

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

Authors: Gabriella A. Bishop^{1*}, David Kleijn¹, Matthias Albrecht², Ignasi Bartomeus³, Rufus Isaacs⁴, Claire Kremen⁵, Ainhoa Magrach^{6,7}, Lauren C. Ponisio⁸, Simon G. Potts⁹, Jeroen Schepers¹, Henrik G. Smith¹⁰, Teja Tschardt¹¹, Jörg Albrecht¹², Jens Åström¹³, Isabelle Badenhauer¹⁴, András Báldi¹⁵, Parthiba Basu^{16†}, Åsa Berggren¹⁷, Nicole Beyer¹⁸, Nico Blüthgen¹⁹, Riccardo Bommarco¹⁷, Berry J. Brosi²⁰, Hamutahl Cohen²¹, Lorna J. Cole²², Kathy R. Denning^{23,24}, Mariano Devoto^{25,26}, Johan Ekroos^{27,28}, Felix Fornoff²⁹, Bryan L. Foster^{23,24}, Mark A.K. Gillespie³⁰, Jose L. Gonzalez-Andujar³¹, Juan P. González-Varo³², Dave Goulson³³, Ingo Grass^{34,35}, Annika L. Hass¹⁸, José M. Herrera³⁶, Andrea Holzschuh³⁷, Sebastian Hopfenmüller³⁸, Jordi Izquierdo³⁹, Birgit Jauker⁴⁰, Eveliina P. Kallioniemi^{41,42}, Felix Kirsch^{18,43}, Alexandra-Maria Klein²⁹, Anikó Kovács-Hostyánszki¹⁵, Jochen Krauss³⁷, Elena Krimmer^{37,44}, William E. Kunin⁴⁵, Supratim Laha⁴⁶, Sandra A.M. Lindström⁴⁷, Yael Mandelik⁴⁸, Gabriel Marcacci^{49,50}, David I. McCracken⁵¹, Marcos Monasterolo⁵², Lora A. Morandin⁵³, Jane Morrison^{31,39,54}, Sonja Mudri Stojnic⁵⁵, Jeff Ollerton^{56,57}, Anna S. Persson⁵⁸, Benjamin B. Phillips⁵⁹, Julia I. Piko^{60,61,62}, Eileen F. Power⁶³, Gabriela M. Quinlan^{64,65}, Maj Rundlöf⁶⁶, Chloé A. Raderschall^{17,67}, Laura G.A. Riggi^{17,68}, Stuart P.M. Roberts⁶⁹, Tohar Roth⁴⁸, Deepa Senapathi⁹, Dara A. Stanley⁷⁰, Ingolf Steffan-Dewenter³⁷, Jane C. Stout⁶³, Louis Sutter⁷¹, Marco F. Tanis⁷², Sam Tarrant⁷³, Lisette van Kolschoten⁷⁴, Adam J. Vanbergen⁷⁵, Montserrat Vilà^{3,76}, Vivien von Königslöw⁷⁷, Ante Vujic⁵⁵, Michiel F. WallisDeVries⁷⁸, Ai Wen⁷⁹, Catrin Westphal¹⁸, Jennifer B. Wickens⁸⁰, Victoria J. Wickens⁸¹, Nicholas I. Wilkinson⁸², Thomas J. Wood⁷², Thijs P.M. Fijen^{1*}

Affiliations:

¹Plant Ecology and Nature Conservation, Wageningen University; Wageningen, 6708PB, The Netherlands.

²Agroecology and Environment, Agroscope; 8046 Zurich, Switzerland.

³Estación Biológica de Doñana (EBD-CSIC); 41092 Sevilla, Spain.

⁴Department of Entomology, Michigan State University; 48824 East Lansing, MI, USA.

⁵Institute for Resources, Environment and Sustainability, University of British Columbia; V6T 1Z4 Vancouver, Canada.

⁶Basque Centre for Climate Change (BC3); 48940 Leioa, Spain.

⁷IKERBASQUE, Basque Foundation for Science; 48009 Bilbao, Spain.

⁸Institute of Ecology and Evolution, Department of Biology, University of Oregon; 97403 Eugene, OR, USA.

⁹Centre for Agri-Environmental Research (CAER), School of Agriculture, Policy and Development, University of Reading; RG6 6AR Reading, UK.

¹⁰Centre for Environmental and Climate Science, Department of Biology, Lund University; 22362 Lund, Sweden.

¹¹Agroecology, University of Göttingen; 37073 Göttingen, Germany.

¹²Senckenberg Biodiversity and Climate Research Centre (SBIK-F); 60325 Frankfurt am Main, Germany.

¹³Terrestrial biodiversity, Norwegian Institute for Nature Research; 7034 Trondheim, Norway.

¹⁴Unité de Recherche Pluridisciplinaire Prairies et Plantes Fourragères, INRAE; 86600 Lusignan, France.

5 ¹⁵Lendület Ecosystem Services Research Group, Institute of Ecology and Botany, HUN-REN Centre for Ecological Research; H-2163 Vácrátót, Hungary.

¹⁶Centre for Agroecology and Pollination Studies, Department of Zoology, University of Calcutta; 700019 Kolkata, India.

10 ¹⁷Department of Ecology, Swedish University of Agricultural Sciences; 75007 Uppsala, Sweden.

¹⁸Functional Agrobiodiversity & Agroecology, Department of Crop Sciences, University of Göttingen; 37077 Göttingen, Germany.

¹⁹Ecological Networks Lab, Technische Universität Darmstadt; 64287 Darmstadt, Germany.

²⁰Department of Biology, University of Washington; 98195 Seattle, WA, USA.

15 ²¹University of California Cooperative Extension Ventura, University of California Agriculture and Natural Resources; 93003 Ventura, CA, USA.

²²Environment Team, Food and Foot Print, SAC Consulting, Scotland's Rural College (SRUC); KA6 5HW Ayr, Scotland.

20 ²³Department of Ecology & Evolutionary Biology, University of Kansas; 66045 Lawrence, KS, USA.

²⁴Kansas Biological Survey & Center for Ecological Research; 66047 Lawrence, KS, USA.

²⁵Cátedra de Botánica General, Facultad de Agronomía, Universidad de Buenos Aires; C1053ABJ C.A. de Buenos Aires, Argentina.

25 ²⁶Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET); C1033AAJ C.A. de Buenos Aires, Argentina.

²⁷Department of Agricultural Sciences, Plant Production Science, University of Helsinki; FI-00014 Helsinki, Finland.

²⁸Helsinki Institute of Sustainability Science, HELSUS, University of Helsinki; FI-00014 Helsinki, Finland.

30 ²⁹Chair of Nature Conservation and Landscape Ecology, Albert-Ludwigs-University of Freiburg; 79106 Freiburg, Germany.

³⁰Department of Civil Engineering and Environmental Sciences, Western Norway University of Applied Sciences; PB 133 Sogndal, Norway.

³¹Instituto de Agricultura Sostenible (CSIC); 14005 Cordoba, Spain.

35 ³²Departamento de Biología, Instituto Universitario de Investigación Marina (INMAR), Universidad de Cádiz; 11510 Puerto Real, Spain.

³³School of Life Sciences, University of Sussex; BN1 9QG Brighton, UK.

³⁴Ecology of Tropical Agricultural Systems, University of Hohenheim; 70599 Stuttgart, Germany.

³⁵Center for Biodiversity and Integrative Taxonomy (KomBioTa), University of Hohenheim; 70599 Stuttgart, Germany.

³⁶Departamento de Biología, Instituto de Investigación Vitivinícola y Agroalimentaria, Universidad de Cádiz; 11510 Cádiz, Spain.

5 ³⁷Department of Animal Ecology and Tropical Biology, Bioncenter, University of Würzburg; 97074 Würzburg, Germany.

³⁸Foundation Cultural Landscape Günztal; 87724 Ottobeuren, Germany.

³⁹Department of Agri-Food Engineering and Biotechnology, Universitat Politècnica de Catalunya; 08860 Castelldefels, Spain.

10 ⁴⁰Justus Liebig University Giessen; 35390 Giessen, Germany.

⁴¹Norwegian Institute for Nature Research; 7485 Trondheim, Norway.

⁴²Norwegian Institute for Bioeconomy Research; 1431 Ås, Norway.

⁴³Thünen Institute of Biodiversity; 38116 Braunschweig, Germany.

15 ⁴⁴Laboratory of Ecological Information, Graduate School of Agriculture, Kyoto University; 606-8502 Kyoto, Japan.

⁴⁵School of Biology, University of Leeds; LS2 9JT Leeds, UK.

⁴⁶Ecology Research Unit, Department of Zoology, University of Calcutta; 700019 Kolkata, India.

⁴⁷Swedish Rural Economy and Agricultural Society; 29109 Kristianstad, Sweden.

20 ⁴⁸Department of Entomology, Institute of Environmental Sciences, The Robert H. Smith Faculty of Agriculture, Food and Environment, The Hebrew University of Jerusalem; 761001 Rehovot, Israel.

⁴⁹Swiss Ornithological Institute; 6204 Sempach, Switzerland.

⁵⁰Conservation Biology Lab, University of Neuchâtel; 2000 Neuchâtel, Switzerland.

25 ⁵¹Integrated Land Management Department, Scotland's Rural College; KA6 5HW Ayr, Scotland.

⁵²Centro Regional de Energía y Ambiente para el Desarrollo Sustentable (CREAS), CONICET-Universidad Nacional de Catamarca; 4700 San Fernando del Valle de Catamarca, Argentina.

30 ⁵³Pollinator Partnership; 94111 San Francisco, CA, USA.

⁵⁴Department of Environment, Agriculture, and Geography, Bishop's University; J1M 1Z7 Sherbrooke, Canada.

⁵⁵Department of Biology and Ecology, Faculty of Sciences, University of Novi Sad; 21000 Novi Sad, Serbia.

35 ⁵⁶Faculty of Arts, Science and Technology, University of Northampton, Waterside Campus; NN1 5PA Northampton, UK.

⁵⁷Kunming Institute of Botany; 650201 Kunming, China.

⁵⁸The Center for Environment and Climate Science, Lund University; 22362 Lund, Sweden.

⁵⁹Environment and Sustainability Institute, University of Exeter; TR10 9FE Penryn, UK.

⁶⁰Forest Nature Conservation Group, University of Göttingen; 37077 Göttingen, Germany.

⁶¹German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig; 04103 Leipzig, Germany.

⁶²Department of Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg; 06108 Halle (Saale), Germany.

⁶³Botany, School of Natural Sciences, Trinity College Dublin; D02 PN40 Dublin, Ireland.

⁶⁴Department of Entomology, Center for Pollinator Research, Huck Institutes of the Life Sciences, Pennsylvania State University; 16802 University Park, PA, USA.

⁶⁵Department of Entomology, Michigan State University; 48824 East Lansing, MI, USA.

⁶⁶Department of Biology, Lund University; 22362 Lund, Sweden.

⁶⁷Department of Plant Protection Biology, Swedish University of Agricultural Sciences; 23422 Lomma, Sweden.

⁶⁸Wageningen Environmental Research; 6708PE Wageningen, The Netherlands.

⁶⁹Agroecology Lab, Université libre de Bruxelles; 1050 Brussels, Belgium.

⁷⁰School of Agriculture and Food Science, University College Dublin; D04 V1W8 Dublin, Ireland.

⁷¹Agroscope Plant-Production Systems; 1964 Conthey, Switzerland.

⁷²NL Biodiversity and Society, Naturalis Biodiversity Center; 2333CR Leiden, The Netherlands.

⁷³Unaffiliated.

⁷⁴Department of Ecology and Genetics, Evolutionary Biology Centre, Uppsala University; 75236 Uppsala, Sweden.

⁷⁵Agroécologie, INRAE, L'Institut Agro Dijon, Université de Bourgogne, Université de Bourgogne Franche-Comté; 21000 Dijon, France.

⁷⁶Department of Plant Biology and Ecology, University of Sevilla; 41012 Sevilla, Spain.

⁷⁷Faculty of Environment and Natural Resources, University of Freiburg; 79106 Freiburg, Germany.

⁷⁸De Vlinderstichting / Dutch Butterfly Conservation; 6700AM Wageningen, The Netherlands.

⁷⁹Biology Department, University of Northern Iowa; 50614-0421 Cedar Falls, IA, USA.

⁸⁰Strategic Programme Generation and Delivery, Natural Environment Research Council; SN2 1EU Swindon, UK.

⁸¹Funding Operations, Natural Environment Research Council; SN2 1EU Swindon, UK.

⁸²RSPB Centre for Conservation Science; EH12 9DH Edinburgh, UK.

† Deceased.

*Corresponding authors. Emails: gabriella.bishop@wur.nl; thijs.fijen@wur.nl

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

5 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.

10 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.

40 Minimum habitat thresholds depend on species group

45 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.

5
10
15
20
25
30
35
40
45
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).

25
30
35
40
45
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.

5 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
10 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
15 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
20 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
25 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
30 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
35 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
40 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
45 compensate landowners with incentives for marked improvements in habitat quality in landscapes where increases in habitat area are not feasible.

References and Notes

- 5 1. R. Dirzo, H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, B. Collen, Defaunation in the Anthropocene. *Science* **345**, 401–406 (2014).
2. G. Ceballos, P. R. Ehrlich, R. Dirzo, Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc. Natl. Acad. Sci.* **114** (2017).
- 10 3. M. Dainese, E. A. Martin, M. A. Aizen, M. Albrecht, I. Bartomeus, R. Bommarco, *et al.*, A global synthesis reveals biodiversity-mediated benefits for crop production. *Sci. Adv.* **5**, eaax0121 (2019).
4. T. H. Oliver, M. S. Heard, N. J. B. Isaac, D. B. Roy, D. Procter, F. Eigenbrod, *et al.*, Biodiversity and Resilience of Ecosystem Functions. *Trends Ecol. Evol.* **30**, 673–684 (2015).
- 15 5. S. Díaz, U. Pascual, M. Stenseke, B. Martín-López, R. T. Watson, Z. Molnár, *et al.*, Assessing nature’s contributions to people. *Science* **359**, 270–272 (2018).
6. F. Isbell, A. Gonzalez, M. Loreau, J. Cowles, S. Díaz, A. Hector, *et al.*, Linking the influence and dependence of people on biodiversity across scales. *Nature* **546**, 65–72 (2017).
- 20 7. Convention on Biological Diversity, Kunming-Montreal Global Biodiversity Framework (2022). <https://www.cbd.int/doc/decisions/cop-15/cop-15-dec-04-en.pdf>.
8. C. Kremen, A. M. Merenlender, Landscapes that work for biodiversity and people. *Science* **362**, eaau6020 (2018).
9. Food and Agriculture Organization of the United Nations - processed by Our World in Data, Agriculture (2023). <https://ourworldindata.org/grapher/breakdown-habitable-land?time=latest>.
- 25 10. D. A. Landis, Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic Appl. Ecol.* **18**, 1–12 (2017).
11. C. Carroll, R. F. Noss, How percentage-protected targets can support positive biodiversity outcomes. *Conserv. Biol.* **36**, e13869 (2022).
- 30 12. L. A. Garibaldi, F. J. Oddi, F. E. Miguez, I. Bartomeus, M. C. Orr, E. G. Jobbágy, *et al.*, Working landscapes need at least 20% native habitat. *Conserv. Lett.* **14**, e12773 (2021).
13. European Commission Directorate General for Environment, *EU Biodiversity Strategy for 2030: Bringing Nature Back into Our Lives*. (Publications Office, LU, 2021; <https://data.europa.eu/doi/10.2779/677548>).
- 35

14. A. Mohamed, F. DeClerck, P. H. Verburg, D. Obura, J. F. Abrams, N. Zafra-Calvo, *et al.*, Securing Nature's Contributions to People requires at least 20%–25% (semi-)natural habitat in human-modified landscapes. *One Earth* **7**, 59–71 (2024).
- 5 15. M. Eraerts, A minimum of 15% semi-natural habitat facilitates adequate wild pollinator visitation to a pollinator-dependent crop. *Biol. Conserv.* **278**, 109887 (2023).
16. D. Kleijn, R. Winfree, I. Bartomeus, L. G. Carvalheiro, M. Henry, R. Isaacs, *et al.*, Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat Commun* **6** (2015).
- 10 17. P. Batáry, L. V. Dicks, D. Kleijn, W. J. Sutherland, The role of agri-environment schemes in conservation and environmental management. *Conserv. Biol.* **29**, 1006–1016 (2015).
18. IPBES, “The assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production” (Zenodo, 2016); <https://doi.org/10.5281/ZENODO.3402856>.
- 15 19. E. B. Lowe, R. Groves, C. Gratton, Impacts of field-edge flower plantings on pollinator conservation and ecosystem service delivery – A meta-analysis. *Agric. Ecosyst. Environ.* **310**, 107290 (2021).
- 20 20. H. Segre, D. Kleijn, I. Bartomeus, M. F. WallisDeVries, M. de Jong, M. Frank van der Schee, *et al.*, Butterflies are not a robust bioindicator for assessing pollinator communities, but floral resources offer a promising way forward. *Ecol. Indic.* **154**, 110842 (2023).
21. P. G. Kevan, Pollinators as bioindicators of the state of the environment: species, activity and diversity. *Agric. Ecosyst. Environ.* **74**, 373–393 (1999).
- 25 22. Department for Environment, Food and Rural Affairs, Overview of assessment of change for all indicators and their component measures, *GOV.UK* (2024). <https://www.gov.uk/government/statistics/england-biodiversity-indicators/overview-of-assessment-of-change-for-all-indicators-and-their-component-measures--2>.
23. Materials and methods are available as supplementary materials.
- 30 24. H. Taki, R. Murao, K. Mitai, Y. Yamaura, The species richness/abundance–area relationship of bees in an early successional tree plantation. *Basic Appl. Ecol.* **26**, 64–70 (2018).
25. J. W. Redhead, S. Dreier, A. F. G. Bourke, M. S. Heard, W. C. Jordan, S. Sumner, *et al.*, Effects of habitat composition and landscape structure on worker foraging distances of five bumble bee species. *Ecol. Appl.* **26**, 726–739 (2016).
- 35 26. M. Toivonen, A. Peltonen, I. Herzon, J. Heliölä, N. Leikola, M. Kuussaari, High cover of forest increases the abundance of most grassland butterflies in boreal farmland. *Insect Conserv. Divers.* **10**, 321–330 (2017).

27. D. Kleijn, F. van Langevelde, Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. *Basic Appl. Ecol.* **7**, 201–214 (2005).
- 5 28. M. Albrecht, A. Knecht, M. Riesen, T. Rutz, D. Ganser, Time since establishment drives bee and hoverfly diversity, abundance of crop-pollinating bees and aphidophagous hoverflies in perennial wildflower strips. *Basic Appl. Ecol.* **57**, 102–114 (2021).
29. T. H. Roulston, K. Goodell, The role of resources and risks in regulating wild bee populations. *Annu. Rev. Entomol.* **56**, 293–312 (2011).
- 10 30. A. Holzschuh, M. Dainese, J. P. González-Varo, S. Mudri-Stojnić, V. Riedinger, M. Rundlöf, *et al.*, Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. *Ecol. Lett.* **19**, 1228–1236 (2016).
- 15 31. D. Kleijn, T. E. W. Linders, A. Stip, J. C. Biesmeijer, F. L. Wäckers, T. Bukovinszky, Scaling up effects of measures mitigating pollinator loss from local- to landscape-level population responses. *Methods Ecol. Evol.* **9**, 1727–1738 (2018).
32. T. P. M. Fijen, G. A. Bishop, C. Ganuza, J. Scheper, D. Kleijn, Analyzing the relative importance of habitat quantity and quality for boosting pollinator populations in agricultural landscapes. *Conserv. Biol.*, doi: 10.1111/cobi.14317 (2024).
- 20 33. R. Rader, I. Bartomeus, L. A. Garibaldi, M. P. D. Garratt, B. G. Howlett, R. Winfree, *et al.*, Non-bee insects are important contributors to global crop pollination. *Proc. Natl. Acad. Sci.* **113**, 146–151 (2016).
34. M. S. Warren, D. Maes, C. A. M. van Swaay, P. Goffart, H. Van Dyck, N. A. D. Bourn, *et al.*, The decline of butterflies in Europe: Problems, significance, and possible solutions. *Proc. Natl. Acad. Sci.* **118**, e2002551117 (2021).
- 25 35. J. Ekroos, M. Kuussaari, Landscape context affects the relationship between local and landscape species richness of butterflies in semi-natural habitats. *Ecography* **35**, 232–238 (2012).
36. E. Öckinger, H. G. Smith, Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. *Oecologia* **149**, 526–534 (2006).
- 30 37. B. Meyer, F. Jauker, I. Steffan-Dewenter, Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic Appl. Ecol.* **10**, 178–186 (2009).
38. E. Öckinger, H. G. Smith, Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *J. Appl. Ecol.* **44**, 50–59 (2007).
- 35 39. D. Senapathi, M. A. Goddard, W. E. Kunin, K. C. R. Baldock, Landscape impacts on pollinator communities in temperate systems: evidence and knowledge gaps. *Funct. Ecol.* **31**, 26–37 (2017).

40. R. Marja, T. Tschardtke, P. Batáry, Increasing landscape complexity enhances species richness of farmland arthropods, agri-environment schemes also abundance – A meta-analysis. *Agric. Ecosyst. Environ.* **326**, 107822 (2022).
- 5 41. T. P. Timberlake, I. P. Vaughan, J. Memmott, Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *J. Appl. Ecol.* **56**, 1585–1596 (2019).
42. T. H. Ricketts, J. Regetz, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, A. Bogdanski, *et al.*, Landscape effects on crop pollination services: are there general patterns? *Ecol. Lett.* **11**, 499–515 (2008).
- 10 43. K. Konno, M. Akasaka, C. Koshida, N. Katayama, N. Osada, R. Spake, *et al.*, Ignoring non-English-language studies may bias ecological meta-analyses. *Ecology and Evolution* **10**, 6373–6384 (2020).
44. L. A. Garibaldi, L. G. Carvalheiro, B. E. Vaissière, B. Gemmill-Herren, J. Hipólito, B. M. Freitas, *et al.*, Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. *Science* **351**, 388–391 (2016).
- 15 45. R. A. Robinson, W. J. Sutherland, Post-war changes in arable farming and biodiversity in Great Britain. *J. Appl. Ecol.* **39**, 157–176 (2002).
46. A. S. Persson, H. G. Smith, Seasonal persistence of bumblebee populations is affected by landscape context. *Agric. Ecosyst. Environ.* **165**, 201–209 (2013).
- 20 47. T. Tschardtke, J. M. Tylianakis, T. A. Rand, R. K. Didham, L. Fahrig, P. Batáry, *et al.*, Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol. Rev.* **87**, 661–685 (2012).
48. C. Maurer, L. Sutter, C. Martínez-Núñez, L. Pellissier, M. Albrecht, Different types of semi-natural habitat are required to sustain diverse wild bee communities across agricultural landscapes. *J. Appl. Ecol.* **59**, 2604–2615 (2022).
- 25 49. Y. Mandelik, R. Winfree, T. Neeson, C. Kremen, Complementary habitat use by wild bees in agro-natural landscapes. *Ecol. Appl.* **22**, 1535–1546 (2012).
50. A. Pindar, N. E. Raine, Safeguarding pollinators requires specific habitat prescriptions and substantially more land area than suggested by current policy. *Sci. Rep.* **13**, 1040 (2023).
- 30 51. R. Winfree, J. R. Reilly, I. Bartomeus, D. P. Cariveau, N. M. Williams, J. Gibbs, Species turnover promotes the importance of bee diversity for crop pollination at regional scales. *Science* **359**, 791–793 (2018).
- 35 52. G. A. Bishop, D. Kleijn, M. Albrecht, I. Bartomeus, R. Isaacs, C. Kremen, *et al.*, Critical habitat thresholds for effective pollinator conservation in agricultural landscapes, Dryad (2025); <https://doi.org/10.5061/dryad.nk98sf82b>

53. G. A. Bishop, D. Kleijn, M. Albrecht, I. Bartomeus, R. Isaacs, C. Kremen, *et al.*, Location data from: “Critical habitat thresholds for effective pollinator conservation in agricultural landscapes”, Zenodo (2025); <https://doi.org/10.5281/zenodo.15497131>
54. E. Pollard, A method for assessing changes in the abundance of butterflies. *Biol. Conserv.* **12**, 115–134 (1977).
55. D. Mueller-Dombois, H. Ellenberg, *Aims and Methods of Vegetation Ecology* (Wiley, New York, NY, 1974).
56. M. J. Page, D. Moher, P. M. Bossuyt, I. Boutron, T. C. Hoffmann, C. D. Mulrow, *et al.*, PRISMA 2020 explanation and elaboration: updated guidance and exemplars for reporting systematic reviews. *BMJ*, n160 (2021).
57. E. Grames, A. Stillamn, M. Tingley, C. Elphick, litsearchr: Automated Search Term Selection and Search Strategy for Systematic Reviews, version R package version 1.0.0 (2020).
58. E. M. Grames, A. N. Stillman, M. W. Tingley, C. S. Elphick, An automated approach to identifying search terms for systematic reviews using keyword co-occurrence networks. *Methods Ecol. Evol.* **10**, 1645–1654 (2019).
59. C. Kohl, E. J. McIntosh, S. Unger, N. R. Haddaway, S. Kecke, J. Schiemann, *et al.*, Online tools supporting the conduct and reporting of systematic reviews and systematic maps: a case study on CADIMA and review of existing tools. *Environ. Evid.* **7**, 8 (2018).
60. C. D. Michener, *The Bees of the World* (Johns Hopkins University Press, Baltimore, Md, 2000).
61. C. Plateaux-Quénu, Subsociality in halictine bees. *Insectes Sociaux* **55**, 335–346 (2008).
62. J. Scheper, R. Bommarco, A. Holzschuh, S. G. Potts, V. Riedinger, S. P. M. Roberts, *et al.*, Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. *J. Appl. Ecol.* **52**, 1165–1175 (2015).
63. K. Dijkstra, Wild plants in the Netherlands and Belgium (2024). <https://wildeplanten.nl/>.
64. J. Hilty, Illinois Wildflowers (2024). <https://www.illinoiswildflowers.info/>.
65. Minnesota Wildflowers (2024). <https://www.minnesotawildflowers.info/>.
66. NatureGate (2024). <https://luontoportti.com/en>.
67. Missouri Botanical Garden, Manual de Plantas de Costa Rica (2024). <http://legacy.tropicos.org/Project/Costa%20Rica>.
68. Missouri Botanical Garden, Harvard University Herbaria, eFloras.org (2024). <http://efloras.org/>.

69. Missouri Native Plant Society, Missouri Plants (2024). <https://missouriplants.com/>.
70. Native Plant Trust, Go Botany (2024). <https://gobotany.nativeplanttrust.org/>.
71. Real Jardín Botánico, CSIC, Flora Iberica (2024). <http://www.floraiberica.es/index.php>.
72. WFO, World Flora Online (2024). <https://worldfloraonline.org/>.
- 5 73. Bundesamt für Kartographie und Geodäsie, Digitales Basis-Landschaftsmodell (2021). <https://gdz.bkg.bund.de/index.php/default/digitale-geodaten/digitale-landschaftsmodelle/digitales-basis-landschaftsmodell-ebenen-basis-dlm-ebenen.html>.
74. Consejería de Sostenibilidad, Medio Ambiente y Economía Azul, Junta de Andalucía, Base cartográfica SIOSE Andalucía 2013 (2015).
10 <https://portalrediam.cica.es/geonetwork/static/eng/catalog.search#/metadata/84849016-eb54-45f2-9b9e-b4104cd2b5f1>.
75. European Environment Agency, CORINE Land Cover 2018 (raster 100 m), Europe, 6-yearly - version 2020_20u1, May 2020, version 20.01, European Environment Agency (2019); <https://doi.org/10.2909/960998C1-1870-4E82-8051-6485205EBBAC>.
- 15 76. European Environment Agency, CORINE Land Cover 2000 (raster 100 m), Europe, 6-yearly - version 2020_20u1, May 2020, version 20.01, European Environment Agency (2019); <https://doi.org/10.2909/DDACBD5E-068F-4E52-A596-D606E8DE7F40>.
77. European Environment Agency, CORINE Land Cover 2006 (raster 100 m), Europe, 6-yearly - version 2020_20u1, May 2020, version 20.01, European Environment Agency (2019); <https://doi.org/10.2909/08560441-2FD5-4EB9-BF4C-9EF16725726A>.
- 20 78. European Environment Agency, CORINE Land Cover 2012 (raster 100 m), Europe, 6-yearly - version 2020_20u1, May 2020, version 20.01, European Environment Agency (2019); <https://doi.org/10.2909/A84AE124-C5C5-4577-8E10-511BFE55CC0D>.
79. R. M. Fuller, G. M. Smith, J. M. Sanderson, R. A. Hill, A. G. Thomson, R. Cox, *et al.*, Land Cover Map 2000 (25m raster, GB), NERC EDS Environmental Information Data Centre (2002); <https://doi.org/10.5285/F802EDFC-86B7-4AB9-B8FA-87E9135237C9>.
- 25 80. Geodienste, Landw. Bewirtschaftung: Nutzungsflächen (2024). https://www.geodienste.ch/services/lwb_nutzungsflaechen?locale=de.
81. G. W. Hazeu, M. Vittek, R. Schuiling, J. D. Bulens, M. H. Storm, G. J. Roerink, *et al.*, “LGN2018: een nieuwe weergave van het grondgebruik in Nederland” (1566–7197, Wageningen Environmental Research, Wageningen, 2020); <https://edepot.wur.nl/523996>.
- 30 82. E. S. F. Heggem, H. Mathisen, J. Frydenlund, *AR50 – Arealressurskart i målestokk 1:50 000. Et heldekkende arealressurskart for jord- og skogbruk* (NIBIO, 2019); <https://nibio.brage.unit.no/nibio-xmlui/handle/11250/2626573>.
- 35

83. Institut Cartogràfic i Geològic de Catalunya, Cubiertas del suelo (2019).
<https://www.icgc.cat/es/Ambitos-tematicos/Territori-sostenible/Cubiertas-del-suelo>.
84. R. D. Morton, C. G. Marston, A. W. O’Neil, C. S. Rowland, Land Cover Map 2018
(25m rasterised land parcels, GB), NERC Environmental Information Data Centre
5 (2020); <https://doi.org/10.5285/25C6451B-5C88-40DA-9A63-C3EC473E4874>.
85. R. D. Morton, C. S. Rowland, C. M. Wood, L. Meek, C. G. Marston, G. M. Smith, Land
Cover Map 2007 (25m raster, GB) v1.2, NERC EDS Environmental Information Data
Centre (2014); <https://doi.org/10.5285/A1F88807-4826-44BC-994D-A902DA5119C2>.
86. Naturvårdsverkets Metadatakatalog för Geodata, Nationella marktäckedata 2018:
10 basskikt.
<https://geodatakatalogen.naturvardsverket.se/geonetwork/srv/swe/catalog.search#/meta-data/8853721d-a466-4c01-afcc-9eae57b17b39>.
87. C. S. Rowland, R. D. Morton, L. Carrasco, G. McShane, A. W. O’Neil, C. M. Wood,
15 Land Cover Map 2015 (25m raster, GB), NERC EDS Environmental Information Data
Centre (2017); <https://doi.org/10.5285/BB15E200-9349-403C-BDA9-B430093807C7>.
88. Scottish Government, Scotland Habitat and Land Cover Map - 2020 (2024).
<https://www.data.gov.uk/dataset/911c87c4-a0d3-4bb8-9089-f7657980113e/scotland-habitat-and-land-cover-map-2020>.
89. L. Yang, S. Jin, P. Danielson, C. Homer, L. Gass, S. M. Bender, *et al.*, A new
20 generation of the United States National Land Cover Database: Requirements, research
priorities, design, and implementation strategies. *ISPRS J. Photogramm. Remote Sens.*
146, 108–123 (2018).
90. D. Zanaga, R. Van De Kerchove, W. De Keersmaecker, N. Souverijns, C. Brockmann,
25 R. Quast, *et al.*, ESA WorldCover 10 m 2020 v100, version v100, Zenodo (2021);
<https://doi.org/10.5281/ZENODO.5571936>.
91. E. Pebesma, Simple Features for R: Standardized Support for Spatial Vector Data. *R J.*
10, 439 (2018).
92. R. J. Hijmans, J. van Etten, M. Sumner, J. Cheng, D. Baston, A. Bevan, *et al.*, raster:
30 Geographic Data Analysis and Modeling, version 3.6-26 (2023); <https://cran.r-project.org/web/packages/raster/index.html>.
93. B. B. Phillips, K. J. Gaston, J. M. Bullock, J. L. Osborne, Road verges support
pollinators in agricultural landscapes, but are diminished by heavy traffic and summer
cutting. *J. Appl. Ecol.* **56**, 2316–2327 (2019).
94. Geofabrik, OpenStreetMap, OpenStreetMap data (2024).
35 <https://download.geofabrik.de/europe/>.
95. Ordnance Survey, OS Open Roads, *Ordnance Survey* (2024).
<https://www.ordnancesurvey.co.uk/products/os-open-roads>.

96. U.S. Geological Survey, USGS National Transportation Dataset (2024).
<https://data.usgs.gov/datacatalog/data/USGS:ad3d631d-f51f-4b6a-91a3-e617d6a58b4e>.
97. Yolo County, Yolo County Street Centerlines Open Data (2024). https://yodata-yolo.opendata.arcgis.com/datasets/f6321ba62a574a60b429f21133836bc6_2/explore?location=38.649186,-121.876677,12.34.
98. Dades obertes de Catalunya, Dades del mapa de Cultius amb origen DUN 2017 (2023).
https://analisi.transparenciacatalunya.cat/Medi-Rural-Pesca/Dades-del-mapa-de-Cultius-amb-origen-DUN-2017/v982-gtrg/about_data.
99. W. Han, Z. Yang, L. Di, R. Mueller, CropScape: A Web service based application for exploring and disseminating US conterminous geospatial cropland data products for decision support. *Comput. Electron. Agric.* **84**, 111–123 (2012).
100. OneSoil, OneSoil Map (2024). <https://map.onesoil.ai/>.
101. Rural Payments Agency, Crop Map of England (CROME) 2018 (2023).
<https://www.data.gov.uk/dataset/fb19d34f-59e6-48e7-820a-fe5fda3019e5/crop-map-of-england-crome-2018>.
102. M. Schwieder, G. O. Tetteh, L. Blickensdörfer, A. Gocht, S. Erasmi, Agricultural land use (raster) : National-scale crop type maps for Germany from combined time series of Sentinel-1, Sentinel-2 and Landsat data (2017 to 2021), version v201, Zenodo (2024);
<https://doi.org/10.5281/ZENODO.10617623>.
103. Scottish Government, Scottish Crop Map 2019 (2021).
<http://www.gov.scot/publications/scottish-crop-map-2019/>.
104. Urząd Marszałkowski Województwa Małopolskiego, Mapa glebowo-rolnicza (2024).
https://miip.geomalopolska.pl/mapa/glebowo_rolnicza.html.
105. R Core Team, R: A language and environment for statistical computing, R Foundation for Statistical Computing (2021); <https://www.r-project.org/>.
106. M. E. Brooks, K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, *et al.*, glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal* **9**, 378–400 (2017).
107. A. H. Aldercotte, D. T. Simpson, R. Winfree, Crop visitation by wild bees declines over an 8-year time series: A dramatic trend, or just dramatic between-year variation? *Insect Conserv. Divers.* **15**, 522–533 (2022).
108. M. van de Pol, J. Wright, A simple method for distinguishing within- versus between-subject effects using mixed models. *Anim. Behav.* **77**, 753–758 (2009).
109. F. Hartig, L. Lohse, DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models, version 0.4.6 (2022); <https://cran.r-project.org/web/packages/DHARMA/index.html>.

110. M. Santon, F. Korner-Nievergelt, N. K. Michiels, N. Anthes, A versatile workflow for linear modelling in R. *Front. Ecol. Evol.* **11**, 1065273 (2023).
111. A. F. Zuur, E. N. Ieno, C. S. Elphick, A protocol for data exploration to avoid common statistical problems: *Data exploration. Methods Ecol. Evol.* **1**, 3–14 (2010).
- 5 112. D. Lüdecke, M. Ben-Shachar, I. Patil, P. Waggoner, D. Makowski, performance: An R Package for Assessment, Comparison and Testing of Statistical Models. *J. Open Source Softw.* **6**, 3139 (2021).
113. J. Fox, S. Weisberg, *An R Companion to Applied Regression* (SAGE, Los Angeles, ed. 3rd, 2019).
- 10 114. J. Fox, S. Weisberg, Visualizing Fit and Lack of Fit in Complex Regression Models with Predictor Effect Plots and Partial Residuals. *J. Stat. Softw.* **87** (2018).
115. D. Lüdecke, ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. *J. Open Source Softw.* **3**, 772 (2018).
- 15 116. H. Wickham, *Ggplot2: Elegant Graphics for Data Analysis* (Springer New York, New York, NY, 2009; <https://link.springer.com/10.1007/978-0-387-98141-3>).
117. S. Garnier, N. Ross, Bob Rudis, A. P. Camargo, M. Sciaini, C. Scherer, Rvision - Colorblind-Friendly Color Maps for R, version 0.6.2, Zenodo (2023); <https://doi.org/10.5281/ZENODO.4679423>.
- 20 118. B. Auguie, A. Antonov, gridExtra: Miscellaneous Functions for “Grid” Graphics, version 2.3 (2017); <https://cran.r-project.org/web/packages/gridExtra/index.html>.
119. A. Magrach, F. P. Molina, I. Bartomeus, Niche complementarity among pollinators increases community-level plant reproductive success. *Peer Community J.* **1**, e1 (2021).
- 25 120. S. Laha, S. Chatterjee, A. Das, B. Smith, P. Basu, Exploring the importance of floral resources and functional trait compatibility for maintaining bee fauna in tropical agricultural landscapes. *J. Insect Conserv.* **24**, 431–443 (2020).
121. N. Beyer, D. Gabriel, F. Kirsch, K. Schulz-Kesting, J. Dauber, C. Westphal, Functional groups of wild bees respond differently to faba bean *Vicia faba* L. cultivation at landscape scale. *J. Appl. Ecol.* **57**, 2499–2508 (2020).
- 30 122. N. Beyer, F. Kirsch, D. Gabriel, C. Westphal, Identity of mass-flowering crops moderates functional trait composition of pollinator communities. *Landsc. Ecol.* **36**, 2657–2671 (2021).
123. R. Bommarco, S. A. M. Lindström, C. A. Raderschall, V. Gagic, O. Lundin, Flower strips enhance abundance of bumble bee queens and males in landscapes with few honey bee hives. *Biol. Conserv.* **263**, 109363 (2021).
- 35 124. B. J. Brosi, G. C. Daily, T. M. Shih, F. Oviedo, G. Duran, The effects of forest fragmentation on bee communities in tropical countryside. *J. Appl. Ecol.* **45**, 773–783 (2008).

125. B. J. Brosi, G. C. Daily, P. R. Ehrlich, Bee community shifts with landscape context in a tropical countryside. *Ecol. Appl.* **17**, 418–430 (2007).
126. H. Cohen, G. P. Smith, H. Sardiñas, J. F. Zorn, Q. S. McFrederick, S. H. Woodard, *et al.*, Mass-flowering monoculture attracts bees, amplifying parasite prevalence. *Proc. R. Soc. B Biol. Sci.* **288**, 20211369 (2021).
127. L. J. Cole, S. Brocklehurst, D. Robertson, W. Harrison, D. I. McCracken, Riparian buffer strips: Their role in the conservation of insect pollinators in intensive grassland systems. *Agric. Ecosyst. Environ.* **211**, 207–220 (2015).
128. L. J. Cole, S. Brocklehurst, D. Robertson, W. Harrison, D. I. McCracken, Exploring the interactions between resource availability and the utilisation of semi-natural habitats by insect pollinators in an intensive agricultural landscape. *Agric. Ecosyst. Environ.* **246**, 157–167 (2017).
129. K. R. Denning, B. L. Foster, Flower visitor communities are similar on remnant and reconstructed tallgrass prairies despite forb community differences. *Restor. Ecol.* **26**, 751–759 (2018).
130. K. R. Denning, B. L. Foster, Taxon-specific associations of tallgrass prairie flower visitors with site-scale forb communities and landscape composition and configuration. *Biol. Conserv.* **227**, 74–81 (2018).
131. J. Scheper, I. Badenhauer, J. Kantelhardt, S. Kirchweger, I. Bartomeus, V. Bretagnolle, *et al.*, Biodiversity and pollination benefits trade off against profit in an intensive farming system. *Proc. Natl. Acad. Sci.* **120**, e2212124120 (2023).
132. J. Ekroos, M. Rundlöf, H. G. Smith, Trait-dependent responses of flower-visiting insects to distance to semi-natural grasslands and landscape heterogeneity. *Landsc. Ecol.* **28**, 1283–1292 (2013).
133. T. P. M. Fijen, J. A. Scheper, B. Boekelo, I. Raemakers, D. Kleijn, Effects of landscape complexity on pollinators are moderated by pollinators’ association with mass-flowering crops. *Proc. R. Soc. B Biol. Sci.* **286**, 20190387 (2019).
134. C. Martínez-Núñez, D. Kleijn, C. Ganuza, D. Heupink, I. Raemakers, W. Vertommen, *et al.*, Temporal and spatial heterogeneity of semi-natural habitat, but not crop diversity, is correlated with landscape pollinator richness. *J. Appl. Ecol.* **59**, 1258–1267 (2022).
135. J. Fründ, K. E. Linsenmair, N. Blüthgen, Pollinator diversity and specialization in relation to flower diversity. *Oikos* **119**, 1581–1590 (2010).
136. D. Goulson, G. C. Lye, B. Darvill, Diet breadth, coexistence and rarity in bumblebees. *Biodivers. Conserv.* **17**, 3269–3288 (2008).
137. D. Goulson, M. E. Hanley, B. Darvill, J. S. Ellis, M. E. Knight, Causes of rarity in bumblebees. *Biol. Conserv.* **122**, 1–8 (2005).
138. I. Grass, J. Albrecht, F. Jauker, T. Diekötter, D. Warzecha, V. Wolters, *et al.*, Much more than bees—Wildflower plantings support highly diverse flower-visitor

communities from complex to structurally simple agricultural landscapes. *Agric. Ecosyst. Environ.* **225**, 45–53 (2016).

- 5 139. A. Holzschuh, C. F. Dormann, T. Tschardtke, I. Steffan-Dewenter, Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proc. R. Soc. B Biol. Sci.* **278**, 3444–3451 (2011).
140. A. Holzschuh, I. Steffan-Dewenter, T. Tschardtke, Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos* **117**, 354–361 (2008).
- 10 141. S. Hopfenmüller, I. Steffan-Dewenter, A. Holzschuh, Trait-Specific Responses of Wild Bee Communities to Landscape Composition, Configuration and Local Factors. *PLoS ONE* **9**, e104439 (2014).
142. B. Jauker, J. Krauss, F. Jauker, I. Steffan-Dewenter, Linking life history traits to pollinator loss in fragmented calcareous grasslands. *Landsc. Ecol.* **28**, 107–120 (2013).
- 15 143. E. Kallioniemi, J. Åström, G. M. Rusch, S. Dahle, S. Åström, J. O. Gjershaug, Local resources, linear elements and mass-flowering crops determine bumblebee occurrences in moderately intensified farmlands. *Agric. Ecosyst. Environ.* **239**, 90–100 (2017).
144. A. Kovács-Hostyánszki, R. Földesi, E. Mózes, Á. Szirák, J. Fischer, J. Hanspach, *et al.*, Conservation of pollinators in traditional agricultural landscapes – New challenges in Transylvania (Romania) posed by EU accession and recommendations for future research. *PLOS ONE* **11**, e0151650 (2016).
- 20 145. E. Krimmer, E. A. Martin, J. Krauss, A. Holzschuh, I. Steffan-Dewenter, Size, age and surrounding semi-natural habitats modulate the effectiveness of flower-rich agri-environment schemes to promote pollinator visitation in crop fields. *Agric. Ecosyst. Environ.* **284**, 106590 (2019).
- 25 146. S. Kühnel, N. Blüthgen, High diversity stabilizes the thermal resilience of pollinator communities in intensively managed grasslands. *Nat. Commun.* **6**, 7989 (2015).
147. T. Roth, M. Coll, Y. Mandelik, The Role of Uncultivated Habitats in Supporting Wild Bee Communities in Mediterranean Agricultural Landscapes. *Diversity* **15**, 294 (2023).
- 30 148. G. Marcacci, I. Grass, V. S. Rao, S. Kumar S, K. B. Tharini, V. V. Belavadi, *et al.*, Functional diversity of farmland bees across rural–urban landscapes in a tropical megacity. *Ecol. Appl.* **32**, e2699 (2022).
149. M. Monasterolo, S. L. Poggio, D. Medan, M. Devoto, Wider road verges sustain higher plant species richness and pollinator abundance in intensively managed agroecosystems. *Agric. Ecosyst. Environ.* **302**, 107084 (2020).
- 35 150. L. A. Morandin, C. Kremen, Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecol. Appl.* **23**, 829–839 (2013).
151. J. Morrison, J. Izquierdo, E. H. Plaza, J. L. González-Andújar, The role of field margins in supporting wild bees in Mediterranean cereal agroecosystems: Which biotic and abiotic factors are important? *Agric. Ecosyst. Environ.* **247**, 216–224 (2017).

152. A. S. Persson, M. Rundlöf, Y. Clough, H. G. Smith, Bumble bees show trait-dependent vulnerability to landscape simplification. *Biodivers. Conserv.* **24**, 3469–3489 (2015).
153. J. Piko, A. Keller, C. Geppert, P. Batáry, T. Tschardtke, C. Westphal, *et al.*, Effects of three flower field types on bumblebees and their pollen diets. *Basic Appl. Ecol.* **52**, 95–108 (2021).
154. E. F. Power, J. C. Stout, Organic dairy farming: impacts on insect–flower interaction networks and pollination. *J. Appl. Ecol.* **48**, 561–569 (2011).
155. G. Quinlan, M. Milbrath, C. Otto, A. Smart, D. Iwanowicz, R. S. Cornman, *et al.*, Honey bee foraged pollen reveals temporal changes in pollen protein content and changes in forager choice for abundant versus high protein flowers. *Agric. Ecosyst. Environ.* **322**, 107645 (2021).
156. L. G. A. Riggi, O. Lundin, Å. Berggren, Mass-flowering red clover crops have positive effects on bumblebee richness and diversity after bloom. *Basic Appl. Ecol.* **56**, 22–31 (2021).
157. J. Scheper, T. Bukovinszky, M. E. Huigens, D. Kleijn, Attractiveness of sown wildflower strips to flower-visiting insects depends on seed mixture and establishment success. *Basic Appl. Ecol.* **56**, 401–415 (2021).
158. S. C. Simanonok, C. R. V. Otto, D. A. Buhl, Floral resource selection by wild bees and honey bees in the Midwest United States: implications for designing pollinator habitat. *Restor. Ecol.* **29**, e13456 (2021).
159. D. Bourke, D. Stanley, E. O’Rourke, R. Thompson, T. Carnus, J. Dauber, *et al.*, Response of farmland biodiversity to the introduction of bioenergy crops: effects of local factors and surrounding landscape context. *GCB Bioenergy* **6**, 275–289 (2014).
160. D. A. Stanley, J. C. Stout, Quantifying the impacts of bioenergy crops on pollinating insect abundance and diversity: a field-scale evaluation reveals taxon-specific responses. *J. Appl. Ecol.* **50**, 335–344 (2013).
161. A. Magrach, J. P. González-Varo, M. Boiffier, M. Vilà, I. Bartomeus, Honeybee spillover reshuffles pollinator diets and affects plant reproductive success. *Nat. Ecol. Evol.* **1**, 1299–1307 (2017).
162. A. Magrach, A. Holzschuh, I. Bartomeus, V. Riedinger, S. P. M. Roberts, M. Rundlöf, *et al.*, Plant-pollinator networks in semi-natural grasslands are resistant to the loss of pollinators during blooming of mass-flowering crops. *Ecography*, n/a-n/a (2017).
163. M. F. Tanis, L. Marshall, J. C. Biesmeijer, L. van Kolfschoten, Grassland management for meadow birds in the Netherlands is unfavourable to pollinators. *Basic Appl. Ecol.* **43**, 52–63 (2020).
164. S. Tarrant, J. Ollerton, M. L. Rahman, J. Tarrant, D. McCollin, Grassland Restoration on Landfill Sites in the East Midlands, UNITED KINGDOM : An Evaluation of Floral Resources and Pollinating Insects. *Restor. Ecol.* **21**, 560–568 (2013).

165. A. J. Vanbergen, B. A. Woodcock, A. Gray, F. Grant, A. Telford, P. Lambdon, *et al.*, Grazing alters insect visitation networks and plant mating systems. *Funct. Ecol.* **28**, 178–189 (2014).
- 5 166. V. von Königslöw, F. Fornoff, A.-M. Klein, Pollinator enhancement in agriculture: comparing sown flower strips, hedges and sown hedge herb layers in apple orchards. *Biodivers. Conserv.*, doi: 10.1007/s10531-021-02338-w (2021).
167. V. von Königslöw, A.-C. Mupepele, A.-M. Klein, Overlooked jewels: Existing habitat patches complement sown flower strips to conserve pollinators. *Biol. Conserv.* **261**, 109263 (2021).
- 10 168. C. N. Weiner, M. Werner, K. E. Linsenmair, N. Blüthgen, Land-use impacts on plant–pollinator networks: interaction strength and specialization predict pollinator declines. *Ecology* **95**, 466–474 (2014).
169. A. Wen, K. J. Elgersma, M. E. Sherrard, L. L. Jackson, J. Meissen, M. C. Myers, Wild bee visitors and their association with sown and unsown floral resources in
15 reconstructed pollinator habitats within an agriculture landscape. *Insect Conserv. Divers.* **15**, 102–113 (2022).
170. N. I. Wilkinson, J. D. Wilson, G. Q. A. Anderson, Agri-environment management for corncrake *Crex crex* delivers higher species richness and abundance across other taxonomic groups. *Agric. Ecosyst. Environ.* **155**, 27–34 (2012).
- 20 171. T. J. Wood, J. Gibbs, N. Rothwell, J. K. Wilson, L. Gut, J. Brokaw, R. Isaacs, Limited phenological and dietary overlap between bee communities in spring flowering crops and herbaceous enhancements. *Ecol. Appl.* **28**, 1924–1934 (2018).
172. N. Blüthgen, S. Kühnel, Flower visitor response to temperature on 40 grassland EPs (ALB, HAI), 2012, version 2, Biodiversity Exploratories Information System (2019);
25 <https://www.bexis.uni-jena.de/ddm/data/Showdata/17526?version=2>.
173. A. Ostrowski, J. Nieschulze, E.-D. Schulze, B. König-Ries, Birgitta (2023), Coordinates and Inventory Overview of all Grid Plots (GPs), version 7, Biodiversity Exploratories Information System (2023).
- 30 174. M. Werner, C. Weiner, K.E. Linsenmair, N. Blüthgen, flower availability 2007 Schwäbische Alb, version 2, Biodiversity Exploratories Information System (2016); <https://www.bexis.uni-jena.de/ddm/data/Showdata/4882?version=2>.
- 35 175. M. Werner, C. Weiner, K.E. Linsenmair, N. Blüthgen, Flower visitor interactions in 2007, Schwäbische Alb, version 2, Biodiversity Exploratories Information System (2016); <https://www.bexis.uni-jena.de/ddm/data/Showdata/4883?version=2>.
- 40 176. C. Weiner, M. Werner, K.E. Linsenmair, N. Blüthgen, flower visitor interactions 2008, version 3, Biodiversity Exploratories Information System (2016); <https://www.bexis.uni-jena.de/ddm/data/Showdata/10160?version=3>.

177. C. Weiner, K.E. Linsenmair, N. Blüthgen, Flower availability 2008 Schorfheide, version 2, Biodiversity Exploratories Information System (2019); <https://www.bexis.uni-jena.de/ddm/data/Showdata/4964?version=2>.

5

178. C. Weiner, K.E. Linsenmair, N. Blüthgen, Flower availability 2008 Hainich, version 2, Biodiversity Exploratories Information System (2019); <https://www.bexis.uni-jena.de/ddm/data/Showdata/4963?version=2>.

10

179. C. Weiner, K.E. Linsenmair, N. Blüthgen, Flower availability 2008 Alb-korrigiert, version 2, Biodiversity Exploratories Information System (2019); <https://www.bexis.uni-jena.de/ddm/data/Showdata/4981?version=2>.

15

Acknowledgments: We would like to thank Jochen Fründ, Clint Otto, and Stacy Simanonok for providing data, Marcel Schwieder for granting access to GIS data, Maarten Postuma for assistance with code, and Klara Leander Oh for assisting in graphics creation.

Funding: This work was supported by the European Union’s Horizon 2020 research and innovation programme under grant agreement no. 862480, SHOWCASE project (<https://showcase-project.eu/>) (GAB, DK, MA, I Bartomeus, SGP, JS, A Báldi, JMH). This article reflects only the views of the authors. Any opinions, findings, conclusions, or recommendations expressed in this article are those of the authors and do not necessarily reflect the views of or imply endorsement by the funding sources. The funding sources had no role in the completion of the study or the creation of the article and are not responsible for any use that may be made of the information this article contains. Additional funding information is as follows:

017-2018 Belmont Forum and BiodivERsA joint call for research proposals, under the BiodivScen ERA-Net COFUND programme, and with the funding organisations AEI, NWO, ECCyT and NSF (TPMF)

Anne M. and Robert T. Bass Stanford Graduate Fellowship in Science and Engineering (BJB)

Basque Government through the Basque Excellence Research Centres (BERC) 2022-2025 (AM)

Bayer Crop Science (VvK, AMK)

BiodivERsA/FACCE-JPI joint call project ECODEAL, national funders Agence Nationale de la Recherche (ANR), Bundesministerium für Bildung und Forschung (BMBF) (01 LC1407A), Swedish Research Council for Environment (FORMAS) (2014-1783), Fonds zur Förderung der wissenschaftlichen Forschung (FWF) (contract I 2045-B25), Ministerio de Economía y Competitividad (MINECO) (PCIN-2014-048), Netherlands Organisation for Scientific Research (NWO) (832.14.007), and Projektträger im Deutschen Zentrum für Luft- und Raumfahrt (PT-DLR) (I Bartomeus, AH, JS, JPGV, EK, ISD, MV, AM, I Badenhauer, JK, RB, DK)

British Ecological Society (DG)

British Ecological Society grant no. SEPG 1563/1968 (AJV)

British Entomology and Natural History Society (DG)

Bundesministerium für Ernährung und Landwirtschaft, grant no. 281 5EPSO 16 (FK, CW, N Beyer)

Conservation Innovation Grant CIG-68-9104-6-101 (CK, LAM)

Cornwall Area of Outstanding Natural Beauty Unit (BBP)

Council of Scientific & Industrial Research sanction no. 09/028(0882)/2012-EMR-I, date 21.08.2012 (PB, SL)

Darwin Initiative project 19-024 (PB, SL)

De Vlinderstichting (MFWdV)

Deutsche Forschungsgemeinschaft grant no. BA 4438/2-1 “Biodiversity and associated ecosystem services in small- vs. large-scale agriculture”, (JIP, ALH)

Deutsche Forschungsgemeinschaft grant no. 279374797 (IG, TT, GM)

Deutsche Forschungsgemeinschaft grant nos. 493487387, 405945293, 289781364 (IG, CW)

Deutsche Forschungsgemeinschaft Priority Program 1374 ‘Infrastructure - Biodiversity Exploratories’ grant nos. LI 150/20-1 and BL 960/2-1 (N Blüthgen)

5 Deutsche Forschungsgemeinschaft-Collaborative Research Center 1047 “Insect Timing” (AH, ISD)

‘DRUID project: Drivers and Repercussions of UK Insect Declines’, funded by the Natural Environment Research Council, grant no. NE/V006916/1 (WEK)

EU Seventh Framework Programme project BeeFun grant no. 631653 (I Bartomeus)

10 EU Seventh Framework Programme project SCALES (“Securing the Conservation of biodiversity across Administrative Levels and spatial, temporal and Ecological Scales”) grant no. 226852 (BJ, JK, ISD)

EU-funded project EASY grant no. QLK5-CT-2002-01495 (AH, ISD, TT)

EU-funded project QUESSA grant no. 311879 (LS, MA)

15 EU Seventh Framework Programme project LIBERATION (www.fp7liberation.eu) grant no. 311781 (DK)

EU Seventh Framework Programme (FP7/2007–2013) project STEP grant no. 244090 (AH, SH, JS, DK, ISD, HGS, JE, MR, JPGV, SGP, SPMR, JBW, VJW, SMS, AV, MV, AM, RB, TT)

European Regional Development Fund (ERDF) (JM, JLGA, JI)

20 EU Sixth Framework Programme integrated project ALARM (Assessing Large scale environmental Risks for biodiversity with tested Methods), Pollinator Module, grant no. GOCE-CT-2003-506675 (BJ, JK, ISD)

EU Horizon 2020 research and innovation programme project SAFEGUARD grant no. 101003476 (AH, JK, ISD)

25 EU Horizon framework programme project RestPoll grant no. 1010082101 (AMK, DK, FF, MA, MR)

FOCA Banco Galicia – Fundación Williams 2015 award (MM, MD)

Foundation for Food and Agriculture grant no. CA18-SS-0000000009 (LCP, HC)

Foundation of the University of Marburg grant no. VB1.2-5.45.26 (J Albrecht, IG)

30 Grassland Heritage Foundation (BLF, KRD)

Helmholtz Association grant no. VH-NG-247 (AH, ISD, TT)

Ikerbasque research fellowship (AM)

Iowa Science Foundation grant no. 19-17 (AW)

35 Irish Department of Agriculture, Fisheries and Food Research Stimulus Fund (RSF), funded under the National Development Plan (2007–2013) grant no. 07512 (EFP, JCS)

Juan de la Cierva program grant no. IJCI-2014-22558 (AM)

Kansas Native Plant Society (BLF, KRD)

Kansas University Field Station (BLF, KRD)

Keren Kayemeth LeIsrael-Jewish National Fund Appelby program (YM, TR)
Koret Foundation (BJB)
'Lendület' program of the Hungarian Academy of Sciences (A Báldi, AKH)
Moore Family Foundation (BJB)
5 National Fund for Research of Argentina (FONCYT) grant no. PICT-2011-0582 (MM, MD)
National Geographic Society Research and Exploration (CK, LAM)
National Science Foundation Graduate Research Fellowship grant no. DGE-1848739 (GMQ)
National Science Foundation grant no. DEB-0919128 (CK, LAM)
National Science Foundation grant nos. DEB-1021158 and DEB-0950100 (BLF, KR D)
10 Natural England (NIW)
Natural Environment Research Council grant no. NE/L002434/1 (BBP)
Natural Sciences and Engineering Research Council of Canada (NSERC) doctoral
scholarship (JM, JLGA, JI)
Natural Environment Research Council – UK Centre for Ecology & Hydrology National
15 Capability grant no. NEC03463 (AJV)
Netherlands Organization for Scientific Research, NWO-ALW Biodiversity Works Program,
grant no. 841.11.001 (JS, DK)
Norwegian Environment Agency grant no. 2012/16642 (EPK, J Åström)
Natural Sciences and Engineering Research Council of Canada Postdoctoral Fellowship
20 (LAM)
Operation Pollinator (TJW, RI)
Peter and Helen Bing (BJB)
Prairie Biotic Research, Inc. (BLF, KR D)
Ramon y Cajal fellowship RYC2021-032251-I (AM)
25 Research Council of Norway, BIOSMART project no. 244608/050 (EPK, J Åström)
Research Council of Norway, NINA – Strategic Institute Program 208434/F40 (EPK, J
Åström)
Research Council of Norway, PolliClover project no. 225019 (EPK, J Åström)
Research programme NWO-Green, which is jointly funded by the Netherlands Organization
30 for Scientific Research (NWO) and Nunhems Netherlands BV (BASF) under project number
870.15.030 (TPMF)
Roy J. Carver Charitable Trust (AW)
Royal Society for the Protection of Birds (NIW)
Rural and Environment Science and Analytical Services Division (RESAS) of the Scottish
35 Government, Theme C - 2022-2027 (LJC, DIM)

Scottish Government Rural Affairs and the Environment Strategic Research Programme 2016–2021, Theme 2: Productive and Sustainable Land Management and Rural Economies (LJC, DIM)

5 Scottish Government’s Strategic Research Programme 2011–2016, Programme 1: Environment (LJC, DIM)

Sherwood Foundation (BJB)

10 SIMBIOSYS Project (<http://www.tcd.ie/research/simbiosys/>, 2007-B-CD-1-S1) as part of the Science, Technology, Research and Innovation for the Environment (STRIVE) Programme, financed by the Irish Government under the National Development Plan 2007–2013, administered on behalf of the Department of the Environment, Heritage and Local Government by the Irish Environmental Protection Agency (DAS, JCS)

SITA Environmental Trust (JO, ST)

Spanish Ministry of Economy and Competitiveness project FLORMAS no. CGL 2012-33801 (JPGV, MV)

15 Spanish Ministry of Economy and Competitiveness projects AGL2012-33736 and AGL2015-64130-R (JM, JLGA, JI)

Spanish Severo Ochoa Program SEV-2012-0262 (JPGV, AM)

Spanish State Research Agency María de Maeztu Excellence Unit accreditation (MDM-2017-0714 and CEX2021-001201-M) funded by MCIN/AEI /10.13039/501100011033 (AM)

20 Stanford University Field Studies and Human Biology Research Experiences for Undergraduates Programs (BJB)

Swedish Government Strategic Research Initiative Biodiversity and Ecosystem Services in a Changing Climate BECC (JE, HGS, MR)

Swedish Research Council FORMAS grant no. 2005-788 (HGS, JE, MR)

25 Swedish Research Council FORMAS grant no. 2016-00361 (A Berggren, LGAR)

Swedish Research Council FORMAS grant no. 2019-01524 (ASP)

Swedish University of Agricultural Sciences (SLU) through the research program EkoForsk (RB, SAML)

Syngenta (JS, DK)

30 Syngenta-CONICET grant no. RD298/14 (MM, MD)

Teresa Heinz Scholarship for Environmental Research (BJB)

The Leverhulme Trust (DG)

The Nature Conservancy (BLF, KRD)

35 UK Insect Pollinator Initiative project ‘AgriLand: Linking agriculture and land use change to pollinator populations’, funded under the Living with Environmental change programme, a collaboration between Biotechnology and Biological Sciences Research Council (BBSRC), the Wellcome Trust, Scottish Government, Department of Environment, Food and Rural Affairs (DEFRA) and Natural Environment Research Council (NERC): grant BB/H014934/1 (MAKG, SGP, DS, WEK, SPMR)

40 UK Landfill Tax Credit Scheme (JO, ST)

University Fund Wageningen (TPMF)

University of Buenos Aires grant no. 20020130200230BA (MM, MD)

University of Northern Iowa Biology Department, College of Humanities, Arts and Sciences,
and Tallgrass Prairie Center (AW)

5 USDA Farm Service Agency grant no. AG-3151-C-17-0013 (AW)

USDA Farm Service Agency Inter-agency Agreement 16IAMRECRPHBTA1 (GMQ)

USDA-NIFA Specialty Crop Research Initiative award 2012-51181-20105 (Developing
Sustainable Pollination Strategies for U.S. Specialty Crops) (TJW, RI)

Winslow Foundation (BJB)

10 Women's League for Israel (YM, TR)

Author contributions:

Conceptualization: GAB, DK, TPMF

Data curation: GAB

15 Formal analysis: GAB

Investigation: GAB, DK, MA, I Bartomeus, RI, CK, AM, LCP, SGP, JS, HGS, TT, J
Albrecht, J Åström, I Badenhauer, A Baldi, PB, A Berggren, N Beyer, N Blüthgen, RB,
BJB, HC, LJC, KRD, MD, JE, FF, BLF, MAKG, JLGA, JPGV, DG, IG, ALH, JMH, AH,
SH, JI, BJ, EPK, FK, AMK, AKH, JK, EK, WEK, SL, SAML, YM, GM, DIM, MM, LAM,
20 JM, SMS, JO, ASP, BBP, JIP, EFP, GMQ, MR, CAR, LGAR, SPMR, TR, DS, DAS, ISD,
JCS, LS, MFT, ST, LvK, AJV, MV, VvK, AV, MFWdV, AW, CW, JBW, VJW, NIW,
TJW, TPMF

Methodology: GAB, DK, TPMF

Supervision: DK, TPMF

25 Validation: GAB, DK, MA, I Bartomeus, RI, CK, AM, LCP, SGP, JS, HGS, TT, J
Albrecht, J Åström, I Badenhauer, A Baldi, PB, A Berggren, N Beyer, N Blüthgen, RB,
BJB, HC, LJC, KRD, MD, JE, FF, BLF, MAKG, JLGA, JPGV, DG, IG, ALH, JMH, AH,
SH, JI, BJ, EPK, FK, AMK, AKH, JK, EK, WEK, SL, SAML, YM, GM, DIM, MM, LAM,
JM, SMS, JO, ASP, BBP, JIP, EFP, GMQ, MR, CAR, LGAR, SPMR, TR, DS, DAS, ISD,
30 JCS, LS, MFT, ST, LvK, AJV, MV, VvK, AV, MFWdV, AW, CW, JBW, VJW, NIW,
TJW, TPMF

Visualization: GAB, TPMF

Writing – original draft: GAB

35 Writing – review & editing: GAB, DK, MA, I Bartomeus, RI, CK, AM, LCP, SGP, JS,
HGS, TT, J Albrecht, J Åström, I Badenhauer, A Baldi, PB, A Berggren, N Beyer, N
Blüthgen, RB, BJB, HC, LJC, KRD, MD, JE, FF, BLF, MAKG, JLGA, JPGV, DG, IG,
ALH, JMH, AH, SH, JI, BJ, EPK, FK, AMK, AKH, JK, EK, WEK, SL, SAML, YM, GM,
DIM, MM, LAM, JM, SMS, JO, ASP, BBP, JIP, EFP, GMQ, MR, CAR, LGAR, SPMR,
TR, DS, DAS, ISD, JCS, LS, MFT, ST, LvK, AJV, MV, VvK, AV, MFWdV, AW, CW,
40 JBW, VJW, NIW, TJW, TPMF

Competing interests: SL declares an additional affiliation as Senior Analyst at the Swedish Board of Agriculture, SE-551 82 Jönköping.

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

Supplementary Materials

Materials and Methods

Supplementary Text

Figs. S1 to S10

Tables S1 to S9

References (54–179)

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

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

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

5

10