Indirect effects dominate ecosystem service losses in response to agricultural intensification

Agustin Vitali [1,*], Darren M. Evans [2], Fredric M. Windsor [3], Laura Dee [4], Anna Eklöf [5], Michael J. Pocock [6], and Shai Pilosof [1,7,*]

[1] *Department of Life Sciences, Ben-Gurion University of the Negev, Beer-Sheva, Israel*

[2] *School of Natural and Environmental Sciences, Newcastle University, Newcastle-upon-Tyne, UK*

[3] *School of Biosciences, Cardiff University, Cardiff, UK*

[4] *Department of Ecology and Evolutionary Biology, University of Colorado Boulder, Boulder, CO, USA*

[5] *Department of Theoretical Biology, Chemistry, and Physics, Linköping University, Linköping, Sweden*

[6] *UK Centre for Ecology Hydrology, Wallingford, Oxfordshire, OX10 8BB, UK*

[7] *The Goldman Sonnenfeldt School of Sustainability and Climate Change, Ben-Gurion University of the Negev, Be'er Sheva, Israel*

[*] *Corresponding author: agustinvitali12@gmail.com, pilos@bgu.ac.il*

Abstract

Feeding a growing human population while preventing biodiversity loss is a major challenge. Land conversion impacts multiple ecosystem services (ESs), including food production and biodiversity-dependent services; yet, the role of indirect effects on ESs within this context, such as parasitoids boosting crop yield by controlling herbivores, remains poorly understood. Using species-network data from an organic agroecosystem with multiple habitats, we simulated the effects of converting extensive to intensive crop production on multiple ESs. Projected land conversion increased crop yield by up to 191% but severely reduced other ESs (e.g., pollination by 95%). However, indirect effects on ES-providing species declined by 97%, revealing undescribed effects of habitat conversion. Comparison to a null model showed that the identity of species lost either mitigates or amplifies these effects, depending on the ES type. Uncovering how land-use changes shape direct and indirect interplay among multiple services is crucial for sustainable agroecosystem management.

Main

Global human population growth is expected to drive a 35% to 56% surge in food demand by 2050, intensifying the challenge of maintaining food security while safeguarding biodiversity[1,2]. The rapid rate of land-use changes, affecting over two-thirds of the Earth's land area, highlights the urgent need to sustainably manage biodiversity and the ecosystem services (ESs) it provides[3,4]. Paradoxically, agriculture—the main driver of biodiversity loss through land-use change—depends on farmland biodiversity. For example, non-crop species affect pollination that ultimately influence agricultural yield[5,6] and other ESs such as pest control and recreational activities[7,8]. Therefore, evaluating the trade-offs and synergies between agricultural expansion, biodiversity conservation, and ES provision is critical[9].

Management decisions in agroecosystems often impact multiple ESs simultaneously. For instance, land practices that increase biodiversity, such as crop rotation with a variety of semi-natural habitats, promote crop yields, nutrient cycling and water regulation[10]. While the effects of agricultural management strategies on biodiversity and specific ES provision are commonly assessed[11,12], it remains challenging to do so for multiple ESs simultaneously[13,14].

Understanding how land-use change affects multiple ESs requires an ecosystem-level approach, as different species provide distinct services and are interlinked within a web of interactions[15–17]. Ecological networks, in which species and their interactions are represented as nodes and links, are an ideal framework for analyzing how direct and indirect interactions affect multiple ESs[16–19]. These networks contain direct interactions, such as pollinators visiting flowers, and indirect interactions, where species populations are mediated by intermediary species. Collectively, direct and indirect interactions shape network structure; that is, the distribution of links among species[19–21]. Indirect interactions can affect the provision of ES[22]. For example, parasitoids can indirectly boost crop yield by controlling herbivores in agroecosystems, and are an important part of integrated pest management[23]. While recent studies have begun to highlight the importance of indirect interactions in the context of ESs[16,24–26], there remains a significant gap in fully integrating their effects into ES assessments and land management strategies.

A recent study used ecological networks to highlight the critical role of species that support ES-providers, demonstrating how they indirectly enhance the robustness of marine food webs against the loss of ESs[24,26]. However, the role of such supporting species in terrestrial ecosystems, particularly within complex communities involving multiple interaction types, remains unexplored[25]. This creates a significant gap in our understanding of how the structure and dynamics of ecological networks can affect ES provision, particularly in the context of agricultural intensification, such as in highly farmed countries like England, where 75% of the land is agricultural, and biodiversity is closely tied to farming practices.

To address this gap, we assessed how land conversion affects the provision of multiple ecosystem services. We simulated sequential land conversion from extensive organic to intensive non-organic crop production across six land management scenarios. We hypothesized that land conversion would erode community structure, triggering cascading effects on both direct and indirect ES provision, such as pollination and parasitoids increasing crop yield (H_1, Fig. 1A and B). However, we also expected these effects to vary depending on the type of ES (H_2, Fig. 1A), as species respond differently to land-use change[27,28]. A key component of our approach was the development of a null model to test whether the identity, rather than the number, of species lost during land conversion mitigates or amplifies their effect on ES provision. Given the critical role species play in indirectly supporting ESs[24], we further hypothesized that land conversion would alter the contribution of species to indirectly affect ES provision (H_3, Fig. 1C), with effects varying across trophic guilds. To test these hypotheses, we used an extensive network dataset from an organic farm with diverse habitats in Somerset, UK[29], describing interactions between 551 species. We extended this dataset by assigning ES to species, allowing us to quantify changes in six ESs—crop production, insect pest control (i.e., natural enemies), pollination, seed dispersal, recreational bird-watching, and recreational butterfly-watching—as well as one ecosystem disservice, crop damage.

We show that converting land to intensive management nearly doubles food production, but at the expense of disrupted community structure and consequent declines in most ES that underpin sustainable crop production. Indirect effects on ES provision had a larger effect than direct ones, revealing the hidden impacts of habitat conversion. Furthermore, the qualitative and quantitative effect of the identity of the species lost varied with ES type. Our findings underscore the importance of indirect effects within complex agroecosystems and offer insights into the mechanisms driving the loss of multiple ES in modified landscapes.

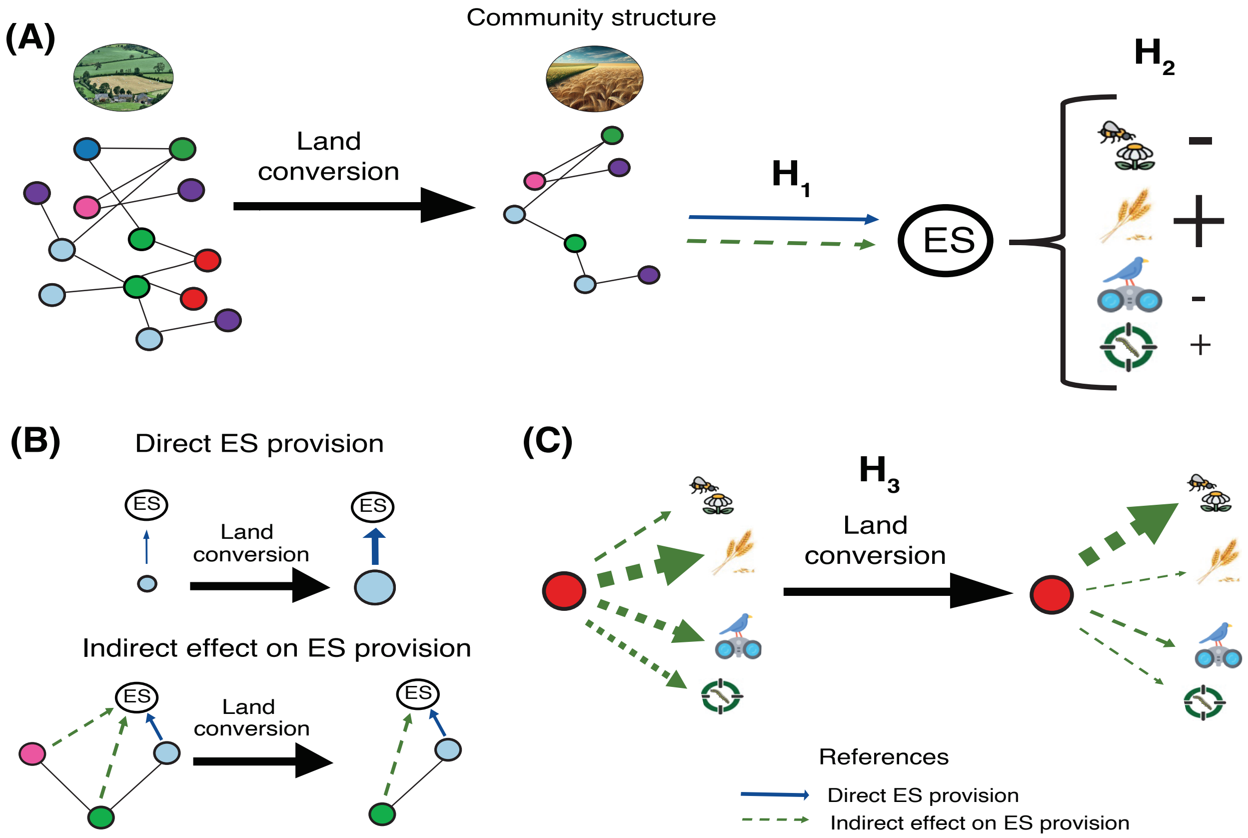

Fig. 1. Hypothesis overview: the cascading effects of land conversion on multiple ecosystem services. (A) We hypothesized that land conversion would influence the direct and indirect ES provision by affecting community structure (H_1). The impact of land conversion on ES would vary depending on the type of ES because species may respond differently to disturbances (H_2)[27,28]. A toy example representing land conversion of the real farm to intensive management illustrates these effects. Colors within the farm represent habitats, with red indicating crop production. Communities are depicted as ecological networks, where nodes and lines represent species and interactions between them, respectively. Node colors indicate the species' trophic guild. **(B)** We defined the effect of land conversion on direct ES provision as the impact on ES-providing species (nodes). Effects on direct provision can occur due to species extinction or changes in abundance, which could change the ES provided by the species. In contrast, impact of land conversion on indirect effects on ES provision is driven by changes in species interactions (links). For instance, the green node interacts with the light blue one, indirectly affecting the ES it provides. A longer cascade starts with the pink node that affects the green one. Arrow width indicates the magnitude of the effect, with thicker arrows indicating greater direct provision or a stronger indirect impact. For simplicity, we only indicated species abundances in this panel by the size of the nodes. **(C)** A previous study emphasized the critical role of indirect effects in ES loss dynamics[24]. We hypothesized that species' roles in indirectly affecting ES provision would change following land conversion (H_3).

Results

We used data from Norwood Farm, a 125 ha organic farm in southwest England[29], characterized by its arable rotation system, absence of agro-chemical inputs, and high diversity of 'weed' plant species. This dataset has become a classical resource in ecological research, supporting studies on community robustness against habitat loss and the importance of plants in supporting multiple ES-providers[17,29–31]. The farm includes 23 fields classified into 10 habitat types, comprising both cultivated (e.g., crops, permanent pasture) and non-cultivated areas (e.g., woodlands, hedgerows). Over two years (2007–2008), antagonistic and mutualistic interactions were identified using a bottom-up approach, where animal groups interacting with shared plants were recorded, and species abundances were estimated through monthly sampling for a wide range of taxa and functional groups. In total, 551 species and 1461 unique interactions between species were recorded, comprising 11 functional groups, including flower-visitors, crops, granivourous mammals, birds, and insects, and parasitoids (Fig. S1; 'Methods').

We simulated land conversion by gradually converting different habitats in the farm into crop production, creating different land management scenarios (Fig. S2). We had a total of six land management scenarios ranging from extensive organic to intensive non-organic crop production. Although simplified, these scenarios represent a diversity of management approaches in agricultural landscapes, offering an in-silico method to explore habitat conversion's impact on multiple ES provision[10,32]. Changes in habitat management could disrupt plant-animal interactions, with bottom-up effects propagating to higher trophic levels, potentially impacting both plants and their dependent animals. As such, the transformation process involved replacing species and their interactions in habitats undergoing conversion with those found in croplands and adjusting species abundances according to the new habitat area. The final land conversion scenario included the removal of all non-crop plants ('weeds'), reflecting conventional agricultural practices in several countries. For each scenario, we pooled species' abundance across habitats to build a simulated ecological network for the whole farm (hereafter 'converted network'). The multipartite networks consisted of species (nodes) connected by unweighted links representing trophic (e.g., plant-aphid feeding), mutualistic (e.g., flower-visitors), or parasitic (e.g., aphid-parasitoids) interactions.

Land conversion was projected to disassemble the community, causing the number of species to decline from 551 under extensive organic management to 46 under intensive non-organic management, i.e. the loss of 92% of species (Fig. 2). The impact varied among trophic guilds. Insect seed-feeders, their parasitoids, rodent ectoparasites, and flower-visitors were the most affected, with extinction rates of 100% for the first three groups and 98% for the last (Fig. S3).

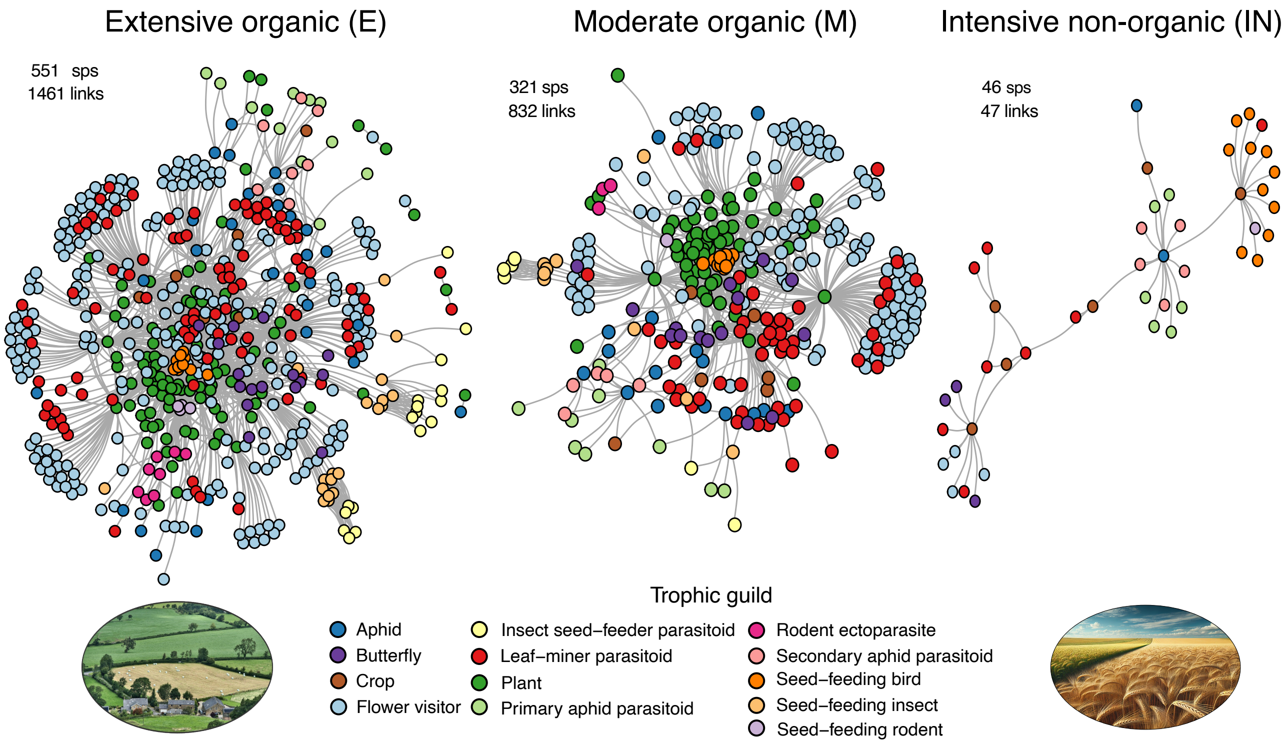

Fig. 2. Land conversion disassembles the community. Each network represents the ecological community at three stages of land-use conversion: the observed extensive organic (E), moderate organic (M), and intensive non-organic (IN). Nodes and links represent species and their interactions, respectively. Node colors correspond to the trophic guild of each species. For clarity, we show only these three scenarios, where extensive organic serves as the starting point, moderate organic represents an intermediate stage, and intensive non-organic reflects the end-point of land conversion

Land conversion decreases the direct provision of ESs

To test how land conversion affects ES provision (H_1, H_2, Fig. 1A), we assigned potential ESs to species based on trophic guilds using literature, databases, and recorded interactions ('Methods'). For example, herbivores interacting with crops were classified as pests causing crop damage. Rather than directly measuring ESs, we used established criteria to assign them, enabling an analysis of the potential impacts of land conversion on ES provision. We described six ESs: recreational bird-watching, recreational butterfly-watching, crop production, insect pest control (i.e., natural enemies), pollination, and seed dispersal, and one ecosystem disservice, crop damage. These assignments are node attributes, meaning any effect on a node (e.g., species extinction) directly affects the associated ES (Fig. 1B). Overall, 306 species (55%) were assigned to one or more ESs.

Second, depending on the type of ES, we estimated the amount of direct ESs provided by each species either as its abundance or as the product of its abundance and biomass ('Methods' and Table S4). Proxies such as abundance, richness, or trait combinations are commonly used to quantify ESs due to the lack of standardized methods across trophic guilds and ES types (e.g., bird-watching vs. crop production)[33]. Then, for each ES, we calculated the proportion of direct ESs retained (PD) and the relative change in the amount of ESs provision (A) after gradual land conversion to a given land management scenario, as $PD_x = \frac{D_x}{D_E}$ and $A_x = \frac{M_x}{M_E}$, respectively. Here, D_x and M_x represent the number and amount of direct ESs provided in the management scenario x, respectively. D_E and M_E correspond to those provided in the extensive farm, and therefore indicate the baseline of the most species-rich network. Finally, we used a generalized linear model (GLM) and a generalized linear mixed model (GLMM) to test whether PD_x and A_x were affected by the extent of land conversion and the type of ES respectively.

The proportion of direct ES provision retained (PD_x) was significantly affected by land conversion and ES type ($\chi^2_{5,42} = 22.616, p < 0.001$ and $\chi^2_{6,42} = 41.142, p < 0.001$; Fig. 3A, Table S5). On average, 31% of direct ESs were lost when the farm was converted to intensive non-organic crop production. However, as predicted by H_2, the impact varied by ES type. For example, direct provision of pollination decreased by nearly 95%, indicating that most pollinator species went extinct at higher land conversion intensities, while bird-watching, seed dispersal, and crop production remained unaffected. Additionally, both the extent of land conversion and ES type significantly influenced the relative change in the amount of ESs (A_x; GLMM, $\chi^2_{5,802} = 66.12, p < 0.001$ and $\chi^2_{6,802} = 44.47, p < 0.001$; Table S5, Fig. 4A). Conversion to intensive non-organic farming increased crop yield by up to 191%. However, this increase came at the expense of other ESs, including butterfly-watching, bird-watching, and seed dispersal (87%, 51%, and 25% decline, respectively). While pollination increased by 42% under intensive organic management, it declined by 2.92-fold under non-organic management, likely due to weed removal and secondary extinctions of flower-visitors (Fig. S3). These results highlight that while intensive non-organic farming may boost crop yield (in terms of land area), it comes with substantial losses in pollination, pest control, and butterfly-watching.

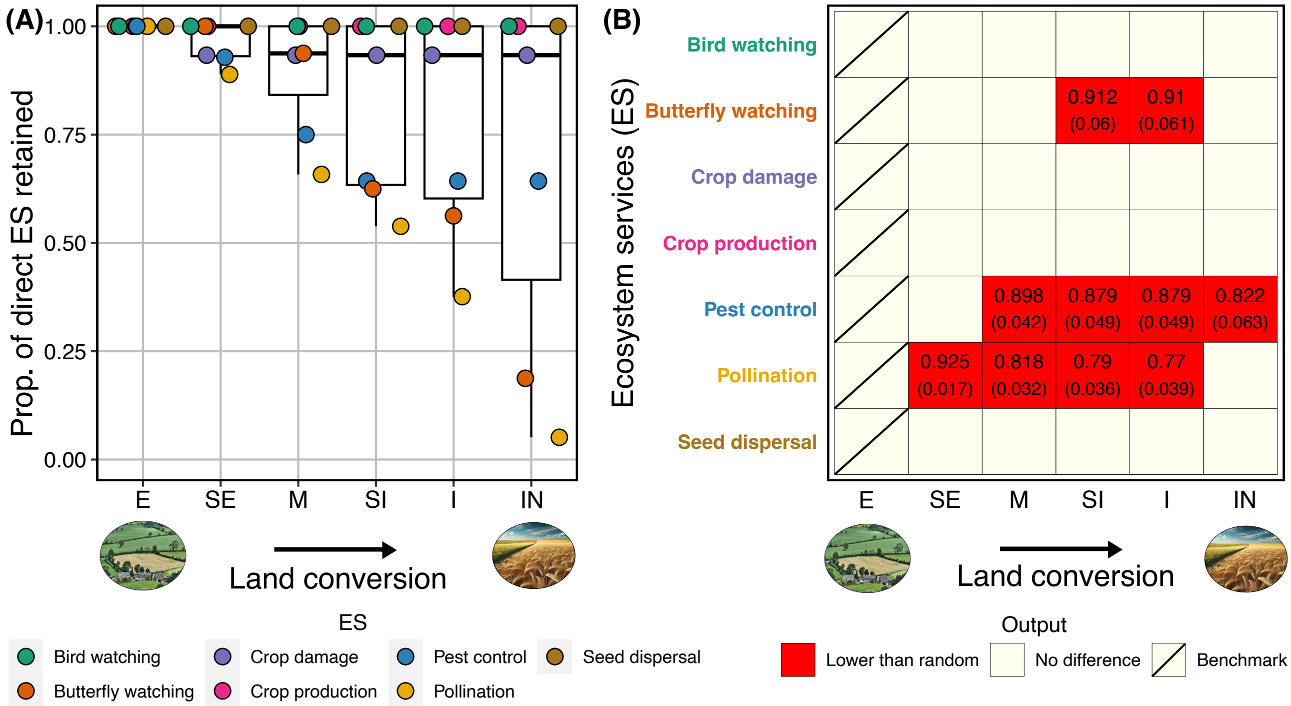

Fig. 3. Impact of land conversion on direct ecosystem services (ES) provision. **(A)** Each boxplot represents the proportion of direct ES retained in comparison to the initial extensive organic farming (PD_x) during land conversion into intensive non-organic crop production. The x-axis is the progression of land-use conversion in various management scenarios from left to right as follows: extensive organic (E), semi-extensive organic (SE), moderate organic (M), semi-intensive organic (SI), intensive organic (I), and intensive non-organic (IN); see details of land management scenarios in Table S2. Dots indicate the proportion of each ES retained, with colors corresponding to different types of ES. The boxplots show the median, 25th, and 75th percentiles across the ESs, with whiskers extending to the minimum and maximum values within 1.5 times the interquartile range. **(B)** Each cell in the heatmap represents the Z-score comparison between the converted and randomized networks for PD_x. The null model tested whether the identity of species that go extinct affects PD_x. Values within the cells indicate the mean (±standard deviation) of the randomized networks. Red cells indicate that the observed PD_x was statistically lower than expected if ES loss was only due to species richness loss, implying a greater-than-expected loss. Hence, land conversion generally leads to non-random loss of ES driven by the identity of species going extinct, particularly in pest control and pollination.

In our land conversion simulation, we gradually replaced species and their interactions with those found in crop production habitats, leading to the extinction of specific species. Consequently, our results could be influenced by both the number of species going extinct and their identities. To tease apart these two effects, we developed a null model in which the same number of species were removed during land conversion as in the original simulation, but at random. We ran the model 500 times per management scenario, estimated PD_x and A_x from the 'randomized networks', and compared these values with the converted ones using Z-scores ('Methods'). Both species numbers and identities influenced direct ES loss, with species identity leading to a greater-than-expected loss of ES-provider species and their associated contributions (Z-score < -1.96, Fig. 3B and Fig. 4B). The impact of species identity varied by ES type. For example, the proportion of retained direct ESs, such as pollination, pest control, and butterfly-watching, was 1.36, 1.24, and 1.22 times lower in the converted networks than in the randomized ones (Fig. S4). This effect was even more pronounced for the amount of ESs provided, with bird-watching, seed dispersal, and crop damage being, on average, 1.68, 1.41, and 1.33 times lower in the converted networks (Fig. S5). These results suggest that ES loss is greater than what is expected under random extinctions during land conversion, a scenario typically considered in biodiversity-ecosystem functioning studies.

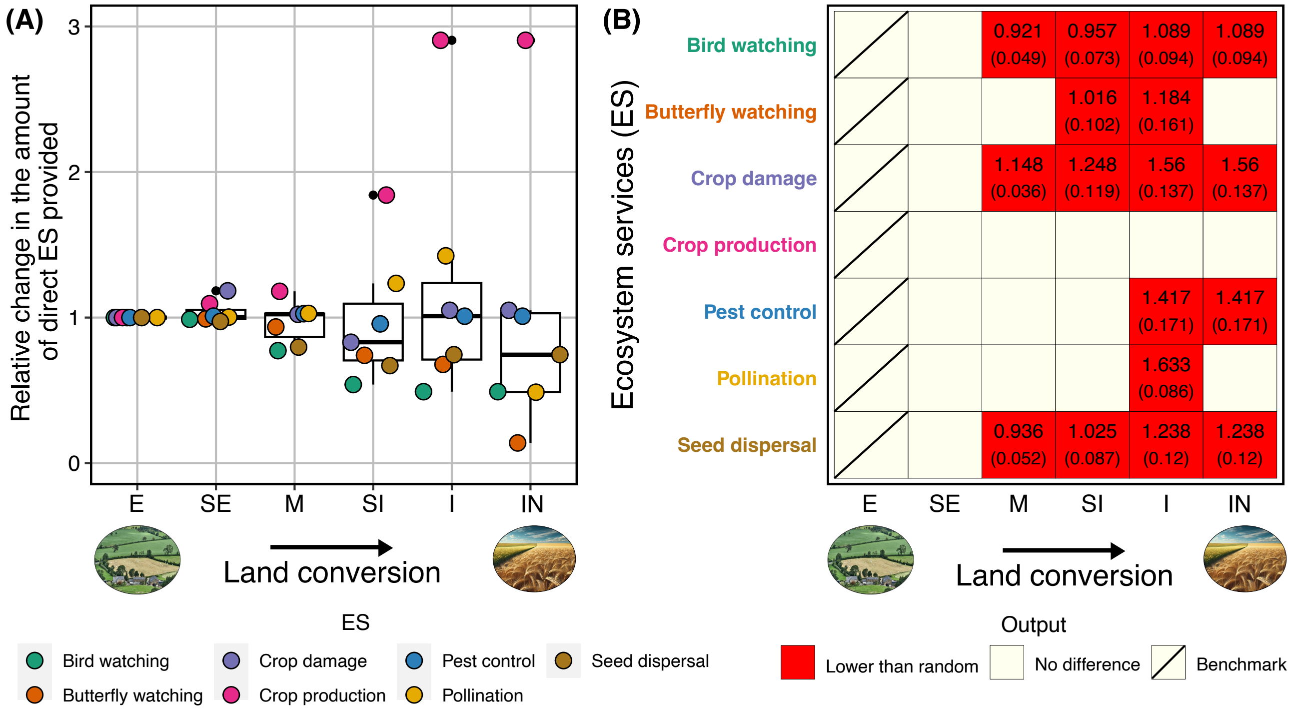

Fig. 4. The effect of land conversion on the amount of ES provision. (A) Each boxplot represents the relative change in the amount of direct ES provision (A_x) during land conversion into intensive non-organic crop production. The x-axis is the progression of land-use conversion in various management scenarios from left to right as follows: extensive organic (E), semi-extensive organic (SE), moderate organic (M), semi-intensive organic (SI), intensive organic (I), and intensive non-organic (IN); see details of land management scenarios in Table S2. Dot colours depict different types of ES. Values greater than 1 indicate an increase in the amount of ES compared to the extensive organic farm following land conversion. The boxplots show the median, 25th, and 75th percentiles across the ESs, with whiskers extending to the minimum and maximum values within 1.5 times the interquartile range. **(B)** Each cell in the heatmap represents the Z-score comparison between the converted and randomized networks for A_x. The null model tested whether the identity of species that go extinct affects A_x. Values within the cells indicate the mean ($\pm$standard deviation) of the randomized networks. Red cells indicate that the observed A_x was statistically lower than expected if ES loss was only due to species richness loss, implying a greater-than-expected loss. Hence, land conversion leads to non-random loss of ES driven by the identity of species going extinct.

Indirect effects on ES decreases linearly following land conversion

While species loss directly affects ES provision, the indirect pathways through which land conversion affects these services remain largely unexplored. Such effects could lead to significant cascading impacts within the network because species depend on one another in ways that land-use change can disrupt[19,21,34,35]. Therefore, to fully grasp the consequences of land conversion, it is essential to consider the indirect effects on ES provision through disrupted species interactions (H_1 and H_2, Fig. 1A and B). To assess a species' indirect contribution to ES, we counted the number of interaction paths connecting each species to those that provide ESs, a measure we term I, and which is a proxy for the indirect effect on an ES ('Methods'). Then, for each ES, we estimated the proportion of indirect effects retained (PI) after converting the extensive farm into each management scenario, calculated as $PI_x = \frac{I_x}{I_E}$, where I_x and I_E represent the number of indirect effects on ESs in the management scenario x, and in the extensive farm, respectively. Additionally, we tested whether PI_x was affected by the extent of land conversion and differed across ES types using a GLM. To assess how the identity of species that go extinct affects the impact of land conversion on indirect effects on ES provision, we estimated PI_x in the previously randomized networks and compared these values with those from the converted networks using Z-scores.

Both the extent of land conversion and ES type affected the proportion of indirect effects on ES that were retained (PI_x; GLM, $\chi^2_{5,42} = 1393.44, p < 0.001$ and $\chi^2_{6,42} = 443.33, p < 0.001$; Fig. 5A, Table S5). Intensive management reduced the number of indirect links to ESs by 97%. Pollination, butterfly-watching, and pest control showed the greatest losses during early conversion stages, from extensive to semi-intensive organic management (rate of loss per stage: 0.1992 ± 0.0405, 0.1981 ± 0.0387, 0.1856 ± 0.0344). Conversely, crop production was most impacted in the final stage of intensification, from intensive organic to intensive non-organic management, with 62% of indirect effects lost (0.1837 ± 0.1099). These reductions stemmed from the loss of agricultural plant 'weeds', which mediate 95% of indirect interactions with ES-providers species (Fig. S3, Fig. S7).

The impact of land conversion on indirect effects varied with the identity of extinct species, showing lower or greater-than-expected loss according to ES type (Z-score > 1.96 or < -1.96; blue and red cells in Fig. 5B). Compared to randomized networks, the converted networks retained more indirect effects for several ESs: 3.65 times higher for crop production, 1.71 for bird-watching, 1.70 for seed dispersal, and 1.54 for crop damage (Fig. S6). Conversely, in the converted network, indirect effects for some ESs declined further (Fig. S6). Overall, random extinctions caused greater indirect effect losses for most ESs, likely due to the high richness of weeds in crop habitats in the organic farm (Fig. S1). In the original simulation, most weeds persisted until the intensive organic scenario (Fig. S3), whereas random extinctions in the null model led to earlier weed extinction and greater indirect effect losses (Fig. S6).

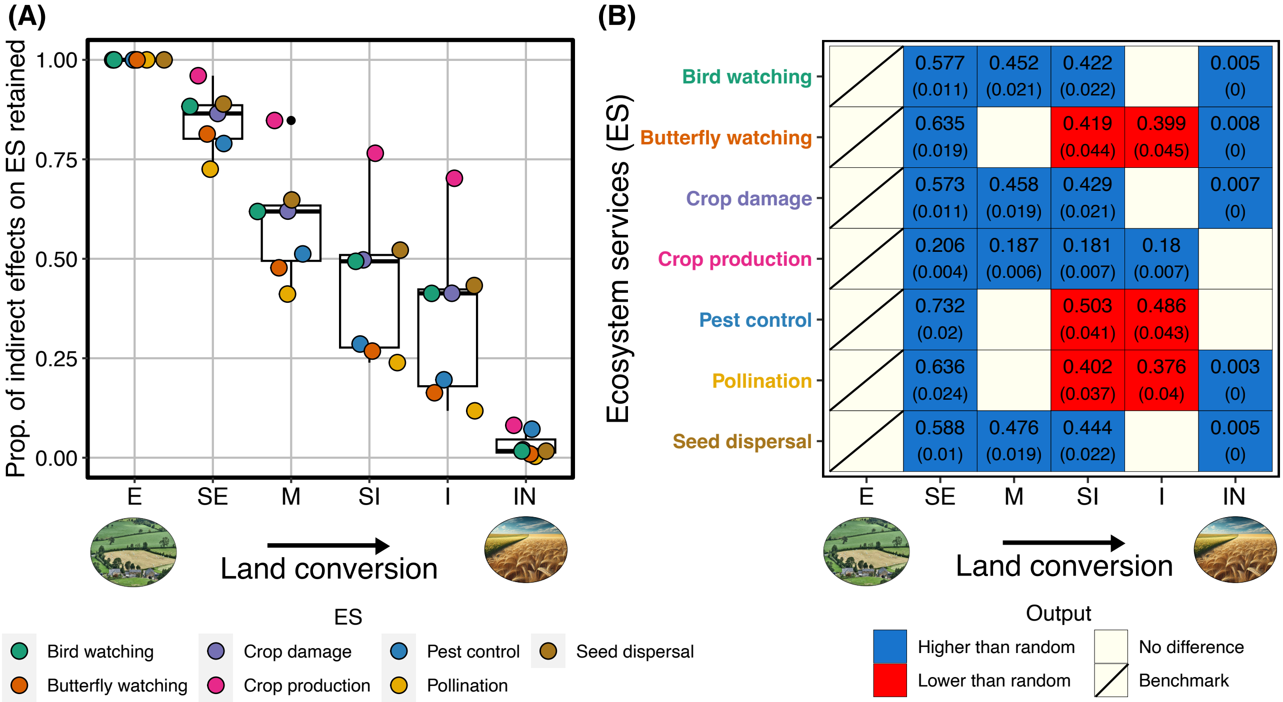

Fig. 5. The effect of land conversion on indirect effects on ES provision. (A) Each boxplot represents the proportion of indirect effects on ES retained in comparison to the initial extensive organic farming (PI_x) during land conversion into intensive non-organic crop production. The x-axis is the progression of land-use conversion in various management scenarios from left to right as follows: extensive organic (E), semi-extensive organic (SE), moderate organic (M), semi-intensive organic (SI), intensive organic (I), and intensive non-organic (IN); see details of land management scenarios in Table S2. Dots indicate the proportion of indirect effects on each ES retained, with colors corresponding to different types of ES. The boxplots show the median, 25th, and 75th percentiles across the ESs, with whiskers extending to the minimum and maximum values within 1.5 times the interquartile range. **(B)** Each cell in the heatmap represents the Z-score comparison between the converted and randomized networks for PI_x. The null model tested whether the identity of species that go extinct affects PI_x. Values within the cells indicate the mean (±standard deviation) of the randomized networks. Red and blue cells indicate that the observed PI_x was statistically lower and higher than expected if indirect effects on ES loss were only due to species richness loss. This suggests a greater or lower-than-expected loss. Hence, land conversion leads to non-random loss of indirect effects on ES driven by the identity of species going extinct.

Conversion to intensive land management affects the indirect contribution of species in ES provision

Given species-specific responses to land-use change[28] and the importance of indirect effects in maintaining ES robustness, we examined how land conversion alters species' indirect contributions to ES provision (H_3, Fig. 1C). We quantified this by measuring the average shortest path between each species and all ES-providing species. This index reflects how closely each species is linked to those directly providing ES, with lower values indicating a shorter 'distance' and, therefore, a stronger indirect impact on ES. We then tested how this metric varied with land conversion extent and trophic guild (Table S5, 'Methods')

The role of species in indirectly affecting ESs varied by trophic guild and land conversion extent (GLM,

$\chi^2_{12,1798} = 785.31, p < 0.001$, and $\chi^2_{5,1798} = 180.43, p < 0.001$; Fig. 6A, Table S5). Seed-feeding birds, rodents, and weeds were closest to ES-providing species, with shortest path distances of 2.54 ± 0.06 (mean $\pm$ se), 2.59 ± 0.10, and 2.80 ± 0.03, respectively (Fig. 6A), highlighting their significant indirect contribution to ES provision. Land conversion generally reduced the indirect role of species, especially in the final stages. The shift from intensive organic to non-organic crop production increased species' shortest path to an ES-provider, requiring at least one additional intermediate species. These findings point to variation between trophic guilds in their influence on the indirect contributions of species to ES provision. Moreover, weed removal during land conversion isolates ES-providing species from the broader network.

To further investigate the effects of key species on ES, we identified the top five most important species within each trophic guild that indirectly affect ES provision in the extensive scenario (hereafter 'core species'), and tested with a GLMM if their role (average shortest path) persists across different extents of land conversion and trophic guilds (Table S5; 'Methods'). The ability of core species to affect ES-providing species was also reduced by the extent of land conversion and differed significantly across trophic guilds, with some guilds being more severely impacted than others (GLMM, $\chi^2_{5,298} = 319.16, p < 0.001$, and $\chi^2_{12,298} = 364.18, p < 0.001$; Fig. 6B, Table S5). Across the simulated land-use intensification stages, 55% of the core species were driven to extinction, including all weeds, flower-visitors, rodent ectoparasites, and seed-feeding insects (gray cells in Fig. 6B). This led to a 1.3-fold increase in the average shortest path of the surviving core species, indicating a diminished indirect effect on ES provision, especially for bird and butterfly-watching, and seed dispersal. Despite land conversion, first- and second-order aphid parasitoids showed stable roles, with only a 6% and 9% increase in shortest path length. This stability likely arises from the fact that 90% of core aphid parasitoids use crop-feeding aphids (pests) as hosts and the promotion of crops during the shift to intensive land management. Our results reveal that land conversion significantly affected core species in most trophic guilds, reducing their indirect contribution to ES provision, particularly crop production, pest control, and pollination.

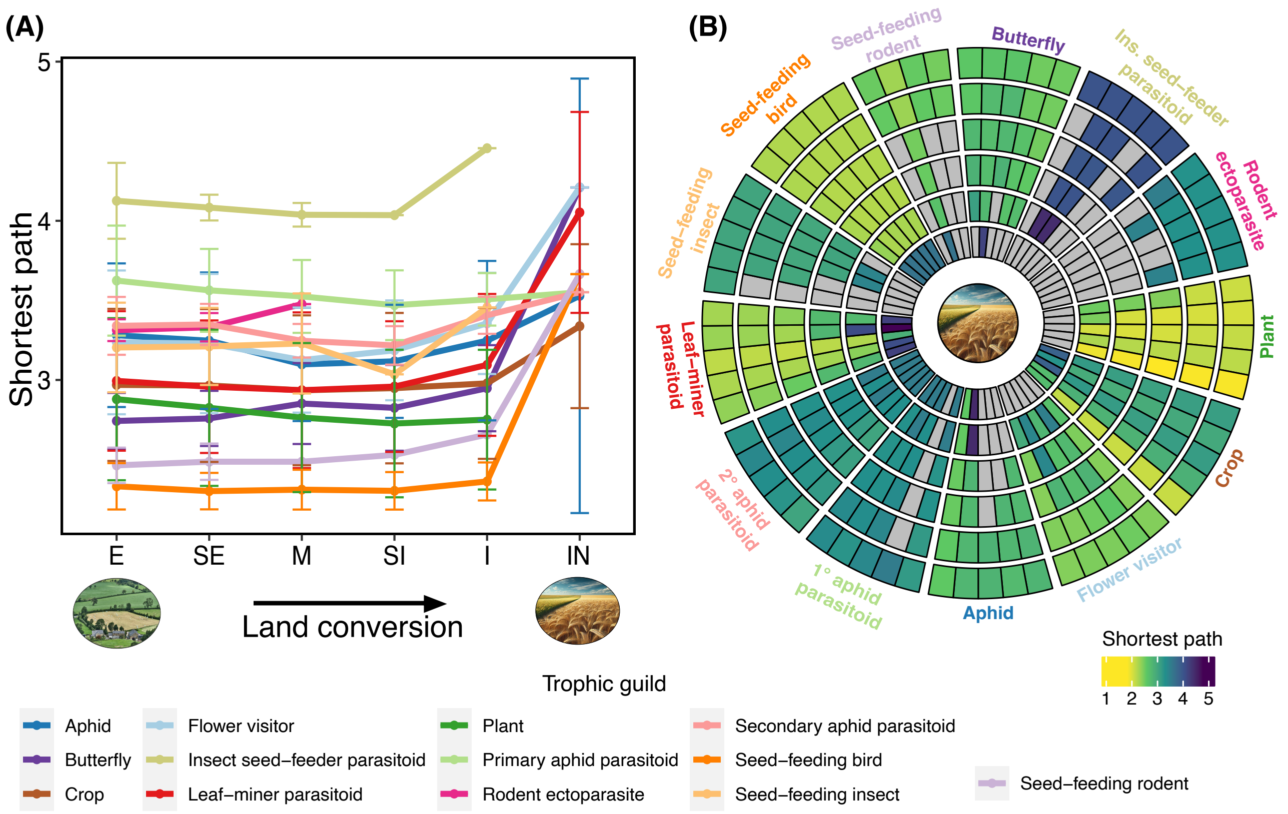

Fig. 6. Land conversion affects species' role in indirectly affecting ES. (A) Changes in the shortest path of species within each trophic guild as an extensive farm is gradually converted into intensive non-organic crop production. The x-axis is the progression of land-use conversion in various management scenarios from left to right as follows: extensive organic (E), semi-extensive organic (SE), moderate organic (M), semi-intensive organic (SI), intensive organic (I), and intensive non-organic (IN); see details of land management scenarios in Table S2. Lower shortest path values indicate a higher indirect impact on ES provision. Dots and error bars indicate the mean shortest path and standard deviation for each trophic guild, with colors corresponding to different guilds. **(B)** Changes in the role of core species within each trophic guild following land conversion. Each slice represents a core species, and each ring corresponds to a different land management scenario, arranged in an increasing gradient of crop production intensity from the outermost to the innermost ring (extensive organic, semi-extensive organic, moderate organic, semi-intensive organic, intensive organic, and intensive non-organic). The cell values indicate the shortest path of the species in a specific land management scenario.

Discussion

Achieving global sustainability targets, such as the Sustainable Development Goals (SDGs) and the Kunming-Montreal Global Biodiversity Framework, requires well-designed policies that account for both direct and indirect effects of land conversion on biodiversity and ecosystem services[36,37]. Yet, indirect effects, such as disruptions to species interactions that support ESs, are often overlooked in land-use planning. Here, we provide a novel network-based approach to model the direct and indirect effects of land conversion on multiple ESs provided by farmland biodiversity. By combining empirical data, literature synthesis, ecological network analyses, and simulations, we reveal the extinction of ecological interactions and their consequences for ES provision, highlighting acute indirect effects.

Our findings show that while intensive conversion increases crop production, it comes at the expense of other ESs, such as pollination and pest control, by driving biodiversity loss and altering species abundances. The loss of pollination, which is vital for 75% of global crops, and of pest control, could significantly threaten future crop production security. Additionally, our null model demonstrates how the identity of the species lost during land conversion shapes ES loss dynamics. Although species extinction following land intensification is evident, the erosion of community structure, reflected in a 97% decline in indirect effects, can only be revealed using a network approach, exposing the far-reaching consequences of disrupted ecological interactions for ES provision.

Identifying the optimal land management strategy to balance multiple ES is challenging. Our results suggest that conserving crop rotation and organic practices while expanding crop area can simultaneously boost food production and the abundance of remaining pollinators. Previous studies have shown that landscape simplification reduces pollinator diversity while increasing the abundance of persistent species, such as *Apis mellifera*, yet, this does not guarantee higher interaction frequency, which could be essential for sustaining effective pollination[38]. Maintaining a diverse pollinator community is key to enhancing the effectiveness and stability of crop pollination, ensuring sustainable food production[39].

We identified the removal of weeds (from intensive organic to non-organic) as one of the most detrimental stages of land conversion, significantly reducing ES provision and the indirect effects that underpin these services. For example, the loss of a pollinator species could indirectly impact recreation activities like bird-watching by reducing the bird population that relies on pollinator-dependent plants for food or nesting resources. This type of land conversion also led to the loss of species, such as non-crop plants, that play important indirect roles in support populations of ES-providers and community stability[24,29,30]. Although weeds do not directly provide ESs, they act as bridges that connect species within the community, offering pathways for energy flow. Their removal not only drives the extinction of ES-providing species but also disrupts community structure by eroding these connections. This disruption isolates remaining species and reduces pathways for energy flow.

To our knowledge, this study is the first to evaluate both direct and indirect effects of land conversion on trade-offs among ES through a network-based framework. While our approach relies on certain assumptions that may limit interpretation, it remains the most efficient way to test the effects of network structure on ES provision, as large-scale land conversion experiments are extremely challenging to conduct. Our approach could be enhanced by incorporating interaction 'rewiring' between species and/or dispersal[40,41]. For instance, the inclusion of dispersal and migration can significantly reduce the risk of species extinction through demographic and genetic rescue[42]. Although assigning ES to species is a common proxy for studying ES provision[24,33], this approach may also influence the precision of the findings. Yet, integrating these processes into complex multitrophic systems remains challenging, primarily due to the extensive trait data required. Additionally, we did not account for competition between plant species, such as weeds and crops, which could affect resource availability and crop yield[43]. Accounting for competition among weeds and crops would further exacerbate the trade-offs we observed among ES from removing weeds. Despite these simplifications, our work underscores the critical role of indirect effects in ecosystem services, demonstrating how species loss can trigger a domino effect, leading to the collapse of multiple services in modified agroecosystems.

Methods

Data

We used data from Norwood Farm, a 125 ha site located in southwest England (51°18.3'N, 2°19.5'W). A full description of the study site, data collection and the 'Norwood Farm Network' is provided in previous publications[29,30,44]. While previous studies with this dataset focused on biodiversity aspects, such as habitat loss and community robustness[30], we explored how land-use intensification impacts multiple ecosystem services via its effects on direct and indirect interactions within a multitrophic ecological network.

Norwood Farm is an organic, mixed lowland farm, where the use of artificial chemical fertilizers and pesticides is prohibited, resulting in a high diversity of 'weed' species in crop and non-crop habitats. The farm employs agricultural rotations to maintain its ecological integrity. The farm comprised 23 fields, which we classified into 10 habitat types: four cultivated (ley, new ley, permanent pasture, and crops) and six non-cultivated (spring fallow, grass margins, mature hedgerows, new hedgerows, rough ground, and woodlands). In the original publication[29], the fields were classified into 12 habitats. However, 'Lucerne' was merged with 'Crop production' and 'Standing trees' was excluded due to its small species count and lack of size-based area classification. This reclassification aligned with our study goals. Details of each habitat are in Table S1.

Antagonistic and mutualistic interactions were identified by monthly sampling over 2 years (2007–2008) using a bottom-up approach, recording animal groups interacting with shared plants. This approach was further supplemented by secondary literature on plant-seed-feeding birds and mammals, as well as plant-flower-visiting butterflies. The aim was to include a broad range of taxa and functional groups, incorporating species recognized as bioindicators and providers of ecosystem services[30]. Those encompass plants (crops and weeds), flower-visitors, herbivores (phytophagus aphids, granivorous insects, birds, and mammals), and their dependants (primary and secondary aphid parasitoids, leaf-miner parasitoids, seed-feeding insect parasitoids, and rodent ectoparasites) (Fig. S1). Samples for each taxonomic group were collected from 3-4 randomly located transects per habitat, per month. Species abundance estimates were scaled-up to provide a total per habitat, and then summed across months and averaged across both years.

Land conversion

To understand the impact of land conversion on ecosystem services provision, we simulated the gradual transformation of Norwood Farm from extensive organic to intensive non-organic crop production management. We developed six land management scenarios representing a continuum from extensive to intensive practices (Table S1 and S2). These scenarios incorporate a range of practices, including grass and hedge field margin management, crop rotation, and unmanaged areas such as woodlands. Although simplified, these scenarios capture the diversity of management approaches used in many agricultural landscapes, providing an *in-silico* method to explore the role of habitat conversion in ecosystem service provision[10,32].

Our simulation of land conversion involved the following steps (Fig. S2). First, we identify habitats that are unique to the extensive management scenario and absent in the management to convert. These habitats are converted into crop lands, starting with those that had the least intensive productive output. For example, the first habitats to be converted were woodlands and rough ground. This process involved replacing the species in the converted habitat and their interactions with those of crop habitats. Second, we adjusted species' abundances in the new habitats proportionally to the land area. Populations that fell below one individual were considered extinct. During this step, we assume that the community reaches equilibrium. Finally, after converting the entire landscape into crop habitats (i.e., intensive organic scenario), we simulated the removal of non-crop plants (weeds) to reflect the most intensive management practice, where a few crop species are typically cultivated over large areas. We assumed that removal of non-crop plants would trigger secondary extinctions, starting with species that exclusively interact with these plants, and cascading through higher trophic levels. This includes species that would remain with no interactions following the removal. It is important to note that we did not consider the spatial component during our land conversion simulation.

Network construction

For each land management scenario, we pooled species' abundances across habitats to construct ecological networks, which are valuable tools for describing and assessing changes in communities structure, ES provision, and potential indirect interactions[16–19]. In total, we constructed six ecological networks that represent the continuum from extensive organic to intensive non-organic crop production. Each network included two components:

1. Set of nodes representing species. We assigned each node three characteristics (i.e., attributes): trophic guild (e.g., aphid, bird), abundance (estimated as the sum of abundances across habitats),

and, for species that provide ES, the types of ES provided (e.g., crop damage, pest control).

2. Unweighted and undirected links representing the presence or absence of ecological interactions between species. These multipartite networks included trophic interactions (e.g., feeding relationships between plants and aphids, seed-feeding insects, and granivorous birds and mammals), mutualistic interactions (e.g., pollination by butterflies and other flower-visitors), and parasitic interactions (e.g., aphid parasitoids, leaf-miner parasitoids, parasitoids of seed-feeding insects, and rodent ectoparasites).

Ecosystem services provision

We estimated the provision of ecosystem services in each network. For each trophic guild, we used criteria derived from a combination of literature reviews, databases, and interactions recorded in our network to assign ESs to species (see full description of criteria in Table S3). While species within the same trophic guild share similar ecological roles, they can provide different ES. In total, we assigned seven types of ESs, however, some species do not provide any ESs. For instance, flower-visitor species provide pollination only if they were documented transporting pollen grains in the literature or databases.

Second, depending on the ES type, we estimated the amount of direct ESs provided by each species either as its abundance (e.g., bird and butterfly-watching) or as the product of its abundance and biomass (e.g., pest control, crop damage; full list in Table S4). In the latter case, this proxy accounts for differences in species abundance and size across trophic guilds, particularly for ESs related to consumption rates. Proxies such as abundance, richness, or trait combinations are commonly used to quantify ESs due to the lack of standardized methods across trophic guilds and ES types (e.g., bird-watching vs. crop production)[33]. Species biomass values were obtained from databases[45–48] and a comprehensive literature review (see appendix S1 in the supplementary information for details).

Third, we estimated the impact of land conversion on indirect effects on ES provision. For each focal species j, we counted the number of paths connecting it to any species i that provides ESs, using this as a proxy for the indirect effect on ESs. Mathematically, we define $I_j = \sum_{i=1}^{S} V(j,i)$, where S is the total number of species that directly provide ESs and $V(j,i)$ denotes the number of paths between the species j and i in the network. For example, in a crop-aphid-parasitoid interaction, the crop indirectly influences the crop damage caused by the aphid, and, consequently, the pest control provided by the parasitoid (Fig. S8). It is important to note that if an intermediate species is removed, the focal species could still generate indirect effects through alternative paths, as two species may be connected by more than one intermediary species. Thus, the loss of a connector species does not necessarily mean that the focal species will lose all its indirect effects. We limited the estimation of indirect effects to two hops (three-node chains) because these effects tend to weaken with more intermediate species, and because calculating all path combinations in large networks is computationally impossible.

To assess the impact of land conversion on ES, we calculated for each ecosystem service the proportion of direct ESs and indirect effects on ESs provision retained (Eq. 1 and 2) and the relative change in the amount of direct ESs provision (Eq. 3) after transforming the extensive farm into each land management scenario.

$$PD_x = \frac{D_x}{D_E} \tag{1}$$

where PD_x denotes the proportion of direct ESs retained after converting the extensive farm to the management scenario x; D_x and D_E represent the number of direct ESs provided in the management scenario x and in the extensive farm, respectively.

$$PI_x = \frac{I_x}{I_E} \tag{2}$$

here, PI_x represents the proportion of indirect effects on ES provision retained after converting the extensive farm to management scenario x; I_x and I_E denote the number of indirect effects of species on ESs in the management scenario x and in the extensive farm.

$$A_x = \frac{M_x}{M_E} \tag{3}$$

where A_x refers to the relative change in the amount of direct ES after converting the extensive farm to the management scenario x; M_x and M_E represent the amount of direct ES in the management scenario x and in the extensive farm.

Finally, we used three GLM and GLMM models to test whether each response variable defined above was affected by the extent of land conversion and type of ecosystem services (Table S5). We used the beta distribution for response variables with positive continuous values between 0 and 1 (PD_x and PI_x), and gamma distribution for values above 1 (A_x), as these variables were not normally distributed[49]. We identified and selected the models that provide the best trade-off between explanatory power and simplicity using the Akaike Information Criterion (AIC) values[50]. We applied a logarithmic transformation to the biomass component of A_x to account for potential skewness. However, since this transformation did not alter the model output (Table S6), we opted to keep the untransformed biomass values in the main analysis to simplify the interpretation. Analyses were performed using R software and glmmTMB, emmeans, and bbmle packages[51–53].

Null model

In our simulation of land conversion, the ES loss patterns we observe may be attributed to both the number of species that go extinct and their identities. To disentangle these factors, we developed a null model that controls for the number of species going extinct, as observed in the original simulation, but alters the identities of those species. The null model keeps the definition and composition of habitats in each land management scenario unchanged (e.g., the semi-intensive organic scenario still comprises crop production, new ley, and ley pasture habitats, Table S2), while modifying the transformation process itself. The transformation of each habitat to crop production consists of two steps:

1. Adding habitats: The simulation begins by adding species and interactions from crop habitats to the habitat being transformed. Additionally, we adjust the abundance of species from the crop habitat in proportion to the area of the habitat being converted.

2. Species removal: We randomly remove non-crop species and their interactions from the new habitat until the number of species matches that in the original simulation. This step controls for species richness while altering species composition as we convert the landscape into a more intensive crop production system.

We performed 500 iterations for each land management scenario and constructed the network for each iteration by pooling species abundance across all habitats (hereafter 'randomized network'). For each randomized network, we estimated the same variables related to each ES as in the simulated managements scenarios (PD_x, PI_x, A_x). We then calculated the Z-scores for each variable and management scenario to assess whether the converted values are significantly higher or lower from the values expected under the randomized networks. We used a ± 1.96 benchmark for determining significance, corresponding to the critical value for a two-tailed test at the 95% confidence level. This means that if the Z-score of a variable for a particular management scenario is greater than 1.96 or lower than -1.96, the observed value is significantly higher or lower than the values expected when species are removed at random. A significant Z-value indicates that the influence of land conversion on ES in the converted network is not only due to the number of species lost but also their identity.

Role and identity of species in indirectly affecting ESs provision

To assess how land conversion affects the role of species in indirectly affecting ESs provision, we first measured the connectivity of each species to those that directly provide ES within each network using the shortest path. This index indicates the minimum number of links needed for a focal species to connect to an ES-provider, representing the 'distance' of each species from those that deliver ES. For instance, to estimate the indirect effect of crop species i on crop damage, we calculated the shortest path between species i and each species that directly provides crop damage. We performed this calculation for each species in relation to every ES and then averaged these values. A lower shortest path value indicates a higher indirect impact on ESs because the species is closer to those that directly provide ESs. Second, we used a GLMM to evaluate whether the role of species in indirectly affecting ES provision is influenced by the extent of land conversion and trophic guild (see model details in Table S5). We used a Gamma distribution for the response variable and the model was selected using AIC criteria.

Recognizing the heterogeneity across species in their indirect effects, we further focused on those most likely to drive indirect effects on ES. Specifically, we identified the top five species within each trophic guild that indirectly impact ES provision in the extensive scenario (i.e., species with the lowest average shortest path), hereafter referred to as 'core species'. We then performed a GLMM to assess whether the role of these core species in indirectly affecting ES persisted after land conversion, including the extent of land conversion and trophic guild as fixed factors, and average shortest path as the response variable (Table S5). We included 'Species' as a random factor, with a Gamma distribution assumed, and used the AIC values for model selection.

Acknowledgments

This research was supported by the Israel Academy of Sciences and Humanities & the Council for Higher Education Excellence Fellowship Program for International Postdoctoral Researchers to AV and the Royal Society International Exchanges to DE and SP (IES/R2/222217).

Author contribution

Conceptualization: AV, SP, DE; Data curation: AV, MP; Formal Analysis: AV, SP; Funding acquisition: DE, SP, AV; Investigation: AV, SP, DE, FW, LD, AE, MP; Methodology: AV, SP; Project administration: AV; Resources: AV, DE, SP; Software: AV; Supervision: SP, DE ; Validation: AV; Visualization: AV; Writing – original draft: AV, SP, DE, FW, LD, AE, MP; Writing – review and editing: AV, SP, DE, FW, LD, AE, MP.

Competing interest

The authors declare no competing interests.

Data and Code Availability

The raw data were taken from Pocock et al., 2012 (doi: https://doi.org/10.1126/science.1214915). The full raw and processed data, as well as code, are available on the following GitHub repository: https://github.com/Ecological-Complexity-Lab/Norwood_farm

References

1. Van Dijk, M., Morley, T., Rau, M. L. & Saghai, Y. A meta-analysis of projected global food demand and population at risk of hunger for the period 2010-2050. *Nat. Food* **2,** 494–501 (2021).
2. Vijay, V. & Armsworth, P. R. Pervasive cropland in protected areas highlight trade-offs between conservation and food security. *Proc. Natl. Acad. Sci. U. S. A.* **118,** e2010121118 (2021).
3. IPBES. *Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services* (ed S. Díaz, J. Settele, E. Brondízio and H. T. Ngo.) (IPBES Secretariat, 2019).
4. Williams, D. R. *et al.* Proactive conservation to prevent habitat losses to agricultural expansion. *Nat. Sustain.* **4,** 314–322 (2020).
5. Power, A. G. Ecosystem services and agriculture: tradeoffs and synergies. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365,** 2959–2971 (2010).
6. Kleijn, D. *et al.* Ecological intensification: Bridging the gap between science and practice. *Trends Ecol. Evol.* **34,** 154–166 (2019).
7. Assessment, M. E. *Ecosystems and human well-being: a framework for assessment* (wri.org, 2003).
8. Zhang, W., Ricketts, T. H., Kremen, C., Carney, K. & Swinton, S. M. Ecosystem services and dis-services to agriculture. *Ecol. Econ.* **64,** 253–260 (2007).
9. WWF International. *Living Planet Report 2022* (WWF International, Gland, Switzerland, 2022).
10. Tamburini, G. *et al.* Agricultural diversification promotes multiple ecosystem services without compromising yield. *Sci Adv* **6** (2020).
11. Priyadarshana, T. S. *et al.* Crop and landscape heterogeneity increase biodiversity in agricultural landscapes: A global review and meta-analysis. *Ecol. Lett.* **27,** e14412 (2024).
12. Beillouin, D., Ben-Ari, T., Malézieux, E., Seufert, V. & Makowski, D. Positive but variable effects of crop diversification on biodiversity and ecosystem services. *Glob. Chang. Biol.* **27,** 4697–4710 (2021).
13. Bennett, E. M., Peterson, G. D. & Gordon, L. J. Understanding relationships among multiple ecosystem services: Relationships among multiple ecosystem services. *Ecol. Lett.* **12,** 1394–1404 (2009).
14. Windsor, F. M. *et al.* Network science: Applications for sustainable agroecosystems and food security. *Perspectives in Ecology and Conservation* **20,** 79–90 (2022).
15. Tylianakis, J. M., Didham, R. K., Bascompte, J. & Wardle, D. A. Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* **11,** 1351–1363 (2008).

16. Dee, L. E. *et al.* Operationalizing Network Theory for Ecosystem Service Assessments. *Trends Ecol. Evol.* **32,** 118–130 (2017).

17. Windsor, F. M. *et al.* Identifying plant mixes for multiple ecosystem service provision in agricultural systems using ecological networks. *J. Appl. Ecol.* **58,** 2770–2782 (2021).

18. Delmas, E. *et al.* Analysing ecological networks of species interactions: Analyzing ecological networks. *Biol Rev* **94,** 16–36 (2019).

19. Guimarães Jr, P. R. The Structure of Ecological Networks Across Levels of Organization. *Annu. Rev. Ecol. Evol. Syst.* **51,** 433–460 (2020).

20. Bascompte, J. Disentangling the web of life. *Science* **325,** 416–419 (2009).

21. Wootton, T. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology, Evolution, and Systematics* **25,** 443–466 (1994).

22. Gutierrez-Arellano, C & Mulligan, M. A review of regulation ecosystem services and disservices from faunal populations and potential impacts of agriculturalisation on their provision, globally. *Nature Conservation* **30,** 1–39 (2018).

23. Miller, K. E., Polaszek, A. & Evans, D. M. A dearth of data: fitting parasitoids into ecological networks. *Trends Parasitol.* **37,** 863–874 (2021).

24. Keyes, A. A., McLaughlin, J. P., Barner, A. K. & Dee, L. E. An ecological network approach to predict ecosystem service vulnerability to species losses. *Nat. Commun.* **12,** 1586 (2021).

25. Felipe-Lucia, M. R. *et al.* Conceptualizing ecosystem services using social–ecological networks. *Trends Ecol. Evol.* **37,** 211–222 (2022).

26. Wilkes, L. N. *et al.* Quantifying co-extinctions and ecosystem service vulnerability in coastal ecosystems experiencing climate warming. *Glob. Chang. Biol.* **30,** e17422 (2024).

27. Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H. & Bellwood, D. R. A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* **28,** 167–177 (2013).

28. Newbold, T. *et al.* Global effects of land use on biodiversity differ among functional groups. *Funct. Ecol.* **34,** 684–693 (2020).

29. Pocock, M. J. O., Evans, D. M. & Memmott, J. The robustness and restoration of a network of ecological networks. *Science* **335,** 973–977 (2012).

30. Evans, D. M., Pocock, M. J. O. & Memmott, J. The robustness of a network of ecological networks to habitat loss. *Ecol. Lett.* **16,** 844–852 (2013).

31. Sauve, A. M. C., Thébault, E., Pocock, M. J. O. & Fontaine, C. How plants connect pollination and herbivory networks and their contribution to community stability. *Ecology* **97,** 908–917 (2016).

32. Van Ruymbeke, K. *et al.* Assessing the impact of farm-management practices on ecosystem services in European agricultural systems: A rapid evidence assessment. *Sustainability* **15,** 12819 (2023).

33. Noriega, J. A. *et al.* Research trends in ecosystem services provided by insects. *Basic Appl. Ecol.* **26,** 8–23 (2018).

34. Pires, M. M. *et al.* The indirect paths to cascading effects of extinctions in mutualistic networks. *Ecology* **101,** e03080 (2020).

35. Vitali, A. *et al.* Invasive species modulate the structure and stability of a multilayer mutualistic network. *Proc. Biol. Sci.* **290,** 20230132 (2023).

36. IUCN. Agriculture and conservation: living nature in a globalised world. *IUCN Flagship Report Series No. 2. Gland, Switzerland: IUCN* (2024).

37. Feeding the future global population. *Nat. Commun.* **15,** 222 (2024).

38. Maurer, C. *et al.* Landscape simplification leads to loss of plant–pollinator interaction diversity and flower visitation frequency despite buffering by abundant generalist pollinators. *Divers. Distrib.* **30** (2024).

39. Requier, F. *et al.* Bee and non-bee pollinator importance for local food security. *Trends Ecol. Evol.* **38,** 196–205 (2023).

40. Quévreux, P. *et al.* Perspectives in modelling ecological interaction networks for sustainable ecosystem management. *J. Appl. Ecol.* **61,** 410–416 (2024).

41. Lázaro, A. & Gómez-Martínez, C. Habitat loss increases seasonal interaction rewiring in plant–pollinator networks. *Funct. Ecol.* **36,** 2673–2684 (2022).

42. Hufbauer, R. A. *et al.* Three types of rescue can avert extinction in a changing environment. *Proc. Natl. Acad. Sci. U. S. A.* **112,** 10557–10562 (2015).

43. Gallandt, E. R. & Weiner, J. in *eLS* 1–9 (John Wiley & Sons, Ltd, Chichester, UK, 2015).

44. Evans, D. M., Pocock, M. J. O., Brooks, J. & Memmott, J. Seeds in farmland food-webs: Resource importance, distribution and the impacts of farm management. *Biol. Conserv.* **144,** 2941–2950 (2011).

45. Brose, U., Williams, R. J. & Martinez, N. D. Allometric scaling enhances stability in complex food webs. *Ecol. Lett.* **9,** 1228–1236 (2006).

46. Cook, P. M. *et al.* Traits data for the butterflies and macro-moths of Great Britain and Ireland. *Ecology* **103,** e3670 (2022).

47. Kendall, L. K. *et al.* Pollinator size and its consequences: Robust estimates of body size in pollinating insects. *Ecol. Evol.* **9,** 1702–1714 (2019).

48. Wilman, H. *et al.* EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals: Ecological Archives E095-178. *Ecology* **95,** 2027–2027 (2014).

49. Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A. & Smith, G. M. *Mixed Effects Models and Extensions in Ecology with R* (Springer New York, 2009).

50. Wagenmakers, E.-J. & Farrell, S. AIC model selection using Akaike weights. *Psychon. Bull. Rev.* **11,** 192–196 (2004).

51. Brooks, Kristensen, Van Benthem & others. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R* (2017).

52. Bolker, B. & Team, R. D. C. bbmle: Tools for general maximum likelihood estimation. *R package version 0. 9* **5** (2010).

53. Searle, S. R., Speed, F. M. & Milliken, G. A. Population Marginal Means in the Linear Model: An Alternative to Least Squares Means. *Am. Stat.* **34,** 216–221 (1980).

Supplementary Information - Indirect effects dominate ecosystem service losses in response to agricultural intensification

Table S1. Description of habitats. The table was extracted from[29] and modified as we reclassified the habitats to align with the paper's goals.

Habitats	**Description**	**Area in 2007 (ha)**	**Area in 2008 (ha)**
Crop production (CP)	Crops (spring-sown barley, oats, winter-sown oats, triticale, wheat and lucerne; *Hordeum vulgare*, *Avena sativa*, ×Triticosecale, *Triticum* sp., *Medicago sativa*). Each type of crop was samply separated and they were part of the organic crop rotation. Lucerne was harvested for sillage.	33	59.8
Spring fallow (SF)	Uncultivated arable fields that remained uncultivated for a whole year.	5.7	0
Woodland (WD)	Three small woods that had been present for more than 100 years.	3	3
Rough ground (RG)	Uncultivated areas around farm buildings and machinery storage area, which were dominated by ruderal vegetation.	2	1.2
Mature hedgerow (MH)	Hedgerow present more than 100 years (recorded on the 1890 Ordnance Survey map). Height and width 4.1 ± 1.5 and 3.6 ± 1.4 m (mean ± SD) respectively.	3.7	3.7
New hedgerow (NH)	Hedgerow planted within the previous 10 years. It was composed by young tress and grass average 1.8 ± 0.7 and 1.3 ± 0.3 m (mean ± SD) respectively.	0.4	0.4
Grass margin (GM)	Uncultivated margins up to 10m wide, introduced voluntarily and mostly removed in 2008 due to a change of farm ownership.	5.5	0.2
Permanent pasture (PP)	Grass that had been established for at least 10 years and used for grazing, hay and silage production.	22.2	22.2
Ley pasture (LP)	Mix of rye grass *Lolium* spp. and red clover (*Trifolium pratense*) that were sown and grown for 2–4 years as part of the organic crop rotation.	48.2	14.3
New ley (NL)	Mix of rye grass and red clover that had been established for less than a year as part of the organic crop rotation.	0	18.1
Excluded	Including access roads, farm buildings and the concrete farm yard.	1.3	2.1

Table S2. Land management scenarios representing a continuum from extensive to intensive practices. Habitat richness indicate the number of different habitats integrating each management scenario. Habitat code refers to the type of habitat present in each scenario. The habitat codes are as follows: Crop production (CP), Spring fallow (SF), Grass margin (GM), Ley pasture (LP), Mature hedgerow (MH), New hedgerow (NH), New ley (NL), Permanent pasture (PP), Rough ground (RG), and Woodland (WD). Details for each habitat can be found in Table S1.

Land management scenario	Practices included	Habitat richness	Habitat codes
Extensive (E)	Organic crop rotation and pastures. Diverse field margin management including trees, shrubs, and grass. Preservation of natural woodlands.	10	CP, SF, GM, LP, MH, NH, NL, PP, RG, WD
Semi-extensive (SE)	Organic crop rotation and pastures. Diverse field margin management including trees, shrubs, and grass.	8	CP, SF, GM, LP, MH, NH, NL, PP
Moderate (M)	Organic crop rotation and pastures with grass margin management.	6	CP, SF, GM, LP, NL, PP
Semi-intensive (SI)	Organic crop rotation.	3	CP, LP, NL
Intensive (I)	Organic crop production.	1	CP
Intensive non-organic (IN)	Crop production without weeds.	1	CP

Table S3. Criteria for assigning the potential direct provision of ecosystem services or disservices to each species based on their trophic guild.

Trophic guild	Direct provision	Condition	Type
Crop	Crop production	-	Service
Plant (weeds)	-	-	-
flower-visitorssitor	Pollination	If the species has been documented transporting pollen grains in the literature. Otherwise, the species does not directly provide pollination.	Service
Bird	Seed dispersal	If the species has been documented dispersing seeds in the literature.	
	Bird-watching	If the species has been documented in the literature as being observed during birding watching.	
	Crop damage	If the species has been documented interacting with crop species.	Disservice
Butterfly	Pollination	If the species has been documented transporting pollen grains in the literature. Otherwise, the species does not directly provide pollination.	Service
	Butterfly-watching	-	
Aphid	Crop damage	If the species has been recorded interacting with crop species. Otherwise, the species does not directly provide crop damage.	Disservice
Seed-feeding insect			
Seed-feeding rodent			
Primary aphid parasitoid	Pest control	If the species has been recorded interacting with species that provide crop damage. Otherwise, the species does not directly provide pest control.	Service
Secondary aphid parasitoid			
Leaf-miner parasitoid			
Insect seed-feeder parasitoid			
Rodent ectoparasite			

Table S4. Estimation of the amount of direct ecosystem services provision. Depending on the type of ES, the amount provided by each species was estimated either by its abundance or by the product of its abundance and biomass. Biomass per species were obtained from a comprehensive literature review and databases (see section S1 in the supplementary information for more details).

Ecosystem (dis)services	**Amount**
Bird-watching	Abundance
Butterfly-watching	Abundance
Crop damage	Abundance * Biomass
Crop production	Abundance * Biomass
Pest control	Abundance * Biomass
Pollination	Abundance * Biomass
Seed dispersal	Abundance * Biomass

Table S5. Description and output of performed models.

Response variable	Model	Fixed factor	Coeff.	Chisq	p - value	df
Prop. direct ES retained (PD_x)	extent of land conversion + type of ES	extent of land conversion	-2.67	22.616	<0.001	5
		type of ES	-2.04	41.142	<0.001	6
Relative change in the amount of direct ES (A_x)	extent of land conversion + type of ES + (1|species_id)	extent of land conversion	0.033	66.122	<0.001	5
		type of ES	0.32	44.471	<0.001	6
Prop. indirect effects of species on ES retained (PI_x)	extent of land conversion + type of ES	extent of land conversion	-8.27	1393.44	<0.001	5
		type of ES	-0.22	443.33	<0.001	6
Shorthest path of sps	extent of land conversion + trophic guild	extent of land conversion	-0.041	180.43	<0.001	5
		trophic guild	-0.047	785.31	<0.001	12
Shorthest path of core sps	extent of land conversion + trophic guild + (1|species_id)	extent of land conversion	0.091	319.18	<0.001	5
		trophic guild	0.0071	364.84	<0.001	12

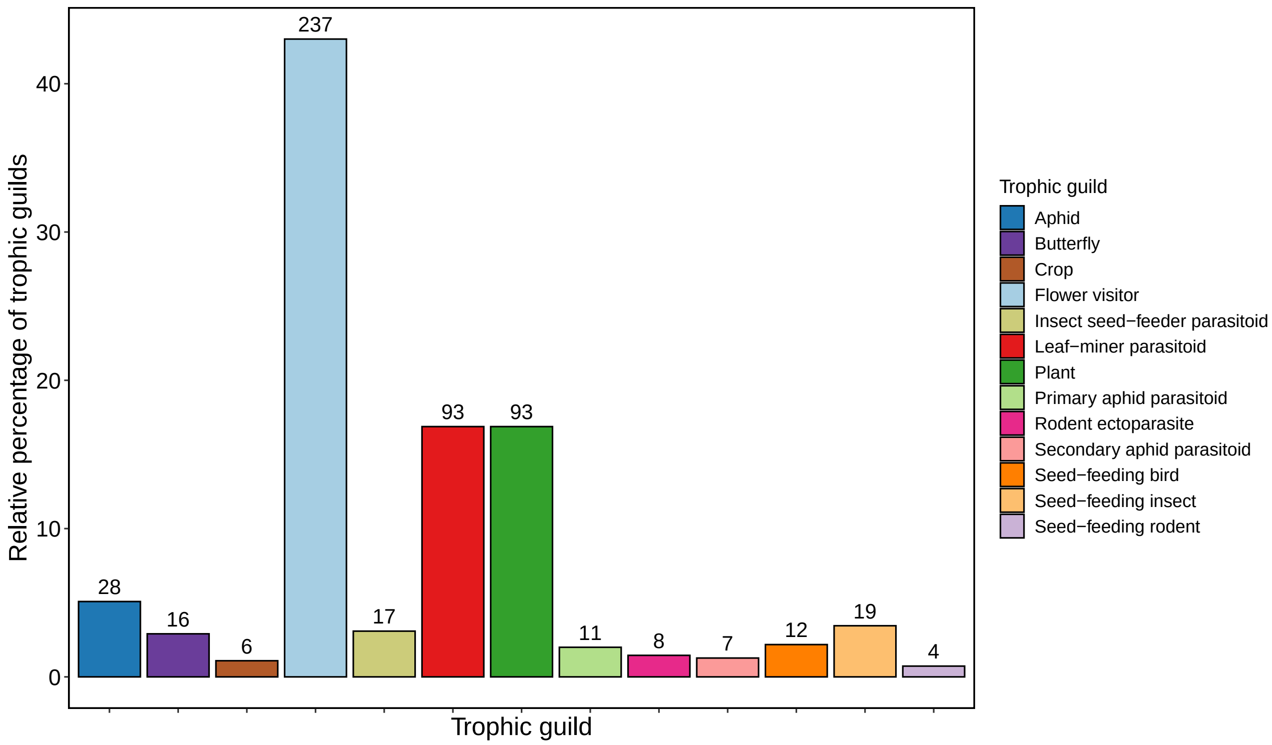

Fig. S1. Relative percentage of trophic guilds in Norwood farm. Each bar represents the percentage of species within a trophic guild. The numbers above the bars indicate the total number of species in each guild.

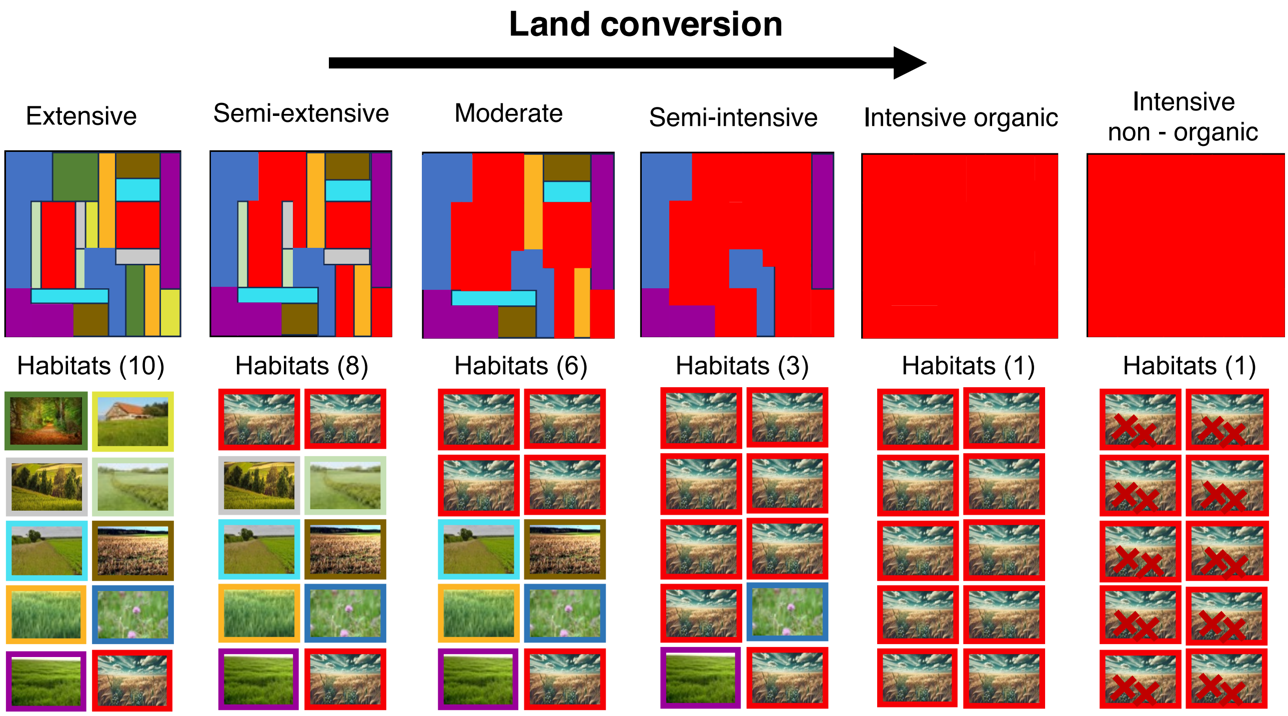

Fig. S2. Process of gradual land conversion from extensive to intensive non-organic crop production management scenario. Our simulation of land conversion consisted of the following steps. First, we identify habitats that are unique to the extensive management scenario and absent in the management to convert. These habitats were converted into crop lands, starting with those that had the least intensive productive output. This process involved replacing the original species and their interactions within these habitats with those typical of crop habitats. Second, we adjusted species' abundances in the new habitats proportionally to the land area. Populations that fell below one individual were considered extinct. During this step, we assume that the community reaches equilibrium. Finally, after converting the entire landscape into crop habitats (i.e., intensive organic scenario), we simulated the removal of non-crop plants to reflect management practices commonly used in several countries, where a few crop species are typically cultivated over large areas. We assumed that removal of non-crop plants would trigger secondary extinctions, starting with species that exclusively consume these plants, and cascading through higher trophic levels. The illustrative examples represent different habitats within each land management scenario. The colors of the rectangles indicate habitat types: Woodland (green), Rough ground (yellow), Mature hedgerow (grey), New hedgerow (light green), Grass margin (light blue), Spring fallow (brown), Permanent pasture (orange), Ley pasture (blue), New ley (purple), and Crop production (red). Each habitat is shown with a color-bordered picture indicating its type. Note that the illustrative examples do not reflect the relative area of each habitat type, and spatial configuration was not considered in the simulation. Details for each land management scenario and habitat can be found in Table S1 and S2.

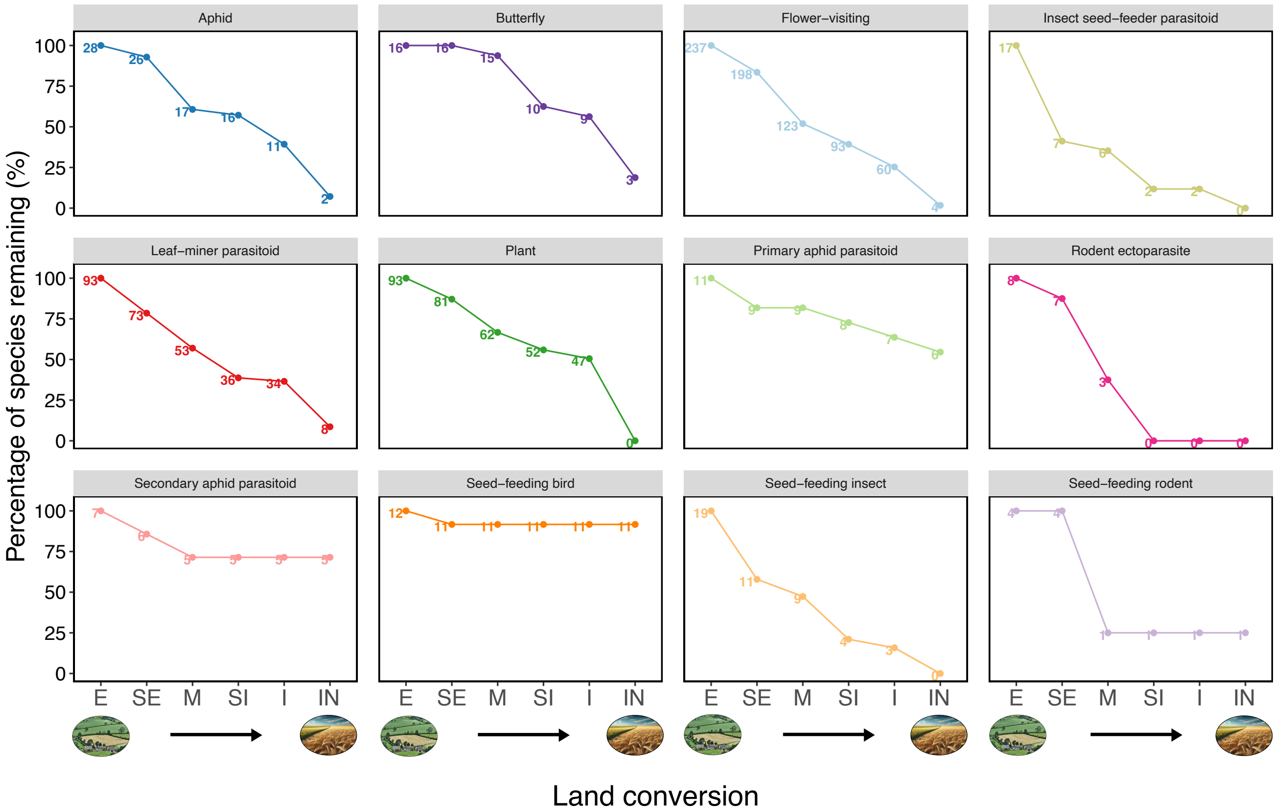

Fig. S3. Percentage of species remaining after land conversion based on trophic guild. Each graph represents the percentage of a specific trophic guild that remains (y-axis) after gradually converting the extensive farm into an intensive non-organic crop production management (x-axis). Each value on the x-axis refers to a different management scenario of crop production, listed from left to right as follows: extensive organic (E), semi-extensive organic (SE), moderate organic (M), semi-intensive organic (SI), intensive organic (I), and intensive non-organic (IN). Numeric values indicate the number of species remaining.

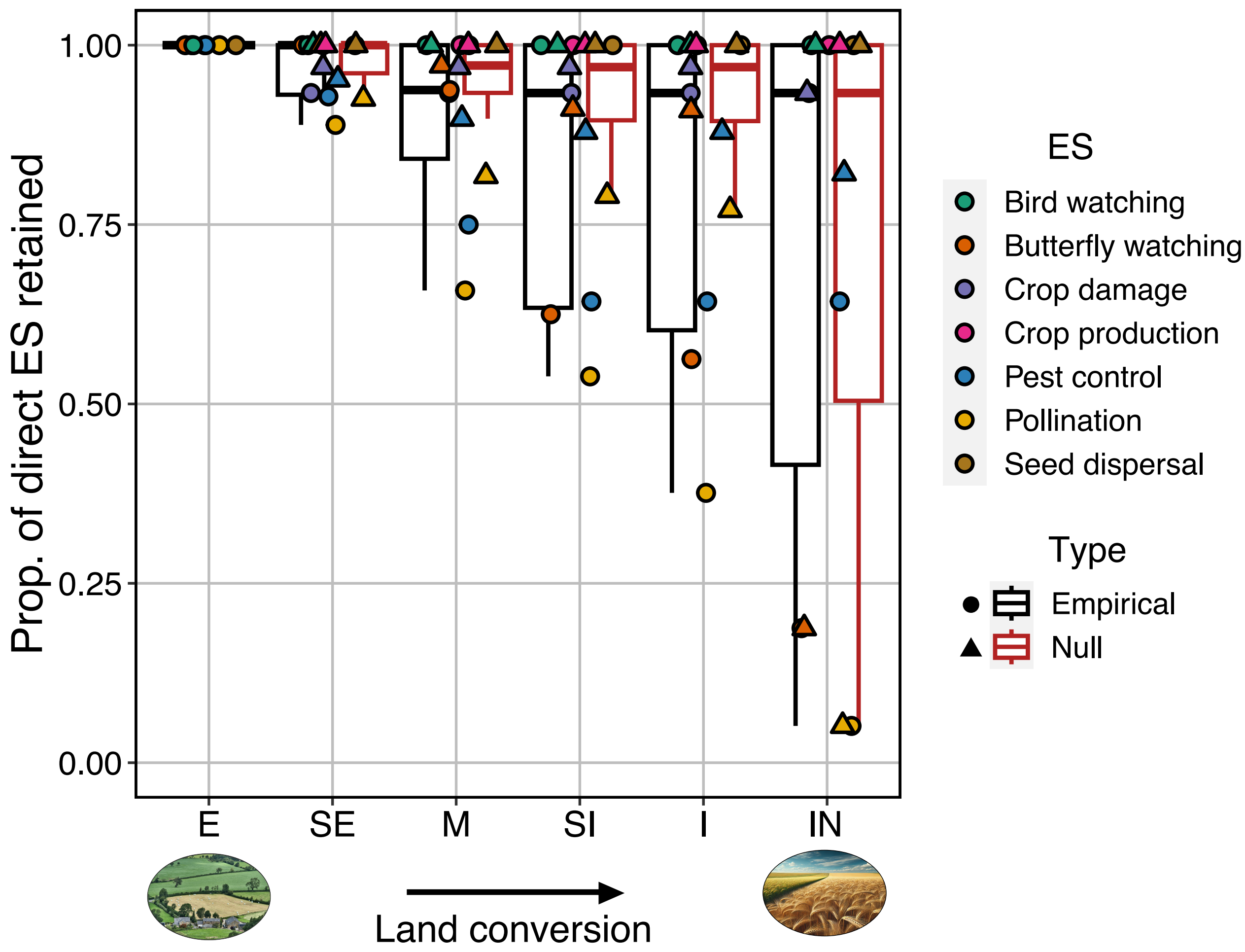

Fig. S4. Proportion of direct ES provision retained after land conversion in the original simulation and null model. Each boxplot represents the proportion of direct ecosystem services (ES) retained (y-axis) after gradually converting an extensive farm into intensive non-organic crop production (x-axis). The x-axis lists the management scenarios from left to right as follows: extensive organic (E), semi-extensive organic (SE), moderate organic (M), semi-intensive organic (SI), intensive organic (I), and intensive non-organic (IN). Black boxplots show the results of the original land conversion simulation, while red boxplots represent the results of the null model, where species were removed randomly during land conversion. Symbols indicate the proportion of direct ES retained (PD_x) following land conversion, with colors corresponding to different types of ES. For the null model, the symbols represent average values. The boxplots show the median, 25th, and 75th percentiles, with whiskers extending to the minimum and maximum values within 1.5 times the interquartile range.

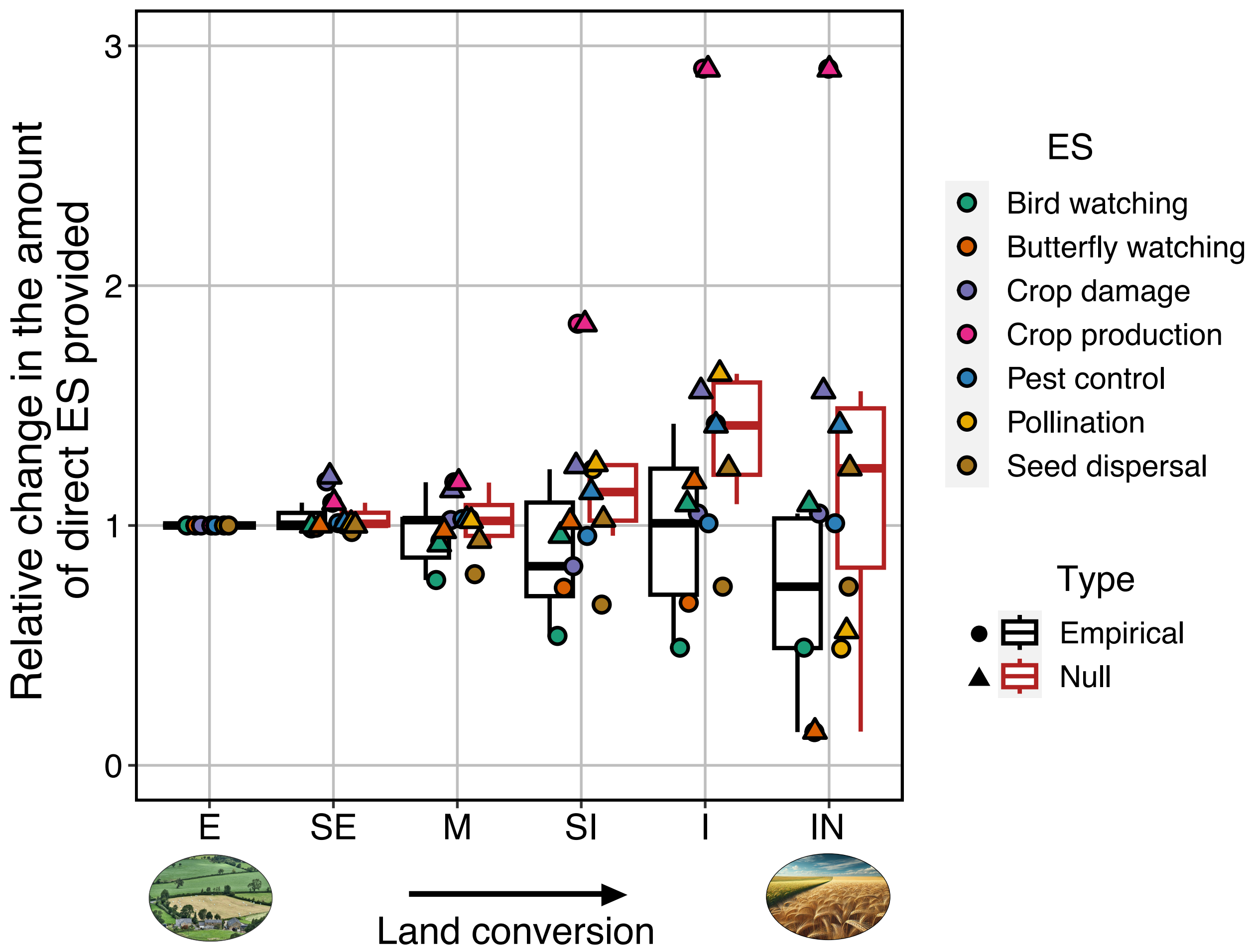

Fig. S5. Relative change in the amount of direct ES provision after land conversion in the original simulation and null model. Each boxplot represents the relative change in the amount of direct ES provision (y-axis) after gradually converting an extensive farm into intensive non-organic crop production (x-axis). The x-axis lists the management scenarios from left to right as follows: extensive organic (E), semi-extensive organic (SE), moderate organic (M), semi-intensive organic (SI), intensive organic (I), and intensive non-organic (IN). Black boxplots show the results of the original land conversion simulation, while red boxplots represent the results of the null model, where species were removed randomly during land conversion. Symbols indicate the relative change in the amount of ES provision (A_x), with colors corresponding to different types of ES. Values greater than 1 indicate an increase in the amount of ES compared to the extensive organic farm following land conversion. For the null model, the symbols represent average values. The boxplots show the median, 25th, and 75th percentiles, with whiskers extending to the minimum and maximum values within 1.5 times the interquartile range.

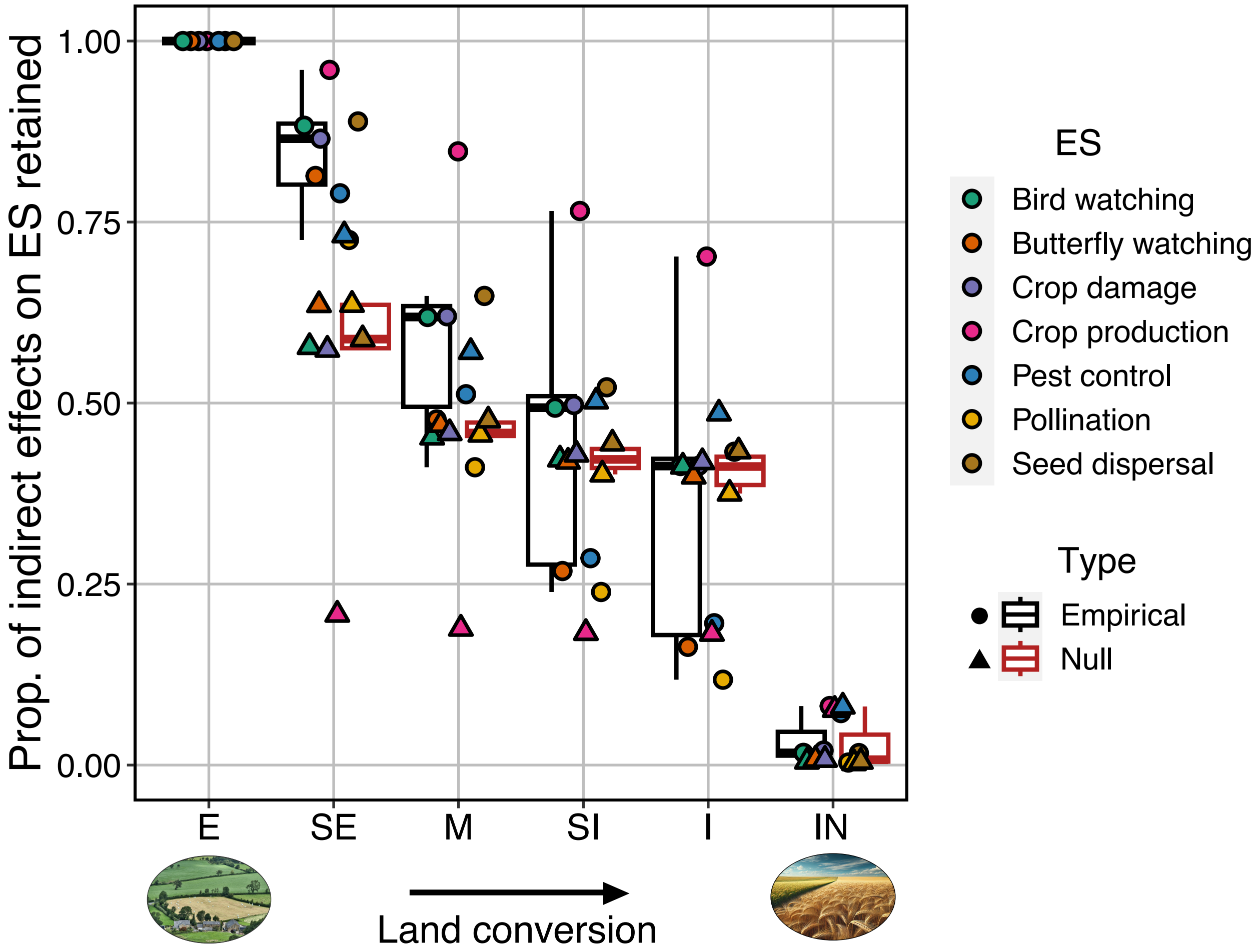

Fig. S6. Proportion of indirect effects on ES retained after land conversion in the original simulation and null model. Each boxplot represents the proportion of indirect effects of species on ecosystem services (ES) retained (y-axis) after gradually converting an extensive farm into intensive non-organic crop production (x-axis). The x-axis lists the management scenarios from left to right as follows: extensive organic (E), semi-extensive organic (SE), moderate organic (M), semi-intensive organic (SI), intensive organic (I), and intensive non-organic (IN). Black boxplots show the results of the original land conversion simulation, while red boxplots represent the results of the null model, where species were removed randomly during land conversion. Symbols indicate the proportion of indirect effects on each ES retained (PI_x), with colors corresponding to different types of ES. For the null model, the symbols represent average values. The boxplots show the median, 25th, and 75th percentiles, with whiskers extending to the minimum and maximum values within 1.5 times the interquartile range.

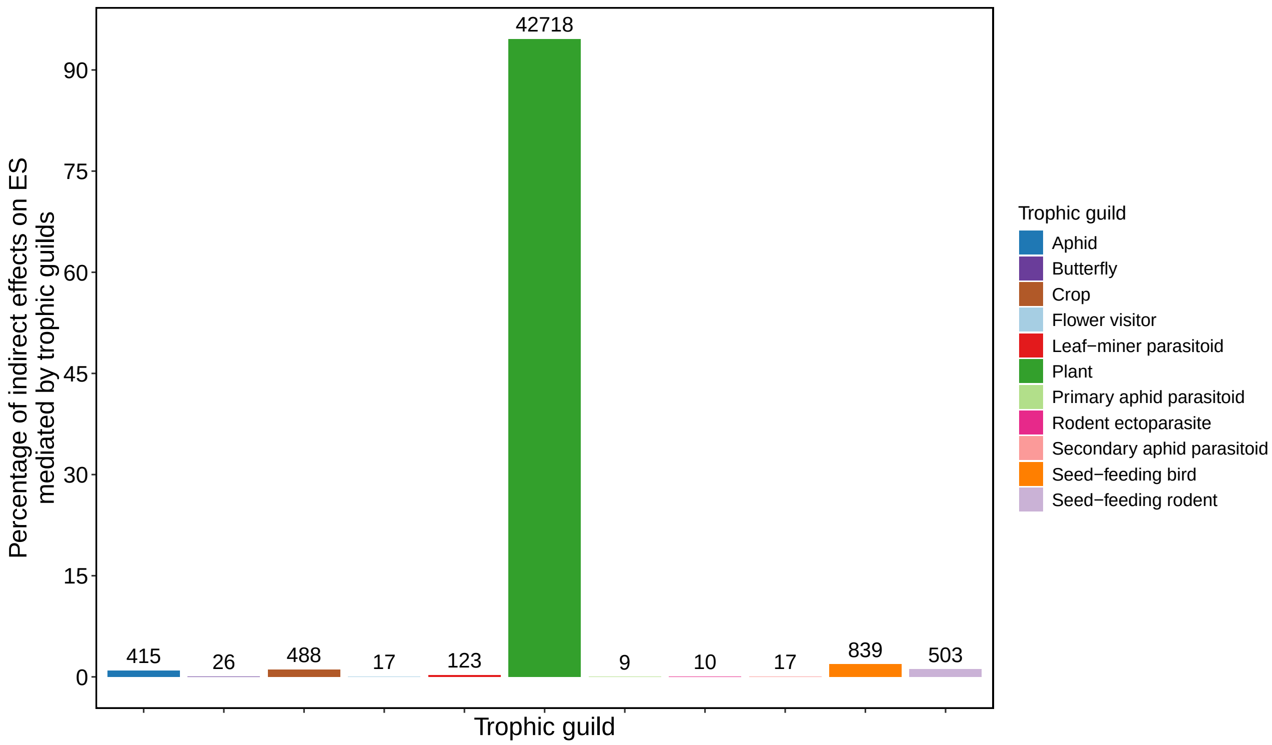

Fig. S7. Percentage of indirect effects on ecosystem services mediated by trophic guilds. Each bar represents the percentage of indirect interactions with ecosystem service providers mediated by a specific trophic guild. The numbers above the bars indicate the total number of times species within each trophic guild act as intermediate nodes in these indirect effects.

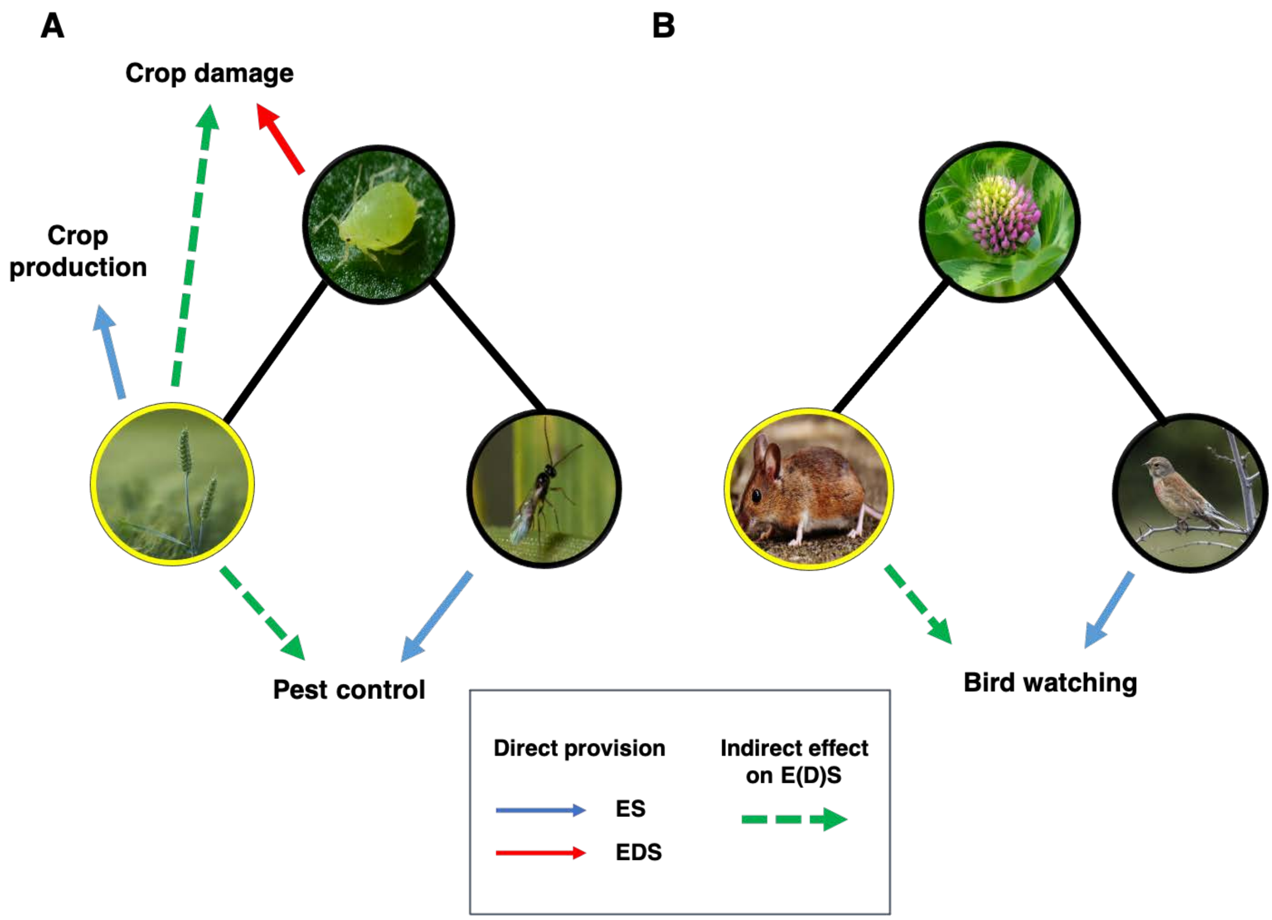

Fig. S8. Examples of potential indirect effects of species on ecosystem services and disservices. In each panel, we illustrate the indirect effects from a target species (crop for Panel A, rodent for Panel B) to simplify the explanation. However, it is essential to note that these effects are estimated for every species in the network. (A) Interaction chain involving a crop, an aphid, and a parasitoid species. Given that the aphid feeds on the crop, the presence of the crop is expected to influence on the abundance of the aphid, and hence, on crop damage. In addition, the parasitoid preys on the aphid, therefore, the crop is also potentially affecting the pest control provided by the parasitoid. (B) Interaction chain involving a rodent, a plant (weed), and a bird species. The rodent could indirectly affect the abundance of the bird by competing for resources, which suggests a potential impact on bird-watching facilitated by the presence of the bird. Hence, the rodent has the potential to indirectly affect bird-watching. It is important to note that the rodent could generate indirect effects on ES even if it is not providing any ES. In the figures, nodes and links represent species and ecological interactions between them. Blue arrows indicate potential provision of ecosystem services (ES), red arrows indicate ecosystem disservices (EDS), and green dashed arrows represent the indirect effects of species on E(D)S. Nodes with yellow border indicates the focal species from which indirect effects are explained.

S1 Estimation and analysis of the amount of direct ES provision

We estimated the amount of direct ESs provided by each species, depending on the type of ES, either as its abundance (bird and butterfly-watching) or as the product of its abundance and biomass (crop production, crop damage, pest control, pollination, seed dispersal). In the latter case, this quantitative proxy allows us to account for differences in species abundance and size across trophic guilds in ESs related to the rate of consumption. Using proxies such as abundance, richness, or trait combinations to quantify ESs is a widely used approach due to the complexity and lack of standardized methods across trophic guilds[33]. Biomass per species was obtained from databases[45–48] and a comprehensive literature review (see list below). In cases where we could not identify the specimen to the species level or no biomass information was available, we used the average biomass of the closest taxonomic level (e.g., genus).

After estimating the amount of ES provided, we calculated the relative change in the amount of direct ESs provision (A_x) after transforming the extensive farm into each management scenario. We did it for each ecosystem services. Then, we performed a GLMM to test whether A_x was affected by the extent of land conversion and type of ecosystem services. We used the gamma distribution as these variables were not normally distributed[49] and added "Species" as random. Finally, to address the potential skewness in biomass distribution and to ensure more balanced comparisons across species, we performed the same model but applying a logarithmic transformation to the biomass data. Since this transformation did not alter the model output (Table S6), we opted to keep the untransformed biomass values in the main analysis to simplify the interpretation. Analyses were performed using R software and glmmTMB, emmeans, and bbmle packages[51–53].

Table S6. Model summary comparing the effect of logarithmic transformation on the response variable A_x.

Log. Transformation	Response variable	Model	Fixed factor	Coeff.	Chisq	p-value	df
no	A_x	extent of land conversion + type of ES + (1|species_id)	extent of land conversion	0.0331	66.122	<0.001	5
			type of ES	0.322	44.471	<0.001	6
yes	A_x	extent of land conversion + type of ES + (1|species_id)	extent of land conversion	0.0332	66.122	<0.001	5
			type of ES	0.323	44.471	<0.001	6

List of literature reviewed to assign biomass to species:

Braschler, B., & Hill, J. K. (2007). Role of larval host plants in the climate-driven range expansion of the butterfly Polygonia c-album. Journal of Animal Ecology, 76(3), 415-423.

Brose, U., Williams, R. J., & Martinez, N. D. (2006). Allometric scaling enhances stability in complex food webs. Ecology letters, 9(11), 1228-1236.

Buitenhuis, R. (2004). A comparative study of the life history and foraging behaviour of aphid hyperparasitoids.

Doctoral dissertation, Université Laval.

Chen, Y. Z., Lin, L., Wang, C. W., Yeh, C. C., & Hwang, S. Y. (2004). Response of two Pieris (Lepidoptera: Pieridae) species to fertilization of a host plant. Zoological Studies, 43(4), 778-786.

Cook, P.M., Tordoff, G.M., Davis, A.M., Parsons, M.S., Dennis, E.B., Fox, R., Botham, M.S., & Bourn, N.A.D. (2021). Traits data for the butterflies and macro-moths of Great Britain and Ireland, 2021. NERC EDS Environmental Information Data Centre.

Corbet, S. A. (2000). Butterfly nectaring flowers: butterfly morphology and flower form. Entomologia Experimentalis et Applicata, 96(3), 289-298.

DeLong, J. P. (2014). The body-size dependence of mutual interference. Biology letters, 10(6), 20140261.

Derbel, S., Noumi, Z., Anton, K. W., & Chaieb, M. (2007). Life cycle of the coleopter Bruchidius raddianae and the seed predation of the Acacia tortilis Subsp. raddiana in Tunisia. Comptes Rendus Biologies, 330(1), 49-54.

Gols, R. (2008). Tritrophic interactions in wild and cultivated brassicaceous plant species. Wageningen University and Research.

Goverde, M., Bazin, A., Shykoff, J. A., & Erhardt, A. (1999). Influence of leaf chemistry of Lotus corniculatus (Fabaceae) on larval development of Polyommatus icarus (Lepidoptera, Lycaenidae): effects of elevated CO2 and plant genotype. Functional Ecology, 13(6), 801-810.

Hentz, M., Ellsworth, P., & Naranjo, S. (1997). Biology and morphology of Chelonus sp. nr. curvimaculatus (Hymenoptera: Braconidae) as a parasitoid of Pectinophora gossypiella (Lepidoptera: Gelechiidae). Annals of the Entomological Society of America, 90(5), 631-639.

Hu, J. (2019). Evolution of Body Mass in Coleoptera: Insights from Museum Specimens and DNA Barcodes. Doctoral dissertation, University of Guelph.

Kendall, L. K., Rader, R., Gagic, V., Cariveau, D. P., Albrecht, M., Baldock, K. C., ... & Bartomeus, I. (2019). Pollinator size and its consequences: Robust estimates of body size in pollinating insects. Ecology and Evolution, 9(4), 1702-1714.

Krämer, F., & Mencke, N. (2012). Flea biology and control: the biology of the cat flea control and prevention with imidacloprid in small animals. Springer Science & Business Media.

Lamb, R. J., MacKay, P. A., & Migui, S. M. (2009). Measuring the performance of aphids: fecundity versus biomass. The Canadian Entomologist, 141(4), 401-405.

Le Lann, C., Visser, B., van Baaren, J., van Alphen, J. J., & Ellers, J. (2012). Comparing resource exploitation and allocation of two closely related aphid parasitoids sharing the same host. Evolutionary Ecology, 26, 79-94.

Nicol, C. M. Y., & Mackauer, M. (1999). The scaling of body size and mass in a host-parasitoid association: influence of host species and stage. Entomologia experimentalis et applicata, 90(1), 83-92.

Pivnick, K. A., & McNeil, J. N. (1986). Sexual differences in the thermoregulation of Thymelicus lineola adults (Lepidoptera: Hesperiidae). Ecology, 67(4), 1024-1035.

Semsar-Kazerouni, M., Siepel, H., & Verberk, W. C. (2022). Influence of photoperiod on thermal responses in body size, growth and development in Lycaena phlaeas (Lepidoptera: Lycaenidae). Current Research in Insect Science, 2, 100034.

Serruys, M., Van Dyck, H. (2014). Development, survival, and phenotypic plasticity in anthropogenic landscapes: trade-offs between offspring quantity and quality in the nettle-feeding peacock butterfly. Oecologia, 176, 379-387.

Svärd, L., & Wiklund, C. (1989). Mass and production rate of ejaculates in relation to monandry/polyandry in butterflies. Behavioral Ecology and Sociobiology, 24, 395-402.

Swenson, S. J., Bell-Clement, J., Schroeder, S., & Prischmann-Voldseth, D. A. (2022). Predatory and Parasitic Insects Associated with Urophora cardui L.(Diptera: Tephritidae) Galls on Canada Thistle, Cirsium arvense L.(Asterales, Asteraceae) in North Dakota. Insects, 13(7), 646.

Symanski, C. (2016). Effects of Diet and Temperature Stressors on Fluctuating Asymmetry of Wing Traits, Mortality and Dry Mass in a Lepidopteran (Vanessa cardui Linnaeus). University of California, Riverside.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals: Ecological Archives E095-178. Ecology, 95(7), 2027-2027.

Xi, X., Li, D., Peng, Y., Eisenhauer, N., & Sun, S. (2016). Experimental warming and precipitation interactively modulate the mortality rate and timing of spring emergence of a gallmaking Tephritid fly. Scientific Reports, 6(1), 32284.

Xi, X., Yang, Y., Yang, Y., Segoli, M., & Sun, S. (2017). Plant-mediated resource partitioning by coexisting parasitoids. Ecology, 98(6), 1660–1670.

References

1. Van Dijk, M., Morley, T., Rau, M. L. & Saghai, Y. A meta-analysis of projected global food demand and population at risk of hunger for the period 2010-2050. *Nat. Food* **2,** 494–501 (2021).
2. Vijay, V. & Armsworth, P. R. Pervasive cropland in protected areas highlight trade-offs between conservation and food security. *Proc. Natl. Acad. Sci. U. S. A.* **118,** e2010121118 (2021).
3. IPBES. *Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services* (ed S. Díaz, J. Settele, E. Brondízio and H. T. Ngo.) (IPBES Secretariat, 2019).
4. Williams, D. R. *et al.* Proactive conservation to prevent habitat losses to agricultural expansion. *Nat. Sustain.* **4,** 314–322 (2020).
5. Power, A. G. Ecosystem services and agriculture: tradeoffs and synergies. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365,** 2959–2971 (2010).
6. Kleijn, D. *et al.* Ecological intensification: Bridging the gap between science and practice. *Trends Ecol. Evol.* **34,** 154–166 (2019).
7. Assessment, M. E. *Ecosystems and human well-being: a framework for assessment* (wri.org, 2003).
8. Zhang, W., Ricketts, T. H., Kremen, C., Carney, K. & Swinton, S. M. Ecosystem services and dis-services to agriculture. *Ecol. Econ.* **64,** 253–260 (2007).
9. WWF International. *Living Planet Report 2022* (WWF International, Gland, Switzerland, 2022).
10. Tamburini, G. *et al.* Agricultural diversification promotes multiple ecosystem services without compromising yield. *Sci Adv* **6** (2020).
11. Priyadarshana, T. S. *et al.* Crop and landscape heterogeneity increase biodiversity in agricultural landscapes: A global review and meta-analysis. *Ecol. Lett.* **27,** e14412 (2024).
12. Beillouin, D., Ben-Ari, T., Malézieux, E., Seufert, V. & Makowski, D. Positive but variable effects of crop diversification on biodiversity and ecosystem services. *Glob. Chang. Biol.* **27,** 4697–4710 (2021).
13. Bennett, E. M., Peterson, G. D. & Gordon, L. J. Understanding relationships among multiple ecosystem services: Relationships among multiple ecosystem services. *Ecol. Lett.* **12,** 1394–1404 (2009).
14. Windsor, F. M. *et al.* Network science: Applications for sustainable agroecosystems and food security. *Perspectives in Ecology and Conservation* **20,** 79–90 (2022).
15. Tylianakis, J. M., Didham, R. K., Bascompte, J. & Wardle, D. A. Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* **11,** 1351–1363 (2008).

16. Dee, L. E. *et al.* Operationalizing Network Theory for Ecosystem Service Assessments. *Trends Ecol. Evol.* **32,** 118–130 (2017).

17. Windsor, F. M. *et al.* Identifying plant mixes for multiple ecosystem service provision in agricultural systems using ecological networks. *J. Appl. Ecol.* **58,** 2770–2782 (2021).

18. Delmas, E. *et al.* Analysing ecological networks of species interactions: Analyzing ecological networks. *Biol Rev* **94,** 16–36 (2019).

19. Guimarães Jr, P. R. The Structure of Ecological Networks Across Levels of Organization. *Annu. Rev. Ecol. Evol. Syst.* **51,** 433–460 (2020).

20. Bascompte, J. Disentangling the web of life. *Science* **325,** 416–419 (2009).

21. Wootton, T. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology, Evolution, and Systematics* **25,** 443–466 (1994).

22. Gutierrez-Arellano, C & Mulligan, M. A review of regulation ecosystem services and disservices from faunal populations and potential impacts of agriculturalisation on their provision, globally. *Nature Conservation* **30,** 1–39 (2018).

23. Miller, K. E., Polaszek, A. & Evans, D. M. A dearth of data: fitting parasitoids into ecological networks. *Trends Parasitol.* **37,** 863–874 (2021).

24. Keyes, A. A., McLaughlin, J. P., Barner, A. K. & Dee, L. E. An ecological network approach to predict ecosystem service vulnerability to species losses. *Nat. Commun.* **12,** 1586 (2021).

25. Felipe-Lucia, M. R. *et al.* Conceptualizing ecosystem services using social–ecological networks. *Trends Ecol. Evol.* **37,** 211–222 (2022).

26. Wilkes, L. N. *et al.* Quantifying co-extinctions and ecosystem service vulnerability in coastal ecosystems experiencing climate warming. *Glob. Chang. Biol.* **30,** e17422 (2024).

27. Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H. & Bellwood, D. R. A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* **28,** 167–177 (2013).

28. Newbold, T. *et al.* Global effects of land use on biodiversity differ among functional groups. *Funct. Ecol.* **34,** 684–693 (2020).

29. Pocock, M. J. O., Evans, D. M. & Memmott, J. The robustness and restoration of a network of ecological networks. *Science* **335,** 973–977 (2012).

30. Evans, D. M., Pocock, M. J. O. & Memmott, J. The robustness of a network of ecological networks to habitat loss. *Ecol. Lett.* **16,** 844–852 (2013).

31. Sauve, A. M. C., Thébault, E., Pocock, M. J. O. & Fontaine, C. How plants connect pollination and herbivory networks and their contribution to community stability. *Ecology* **97,** 908–917 (2016).

32. Van Ruymbeke, K. *et al.* Assessing the impact of farm-management practices on ecosystem services in European agricultural systems: A rapid evidence assessment. *Sustainability* **15,** 12819 (2023).

33. Noriega, J. A. *et al.* Research trends in ecosystem services provided by insects. *Basic Appl. Ecol.* **26,** 8–23 (2018).

34. Pires, M. M. *et al.* The indirect paths to cascading effects of extinctions in mutualistic networks. *Ecology* **101,** e03080 (2020).

35. Vitali, A. *et al.* Invasive species modulate the structure and stability of a multilayer mutualistic network. *Proc. Biol. Sci.* **290,** 20230132 (2023).

36. IUCN. Agriculture and conservation: living nature in a globalised world. *IUCN Flagship Report Series No. 2. Gland, Switzerland: IUCN* (2024).

37. Feeding the future global population. *Nat. Commun.* **15,** 222 (2024).

38. Maurer, C. *et al.* Landscape simplification leads to loss of plant–pollinator interaction diversity and flower visitation frequency despite buffering by abundant generalist pollinators. *Divers. Distrib.* **30** (2024).

39. Requier, F. *et al.* Bee and non-bee pollinator importance for local food security. *Trends Ecol. Evol.* **38,** 196–205 (2023).

40. Quévreux, P. *et al.* Perspectives in modelling ecological interaction networks for sustainable ecosystem management. *J. Appl. Ecol.* **61,** 410–416 (2024).

41. Lázaro, A. & Gómez-Martínez, C. Habitat loss increases seasonal interaction rewiring in plant–pollinator networks. *Funct. Ecol.* **36,** 2673–2684 (2022).

42. Hufbauer, R. A. *et al.* Three types of rescue can avert extinction in a changing environment. *Proc. Natl. Acad. Sci. U. S. A.* **112,** 10557–10562 (2015).

43. Gallandt, E. R. & Weiner, J. in *eLS* 1–9 (John Wiley & Sons, Ltd, Chichester, UK, 2015).

44. Evans, D. M., Pocock, M. J. O., Brooks, J. & Memmott, J. Seeds in farmland food-webs: Resource importance, distribution and the impacts of farm management. *Biol. Conserv.* **144,** 2941–2950 (2011).

45. Brose, U., Williams, R. J. & Martinez, N. D. Allometric scaling enhances stability in complex food webs. *Ecol. Lett.* **9,** 1228–1236 (2006).

46. Cook, P. M. *et al.* Traits data for the butterflies and macro-moths of Great Britain and Ireland. *Ecology* **103,** e3670 (2022).

47. Kendall, L. K. *et al.* Pollinator size and its consequences: Robust estimates of body size in pollinating insects. *Ecol. Evol.* **9,** 1702–1714 (2019).

48. Wilman, H. *et al.* EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals: Ecological Archives E095-178. *Ecology* **95,** 2027–2027 (2014).

49. Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A. & Smith, G. M. *Mixed Effects Models and Extensions in Ecology with R* (Springer New York, 2009).

50. Wagenmakers, E.-J. & Farrell, S. AIC model selection using Akaike weights. *Psychon. Bull. Rev.* **11,** 192–196 (2004).

51. Brooks, Kristensen, Van Benthem & others. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R* (2017).

52. Bolker, B. & Team, R. D. C. bbmle: Tools for general maximum likelihood estimation. *R package version 0. 9* **5** (2010).

53. Searle, S. R., Speed, F. M. & Milliken, G. A. Population Marginal Means in the Linear Model: An Alternative to Least Squares Means. *Am. Stat.* **34,** 216–221 (1980).