

A global synthesis reveals biodiversity-mediated benefits for crop production

Matteo Dainese^{1,2*}, Emily A. Martin², Marcelo A. Aizen³, Matthias Albrecht⁴, Ignasi Bartomeus⁵, Riccardo Bommarco⁶, Luisa G. Carvalheiro^{7,8}, Rebecca Chaplin-Kramer⁹, Vesna Gagic¹⁰, Lucas A. Garibaldi¹¹, Jaboury Ghazoul¹², Heather Grab¹³, Mattias Jonsson⁶, Daniel S. Karp¹⁴, Christina M. Kennedy¹⁵, David Kleijn¹⁶, Claire Kremen¹⁷, Douglas A. Landis¹⁸, Deborah K. Letourneau¹⁹, Lorenzo Marini²⁰, Katja Poveda¹³, Romina Rader²¹, Henrik G. Smith^{22,23}, Teja Tschardt²⁴, Georg K.S. Andersson²², Isabelle Badenhauer^{25,26}, Svenja Baensch^{24,27}, Antonio Diego M. Bezerra²⁸, Felix J.J.A. Bianchi²⁹, Virginie Boreux¹², Vincent Bretagnolle³⁰, Berta Caballero-Lopez³¹, Pablo Cavigliasso³², Aleksandar Ćetković³³, Natacha P. Chacoff³⁴, Alice Classen², Sarah Cusser³⁵, Felipe D. da Silva e Silva^{36,37}, G. Arjen de Groot³⁸, Jan H. Dudenhöffer³⁹, Johan Ekroos²², Thijs Fijen¹⁵, Pierre Franck⁴⁰, Breno M. Freitas⁴¹, Michael P.D. Garratt⁴², Claudio Gratton⁴³, Juliana Hipólito¹¹, Andrea Holzschuh², Lauren Hunt⁴⁴, Aaron L. Iverson¹³, Shalene Jha⁴⁵, Tamar Keasar⁴⁶, Tania N. Kim⁴⁷, Miriam Kishinevsky⁴⁸, Björn K. Klatt^{23,24}, Alexandra-Maria Klein⁴⁹, Kristin M. Krewenka⁵⁰, Smitha Krishnan^{12,51}, Ashley E. Larsen⁵², Claire Lavigne⁴⁰, Heidi Lier⁵³, Bea Maas⁵⁴, Rachel E. Mallinger⁵⁵, Eliana Martinez Pachon⁵⁶, Alejandra Martínez-Salinas⁵⁷, Timothy D. Meehan⁵⁸, Matthew G.E. Mitchell⁵⁹, Gonzalo A.R. Molina⁶⁰, Maike Nesper¹², Lovisa Nilsson²², Megan E. O'Rourke⁶¹, Marcell K. Peters², Milan Plečák³³, Simon G. Potts⁴², Davi de L. Ramos⁶², Jay A. Rosenheim⁶³, Maj Rundlöf²³, Adrien Rusch⁶⁴, Agustín Sáez⁶⁵, Jeroen Scheper^{15,38}, Matthias Schleuning⁶⁶, Julia Schmack⁶⁷, Amber R. Sciligo⁶⁸, Colleen Seymour⁶⁹, Dara A. Stanley⁷⁰, Rebecca Stewart²², Jane C. Stout⁷¹, Louis Sutter⁴, Mayura B. Takada⁷², Hisatomo Taki⁷³, Giovanni Tamburini⁶, Matthias Tschumi⁴, Blandina F. Viana⁷⁴, Catrin Westphal²⁷, Bryony K. Willcox²¹, Stephen D. Wratten⁷⁵, Akira Yoshioka⁷⁶, Carlos Zaragoza-Trello⁵, Wei Zhang⁷⁷, Yi Zou⁷⁸, Ingolf Steffan-Dewenter²

¹Institute for Alpine Environment, Eurac Research, Viale Druso 1, 39100 Bolzano, Italy

²Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Am Hubland, 97074 Würzburg, Germany

³Grupo de Ecología de la Polinización - INIBIOMA (Universidad Nacional del Comahue-CONICET), 8400 Bariloche, Rio Negro, Argentina

⁴Agroecology and Environment, Agroscope, Reckenholzstrasse 191, 8046 Zurich, Switzerland

⁵Estación Biológica de Doñana (EBD-CSIC), Integrative Ecology, E-41092 Sevilla, Spain

⁶Swedish University of Agricultural Sciences, Department of Ecology, 750 07 Uppsala, Sweden

⁷Departamento de Ecologia, Universidade Federal de Goias (UFG), Goiânia, Brazil

⁸Faculdade de Ciencias, Centre for Ecology, Evolution and Environmental Changes (CE3C), Universidade de Lisboa, Lisboa, Portugal

⁹Natural Capital Project, Stanford University, Stanford, California, USA

¹⁰CSIRO, GPO Box 2583, Brisbane, QLD 4001, Australia

¹¹Instituto de Investigaciones en Recursos Naturales, Agroecología y Desarrollo Rural (IRNAD), Sede Andina, Universidad Nacional de Río Negro (UNRN) y CONICET. Mitre 630, CP 8400, San Carlos de Bariloche, Río Negro, Argentina

¹²Department of Environmental Systems Science, ETH Zurich, Universitätstrasse 16, 8092 Zurich, Switzerland

¹³Cornell University, Department of Entomology, Ithaca, NY 14853, USA

¹⁴Department of Wildlife, Fish, and Conservation Biology; University of California Davis, Davis, CA 95616, USA

¹⁵Global Lands Program, The Nature Conservancy, 117 E. Mountain Avenue, Fort Collins, CO 80524, USA

- 16Plant Ecology and Nature Conservation Group, Wageningen University, Droevendaalsesteeg 3a, Wageningen
6708 PB, The Netherlands
- 17IRES and Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia, Canada
- 18Michigan State University, Department of Entomology and Great Lakes Bioenergy Research Center, 204 CIPS,
578 Wilson Ave, East Lansing, MI 48824, USA
- 19Department of Environmental Studies, University of California, Santa Cruz, CA USA 95064
- 20DAFNAE, University of Padova, viale dell'Università 16, 35020, Legnaro, Padova, Italy
- 21School of Environment and Rural Science, University of New England, Armidale, 2350, Australia
- 22Centre for Environmental and Climate Research, Lund University, S-223 62 Lund, Sweden
- 23Department of Biology, Lund University, S-223 62 Lund, Sweden
- 24Agroecology, Department of Crop Sciences, University of Göttingen, Germany
- 25USC1339 INRA-CNRS, CEBC UMR 7372, CNRS & Université de La Rochelle, Beauvoir sur Niort, 79360,
France
- 26INRA, URP3F Unité de Recherche Pluridisciplinaire Prairie et Plantes Fourragères, Lusignan, 86600, France
- 27Functional Agrobiodiversity, Department of Crop Sciences, University of Göttingen, Germany
- 28Departamento de Zootecnia – CCA, Universidade Federal do Ceará, 60.356-000, Fortaleza, CE, Brazil
- 29Farming Systems Ecology, Wageningen University & Research, P.O. Box 430, 6700 AK Wageningen, The
Netherlands
- 30LTSE Zone Atelier Plaine & Val de Sevre, CEBC UMR 7372, CNRS & Université de La Rochelle, Beauvoir sur
Niort, 79360, France
- 31Arthropods Department, Natural Sciences Museum of Barcelona, 08003 Barcelona, Spain
- 32Instituto Nacional de Tecnología Agropecuaria, Estación Experimental Concordia. Estacion Yuqueri y vias del
Ferrocarril s/n (3200), Entre Rios. Argentina
- 33Faculty of Biology, University of Belgrade, Studentski trg 16, 11000 Belgrade, Serbia
- 34Instituto de Ecología Regional - IER (Universidad Nacional de Tucumán-CONICET), 4107 Yerba Buena,
Tucumán, Argentina
- 35W.K. Kellogg Biological Station, Michigan State University, Michigan, USA
- 36Federal Institute of Education, Science and Technology of Mato Grosso, Campus of Barra do Garças/MT, 78600-
000, Brazil
- 37Center of Sustainable Development, University of Brasília (UnB) – Campus Darcy Ribeiro, Asa Norte, Brasília-
DF, 70910-900, Brazil
- 38Wageningen Environmental Research, Wageningen University & Research, P.O. Box 47, 6700 AA Wageningen,
The Netherlands
- 39Natural Resources Institute, University of Greenwich, Central Avenue, Chatham Maritime, Kent, ME44TB, UK
- 40INRA, UR 1115, Plantes et Systèmes de culture horticoles, 84000 Avignon, France
- 41Departamento de Zootecnia – CCA, Universidade Federal do Ceará, 60.356-000, Fortaleza, CE, Brazil
- 42Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, Reading University,
RG6 6AR, UK
- 43Department of Entomology, University of Wisconsin, Madison, WI 53705, USA
- 44Human-Environment Systems, Ecology, Evolution, and Behavior, Department of Biological Sciences, Boise State
University, Boise, ID, USA
- 45Department of Integrative Biology, University of Texas at Austin, 205 W 24th Street, 401 Biological Laboratories,
Austin, TX 78712, USA
- 46Department of Biology and Environment, University of Haifa - Oranim, Tivon 36006, Israel
- 47Kansas State University Department of Entomology, 125 Waters Hall, Manhattan, KS 66503 USA
- 48Department of Evolutionary and Environmental Biology, University of Haifa, 3498838 Haifa, Israel
- 49Chair of Nature Conservation and Landscape Ecology, University of Freiburg, Tennenbacher Straße 4, 79106
Freiburg, Germany
- 50Institute for Plant Science and Microbiology, University of Hamburg, Hamburg, Germany
- 51Ashoka Trust for Research in Ecology and the Environment (ATREE), Bangalore, India
- 52Bren School of Environmental Science & Management, University of California, Santa Barbara, CA 93106-5131,
USA
- 53Seattle University, Department of Environmental Studies, 901 12th Avenue, Seattle, WA 9812, USA
- 54Department of Botany and Biodiversity Research, Division of Conservation Biology, Vegetation Ecology and
Landscape Ecology, University of Vienna, Rennweg 14, 1030 Vienna, Austria

- ⁵⁵University of Florida, Department of Entomology and Nematology, 1881 Natural Area Drive, Gainesville, FL, USA 32601
- ⁵⁶Agrosavia, Centro de Investigación Obonuco. Km 5 vía Obonuco - Pasto, Nariño. Colombia
- ⁵⁷Agriculture, Livestock and Agroforestry Program, Tropical Agricultural Research and Higher Education Center (CATIE), Cartago, Turrialba, 30501, Costa Rica
- ⁵⁸National Audubon Society, Boulder, CO 80305, USA
- ⁵⁹Institute for Resources, Environment and Sustainability, University of British Columbia, Vancouver, British Columbia, Canada
- ⁶⁰Cátedra de Avicultura, Cunicultura y Apicultura - Facultad de Agronomía, Universidad de Buenos Aires - CABA (C1417DSE), Argentina
- ⁶¹School of Plant and Environmental Sciences, Virginia Tech, Blacksburg, VA, USA
- ⁶²Department of Ecology, University of Brasília (UnB) - Campus Universitário Darcy Ribeiro, Brasília - DF, 70910-900, Brazil
- ⁶³Department of Entomology and Nematology, University of California, Davis, CA 95616, USA
- ⁶⁴INRA, UMR 1065 Santé et Agroécologie du Vignoble, ISVV, Université de Bordeaux, Bordeaux Sciences Agro, F-33883 Villenave d'Ornon Cedex, France
- ⁶⁵INIBIOMA, Universidad Nacional del Comahue, CONICET, Quintral 1250, Bariloche (8400), Argentina
- ⁶⁶Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Senckenberganlage 25, 60325 Frankfurt am Main, Germany
- ⁶⁷Centre for Biodiversity and Biosecurity, University of Auckland, Auckland, New Zealand
- ⁶⁸Department of Environmental Science, Policy & Management, University of California Berkeley, USA
- ⁶⁹South African National Biodiversity Institute, Kirstenbosch Research Centre, Private Bag X7, Claremont, 7735, South Africa
- ⁷⁰School of Agriculture and Food Science and Earth Institute, University College Dublin, Belfield, Dublin 4, Ireland
- ⁷¹School of Natural Sciences, Trinity College Dublin, Dublin 2, Ireland
- ⁷²Institute for Sustainable Agro-Ecosystem Services, School of Agriculture and Life Sciences, The University of Tokyo, 188-0002 Tokyo, Japan
- ⁷³Forestry and Forest Products Research Institute, 1 Matsunosato, Tsukuba, Ibaraki 305-8687, Japan
- ⁷⁴Instituto de Biologia, Universidade Federal da Bahia, 40170-210 Salvador, Brazil
- ⁷⁵Bio-Protection Research Centre, Lincoln University, Lincoln, New Zealand
- ⁷⁶Fukushima Branch, National Institute for Environmental Studies, Japan
- ⁷⁷Environment and Production Technology Division, International food policy research institute, Washington DC, USA
- ⁷⁸Department of Health and Environmental Sciences, Xi'an- Jiaotong Liverpool University, Suzhou, China

*Correspondence to: Matteo.Dainese@eurac.edu

ABSTRACT

Human land use threatens global biodiversity and compromises multiple ecosystem functions critical to food production. Whether crop yield-related ecosystem services can be maintained by few abundant species or rely on high richness remains unclear. Using a global database from 89 crop systems, we partition the relative importance of abundance and species richness for pollination, biological pest control and final yields in the context of on-going land-use change. Pollinator and enemy richness directly supported ecosystem services independent of abundance. Up to 50% of the negative effects of landscape simplification on ecosystem services was due to richness losses of service-providing organisms, with negative consequences for crop yields. Maintaining the biodiversity of ecosystem service providers is therefore vital to sustain the flow of key agroecosystem benefits to society.

INTRODUCTION

Natural and modified ecosystems contribute a multitude of functions and services that support human well-being (1, 2). It has long been recognized that biodiversity plays an important role in the functioning of ecosystems (3), but the dependence of ecosystem services on biodiversity is under debate. An early synthesis revealed inconsistent results (4), whereas subsequent studies suggest that a few dominant species may supply the majority of ecosystem services (5, 6). It thus remains unclear whether a few dominant or many complementary species are needed to supply ecosystem services. A major limitation to resolving these relationships is a lack of evidence from real-world human-driven biodiversity changes (7, 8). For instance, changes in richness or abundance of service-providing organisms in response to land-clearing for agriculture (9, 10), could alter the flow of benefits to people.

Over the past half-century, the need to feed a growing world population has led to dramatically expanded and intensified agricultural production, transforming many regions into simplified landscapes (11). This transformation has contributed to enhanced agricultural production, but has also led to the degradation of the global environment. The loss of biodiversity can disrupt key intermediate services to agriculture, such as crop pollination (12) and biological pest control (13), that underpin the final provisioning service of crop production (14). Indeed, the recent stagnation or even decline of crop yields with ongoing intensification (15) indicates which alternative pathways are necessary to maintain future stable and sustainable crop production (16–18). An improved understanding of global biodiversity-driven ecosystem services in agroecosystems and their cascading effects on crop production, is urgently needed to forecast future supplies of ecosystem services and to pursue strategies for sustainable management (8).

We compiled an extensive database comprising 89 crop systems that measured richness and abundance of pollinators and pest natural enemies, and associated ecosystem services at 1,475 sampling locations around the world (Fig. 1A). Our study is focused on the ecosystem services of pollination and biological pest control, because these services are essential to crop production and have been the focus of much research in recent decades (1). We quantified pollinator and pest natural enemy richness as the number of unique taxa sampled from each location (field), and abundance as the sum of individuals sampled per field. We calculated a standardized index of pollination services using measures of pollination success and plant reproduction, and of pest control services using measures of natural enemy activity and crop damage (19). We also characterized the 1-km landscape surrounding each field by measuring the percentage of cropland and used this metric as a measure of landscape simplification (20, 21). Using a Bayesian multilevel modelling approach, we addressed three fundamental, yet unresolved questions in the biodiversity-ecosystem function framework: (i) are pollinator and natural enemy richness consistently related to pollination and pest control services independent of abundance?; (ii) does landscape simplification indirectly impact ecosystem services mediated by a loss of local community diversity?; and lastly, (iii) how strong are the cascading effects of landscape simplification on final crop production?

RESULT AND DISCUSSION

Importantly, we found clear evidence that richness of service-providing organisms positively influenced ecosystem service delivery. This was detected for both pollination (Fig. 1B

and table S2) and pest control (Fig. 1C and table S2), and in almost all crop systems (figs. S1 and S2). By a path analysis – where we tested the assumption that richness drives abundance resource use in addition to the classic view where richness is a function of the local community size (19, 22) – we further showed that these positive relationships were determined by both direct and mediated effects of richness and abundance of service-providing organisms on ecosystem services (fig. S3, table S3 and S4). The integration of different aspects of community structure in a single analysis revealed a more multilayered relationship between biodiversity and ecosystem services than has been previously acknowledged. These results complement previous findings for pollination (6, 14, 23) and pest control (24) and indicate that: (i) both richness and abundance contribute to support these two key ecosystem services in agriculture; and (ii) abundance and richness influence each other and cannot be interpreted in isolation. Hence, we find strong support for the role of species-rich communities in supporting pollination and pest control services.

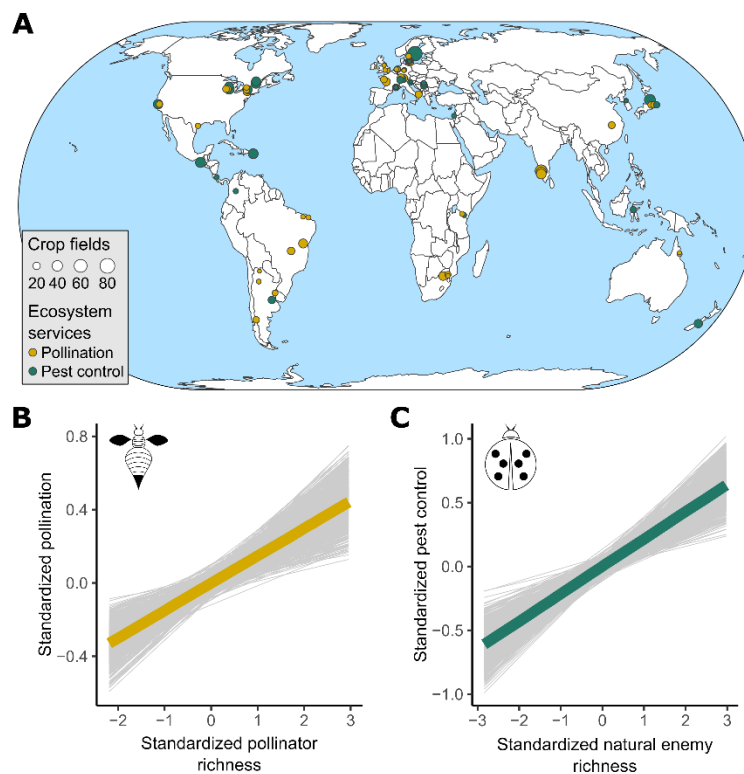


Fig. 1. Distribution of analyzed crop systems and effects of richness on ecosystem services provisioning. (A) Global distribution of the 89 crop systems. Crop systems were defined as a given crop species, in a particular region and year (further details of crop systems are given in table S1). (B) Global effect of pollinator richness on pollination ($N = 821$ fields of 52 crop systems). (C) Global effect of natural enemy richness on pest control ($N = 654$ fields of 37 crop systems). The thick line in each plot represents the median of the posterior distribution of the model. Light grey lines represent 1,000 random draws from the posterior. The lines are included to depict uncertainty of the modelled relationship.

Further, we found that landscape simplification indirectly affected ecosystem services by reducing the richness of service-providing organisms. Roughly a third of the negative effects of landscape simplification on pollination were due to a loss in pollinator richness (Fig. 2A and

table S5). This effect was even greater for pest control where natural enemy richness mediated about 50% of the total effect of landscape simplification (Fig. 2B and table S5). A consistent richness-mediated effect was also confirmed when we tested the direct and indirect effects of landscape simplification on ecosystem services via changes in both richness and abundance (fig. S4 and table S6). Importantly, the effect of landscape simplification on ecosystem services was minimized when not considering the mediated effect of richness, especially for pest control. Indeed, we did not find a direct landscape simplification effect on pest control (all highest density intervals overlapped zero; Fig. 2B and table S5). Together, these results demonstrate strong negative indirect effects of landscape simplification on biodiversity-driven ecosystem services in agroecosystems, and the importance of the richness of service-providing organisms in mediating these effects.

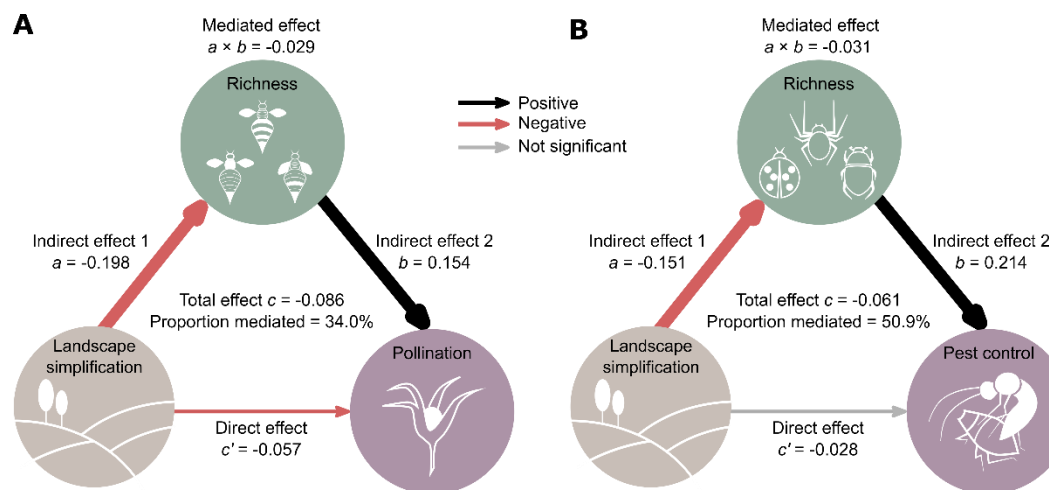


Fig. 2. Direct and indirect effects of landscape simplification on richness of service-providing organisms and associated ecosystem services. (A) Path model of landscape simplification as a predictor of pollination, mediated by pollinator richness ($N = 821$ fields of 52 crop systems). (B) Path model of landscape simplification as a predictor of pest control, mediated by natural enemy richness ($N = 654$ fields of 37 crop systems). Coefficients of the three causal paths (a , b , c') correspond to the median of the posterior distribution of the model. The proportion mediated is the mediated effect ($a \times b$) divided by the total effect (c). Black and red arrows represent positive or negative effects, respectively. Arrow widths are proportional to highest density intervals (HDIs). Grey arrows represent non-significant effects (HDIs overlapped zero).

Finally, for a subset of the data that had crop production information (676 fields of 42 crop systems) we found that the cascading effects of landscape simplification mediated through richness and associated ecosystem services led to lower crop production. This was detected for both pollination (Fig. 3A and table S7) and pest control (Fig. 3B and table S7). Specifically, landscape simplification reduced both pollinator and natural enemy richness which had indirect consequences for pollination and pest control and, in turn, decreased crop production. Pollinator abundance was also negatively affected by landscape simplification, but in contrast to richness, abundance had no significant effect on pollination services (Fig. 3A). Effects of landscape simplification on natural enemy abundance were even weaker (Fig. 3B). For pest control, a positive link with crop production was detected in fields where the study area was not sprayed with insecticides during the course of the experiment (Fig. 3B), but not when considering all sites combined (with and without insecticide use; fig. S5). In sprayed areas, we did not find a

pest control effect (all highest density intervals overlapped zero), probably because effects were masked by insecticide use (25, 26). Importantly, a positive link with crop production was detected even though measures used to estimate pest control (natural enemy and pest activity) were not direct components of crop production, as was the case of pollination measures (fruit or seed set). Though only available from a subset of the data, this result underpins that the effects of landscape simplification can cascade up to reducing the final provisioning service of crop production.

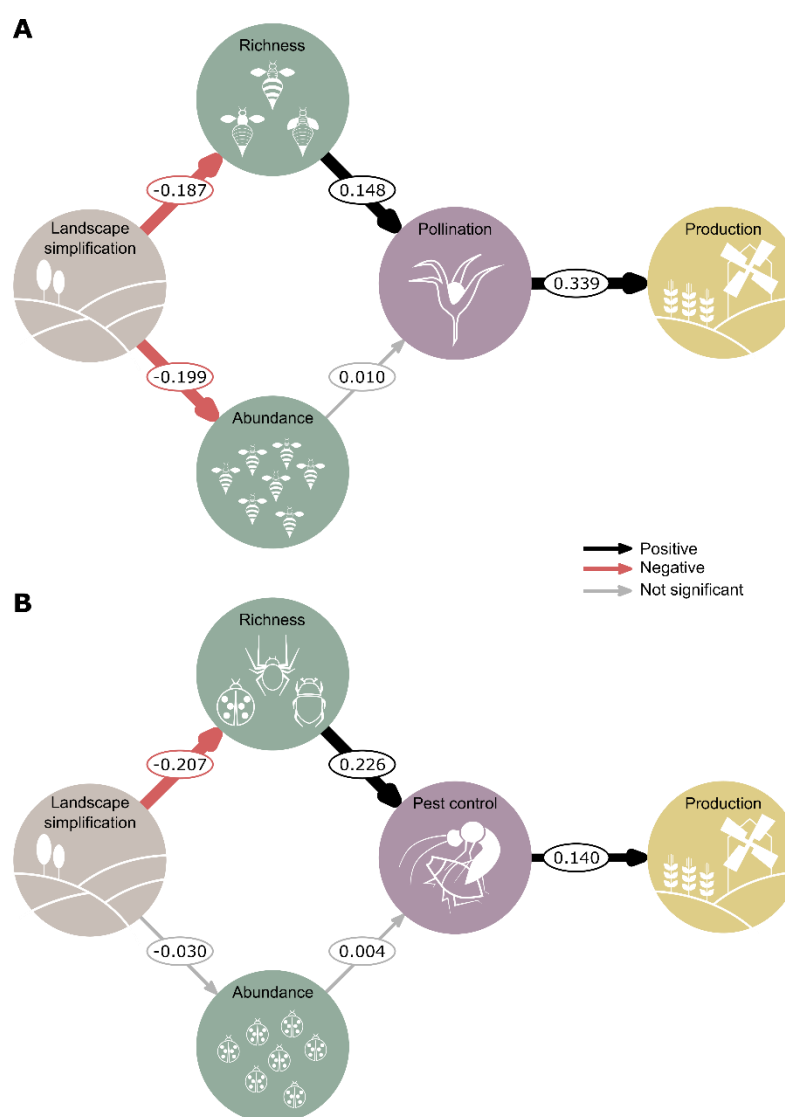


Fig. 3. Direct and cascading effects of landscape simplification on final crop production via changes in richness, abundance and ecosystem services. (A) Path model representing direct and indirect effects of landscape simplification on final crop production through changes in pollinator richness, abundance and pollination ($N = 440$ fields of 27 crop systems). **(B)** Path model representing direct and indirect effects of landscape simplification on final crop production through changes in natural enemy richness, abundance and pest control (only insecticide-free areas were considered in the model ($N = 184$ fields of 14 crop systems)). Path coefficients are effect sizes estimated from the median of the posterior distribution of the model. Black and red arrows represent positive or negative effects, respectively. Arrow widths are proportional to highest density intervals (HDIs). Grey arrows represent non-significant effects (HDIs overlapped zero).

Our findings suggest that some previously inconsistent responses of natural enemy abundance and activity to surrounding landscape composition (27) can be reconciled by considering richness in addition to abundance. Although richness and abundance are often correlated, their response to environmental variation can differ. This was evident in the path analysis showing a strong effect of landscape simplification on richness, but only a marginal effect on abundance (fig. S4b). Moreover, effect sizes for natural enemy abundances in individual crop systems (fig. S6) showed similarly inconsistent responses to the previous synthesis (27). For pest control, both results are instead well aligned (Fig. 2B).

Using an integrative model to assess key ecological theory, we demonstrate that the negative effects of landscape simplification on service supply and final crop production are primarily mediated by loss of species. We found strong evidence for positive biodiversity-ecosystem service relationships, highlighting that managing landscapes to enhance the richness of service-providing organisms (28) is a promising pathway towards a more sustainable food production globally. In an era of rapid environmental changes, preserving biodiversity-driven services will consistently confer greater resilience to agroecosystems, such that we could expect improved crop production under a broader range of potential future conditions.

MATERIALS AND METHODS

Database compilation

We compiled data from crop studies where measures of richness and abundance of service-providing organisms (pollinators or natural enemies) and associated ecosystem services (pollination and biological pest control) were available for the same sites. If available, we also included information on yield. Studies were identified by first searching the reference lists of recent meta-analyses (6, 14, 27, 29, 30) and then directly contacting researchers. For pest control, data were mostly provided from a recent pest control database (27). Of 191 researchers initially contacted, 86 provided data that met our criteria. Overall, we analyzed data from 89 crop systems and 1,475 fields in 27 countries around the world (table S1). Crop systems were defined as a given crop species, in a particular region and year (14). Twenty-nine crops were considered, including a wide array of annual and perennial fruit, seed, nut, stimulant, pulse, cereal and oilseed crops. Crop systems represented the spectrum of management practices, that is, conventional, low-input conventional, integrated pest management and organic farming. In 76% of fields, pest control experiments were performed in insecticide-free areas. In some fields this information was not available (7%) or insecticides were applied (17%). As similar studies were frequently performed in the same area, occasionally in the same year, and studies with multiple years usually used different sites each year, we did not nest year within study. Instead, we considered each year of multi-year studies (that is, 10 studies) to be an independent dataset and used study-year combinations as the highest hierarchical unit.

Pollinator and pest natural enemy richness and abundance

Studies used a broad range of methods, which we categorized as active or passive (31) to sample pollinators or natural enemies. Active sampling methods included netting pollinators seen on crop flowers, hand-collecting individuals on plants, observational counting, sweep-netting, and vacuum sampling. Passive sampling methods were malaise traps, pan traps, pitfall traps, and

sticky cards. Active sampling was performed in 85% of pollinator sampling fields and in 50% of natural enemy sampling fields.

Pollinators included representatives from the orders Hymenoptera, Diptera, Lepidoptera, and Coleoptera. Bees (Hymenoptera: Apoidea) were the most commonly observed pollinators and included *Apis* bees (Apidae: *Apis mellifera*, *Apis cerana*, *Apis dorsata*, *Apis florea*), stingless bees (Apidae: Meliponini), bumble bees (Apidae: *Bombus* spp.), carpenter bees (Apidae: Xylocopini), small carpenter bees (Apidae: Ceratinini), sweat bees (Halictidae), long-horned bees (Apidae: Eucerini), plasterer bees (Colletidae), mining bees (Andrenidae), and mason bees (Megachilidae). Non-bee taxa included syrphid flies (Diptera: Syrphidae), other flies (Diptera: Calliphoridae, Tachinidae, and Muscidae), butterflies and moths (Lepidoptera), various beetle families (Coleoptera) and hymenopterans including ants (Formicidae) and the paraphyletic group of non-bee aculeate wasps.

Natural enemies included ground beetles (Coleoptera), flies (Diptera), spiders (Aranea), hymenopterans including ants (Formicidae) and wasps, bugs (Hemiptera), thrips (Thysanoptera), net-winged insects (Neuroptera), bats and birds.

We calculated pollinator and natural enemy richness as the number of unique taxa sampled per crop system, method and field. A taxon was defined as a single biological type (that is, species, morphospecies, genus, family) determined at the finest taxonomic resolution to which each organism was identified. In almost 70% of cases, taxonomic resolution was to species-level (averaged proportion among all studies), but sometimes it was based on morphospecies- (15%), genus- (8%) or family-levels (7%). Taxon richness per field varied between 1 and 49 for pollinators and between 1 and 40 for natural enemies. Abundance reflects the sum of individuals sampled per crop system, method and field. Pollinator richness and abundance were calculated either including or excluding honey bees (*Apis mellifera*). *Apis mellifera* was considered as the only species within the honey bee group for consistency across all datasets (30). Other *Apis* bees (that is, *Apis cerana*, *Apis dorsata*, *Apis florea*) were not pooled into the honey bee category as the large majority of observed individuals are derived from feral populations. Feral and managed honey bees were analysed as a single group because they cannot be distinguished during field observations. Feral honey bees were uncommon in most studies except for those in Africa and South America (*Apis mellifera* is native in Africa, while it was introduced to the Americas). In studies with subsamples within a field (that is, plots within fields or multiple sampling rounds within fields), we calculated the total number of individuals and unique taxa across these subsamples.

Pollination and pest control services

As different methods were used to quantify pollination or pest control services across studies, standardization was necessary to put all the indices on equivalent terms. Therefore, we transformed each index y in each field i in each crop system j using z -scores. We preferred the use of z -scores over other transformations (for example, division by the maximum), because z -scores do not constrain the variability found in the raw data, as do other indices that are bounded between 0 and 1. We used the proportion of flowers that set fruit (that is, fruit set), the average number of seeds per fruits (that is, seed set), or the estimated measures of pollinator contribution to plant reproduction (that is, differences in fruit weight between plants with and without insect pollination, hereafter Δ fruit weight) as measures of pollination services. We then converted

these measures into the pollination index. The pest control index was calculated using measures of natural enemy activity or pest activity. Natural enemy activity was measured by sentinel pest experiments where pests were placed in crop fields and predation or parasitism rates were monitored, or field exclosure experiments where cages were used to exclude natural enemies to quantify differences in pest abundance or crop damage between plants with and without natural enemies. Pest activity was measured as the fraction or amount of each crop consumed, infested, or damaged. We inverted standardized values of pest activity by multiplying by -1, as low values indicate positive contributions to the ecosystem service.

Crop production

Depending on the crop type, marketable crop yield is not only valued by farmers in terms of area-based yield, but also in terms of fruit or seed weight [for example, in coffee, sunflower or strawberry fields; (32, 33)] or seed production per plant [for example, in seed production fields; (34)]. Moreover, area-based yield and within-plant yield are often correlated (35, 36). Thus, we used both area-based yield and within-plant yield as measures of final crop production. Within-plant yield was measured by the total number (or mass) of seeds or fruits per plant, or by fruit or seed weight. Also in this case, we standardized variables (z -scores) to put all the indices on equivalent terms.

Landscape simplification

Landscapes were characterized by calculating the percentage of cropland (annual and perennial) within a 1 km radius around the center of each crop field. This landscape metric has been used as a relevant proxy for characterizing landscape simplification (20, 21) and is often correlated with other indicators of landscape complexity (37, 38). Moreover, we used this metric because cropland data are readily accessible from publicly available land cover data and are more accurate than other land use types such as forests and grasslands (39), especially when detailed maps are not available. The 1 km spatial extent was chosen to reflect the typical flight and foraging distances of many insects including pollinators (40, 41) and natural enemies (42, 43). For studies where this information was not supplied by the authors, land uses were digitized using GlobeLand30 (44), a high-resolution map of Earth's land cover. The derived land-cover maps were verified and, if necessary, corrected using a visual inspection of satellite images (Google Earth®). We then calculated the percentage of cropland within the radius using Quantum GIS 2.18 (Open Source Geospatial Foundation Project, <http://qgis.osgeo.org>). The average percentage of cropland was 67.5% for pollination studies and 41.5% for natural enemy studies.

Data analysis

Data standardization. Before performing the analyses, we standardized the predictors (abundance, richness and landscape simplification) using z -scores within each crop system. This standardization was necessary to allow comparisons between studies with differences in methodology and landscape ranges (45). By doing this the focus of our analysis is on within-study effects rather than between-study effects (46, 47).

Relationship between richness and ecosystem services. The relationship between richness of service-providing organisms and related ecosystem services (Fig. 1B and 1C) was estimated from a Bayesian multilevel (partial pooling) model that allowed the intercept and the slope to vary among crop systems (also commonly referred to as random intercepts and slopes), following the equation:

$$\begin{aligned} ES_i &\sim N(\alpha_{j[i]} + \beta_{j[i]} RIC_i, \sigma_j) \\ \alpha_j &\sim N(\mu_\alpha, \sigma_\alpha) \\ \beta_j &\sim N(\mu_\beta, \sigma_\beta) \end{aligned}$$

where ES_i is the ecosystem service index (pollination or pest control depending on the model), RIC_i is richness of service-providing organisms (pollinator or natural enemy richness depending on the model), and $j[i]$ represents observation i of crop system j . This partial-pooling model estimates both crop system-level responses [yielding an estimate for each crop system (β_j)] and the distribution from which the crop system-level estimates are drawn, yielding a higher-level estimate of the overall response across crop systems (μ_β). In addition, it accounts for variation in variance and sample size across observations (for example, crop systems, studies). The intercepts α_j and slopes β_j varied between crop systems according to a normal distribution with mean μ and standard deviation σ . Independent within-crop system errors also followed a normal distribution $\varepsilon_i \sim N(0, \sigma)$. We used weakly informative priors: Normal (0,10) for the population-level parameters (α, β) and half-Student- t (3, 0, 5) for the group-level standard deviation and residual standard deviation.

Direct and mediated effects of richness and abundance on service provisioning. As natural communities vary not only in number of species but also in number of individuals (abundance), it is important to incorporate these attributes when assessing or modelling biodiversity effects (48, 49). According to a revised version of the ‘more individuals hypothesis’ (22), we cannot necessarily infer that an increase in the number of individuals of a community causes an increase in the number of species in a unidirectional way, but theory also indicates that more species can exploit more diverse resources and may therefore maintain more individuals than species-poor communities. In a Bayesian multivariate response model with causal mediation effects (hereafter, mediation model), a form of path analysis, we thus verified two alternative paths between richness, abundance and ecosystem services. We tested (i) whether richness *per se* directly influences ecosystem services or is instead mediated by abundance (fig. S3a, b), and (ii) whether abundance *per se* directly influences ecosystem services or is instead mediated by richness (fig. S3c, d). Prior to analysis, we checked for data collinearity among abundance and richness by calculating the variance inflation factor (VIF). No signal of collinearity was detected in either model (VIFs were below 1.5). Mediation analysis is a statistical procedure to test whether the effect of an independent variable X on a dependent variable Y ($X \rightarrow Y$) is at least partly explained via the inclusion of a third hypothetical variable, the mediator variable M ($X \rightarrow M \rightarrow Y$) (50). The three causal paths a , b , and c' correspond to X ’s effect on M , M ’s effect on Y , and X ’s effect on Y having taken M into account, respectively. The three causal paths correspond to parameters from two regression models, one in which M is the outcome and X the predictor, and one in which Y is the outcome and X and M the simultaneous predictors (fig. S7). From these parameters, we can compute the mediation effect (the product ab ; also known as the indirect effect), and the total effect of X on Y ,

$$c = c' + ab$$

Thus, the total causal effect of X , which is captured by the parameter c , can be decomposed precisely into two components, a direct effect c' and an indirect (mediation) effect ab (the product of paths a and b). To illustrate we first show the univariate multilevel (partial pooling) models following these equations:

$$ABU_i \sim N(\alpha_{j[i]} + \beta_{j[i]} RIC_i, \sigma_j) \quad (1)$$

$$RIC_i \sim N(\alpha_{j[i]} + \beta_{j[i]} ABU_i, \sigma_j) \quad (2)$$

$$ES_i \sim N(\alpha_{j[i]} + \beta_{j[i]} RIC_i + \beta_{j[i]} ABU_i, \sigma_j) \quad (1, 2)$$

where ABU_i is abundance, RIC_i is richness of service-providing organisms, ES_i is the ecosystem service index, and the index $j[i]$ represents observation i of crop system j . We specified both multivariate multilevel models in a matrix-vector notion (45), as follows:

$$Y_i \sim N(X_i B_r[i], \Sigma_j)$$

$$B_r \sim N(M_B, \Sigma_B)$$

where Y_i is the matrix of response variables with observations i as rows and variables r as columns, X_i is the matrix of all predictors for response r , B_r are the regression parameters (α and β) for response r , M_B represents the mean of the distribution of the regression parameters, and Σ_B is the covariance matrix representing the variation of the regression parameters in the population groups. We used weakly informative priors: Normal (0,10) for the population-level parameters (α , β) and half-Student-t (3, 0, 5) for the group-levels standard deviation and residual standard deviation. In building the model, we ensured that no residual correlation between ES_i and ABU_i or ES_i and RIC_i was estimated [see ‘*set_rescor*’ function in the package *brms*; (51)]. The mediation analysis was implemented using the R package *sjstats* [v 0.15.0; (52)].

Direct and indirect effects of landscape simplification on ecosystem services. To estimate the direct and indirect effects of landscape simplification on richness and associated ecosystem services, we employed two models. First, we developed a mediation model to test whether landscape simplification directly influences ecosystem services or is mediated by richness. The model included the ecosystem service index as response, landscape simplification as predictor, and richness as mediator (Fig. 2). The separate regression models that made up the Bayesian multivariate multilevel model followed these equations:

$$RIC_i \sim N(\alpha_{j[i]} + \beta_{j[i]} LAND_i, \sigma_j)$$

$$ES_i \sim N(\alpha_{j[i]} + \beta_{j[i]} RIC_i + \beta_{j[i]} LAND_i, \sigma_j)$$

We then compiled a multilevel path analysis testing the direct and indirect effects of landscape simplification on ecosystem services via changes in both richness and abundance (fig. S4). The separate regression models that made up the model followed these equations:

$$RIC_i \sim N(\alpha_{j[i]} + \beta_{j[i]} LAND_i, \sigma_j)$$

$$ABU_i \sim N(\alpha_{j[i]} + \beta_{j[i]} LAND_i, \sigma_j)$$

$$ES_i \sim N(\alpha_{j[i]} + \beta_{j[i]} RIC_i + \beta_{j[i]} ABU_i + \beta_{j[i]} LAND_i, \sigma_j)$$

where RIC_i is richness of service-providing organisms, $LAND_i$ is landscape simplification measured as the percentage of arable land surrounding each study site, ABU_i is abundance, ES_i is the ecosystem service index, and the index $j[i]$ represents observation i of crop system j . We then specified multivariate multilevel models in a matrix-vector notion, as explained above.

Cascading effects of landscape simplification on final crop production. For 42 crop systems and 676 fields (pollination model, $N = 440$ fields of 27 crop systems; pest control model, $N = 236$ fields of 15 crop systems; table S1), the data allowed us to employ a multilevel path analysis to examine cascading effects of landscape simplification on final crop production via changes in richness, abundance and ecosystem services. In this model, we expected that: (i) landscape simplification would have a direct effect on richness and abundance of service-providing organisms, (ii) richness and abundance of service-providing organisms would relate positively to intermediate services, which in turn, (iii) would increase final crop production (Fig. 3). The separate regression models that made up the path model followed these equations:

$$RIC_i \sim N(\alpha_{j[i]} + \beta_{j[i]} LAND_i, \sigma_j) \quad (1)$$

$$ABU_i \sim N(\alpha_{j[i]} + \beta_{j[i]} LAND_i, \sigma_j) \quad (1)$$

$$ES_i \sim N(\alpha_{j[i]} + \beta_{j[i]} RIC_i + \beta_{j[i]} LAND_i, \sigma_j) \quad (2)$$

$$PROD_i \sim N(\alpha_{j[i]} + \beta_{j[i]} ES_i, \sigma_j) \quad (3)$$

where RIC_i is richness of service-providing organisms, $LAND_i$ is landscape simplification measured as the percentage of arable land surrounding each study site, ABU_i is abundance, ES_i is the ecosystem service index, $PROD_i$ is crop production, the index $j[i]$ represents observation i of crop system j . We specified a multivariate multilevel model in a matrix-vector notion, as explained above.

Parameter estimation. All analyses were conducted in Stan through R (v. 3.4.3) using the package brms [v 2.2.0; (51)]. Stan provides efficient MCMC sampling via a No-U-Turn Hamiltonian Monte Carlo approach (53). Each model was run with four independent Markov chains of 5,000 iterations, discarding the first 2,500 iterations per chain as warm-up and resulting in 10,000 posterior samples overall. Convergence of the four chains and sufficient sampling of posterior distributions were confirmed by: (i) the visual inspection of parameter traces, (ii) ensuring a scale reduction factor (\hat{R}) below 1.01, and (iii) effective size (n_{eff}) of at least 10% of the number of iterations. For each model, posterior samples were summarized based on the Bayesian point estimate (median), standard error (median absolute deviation), and posterior uncertainty intervals by highest density intervals (HDIs), a type of credible interval which contains the required mass such that all points within the interval have a higher probability density than points outside the interval (54). The advantage of the Bayesian approach is the possibility not only to estimate expected values for each parameter, but also the uncertainty associated with these estimates (55). Thus, we calculated 80%, 90% and 95% HDIs for parameter estimates.

Sensitivity analyses. Given that different methods were used in different studies to quantify richness, ecosystem services and final crop production, we measured the sensitivity of our results to methodological differences.

(i) We verified whether treating each annual data set from multi-year studies separately could incorrectly account for the dependence of the data. We refitted the model testing the relationship between richness and ecosystem services including year nested within crop system (that is, crop system defined as crop-region combination). Then, we compared models (year-independent model vs. year-nested model) using leave-one-out cross-validation (LOO), a fully Bayesian model selection procedure for estimating pointwise out-of-sample prediction accuracy (56). We

calculated the expected log pointwise predictive density (\widehat{elpd}_{loo}), using the log-likelihood evaluated at the posterior simulations of the parameter values. Model comparison was implemented using R package loo [v 2.0.0; (57)]. We found that the year-nested model had a lower average predictive accuracy than the year-independent model for both pollination ($\Delta\widehat{elpd}_{loo} = -1.79$) and pest control ($\Delta\widehat{elpd}_{loo} = -1.09$), and therefore retained the year-independent model in our analysis.

(ii) We verified whether taxonomic resolution influenced the interpretation of results. We recalculated richness considering only organisms classified at the fine taxonomy level (species- or morphospecies-levels) and refitted the model testing the effect of richness on ecosystem services. We found no evidence that taxonomic resolution influenced our results. With a fine taxonomic resolution, the effects of richness on ecosystem services ($\beta_{\text{pollinators}} = 0.1535$, 90% HDIs = 0.0967 to 0.2141; $\beta_{\text{enemies}} = 0.2262$, 90% HDIs = 0.1420 to 0.3022; table S2) were nearly identical to the estimates presented in the main text ($\beta_{\text{pollinators}} = 0.1532$, 90% HDIs = 0.0892 to 0.2058; $\beta_{\text{enemies}} = 0.2132$, 90% HDIs = 0.1451 to 0.2810; table S2).

(iii) We verified whether the sampling methods used to collect pollinators (active vs. passive sampling techniques) influenced the relationship between pollinator richness and pollination using Bayesian hypothesis testing (51). Passive methods do not directly capture flower visitors and may introduce some bias (for example, they may underestimate flower visitors). However, our estimate was not influenced by sampling method (the one-sided 90% credibility interval overlapped zero; table S9). In accordance with this finding, the evidence ratio showed that the hypothesis tested (that is, estimates of studies with active sampling > estimates of studies with passive sampling) was only 0.78 times more likely than the alternative hypothesis.

(iv) We verified whether methodological differences in measuring pollination and pest control services influenced the relationship between richness and ecosystem services. Using Bayesian hypothesis testing, we tested whether the estimates differed among methods. The two-sided 95% credibility interval overlapped zero in all comparisons (estimates did not differ significantly; table S10) indicating that our estimate was not influenced by methodological differences in measuring ecosystem services. Furthermore, we tested effects including only inverted pest activity as a reflection of pest control. We found positive effects of natural enemy richness on inverted pest activity ($\beta = 0.1307$, 90% HDIs = 0.0102 to 0.2456), indicating that results were robust to the type of pest control measure considered.

(v) As honey bees are the most important and abundant flower visitors in some locations, we verified the potential influence of honey bees on our results by refitting the mediation model with honey bees. A positive direct contribution of richness to pollination was confirmed even after including honey bees (fig. S8). However, abundance was more important than richness when honey bees were considered.

(vi) Insecticide application during the course of the experiment could mask the effect of pest control on crop production (25, 26). We verified the potential influence of insecticide application on our results by refitting the model considering only fields where the study area was not sprayed with insecticide during the course of the experiment ($N = 184$ fields of 14 crop systems). Indeed, we found a pest control effect that was masked when considering all sites combined (with and without insecticide; fig. S5). We therefore show the insecticide-free model in the main text (Fig. 3).

(vii) We verified the consistency of our results considering only studies that measured area-based yield (sub-model). Only significant terms were retained in a simplified model. We found no evident differences between the sub-model (fig. S9) and the full model presented in the main text (Fig. 3).

REFERENCES

1. Millennium Ecosystem Assessment, *Ecosystems and Human Well-being: Biodiversity Synthesis* (World Resources Institute, 2005).
2. S. Díaz *et al.*, Assessing nature's contributions to people. *Science*. **359**, 270–272 (2018).
3. D. Tilman, F. Isbell, J. M. Cowles, Biodiversity and ecosystem functioning. *Annu. Rev. Ecol. Evol. Syst.* **45**, 471–493 (2014).
4. B. J. Cardinale *et al.*, Biodiversity loss and its impact on humanity. *Nature*. **486**, 59–67 (2012).
5. R. Winfree, J. W. Fox, N. M. Williams, J. R. Reilly, D. P. Cariveau, Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecol. Lett.* **18**, 626–635 (2015).
6. D. Kleijn *et al.*, Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat. Commun.* **6**, 7414 (2015).
7. P. Balvanera *et al.*, Linking biodiversity and ecosystem services: current uncertainties and the necessary next steps. *BioScience*. **64**, 49–57 (2014).
8. F. Isbell *et al.*, Linking the influence and dependence of people on biodiversity across scales. *Nature*. **546**, 65–72 (2017).
9. R. Chaplin-Kramer, M. E. O'Rourke, E. J. Blitzer, C. Kremen, A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecol. Lett.* **14**, 922–932 (2011).
10. C. M. Kennedy *et al.*, A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol. Lett.* **16**, 584–599 (2013).
11. J. A. Foley *et al.*, Global consequences of land use. *Science*. **309**, 570–574 (2005).
12. T. H. Ricketts *et al.*, Landscape effects on crop pollination services: are there general patterns? *Ecol. Lett.* **11**, 499–515 (2008).
13. F. J. J. A. Bianchi, C. J. H. Booij, T. Tscharntke, Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc. R. Soc. Biol. Sci.* **273**, 1715–1727 (2006).
14. L. A. Garibaldi *et al.*, Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*. **339**, 1608–1611 (2013).
15. D. K. Ray, N. Ramankutty, N. D. Mueller, P. C. West, J. A. Foley, Recent patterns of crop

- yield growth and stagnation. *Nat. Commun.* **3**, 1293–1297 (2012).
16. J. A. Foley *et al.*, Solutions for a cultivated planet. *Nature*. **478**, 337–342 (2011).
17. R. Bommarco, D. Kleijn, S. G. Potts, Ecological intensification: harnessing ecosystem services for food security. *Trends Ecol. & Evol.* **28**, 230–238 (2013).
18. J. Pretty, Intensification for redesigned and sustainable agricultural systems. *Science*. **362**, eaav0294 (2018).
19. Materials and methods are available as supplementary materials.
20. T. D. Meehan, B. P. Werling, D. A. Landis, C. Gratton, Agricultural landscape simplification and insecticide use in the Midwestern United States. *Proc. Natl. Acad. Sci. United States Am.* **108**, 11500–11505 (2011).
21. M. Dainese *et al.*, Landscape simplification weakens the association between terrestrial producer and consumer diversity in Europe. *Glob. Chang. Biol.* **23**, 3040–3051 (2017).
22. D. Storch, E. Bohdalková, J. Okie, The more-individuals hypothesis revisited: the role of community abundance in species richness regulation and the productivity–diversity relationship. *Ecol. Lett.* **21**, 920–937 (2018).
23. R. Winfree *et al.*, Species turnover promotes the importance of bee diversity for crop pollination at regional scales. *Science*. **359**, 791–793 (2018).
24. D. K. Letourneau, J. A. Jedlicka, S. G. Bothwell, C. R. Moreno, Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Annu. Rev. Ecol. Evol. Syst.* **40**, 573–592 (2009).
25. H. Liere *et al.*, Trophic cascades in agricultural landscapes: indirect effects of landscape composition on crop yield. *Ecol. Appl.* **25**, 652–661 (2015).
26. V. Gagic *et al.*, Combined effects of agrochemicals and ecosystem services on crop yield across Europe. *Ecol. Lett.* **20**, 1427–1436 (2017).
27. D. S. Karp *et al.*, Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proc. Natl. Acad. Sci. United States Am.* **15**, E7863–E7870 (2018).
28. C. Kremen, A. M. Merenlender, Landscapes that work for biodiversity and people. *Science*. **362**, eaav6020 (2018).
29. L. A. Garibaldi *et al.*, Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. *Science*. **351**, 388–391 (2016).
30. R. Rader *et al.*, Non-bee insects are important contributors to global crop pollination. *Proc. Natl. Acad. Sci. United States Am.* **113**, 146–151 (2016).
31. E. M. Lichtenberg *et al.*, A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. *Glob. Chang. Biol.* **23**,

- 4946–4957 (2017).
32. L. G. Carvalheiro *et al.*, Natural and within-farmland biodiversity enhances crop productivity. *Ecol. Lett.* **14**, 251–259 (2011).
33. V. Boreux, C. G. Kushalappa, P. Vaast, J. Ghazoul, Interactive effects among ecosystem services and management practices on crop production: pollination in coffee agroforestry systems. *Proc. Natl. Acad. Sci. United States Am.* **110**, 8387–8392 (2013).
34. T. P. M. Fijen *et al.*, Insect pollination is at least as important for marketable crop yield as plant quality in a seed crop. *Ecol. Lett.* **21**, 1704–1703 (2018).
35. I. Bartomeus, V. Gagic, R. Bommarco, Pollinators, pests and soil properties interactively shape oilseed rape yield. *Basic Appl. Ecol.* **16**, 737–745 (2015).
36. G. Schneider, J. Krauss, V. Riedinger, A. Holzschuh, I. Steffan-Dewenter, Biological pest control and yields depend on spatial and temporal crop cover dynamics. *J. Appl. Ecol.* **52**, 1283–1292 (2015).
37. T. Tscharntke, A. M. Klein, A. Kruess, I. Steffan-Dewenter, C. Thies, Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecol. Lett.* **8**, 857–874 (2005).
38. D. A. Landis, Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic Appl. Ecol.* **18**, 1–12 (2017).
39. R. Tropek *et al.*, Comment on “High-resolution global maps of 21st-century forest cover change.” *Science*. **344**, 981 (2014).
40. M. Rundlöf, J. Bengtsson, H. G. Smith, Local and landscape effects of organic farming on butterfly species richness and abundance. *J. Appl. Ecol.* **45**, 813–820 (2008).
41. A. Holzschuh *et al.*, Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. *Ecol. Lett.* **19**, 1228–1236 (2016).
42. C. Thies, T. Tscharntke, Landscape structure and biological control in agroecosystems. *Science*. **285**, 893–895 (1999).
43. A. Rusch *et al.*, Agricultural landscape simplification reduces natural pest control: a quantitative synthesis. *Agric. Ecosyst. Environ.* **221**, 198–204 (2016).
44. J. Chen, Y. Ban, S. Li, China: Open access to Earth land-cover map. *Nature*. **514**, 434 (2014).
45. A. Gelman, J. Hill, *Data Analysis Using Regression and Multilevel Hierarchical Models* (Cambridge University Press, Cambridge, 2007).
46. 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).

47. H. Schielzeth, Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.* **1**, 103–113 (2010).
48. B. J. Cardinale *et al.*, Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*. **443**, 989–992 (2006).
49. J. Reiss, J. R. Bridle, J. M. Montoya, G. Woodward, Emerging horizons in biodiversity and ecosystem functioning research. *Trends Ecol. & Evol.* **24**, 505–514 (2009).
50. D. P. MacKinnon, A. J. Fairchild, M. S. Fritz, Mediation Analysis. *Annu. Rev. Psychol.* **58**, 593–614 (2007).
51. P.-C. Bürkner, brms: an R package for Bayesian multilevel models using Stan. *J. Stat. Softw.* **80**, 1–27 (2017).
52. D. Lüdtke, sjstats: Statistical Functions for Regression Models. (2018), doi:10.5281/ZENODO.1308979.
53. B. Carpenter *et al.*, Stan: a probabilistic programming language. *J. Stat. Softw.* **76**, 1–37 (2017).
54. J. K. Kruschke, *Doing Bayesian Data Analysis: A Tutorial with R, JAGS, and Stan* (Academic Press, Boston, ed. 2, 2015).
55. R. McElreath, *Statistical Rethinking: A Bayesian Course with Examples in R and Stan* (CRC Press, 2016).
56. A. Vehtari, A. Gelman, J. Gabry, Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat. Comput.* **27**, 1413–1432 (2017).
57. A. Vehtari, J. Gabry, X. Yao, A. Gelman, loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models. R package version 2.0.0 (2018), (available at <https://cran.r-project.org/package=loo>).

ACKNOWLEDGMENTS

This work was funded by EU-FP7 LIBERATION (311781) and Biodiversa-FACCE ECODEAL (PCIN-2014–048). For all further acknowledgements see the Supplementary Materials. We thank R. Carloni for producing icons in Figures 1 to 3.

AUTHOR CONTRIBUTIONS

M.D., E.A.M. and I.S.D. conceived the study. M.D. performed statistical analyses and wrote the manuscript draft. The authors named from E.A.M. to T.T and I.S.D. discussed and revised earlier versions of manuscript. The authors named from G.K.S.A. to Y.Z. are listed alphabetically, as they contributed equally in gathering field data and providing several important corrections to subsequent manuscript drafts.

COMPETING INTERESTS

Authors declare no competing interests.

DATA AND MATERIALS AVAILABILITY

The data and R script files used in this study are available from the corresponding authors.