding to (a) Model 3 and (b) Model 5 from the Mantel path analysis. SEMs are simplified for clarity: Variables in bold are site scores from the first two axes of separate PCAs at each level. Habitat configuration metrics consist of edge density and connectivity index variables, and site selection drivers comprise the variables habitat diversity, honeybee density and floral resource availability.

3 | RESULTS

Over the 2 years of study, we identified 294 species of insect, of which 108 species were hoverflies (~39% of total UK fauna; 14,710 individuals identified) and 116 species were wild bees (~43% of total UK fauna; 5142 individuals identified). The remaining 70 species were from wasp, butterfly or other fly families (Table S2). In addition, we surveyed 470 species of flowering plants containing nectar and/or pollen that was accessible to pollinating insects.

Unsurprisingly there was a strong regional impact on the plant and pollinator communities. According to the between-group analyses of the plant and pollinator species data tables, the regional grouping of the study sites accounted for a significant (Monte Carlo permutation test $p = 0.001$) proportion of the variance in abundances of species (All pollinators: 15.8%, wild bees: 15.1%, hoverflies: 15.0%, flowering plants: 20.5%). The environmental matrix was also subject to a strong region impact ($p = 0.001$, proportion of variance = 29.6%). These findings highlighted the need to account for spatial clustering in our analyses. Dissimilarities between regions (Figure S1) also suggest that regional conditions acted as a broad environmental filter on plant and pollinator communities.

> Objective 1. The flowering plant community as mediator between environmental factors and the pollinator community.

The best fitting model to the data depended on the taxonomic groups used in the pollinator community matrix (Figure 4). When all pollinators (including all wasps and butterflies) were used, or when only hoverflies were used, Model 3 was the best fitting model

suggesting that the environmental variables only impacted the pollinator community composition indirectly via effects on the flowering plant community. When the pollinator community was restricted to wild bees only, Model 5 was the best fitting model, suggesting both a direct effect of environmental variables on the composition of the pollinator community, and an indirect effect via the flowering plant community.

> Objective 2. The response and effect traits of plants as mediator between environmental factors and the pollinator functional traits.

The first two axes of the habitat composition PCA explained 60.3% of the variance in habitat cover distribution (axis 1: 36.7%, axis 2: 23.6%). Loadings indicated that axis 1 (hereafter '*Habitat 1*') represented a gradient from open SNH (negative loading) to improved grassland and abundance of linear features (positive loadings), while axis 2 ('*Habitat 2*') mainly represented a gradient from high to low arable land use (Table 2). The first plant response trait axis (hereafter '*Response 1*'; 46.8%) revealed a gradient with larger negative loadings for SLA, annual life span and seed mass, and positive loadings for perennialism and late flowering (Table 2). The second axis ('*Response 2*', 25.3%) was mainly a gradient of height and seed number, with negative loadings for tall species producing many seeds. The effect traits PCA revealed a complex set of gradients due to the presence of several categorical variables (Table 2). The first axis (hereafter '*Effects 1*', 34.2%) had strong negative loadings for flowers with partly hidden nectar sources (a Müller flower shape category), high nectar scores, high UV reflectance and a tendency to be pollinated by insects (rather than wind or selfing), while there were positive loadings for blue/violet flowers, and the Müller (1881)

FIGURE 4 Table of multivariate relationships between the environmental variables (ENV), the flower community (FLW) and the pollinator community (POL), when the latter consists of all pollinators captured, wild bees only or hoverflies only. Cell values correspond to spatially-corrected simple (above the diagonal) and partial Mantel statistics (below the diagonal), which are based on the Pearson's product–moment correlation. Bold values indicate significance at the $p < 0.001$ level after Bonferroni correction. Flower and pollinator abundances were Hellinger transformed. Significance was assessed with 4999 permutations. Models 3 and 5 are reproduced from Figure 2 to illustrate the confirmed models for each community.

All Pollinators - Model 3

	ENV	FLW	POL
ENV		**0.44**	0.33
FLW	0.34		**0.46**
POL	0.07	**0.42**	

Hoverflies - Model 3

	ENV	FLW	POL
ENV		**0.44**	0.26
FLW	**0.38**		0.37
POL	0.05	0.34	

Wild bees - Model 5

	ENV	FLW	POL
ENV		**0.44**	0.40
FLW	0.31		0.34
POL	0.24	0.29	

Model 3: Indirect environmental impacts on pollinator community via floral community

Environmental drivers → Flower community → Pollinator community

Model 5: Direct environmental impacts on pollinator community and indirect effects via floral community

Environmental drivers → Flower community; Environmental drivers → Pollinator community; Flower community → Pollinator community

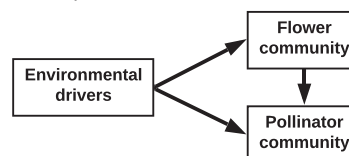**TABLE 2** Loadings from the first two PCA axes for habitat composition, plant response traits and plant effect traits.

Habitat composition	Axis 1	Axis 2	Plant response traits	Axis 1	Axis 2	Plant effect traits	Axis 1	Axis 2
Arable	0.08	−0.82	First flower month	0.37	−0.37	Blue/Violet flowers	0.30	0.14
Improved	0.56	0.30	Canopy height	−0.23	−0.50	Red/Pink flowers	−0.10	0.51
Woodland SNH	0.15	0.11	SLA	−0.43	0.28	White/Yellow flower	−0.10	−0.54
Conifer	−0.35	0.10	Seed number	0.02	−0.63	'Fly' flowers	0.18	−0.07
Open SNH	−0.45	0.42	Seed mass	−0.43	0.09	Hidden nectar flowers	−0.01	0.39
Linear features	0.58	0.19	Annual life span	−0.46	−0.23	Hymenoptera flowers	0.29	0.08
			Biennial life span	−0.13	0.14	Open nectar flowers	0.33	−0.10
			Perennial life span	0.46	0.22	Part hidden flowers	−0.38	−0.28
						Pollen flowers	0.29	0.10
						Flowering duration	0.16	−0.38
						Nectar score	−0.32	0.16
						UV reflectance	−0.28	0.05
						Insect pollinated	−0.39	0.07

flower shape categories: open nectar sources, pollen flower types and flowers favoured by Hymenoptera. The second axis ('*Effects 2*', 23.6%) appeared to represent a gradient from white/yellow flowers with partly hidden nectar (Müller, 1881) and a long flowering season, to red/pink flowers with hidden nectar sources (Müller, 1881) and a shorter season.

The wild bee PCA axes explained 43.4% and 19.7% of the variance, respectively, and the first axis ('*Bee 1*') represented a gradient of large, long-tongued and social species with a long active season and tendency towards multivoltinism, to small, solitary species and a tendency towards a later start to the active season (Table 3). The second axis ('*Bee 2*') appeared to mainly represent a gradient from parasitic to polylectic species. The hoverfly PCA axes explained

43.9% and 27.7% of the variance in trait distribution, with the first axis ('*Hoverfly 1*') representing a phenological gradient from species with a long active season, to those with a late season start and a tendency towards univoltinism (Table 3). The second axis ('*Hoverfly 2*') had high positive loadings for body size and adult diet (nectar only feeding).

As Model 5 was the best fitting Mantel path model for the wild bee community, we fit the corresponding SEM to wild bee traits and it was initially a poor fit to the data (Fisher's $C_{40} = 81.3$, $p = 0.002$; a low p-value indicates poor model fit). To achieve 'good fit', the model required the addition of three paths: a correlated errors links between the two Effect axes, and links from edge density and *Habitat 2* to *Effect 1*. With these paths added, the model was an adequate fit to

Wild bee traits	Axis 1	Axis 2	Hoverfly traits	Axis 1	Axis 2
Body size	−0.36	−0.06	Body size	−0.27	0.58
Cleotoparasitic	0.20	−0.23	Active season start	0.56	−0.27
Social	−0.37	0.07	Duration of season	−0.62	−0.09
Social parasite	0.02	−0.52	Adult diet	0.19	0.71
Solitary	0.35	0.11	Voltinism	0.43	0.27
No diet preference (parasitic)	0.13	−0.55			
Oligolectic	0.08	−0.06			
Polylectic	−0.16	0.52			
Active season start	0.26	0.17			
Duration of season	−0.35	−0.08			
Univoltine	0.03	−0.06			
Bivoltine	−0.31	−0.09			
Multivoltine	−0.34	−0.13			
Tongue length guild	−0.33	−0.11			

TABLE 3 Loadings from the first two PCA axes for wild bee traits and hoverfly traits.

the data ($C_{38} = 51.5$, $p = 0.07$; Figure 5a). These additional paths were also required for the wild bee FDis and FRic models (FDis: $C_{30} = 36.3$, $p = 0.198$; FRic: $C_{30} = 36.3$, $p = 0.113$; Figure 5b,c).

Model 3 was the best fitting Mantel path model for the hoverfly community, and the corresponding SEM also required the addition of the three paths described above. However, this only resulted in an adequate fit for the trait model ($C_{64} = 82.3$, $p = 0.062$; Figure 6a). The FDis model also required a link between connectivity and FDis ($C_{42} = 54.8$, $p = 0.089$; Figure 6b), and FRic required a link from connectivity to *Effects 2* ($C_{42} = 53.2$, $p = 0.115$; Figure 6c).

In general, both sets of models showed some support for the response-effect framework, with the strong influence of the habitat composition gradients on *Response 1* suggesting that plant species with traits such as high SLA and seed mass, early flowering and annual life span tended to be associated with the arable and improved grassland cover types, as well as linear features such as fence lines, stonewalls and water ditches. However, a positive link from *Habitat 2* to *Response 2* showed some complexity to this pattern, with tall and late flowering species also favouring arable land. *Effect 1* had the strongest link from *Response 1*, suggesting that communities dominated by fast-growing species tended to be those dominated by species with either open nectar and pollen flower types, or with blue- and violet-coloured flowers. However, the impacts of *Habitat 2* (negative) and edge density (positive) on *Effect 1* again highlighted complexity not captured solely by the response-effect structure.

The strong link from *Effect 1* to *Bee 1* further suggests that certain flower types tended to attract small and solitary species that are active early in the season. The strongest direct impact of the environmental variables was a positive link between honeybee density and *Bee 1*, functional dispersion and functional richness. Similar to the bee SEM, *Effect 1* had a strong positive link to the hoverfly size gradient (*Hoverfly*

2), although in the opposite direction to bees. Larger hoverflies and those preferring to feed on nectar only were associated with this effect trait axis. In contrast to the bee model, *Effect 1* had a positive, though weaker, effect on hoverfly FDis, but not hoverfly FRic.

4 | DISCUSSION

In this study, we found that the links between land-use patterns and species communities were generally stronger for flowering plants than for pollinators and that links between land use and pollinator communities were largely (for bees) or wholly (for hoverflies) mediated by floral resources. Furthermore, we found strong support for the ability of the response-effect trait framework to explain the mechanisms underlying this mediation, although our large-scale and exploratory application of the framework revealed some additional complexities. We recommend that future studies of land use and pollinator biodiversity consider such indirect effects in project design and analysis more explicitly.

4.1 | Regional patterns—A broad environmental filter

Our pollinator and plant data indicated that the regions we studied in the UK had relatively distinct pollinator and flowering plant communities. Those in the southern-England regions were highly dissimilar to those in Scotland, although there was considerable overlap in assemblages between northern England and southern Scotland. These patterns are unsurprising given the regional differences in topography, climate and land use in Britain, from the low-lying, warmer and more arable southern regions to the
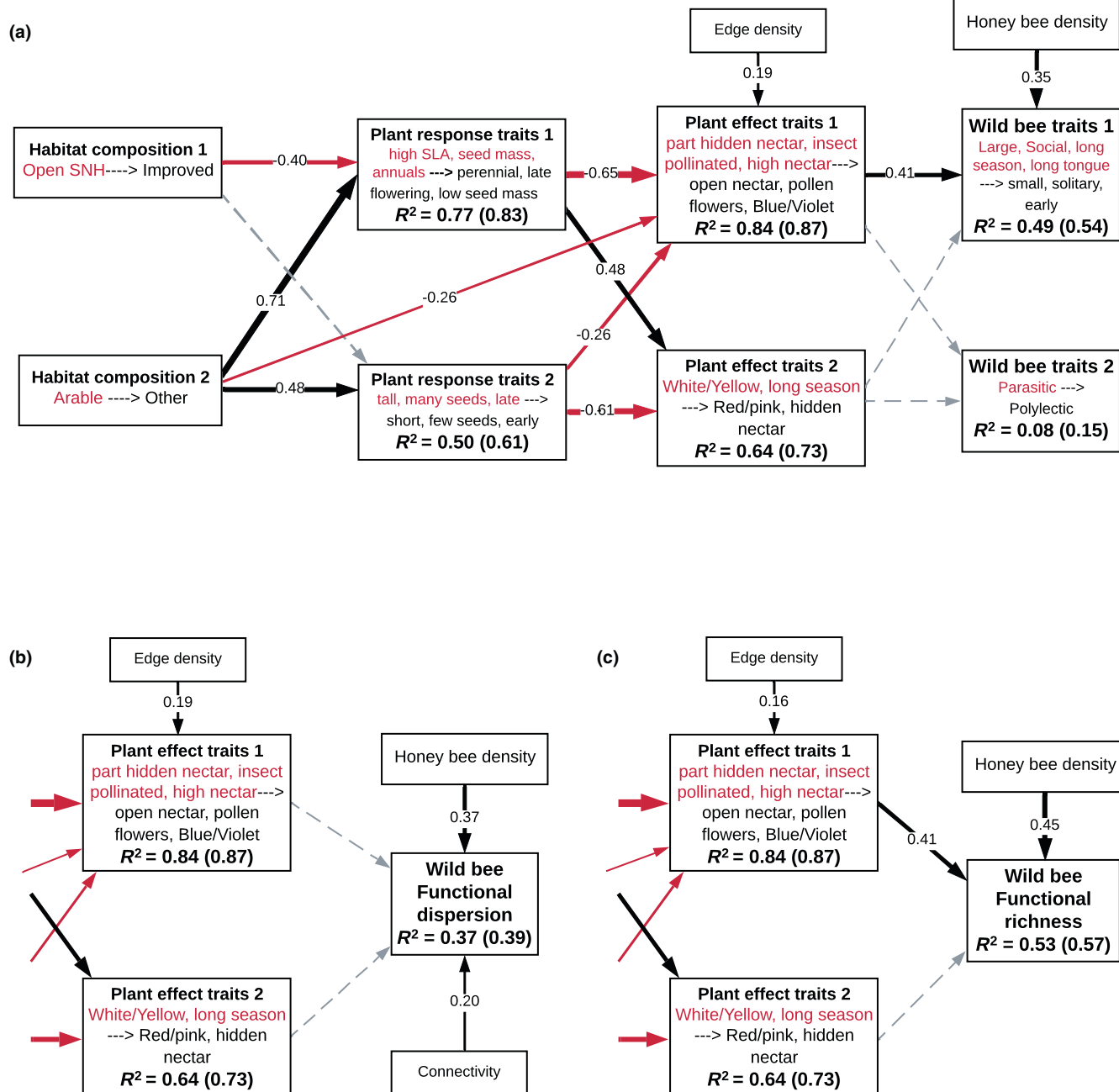
FIGURE 5 Path models exploring the indirect link between wild bee (a) functional traits, (b) functional dispersion, and (c) functional richness and environmental variables via plant response and effect traits. The left-hand side of the models are the same for all three responses and has been omitted in (b) and (c) to save space. Note also that most non-significant relationships are omitted for clarity. Red text indicates negative loadings for habitat/trait PCA axes; black text indicates positive loadings. Red arrows = negative effects; black arrows = positive effects; and grey, dashed arrows = non-significant relationships ($p > 0.05$). The thickness of arrows corresponds to the size of the standardised coefficients (displayed numerically). The first r-squared value is marginal (only fixed effects) and the second in brackets is conditional (both fixed and random effects). See Appendix S2 for full results.

mountainous, wetter and more abundant heath- and moorlands of northern Scotland (Mayes & Wheeler, 2013). We have not explored this further, but regional dissimilarities have been found elsewhere as a broad-scale environmental filter to community assembly (de Bello et al., 2013), and these strong patterns along topographic and climatic gradients support the existence of a large-scale regional environmental filter in Britain.

4.2 | Within-region environmental filters

When the regional effect was accounted for, the Mantel path models linking the *dissimilarity* of pollinators, flowering plants and environmental factors strongly suggested that land use provided within-region environmental filtering and that plant communities likely mediated this process on pollinators. These results
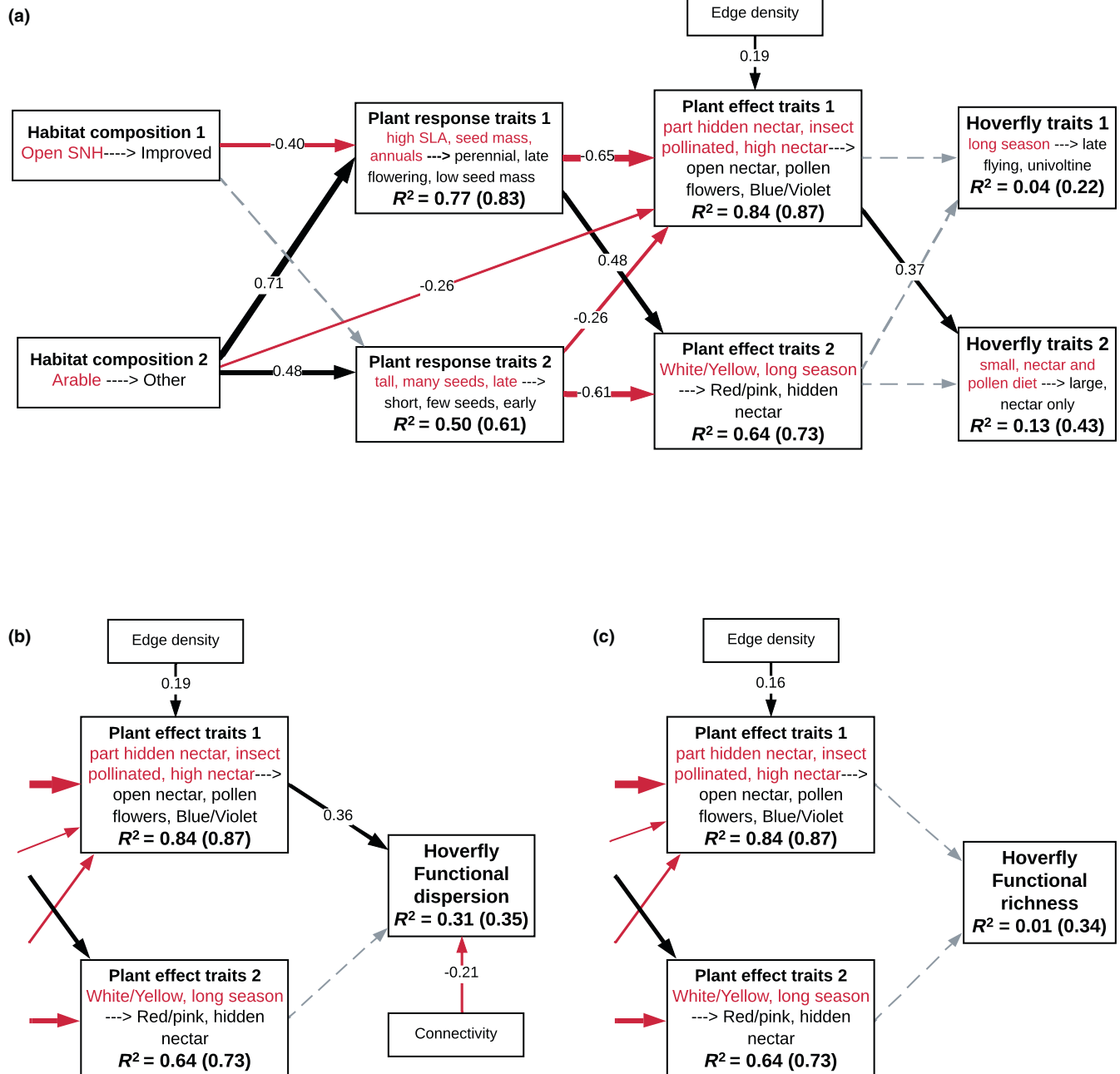
(a)

(b)

(c)

FIGURE 6 Path models exploring the indirect link between hoverfly (a) functional traits, (b) functional dispersion, and (c) functional richness and habitat composition via plant response and effect traits. The left-hand side of the models is the same for all three responses and has been omitted in (b) and (c) to save space. Red text indicates main negative loadings for habitat/trait PCA axes; black text indicates main positive loadings. Red arrows = negative effects; black arrows = positive effects; and grey, dashed arrows = non-significant relationships ($p > 0.05$). Note that most non-significant relationships are omitted for clarity. The thickness of arrows corresponds to the size of the standardised coefficients (displayed numerically). The first r-squared value is marginal (only fixed effects) and the second in brackets is conditional (both fixed and random effects). See Appendix S2 for full results.

are similar to those of Frenette-Dussault et al. (2013), who found that vegetation structure mediated environmental effects on ant communities, suggesting a coarse environmental filter and a finer, microclimatic filter of vegetation structure. A similarly hierarchical filtering process may have occurred in our landscapes, perhaps due to plants' relatively limited dispersal, strong dependence on local conditions and slow reactions to habitat change

(Winsa et al., 2017), whereas more mobile insect pollinators are able to quickly track the availability of food resources (Kremen et al., 2018).

We note, however, that the full mediation role of plants was only found for the entire pollinator community and for hoverflies separately. When we restricted our analysis to wild bees, the best model comprised both direct and indirect links between the

environmental factors and the wild bee community, suggesting a complex filtering process. This is perhaps unsurprising given the importance of suitable nesting substrates to many bee species (Roulston & Goodell, 2011), and the impact of land use and land management on these resources (Bennett et al., 2014; Kells & Goulson, 2003). However, we have not explicitly assessed nesting resources at our sites, and support calls to improve our understanding of these requirements (Image et al., 2022). Future iterations of this modelling approach could then incorporate probable indirect links between land use and pollinators via multiple resources to greatly improve our overall understanding of landscape-scale pollinator communities. Furthermore, the different findings for our species groups suggest that this analysis is sensitive to target taxa and that investigation of smaller targeted groups may be needed to corroborate these patterns. Nevertheless, the partial mediating effect of the plant community remains plausible because the quality of floral resources is considered an important factor in pollinator community structure (Potts et al., 2003), with many pollinators demonstrating flowering plant preferences based on flower structure, size and colour (Carvell et al., 2006).

4.3 | Response-effect framework—land-use effects on plant response traits

Our piecewise SEM analysis suggested further insights into the mechanisms behind the above results via an exploratory adaptation of the response-effect trait framework. The left-hand side of the SEM diagrams highlighted the role of land use in structuring plant communities, with sites dominated by intensive land use types such as arable and improved grassland strongly linked to plant communities exhibiting fast resource-use traits, as shown elsewhere (Smart et al., 2006; Storkey et al., 2013). Trait values such as high specific leaf area and annual life span are associated with a resource acquisition strategy typical of highly fertile habitats (Cebrián-Piqueras et al., 2021; Lavorel & Grigulis, 2012), early successional plant communities (Gaba et al., 2017; Lavorel & Grigulis, 2012), disturbed environments (i.e. those subject to regular tilling, mowing and grazing; Storkey et al., 2013), and agricultural field margins (Blaix & Moonen, 2020). By contrast, less intensive SNH were associated with 'resource conservation' traits such as perennialism, slow resource use and later flowering (Lavorel & Grigulis, 2012; Storkey et al., 2013). These are typical dominant traits of low fertility and later successional habitats, such as heathlands and woodlands (Robleño et al., 2018; Solé-Senan et al., 2018).

In addition, the plant response trait axis '*Response 2*' appeared to represent the 'plant size' gradient (Lavorel & Grigulis, 2012), which has been posited as an independent axis to gradients of leaf economics (typified by high to low SLA), and is often related to seed number (Cebrián-Piqueras et al., 2021; Lavorel & Grigulis, 2012), as we found here. We found that taller flowering plants were associated with arable land use, which is likely to reflect the predominance of tree and weed species in field margins (Rotchés-Ribalta et al., 2018). However, the lack of strong association with improved grassland and linear features is contrary to studies of grassland disturbance reporting a predominance of shorter plants (Lienin & Kleyer, 2012; Robleño et al., 2018; Storkey et al., 2013). Nevertheless, as Lavorel and Grigulis (2012) pointed out for grasslands, short height is commensurate with the resource conservation strategy found in late successional and low fertility habitats such as our SNH habitats.

4.4 | Response-effect relationships and links to land use

The response-effect framework suggests that the correlation between the two plant trait types will determine the impact of environmental drivers on functioning (Lavorel et al., 2013; Lavorel & Garnier, 2002), and while we did not specifically test certain trait pairings, our exploratory approach found strong links between response- and floral (effect) traits. Although little is understood about how floral traits relate to other plant functional traits (E-Vojtkó et al., 2020; Goulnik et al., 2021), similar associations have been found elsewhere (Blaix & Moonen, 2020; Robleño et al., 2018; Solé-Senan et al., 2017). In general, grasslands also support many annual weedy species that are able to self-pollinate, are likely to invest less in pollinator attraction, frequently have white flowers and can flower for long periods (Gaba et al., 2017).

Given the links between habitat composition and response traits, the associations here also support general patterns of floral trait associations with land-use intensity. A review of grassland floral traits by Goulnik et al. (2021) reported that intensive management of grasslands can lead to reductions in nectar tube depth, amount of nectar reward, pollen quality and attractiveness of flowers. Conversely, the authors also suggested a change in colour dominance with intensity from blue to white. Our results suggested both blue/violet and white/yellow flowers were linked to more intensive land uses, and other studies have reported a range of associations between flower colour and management intensity dependent on season (Rotchés-Ribalta et al., 2018) and region (Robleño et al., 2018). However, flower colour is only one factor in pollinator attractiveness; UV reflectance is also a factor in visual attractiveness (Ricou et al., 2014) and may be a more precise measure of pollinator attraction. In our study, this had a negative loading on *Effect 2* and was subsequently associated with plant communities linked to more intensive land uses.

4.5 | Effect and pollinator trait links

We found contrasting effects in the associations between plant effect traits and the traits of bees and hoverflies. The strongest link was between larger species of social bee with long active seasons, such as bumblebees, and high reward plant communities that

accommodated high proportions of partially hidden nectar flowers (several members of Brassicaceae, Rosaceae, Ranunculaceae and Caryophyllaceae), favoured by medium to long-tongued species (Müller, 1881). By contrast, smaller hoverflies with nectar and pollen diets were weakly associated with these traits. The same link suggested that smaller, solitary bee species (and larger hoverflies) were associated with plant communities dominated by open nectar sources (e.g. Apiaceae, Rubiaceae, Hypericaceae), 'pollen' plants and blue-violet flowers. Larger bumblebees have been associated with high reward flowers elsewhere (Solé-Senan et al., 2018; Vaudo et al., 2015) and may outcompete hoverflies for resources (Hogg et al., 2011). Similarly, smaller solitary bees have been associated with lower nectar quantities and pollen lower in amino acids (Vaudo et al., 2015), and hoverfly body size relates to flower size preferences in some sub-families (Klecka et al., 2018). However, not enough is known about hoverfly diet preferences, and the low explanatory power of our models may reflect their generalist, opportunistic flower choices (Branquart & Hemptinne, 2000), and indicate that their distribution depends more on larval requirements than flower traits. If this is the case, it is surprising that our SEMs did not find stronger direct links between hoverfly traits and the environmental variables, and further research into these links is recommended.

The wild bee SEM also found a strong impact of honeybee density on *Bee 1* and functional diversity, and this link may explain why Model 5 was the better fitting Mantel path model. A high density of managed honeybees in our landscapes appeared to enhance functional diversity, and favoured small, solitary species of wild bee. This may suggest that honeybees compete for resources with larger, social bees, supporting recent review findings (Iwasaki & Hogendoorn, 2022), and this is considered more likely in areas of uniform land cover and scarce floral resources (Herbertsson et al., 2016). Such competition may enhance functional diversity by encouraging a greater range of solitary bee species with varied traits, particularly when bumblebees are lacking. However, we also cannot rule out the possibility that this result is an artefact of our honeybee density data, which are more certain in southern regions where more solitary bee species were caught (Gillespie et al., 2022).

The general pattern shown by the SEM analysis suggests that via dominant plant traits, intensive land uses favoured smaller and solitary bee species with early active periods (and large hoverflies), and that less disturbed open SNH habitats supported larger and social bee species (and small hoverflies). While previous work attempting to test such links directly have reported conflicting results concerning the sensitivity of traits such as body size to land use (Bartomeus et al., 2018; De Palma et al., 2015; Rader et al., 2014), our indirect approach showed congruence with the patterns detected in the review of grassland floral trait patterns by Goulnik et al. (2021). They described floral traits as becoming generalised in frequently disturbed and intensively managed habitats, increasing in ruderal species associated with fewer insect pollinated plants, smaller nectar tube depth and lower nectar rewards and pollen quality. This may lead to fewer large, long-tongued and social bees that require more resources to develop colonies (Cane & Tepedino, 2017), and more

oligolectic solitary bees that favour lower quality pollen (Weiner et al., 2010). Many nectar and pollen feeding hoverflies on the other hand, may be favoured in these situations due to shorter tongue length, a stronger ability to store protein and fewer constraints on nesting sites (van Rijn et al., 2013). Although the review by Goulnik et al. (2021) only covers grasslands, and no other habitat types have been treated to such a holistic overview, the patterns in plant and pollinator coexistence provide important insights into the filtering role that flowering plants may play in pollinator community composition. Previously conflicting results concerning the impact of land use composition may occur because the direct signal on pollinator communities is obscured by these mediating effects on favoured food resources in the plant community (Forrest et al., 2015).

4.6 | Effects on functional dispersion and richness

The wild bee functional richness SEM suggested greater trait richness was associated with flowering plants linked to more intensive land uses. This appears contrary to previous work, where greater functional richness and dispersion were associated with agroforestry compared to arable land uses (Staton et al., 2022), and where functional dispersion was associated with low intensity land uses (Forrest et al., 2015; Roquer-Beni et al., 2021). Whether the increased functional richness found here translates to increased function is beyond the scope of this study and remains to be tested. However, our results do highlight previously unexplored complexity, suggesting that non-target flowering plants occurring among intensively managed landscapes are important to pollinator functional diversity. For example, in landscapes with a high proportion of arable land, the flowering plant community may consist of both fast-growing, early flowering species, and tall, late flowering species, probably growing at field edges. These plants were associated with effect traits favoured by small, solitary species which apparently drive functional richness here. With the addition of the effect of edge density and habitat composition on *Effect 1*, our models suggest that managing a range of habitats and linear features in disturbed landscapes with a diverse flowering plant composition are likely to be most important to functional richness.

The weaker effects we found on hoverfly trait distribution and functional diversity may reflect the limited traits we used for hoverflies, or may be a result of differing behaviour of this group. Hoverflies are not central-place foragers like bees, are generally less specialised in their floral dependencies, do not collect resources for larvae and are not restricted by the need for proximal forage resources (Winsa et al., 2017). Therefore, the filters impacting trait dispersion are likely linked to the diversity of larval food resources, which have not been included in our analysis. Nevertheless, the positive link of *Effect 1* on *Hoverfly 2* and hoverfly functional dispersion suggests body size is a key driver of functional diversity.

As with the Mantel path analysis, our SEMs found that the responses of pollinator community to both plant resources and

environmental factors depended on the focal taxa. Contrasting responses of bees and hoverflies have been reported elsewhere (Roquer-Beni et al., 2021; Staton et al., 2022), and some authors have suggested that assessments of landscape effects on hoverflies may be required at coarser spatial scales (Staton et al., 2022). In any case, these patterns highlight the importance of considering the differing resource needs of smaller taxonomic groups, and we recommend that further research aims to identify which flower-pollinator associations are important and most responsive in different regional contexts.

4.7 | Weaknesses

We note that these findings should be interpreted with a degree of caution because the pollinators were not recorded visiting the flowering plants but were caught in the same locations. We cannot therefore prove that it is the flowering plant community that attracted the pollinators to our landscapes per se. In addition, it should also be noted that pan-traps used to collect insects do not always provide an accurate reflection of pollinator communities (e.g. Hutchinson et al., 2022). Similarly, we were limited by the published trait information available for many species, which made the results of the Mantel tests difficult to compare to those of the SEM, for example. We recommend that future work aimed at corroborating our findings is based on individually measured values of carefully selected traits. Finally, our findings may be limited by our use of PCA axes to represent gradients. The first two axes did not reach a commonly used threshold of 80% variance explained and may not have fully captured the most important gradients, or fully accounted for the spatial clustering of our sites. However, we would iterate that the SEM analysis was an exploratory approach rather than confirmatory, and that our findings provide important insights for designing future research approaches.

5 | CONCLUSIONS

We have demonstrated that pollinator community assemblage is determined by a complex suite of factors including broad regional filters, habitat composition and configuration, and their impacts on the foraging resources of the local pool of pollinators. It is also important to note that our findings depended on the focal taxonomic group, highlighting different resource needs and responses to landscape-scale pressures. In general, it seems that functionally diverse pollinator communities can be found even in intensively managed landscapes, particularly through the maintenance or enhancement of diverse, locally important plant communities, rather than large-scale alteration of the habitat matrix. We therefore recommend more mechanistic research on the role of floral resources and their diverse and complementary roles in pollinator nutrition. We further suggest that future research should begin to explicitly model the indirect effects of land use via fundamental resources. Much previous research uses a direct, linear effects modelling approach to assess both broad landscape effects and more local resource provision effects on pollinator abundance, diversity and visitation (Gillespie et al., 2022; Hopfenmüller et al., 2014; Jauker et al., 2013; Martin et al., 2019). These studies have provided important insights into the links between pollinator populations and floral resources (e.g. Holland et al., 2015), and habitat composition and configuration (e.g. Ekroos et al., 2015). However, habitat composition and configuration effects are likely to act indirectly through changes in resource availability, and resources such as foraging plants and nesting locations are sometimes more direct factors (Roulston & Goodell, 2011). Research approaches such as the response-effect trait framework (Lavorel et al., 2013), can be instrumental in understanding the tight link between trophic levels and their environments, and we recommend that future studies are designed and analysed with direct and indirect effects in mind.

AUTHOR CONTRIBUTIONS
W.E. Kunin, J. Biesmeijer, N. Boatman, G.E. Budge, J. Memmott, R.D Morton, S.G. Potts, S.M. Smart and S.P.M. Roberts conceived and designed the field study, assisted in acquiring funding, and provided supervision and project administration. M. Baude, A. Crowe, N. Davies, R. Evans, E. Moss, C. Rowland, D. Senapathi and C. Wood contributed to methodological design, site selection, data collection and data analysis. Further data collection was carried out by field assistants, supervised by M.A.K. Gillespie, who also conducted the data analysis and led the writing effort. All authors provided critical input in writing and all authors approved of the final version to be published.

CONFLICT OF INTEREST STATEMENT

We declare we have no competing interests.

DATA AVAILABILITY STATEMENT

The species and environmental data that supports the findings of this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.stqjq2cbx (Gillespie et al., 2024). The bee traits data are available on request from Stuart Roberts. The hoverfly traits data are available on request from https://pollinators.ie/record-pollinators/hoverflies/syrph-the-net/. The plant traits data are publicly available via the TRY database: https://www.try-db.org/TryWeb/Home.php.

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REFERENCES

Bartomeus, I., Cariveau, D. P., Harrison, T., & Winfree, R. (2018). On the inconsistency of pollinator species traits for predicting either response to land-use change or functional contribution. *Oikos*, *127*(2), 306–315. https://doi.org/10.1111/oik.04507

Bennett, J. A., Gensler, G. C., & Cahill, J. F. (2014). Small-scale bee patch use is affected equally by flower availability and local habitat configuration. *Basic and Applied Ecology*, *15*(3), 260–268. https://doi.org/10.1016/j.baae.2014.03.004

Blaix, C., & Moonen, A.-C. (2020). Structural field margin characteristics affect the functional traits of herbaceous vegetation. *PLoS One*, *15*(9), e0238916. https://doi.org/10.1371/journal.pone.0238916

Branquart, E., & Hemptinne, J. L. (2000). Selectivity in the exploitation of floral resources by hoverflies (Diptera: Syrphinae). *Ecography*, *23*(6), 732–742. https://doi.org/10.1034/j.1600-0587.2000.230610.x

Bunce, R. G. H., Barr, C. J., Clarke, R. T., Howard, D. C., & Lane, A. M. J. (1996). ITE Merlewood land classification of Great Britain. *Journal of Biogeography*, *23*(5), 625–634. https://doi.org/10.1111/j.1365-2699.1996.tb00023.x

Cane, J. H., & Tepedino, V. J. (2017). Gauging the effect of honey bee pollen collection on native bee communities. *Conservation Letters*, *10*(2), 205–210. https://doi.org/10.1111/conl.12263

Carvell, C., Westrich, P., Meek, W. R., Pywell, R. F., & Nowakowski, M. (2006). Assessing the value of annual and perennial forage mixtures for bumblebees by direct observation and pollen analysis. *Apidologie*, *37*(3), 326–340. https://doi.org/10.1051/apido:2006002

Cebrián-Piqueras, M. A., Trinogga, J., Trenkamp, A., Minden, V., Maier, M., & Mantilla-Contreras, J. (2021). Digging into the roots: Understanding direct and indirect drivers of ecosystem service trade-offs in coastal grasslands via plant functional traits. *Environmental Monitoring and Assessment*, *193*(1), 271. https://doi.org/10.1007/s10661-020-08817-x

Coutinho, J. G. E., Hipólito, J., Santos, R. L. S., Moreira, E. F., Boscolo, D., & Viana, B. F. (2021). Landscape structure is a major driver of bee functional diversity in crops. *Frontiers in Ecology and Evolution*, *9*(53). https://doi.org/10.3389/fevo.2021.624835

Crabot, J., Clappe, S., Dray, S., & Datry, T. (2019). Testing the Mantel statistic with a spatially-constrained permutation procedure. *Methods in Ecology and Evolution*, *10*(4), 532–540. https://doi.org/10.1111/2041-210X.13141

de Bello, F., Lavorel, S., Lavergne, S., Albert, C. H., Boulangeat, I., Mazel, F., & Thuiller, W. (2013). Hierarchical effects of environmental filters on the functional structure of plant communities: A case study in the French Alps. *Ecography*, *36*(3), 393–402. https://doi.org/10.1111/j.1600-0587.2012.07438.x

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*(6), 1567–1577. https://doi.org/10.1111/1365-2664.12524

Delnevo, N., van Etten, E. J., Byrne, M., Petraglia, A., Carbognani, M., & Stock, W. D. (2020). Habitat fragmentation restricts insect pollinators and pollen quality in a threatened Proteaceae species. *Biological Conservation*, *252*, 108824. https://doi.org/10.1016/j.biocon.2020.108824

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., ... Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, *529*(7585), 167–171. https://doi.org/10.1038/nature16489

Duflot, R., Ernoult, A., Aviron, S., Fahrig, L., & Burel, F. (2017). Relative effects of landscape composition and configuration on multi-habitat gamma diversity in agricultural landscapes. *Agriculture, Ecosystems & Environment*, *241*, 62–69. https://doi.org/10.1016/j.agee.2017.02.035

Ekroos, J., Jakobsson, A., Wideen, J., Herbertsson, L., Rundlöf, M., & Smith, H. G. (2015). Effects of landscape composition and configuration on pollination in a native herb: A field experiment. *Oecologia*, *179*(2), 509–518. https://doi.org/10.1007/s00442-015-3370-y

Else, G., & Edwards, M. (2018). *Handbook of the bees of the British Isles*. Ray Society.

E-Vojtkó, A., de Bello, F., Durka, W., Kühn, I., & Götzenberger, L. (2020). The neglected importance of floral traits in trait-based plant community assembly. *Journal of Vegetation Science*, *31*(4), 529–539. https://doi.org/10.1111/jvs.12877

Fitter, A. H., & Peat, H. J. (1994). The ecological Flora database. *Journal of Ecology*, *82*(2), 415–425. https://doi.org/10.2307/2261309

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*(3), 706–715. https://doi.org/10.1111/1365-2664.12433

Frenette-Dussault, C., Shipley, B., & Hingrat, Y. (2013). Linking plant and insect traits to understand multitrophic community structure in arid steppes. *Functional Ecology*, *27*(3), 786–792. https://doi.org/10.1111/1365-2435.12075

Gaba, S., Perronne, R., Fried, G., Gardarin, A., Bretagnolle, F., Biju-Duval, L., Colbach, N., Cordeau, S., Fernández-Aparicio, M., Gauvrit, C.,

Gibot-Leclerc, S., Guillemin, J.-P., Moreau, D., Munier-Jolain, N., Strbik, F., & Reboud, X. (2017). Response and effect traits of arable weeds in agro-ecosystems: A review of current knowledge. *Weed Research*, 57(3), 123–147. https://doi.org/10.1111/wre.12245

Gabriel, D., Sait, S. M., Kunin, W. E., & Benton, T. G. (2013). Food production vs. biodiversity: Comparing organic and conventional agriculture. *Journal of Applied Ecology*, 50(2), 355–364. https://doi.org/10.1111/1365-2664.12035

Garibaldi, L. A., Steffan-Dewenter, I., Kremen, C., Morales, J. M., Bommarco, R., Cunningham, S. A., Carvalheiro, L. G., Chacoff, N. P., Dudenhöffer, J. H., Greenleaf, S. S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M. M., Morandin, L. A., Potts, S. G., Ricketts, T. H., Szentgyörgyi, H., … Klein, A. M. (2011). Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecology Letters*, 14(10), 1062–1072. https://doi.org/10.1111/j.1461-0248.2011.01669.x

Gillespie, M. A. K., Baude, M., Biesmeijer, J., Boatman, N., Budge, G. E., Crowe, A., Davies, N., Evans, R., Memmott, J., Morton, R. D., Moss, E., Murphy, M., Pietravalle, S., Potts, S. G., Roberts, S. P. M., Rowland, C., Senapathi, D., Smart, S. M., Wood, C., & Kunin, W. E. (2022). Landscape-scale drivers of pollinator communities may depend on land-use configuration. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 377(1853), 20210172. https://doi.org/10.1098/rstb.2021.0172

Gillespie, M. A. K., Baude, M., Biesmeijer, J., Boatman, N., Budge, G. E., Crowe, A., Davies, N., Evans, R., Memmott, J., Morton, R. D., Moss, E., Potts, S. G., Roberts, S. P. M., Rowland, C., Senapathi, D., Smart, S. M., Wood, C., & Kunin, W. E. (2024). Data from: Flowering plant communities mediate the effects of habitat composition and configuration on wild pollinator communities submitted. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.stqjq2cbx

Gillespie, M. A. K., Baude, M., Biesmeijer, J., Boatman, N., Budge, G. E., Crowe, A., Memmott, J., Morton, R. D., Pietravalle, S., Potts, S. G., Senapathi, D., Smart, S. M., & Kunin, W. E. (2017). A method for the objective selection of landscape-scale study regions and sites at the national level. *Methods in Ecology and Evolution*, 8, 1468–1476. https://doi.org/10.1111/2041-210X.12779

Goulnik, J., Plantureux, S., Dajoz, I., & Michelot-Antalik, A. (2021). Using matching traits to study the impacts of land-use intensification on plant–pollinator interactions in European Grasslands: A review. *Insects*, 12(8), Article 8. https://doi.org/10.3390/insects12080680

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(6229), 1255957. https://doi.org/10.1126/science.1255957

Herbertsson, L., Lindstrom, S. A. M., Rundlof, M., Bornmarco, R., & Smith, H. G. (2016). Competition between managed honeybees and wild bumblebees depends on landscape context. *Basic and Applied Ecology*, 17(7), 609–616. https://doi.org/10.1016/j.baae.2016.05.001

Hogg, B. N., Bugg, R. L., & Daane, K. M. (2011). Attractiveness of common insectary and harvestable floral resources to beneficial insects. *Biological Control*, 56(1), 76–84. https://doi.org/10.1016/j.biocontrol.2010.09.007

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(3), 354–361. https://doi.org/10.1111/j.2007.0030-1299.16303.x

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E. K., Hungate, B. A., Matulich, K. L., Gonzalez, A., Duffy, J. E., Gamfeldt, L., & O'Connor, M. I. (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, 486(7401), Article 7401. https://doi.org/10.1038/nature11118

Hopfenmüller, S., Steffan-Dewenter, I., & Holzschuh, A. (2014). Trait-specific responses of wild bee communities to landscape composition, configuration and local factors. *PLoS One*, 9(8), e104439. https://doi.org/10.1371/journal.pone.0104439

Humphrey, J. W., Ferris, R., Jukes, M. R., & Peace, A. J. (2002). The potential contribution of conifer plantations to the UK biodiversity action plan. *Botanical Journal of Scotland*, 54(1), 49–62. https://doi.org/10.1080/03746600208685028

Hutchinson, L. A., Oliver, T. H., Breeze, T. D., O'Connor, R. S., Potts, S. G., Roberts, S. P. M., & Garratt, M. P. D. (2022). Inventorying and monitoring crop pollinating bees: Evaluating the effectiveness of common sampling methods. *Insect Conservation and Diversity*, 15(3), 299–311. https://doi.org/10.1111/icad.12557

Image, M., Gardner, E., Clough, Y., Smith, H. G., Baldock, K. C. R., Campbell, A., Garratt, M., Gillespie, M. A. K., Kunin, W. E., McKerchar, M., Memmott, J., Potts, S. G., Senapathi, D., Stone, G. N., Wackers, F., Westbury, D. B., Wilby, A., Oliver, T. H., & Breeze, T. D. (2022). Does agri-environment scheme participation in England increase pollinator populations and crop pollination services? *Agriculture, Ecosystems & Environment*, 325, 107755. https://doi.org/10.1016/j.agee.2021.107755

Iwasaki, J. M., & Hogendoorn, K. (2022). Mounting evidence that managed and introduced bees have negative impacts on wild bees: An updated review. *Current Research in Insect Science*, 2, 100043. https://doi.org/10.1016/j.cris.2022.100043

Jauker, B., Krauss, J., Jauker, F., & Steffan-Dewenter, I. (2013). Linking life history traits to pollinator loss in fragmented calcareous grasslands. *Landscape Ecology*, 28(1), 107–120. https://doi.org/10.1007/s10980-012-9820-6

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Carolina Alcázar, C., Aleixo, I., Ali, H., … Wirth, C. (2020). TRY plant trait database—Enhanced coverage and open access. *Global Change Biology*, 26(1), 119–188. https://doi.org/10.1111/gcb.14904

Kells, A. R., & Goulson, D. (2003). Preferred nesting sites of bumble-bee queens (Hymenoptera: Apidae) in agroecosystems in the UK. *Biological Conservation*, 109(2), 165–174. https://doi.org/10.1016/s0006-3207(02)00131-3

Kennedy, C. M., Lonsdorf, E., Neel, M. C., Williams, N. M., Ricketts, T. H., Winfree, R., Bommarco, R., Brittain, C., Burley, A. L., Cariveau, D., Carvalheiro, L. G., Chacoff, N. P., Cunningham, S. A., Danforth, B. N., Dudenhöffer, J.-H., Elle, E., Gaines, H. R., Garibaldi, L. A., Gratton, C., … Kremen, C. (2013). A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters*, 16(5), 584–599. https://doi.org/10.1111/ele.12082

Klecka, J., Hadrava, J., Biella, P., & Akter, A. (2018). Flower visitation by hoverflies (Diptera: Syrphidae) in a temperate plant-pollinator network. *PeerJ*, 6, e6025. https://doi.org/10.7717/peerj.6025

Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J. M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G. M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., … Peco, B. (2008). The LEDA Traitbase: A database of life-history traits of the Northwest European flora. *Journal of Ecology*, 96(6), 1266–1274. https://doi.org/10.1111/j.1365-2745.2008.01430.x

Klotz, A. H., Kühn, I., & Durka, W. (2002). *BIOLFLOR—Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland* (Vol. 38). Bundesamt für Naturschutz.

Kremen, C. (2018). The value of pollinator species diversity. *Science*, 359(6377), 741–742. https://doi.org/10.1126/science.aar7614

Kremen, C., M'Gonigle, L. K., & Ponisio, L. C. (2018). Pollinator community assembly tracks changes in floral resources as restored

hedgerows mature in agricultural landscapes. *Frontiers in Ecology and Evolution*, 6, 170. https://doi.org/10.3389/fevo.2018.00170

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91(1), 299–305. https://doi.org/10.1890/08-2244.1

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, 16(5), 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Lavorel, S., & Grigulis, K. (2012). How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. *Journal of Ecology*, 100(1), 128–140. https://doi.org/10.1111/j.1365-2745.2011.01914.x

Lavorel, S., Storkey, J., Bardgett, R. D., de Bello, F., Berg, M. P., Le Roux, X., Moretti, M., Mulder, C., Pakeman, R. J., Díaz, S., & Harrington, R. (2013). A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *Journal of Vegetation Science*, 24(5), 942–948. https://doi.org/10.1111/jvs.12083

Le Provost, G., Badenhausser, I., Violle, C., Requier, F., D'Ottavio, M., Roncoroni, M., Gross, L., & Gross, N. (2021). Grassland-to-crop conversion in agricultural landscapes has lasting impact on the trait diversity of bees. *Landscape Ecology*, 36(1), 281–295. https://doi.org/10.1007/s10980-020-01141-2

Lefcheck, J. S. (2016). PIECEWISESEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7(5), 573–579. https://doi.org/10.1111/2041-210x.12512

Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129(2), 271–280. https://doi.org/10.1007/s004420100716

Liccari, F., Boscutti, F., Bacaro, G., & Sigura, M. (2022). Connectivity, landscape structure, and plant diversity across agricultural landscapes: Novel insight into effective ecological network planning. *Journal of Environmental Management*, 317, 115358. https://doi.org/10.1016/j.jenvman.2022.115358

Lienin, P., & Kleyer, M. (2012). Plant trait responses to the environment and effects on ecosystem properties. *Basic and Applied Ecology*, 13(4), 301–311. https://doi.org/10.1016/j.baae.2012.05.002

Martin, E. A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M. P. D., Holzschuh, A., Kleijn, D., Kovács-Hostyánszki, A., Marini, L., Potts, S. G., Smith, H. G., Al Hassan, D., Albrecht, M., Andersson, G. K. S., Asís, J. D., Aviron, S., Balzan, M. V., … Steffan-Dewenter, I. (2019). The interplay of landscape composition and configuration: New pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecology Letters*, 22(7), 1083–1094. https://doi.org/10.1111/ele.13265

Mayes, J., & Wheeler, D. (2013). Regional weather and climates of the British Isles—Part 1: Introduction. *Weather*, 68(1), 3–8. https://doi.org/10.1002/wea.2041

McGarigal, K., Cushman, S., & Ene, E. (2023). *Fragstats v4: Spatial pattern analysis program for categorical maps*. [computer software]. https://www.fragstats.org

Morton, D., Rowland, C., Wood, C., Meek, L., Marston, C., Smith, G., Wadsworth, R., & Simpson, I. C. (2011). *Final report for LCM2007-the new UK land cover map* (countryside survey). Centre for Ecology & Hydrology.

Morton, R. D., Rowland, C. S., Wood, C. M., Meek, L., Marston, C. G., & Smith, G. M. (2014). *Land cover map 2007 (25m raster, GB) v1.2*. [Dataset]. https://doi.org/10.5285/a1f88807-4826-44bc-994d-a902da5119c2

Müller, H. (1881). *Alpenblumen*. Engelmann.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2019). *Vegan: Community ecology package*. [computer software].

Pakeman, R. J., & Stockan, J. (2013). Using plant functional traits as a link between land use and bee foraging abundance. *Acta Oecologica*, 50, 32–39. https://doi.org/10.1016/j.actao.2013.04.004

Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., Dicks, L. V., Garibaldi, L. A., Hill, R., Settele, J., & Vanbergen, A. J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, 540(7632), Article 7632. https://doi.org/10.1038/nature20588

Potts, S. G., Vulliamy, B., Dafni, A., Ne'eman, G., & Willmer, P. (2003). Linking bees and flowers: How do floral communities structure pollinator communities? *Ecology*, 84(10), 2628–2642. https://doi.org/10.1890/02-0136

R Core Team. (2023). *R: A language and environment for statistical computing* [computer software]. R Foundation for Statistical Computing.

Rader, R., Bartomeus, I., Tylianakis, J. M., & Laliberté, E. (2014). The winners and losers of land use intensification: Pollinator community disassembly is non-random and alters functional diversity. *Diversity and Distributions*, 20(8), 908–917. https://doi.org/10.1111/ddi.12221

Ricou, C., Schneller, C., Amiaud, B., Plantureux, S., & Bockstaller, C. (2014). A vegetation-based indicator to assess the pollination value of field margin flora. *Ecological Indicators*, 45, 320–331. https://doi.org/10.1016/j.ecolind.2014.03.022

Robleño, I., Storkey, J., Solé-Senan, X. O., & Recasens, J. (2018). Using the response–effect trait framework to quantify the value of fallow patches in agricultural landscapes to pollinators. *Applied Vegetation Science*, 21(2), 267–277. https://doi.org/10.1111/avsc.12359

Roquer-Beni, L., Alins, G., Arnan, X., Boreux, V., García, D., Hambäck, P. A., Happe, A.-K., Klein, A.-M., Miñarro, M., Mody, K., Porcel, M., Rodrigo, A., Samnegård, U., Tasin, M., & Bosch, J. (2021). Management-dependent effects of pollinator functional diversity on apple pollination services: A response–effect trait approach. *Journal of Applied Ecology*, 58(12), 2843–2853. https://doi.org/10.1111/1365-2664.14022

Rotchés-Ribalta, R., Winsa, M., Roberts, S. P. M., & Öckinger, E. (2018). Associations between plant and pollinator communities under grassland restoration respond mainly to landscape connectivity. *Journal of Applied Ecology*, 55(6), 2822–2833. https://doi.org/10.1111/1365-2664.13232

Roulston, T. H., & Goodell, K. (2011). The role of resources and risks in regulating wild bee populations. In. *Annual Review of Entomology*, 56, 293–312.

Shipley, B. (2000). A new inferential test for path models based on directed acyclic graphs. *Structural Equation Modeling: A Multidisciplinary Journal*, 7(2), 206–218. https://doi.org/10.1207/s15328007sem0702_4

Smart, S. M., Marrs, R. H., Le Duc, M. G., Thompson, K., Bunce, R. G. H., Firbank, L. G., & Rossall, M. J. (2006). Spatial relationships between intensive land cover and residual plant species diversity in temperate farmed landscapes. *Journal of Applied Ecology*, 43(6), 1128–1137. https://doi.org/10.1111/j.1365-2664.2006.01231.x

Solé-Senan, X. O., Juárez-Escario, A., Conesa, J. A., & Recasens, J. (2018). Plant species, functional assemblages and partitioning of diversity in a Mediterranean agricultural mosaic landscape. *Agriculture, Ecosystems & Environment*, 256, 163–172. https://doi.org/10.1016/j.agee.2018.01.014

Solé-Senan, X. O., Juárez-Escario, A., Robleño, I., Conesa, J. A., & Recasens, J. (2017). Using the response-effect trait framework to disentangle the effects of agricultural intensification on the provision of ecosystem services by Mediterranean arable plants. *Agriculture, Ecosystems & Environment*, 247, 255–264. https://doi.org/10.1016/j.agee.2017.07.005

Speight, M., Monteil, C., Castella, E., & Sarthou, J.-P. (2013). *Syrph the net on CD, issue 9, the database of European Syrphidae*. Syrph the Net Publications.

Staton, T., Walters, R. J., Breeze, T. D., Smith, J., & Girling, R. D. (2022). Niche complementarity drives increases in pollinator functional diversity in diversified agroforestry systems. *Agriculture, Ecosystems & Environment, 336*, 108035. https://doi.org/10.1016/j.agee.2022.108035

Storkey, J., Brooks, D., Haughton, A., Hawes, C., Smith, B. M., & Holland, J. M. (2013). Using functional traits to quantify the value of plant communities to invertebrate ecosystem service providers in arable landscapes. *Journal of Ecology, 101*(1), 38–46. https://doi.org/10.1111/1365-2745.12020

Stubbs, A., & Falk, S. (2002). *British hoverflies: An illustrated identification guide* (2nd ed.). British Entomological and Natural History Society.

Theodorou, P., Herbst, S. C., Kahnt, B., Landaverde-Gonzalez, P., Baltz, L. M., Osterman, J., & Paxton, R. J. (2020). Urban fragmentation leads to lower floral diversity, with knock-on impacts on bee biodiversity. *Scientific Reports, 10*(1), 11. https://doi.org/10.1038/s41598-020-78736-x

Thioulouse, J., Dray, S., Dufour, A.-B., Siberchicot, A., Jombart, T., & Pavoine, S. (2018). *Multivariate analysis of ecological data with ade4*. Springer. https://doi.org/10.1007/978-1-4939-8850-1

Thomas, J. A., Edwards, M., Simcox, D. J., Powney, G. D., August, T. A., & Isaac, N. J. B. (2015). Recent trends in UK insects that inhabit early successional stages of ecosystems. *Biological Journal of the Linnean Society, 115*(3), 636–646. https://doi.org/10.1111/bij.12527

van Rijn, P. C. J., Kooijman, J., & Wäckers, F. L. (2013). The contribution of floral resources and honeydew to the performance of predatory hoverflies (Diptera: Syrphidae). *Biological Control, 67*(1), 32–38. https://doi.org/10.1016/j.biocontrol.2013.06.014

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

Wagner, D. L. (2020). Insect declines in the Anthropocene. *Annual Review of Entomology, 65*(1), 457–480. https://doi.org/10.1146/annurev-ento-011019-025151

Weiner, C. N., Hilpert, A., Werner, M., Linsenmair, K. E., & Blüthgen, N. (2010). Pollen amino acids and flower specialisation in solitary bees. *Apidologie, 41*(4), 476–487. https://doi.org/10.1051/apido/2009083

Williams, N. M., Crone, E. E., Roulston, T. H., Minckley, R. L., Packer, L., & Potts, S. G. (2010). Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation, 143*(10), 2280–2291. https://doi.org/10.1016/j.biocon.2010.03.024

Winfree, R., Aguilar, R., Vazquez, D. P., LeBuhn, G., & Aizen, M. A. (2009). A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology, 90*(8), 2068–2076.

Winsa, M., Öckinger, E., Bommarco, R., Lindborg, R., Roberts, S. P. M., Wärnsberg, J., & Bartomeus, I. (2017). Sustained functional composition of pollinators in restored pastures despite slow functional restoration of plants. *Ecology and Evolution, 7*(11), 3836–3846. https://doi.org/10.1002/ece3.2924

Woodcock, B. A., Harrower, C., Redhead, J., Edwards, M., Vanbergen, A. J., Heard, M. S., Roy, D. B., & Pywell, R. F. (2014). National patterns of functional diversity and redundancy in predatory ground beetles and bees associated with key UK arable crops. *Journal of Applied Ecology, 51*(1), 142–151. https://doi.org/10.1111/1365-2664.12171

Zattara, E. E., & Aizen, M. A. (2021). Worldwide occurrence records suggest a global decline in bee species richness. *One Earth, 4*(1), 114–123. https://doi.org/10.1016/j.oneear.2020.12.005

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Additional methodological details.
Appendix S2: Additional results.