Title: Critical habitat thresholds for effective pollinator conservation in agricultural landscapes

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Abstract: Biodiversity in human-dominated landscapes is declining, but evidence-based conservation targets to guide international policies for such landscapes are lacking. We present a framework for informing habitat conservation policies based on the enhancement of habitat quantity and quality and define thresholds of habitat quantity at which it becomes effective to also prioritize habitat quality. We applied this framework to insect pollinators, an important part of agroecosystem biodiversity, by synthesizing 59 studies from 19 countries. Given low habitat quality, hoverflies had the lowest threshold at 6% semi-natural habitat cover, followed by solitary bees (16%), bumble bees (18%), and butterflies (37%). These figures represent minimum habitat thresholds in agricultural landscapes, but when habitat quantity is restricted, marked increases in quality are required to reach similar outcomes.

Main Text: We are currently in a period of rapid biodiversity loss (*1*), a trend so drastic that scientists have raised the alarm of a possible global sixth mass extinction event (*2*). Species loss causes an associated decline in ecosystem functioning (*3*, *4*), which jeopardizes the delivery of critical ecosystem services on which humans rely (*5*, *6*). In an effort to slow and reverse this decline, conservation targets have been formulated for expanding protected areas, such as the Global Biodiversity Framework (GBF) target to conserve 30% of land, waters and sea by 2030 (*7*). The GBF also recognizes the role of human-dominated landscapes in biodiversity conservation, as all areas need to be managed to prevent biodiversity loss, and indicates that restoration should be conducted in 30% of degraded ecosystems and that biodiversity-friendly practices should be substantially increased (*7*). Conservation in so-called working landscapes (*8*), namely the agricultural areas that cover 44% of global habitable land (*9*), is essential to ensure the provision of services such as food production, soil retention, and cultural values (*6*, *10*). However, few area-based conservation targets exist for biodiversity within working landscapes, despite such targets being essential and persistent pillars of global conservation policies due to their feasibility and measurability at scale (*11*). Targets to date either remain general approximations (*12*, *13*) or focus exclusively on ecosystem service provision (*14*, *15*), which excludes the host of species that are not primary service providers (*16*). To enact biodiversity conservation in working landscapes, there is therefore an urgent need to determine evidence-based targets for international policy.

Here we present a framework to inform habitat requirements in decision making based on the response of species to changes in habitat quantity and quality, which can directly support conservation policy and practice. Currently enacted conservation policies in agricultural landscapes promote or in some cases mandate local-scale greening measures that typically either aim to increase habitat quantity, for example by planting native hedgerows, or aim to improve habitat quality, for example through the extensification of grassland management (*12, 17*). There is evidence that both strategies can contribute to biodiversity conservation (*17*), but how they interplay to impact species populations at landscape levels is unknown. Complex landscapes with greater natural habitat coverage generally support higher biodiversity levels in agricultural areas (*3*), but the need for food production imposes an inherent limit on natural habitat area in agricultural landscapes (*12*). It is therefore also important to invest in improving habitat quality, but these two strategies should be applied in a way that maximizes conservation impacts. Assuming greater species abundance with larger habitat area (Fig. 1A), the effect of enhancing habitat quality on species abundance will increase with increasing habitat area (Fig. 1B), as larger areas of habitat will have a greater effect than small ones. This leads to a habitat quantity threshold at which it is more effective to also enhance habitat quality (Fig. 1C). An effective minimum in terms of habitat area conservation can thus be defined as the point at which the marginal benefit for the population size of a focal species group from further increasing habitat area is less than that from improving habitat quality (Fig. 1C). Investing in habitat area up until this point, and also in habitat quality improvements after this point, represents an application of conservation policy in agricultural landscapes that is most beneficial in terms of outcomes for biodiversity.

We utilize this framework to calculate minimum habitat thresholds for the conservation of insect pollinators, a species group linked to food production that faces multiple threats recognized at the highest levels of international policymaking (*7*, *18*). Conservation efforts in agricultural areas generally positively impact local pollinator densities because of increased floral resource availability (*19*), an aspect of habitat quality that can directly indicate suitability for insect pollinators since they rely on floral resources to complete their life cycles (*20*). Pollinators have been proposed as useful bioindicators of ecosystem health (*21*) and are already monitored as such to estimate conservation progress (*22*), so results for this group are highly relevant for decision making in habitat conservation. However, to inform an evidence-based threshold for such policies that are increasingly aimed at pollinators, we need to know the relative impact of increasing habitat quantity or quality for conserving pollinator populations.

To determine a minimum habitat threshold across a wide range of agroecosystems, we synthesized 59 datasets representing 24487 sampling events of 178885 individual insect pollinators in 1250 agricultural landscapes from 19 countries (predominantly US and in Europe, figs. S1-S2; tables S1-S2). Pollinators were sampled in various types of natural and semi-natural habitats (hereafter referred to collectively as semi-natural habitats), but not crop fields, and included four main wild pollinator groups in temperate areas: bumble bees, solitary bees, hoverflies, and butterflies. Our systematic literature screen (see materials and methods, *23*) also identified a small number of datasets from the tropics (n=3), from which we could analyze bees as a pollinator group. First, we tested the effects of habitat quantity and quality on the local densities of pollinators in semi-natural habitats using mixed effects models (*23*). We focused on pollinator densities (abundance measurements) but not species richness because densities can be linearly extrapolated to landscape-level abundances in relation to habitat area (*24*). (Abundance and richness were highly correlated, see fig. S3.) We used local flower abundance (percentage cover) and richness as habitat quality indicators, and the amount of semi-natural habitat in the surrounding landscape (500 m radius (*25–28*)) as a habitat quantity indicator. While nesting and oviposition resources are also key components of habitat quality for insect pollinators, we focused on floral resources because they are more readily measured and are generally the most limiting resource for insect pollinators (*20, 29*). We included the presence of mass-flowering crops in study landscapes as a covariate, because these crops can alter pollinator population dynamics in agroecosystems (*30*). To examine how these local relationships translate to landscape-level abundances (*31*), we extrapolated modelled pollinator densities to the landscape scale by multiplying densities by the area coverage of semi-natural habitat in a landscape (*23*). Following the method of Fijen et al. (*32*), we used 20 quantiles representing the range of habitat quantity and quality measured in our datasets to vary levels of these variables in our predictions. At each of the 400 quantity-quality combinations, we calculated the relative gain in landscape-level pollinator abundance from enhancing habitat quantity or quality by one quantile step (*23*). With these calculations we identified the landscape context in which the marginal benefit of increasing habitat quality equals that of increasing habitat quantity, that is, how much semi-natural habitat should be conserved to support insect pollinators before also investing in habitat quality enhancements. These baseline minimums can be used to guide conservation practice in working landscapes.

Minimum habitat thresholds depend on species group

We found habitat coverage minimums that ranged from 5.5-38.1% (Fig. 2) depending on species group. In temperate regions, hoverflies had the lowest minimum habitat quantity level, at 5.5% semi-natural habitat cover, and butterflies the highest, at 37.0% (Figs. 2C-2D). Bumble bees and solitary bees had similar minimums, at 17.9% and 15.9%, respectively (Figs. 2A-2B). In the tropics, however, bees seemed to benefit from greater habitat area, as the minimum habitat coverage for this group was 38.1% (Fig. 2E). These differences across species groups suggest that there is no one-size-fits-all approach to pollinator conservation in agricultural areas, but that reaching minimums of 16-18% semi-natural habitat cover has greater impact than quality enhancements in temperate regions for both bees and hoverflies, the two groups that provide the majority of pollination (and, in the case of aphidophagous hoverflies, pest control) services to agriculture (*33*). Butterfly communities might only thrive in more complex landscapes with greater overall habitat coverage (*34–36*), indicating the importance of conserving larger habitat areas in landscapes where it is feasible to do so, to ensure effective butterfly conservation.

These differences in habitat minimums can largely be explained by differences in drivers of local pollinator densities across species groups (see figs. S5-S10 and tables S3-S7). For example, hoverflies had high densities (and large total abundances; Fig. 3C; fig. S4C; fig. S8), and comparatively strong relationships with floral resource variables (significantly predicted by flower richness, but marginally by flower cover; fig. S5B), so the relative gain in landscape-level abundance from enhancing habitat quality increased more rapidly than for other species groups (Fig. 2). The feeding ecology of hoverflies is diverse, but these high densities in relatively simple landscapes may be due to a majority of hoverfly individuals, made up of common species, utilizing cropland as oviposition sites to meet larval feeding requirements (*37*). Butterflies, on the other hand, were the only group whose density was significantly positively related to semi-natural habitat cover (fig. S5C), and had low densities (and relatively low total abundances; Fig. 3D; fig. S4D; fig. S9). Despite a positive relationship with flower cover (fig. S5C), habitat quantity thus had a strong influence on landscape-level butterfly abundance. While some butterflies, such as *Pieris rapae*, also can oviposit on crops, butterfly larval habitat requirements are often specialized, so butterflies are generally very sensitive to landscape simplification (*36*). This general reliance on surrounding habitat could explain the low butterfly densities in simplified agricultural areas (*35*, *38*), and could be driven by the importance of larger semi-natural habitat elements that act as butterfly population sources (*38*).

Furthermore, bees and hoverflies had comparatively lower habitat thresholds because of weak to absent effects of semi-natural habitat cover on local densities (figs. S5A-B; marginal effect fig. S5D; opposing trends fig. S6D), which challenges the generally held assumption that these groups are positively affected by surrounding landscape habitat quantity (*39*). While these groups have been found to respond to landscape resources at a number of scales, landscape effects on local densities are typically observed for pollinators within crop fields (*3*, *39*), whereas here we examine landscape effects on local densities in semi-natural habitats. Since crop fields are often disturbed habitats that do not provide permanent resources for pollinators, they are used transiently by pollinators that concentrate within fields from the surrounding landscape (*30*). Our finding suggests that in semi-natural habitat patches, which provide permanent resources for pollinators, bee and hoverfly densities and in turn the carrying capacity of a habitat patch are primarily determined by local habitat parameters (*40*), such as habitat quality. As with hoverflies, bumble bee and tropical bee densities were positively predicted by both flower cover and richness (figs. S6A-B; fig. S5D), while solitary bees were only significantly related to flower richness (fig. S5A). These results indicate that habitat quality enhancements can support bees and hoverflies regardless of surrounding landscape context. While our results refer to pollinator densities and not species richness, the strong effects of flower richness could be due to the support of a wider diversity of pollinator species (fig. S3), for example pollen specialists (*20*). Thus, our findings also suggest that when enhancing habitat quality, a particular emphasis should be placed on increasing the diversity of floral resources available to pollinators (*20*), rather than large displays of only a few flower species that may limit phenological resource availability (*41*).

The minimum habitat threshold for tropical bees should be interpreted with caution because only three studies, representing two countries and five study years, were analyzed for this group.

While conservation strategies should be context-dependent, our results tentatively suggest that in general relatively large amounts of semi-natural habitat should be conserved to support bees in the tropics. This could be due to tropical bee communities being relatively dominated by social bees (e.g., Apini and Meliponini), which are typically more sensitive to habitat loss and require season-long availability of diverse floral resources (*42*). Our results may have also been driven by the relatively small range in habitat quality represented by these three studies, which would have created relatively small marginal gains in landscape bee abundance with each quantile step. The number of studies detected for inclusion in our synthesis was likely biased due to our search language being English (*23*, *43*), as the three studies we included were conducted by English-speaking teams. Despite these uncertainties, habitat conservation for pollinators in the tropics will likely be important due to the high proportion of small farms that rely on biodiversity-mediated ecosystem service provision in these areas (*44*).

Conservation below, within, and beyond minimum habitat thresholds

Our framework for defining minimum habitat thresholds relies on the dual effects of habitat quantity and quality on upscaled landscape-level pollinator abundance. These thresholds assume that landscape habitat quality is low (Q1 in Fig. 2), which supports them as absolute minimums up to which habitat area conservation should be prioritized. With greater habitat quality, similar abundances are achieved with lower habitat cover than our minimums (fig. S4). However, our findings indicate that with greater habitat quality, the habitat quantity threshold actually increases (Fig. 2). This is because the gains from further improving the quality of a habitat that is already high in quality are smaller than those attained by increasing the area of high-quality habitat in the landscape. In other words, increases in habitat quality see diminishing returns in landscape-level abundances (Fig. 3). Hence, above our minimum habitat targets, the focus of conservation should be on a combination of quantity and quality enhancements. Furthermore, our data confirmed that in agricultural landscapes, both semi-natural habitat quality and quantity are typically low (*45*): across the temperate datasets, half of all surveys recorded flower cover and semi-natural habitat cover in the lowest quarter of the range (Fig. 3). This indicates that our framework, which is grounded in the restoration of intensive agricultural landscapes, is a realistic conceptualization that can inform conservation policy and practice. The framework can likely be generalized to various intensive agricultural contexts for pollinator conservation but also for other species groups for which simple habitat indicators can be defined. This prevalence of simple landscapes also indicates, however, that landscapes with large areas of existing semi-natural habitat should be conserved as much as possible, since they are likely important, and rare, harbors of farmland biodiversity.

Within our calculations of habitat minimums we assumed an equal feasibility of enhancing habitat quantity and quality (*23*), which does not consider the context-dependent costs or effort to increase quantity or quality that inherently influence the relative effectiveness of applying these conservation measures. For example, increasing habitat area may in some contexts be relatively more costly due to necessitating losses in agricultural production. To achieve the same increases in landscape pollinator abundances as increasing habitat quantity, habitat quality would have to be greatly enhanced. Given a landscape that could only sustain maximum 5% semi-natural habitat coverage, the quality of that habitat would have to be improved by increasing flower cover to approximately 4.8% and adding approximately 3.8 flower species (assuming equivalent nesting resource availability) to reach an equivalent bumble bee community size as supported by 17.9% habitat cover (fig. S4). While these numbers may sound meager, this flower cover level is greater than 82% of all observations across studies, indicating that it is a rather rare occurrence in agricultural landscapes. This tradeoff shows that in simple landscapes where increasing pollinator habitat may not be an option, efforts to enhance the quality of existing habitat should aim to increase flower abundance and diversity significantly.

Conservation tools outside of semi-natural habitats also have the potential to support pollinators. Our results showed that mass-flowering crop presence elevated bumble bee and solitary bee densities (figs. S6C-D; fig. S5A), but not those of other groups (figs. S5B-D). For bumble bees, however, this effect only occurred in simple landscapes (fig. S6C), possibly due to the presence of sufficient alternative floral resources in complex ones (*46*). Because we modelled average pollinator densities across all surveys in a given landscape regardless of crop flowering period (*23*)*,* we likely captured an overall effect of mass-flowering crop presence, as opposed to detecting specific dilution, concentration, or spillover dynamics (*47*). However, these patterns are likely driven by abundant, common species that preferentially visit agricultural crops (*16*). This general effect suggests that mass-flowering crops, although non-permanent resources due to blooming periods and crop rotation, can complement the restoration and enhancement of semi-natural habitats in supporting part of the bee community in temperate agricultural areas.

Finally, while habitat minimums provide useful guidelines, the types of habitats relevant to specific local contexts and their configuration should also be considered in conservation. For the purposes of estimating pollinator community sizes across landscapes, we assumed equal value of different types of semi-natural habitats, as well as equal distribution of pollinators among these habitat types (*23*). This might overestimate community sizes, leading to lower estimates of minimum habitat quantity due to more rapid increases in marginal benefits from habitat quality. In reality, we know that different pollinators prefer certain habitat types, for example due to their foraging, nesting or oviposition requirements (*34*, *48*), and that they can move between habitat types depending on their resource needs in space and time (*49*). This means that within the minimum recommendations for semi-natural habitat coverage, multiple types of semi-natural habitat (e.g., woody and herbaceous) should be conserved as much as possible (*50*) to increase nesting resources and the temporal continuity of floral resources (*41*, *49*). Conserving a variety of habitat types and ensuring connectivity of habitat patches has the potential to support a more diverse pollinator community (*39*, *50*), which is important for ecosystem functioning and resilience (*51*).

The minimum habitat thresholds identified in our synthesis can guide the design of conservation strategies by balancing quantity and quality enhancements for pollinators in working landscapes. The application of this framework to management decisions or other species groups should be further informed by local knowledge and conservation priorities, such as species of conservation concern and the specific resources they need for viable populations, which is not captured by our study. Overall, our findings demonstrate that current policy targets, such as the EU Biodiversity Strategy for 2030 goal of 10% high-diversity landscape features in agricultural areas (*13*), and the GBF restoration indicator of 10% natural cover in agricultural lands (*7*), are well below the thresholds that would most benefit pollinators, given that on average habitat quality is low. Future conservation policy for working landscapes should more strongly emphasize the need to conserve and restore more semi-natural habitat areas to achieve biodiversity gains, and should compensate landowners with incentives for marked improvements in habitat quality in landscapes where increases in habitat area are not feasible.

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Data and materials availability: Data and code are available via the Dryad Digital Repository (*52*). Study locations are available via Zenodo (*53*) by request only and will be made available for research purposes. Some study locations must be requested separately; this information can be found in the Zenodo entry and in Table S9.

Supplementary Materials

Materials and Methods

Supplementary Text

Figs. S1 to S10

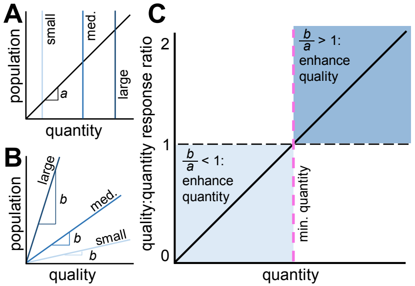
Tables S1 to S9

References (*54–179*)

Fig. 1. Minimum habitat quantity level for application of conservation measures as defined by the relative effectiveness of enhancing habitat quantity or quality. (A) Population size increases with increasing habitat quantity (*a*, which itself depends on habitat quality). This causes (B) the effect of habitat quality on population size (*b*) to increase with increasing habitat quantity (from small to medium [med.] to large), as enhancing larger habitat areas will have a greater effect than enhancing small ones. This leads to (C) increasing quality:quantity population response ratios (*b*/*a*) with increasing habitat quantity. The habitat quantity level at which the population response ratio = 1 can be seen as a minimum (min.) quantity level after which application of conservation practice should also enhance habitat quality.

Fig. 2. Relationships between the habitat quality to quantity population response ratio and the cover of landscape semi-natural habitat (SNH) for landscape-level pollinator abundances. (A) bumble bees, (B) solitary bees, (C) hoverflies, and (D) butterflies in temperate regions, and (E) tropical bees. Ratios < 1 indicate that increasing habitat quantity is most beneficial, while those > 1 indicate that habitat quality should also be prioritized. Q1-Q20 indicate quantiles of flower availability (flower cover and richness) based on the observed range across all studies (one quantile = 5% of the range). Minimum values of landscape SNH are marked where increasing habitat quality becomes more beneficial than increasing habitat quantity, assuming the lowest level of habitat quality (flower cover and richness quantile Q1; at Q20 the only option is to increase habitat quantity, so it is not shown).

Fig. 3. The relative gain in landscape-level pollinator abundances from increasing habitat quantity or quality. (A) bumble bees, (B) solitary bees, (C) hoverflies, and (D) butterflies in temperate regions, and (E) tropical bees. Quantity and quality are expressed across the 20 quantiles of the ranges observed in the datasets. Rightward or upward arrows indicate that increasing habitat quantity or quality is most beneficial, respectively. Arrow transparency indicates the number of samples that fall within a given quantity-quality combination (darkest arrows, highest number of samples; lightest arrows, no samples). Q1-Q20 indicate quantiles of flower availability (flower cover and richness) based on the observed range across all studies (one quantile = 5% of the range). SNH, semi-natural habitat.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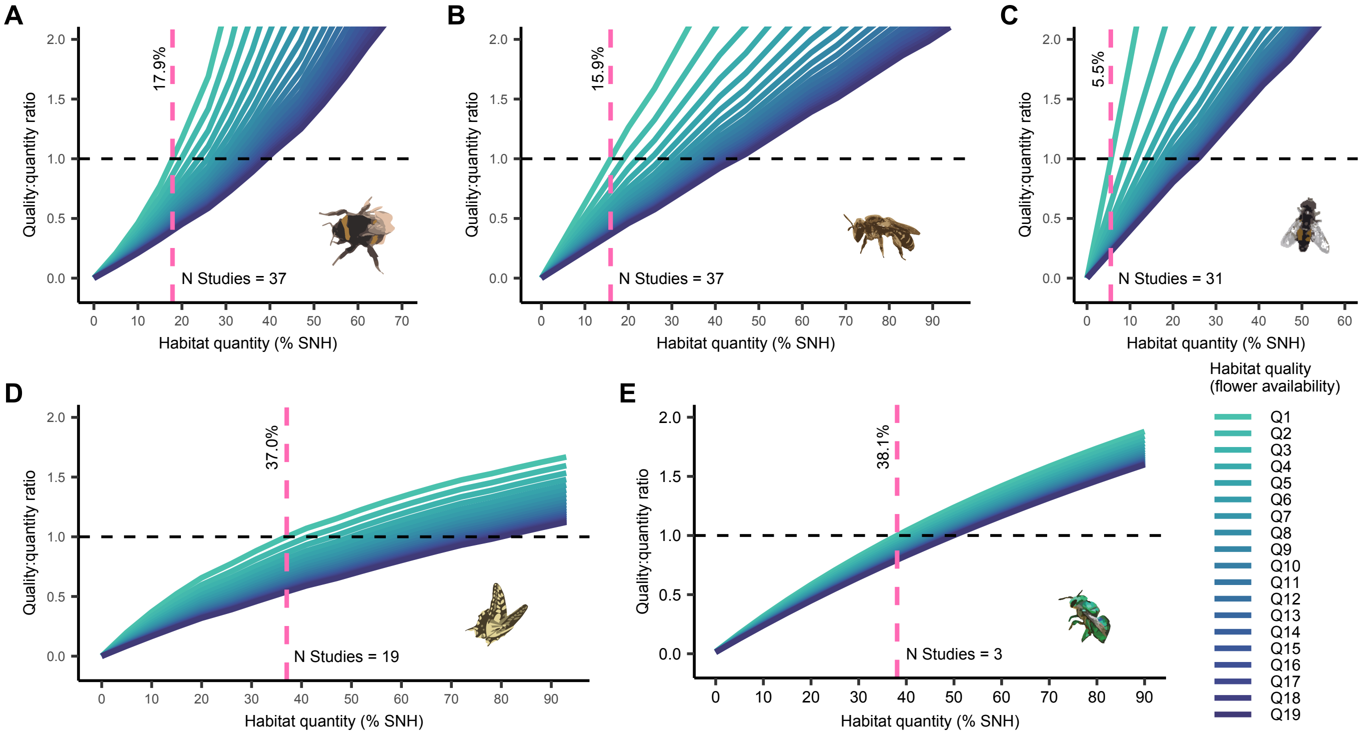
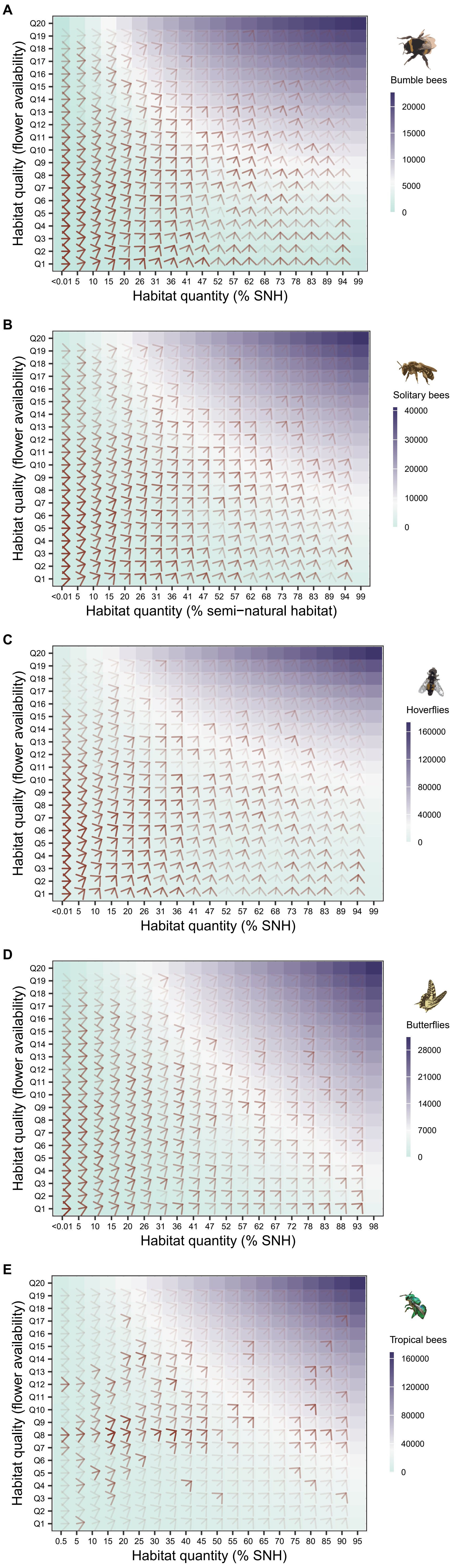

A
17.9%
N Studies = 37
Quality:quantity ratio
Habitat quantity (% SNH)
0.0
0.5
1.0
1.5
2.0
0
10
20
30
40
50
60
70
B
15.9%
N Studies = 37
Quality:quantity ratio
Habitat quantity (% SNH)
0
10
20
30
40
50
60
70
80
90
C
5.5%
N Studies = 31
Quality:quantity ratio
Habitat quantity (% SNH)
0
10
20
30
40
50
60
D
37.0%
N Studies = 19
Quality:quantity ratio
Habitat quantity (% SNH)
0
10
20
30
40
50
60
70
80
90
E
38.1%
N Studies = 3
Quality:quantity ratio
Habitat quantity (% SNH)
0
10
20
30
40
50
60
70
80
90
Habitat quality
(flower availability)
Q1
Q2
Q3
Q4
Q5
Q6
Q7
Q8
Q9
Q10
Q11
Q12
Q13
Q14
Q15
Q16
Q17
Q18
Q19


A
Habitat quality (flower availability)
Q20
Q19
Q18
Q17
Q16
Q15
Q14
Q13
Q12
Q11
Q10
Q9
Q8
Q7
Q6
Q5
Q4
Q3
Q2
Q1
<0.01 5 10 15 20 26 31 36 41 47 52 57 62 68 73 78 83 89 94 99
Habitat quantity (% SNH)
Bumble bees
20000
15000
10000
5000
0
B
Habitat quality (flower availability)
<0.01 5 10 15 20 26 31 36 41 47 52 57 62 68 73 78 83 89 94 99
Habitat quantity (% semi−natural habitat)
Solitary bees
40000
30000
20000
10000
0
C
Habitat quality (flower availability)
<0.01 5 10 15 20 26 31 36 41 47 52 57 62 68 73 78 83 89 94 99
Habitat quantity (% SNH)
Hoverflies
160000
120000
80000
40000
0
D
Habitat quality (flower availability)
<0.01 5 10 15 20 26 31 36 41 47 52 57 62 67 72 78 83 88 93 98
Habitat quantity (% SNH)
Butterflies
28000
21000
14000
7000
0
E
Habitat quality (flower availability)
0.5 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95
Habitat quantity (% SNH)
Tropical bees
160000
120000
80000
40000
0

Science
AAAS

Supplementary Materials for

Critical habitat thresholds for effective pollinator conservation in agricultural landscapes

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The PDF file includes:

Materials and Methods
Figs. S1 to S10
Tables S1 to S9
References (*54–179*)

Materials and Methods

Criteria definition

We predefined a list of criteria for the inclusion of datasets based on our research objective, which was to synthesize the effects of habitat quantity and quality variables on local pollinator densities and landscape pollinator abundances. We defined four main topic-based criteria (Box 1 "Criteria") to ensure studies measured wild insect pollinators and flowers in semi-natural habitats within agricultural areas. We focused on bees, hoverflies, and butterflies (including burnet moths) because they are best studied in agricultural landscapes due to their contributions to crop pollination (*33*) and their conservation concern (*34*). We used floral resources as habitat quality indicators because they are important to all the pollinator groups within our study (*20, 29*). While nesting and oviposition resources can also be considered habitat quality indicators because they are important for pollinator reproduction, we chose to focus on floral resources because these are more easily and commonly measured and because resources for reproduction are generally captured by the amount of non-productive habitat in a given landscape (*29*). We considered all natural and semi-natural herbaceous and woody habitats, including extensive grasslands and perennial (older than one year) wildflower strips but excluding rotational or otherwise intensively managed areas, as semi-natural habitats. We defined seven specific criteria related to sampling methods and sample size for standardization and data quality purposes. We required studies to have sampled pollinators in a defined surface area and for a defined time duration to be able to calculate a standardized density of pollinators per area and sampling time, which was necessary for upscaling pollinator densities to the landscape scale. Butterfly sampling was not required to have a defined sampling duration because the standard accepted method in the field for sampling this group ("Pollard walks"; (*54*)) is not timed. We furthermore required studies to have sampled both flower richness and flower cover, since we use these variables as habitat quality proxies. We required flower cover to be measured quantitatively, such as flower counts or area coverage, so that flower cover for all studies could be uniformly calculated in units of percentage cover. Studies had to have measured pollinators in different landscapes (i.e., sufficient spatial replication; minimum 500 m radius), with at least ten landscapes and 20 total data points (sampling events). This allowed us to evaluate the effect of landscape context (% semi-natural habitat cover) and have a base level of replication to do so. If datasets met these requirements, we asked data owners to confirm two additional criteria. We required site coordinates for calculating surrounding landscape characteristics and spatial autocorrelation. We also required that studies covered a minimum gradient of 10% in semi-natural habitat cover, that is, that the study sampled a variety of landscape contexts, since evaluating the effects of habitat quantity and quality across a range of landscape contexts was a primary research objective.

Box 1. Criteria

Title-abstract screening

a. Species groups: wild bees, wild bumble bees, hoverflies, or butterflies (including burnet moths)
b. Locations: agricultural landscapes
c. Habitat types: semi-natural habitats (not crop fields)
d. Environmental variables: flowers

Full-text screening

a. Sampling method: defined area (not e.g. pan traps)
b. Sampling method: defined time per unit area (excl. butterflies)
c. Environmental variables: floral richness and floral cover at the time of pollinator sampling
d. Sampling method: quantitative* measure of floral cover
e. Locations: different landscapes (buffer min. 500 m)**
f. Sample size: at least 10 landscapes
g. Sample size: at least 20 data points

Additional screening

a. Data: coordinate availability
b. Locations: range in landscape semi-natural habitat cover > 10%

*We accepted studies that counted flowers or that measured flower area or percentage cover. We only accepted studies using qualitative scales if the scale could be readily and accurately translated into percentage cover (e.g., Domin scale; (*55*)).
**The study might not have organized its sampling locations into landscapes, but we required enough spatial replication to do so.

Literature search and screening

We followed guidelines from the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) (*56*) in conducting our literature screening. We utilized two literature databases to evaluate published literature, and additionally solicited research networks for unpublished datasets. We first created a “naïve” search string based on our four main topic criteria. This search string of 19 terms (Box 2 “Search strings”) was expanded to a string of 87 terms using litsearchr, an R package that performs quasi-automatic search string development for systematic reviews (*57*), according to the approach of Grames et al. (*58*). We retrieved articles in English from Web of Science and Scopus on 19/09/22. We first screened titles and abstracts based on our first four criteria. When relevant review or synthesis papers were encountered, we retained these (17 in total) for reference “snowballing”, i.e., adding the studies that those papers cited and/or synthesized to the overall group of studies for screening. Studies that met our criteria at the title and abstract stage were evaluated based on the full text for our seven additional criteria. All screening was performed by one author using the online tool CADIMA (*59*). When a study met all of our full-text criteria, we contacted the corresponding author to request the dataset and to evaluate our two additional criteria, which could not always be deduced from the text. We additionally gathered eight datasets external to our literature screen that met our criteria. The PRISMA flow diagram representing our study screening is presented in fig. S1.

Box 2. Search strings

“Naïve” search string

("pollinator*" OR "bee*" OR "bumblebee*" OR "hoverfl*" OR "hover fl*" OR "butterfl*") AND ("floral resource*" OR "flower*" OR "forb*") AND ("landscape*" OR "semi-natural habitat*" OR "natural habitat*") AND ("agricultur*" OR "agroeco*" OR "farm*")

Final Scopus search string

(“floral* visitor*” OR “flower-visit* insect*” OR “flower* visitor*” OR “hover* flies” OR “pollin* insect*” OR apida* OR apoidea* OR bee OR bombus* OR butterfl* OR hoverfl* OR lasioglossum* OR lepidoptera* OR osmia* OR pollin* OR syrphid* OR bumble bee*) AND (“forag* avail*” OR “forag* plant*” OR “forag* resourc*” OR “habitat* qualit*” OR “resourc* abund*” OR “resourc* avail*” OR “resourc* provis*” OR floral* OR flower* OR forb* OR nectar* OR pollen*) AND (“adjac* habitat*” OR “buffer* strip*” OR “field* border*” OR “field* boundar*” OR “field* margin*” OR “flower-rich* habitat*” OR “flower* field*” OR “flower* patch*” OR “flower* strip*” OR “forag* habitat*” OR “habitat* featur*” OR “habitat* patch*” OR “habitat* type*” OR “landscap* element*” OR “landscap* featur*” OR “natur* area*” OR “natur* habitat*” OR “non-crop* habitat*” OR “pollin* habitat*” OR “suitabl* habitat*” OR “wood* habitat*” OR “field* edge” OR “forest* edge” OR grassland* OR hedg* OR pastur* OR “road* verg*” OR semi-natur* OR “wildflow* plant*”) AND (“agricultur* area*” OR “agricultur* ecosystem*” OR “agricultur* environ*” OR “agricultur* field*” OR “agricultur* habitat*” OR “agricultur* manag*” OR “agricultur* practic*” OR “agricultur* product*” OR “agricultur* region*” OR “agricultur* site*” OR “agricultur* system*” OR “arabl* field*” OR “cultiv* field*” OR “cultiv* land*” OR “manag* agricultur*” OR “manag* field*” OR “manag* grassland*” OR “manag* landscap*” OR “rural* landscap*” OR agri-environ* OR “agricultur* land*” OR agricultur* OR agro-ecosystem* OR agroecosystem* OR “arabl* land*” OR crop* OR cultiv* OR farm* OR “adjac* field*”)

(cont. below)

Box 2 (cont.). Search strings

Final Web of Science search string (variation in formatting)

(((TI=(“floral* visitor*” OR “flower-visit* insect*” OR “flower* visitor*” OR “hover* flies” OR “pollin* insect*” OR apida* OR apoidea* OR bee OR bombus* OR butterfl* OR hoverfl* OR lasioglossum* OR lepidoptera* OR osmia* OR pollin* OR syrphid* OR bumblebee*)) OR (AB= (“floral* visitor*” OR “flower-visit* insect*” OR “flower* visitor*” OR “hover* flies” OR “pollin* insect*” OR apida* OR apoidea* OR bee OR bombus* OR butterfl* OR hoverfl* OR lasioglossum* OR lepidoptera* OR osmia* OR pollin* OR syrphid* OR bumblebee*)) OR (AK= (“floral* visitor*” OR “flower-visit* insect*” OR “flower* visitor*” OR “hover* flies” OR “pollin* insect*” OR apida* OR apoidea* OR bee OR bombus* OR butterfl* OR hoverfl* OR lasioglossum* OR lepidoptera* OR osmia* OR pollin* OR syrphid* OR bumble bee*))) AND ((TI= (“forag* avail*” OR “forag* plant*” OR “forag* resourc*” OR “habitat* qualit*” OR “resourc* abund*” OR “resourc* avail*” OR “resourc* provis*” OR floral* OR flower* OR forb* OR nectar* OR pollen*)) OR (AB= (“forag* avail*” OR “forag* plant*” OR “forag* resourc*” OR “habitat* qualit*” OR “resourc* abund*” OR “resourc* avail*” OR “resourc* provis*” OR floral* OR flower* OR forb* OR nectar* OR pollen*)) OR (AK= (“forag* avail*” OR “forag* plant*” OR “forag* resourc*” OR “habitat* qualit*” OR “resourc* abund*” OR “resourc* avail*” OR “resourc* provis*” OR floral* OR flower* OR forb* OR nectar* OR pollen*))) AND ((TI= (“adjac* habitat*” OR “buffer* strip*” OR “field* border*” OR “field* boundar*” OR “field* margin*” OR “flower-rich* habitat*” OR “flower* field*” OR “flower* patch*” OR “flower* strip*” OR “forag* habitat*” OR “habitat* featur*” OR “habitat* patch*” OR “habitat* type*” OR “landscap* element*” OR “landscap* featur*” OR “natur* area*” OR “natur* habitat*” OR “non-crop* habitat*” OR “pollin* habitat*” OR “suitabl* habitat*” OR “wood* habitat*” OR “field* edge” OR “forest* edge” OR grassland* OR hedg* OR pastur* OR “road* verg*” OR semi-natur* OR “wildflow* plant*”)) OR (AB= (“adjac* habitat*” OR “buffer* strip*” OR “field* border*” OR “field* boundar*” OR “field* margin*” OR “flower-rich* habitat*” OR “flower* field*” OR “flower* patch*” OR “flower* strip*” OR “forag* habitat*” OR “habitat* featur*” OR “habitat* patch*” OR “habitat* type*” OR “landscap* element*” OR “landscap* featur*” OR “natur* area*” OR “natur* habitat*” OR “non-crop* habitat*” OR “pollin* habitat*” OR “suitabl* habitat*” OR “wood* habitat*” OR “field* edge” OR “forest* edge” OR grassland* OR hedg* OR pastur* OR “road* verg*” OR semi-natur* OR “wildflow* plant*”)) OR (AK= (“adjac* habitat*” OR “buffer* strip*” OR “field* border*” OR “field* boundar*” OR “field* margin*” OR “flower-rich* habitat*” OR “flower* field*” OR “flower* patch*” OR “flower* strip*” OR “forag* habitat*” OR “habitat* featur*” OR “habitat* patch*” OR “habitat* type*” OR “landscap* element*” OR “landscap* featur*” OR “natur* area*” OR “natur* habitat*” OR “non-crop* habitat*” OR “pollin* habitat*” OR “suitabl* habitat*” OR “wood* habitat*” OR “field* edge” OR “forest* edge” OR grassland* OR hedg* OR pastur* OR “road* verg*” OR semi-natur* OR “wildflow* plant*”))) AND ((TI= (“agricultur* area*” OR “agricultur* ecosystem*” OR “agricultur* environ*” OR “agricultur* field*” OR “agricultur* habitat*” OR “agricultur* manag*” OR “agricultur* practic*” OR “agricultur* product*” OR “agricultur* region*” OR “agricultur* site*” OR “agricultur* system*” OR “arabl* field*” OR “cultiv* field*” OR “cultiv* land*” OR “manag* agricultur*” OR “manag* field*” OR “manag* grassland*” OR “manag* landscap*” OR “rural* landscap*” OR agri-environ* OR “agricultur* land*” OR agricultur* OR agro-ecosystem* OR agroecosystem* OR “arabl* land*” OR crop* OR cultiv* OR farm* OR “adjac* field*”)) OR (AB= (“agricultur* area*” OR “agricultur* ecosystem*” OR “agricultur* environ*” OR “agricultur* field*” OR “agricultur* habitat*” OR “agricultur* manag*” OR “agricultur* practic*” OR “agricultur* product*” OR “agricultur* region*” OR “agricultur* site*” OR “agricultur* system*” OR “arabl* field*” OR “cultiv* field*” OR “cultiv* land*” OR “manag* agricultur*” OR “manag* field*” OR “manag* grassland*” OR “manag* landscap*” OR “rural* landscap*” OR agri-environ* OR “agricultur* land*” OR agricultur* OR agro-ecosystem* OR agroecosystem* OR “arabl* land*” OR crop* OR cultiv* OR farm* OR “adjac* field*”)) OR (AK= (“agricultur* area*” OR “agricultur* ecosystem*” OR “agricultur* environ*” OR “agricultur* field*” OR “agricultur* habitat*” OR “agricultur* manag*” OR “agricultur* practic*” OR “agricultur* product*” OR “agricultur* region*” OR “agricultur* site*” OR “agricultur* system*” OR “arabl* field*” OR “cultiv* field*” OR “cultiv* land*” OR “manag* agricultur*” OR “manag* field*” OR “manag* grassland*” OR “manag* landscap*” OR “rural* landscap*” OR agri-environ* OR “agricultur* land*” OR agricultur* OR agro-ecosystem* OR agroecosystem* OR “arabl* land*” OR crop* OR cultiv* OR farm* OR “adjac* field*”)))

Data preparation

We extracted data on three local-scale and two landscape-scale variables from each dataset. The three local-scale variables were pollinator (bumble bee, solitary bee, hoverfly, butterfly) densities, flower cover, and flower richness. We separated bumble bees and solitary bees due to their differences in life history and different geographic distributions (*60*). While Halictidae do exhibit social behaviors (*61*), here we separate truly eusocial bees (*Bombus*) from other bees and for simplicity refer to all non-*Bombus* bees in temperate regions as solitary. We separately analyzed datasets from the tropics, and we had enough data to include bees from tropical regions as a pollinator group, but not enough data for other species groups. In the tropics social bees (e.g., wild *Apis* spp.) can make up a majority of the bee community (*60*), so these were combined with other wild bees. *Apis mellifera* counts were excluded from all datasets because they were always managed, and our study focused on the conservation of wild pollinators. The landscape-scale variables were the percentage cover of semi-natural habitat and the presence of a blooming mass-flowering crop in the surrounding landscape (500 m radius) during the sampling period.

Local variables

Pollinator densities and floral resources (flower cover and richness of plants in bloom) were first calculated on the lowest sampling unit per study (e.g., quadrat or transect). If flower data were provided as counts, the flower area was calculated according to the methods of Scheper et al. (*62*) by multiplying the number of flowers per species (in some cases approximate, if flowers were recorded in umbels, heads, or stems) by an average flower area based on direct measurements and key botanical resources (*63–72*) and summing the area across species to yield total flower area. This area was divided by the sampling area to result in percentage flower cover. When flowers were sub-sampled (e.g., in sub-quadrats) within the sampling area, flower cover was first calculated per sub-sample and then averaged across sub-samples, while flower richness was calculated as the total number of unique species across sub-samples. To combine studies into one model, data were aggregated to landscapes within studies, which was the lowest common grouping factor across studies. This allowed us to model general relationships between habitat variables and pollinator densities regardless of differences across studies in sampling periods or number of surveys. We furthermore aggregated data across sampled habitat types to generalize these aforementioned relationships, which themselves capture inherent quality differences among habitats. Floral resource variables were averaged across samples within landscapes. Bee and hoverfly densities were standardized per landscape according to the following equation:

$$D = \frac{\sum_{i=1}^{n} P_i}{\sqrt{\frac{\sum_{i=1}^{n} A_i \times \sum_{i=1}^{n} T_i}{150 \times 15}}}$$

with D being the average pollinator density per 150 m^2 and 15 min sampling effort, P_i being the abundance of pollinators recorded in a sample within a landscape, and A_i and T_i being the area and time surveyed per sample within a landscape, in m^2 and min, respectively. We chose to standardize to densities per 150 m^2 and 15 min because these were the median survey efforts used for bees and hoverflies. For butterflies, the equation was slightly different, because surveys were not necessarily timed. In addition, the median survey area was larger (300 m^2), so we divided the sum of butterflies by the sum of area surveyed over 300, per landscape. If a study had

≥ 50% of landscapes with zero pollinators recorded for a given species group, we excluded that species group from the study for data quality purposes.

Landscape composition

While landscape composition can be represented by several variables, we chose total pollinator habitat quantity as a landscape habitat indicator so that we could model pollinator density responses to landscape habitat availability and to extrapolate local densities to landscape abundances (see subsection Analysis). We calculated the % semi-natural habitat in a 500 m radius surrounding the center of each study landscape. We chose this radius because it captured a landscape habitat resources scale relevant to all pollinator groups included in our study (*25–28*), in particular because it represents the upper end of average foraging distances for the central-place foraging pollinators in our study (*25*). For studies that did not have sampling locations already grouped into landscapes, individual sampling sites were manually assigned to groups to create landscapes of minimum 500 m radius (i.e., minimum 1 km apart). The center of a landscape was defined as the geodesic centroid between grouped sampling locations, when applicable. Using these points, the semi-natural habitat cover was calculated in a 500 m buffer based on available land use/land cover GIS data relevant to the study area and period (*73–90*) using the sf (*91*) and raster (*92*) R packages. Semi-natural habitat was defined as forests (plantations were not distinguishable), shrublands, heath, (semi-)natural grasslands, wetlands, and (semi-)natural vegetation elements within the agricultural matrix. The only exception to this was Study G (table S1), for which we only included the habitat type in which sampling occurred (grasslands), because otherwise nearly the entire study area was estimated to be semi-natural habitat by the available data source (*90*) due to the high classification of tree cover. If no GIS data were available, or if zeroes were produced due to the coarseness of GIS data layers, we either a) used the semi-natural habitat cover in a 500 m radius provided by the dataset, b) estimated road verge semi-natural habitat cover, often the only remnant pollinator habitat in nearly cleared agricultural landscapes (*93*), by applying a 1 m buffer around roads in the study landscapes (*73*, *94–97*), or c) estimated semi-natural habitat cover manually by tracing habitat patches using satellite images in GoogleEarth. We furthermore estimated the presence or absence of a blooming mass-flowering crop (Yes/No) in study landscapes (at any point in the study period, since samples were averaged within landscapes) based on available cropland GIS layers (*98–104*) and information provided by the data owners.

Analysis

All statistical analyses were conducted in R version 4.1.2 (*105*). We constructed linear mixed models using glmmTMB (*106*) for the four separate pollinator groups (bumble bees, solitary bees, hoverflies, and butterflies) from temperate regions, and an additional model for bees from tropical regions. These models tested the effects of local and landscape variables on the local densities of pollinators in semi-natural habitats. The $\log_{10}(+1)$-transformed densities of pollinators were used as response variables, and flower richness, flower cover, % semi-natural habitat, and blooming mass-flowering crop presence were predictor variables. We included an interaction between blooming mass-flowering crop presence and % semi-natural habitat to test if the effect of crop floral resources on pollinator densities depended on the amount of alternative habitat available in the landscape (and therefore alternative floral resources). We did not include an interaction between flower variables and % semi-natural habitat (habitat quality and habitat quantity interaction) since here these variables represent effects on the local scale only. While a plausible interaction, it did not represent our research objective, which was to explore the combined effects of habitat quantity and quality on pollinator abundance at the landscape scale instead (see below). We did however check that we were not missing this interaction (see below). We furthermore included the average survey area and average survey minutes per landscape as covariates to control for the effect of actual survey effort on our calculated densities. Because they were right-skewed, average survey area, average survey minutes, flower cover, and flower richness were all log-transformed to improve the linearity of the modelled relationship. All continuous predictor variables were standardized (i.e., z-scores) across all studies to aid model convergence and to compare effect sizes. We additionally added weights to each datapoint using the number of observations per landscape (on which the standardized pollinator densities were based) to control for variation in sample sizes, and therefore robustness of the relationships, both within and across studies.

Following the methods of Dainese et al. (*3*), we used study-year combinations as the highest hierarchical unit because the majority of studies (n=40) only had one year of data collection and studies with multiple years often varied site locations across years. Furthermore, interannual variability in pollinator abundances (*107*) can allow different years of data collection within the same study to be regarded separately. Study-year was thus fit as a random intercept to capture differences between studies, and random slopes were fit for each study-year for both of the floral resource variables. This allowed us to control for differences among studies in flower abundance sampling methods and in the total area of the flower survey, which would influence floral richness. We did not include a random slope for semi-natural habitat cover because it was calculated uniformly for all datasets, and because we aimed to model the effect of this variable across its entire range instead of only within the ranges in each individual study. Because random slopes caused model convergence issues in the tropical bees model (due to the small number of studies), we instead centered floral resource variables within studies before standardizing across studies, which approximates within-study relationships between floral resources and pollinator density (*108*). However, this prevents floral resource variables from being expressed on an absolute scale in landscape-scale extrapolations (see below). Due to the presence of spatial autocorrelation in the four temperate region models, which was evaluated with the DHARMa package (*109*) and by comparing semivariograms to expected semivariances (*110*), we included a Matern correlation structure using the spatial coordinates of each study landscape. We inspected residual plots to evaluate model assumptions, and we confirmed that all variance inflation factors were below 4 (*111*) using the performance package (*112*). Partial residual plots were inspected using the effects package (*113*) to ensure the linearity of relationships and the absence of unmodelled interactions (*114*). We used log-likelihood ratio tests to evaluate model fixed effects and dropped the interaction term from the model if it was not significant.

Since mass-flowering crop presence was not necessarily a within-study factor for every study (i.e., some studies had all landscapes with mass-flowering crops, or all landscapes without), we checked the robustness of our results for this fixed effect by repeating our models with only the subset of studies that had mass-flowering crop presence as a within-study factor. This check revealed that effects for this factor were consistent (table S8).

As a secondary analysis step, we extrapolated pollinator densities to the landscape scale to evaluate the relative impact of improving habitat quantity or quality in different landscape contexts. Following the method of Fijen et al. (*32*), we separated both habitat quantity (% landscape semi-natural habitat) and habitat quality (both floral resource variables) into 20 quantiles (i.e., steps representing 5% of the range) along the entire range observed in the included studies. For the tropics model, this was a relative range for the floral resource variables, since we centered these variables within studies and thus the values were not comparable across studies. We then created a matrix made up of predicted pollinator densities based on our models at each of the combinations between the 20 quantity and quality quantiles, while holding crop flowering and sampling effort constant (mass-flowering crop = no; area surveyed = 150 m^2 [or, for butterflies, 300 m^2]; time surveyed = 15 min). For the bumble bee model, which had a significant interaction between mass-flowering crop flowering and landscape semi-natural habitat (Fig. 4D; table S3), we predicted at an "average" level of mass-flowering crop flowering to more accurately model the effect of habitat quantity (*115*). Next we extrapolated these pollinator densities to the landscape scale by multiplying the (back-transformed) density per m^2 (predicted density / 150 or 300) by the coverage in m^2 of semi-natural habitat in the landscape (% semi-natural habitat of the given quantile / 100 * π * 500^2) (*31*, *46*), assuming a linear abundance-area relationship (*24*). Using these results we calculated the quality:quantity population response ratio by dividing the population increase with one quantile increase in habitat quality by the population increase with one quantile increase in habitat quantity for each quality-quantity combination in the matrix. This ratio assumes equal feasibility of enhancing either quality or quantity by one quantile. We defined the habitat quantity level at which the ratio = 1 for the lowest quality quantile as the minimum recommended landscape habitat coverage for application of habitat conservation measures for pollinator community size. All plots were constructed using the ggeffects (*115*), ggplot2 (*116*), viridis (*117*), and gridExtra (*118*) packages.

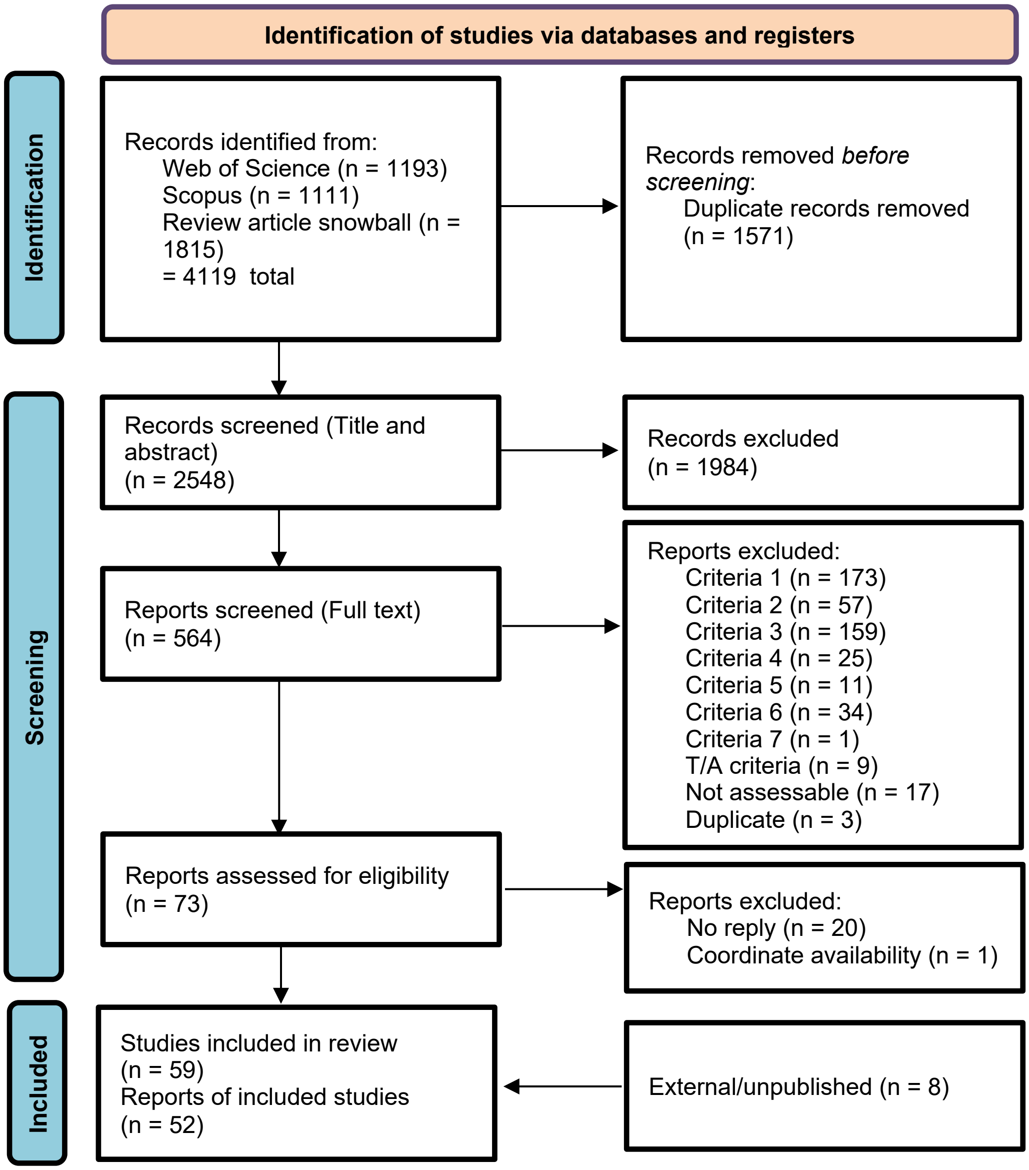


Fig. S1.

PRISMA flow diagram of study selection. T/A = Title / abstract. The total tally of included studies does not align with the total tally of reports (published articles) because some datasets are reported in multiple publications, and some publications report on multiple datasets.

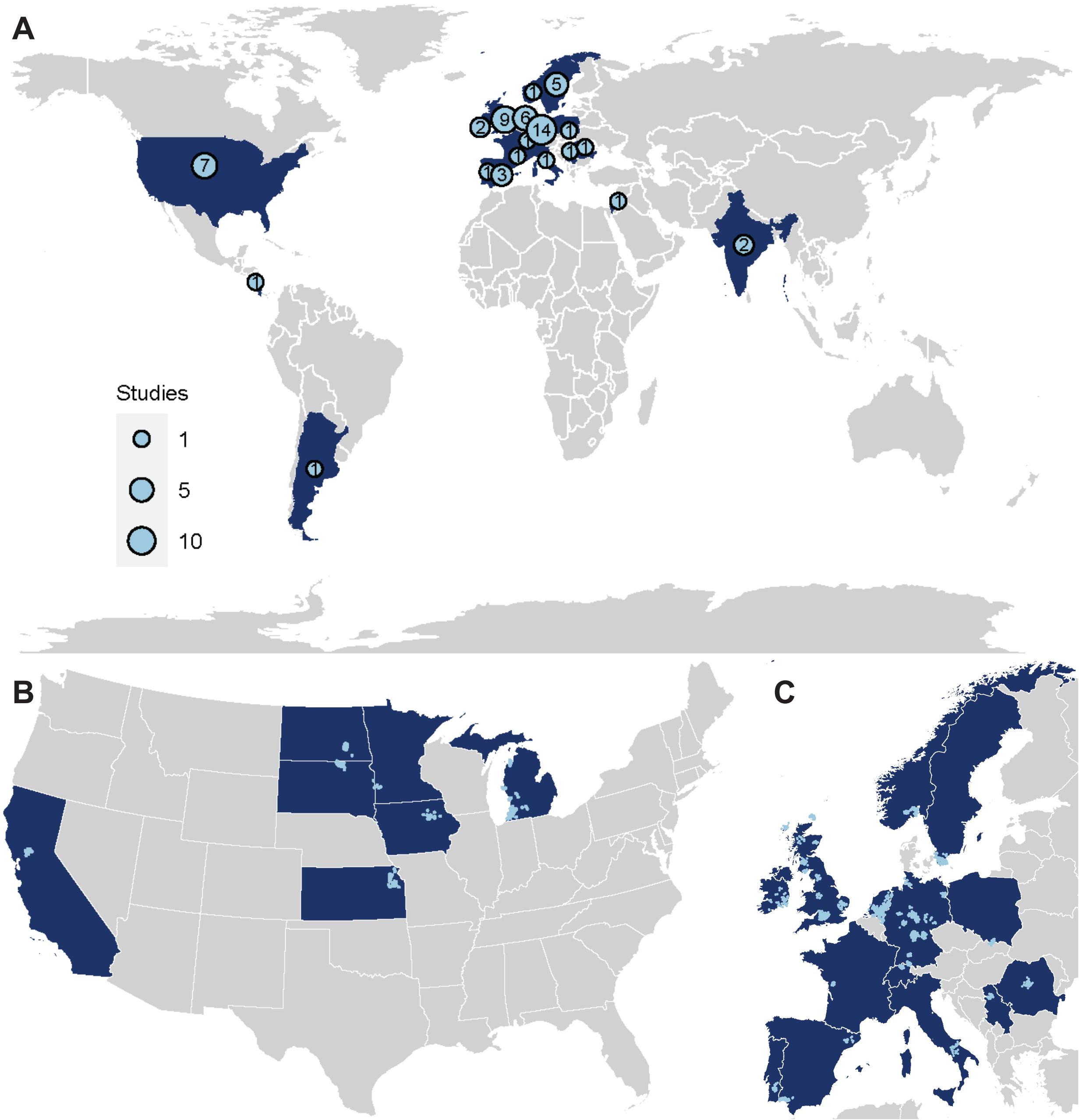


Fig. S2.

Countries from which datasets were collected. (A) Number of studies per country, (B) study landscapes in the USA, (C) study landscapes in Europe. Random jitter has been added to points to obscure exact locations and improve visibility.

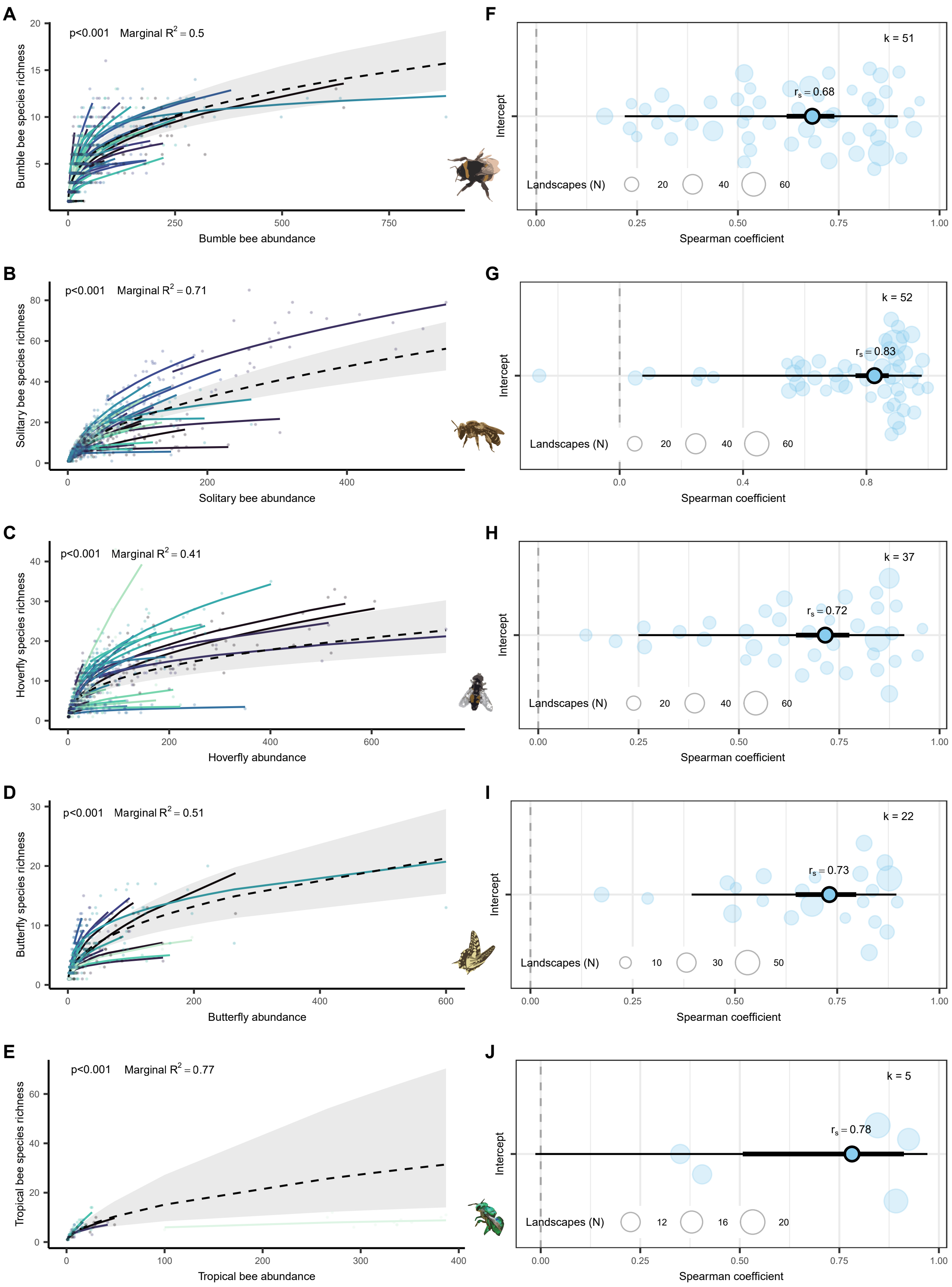
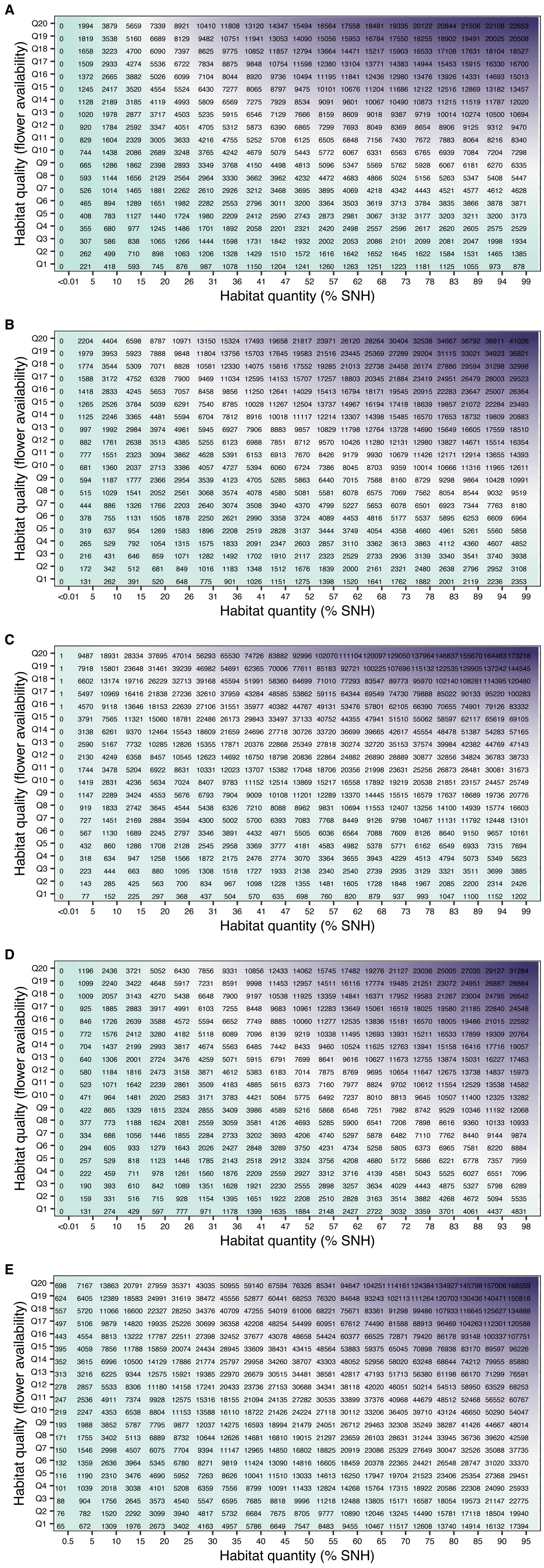

A
p<0.001 Marginal R² = 0.5
Bumble bee species richness
Bumble bee abundance
0
250
500
750
5
10
15
20
F
k = 51
rs = 0.68
Intercept
Landscapes (N)
20
40
60
Spearman coefficient
0.00
0.25
0.50
0.75
1.00
B
p<0.001 Marginal R² = 0.71
Solitary bee species richness
Solitary bee abundance
0
200
400
20
40
60
80
G
k = 52
rs = 0.83
Intercept
Landscapes (N)
20
40
60
Spearman coefficient
0.0
0.4
0.8
C
p<0.001 Marginal R² = 0.41
Hoverfly species richness
Hoverfly abundance
0
200
400
600
10
20
30
40
H
k = 37
rs = 0.72
Intercept
Landscapes (N)
20
40
60
Spearman coefficient
0.00
0.25
0.50
0.75
1.00
D
p<0.001 Marginal R² = 0.51
Butterfly species richness
Butterfly abundance
0
200
400
600
10
20
30
I
k = 22
rs = 0.73
Intercept
Landscapes (N)
10
30
50
Spearman coefficient
0.00
0.25
0.50
0.75
1.00
E
p<0.001 Marginal R² = 0.77
Tropical bee species richness
Tropical bee abundance
0
100
200
300
400
20
40
60
J
k = 5
rs = 0.78
Intercept
Landscapes (N)
12
16
20
Spearman coefficient
0.00
0.25
0.50
0.75
1.00

Fig. S3.

Relationships between species abundance and richness. Bumble bees (A, F), solitary bees (B, G), hoverflies (C, H), and butterflies (D, I) in temperate regions, and tropical bees (E, J). (A-E) Linear mixed models of species richness per landscape weighted by sample size, with study-years marked with different colors and the overall trend marked with a dashed line and 95% CI. (F-I) Meta-analytic models of Spearman coefficients per study-year, calculated across landscapes within study-years. k indicates the number of study-years included in the model; not all studies had species richness information available.



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Q19	0	1819	3538	5160	6689	8129	9482	10751	11941	13053	14090	15056	15953	16784	17550	18255	18902	19491	20025	20508
Q18	0	1658	3223	4700	6090	7397	8625	9775	10852	11857	12794	13664	14471	15217	15903	16533	17108	17631	18104	18527
Q17	0	1509	2933	4274	5536	6722	7834	8875	9848	10754	11598	12380	13104	13771	14383	14944	15453	15915	16330	16700
Q16	0	1372	2665	3882	5026	6099	7104	8044	8920	9736	10494	11195	11841	12436	12980	13476	13926	14331	14693	15013
Q15	0	1245	2417	3520	4554	5524	6430	7277	8065	8797	9475	10101	10676	11204	11686	12122	12516	12869	13182	13457
Q14	0	1128	2189	3185	4119	4993	5809	6569	7275	7929	8534	9091	9601	10067	10490	10873	11215	11519	11787	12020
Q13	0	1020	1978	2877	3717	4503	5235	5915	6546	7129	7666	8159	8609	9018	9387	9719	10014	10274	10500	10694
Q12	0	920	1784	2592	3347	4051	4705	5312	5873	6390	6865	7299	7693	8049	8369	8654	8906	9125	9312	9470
Q11	0	829	1604	2329	3005	3633	4216	4755	5252	5708	6125	6505	6848	7156	7430	7672	7883	8064	8216	8340
Q10	0	744	1438	2086	2689	3248	3765	4242	4679	5079	5443	5772	6067	6331	6563	6765	6939	7084	7204	7298
Q9	0	665	1286	1862	2398	2893	3349	3768	4150	4498	4813	5096	5347	5569	5762	5928	6067	6181	6270	6335
Q8	0	593	1144	1656	2129	2564	2964	3330	3662	3962	4232	4472	4683	4866	5024	5156	5263	5347	5408	5447
Q7	0	526	1014	1465	1881	2262	2610	2926	3212	3468	3695	3895	4069	4218	4342	4443	4521	4577	4612	4628
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Q5	0	408	783	1127	1440	1724	1980	2209	2412	2590	2743	2873	2981	3067	3132	3177	3203	3211	3200	3173
Q4	0	355	680	977	1245	1486	1701	1892	2058	2201	2321	2420	2498	2557	2596	2617	2620	2605	2575	2529
Q3	0	307	586	838	1065	1266	1444	1598	1731	1842	1932	2002	2053	2086	2101	2099	2081	2047	1998	1934
Q2	0	262	499	710	898	1063	1206	1328	1429	1510	1572	1616	1642	1652	1645	1622	1584	1531	1465	1385
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Q19	0	1979	3953	5923	7888	9848	11804	13756	15703	17645	19583	21516	23445	25369	27289	29204	31115	33021	34923	36821
Q18	0	1774	3544	5309	7071	8828	10581	12330	14075	15816	17552	19285	21013	22738	24458	26174	27886	29594	31298	32998
Q17	0	1588	3172	4752	6328	7900	9469	11034	12595	14153	15707	17257	18803	20345	21884	23419	24951	26479	28003	29523
Q16	0	1418	2833	4245	5653	7057	8458	9856	11250	12641	14029	15413	16794	18171	19545	20915	22283	23647	25007	26364
Q15	0	1265	2526	3784	5039	6291	7540	8785	10028	11267	12504	13737	14967	16194	17418	18639	19857	21072	22284	23493
Q14	0	1125	2246	3365	4481	5594	6704	7812	8916	10018	11117	12214	13307	14398	15485	16570	17653	18732	19809	20883
Q13	0	997	1992	2984	3974	4961	5945	6927	7906	8883	9857	10829	11798	12764	13728	14690	15649	16605	17559	18510
Q12	0	882	1761	2638	3513	4385	5255	6123	6988	7851	8712	9570	10426	11280	12131	12980	13827	14671	15514	16354
Q11	0	777	1551	2323	3094	3862	4628	5391	6153	6913	7670	8426	9179	9930	10679	11426	12171	12914	13655	14393
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Q9	0	594	1187	1777	2366	2954	3539	4123	4705	5285	5863	6440	7015	7588	8160	8729	9298	9864	10428	10991
Q8	0	515	1029	1541	2052	2561	3068	3574	4078	4580	5081	5581	6078	6575	7069	7562	8054	8544	9032	9519
Q7	0	444	886	1326	1766	2203	2640	3074	3508	3940	4370	4799	5227	5653	6078	6501	6923	7344	7763	8180
Q6	0	378	755	1131	1505	1878	2250	2621	2990	3358	3724	4089	4453	4816	5177	5537	5895	6253	6609	6964
Q5	0	319	637	954	1269	1583	1896	2208	2519	2828	3137	3444	3749	4054	4358	4660	4961	5261	5560	5858
Q4	0	265	529	792	1054	1315	1575	1833	2091	2347	2603	2857	3110	3362	3613	3863	4112	4360	4607	4852
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Q2	0	172	342	512	681	849	1016	1183	1348	1512	1676	1839	2000	2161	2321	2480	2638	2796	2952	3108
Q1	0	131	262	391	520	648	775	901	1026	1151	1275	1398	1520	1641	1762	1882	2001	2119	2236	2353

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Q19	1	7918	15801	23648	31461	39239	46982	54691	62365	70006	77611	85183	92721	100225	107696	115132	122535	129905	137242	144545
Q18	1	6602	13174	19716	26229	32713	39168	45594	51991	58360	64699	71010	77293	83547	89773	95970	102140	108281	114395	120480
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Q15	0	3791	7565	11321	15060	18781	22486	26173	29843	33497	37133	40752	44355	47941	51510	55062	58597	62117	65619	69105
Q14	0	3138	6261	9370	12464	15543	18609	21659	24696	27718	30726	33720	36699	39665	42617	45554	48478	51387	54283	57165
Q13	0	2590	5167	7732	10285	12826	15355	17871	20376	22868	25349	27818	30274	32720	35153	37574	39984	42382	44769	47143
Q12	0	2130	4249	6358	8457	10545	12623	14692	16750	18798	20836	22864	24882	26890	28889	30877	32856	34824	36783	38733
Q11	0	1744	3478	5204	6922	8631	10331	12023	13707	15382	17048	18706	20356	21998	23631	25256	26873	28481	30081	31673
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Q19	0	1099	2240	3422	4648	5917	7231	8591	9998	11453	12957	14511	16116	17774	19485	21251	23072	24951	26887	28884
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Q17	0	925	1885	2883	3917	4991	6103	7255	8448	9683	10961	12283	13649	15061	16519	18025	19580	21185	22840	24548
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Q15	0	772	1576	2412	3280	4182	5118	6089	7096	8139	9219	10338	11495	12693	13931	15211	16533	17899	19309	20764
Q14	0	704	1437	2199	2993	3817	4674	5563	6485	7442	8433	9460	10524	11625	12763	13941	15158	16416	17716	19057
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Q5	0	257	529	818	1123	1446	1785	2143	2518	2912	3324	3756	4208	4680	5172	5686	6221	6778	7357	7959
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Q3	0	190	393	610	842	1089	1351	1628	1921	2230	2555	2898	3257	3634	4029	4443	4875	5327	5798	6289
Q2	0	159	331	516	715	928	1154	1395	1651	1922	2208	2510	2828	3163	3514	3882	4268	4672	5094	5535
Q1	0	131	274	429	597	777	971	1178	1399	1635	1884	2148	2427	2722	3032	3359	3701	4061	4437	4831

	0.5	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95
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Q18	557	5720	11066	16600	22327	28250	34376	40709	47255	54019	61006	68221	75671	83361	91298	99486	107933	116645	125627	134888
Q17	497	5106	9879	14820	19935	25226	30699	36358	42208	48254	54499	60951	67612	74490	81588	88913	96469	104263	112301	120588
Q16	443	4554	8813	13222	17787	22511	27398	32452	37677	43078	48658	54424	60377	66525	72871	79420	86178	93148	100337	107751
Q15	395	4059	7856	11788	15859	20074	24434	28945	33609	38431	43415	48564	53883	59375	65045	70898	76938	83170	89597	96226
Q14	352	3615	6996	10500	14129	17886	21774	25797	29958	34260	38707	43303	48052	52956	58020	63248	68644	74212	79955	85880
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Q11	247	2536	4911	7374	9928	12575	15316	18155	21094	24135	27282	30535	33899	37376	40968	44679	48512	52468	56552	60767
Q10	219	2247	4353	6538	8804	11153	13588	16110	18722	21426	24224	27118	30112	33206	36405	39710	43124	46650	50290	54047
Q9	193	1988	3852	5787	7795	9877	12037	14275	16593	18994	21479	24051	26712	29463	32308	35249	38287	41426	44667	48014
Q8	171	1755	3402	5113	6889	8732	10644	12626	14681	16810	19015	21297	23659	26103	28631	31244	33945	36736	39620	42598
Q7	150	1546	2998	4507	6075	7704	9394	11147	12965	14850	16802	18825	20919	23086	25329	27649	30047	32526	35088	37735
Q6	132	1359	2636	3964	5345	6780	8271	9819	11424	13090	14816	16605	18459	20378	22365	24421	26548	28747	31020	33370
Q5	116	1190	2310	3476	4690	5952	7263	8626	10041	11510	13033	14613	16250	17947	19704	21523	23406	25354	27368	29451
Q4	101	1039	2018	3038	4101	5208	6359	7556	8799	10091	11433	12824	14268	15764	17315	18922	20586	22308	24090	25933
Q3	88	904	1756	2645	3573	4540	5547	6595	7685	8818	9996	11218	12488	13805	15171	16587	18054	19573	21147	22775
Q2	76	782	1520	2292	3099	3940	4817	5732	6684	7675	8705	9777	10890	12046	13245	14490	15781	17118	18504	19940
Q1	65	672	1309	1976	2673	3402	4163	4957	5786	6649	7547	8483	9455	10467	11517	12608	13740	14914	16132	17394

Fig. S4.

The relative gain in landscape-level pollinator abundances from increasing habitat quantity and quality. (A) bumble bees, (B) solitary bees, (C) hoverflies, and (D) butterflies in temperate regions, and (E) tropical bees. Quantity and quality are expressed across the 20 quantiles of the ranges observed in the datasets. Matrix values represent back-transformed predicted abundances, rounded to the nearest integer. Q1-Q20 indicate quantiles of flower availability (flower cover and richness). Shading indicates the transition from low to high pollinator abundances. SNH, semi-natural habitat.

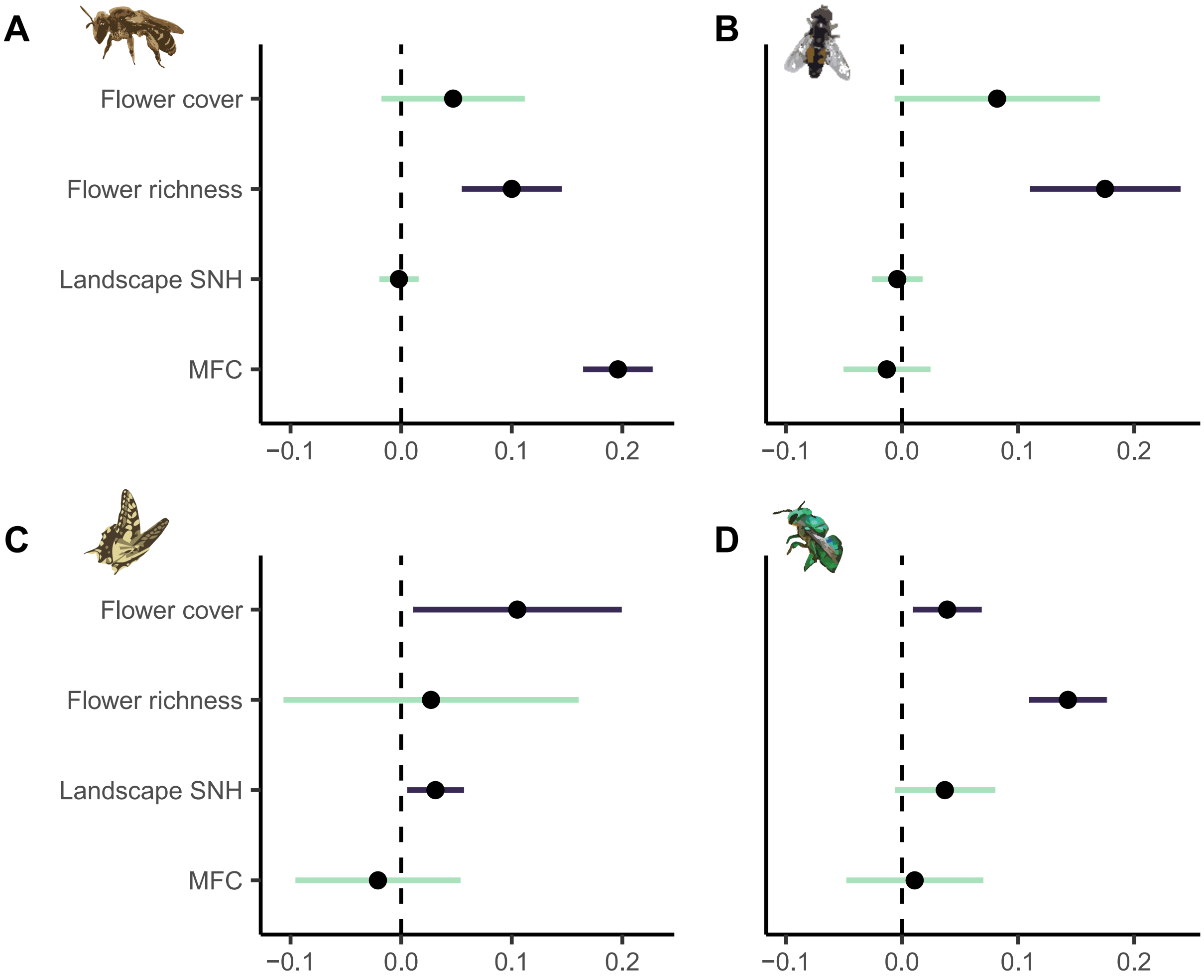

Fig. S5.

Standardized beta coefficients and 95% confidence intervals for linear mixed model main effects predicting local pollinator densities (log scale). (A) solitary bees, (B) hoverflies, and (C) butterflies in temperate regions, and (D) tropical bees. See fig. S5 for bumble bee model main and interaction effects. Dark confidence intervals do not overlap zero ($p < 0.05$). MFC, mass-flowering crop presence. SNH, semi-natural habitat. For effects visualizations, see figs. S7-S10, and for coefficient evaluations see tables S4-S7.

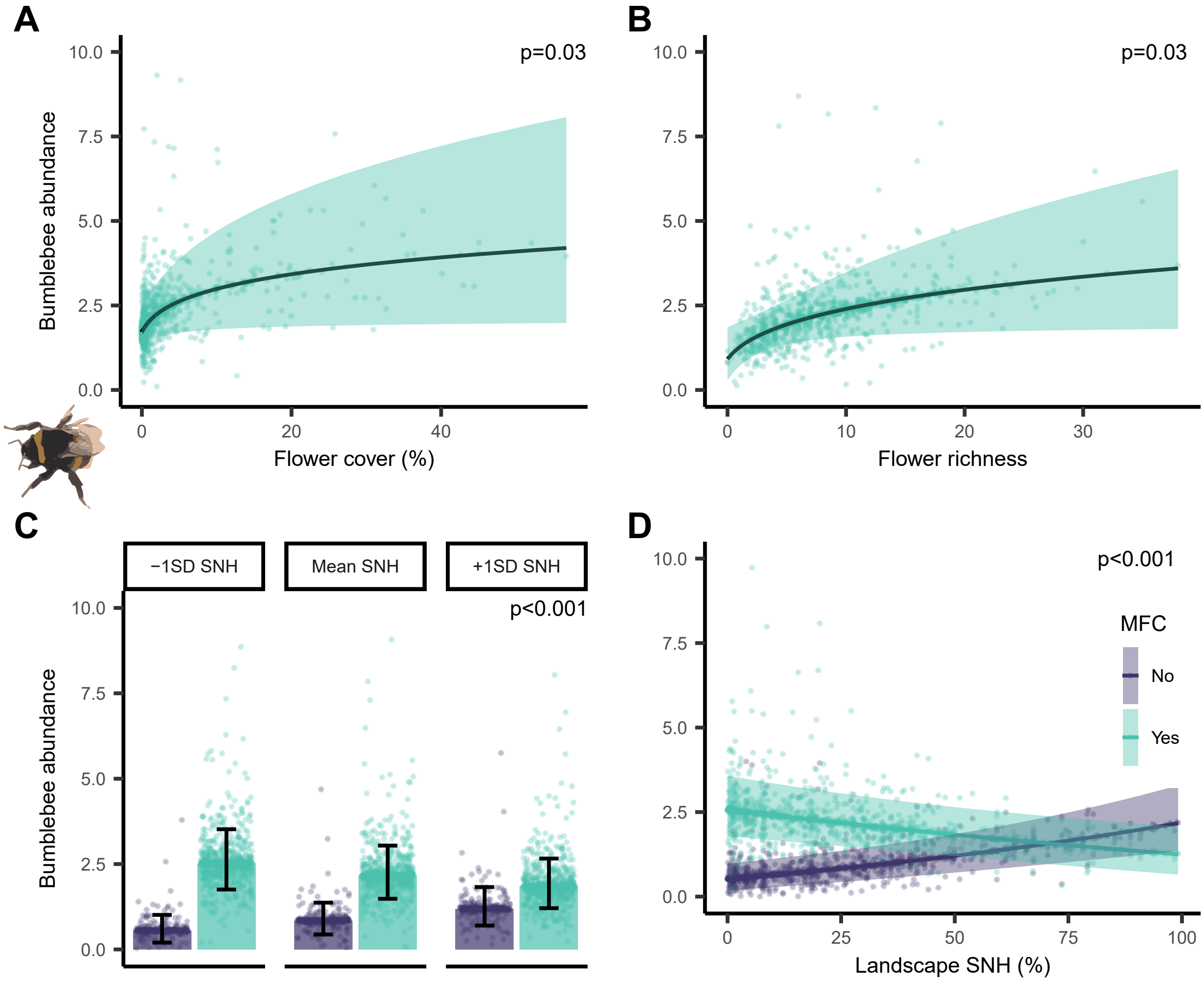

Fig. S6.

Conditional effects of local and landscape habitat parameters on local bumble bee densities. (A) flower cover, (B) flower richness, (C) mass-flowering crop (MFC) presence, and D) landscape semi-natural habitat (SNH). Panels (C) and (D) illustrate the significant interaction between SNH and MFC presence. Abundances are expressed per 150 m^2 and 15 min sampling. Points represent back-transformed partial residuals. SD, standard deviation. For model coefficients, see table S3.

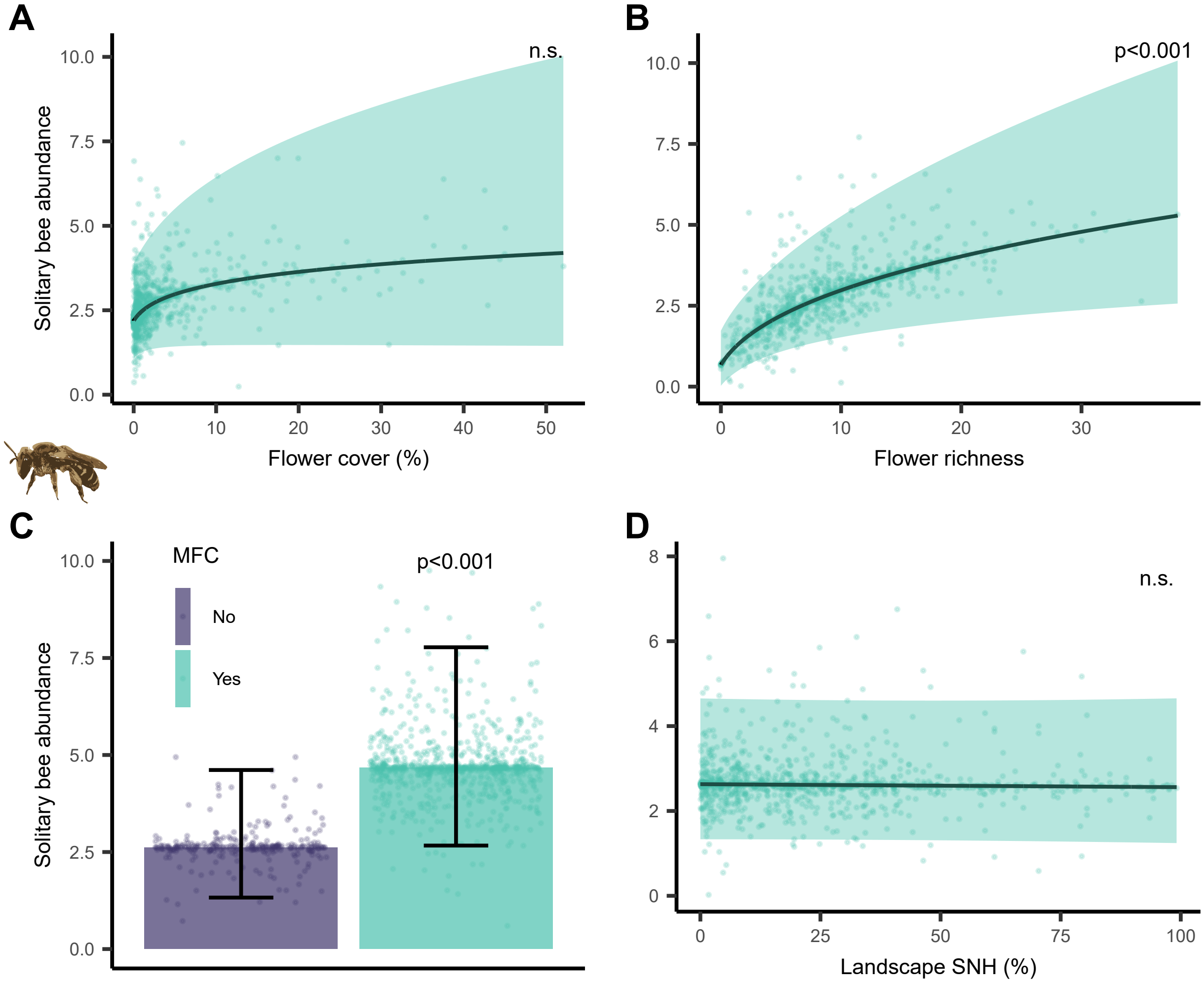

Fig. S7.

Conditional effects of local and landscape habitat parameters on local solitary bee densities in temperate regions. (A) flower cover, (B) flower richness, (C) mass-flowering crop (MFC) presence, and (D) landscape semi-natural habitat (SNH). Abundances are expressed per 150 m^2 and 15 min sampling. Points represent back-transformed partial residuals. SD, standard deviation. For model coefficients, see table S4.

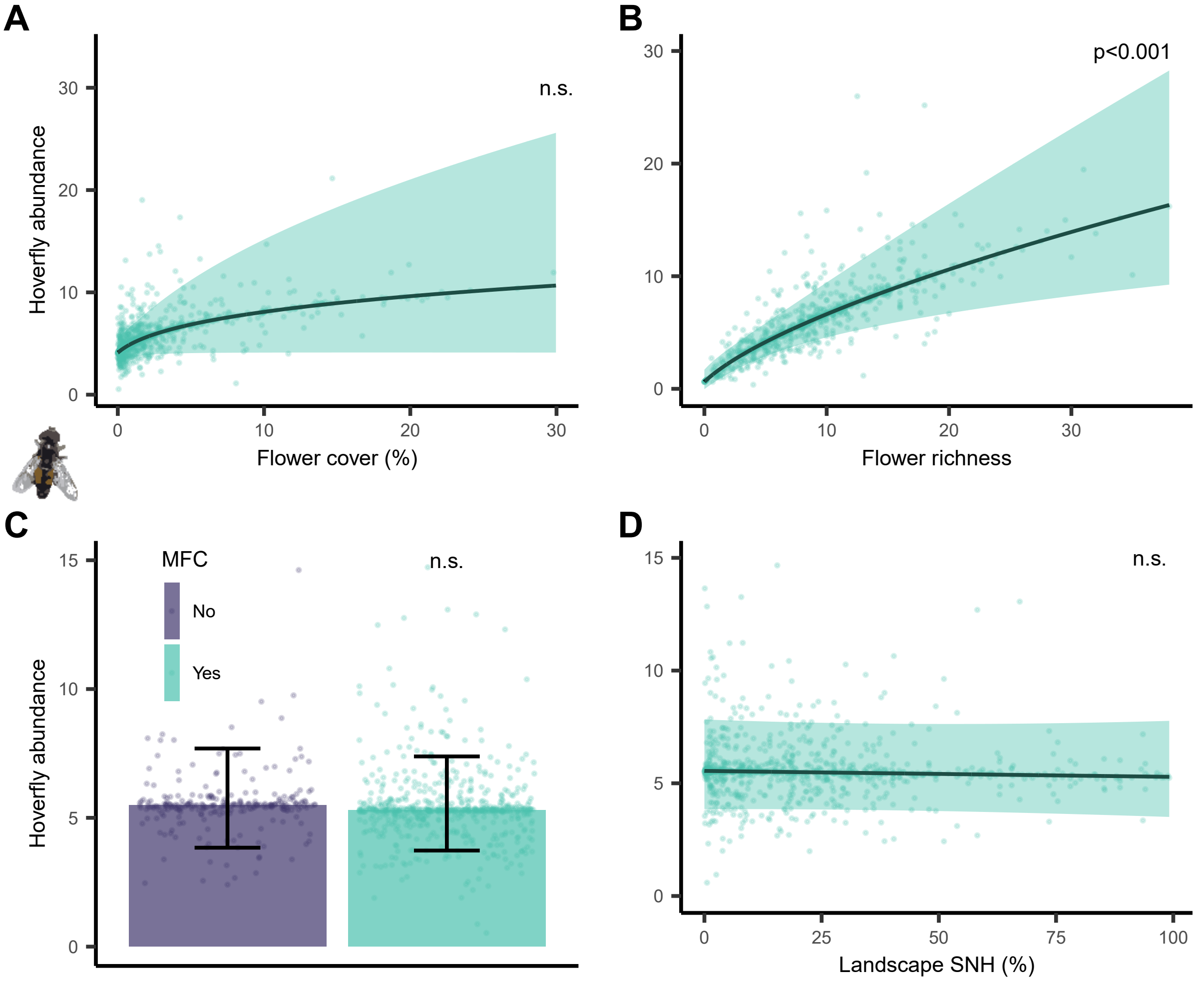

Fig. S8.

Conditional effects of local and landscape habitat parameters on local hoverfly densities in temperate regions. (A) flower cover, (B) flower richness, (C) mass-flowering crop (MFC) presence, and (D) landscape semi-natural habitat (SNH). Abundances are expressed per 150 m^2 and 15 min sampling. Points represent back-transformed partial residuals. SD, standard deviation. For model coefficients, see table S5.

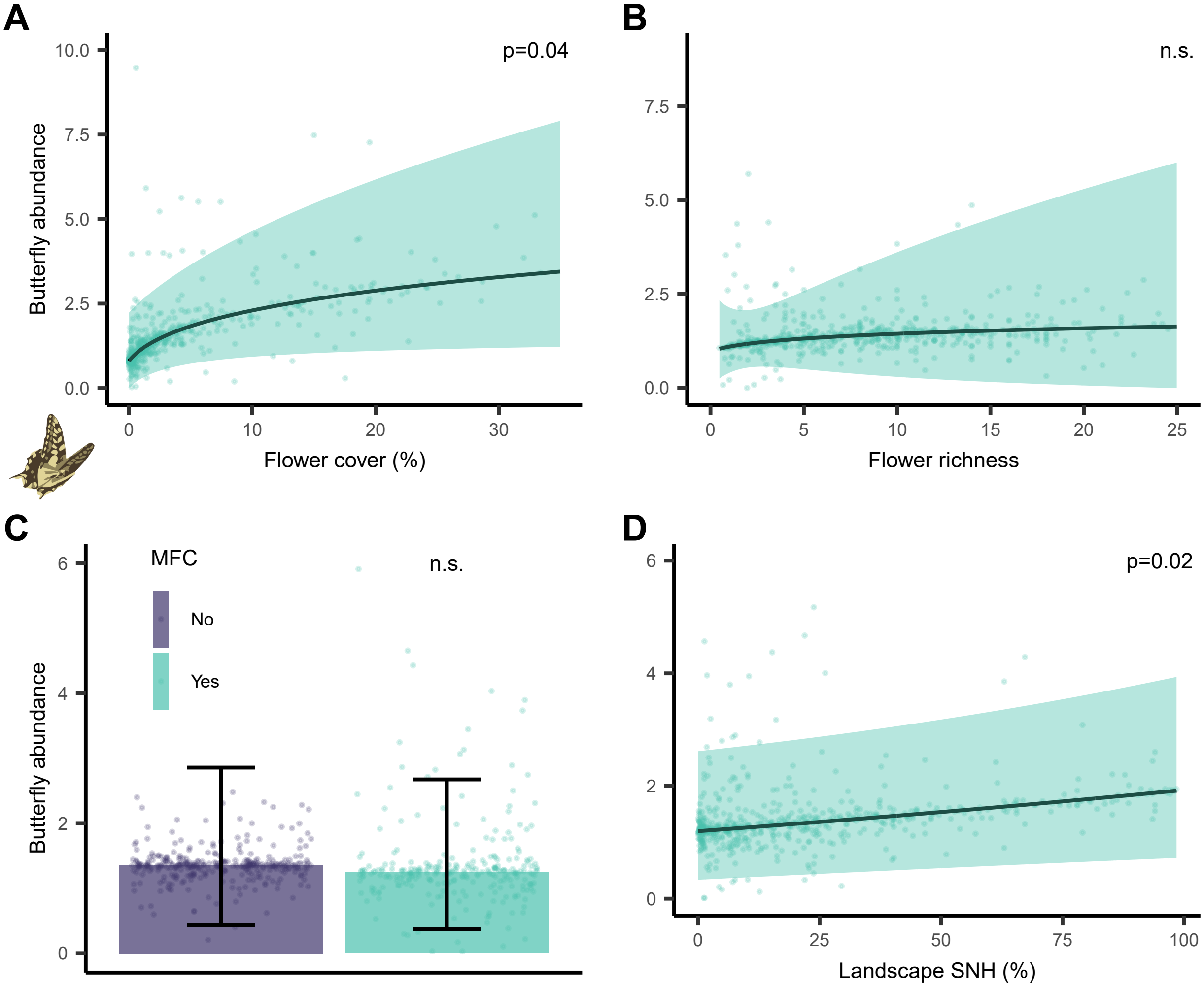

Fig. S9.

Conditional effects of local and landscape habitat parameters on local butterfly densities in temperate regions. (A) flower cover, (B) flower richness, (C) mass-flowering crop (MFC) presence, and (D) landscape semi-natural habitat (SNH). Abundances are expressed per 300 m^2. Points represent back-transformed partial residuals. SD, standard deviation. For model coefficients, see table S6.

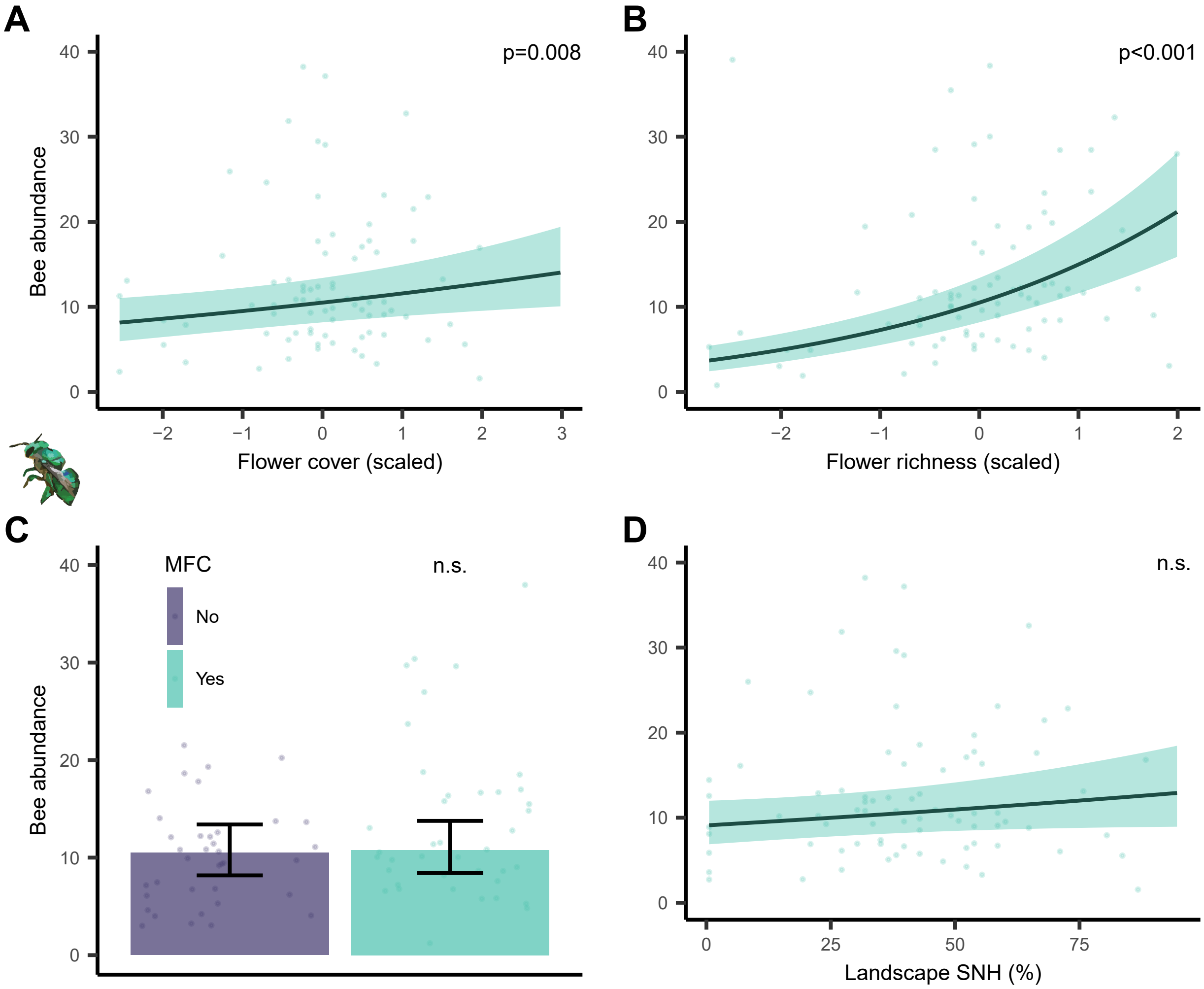

Fig. S10.

Conditional effects of local and landscape habitat parameters on local tropical bee densities. (A) flower cover, (B) flower richness, (C) mass-flowering crop (MFC) presence, and (D) landscape semi-natural habitat (SNH). Abundances are expressed per 150 m^2 and 15 min sampling. Points represent back-transformed partial residuals. SD, standard deviation. For model coefficients, see table S7.

Table S1.

Studies included in the synthesis. Landscapes are counted within year, and samples within landscapes.

Study	Country	Bumble bees	Solitary bees	Hoverflies	Butterflies	Tropical bees	Sampling effort		Habitat type	N Years	N Landscapes	N Samples	Publication
							m^2	min					
A	UK				X		Various	NA	Various	1	95	4173	Unpublished
B	Spain	X	X	X			200	30	Forest	1	16	112	(*119*)[a]
C	India					X	9	90	Various	1	20	60	(*120*)
D	Germany	X	X	X			400	10	Field margins	1	30	630	(*121*)
E	Germany	X	X	X			250	5	Various	1	30	540	(*122*)
F	Sweden	X					50	20	Various	1	17	152	(*123*)
G	Costa Rica					X	400	15	Grasslands	3	49	95	(*124*, *125*)
H	USA	X	X				200	60	Various	1	12	71	(*126*)
I	UK				X		400	NA	Riparian margins	2	19	366	(*127*)
J	UK				X		400	NA	Various	2	31	343	(*128*)
K	USA	X	X	X	X		10000	60	Grasslands	3	30	98	(*129*, *130*)
L	France	X	X	X			150	15	Various	1	25	206	(*131*)[a]
M	Sweden	X		X	X		150	15	Various	1	12	72	(*132*)
N	Netherlands	X	X	X	X		150	15	Various	1	16	131	Unpublished
O	Italy	X	X	X			150	15	Various	1	26	587	(*133*, *134*)
P	Netherlands	X	X	X	X		450[b]	45	Various	1	41	165	(*20*)[a]
Q	Germany	X	X	X			2	15	Grasslands	1	17	459	(*135*)
R	Poland	X					31416	60	Various	1	32	32	(*136*)
S	UK	X					31416	60	Various	1	41	46	(*137*)
T	Germany	X	X	X			200	240	Wildflower strips	1	14	28	(*138*)
U	Portugal		X				150	15	Various	1	29	79	Unpublished
V	Germany	X	X				100	15	Grasslands	1	32	32	(*139*)
W	Germany	X	X				Various	15	Field margins	1	27	198	(*140*)
X	Germany	X	X				100	45	Grasslands	1	23	115	(*141*)
Y	Germany	X	X	X			Various		Grasslands	1	27	192	(*37*, *142*)
Z	Norway	X					200	5	Various	2	52	3676	(*143*)
AA	Netherlands	X	X	X			20	10	Various	2	40	606	(*31*)
AB	Romania	X	X	X	X		300	20	Various	1	28	217	(*144*)
AC	Germany	X	X	X			Various		Wildflower strips	1	19	37	(*145*)
AD	Germany	X	X	X	X		1800	360	Grasslands	1	28	143	(*146*)[c]
AE	Israel		X				800	60	Various	2	30	30	(*147*)[a]
AF	India					X	100	10	Various	1	12	117	(*148*)
AG	Argentina		X	X	X		Various	240	Road verges	2	40	40	(*149*)
AH	USA		X	X			1	4	Various	1	16	455	(*150*)
AI	Spain		X	X			10	5	Field margins	1	17	340	(*151*)
AJ	Sweden	X					100	10	Various	1	12	363	(*152*)
AK	UK	X		X	X		100	10	Road verges	1	19	285	(*93*)
AL	Germany	X					100	10	Various	1	11	20	(*153*)
AM	Ireland				X		200	NA	Hedges	1	20	120	(*154*)
AN	USA	X	X				40	5	Various	1	12	964	(*155*)[d]
AO	Sweden	X	X	X	X		100	10	Various	1	20	235	(*156*)
AP	Netherlands	X	X	X	X		250	25	Various	1	10	40	(*157*)
AQ	USA		X				40	5	Grasslands	2	35	48	(*158*)
AR	Ireland				X		Various	NA	Grasslands	1	25	150	(*159*, *160*)
AS	Spain		X	X			150	15	Various	2	30	226	(*30*, *161*)
AT	UK	X	X	X			150	15	Various	3	47	550	(*30*, *62*, *162*)
AU	Sweden	X	X	X			150	15	Various	2	32	635	(*30*, *62*, *162*)
AV	Serbia	X	X	X			150	15	Various	2	31	218	(*30*)
AW	Netherlands	X	X	X			150	15	Various	3	50	799	(*30*, *62*)
AX	Germany	X	X	X			150	15	Various	2	32	666	(*30*, *62*, *162*)
AY	Switzerland	X	X	X	X		150	20	Various	2	34	552	(*48*)
AZ	Netherlands				X		1000	NA	Grasslands	1	11	64	(*163*)
BA	UK	X		X			200	30	Grasslands	1	18	71	(*164*)
BB	UK			X			200	10	Forest	1	10	22	(*165*)
BC	Germany	X	X	X	X		1	5	Various	3	43	2340	(*166*, *167*)
BD	Germany	X	X	X	X		1800	360	Grasslands	1	70	160	(*168*)[c]

BE	USA		X				10000	60	Wildflower strips	1	11	33	(*169*)
BF	UK				X		Various	NA	Grasslands	2	31	654	(*170*)
BG	USA	X	X				Various		Various	3	56	320	(*171*)

[a] Unpublished at the time of literature screen.

[b] For bees and hoverflies only. Butterfly surveys varied in area and were untimed.

[c] These publications are supported by data references (*172-173*) and (*173-179*), respectively.

[d] Not gathered from literature screen.

Table S2.
Sample sizes per species group. Landscapes are counted within study-year, and samples are sampling events within landscapes.

Species group	Studies	Study-years	Landscapes	Samples
Bumble bees	37	55	1107	16675
Solitary bees	37	58	1124	13294
Hoverflies	31	47	885	11156
Butterflies	19	29	613	9994
Tropical bees	3	5	81	272

Table S3.

Bumble bee model terms evaluated by log-likelihood ratio tests. SNH = semi-natural habitat; MFC = mass-flowering crop. The “no” level of MFC Bloom is captured in the intercept, meaning that the coefficients for landscape SNH and MFC Bloom here are representative of the “yes” level, as well as the slope of the interaction between landscape SNH and MFC Bloom. The single terms of landscape SNH and MFC Bloom are not evaluated with log-likelihood ratio tests because the interaction term is retained in the model. Coefficients are represented on the log scale.

Variable	Coefficient	SE	Chisq	P
Flower cover	0.062	0.028	4.683	**0.030**
Flower richness	0.060	0.027	4.726	**0.030**
Landscape SNH	0.075	0.012	-	-
MFC Bloom	0.235	0.018	-	-
SNH:MFC Bloom	-0.122	0.016	58.839	**<0.001**

Table S4.

Solitary bee model terms evaluated by log-likelihood ratio tests. SNH = semi-natural habitat; MFC = mass-flowering crop. The “no” level of MFC Bloom is captured in the intercept, meaning that the coefficient for MFC Bloom here is representative of the “yes” level. The interaction term is not included in the final model. Coefficients are represented on the log scale.

Variable	Coefficient	SE	Chisq	P
Flower cover	0.047	0.033	2.001	0.157
Flower richness	0.100	0.023	15.738	**<0.001**
Landscape SNH	-0.002	0.009	0.043	0.836
MFC Bloom	0.196	0.016	158.149	**<0.001**
SNH:MFC Bloom	-	-	0.867	0.352

Table S5.

Hoverfly model terms evaluated by log-likelihood ratio tests. SNH = semi-natural habitat; MFC = mass-flowering crop. The “no” level of MFC Bloom is captured in the intercept, meaning that the coefficient for MFC Bloom here is representative of the “yes” level. The interaction term is not included in the final model. Coefficients are represented on the log scale.

Variable	Coefficient	SE	Chisq	P
Flower cover	0.082	0.045	3.257	0.071
Flower richness	0.175	0.033	22.235	**<0.001**
Landscape SNH	-0.004	0.011	0.132	0.716
MFC Bloom	-0.013	0.019	0.470	0.493
SNH:MFC Bloom	-	-	0.374	0.541

Table S6.

Butterfly model terms evaluated by log-likelihood ratio tests. SNH = semi-natural habitat; MFC = mass-flowering crop. The "no" level of MFC Bloom is captured in the intercept, meaning that the coefficient for MFC Bloom here is representative of the "yes" level. The interaction term is not included in the final model. Coefficients are represented on the log scale.

Variable	Coefficient	SE	Chisq	P
Flower cover	0.105	0.048	4.402	**0.036**
Flower richness	0.027	0.068	0.157	0.692
Landscape SNH	0.031	0.013	5.443	**0.020**
MFC Bloom	-0.021	0.038	0.300	0.584
SNH:MFC Bloom	-	-	0.024	0.876

Table S7.

Tropical bee model terms evaluated by log-likelihood ratio tests. SNH = semi-natural habitat; MFC = mass-flowering crop. The “no” level of MFC Bloom is captured in the intercept, meaning that the coefficient for MFC Bloom here is representative of the “yes” level. The interaction term is not included in the final model. Coefficients are represented on the log scale.

Variable	Coefficient	SE	Chisq	P
Flower cover	0.039	0.015	7.029	**0.008**
Flower richness	0.143	0.017	59.749	**<0.001**
Landscape SNH	0.037	0.022	2.888	0.089
MFC Bloom	0.011	0.030	0.131	0.718
SNH:MFC Bloom	-	-	0.109	0.741

Table S8.

The effect of mass-flowering crop (MFC) presence evaluated by log-likelihood ratio tests on models with a subset of the datasets that had this variable as a within-study factor. SNH = semi-natural habitat.

Model	SNH:MFC Bloom		MFC Bloom	
	Chisq	P	Chisq	P
Bumble bees	109.694	**<0.001**	-	-
Solitary bees	0.293	0.588	379.260	**<0.001**
Hoverflies	2.431	0.119	0.270	0.604
Butterflies	0.306	0.580	0.360	0.549
Tropical bees	0.288	0.592	0.448	0.503

Table S9.

Contact information for requesting study locations for certain datasets included in this synthesis. Location data can be requested via the listed point of contact and will be made available for research purposes. Location data from other datasets are available via Zenodo (*53*).

Study	Publication	Primary contact	Primary email	Secondary contact	Secondary email
C	(*120*)	Supratim Laha	Avainlove@gmail.com	Arnob Chatterjee	chatterjeearnob@gmail.com
K	(*129*, *130*)	Kathy Denning	Denning@ku.edu	Bryan Foster	bfoster@ku.edu
O	(*133*, *134*)	Thijs Fijen	Thijs.fijen@wur.nl	David Kleijn	David.kleijn@wur.nl
AD, BD	(*146*, *168*); dataset: (*173*)	Biodiversity Exploratories	Beo@senckenberg.de	Victoria Griessmeier	Victoria.Griessmeier@senckenberg.de
AN	(*155*)	Gabriela Quinlan	Gshbe15@gmail.com	Rufus Isaacs	isaacsr@msu.edu
AQ	(*158*)	Clint Otto	Cotto@usgs.gov	Stacy Simanonok	ssimanonok@columbialandtrust.org
BE	(*169*)	Ai Wen	Ai.wen@uni.edu	Kenneth Elgersma	kenneth.elgersma@uni.edu