

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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Supplementary Materials

5

Materials and Methods

Supplementary Text

Figs. S1 to S10

Tables S1 to S8

References (53–177)

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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.

Supplementary Materials for
Critical habitat thresholds for effective pollinator conservation in agricultural landscapes

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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”; (53)) 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; (54)).

**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) (55) 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 (56), according to the approach of Grames et al. (57). 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 (58). 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 butterfly* 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 butterfly* 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 butterfly* OR hoverfl* OR lasioglossum* OR lepidoptera* OR osmia* OR pollin* OR syrphid* OR bumblebee*))) 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 (57). While Halictidae do exhibit social behaviors (58), 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 (57), 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. (61) 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 (62–71) 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 m² 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 m² and min, respectively. We chose to standardize to densities per 150 m² 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 m²), so we divided the sum of butterflies by the sum of area surveyed over 300, per landscape. If a study had

$\geq 50\%$ 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 (72–89) using the *sf* (90) and *raster* (91) 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 (89) 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 (92), by applying a 1 m buffer around roads in the study landscapes (72, 93–96), 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 (97–103) and information provided by the data owners.

Analysis

All statistical analyses were conducted in R version 4.1.2 (104). We constructed linear mixed models using *glmmTMB* (105) 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 (106) 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 (107). 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 (108) and by comparing semivariograms to expected semivariances (109), 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 (110) using the performance package (111). Partial residual plots were inspected using the effects package (112) to ensure the linearity of relationships and the absence of unmodelled interactions (113). 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 m² [or, for butterflies, 300 m²]; 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 (114). Next we extrapolated these pollinator densities to the landscape scale by multiplying the (back-transformed) density per m² (predicted density / 150 or 300) by the coverage in m² of semi-natural habitat in the landscape (% semi-natural habitat of the given quantile / 100 * π * 500²) (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 ggplot2 (115), viridis (116), ggeffects (114), and gridExtra (117) packages.

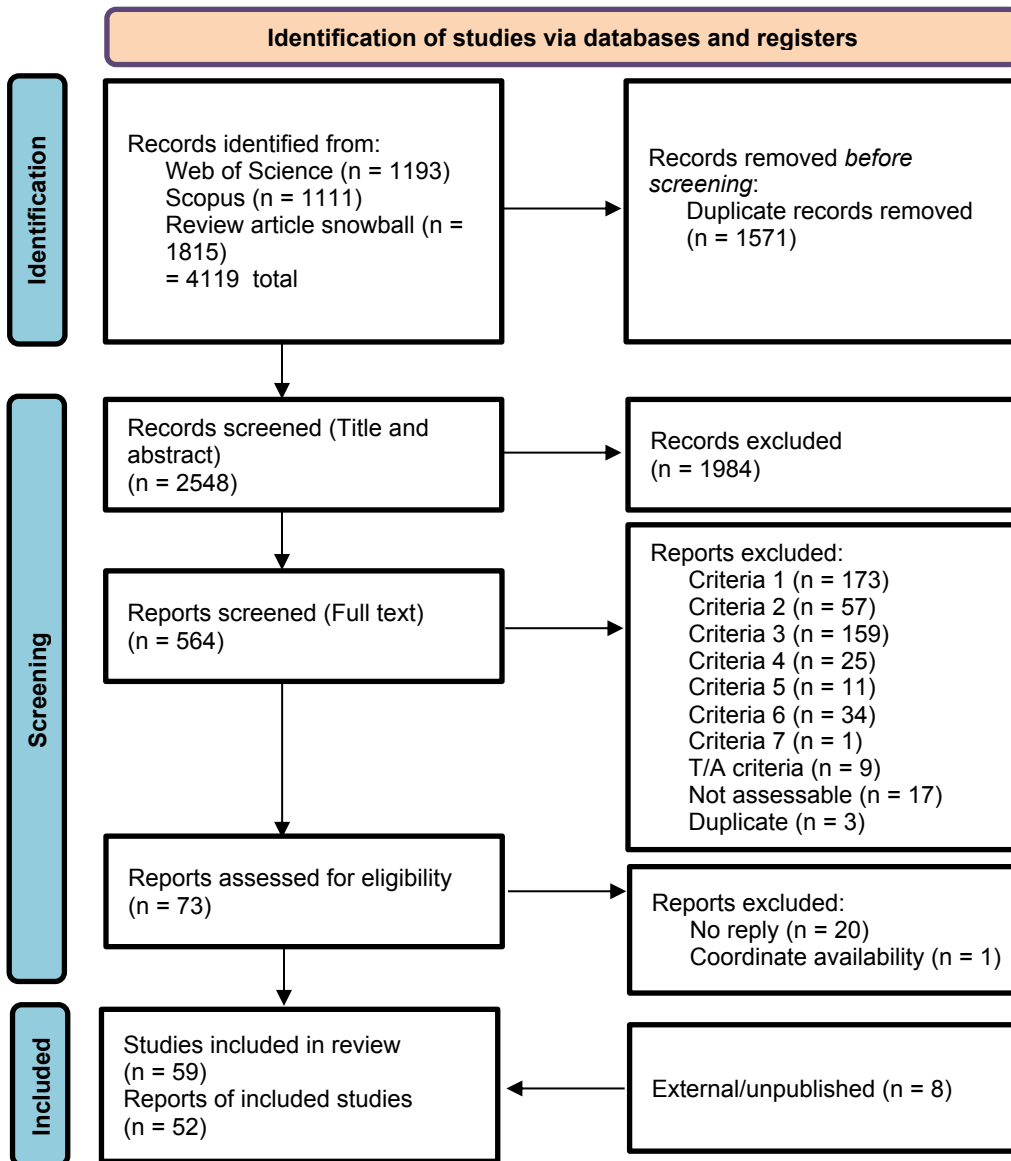


Fig. S1.

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.

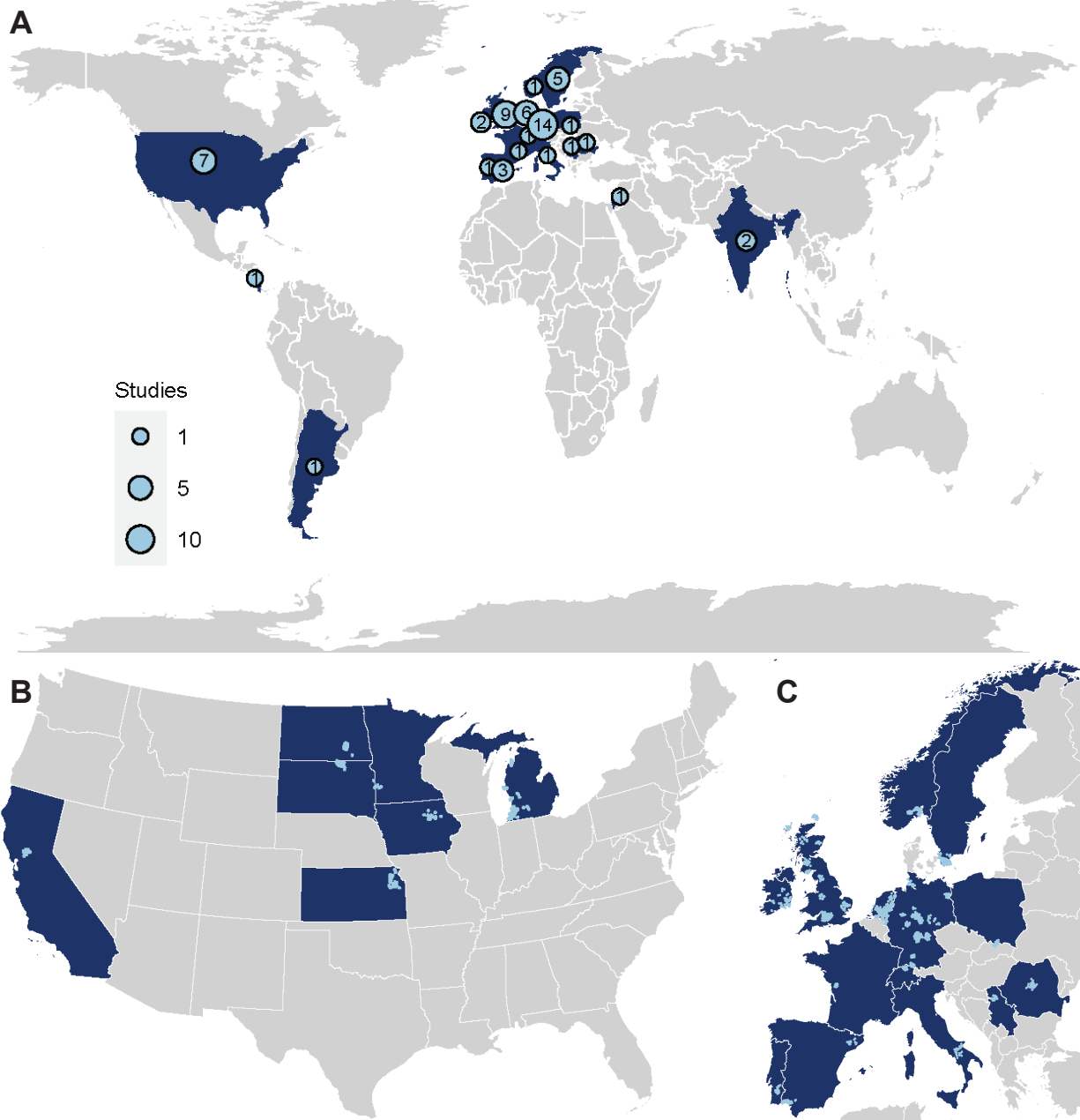


Fig. S2.

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.

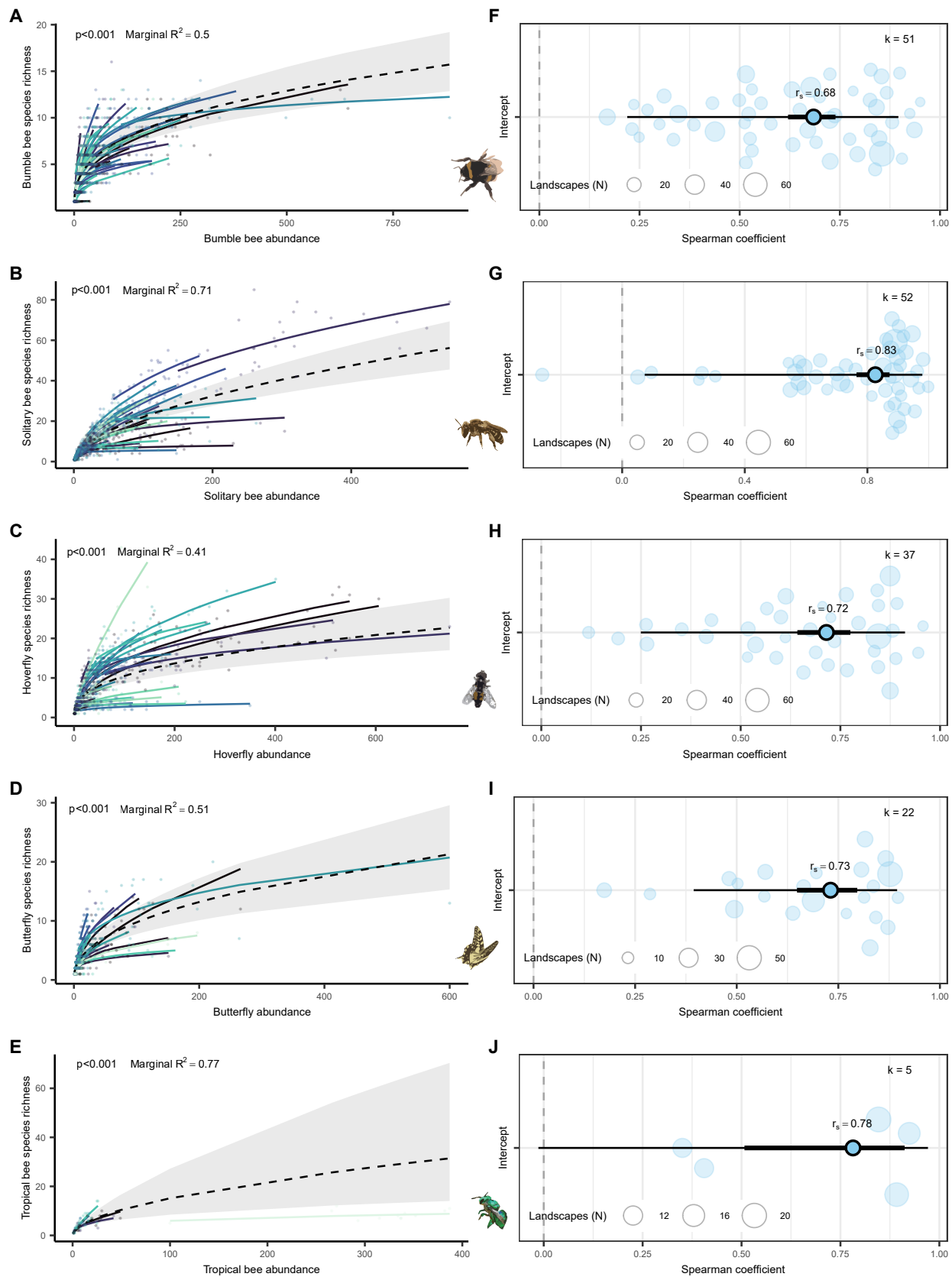
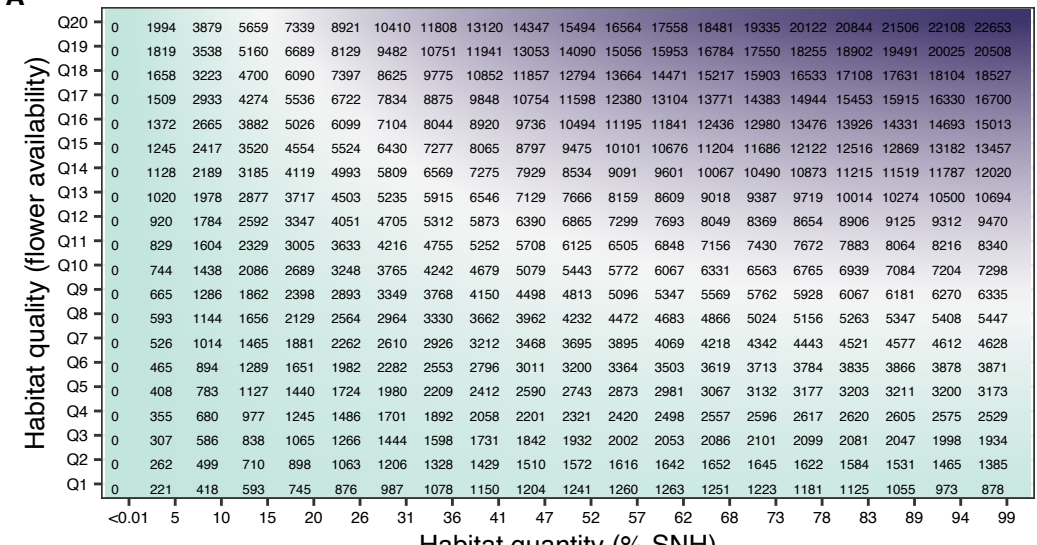


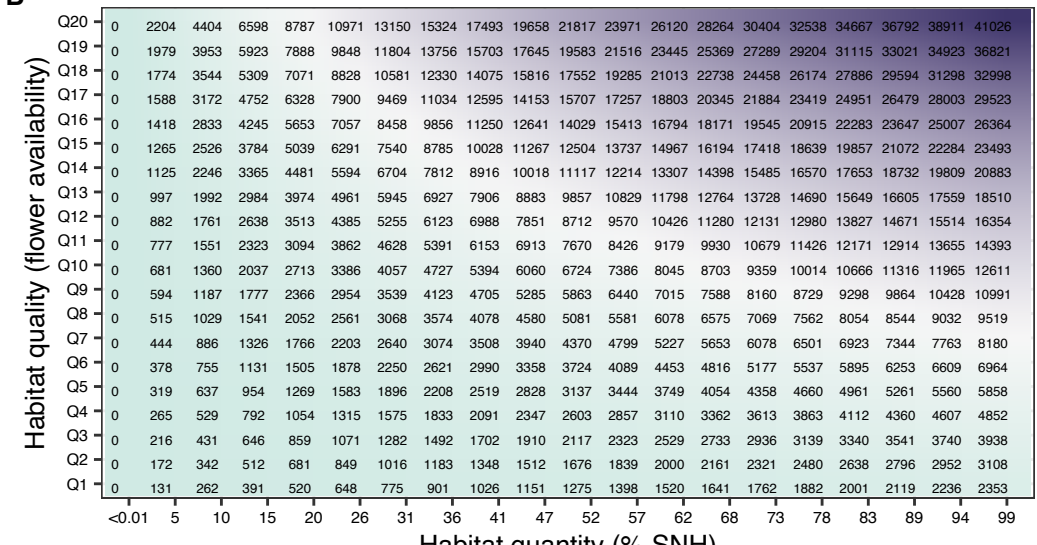
Fig. S3.

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.

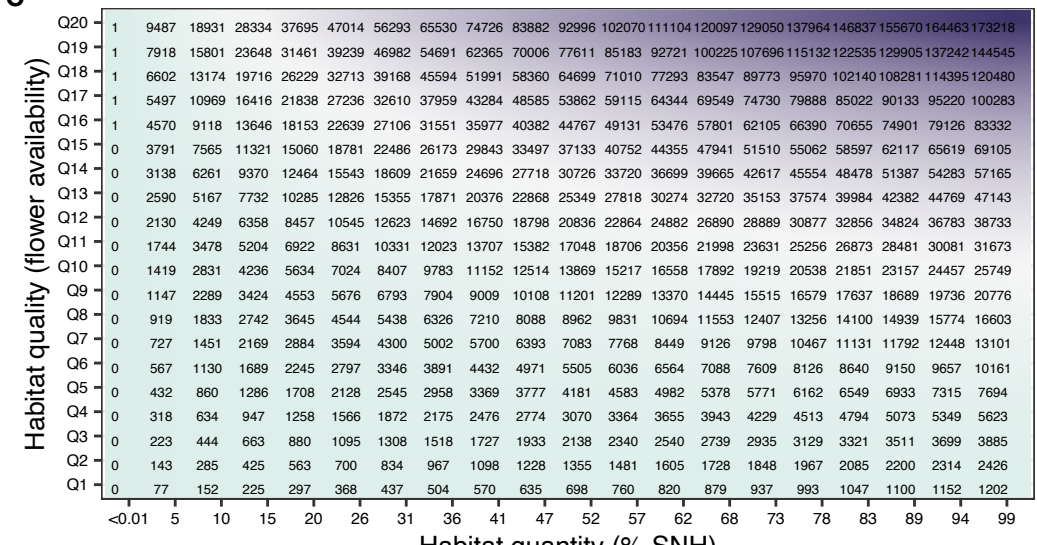
A



B



C



D</

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.

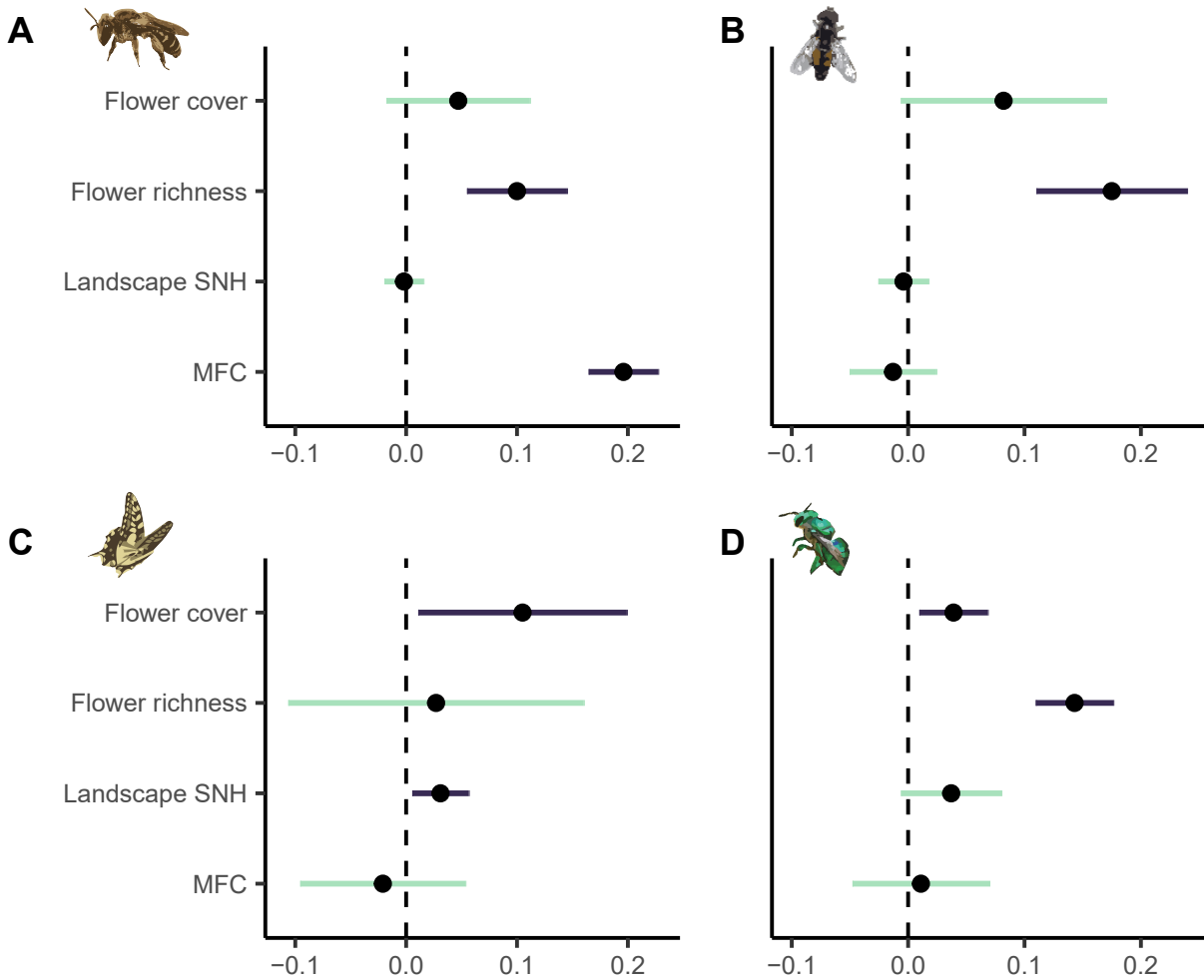


Fig. S5.

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.

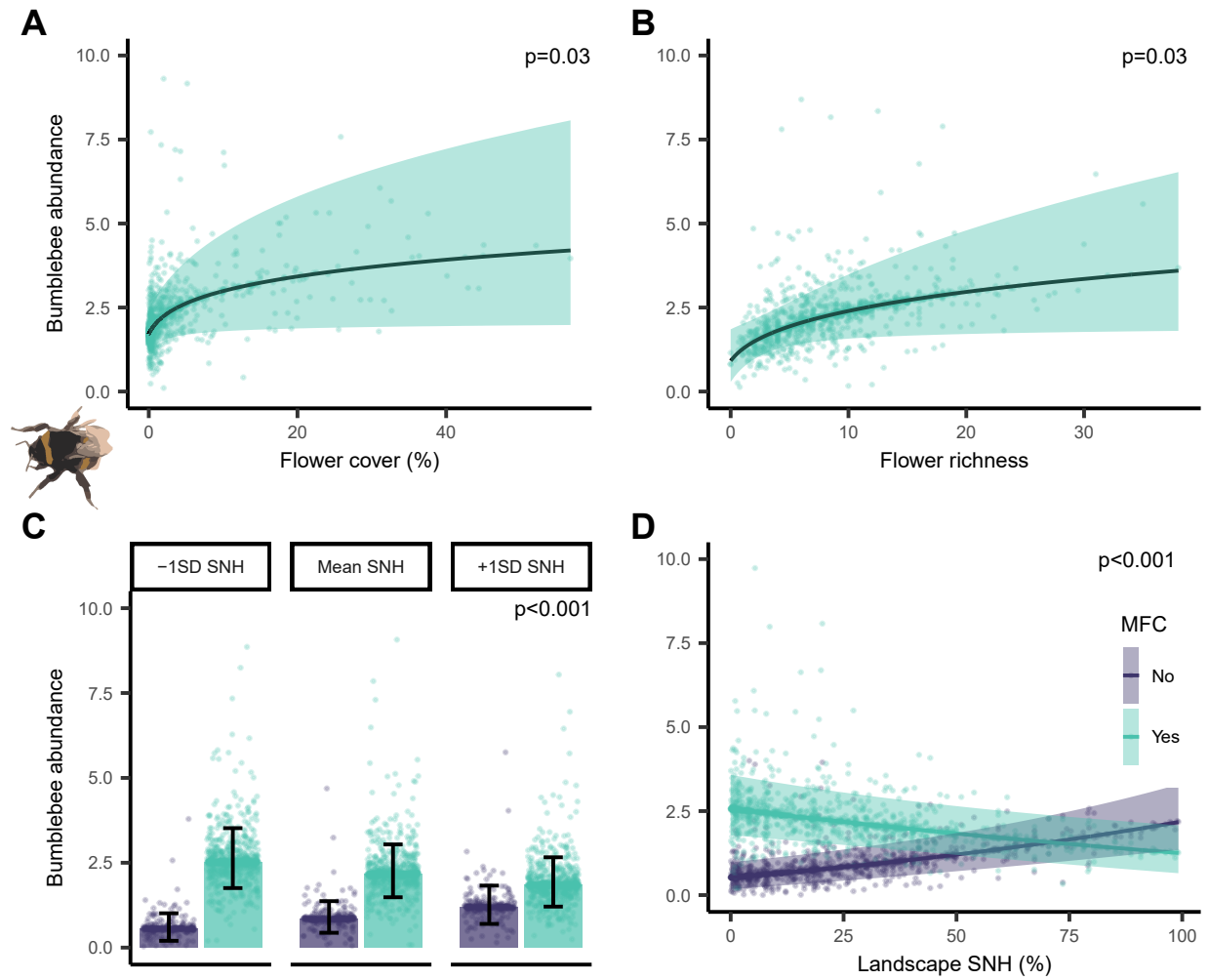


Fig. S6.

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 m² and 15 min sampling. Points represent back-transformed partial residuals. SD, standard deviation. For model coefficients, see table S3.

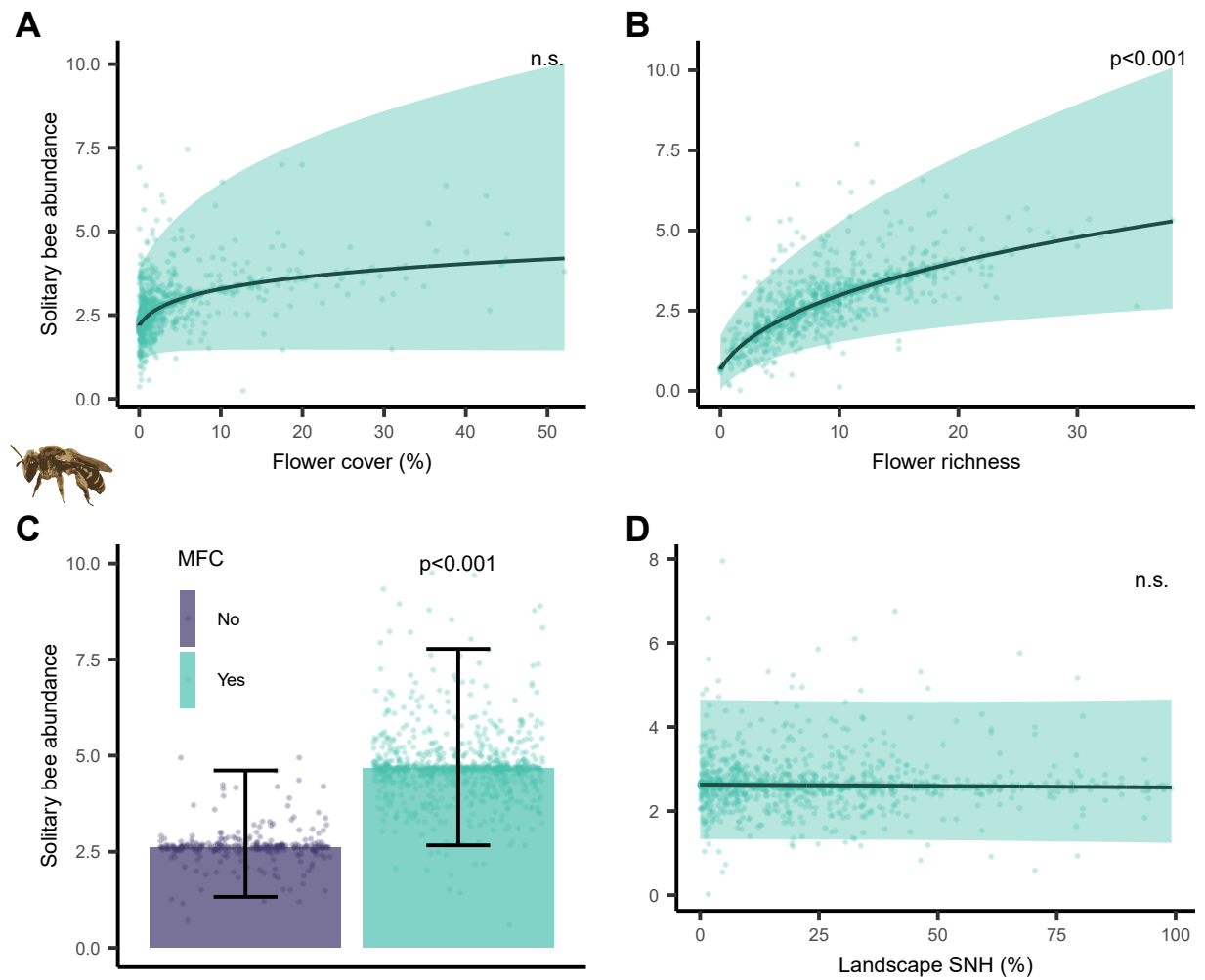


Fig. S7.

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 m² and 15 min sampling. Points represent back-transformed partial residuals. SD, standard deviation. For model coefficients, see table S4.

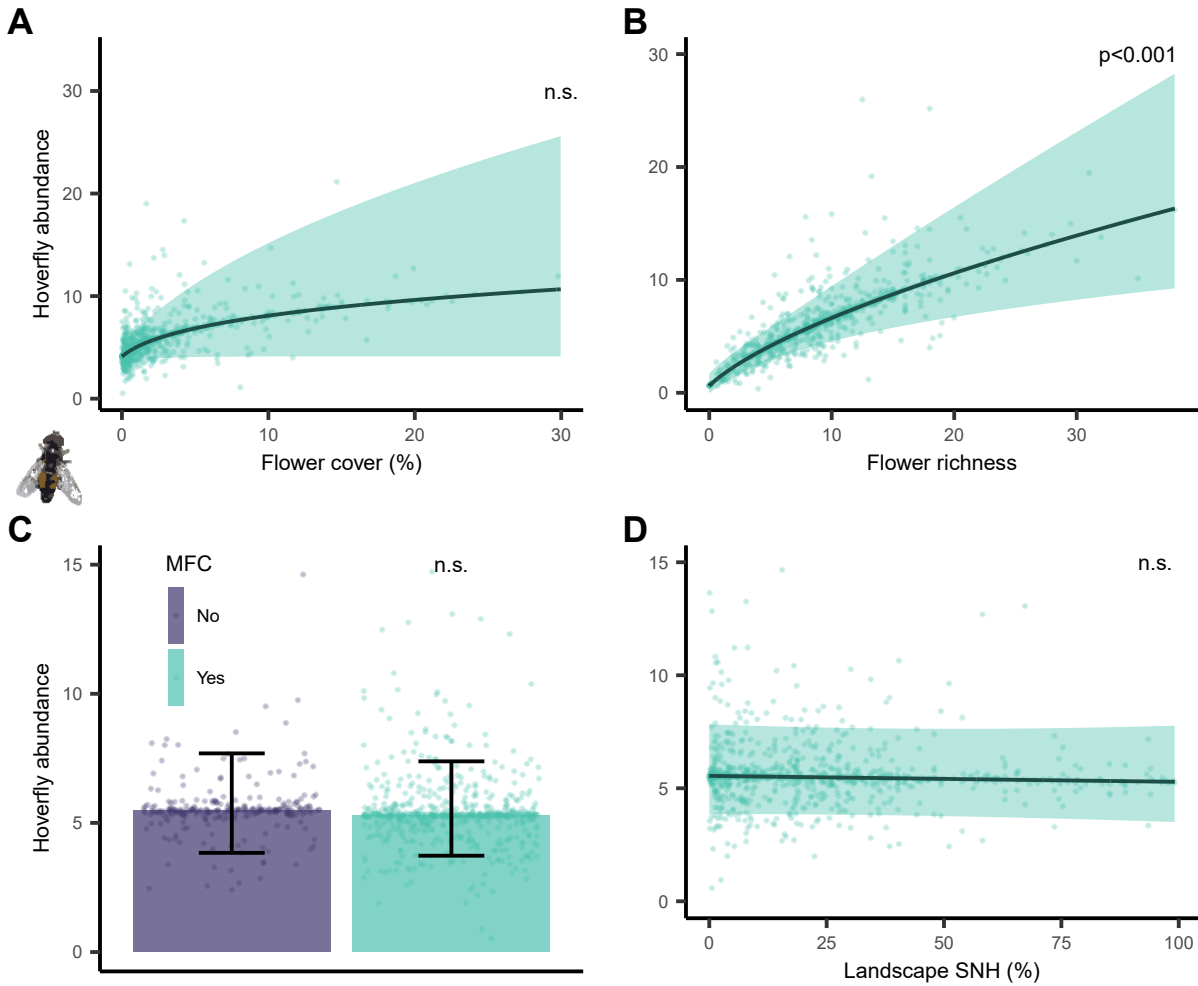


Fig. S8.

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 m² and 15 min sampling. Points represent back-transformed partial residuals. SD, standard deviation. For model coefficients, see table S5.

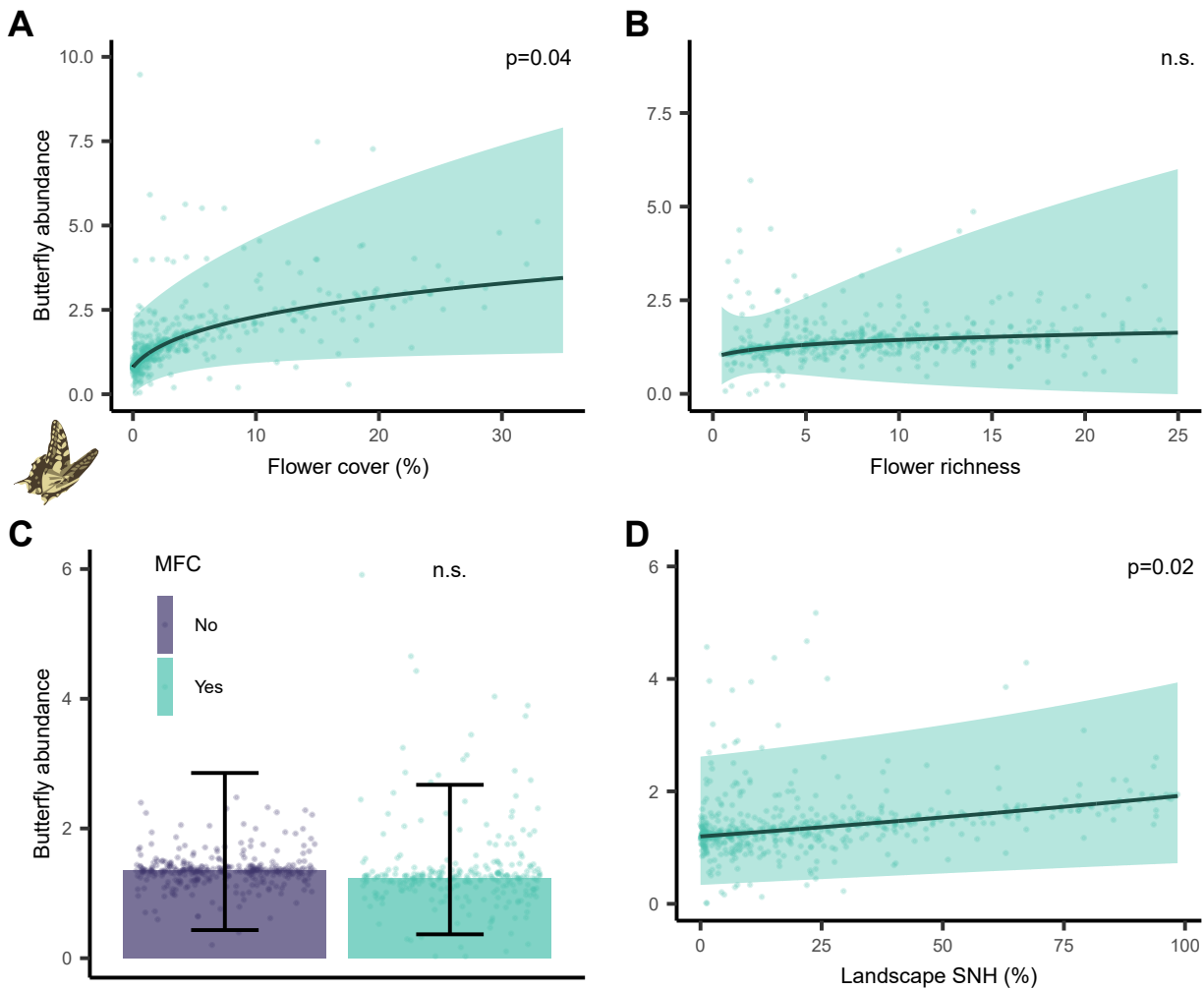


Fig. S9.

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 m². Points represent back-transformed partial residuals. SD, standard deviation. For model coefficients, see table S6.

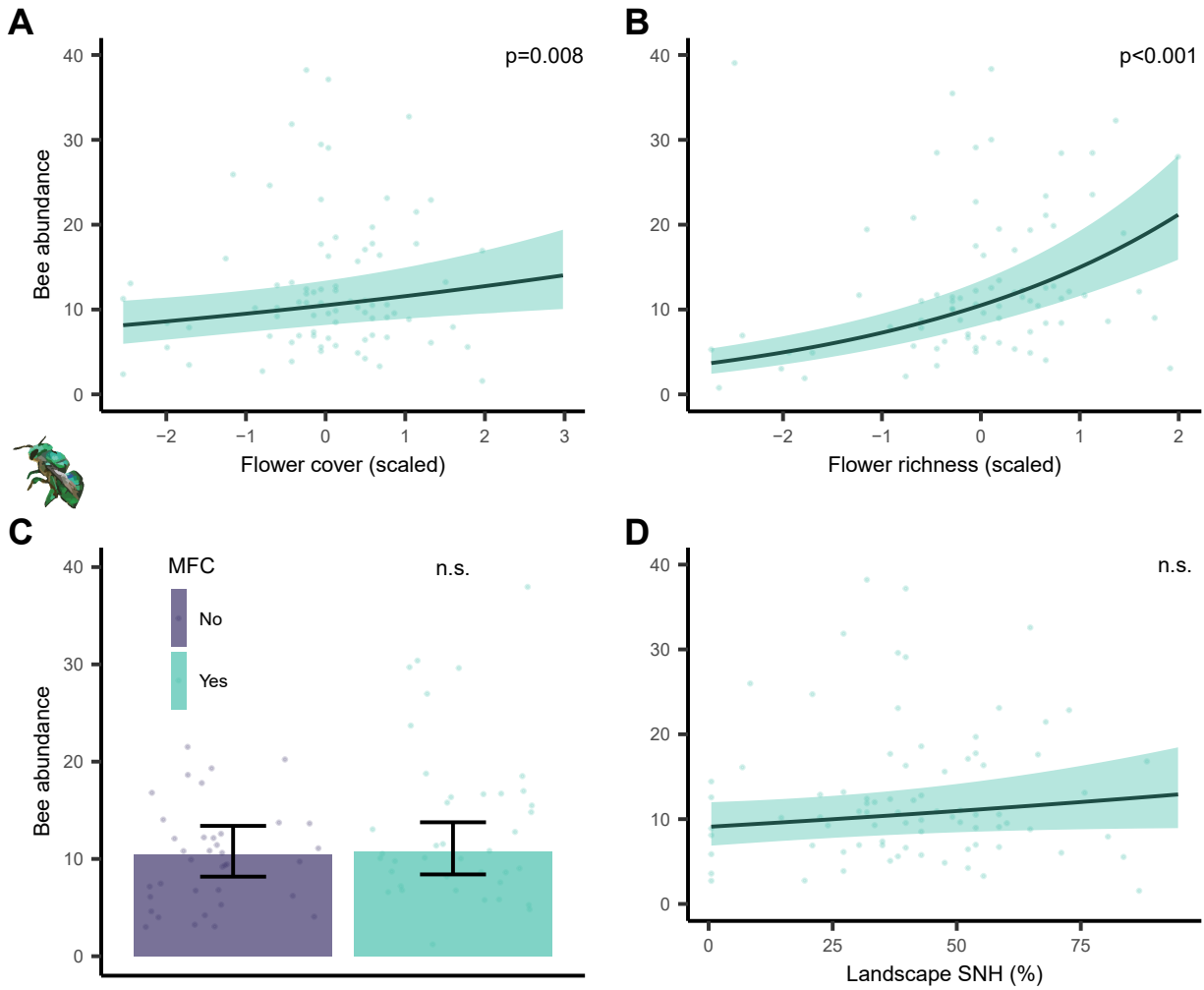


Fig. S10.

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 m² 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	(118) ^a
C	India					X	9	90	Various	1	20	60	(119)
D	Germany	X	X	X			400	10	Field margins	1	30	630	(120)
E	Germany	X	X	X			250	5	Various	1	30	540	(121)
F	Sweden	X					50	20	Various	1	17	152	(122)
G	Costa Rica					X	400	15	Grasslands	3	49	95	(123, 124)
H	USA	X	X				200	60	Various	1	12	71	(125)
I	UK				X		400	NA	Riparian margins	2	19	366	(126)
J	UK				X		400	NA	Various	2	31	343	(127)
K	USA	X	X	X	X		10000	60	Grasslands	3	30	98	(128, 129)
L	France	X	X	X			150	15	Various	1	25	206	(130) ^a
M	Sweden	X		X	X		150	15	Various	1	12	72	(131)
N	Netherlands	X	X	X	X		150	15	Various	1	16	131	Unpublished
O	Italy	X	X	X			150	15	Various	1	26	587	(132, 133)
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	(134)
R	Poland	X					31416	60	Various	1	32	32	(135)
S	UK	X					31416	60	Various	1	41	46	(136)
T	Germany	X	X	X			200	240	Wildflower strips	1	14	28	(137)
U	Portugal		X				150	15	Various	1	29	79	Unpublished
V	Germany	X	X				100	15	Grasslands	1	32	32	(138)
W	Germany	X	X				Various	15	Field margins	1	27	198	(139)
X	Germany	X	X				100	45	Grasslands	1	23	115	(140)
Y	Germany	X	X	X			Various		Grasslands	1	27	192	(37, 141)
Z	Norway	X					200	5	Various	2	52	3676	(142)
AA	Netherlands	X	X	X			20	10	Various	2	40	606	(31)
AB	Romania	X	X	X	X		300	20	Various	1	28	217	(143)
AC	Germany	X	X	X			Various		Wildflower strips	1	19	37	(144)
AD	Germany	X	X	X	X		1800	360	Grasslands	1	28	143	(145) ^c
AE	Israel		X				800	60	Various	2	30	30	(146) ^a
AF	India					X	100	10	Various	1	12	117	(147)
AG	Argentina		X	X	X		Various	240	Road verges	2	40	40	(148)
AH	USA		X	X			1	4	Various	1	16	455	(149)
AI	Spain		X	X			10	5	Field margins	1	17	340	(150)
AJ	Sweden	X					100	10	Various	1	12	363	(151)
AK	UK	X		X	X		100	10	Road verges	1	19	285	(92)
AL	Germany	X					100	10	Various	1	11	20	(152)
AM	Ireland				X		200	NA	Hedges	1	20	120	(153)
AN	USA	X	X				40	5	Various	1	12	964	(154) ^d
AO	Sweden	X	X	X	X		100	10	Various	1	20	235	(155)
AP	Netherlands	X	X	X	X		250	25	Various	1	10	40	(156)
AQ	USA		X				40	5	Grasslands	2	35	48	(157)
AR	Ireland				X		Various	NA	Grasslands	1	25	150	(158, 159)
AS	Spain		X	X			150	15	Various	2	30	226	(30, 160)
AT	UK	X	X	X			150	15	Various	3	47	550	(30, 61, 161)
AU	Sweden	X	X	X			150	15	Various	2	32	635	(30, 61, 161)
AV	Serbia	X	X	X			150	15	Various	2	31	218	(30)
AW	Netherlands	X	X	X			150	15	Various	3	50	799	(30, 61)
AX	Germany	X	X	X			150	15	Various	2	32	666	(30, 61, 161)
AY	Switzerland	X	X	X	X		150	20	Various	2	34	552	(48)
AZ	Netherlands				X		1000	NA	Grasslands	1	11	64	(162)
BA	UK	X		X			200	30	Grasslands	1	18	71	(163)
BB	UK			X			200	10	Forest	1	10	22	(164)
BC	Germany	X	X	X	X		1	5	Various	3	43	2340	(165, 166)
BD	Germany	X	X	X	X		1800	360	Grasslands	1	70	160	(167) ^c

BE	USA		X				10000	60	Wildflower strips	1	11	33	(168)
BF	UK				X		Various	NA	Grasslands	2	31	654	(169)
BG	USA	X	X				Various		Various	3	56	320	(170)

^aUnpublished at the time of literature screen.

^bFor bees and hoverflies only. Butterfly surveys varied in area and were untimed.

^cThese publications are supported by data references (171) and (172-177), respectively.

^dNot 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