

RESEARCH ARTICLES

CONSERVATION BIOLOGY

Critical habitat thresholds for effective pollinator conservation in agricultural landscapes

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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.

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 owing 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 affect 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 use 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 policy-making (7, 18). Conservation efforts in agricultural areas generally positively affect local pollinator densities because of increased floral resource availability (19), an aspect of habitat quality that can directly indicate suitability for insect pollinators because 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 24,487

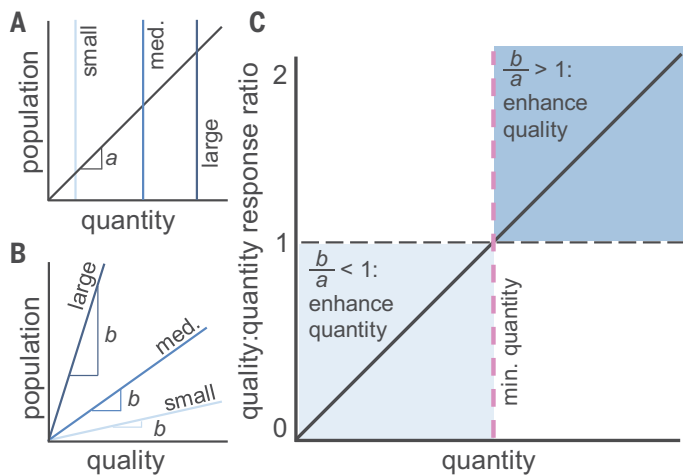


Fig. 1. Minimum habitat quantity level for application of conservation measures as defined by the relative effectiveness of enhancing habitat quantity or quality. (A) Population size increases with increasing habitat quantity (a , which itself depends on habitat quality). This causes (B) the effect of 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.

sampling events of 178,885 individual insect pollinators in 1250 agricultural landscapes from 19 countries (predominantly the US and in Europe, figs. S1 and S2 and tables S1 and 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. Although 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 modeled 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

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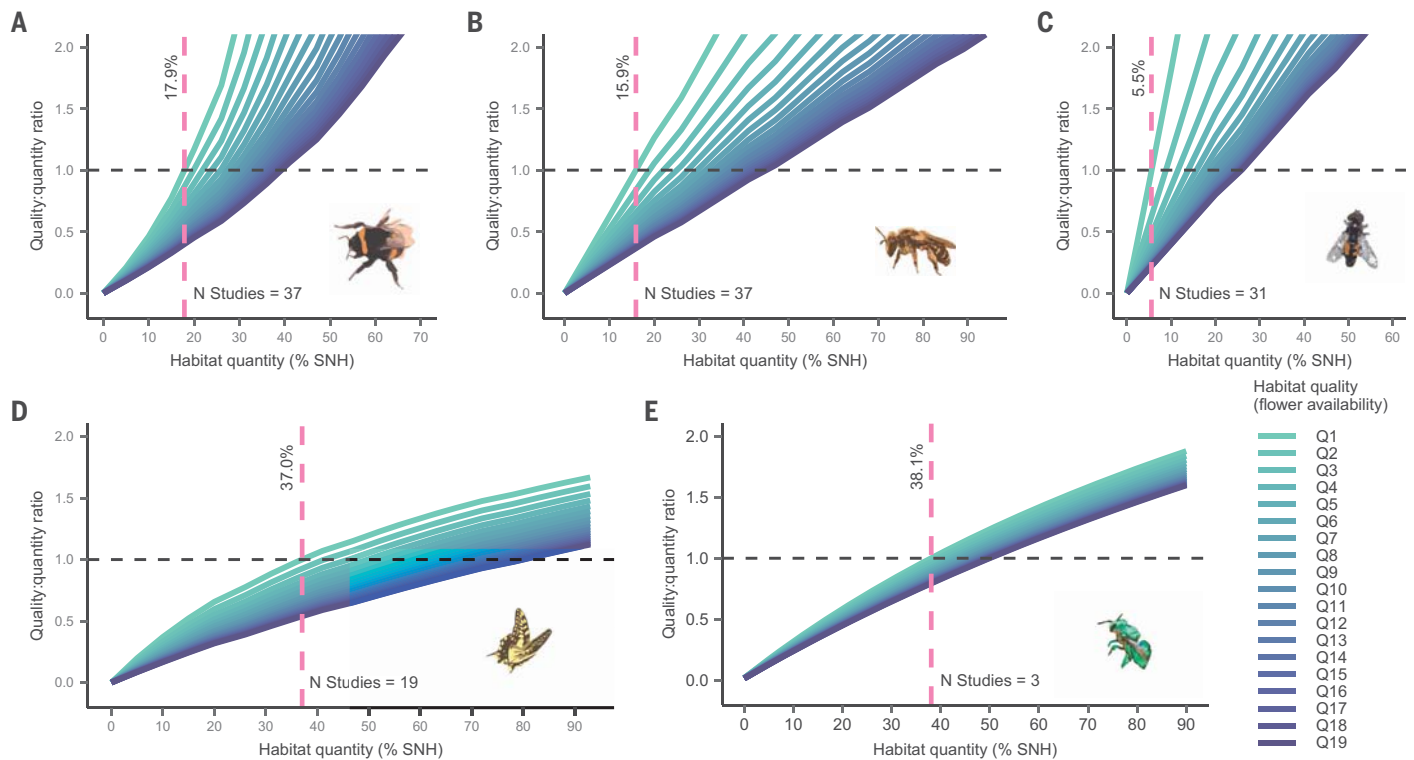


Fig. 2. Relationships between the habitat quality:quantity population response ratio and the cover of landscape semi-natural habitat (SNH) for landscape-level pollinator abundances. (A) Bumble bees, (B) solitary bees, (C) hoverflies, and (D) butterflies in temperate regions, and (E) tropical bees. Ratios <1 indicate that increasing habitat quantity is most beneficial, whereas those >1 indicate that habitat quality should also be prioritized. Q1 to 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).

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 to 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% (Fig. 2, C and D). Bumble bees and solitary bees had similar minimums, at 17.9% and 15.9%, respectively (Fig. 2, A and B). 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 to 18% semi-natural habitat cover has a 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 (figs. S5 to S10 and tables S3 to S7). For example, hoverflies had high densities (and large total abundances; Fig. 3C and figs. S4C and 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, using cropland as oviposition sites to meet larval feeding requirements (37). Butterflies, by contrast, 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 and figs. S4D and S9). Despite a positive relationship with flower cover (fig. S5C), habitat quantity thus had a strong influence on landscape-level butterfly abundance. Although 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 (fig. S5, A and 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). Although 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. Because crop fields are often disturbed habitats that do not provide permanent resources for pollinators, they are used transiently by pollinators that concentrate

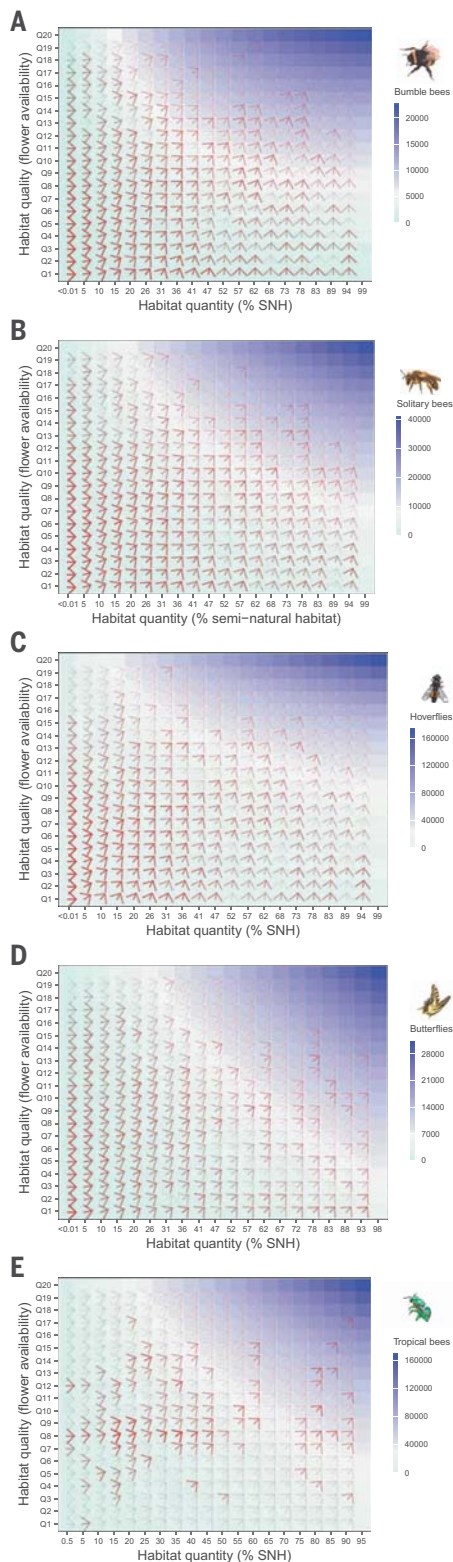


Fig. 3. The relative gain in landscape-level pollinator abundances from increasing habitat quantity or quality. (A) Bumble bees, (B) solitary bees, (C) hoverflies, and (D) butterflies in temperate regions, and (E) tropical bees. Quantity and quality are expressed across the 20 quantiles of the ranges 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 to 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.

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. S5D and S6, A and B), whereas 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. Although 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. Although 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 because of 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 owing 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; i.e., 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, because 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 owing 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 a maximum 5% semi-natural habitat coverage, the quality of that habitat would have to be improved by increasing flower cover to ~4.8% and adding ~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). Although 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 trade-off 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 substantially.

Conservation tools outside of semi-natural habitats also have the potential to support pollinators. Our results showed that mass-flowering crop presence increased bumble bee and solitary bee densities (figs. S5A and S6, C and D), but not those of other groups (fig. S5, B to D). For bumble bees, however, this effect only occurred in simple landscapes (fig. S6C), possibly owing to the presence of sufficient alternative floral resources in complex ones (46). Because we modeled 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 nonpermanent 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, although 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 because of more rapid increases in marginal benefits from habitat quality. In reality, we know that different pollinators prefer certain habitat types—for example, owing 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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Some study locations must be requested separately; this information can be found in the Zenodo entry and in table S9. **License information:** Copyright © 2025 the authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original US government works. <https://www.science.org/about/science-licenses-journal-article-reuse>

SUPPLEMENTARY MATERIALS

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