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RESEARCH ARTICLE

Woodland, cropland and hedgerows promote pollinator abundance in intensive grassland landscapes, with saturating benefits of flower cover

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Abstract

1. Pollinating insects provide economic value by improving crop yield. They are also functionally and culturally important across ecosystems outside of cropland. To understand landscape-level drivers of pollinator declines, and guide policy and intervention to reverse declines, studies must cover (a) multiple insect and plant taxa and (b) a range of agricultural and semi-natural land uses. Furthermore, in an era of woodland restoration initiatives and rewilding ideologies, the contribution of woodland and woody linear features (WLFs; e.g. hedgerows) to pollinator abundance demands further investigation.
2. We demonstrate fine-scale analysis of high-quality, co-located measurements from a national environmental survey. We relate pollinator transect counts to ground-truth habitat and WLF maps across 300 1 km squares in Wales, UK. We look at effects of habitat type, flower cover, WLF density and habitat diversity on summer abundance (July and August) of eight insect groups, representing three insect orders (Lepidoptera, Hymenoptera and Diptera).
3. Compared with improved grassland (the dominant habitat in Wales), pollinator abundance is consistently higher in cropland and woodland—especially broadleaved woodland. For mining bees and two hoverfly groups, abundance is predicted to be at least 1.5× higher in woodland ecosystems than elsewhere. Furthermore, we estimate contributions of WLFs to abundance in agriculturally improved habitats to be up to 14% for honeybees and up to 21% for hoverflies.
4. The abundance of all insect groups increases with flower cover, which is a key mechanism through which woodland, cropland and grassland support pollinators. Importantly, we observe diminishing returns of increasing flower cover for abundance of non-*Apis* pollinator groups, expecting roughly twice the increase in abundance per % flower cover from 0% to 5%, as compared with 10% to 15%.

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However, the shape of the relationship was inverted for honeybees, which showed steeper increases in abundance at higher flower cover.

5. *Synthesis and applications*. We provide a holistic view of the drivers of pollinator abundance in Wales, in which flower cover, woodland, hedgerows and cropland are critical. We propose a key role for woodland creation, hedge-laying and farmland heterogeneity within future land management incentive schemes. Finally, we suggest targeting of interventions to maximise benefits for non-*Apis* pollinators. Specifically, increasing floral provision in areas where existing flower cover is low—for example, in flower-poor improved grasslands—could effectively increase pollinator abundance and diversity while prioritising wild over managed species.

KEYWORDS

agri-environment schemes, bumblebees, butterflies, ecosystem services, forest restoration, landscape-scale conservation, plant–pollinator interactions, semi-natural habitat

1 | INTRODUCTION

'Pollinators' describe a wide variety of wild and managed animals, particularly insects, that enable pollination and fertilisation of flowers (Potts et al., 2016). Pollinators provide economic benefits by enhancing global food production, 35% of which comes from animal-pollinated crops (Klein et al., 2007). However, they are also functionally critical to sustain populations of wild plant and animal species, while some groups—especially bees—carry immense social and cultural value (Christmas et al., 2018).

Many pollinator species are declining (Wagner et al., 2021), but rates of decline and consequences for pollination function remain unclear. Trends from volunteer-submitted records in Great Britain (GB) show that, since 1970, more moth, bee, hoverfly and butterfly species are declining than increasing (Fox et al., 2014; Powney et al., 2019; Thomas et al., 2004). Similar declines are evidenced in wider Europe and the United States, with relatively few data available elsewhere (Sánchez-Bayo & Wyckhuys, 2019). Although pollinator declines are often concentrated in rare species (Powney et al., 2019), recent studies have documented severe declines in insect biomass (e.g. Hallmann et al., 2017; Seibold et al., 2019) generating significant media attention and public concern under the banner of 'insectageddon'. Nonetheless, insect biodiversity assessments are severely data limited; thus, the magnitudes and drivers of insect declines are open to debate (Thomas et al., 2019).

Given the economic, functional and cultural value of pollinators, we need to understand the drivers of pollinator decline and recovery. Insect declines vary based on species traits, while habitat change, pollution and climate change are the most commonly reported drivers (Sánchez-Bayo & Wyckhuys, 2019). Pesticides, parasites and pathogens also play a key role for pollinator declines—especially for honeybees and bumblebees (Goulson et al., 2015; Woodcock et al., 2016). High-level drivers of pollinator declines (e.g. habitat change) may act indirectly via intermediate drivers, such as flower cover (Davidson et al., 2020). In GB, land-use change and agricultural intensification probably underpinned 20th-century declines in forage plants for bumblebees and overall nectar provision (Baude et al., 2016; Carvell et al., 2006). Furthermore, in England and Wales, changes in availability of nectar forage plants were recently explicitly linked to shifts in honeybee foraging (Jones et al., 2021).

Agri-environment schemes (AESs) provide financial incentives for environmentally friendly management on farmland. Some AES interventions, for example, wildflower meadow restoration, provide resources for both larval and adult stages of desirable insect species (Alison et al., 2017) with potential benefits for plant reproduction and crop yield (Albrecht et al., 2007). However, outstanding questions remain with respect to (a) floral resource thresholds at which AESs can sustain pollinator populations (Dicks et al., 2015); (b) optimal spatial targeting of AES interventions for biodiversity and ecosystem services (Alison et al., 2016; Boetzl et al., 2019); (c) providing floral resources for pollinators during periods of deficit (e.g. March and August/September, Timberlake et al., 2019); and (d) which interventions should be prioritised to maximise provision for pollinators (Breeze et al., 2014). Recent studies confirm landscape-scale benefits of woody linear features (WLFs) for multiple insect groups (Garratt et al., 2017; Maskell et al., 2019; Sullivan et al., 2017). However, given rising interest in agroforestry and potential benefits for pollinators across Europe (Varah et al., 2020), studies need to quantify the contribution of WLFs for multiple pollinator groups across multiple habitat types.

Beyond hedgerows, effects of woodland and woodland creation on pollinators are very poorly understood. Marginal land in the EU may be on a trajectory towards agricultural abandonment and reforestation (Stürck et al., 2018), and may be influenced by a popular notion of 'rewilding' (Merckx & Pereira, 2015). In the United Kingdom, devolved administrations have pledged creation of a National Forest 'the length and breadth of Wales' (Welsh Government, 2020) and new planting of 11 million trees in England (Forestry Commission, 2019). Studies of semi-natural grassland demonstrate positive effects of woodland in the surrounding landscape on pollinator abundance (Bergman et al., 2018; Sjödin et al., 2008). However, the benefits of woodland are unclear for most pollinator groups, because studies are usually (a) focussed on bees, (b) restricted to agricultural or urban land (Senapathi et al., 2017) and/or (c) incorporate woodland within coarse habitat categories (Baldock et al., 2015). Interestingly, of the few studies that directly compare woodland to open habitats, several report that bee abundance or diversity is actually lower in woodland (Bartual et al., 2019; Scherber et al., 2019; Winfree et al., 2007).

Here we present analysis of high-resolution, co-located measurements from a national environmental survey of Wales, a region dominated by intensive grassland agriculture and open upland habitats. We address three key questions about the abundance of pollinators across three insect orders (Lepidoptera, Hymenoptera and Diptera), as well as species diversity within Lepidoptera feeding groups. We ask the following questions: (a) How does pollinator abundance vary across woodland and other wider countryside habitats? (b) What is the contribution of WLFs to pollinator abundance in non-woodland habitats? (c) What is the shape of the relationship between flower cover and pollinator abundance? Finally, we discuss important policy implications of this work with respect to land management incentives and AES targeting.

2 | MATERIALS AND METHODS

2.1 | Study region and data

Our study region, Wales, is the region of the United Kingdom most dominated by agriculture. 88% of land in Wales is farmed, of which 75% is permanent pasture (Armstrong, 2016). Furthermore, 80% of farmland in Wales is considered as 'less favourable areas' or LFA land, reflecting the upland terrain and wet climate of the country (Armstrong, 2016). Cattle and sheep account for most of the agricultural output, the latter prevailing in the uplands. Lowland grasslands are typically intensively farmed and dominated by productive grasses (e.g. *Lolium* spp.) with low cover of forbs (e.g. *Trifolium repens*). Only 14% of farmland in Wales is considered 'croppable' (Armstrong, 2016). The vast majority of cropland in Wales produces cereals, with occasional root vegetables, potatoes, oilseed rape and peas (Maskell et al., 2020a).

Data on pollinating insects, flower cover, habitats and WLFs across Wales were collected through the Glastir Monitoring & Evaluation Programme (GMEP; Emmett & the GMEP Team, 2017) and provided by the Welsh Government. GMEP constituted field surveys of plants, pollinators, birds, soils, freshwaters, habitats and landscape features within 300 1 km squares across Wales. GMEP monitoring took place from 2013 to 2016, with survey visits to 60 squares in 2013, 90 squares in 2014 and 75 squares per year in 2015–2016. Data were only collected in areas of the square where explicit permission was provided by land managers.

2.2 | Pollinator and flower surveys

Two visits were made to each GMEP square by trained insect and flower surveyors—one in July and one in August. Visits were made between 10 a.m. and 4 p.m. on warm, dry, calm days following the UK Wider Countryside Butterfly Survey method (Brereton et al., 2011). During each visit, two 1 km transects, divided into 200 m sections, were surveyed for adult butterflies (Lepidoptera: Rhopalocera), bees (Apoidea) and hoverflies (Syrphidae). Surveyors established transects aiming for an ideal of two 1 km survey lines that are straight, parallel, separated by 500 m, and running North-South or East-West across the square (Brereton et al., 2011). However, practical considerations including permissions, pathways, linear features and barriers caused deviations from that ideal (Figure 1b); thus, most transects were opportunistic in their design (following routes of high accessibility). Pollinator transects were walked at a steady, even pace. All identifiable insects observed within a 5 m 'box' around the observer were recorded. Butterflies were identified to species level; bees were identified as honeybees, bumblebees or one of two groups of solitary bee based on pollen collection strategy (pollen on legs: mining bees, e.g. *Andrena*; pollen on abdomen: leafcutter or mason bees, family Megachilidae); hoverflies were identified to one of three morphological groupings, which were broadly reflective of larval feeding strategies (predatory, detritivorous or herbivorous; see Botham et al., 2020 for more details).

Percentage flower cover (*not* vegetative cover) within 5 m of each transect section was recorded using a DAFOR scale (Dominant > 30% ≥ Abundant > 10% ≥ Frequent > 5% ≥ Occasional > 1% ≥ Rare > 0%) for each of 10 plant groups (Apiaceae, Asteraceae [yellow], Asteraceae [purple], Dipsaceae, Ericaeae, Fabaceae, Lamiaceae, Rosaceae, Scrophulariaceae or 'other'). Flower cover was an absolute measure, not a relative measure (i.e. cover of different families were *not* expected to sum to 100). Temperature, percent sunshine and wind speed (Beaufort scale) were also recorded on-site for each visit. Surveyors entered pollinator and flower data, and digitised the route for each transect section, using a secure online portal. Further information on pollinator and flower survey methodology is available in supporting documentation for the published dataset (Botham et al., 2020).

2.3 | Habitat and woody linear feature surveys

Habitat and linear feature surveys were carried out in all GMEP squares during the same year as pollinator and flower surveys. Following the methodology of the Countryside Survey of Great Britain (Wood et al., 2018), every permitted and accessible land parcel in the square was assigned a UK Biodiversity Action Plan (BAP) broad habitat type. A range of linear features (<5 m wide, minimum

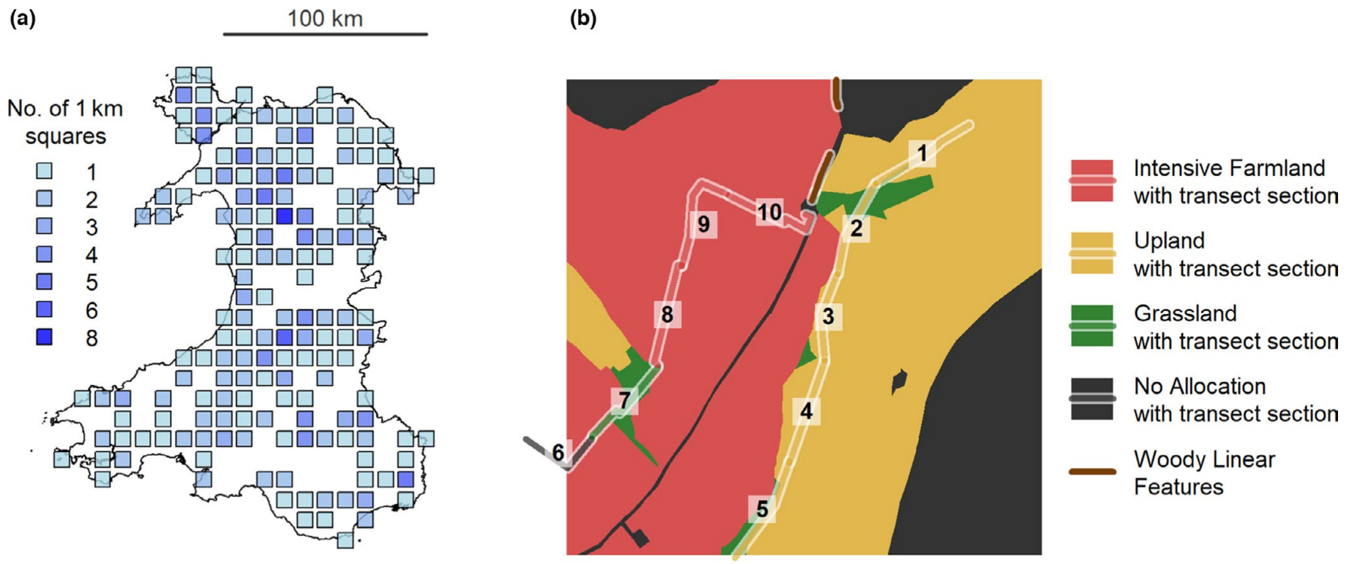

FIGURE 1 (a) Map of Wales, displaying the distribution of 300 1 × 1 km Glastir Monitoring and Evaluation Programme (GMEP) survey squares at 10 km resolution. (b) Example GMEP survey square, showing mapped ecosystems and two 1 km pollinator transects, each formed of five 200 m transect sections (labelled 1–10). Transect sections are allocated as Intensive Farmland (red), Upland (yellow) or Grassland (green) based on the dominant underlying habitat. Woody linear features are also shown (brown lines without numbers)

length 20 m) were recorded in and around those parcels, including WLFs. Further information on habitat and landscape feature survey methodology is available in supporting documentation for the published datasets (Maskell et al., 2020a, 2020b).

Habitat, WLF and elevation variables were extracted for each transect section using ArcGIS Desktop 10.6 (ESRI). To compare transect sections in different habitats, we classified the underlying broad habitat for 200 m pollinator transect sections through intersection with habitat polygons. For each section, the broad habitat accounting for the greatest proportion of its length was assigned as the dominant habitat type. During this process, we sought to maximise sample size while avoiding unrepresentative classifications related to missing or ambiguous habitat data. As such, we made no dominant habitat assignment if (a) the dominant broad habitat accounted for <100 m of the section, (b) a section had incomplete (<90%) overlap with habitat survey data or (c) the dominant broad habitat was recorded as 'Mosaic'. We also calculated the Shannon index of habitat diversity for each transect section, taking into account the total number of broad habitats and the dominance among them (Firbank et al., 2008; Maskell et al., 2019). To relate flower cover and insect counts to habitat classifications at the finest possible scale and resolution, our habitat intersections were length-based, and not area or buffer based. However, a Euclidean buffer was necessary to extract the total density of WLFs (m/ha) within 10 m of each transect section, including managed WLFs (hedges), unmanaged WLFs (lines of trees) and forestry linear features (belts of trees or scrub). Outside of GMEP survey data, a 5-m resolution raster of elevation was provided by Welsh Government (the Nextmap Britain DTM by Intermap Technologies). The elevation of each transect section was taken as the mean elevation of all vertices in the digitised transect section. The final modelled dataset included pollinator counts from 4,449 section-visits across 295 1 km squares (Appendix A1).

2.4 | Data analysis and model selection

We used generalised linear mixed-effects models (GLMMs) to address our key questions about (a) woodland and other habitats, (b) WLFs and (c) flower cover while accounting for confounding effects of habitat diversity and other environmental variables. Of 300 GMEP survey squares, 150 comprised a representative, stratified random sample of the wider countryside of Wales. The remaining 150 squares comprised a 'targeted component' and were selected based on numerous criteria associated with Glastir, an AES which started in 2012 (Wood et al., 2021). To effectively capture relationships between pollinators and environmental variables, we used data from all 300 survey squares to produce statistical models. Then, to make unbiased inferences relevant to the wider countryside of Wales, we make predictions based on just the 150 stratified random squares.

Insect abundance per section-visit was considered as the response variable in models for each of eight insect groups: (a) bumblebees, (b) honeybees, (c) mining bees, (d) butterflies with grass larval food plants (hereafter 'grass-feeding butterflies'), (e) butterflies with forb larval food plants ('forb-feeding butterflies'), (f) hoverflies with larvae that are predatory ('predatory hoverflies'), (g) hoverflies with larvae that are detritivorous ('detritivorous hoverflies'), (h) hoverflies with larvae that are phytophagous ('phytophagous hoverflies'). Due to extremely high incidence of zeroes, in-depth analyses were not possible for leafcutter or mason bees (only 34 individuals in the modelled dataset) or butterflies with woody larval food plants (24 individuals). Specifically, convergence failures occurred for the most complex models for those two insect groups. This suggested insufficient power to address our key questions for groups with very low prevalence; we experienced 100% model convergence for all other groups. For each of the eight more prevalent insect groups, we fitted a set of zero-inflated negative binomial GLMMs (log-link) in R v3.6.3. using the package glmmTMB v0.2.3. (R Core Team; Brooks et al., 2017). To account for surveyor differences, spatial and temporal autocorrelation, and pseudo-replication, we included random intercepts for surveyor ID, date of survey and transect section ID nested within survey square. Furthermore, for grass- and forb-feeding butterflies, data were available on species richness and composition (Table S1). To address our key questions with respect to alpha diversity of these two groups, we also fitted a set of Poisson GLMMs using species richness as the response.

We allowed effects of eight predictors as fixed effects in GLMMs: (a) *Habitat* or *Ecosystem* type. *Habitat* is a 10-level factor nested within *Ecosystem*, which is a four-level factor (Intensive Farmland ecosystem: cropland or intensive grassland habitat. Grassland ecosystem: marshy or neutral grassland habitat. Woodland ecosystem: broadleaved or coniferous woodland. Upland ecosystem: acid grassland, bog, bracken or dwarf shrub heath habitat). (b) *Flower cover*, the sum of the midpoints of DAFOR divisions (values rounded up: 65%, 20%, 8%, 4% and 1%) for all recorded plant families during a section-visit. One surveyor had invalid flower cover measurements which consistently summed to ~100, and these were removed from summaries of flower cover data. However, we made full use of that surveyor's insect counts in GLMMs by imputing flower cover based on habitat type; invalid values were replaced with the mean flower cover recorded by other surveyors in the relevant habitat type. Preliminary analysis suggested strong, nonlinear effects of *Flower cover* on insect abundance. To understand the shape of the relationship between *Flower cover* and insect abundance, we posited linear ($y \sim x$), saturating (logarithmic; $y \sim \ln(x)$), exponential ($y \sim e^x$) or quadratic ($y \sim x + x^2$) effects of this variable. (c) *WLF density* (m/ha) within 10 m of the transect section. (d) Shannon *Habitat diversity* within a section. (e) *Elevation* of transect section (m). To aid model fitting, elevation was rescaled to hectometre (100 m) units. (f) *Sunshine* (%). (g) *Temperature* (°C). (8) *Wind speed* (Beaufort scale, included as a continuous predictor ranging from 0 to 6).

For each insect group, we defined a maximal model of the form *Abundance* ~ [*Habitat*|*Ecosystem*] + [*Flower cover*|ln(*Flower cover*)|$e^{\textit{Flower cover}}$|*Flower cover* + *Flower cover*^{2}] + *WLF density* + *Habitat diversity* + *Elevation* + *Sunshine* + *Temperature* + *Wind speed*. We fitted all possible subsets of this model using R package MuMIn v1.43.17 (Barton, 2020). *Habitat* and *Ecosystem* were mutually exclusive, as were different functions of *Flower cover*. We used model selection based on second-order Akaike's Information Criterion (AICc; Burnham & Anderson, 2002). Recognising that model selection by AICc may lead to overfitting in the presence of unobserved heterogeneity (Brewer et al., 2016), we make inferences and predictions based on the simplest model with ΔAICc ≤ 2 (hereafter the 'best model'). We also highlight effects in other models with ΔAICc ≤ 2, and present the number of models with ΔAICc ≤ 6 (disregarding more complex, nested versions of the lowest AICc model; Richards, 2008). To understand the proportion of variation in insect abundance that could be explained by the best model, we present R^2 statistics based on the methods of Nakagawa et al. (2017; using a function from Ben Bolker found at https://github.com/glmmTMB). Specifically, $R^2_{\mathrm{GLMM(m)}}$ is used to represent the proportion of the total variance explained by the fixed effects, while $R^2_{\mathrm{GLMM(c)}}$ is used to represent the proportion of the variance explained by both fixed and random effects.

After model selection, we addressed question (a) 'how does pollinator abundance vary across woodland and other wider countryside habitats?' by making representative predictions of insect abundance across dominant habitats and ecosystems of Wales. Predictions were made based on observed values of environmental predictors across 150 1 km squares, representing a stratified random sample of Wales. In other words, using best models and observed data, we predicted the abundance of each insect group on each transect section that was (a) included in the final modelled dataset and (b) included in the stratified random half of the GMEP survey. This prevented extrapolation, and ensured that inference was based on observed, nationally representative combinations of predictor values. Predicted abundances were then averaged across *Habitat* or *Ecosystem* type (depending which was present in the best model). This approach accounted for direct effects of *Habitat* or *Ecosystem* type on insect abundance, as well as additive effects of other environmental predictors such as *Flower cover* and weather. We addressed question (b) 'what is the contribution of WLFs to pollinator abundance in non-woodland habitats?' by making a second set of predictions, for which *WLF density* was reduced to zero while other environmental predictors were held constant. This indicated the magnitude of the additive contribution of WLFs to insect abundance, which is expected to be greater in habitats or ecosystems where *WLF density* is highest. Finally, we addressed question (c) 'what is the shape of the relationship between flower cover and pollinator abundance?' by making a third set of predictions, varying flower cover from 0% to 67% while holding other environmental predictors constant (67% is the 99th percentile of flower cover in the modelled dataset). Predictions for each group were scaled to fall between 0 and 1.

3 | RESULTS

In all, 15,329 bumblebees, 3,294 honeybees, 702 mining bees, 12,605 grass-feeding butterflies (12 species), 5,652 forb-feeding butterflies (17 species), 10,330 predatory hoverflies, 9,743 detritivorous hoverflies and 1,384 herbivorous hoverflies were represented in the modelled dataset. The dominant habitat allocations were intensive grassland (30%), neutral grassland (26.2%), acid grassland (14.7%), heathland (8%) and bog (6.4%); all other habitats had 2.2%–3.6% representation (Table S2). For bumblebees and all hoverfly groups, we adopted a best model which was simpler than the lowest AICc model (having fewer parameters, but ΔAICc ≤ 2; Table 1).

TABLE 1 Directions of effects of predictors on abundance of eight insect groups. Positive (+), negative (−) and categorical (±) effects are shown from the best model for each group, which is the simplest model within two Akaike's Information Criterion (AICc) units of the lowest-AICc model. Square brackets indicate predictors that were not present in the best model, but were present in lowest AICc model. Also shown are theta (the dispersion parameter for conditional abundance), number of parameters, log-likelihood, AICc and AICc-rank, ΔAICc from the lowest AICc model, the number of models within six (and two) AICc units of the lowest AICc model (disregarding models in which the best model was fully nested; Richards, 2008), and marginal (m) and conditional (c) R^2 values (Nakagawa et al., 2017). Sunshine, temperature and wind speed were included in all models; effect directions are included below if the *p*-value for the corresponding Wald-*Z* statistic was <0.05

Insect group	*Habitat*	*Ecosystem*	*Flower cover*	*WLF density*	*Habitat diversity*	*Elevation*	*Sunshine*	*Temperature*	*Wind speed*	Theta	*N* pars	Log-likelihood	AICc (rank)	ΔAICc to lowest AICc model	*N* models with ΔAICc < 6 (<2)	$R^2_{\mathrm{GLMM(m)}}$ ($R^2_{\mathrm{GLMM(c)}}$)
Bumblebees			+ (ln)		[+]		−	+	−	2.10	10	−8,631.90	17,283.85 (2)	1.09	6 (1)	0.16 (0.76)
Honeybees	±		+ (ln)	+		−		+	−	0.54	21	−3,072.94	6,188.10 (1)	0.00	4 (0)	0.40 (0.77)
Mining bees		±	+ (ln)			−				0.88	14	−1,422.11	2,872.32 (1)	0.00	11 (0)	0.09 (0.54)
Butterflies: Grass l.f.p.[a]	±		+ (ln)		+	−		+	−	1.20	21	−7,421.81	14,885.82 (1)	0.00	2 (0)	0.19 (0.72)
Butterflies: Forb l.f.p.[a]	±		+ (ln)		+	−	+	+		1.41	21	−4,892.58	9,827.37 (1)	0.00	2 (0)	0.23 (0.70)
Hoverflies: Predators	±		+ (ln)	+	[+]	−		−		1.44	21	−6,171.93	12,386.07 (2)	1.10	1 (1)	0.16 (0.77)
Hoverflies: Detritivores	[±]	±	+ (ln)	+	[+]	−			−	0.81	15	−5,597.06	11,224.23 (3)	0.80	7 (3)	0.24 (0.75)
Hoverflies: Herbivores	[±]	±	+ (ln)	+		−			−	0.47	15	−2,116.78	4,263.66 (2)	0.64	9 (2)	0.14 (0.6)

Abbreviations: AICc, second-order Akaike's Information Criterion; GLMM, generalised linear mixed-effects model; l.f.p., larval food plant; WLF, woody linear feature.

[a] For butterflies, the same parameters were included in the best model for species richness as in the best model for abundance.

Closely competing models with ΔAICc ≤ 2 were consistent in their inclusion of parameters related to (a) woodland and other habitats, (b) WLFs and (c) flower cover.

All pollinator groups were positively affected by flower cover (Table 1), and this mediated differences in pollinator abundance across habitats and ecosystems. Flower cover was highest along broadleaved woodland, cropland and neutral grassland transect sections (Figure 2). The dominant flower groups in those habitats were Rosaceae, yellow Asteraceae and Fabaceae, respectively. Habitat or ecosystem type also directly affected the abundance of all pollinator groups except for bumblebees (Table 1; Figure 3a). Ultimately, broadleaved woodland habitats, or woodland ecosystems, were top ranked for predicted abundance of honeybees, mining bees, detritivorous and herbivorous hoverflies (Figure 3b,c,g,h). Cropland was top ranked for forb-feeding butterflies and predatory hoverflies (Figure 3e,f), while neutral grassland was very narrowly top ranked for grass-feeding butterflies (Figure 3d). The best models for butterfly species richness included the same parameters as the best models for butterfly abundance. Furthermore, patterns of species richness across habitats were similar to patterns of abundance (Figure S1), indicating that common drivers underpin local-scale abundance and species richness of butterflies.

WLF density positively affected abundance of honeybees and all three hoverfly groups, accounting for half of the pollinator groups in our study (Table 1). WLF density was highest in cropland and intensive grassland habitats (Table S2). This was strongly reflected in the additive contribution of WLFs to insect abundance in non-woodland habitats and ecosystems (Figure 3b,f,g,h). The contribution of WLFs was generally greatest for herbivorous hoverflies (up to 21% on intensive farmland) and predatory hoverflies (up to 20% in cropland), but was also substantial for honeybees (up to 14% in cropland) and detritivorous hoverflies (up to 11% on intensive farmland). WLF density did not negatively affect the abundance of any insect group.

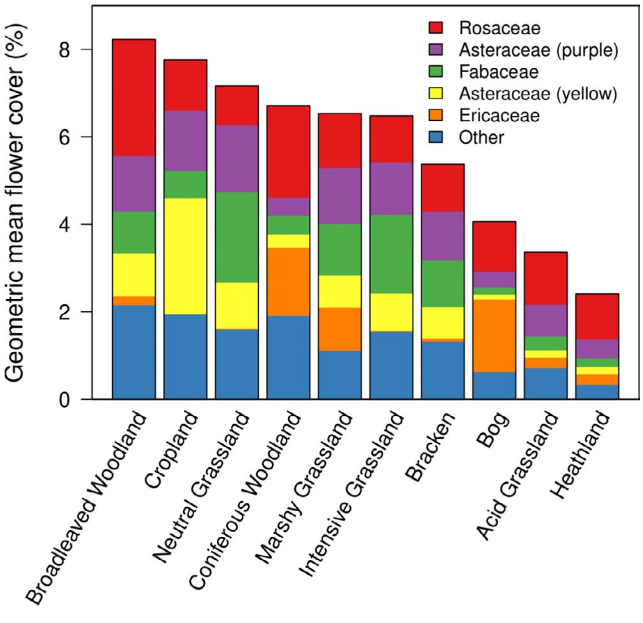

FIGURE 2 Flower cover across habitat types in Wales. Bars are fractionated based on the relative mean cover of each plant family within each habitat type

For all pollinator groups, the best fit for flower cover involved a saturating relationship (logarithmic; $y \sim \ln(x)$) on the scale of the linear predictor (e.g. Figure S2). On the scale of the response, the resulting relationship between flower cover and abundance or species richness was concave (i.e. saturating) for non-*Apis* pollinators but convex for honeybees (Figure 4). In other words, as flower cover increased, there were diminishing returns for abundance and species richness of wild pollinator groups.

4 | DISCUSSION

We present a uniquely comprehensive, national-scale assessment of pollinator abundance across habitats and ecosystems in mid- to late-summer. Representing three insect orders, we identify a critical role for woodlands in Wales, particularly broadleaved woodlands, but also WLFs on farmland. These findings come at a critical time: Insect declines are receiving more public attention than ever before, despite chronic data limitations (Hallmann et al., 2017; Seibold et al., 2019; Thomas et al., 2019). Farming on marginal grasslands across Europe is increasingly unprofitable (Merckx & Pereira, 2015), an issue which may be exacerbated in Wales after UK exit from the European Union (Welsh Government, 2018). Demand for wild spaces for recreation is very high, with tree cover expansion schemes pledged by local governments aiming to provide both recreational space and climate change mitigation (Welsh Government, 2020). We find that woodlands are top ranked for abundance of mining bees, detritivorous hoverflies and herbivorous hoverflies—and highly ranked for abundance of other pollinator groups. These results may portend future increases under native woodland expansion; previous studies have shown that, given appropriate management, pollinators readily colonise new native woodlands (Fuller et al., 2018).

We demonstrate flower cover as a cross-cutting mechanism affecting local abundance of pollinators, with implications for agri-environmental targeting. A key finding was consistent, nonlinear, saturating effects of flower cover on the abundance of wild pollinator groups (i.e. non-*Apis* pollinators; though feral *Apis mellifera* colonies may exist in Wales). Compared with an increase from 10% to 15%, an increase in flower cover from 0% to 5% corresponded to roughly twice the increase in abundance or richness of wild pollinator groups (Figure 4). This implies that interventions to increase floral cover for wild pollinators may be most effective in areas which are presently most flower-poor; in our study, this would include upland and intensive grassland habitats (Figure 2). However, upland habitats also present hostile climates for pollinators (Table S2); bumblebees occurred frequently in upland habitats, but this was not the case for other pollinator groups (Figure 3). Another important finding was that honeybees showed a distinct, non-saturating response to flower cover. This builds upon the work of Neilsen et al. (2012) showing increased visitation frequencies of wild pollinators where

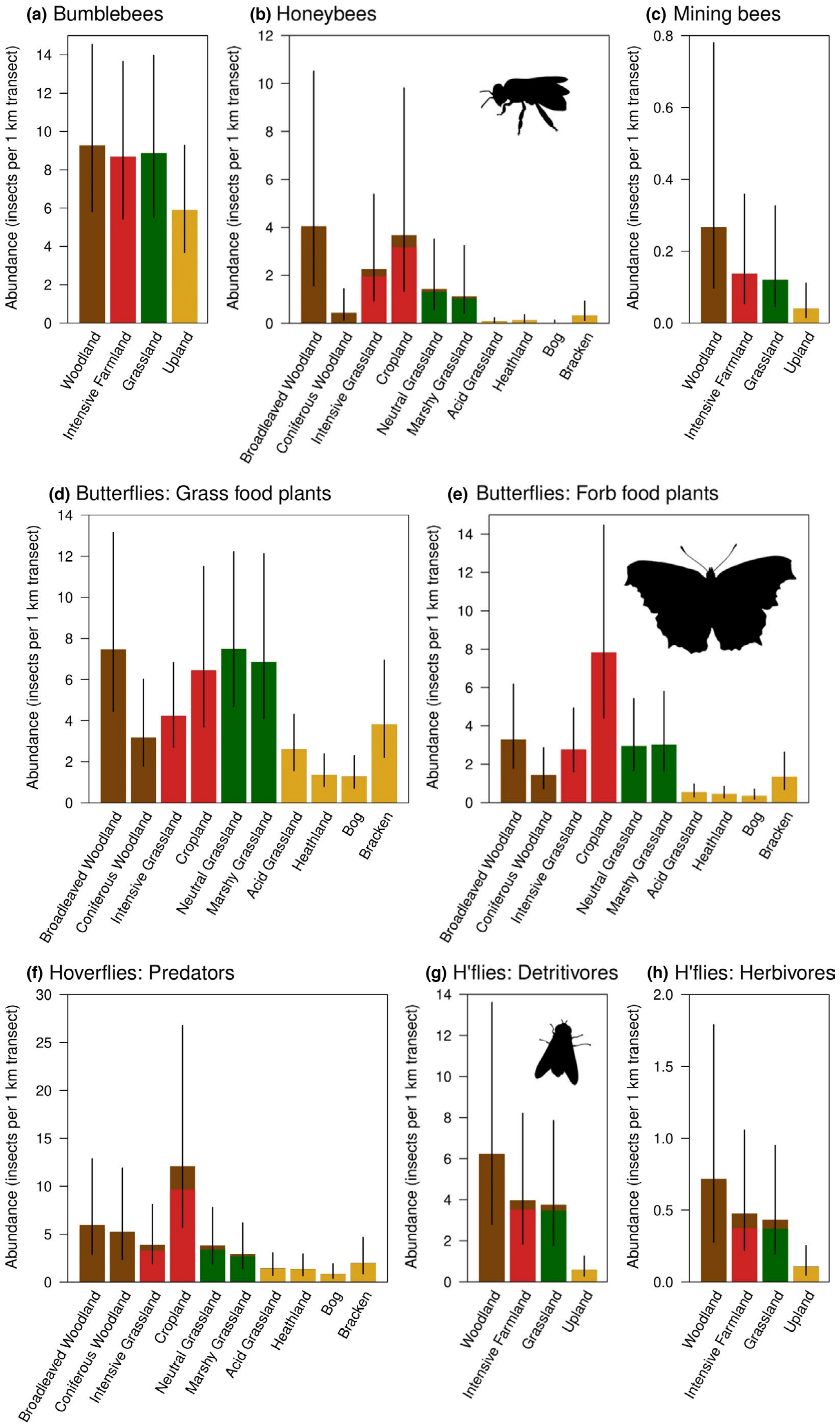
(a) Bumblebees
Abundance (insects per 1 km transect)
0
2
4
6
8
10
12
14
Woodland
Intensive Farmland
Grassland
Upland
(b) Honeybees
Abundance (insects per 1 km transect)
0
2
4
6
8
10
12
Broadleaved Woodland
Coniferous Woodland
Intensive Grassland
Cropland
Neutral Grassland
Marshy Grassland
Acid Grassland
Heathland
Bog
Bracken
(c) Mining bees
Abundance (insects per 1 km transect)
0.0
0.2
0.4
0.6
0.8
Woodland
Intensive Farmland
Grassland
Upland
(d) Butterflies: Grass food plants
Abundance (insects per 1 km transect)
0
2
4
6
8
10
12
14
Broadleaved Woodland
Coniferous Woodland
Intensive Grassland
Cropland
Neutral Grassland
Marshy Grassland
Acid Grassland
Heathland
Bog
Bracken
(e) Butterflies: Forb food plants
Abundance (insects per 1 km transect)
0
2
4
6
8
10
12
14
Broadleaved Woodland
Coniferous Woodland
Intensive Grassland
Cropland
Neutral Grassland
Marshy Grassland
Acid Grassland
Heathland
Bog
Bracken
(f) Hoverflies: Predators
Abundance (insects per 1 km transect)
0
5
10
15
20
25
30
Broadleaved Woodland
Coniferous Woodland
Intensive Grassland
Cropland
Neutral Grassland
Marshy Grassland
Acid Grassland
Heathland
Bog
Bracken
(g) H'flies: Detritivores
Abundance (insects per 1 km transect)
0
2
4
6
8
10
12
14
Woodland
Intensive Farmland
Grassland
Upland
(h) H'flies: Herbivores
Abundance (insects per 1 km transect)
0.0
0.5
1.0
1.5
2.0
Woodland
Intensive Farmland
Grassland
Upland

FIGURE 3 Predicted abundance and 95% confidence intervals (CIs) across habitat or ecosystem types for (a) bumblebees, (b) honeybees and (c) mining bees; (d) butterflies with grass larval food plants and (e) forb larval food plants; (f) hoverflies with predatory larvae, (g) detritivorous larvae and (h) herbivorous larvae. For non-woodland habitats and ecosystems, the proportional additive effect of WLFs on abundance is shown in the brown upper fractions of bars. Ecosystem types are amalgamations of habitat types as follows: woodland (broadleaved and coniferous; brown), grassland (neutral and marshy; green), intensive farmland (intensive grassland and cropland; red) and upland (bracken, heath, acid grassland and bog; yellow). Predictions and CIs across habitats or ecosystems were produced using the best model for each insect group, based on mean values for environmental variables across a stratified random sample of 150 1 km squares in Wales (Table S2). Note that direct effects of habitat or ecosystem type were not included in the best model for bumblebees (Table 1)

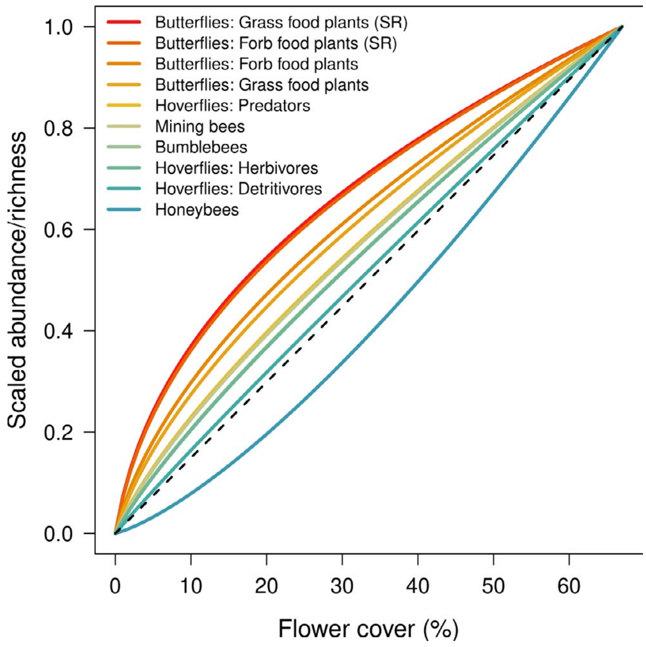

FIGURE 4 Effects of flower cover on scaled abundance of eight pollinator groups, with effects on species richness (SR) also shown for two groups. Relationships between abundance/richness and percent flower cover were principally concave (i.e. saturating) for wild pollinator groups and convex for honeybees. Coloured solid lines represent scaled predictions from the best model for each pollinator group. Predictions were made at the scale of the response (i.e. counts of individuals or species), then rescaled to show proportional change between the minimum count (at flower cover = 0) and the maximum count (at flower cover = 67%, the 99th percentile of the observed data) for each group. The dashed black line represents linearity

floral populations are sparse, but increased visitation of honeybees to larger flower patches. A likely explanation for these results relates to social foraging behaviour in honeybees (Seeley, 1986); specifically, communication through dances and oral fluid exchange might allow colonies to focus foraging effort on highly rewarding sites (Balbuena et al., 2012). Crucially, we show that the strength of competition between honeybees and wild pollinators (Thomson & Page, 2020) may be most severe in more flower-dense environments.

Previous work in Great Britain has estimated that per-area nectar productivity in broadleaved woodland is second only to that in calcareous grassland (Baude et al., 2016). We confirm high floral provision of broadleaved woodlands in Wales, particularly in the family Rosaceae (Figure 2), and demonstrate that high floral cover in woodland propagates to high abundances of key pollinator groups. This finding is bolstered by DNA meta-barcoding work led by the National Botanic Garden of Wales which has shown how a core set of plants, typical of woodlands and hedgerows, can dominate honeybee forage in the early season (De Vere et al., 2017). Further work highlighted how brambles (*Rubus* spp.), a dominant ground flora in many Welsh woodlands, are an increasing and important resource for honeybees throughout the summer months (Jones et al., 2021). These flowers are also critical for hoverflies; *R. fruticosus* agg. pollen is prevalent on hoverflies sampled in Welsh grasslands (Lucas et al., 2018). Floral provision well above ground-level, though rarely quantified, could also be crucial. For example, ivy *Hedera helix* is a major nectar provider in woodland ecosystems (Baude et al., 2016) and an increasingly dominant component of WLFs across Wales (Smart et al., 2017).

To ensure population-level increases, it is crucial to provide both nesting resources and food for larvae for wild pollinators. Woodlands in Wales and wider GB probably provide undisturbed nesting sites for many wild bee species, as indicated by recent modelling (Gardner et al., 2020). Woodland edges also provide larval food plants and buffered temperatures for dominant grass-feeding butterflies such as Ringlet *Aphantopus hyperantus* and Speckled Wood *Pararge aegeria* (Karlsson & Wiklund, 2005). Positive effects of woodland cover on hoverflies have previously been attributed to a supply of forest-specialist aphids (Sjödin et al., 2008), but benefits for detritivorous hoverflies probably relate to supply of moist, decaying plant material. Refugia and moderate microclimates provided by woodlands and WLFs are also critical. For example, the dominant predatory hoverfly *Episyrphus balteatus* has been observed to overwinter in forest edges in Southern France at various life stages (Sarthou et al., 2005).

Our focus on overall abundance of pollinator groups, giving emphasis to common and widespread species, ensures relevance to the magnitude of pollination function (Winfree et al., 2015). However, positive outcomes for pollinator abundance do not preclude negative outcomes for wild pollinator diversity (Zou et al., 2017). This seems particularly likely on cropland—a high-intensity land use, generally associated with low biodiversity—where we observed strikingly high abundances of forb-feeding butterflies and predatory hoverflies. Agricultural pest species were quite dominant in cropland butterfly communities (e.g. *Pieris rapae*, Table S1; almost 15% of individuals on cropland). Still, abundance and species richness of forb-feeding butterflies responded similarly to habitat type (Figure S1). As such, we attribute high pollinator biodiversity on cropland to (a) high availability of food for larvae, whether crops and weeds for butterflies (e.g. nettles for *Aglais urticae* caterpillars) or aphid prey for hoverflies (e.g. *Episyrphus balteatus*); (b) high floral cover among crops and margins (Figure 2); and (c) added floral resource heterogeneity, considering that cropland is not a dominant land use in Wales.

Until now, remarkably few studies have compared pollinator abundance between woodland and open farmland at scale. Interestingly, two studies which have previously compared woodland to open habitats have reported higher bee abundance in open habitats (Bartual et al., 2019; Scherber et al., 2019; Winfree et al., 2007), contrary to our findings. One explanation for this apparently conflicting result relates to woodland edges; these can support very high abundances of pollinator species (Sarthou et al., 2005), and were a component of woodland transects in this study. Further work is needed to compare pollinator abundance between woodland and open habitats in other regions, using a variety of survey methods not considered here (e.g. pan traps; malaise traps). Future studies might also survey pollinators within a wider seasonal window so that species with early or late flight periods are well represented; the present study only captures data on flowers and pollinators in July and August. Finally, future studies should use more advanced analytical methods to better understand the mechanisms behind effects of habitat composition and heterogeneity. For example, proportional covers of habitats could be represented as a set of mutually constrained continuous predictors, rather than using qualitative habitat categories, and models could include parameters that capture complementarity and redundancy between distinct habitat types. Ordination is one tool that can be used to condense several, highly correlated landscape-level drivers into salient predictors relating to land-use intensity and heterogeneity, and this approach has already been used to successfully predict pollinator diversity across Wales (Maskell et al., 2019).

Finally, we find disparity between *Apis* and non-*Apis* pollinators in the shape of the response to flower cover. As such, optimal agri-environmental management solutions will differ between honeybees and wild pollinators. More specifically, honeybees are expected to benefit greatly from introduction of highly concentrated floral resources, for example, dense patches of *Rosaceae* shrubs, to farmland with medium flower cover. On the contrary, wild pollinators can effectively utilise flowers established at low densities, for example, through a diverse seed mix including Asteraceae and Fabaceae, especially at sites which previously had almost zero flower cover (Alison et al., 2017; Freitag et al., 2021). Our findings therefore renew previous recommendations to target floral enhancements to flower-poor intensive grasslands—particularly to encourage species such as *Trifolium pratense*, *Lotus corniculatus* and *Centaurea nigra*. Still, any floral enrichments must be complemented by appropriate low-input, low-intensity grazing to ensure sustained increases in flower cover and pollinator abundance (Freitag et al., 2021).

5 | CONCLUSIONS

The importance of woodland for pollinators may have been under emphasised, especially in regions dominated by intensive grassland. To successfully reverse pollinator declines, future policies need to give balanced consideration to woodland restoration alongside well-known in-field AES interventions. If new land management schemes adopt 'payments for ecosystem services' frameworks, potential benefits of woodland and WLFs for pollinators should be accounted for. However, the context of woodland restoration must not be ignored. Pollinator benefits are most likely to be realised if native woodlands, rich in edges and managed gaps, are created on land which is currently flower-poor. We also propose further investigation into the role of agro-forestry in intensive grassland regions, and possible synergies between animal welfare, climate change mitigation and pollinator biodiversity.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

J.A. designed the study, carried out the data analysis and led the writing of the manuscript; A.G., L.C.M., J.S., S.M.S., B.L.W., C.M.W. and B.A.E. coordinated the GMEP field survey, of which M.B. and G.T. coordinated pollinator surveys. All authors made critical contributions to drafts of the manuscript.

DATA AVAILABILITY STATEMENT

Data used for these analyses are publicly available, at coarse spatial resolutions, from the NERC Environmental Information Data Centre (EIDC; Botham et al., 2020; Maskell et al., 2020a, 2020b). To enable reproduction of our analyses, we provide a lookup table of habitats, WLFs and elevation of each transect section on Dryad Digital

Repository (Alison, 2021). This table can be linked to the publicly available data on pollinator counts based on square ID and section ID (except for one discontinued square with ID marked 'NA').

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