SCIENCE ADVANCES | RESEARCH ARTICLE

APPLIED ECOLOGY

Biodiversity-friendly landscapes: A paradox for conservation?

Eliane Seraina Meier[1]*, **Alexander Indermaur**[1], **Eva Knop**[1,2]

Human-induced global change may cause the sixth mass extinction of species. The moderate success of patch-scale biodiversity conservation measures has led to the concept of creating biodiversity-friendly landscapes. However, these landscapes potentially present a paradox: They may increase local biodiversity and thereby strengthen biotic resistance of native communities to global change winners, i.e., species that thrive under global change, such as invasive alien species or temperature- or nutrient-tolerant species. However, they may also improve landscape-scale habitat conditions, such as habitat connectivity, which facilitates the dispersal of global change winners, thereby accelerating biodiversity loss. Despite increasing investment in biodiversity-friendly landscapes, this paradox and underlying processes remain largely unquantified. We analyzed 2050 repeated, systematic vegetation surveys across the Swiss farmland and found the hypothesized facilitating and inhibitory effects on global change winners, but, overall, the inhibitory effects were stronger. This supports the call for a shift from patch-scale conservation to landscape-wide strategies to stop the ongoing decline of farmland biodiversity.

INTRODUCTION

Biodiversity is currently declining at an unprecedented rate, leading scientists to be concerned that, if no immediate measures are taken (*1*), we are facing the sixth mass extinction of species (*2*). The major driver of this species decline is considered to be global change, which includes climate change, land-use change, pollution, direct exploitation, and the introduction of nonnative species (*3*, *4*). However, certain species benefit from global change, the so-called global change winners (*5*, *6*). Global change helps winners disperse and outcompete native species (*7*) and thereby leads to a homogenization of species communities (*8*), which further accelerates biodiversity decline (*9*, *10*). On the basis of the most important global change drivers, three groups of species may profit particularly from global change: species adapted to warm climates (*11*–*13*), species adapted to nutrient-rich environments (*14*), and nonnative species that are easily transported and manage to expand into other ecosystems (*15*). As a result of the increase in these three groups of global change winners, changes in community functioning due to changing abiotic conditions from global change could be exacerbated (*16*).

Despite many relevant studies on the individual direct effects of factors altered by global change (e.g., temperature or land use) on various species and species groups (*12*, *17*), the mechanisms of community reorganization due to global change are still under debate (*18*–*21*). In particular, it remains unclear whether, and at what spatial scale, measures aimed at conserving and promoting biodiversity (further referred to as biodiversity conservation measures) strengthen the stability of ecosystems. Ecosystem stability is key to preventing marked changes in biotic communities that occur when certain organisms disperse across the landscape, become dominant, and outcompete others locally, ultimately leading to large-scale species loss (*22*–*26*). We probably lack this knowledge because studies on biodiversity conservation measures often focus on conserving losers of global change at the patch scale and in the short term (*27*).

A better understanding of the effects of biodiversity conservation measures at different spatial scales on global change winners is particularly relevant, as biodiversity conservation measures at the local scale have recently been critically debated (*28*, *29*). Scientists are even calling for a paradigm shift in nature conservation, namely, away from local measures toward measures that create biodiversity-friendly landscapes (*28*, *29*). The idea is to create landscapes that provide suitable habitat conditions for viable metacommunities, e.g., sufficient habitat area (*30*), sufficient habitat connectivity (*31*–*33*), and sufficient habitat richness (*34*). These suitable habitat conditions in the landscape can be created, for example, by enlarging the area with biodiversity conservation measures [i.e., based on the relationships between area, habitat diversity, and species diversity (*35*) and the relationship between habitat area and habitat connectivity (*32*)]. However, when it comes to coping with global change winners, biodiversity-friendly landscapes may represent a conservation paradox. The term "paradox" is used in literature in different ways. Here, we use the term paradox to describe two processes that have opposite effects on global change winners at different spatial scales, although they are caused by the same biodiversity conservation measure (Fig. 1).

Biodiversity-friendly landscapes have the potential to inhibit the establishment of global change winners through local-scale processes, while facilitating them through landscape-scale processes (Fig. 1). With a focus on local-scale processes (Fig. 1), improving habitat conditions in the landscape through biodiversity-friendly landscapes may further increase local-scale biodiversity compared to biodiversity conservation measures that solely target local management, such as prohibiting fertilizers and pesticides on specific agricultural fields to mitigate direct harm to biodiversity in those areas (*28*, *34*, *36*, *37*). Increased local-scale biodiversity may, in turn, reduce the vulnerability of the local community to the establishment of emerging invaders, i.e., increase its biotic resistance, which is the ability of an ecosystem to maintain its original community and resist change (*38*). These biotic resistance effects have already been demonstrated in various ecosystems (*38*–*43*) and are largely explained by the fact that more diverse communities produce more biomass, occupy more niches, and use more resources than less diverse communities, which can be attributed to complementarity effects (*44*) and sampling effects (*45*). With a focus on landscape-scale processes (Fig. 1),

---

[1] Agroecology and Environment, Agroscope, Reckenholzstrasse 191, CH-8046 Zürich, Switzerland. [2] Department of Evolutionary Biology and Environmental Studies, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland.
*Corresponding author. Email: eliane.meier@agroscope.admin.ch, meier.eliane@gmail.com

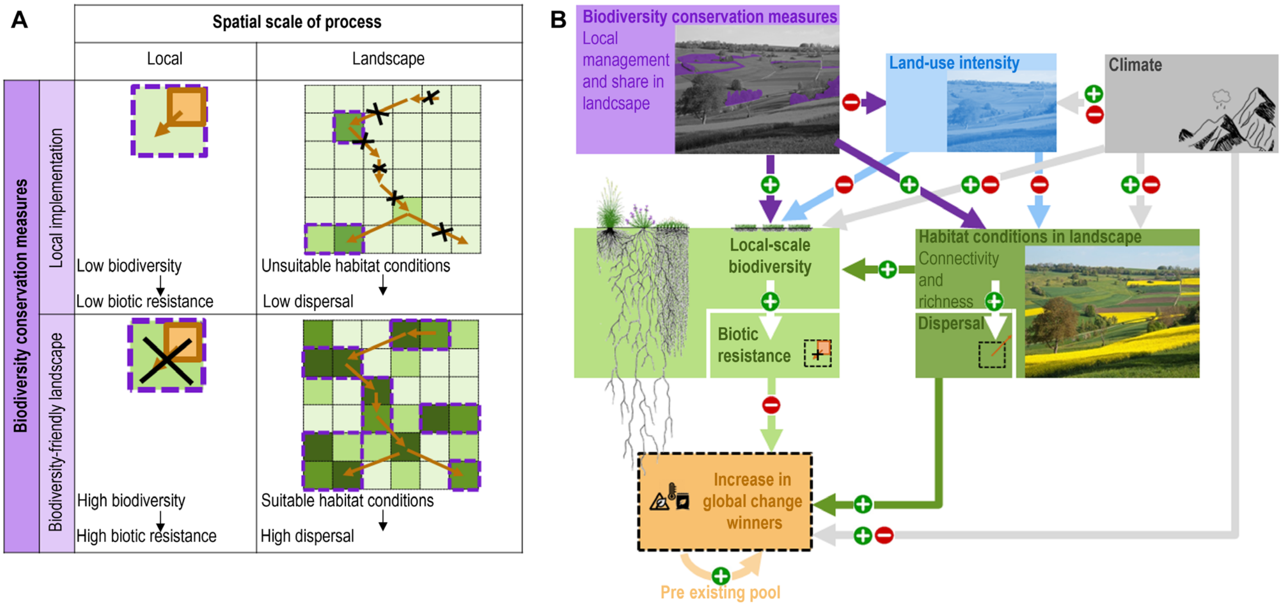

Fig. 1. Paradox of biodiversity conservation measures with regard to their expected effects on the increase in global change winners. (**A**) Depending on the spatial scale at which biodiversity conservation measures are implemented, two counteracting processes may occur: On one hand, biodiversity-friendly landscapes may increase local-scale biodiversity and thus strengthen the biotic resistance to the establishment of global change winners. On the other hand, biodiversity-friendly landscapes may also improve habitat conditions at the landscape scale, which, in turn, may facilitate the dispersal of global change winners within the landscape. (**B**) Conceptual model depicting the expected effects of biodiversity conservation measures on the increase in global change winners, while controlling for climate, land-use intensity, and the preexisting pool of global change winners. CREDIT: G. BRÄNDLE/ *AGROSCOPE*.

biodiversity conservation measures that target biodiversity-friendly landscapes may facilitate the dispersal of species across the landscape. While this may support global-change losers by enhancing habitat conditions that enable viable metacommunities (e.g., habitat connectivity), it may also unintentionally benefit global change winners. If global change winners benefit from improved habitat conditions, then they could spread more rapidly, potentially at the expense of global change losers, thereby further accelerating biodiversity loss (*9*, *10*). To our knowledge, this conservation paradox of biodiversity-friendly landscapes has not yet been quantified. Consequently, it remains unclear whether the potentially inhibiting effects on global change winners outweigh the potentially facilitating effects, or vice versa. If the latter is true and biodiversity-friendly landscapes unintentionally provide a strong advantage to global change winners, then the concept may fail to achieve its intended conservation goals under global change.

Here, we quantify the potentially counteracting effects of biodiversity conservation measures at different spatial scales on the increase of global change winners. Specifically, we asked the following questions: (i) Do biodiversity conservation measures targeting biodiversity-friendly landscapes increase local-scale biodiversity compared to the local management of biodiversity conservation measures, and does this increase lead to increased biotic resistance against the establishment of global change winners (Fig. 1), thereby reducing the increase in global change winners (Fig. 1)? (ii) Do biodiversity conservation measures targeting biodiversity-friendly landscapes increase habitat richness and connectivity at the landscape scale, and does this increase facilitate the dispersal of global change winners (Fig. 1), thereby leading to an increase in global change winners (Fig. 1)? (iii) Is the overall effect of biodiversity conservation measures targeting biodiversity-friendly landscapes on global change winners inhibitory or facilitatory?

We used structural equation modeling (SEM) (*46*) to analyze the potentially counteracting effects on the increase in global change winners, while controlling for land-use intensity, climate, and the preexisting pool of global change winners (Fig. 1). Our analysis was based on repeated vegetation surveys conducted on 2050 sample plots in farmlands distributed across 125 landscapes (squares of 1 km^2) along the main climate and land-use gradients in Switzerland (Fig. 2) (*47*). The selection of 1-km^2 landscapes was guided by ecological relevance, as this spatial scale has been demonstrated to capture key species interactions, habitat connectivity, and land-use dynamics (*48*, *49*), aligns with commonly used spatial resolutions in related studies (*50*, *51*), and enhances the applicability of our findings for management and policy decisions. However, we acknowledge that results may vary depending on the chosen spatial extent. We focused on farmland because farmland biodiversity is under particular pressure due to global change (*4*) and because farmland covers a large area worldwide (*52*), making it a crucial area for biodiversity conservation measures. In our study, the most important biodiversity conservation measures were ecological focus areas, which are either unproductive set-aside areas or fields that yield less because of, e.g., later cutting dates and lower nutrient inputs (*53*–*56*). The extent to which the biodiversity conservation measures were aimed at biodiversity-friendly landscapes was assessed on the basis of the share of biodiversity conservation measures in the landscape. Furthermore, three major groups of global change winners in agricultural landscapes, i.e., invasive neophytes, thermophytes, and nutriophytes, were tracked by two measures of their increase, i.e., increase in cover and occurrence, for which we formulated separate

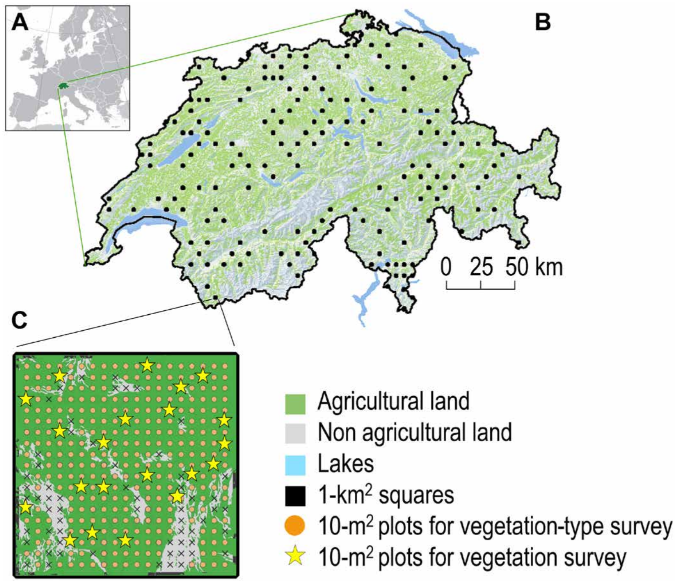

Fig. 2. Overview of study area and survey. (**A**) The study area within Europe, (**B**) the 125 surveyed landscapes (squares of 1 km^2) within the study area, and (**C**) the vegetation-type surveys in 10-m^2 plots on a 50 m–by–50 m grid within an exemplary landscape (i.e., a maximum of 361 plots per landscape) and the ~20 plots selected from these for vegetation surveys (total: 2050).

SEMs. The increase in cover may be determined particularly by the suitability of the local habitat, whereas the increase in occurrence may be determined particularly by the permeability of the landscape for movement (*57*). However, as these two measures may also be interrelated, we considered them complementary proxies of their overall increase. The two measures of increase were derived from four different baseline years (i.e., 2015–2018) over a period of 5 years (i.e., up to 2020–2023), while, for all the other factors in the model, we used the data from the baseline years (*58*). See Materials and Methods for details.

RESULTS

The global model fit of the final SEMs was reasonable for both the increase in cover of global change winners (χ^2/df = 9.41; Fig. 3) and the increase in occurrence of global change winners (χ^2/df = 14.09; Fig. 4).

Biotic resistance effects

Biodiversity conservation measures, especially those aiming for biodiversity-friendly landscapes, were associated with higher local-scale biodiversity (Fig. 3 and table S4). In turn, higher local-scale biodiversity increased the biotic resistance to global change winners (Fig. 3 and table S4). Specifically, the local implementation of biodiversity conservation measures and the low local land-use intensity that partly depend on these, as well as a high share of biodiversity

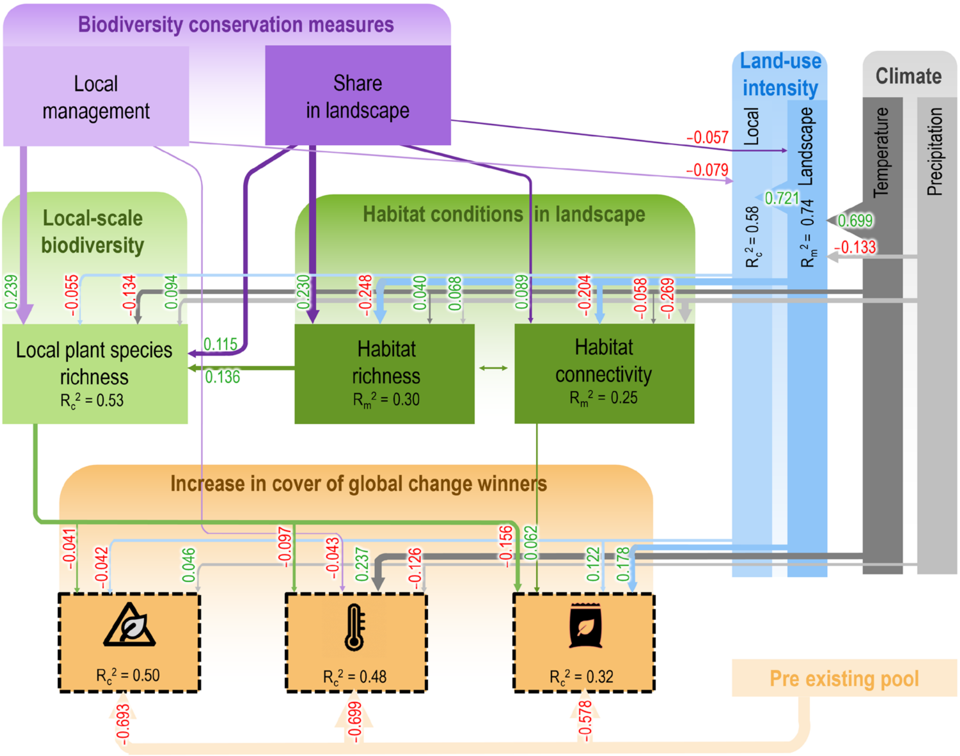

Fig. 3. SEM for the increase in cover of global change winners. Results of the SEM to test for direct and indirect effects of biodiversity conservation measures on the increase in cover of global change winners (left, invasive neophytes; middle, thermophytes; right, nutriophytes) while controlling for land-use intensity and climate. The magnitude of the standardized coefficients is indicated beside the respective arrows, and the thickness of the paths is proportional to the magnitude of the standardized coefficient. R_c^2 represents the conditional coefficient of determination, and R_m^2 represents the marginal coefficient of determination. See table S1 for more details on the results and fig. S1 for bivariate plots of direct effects.

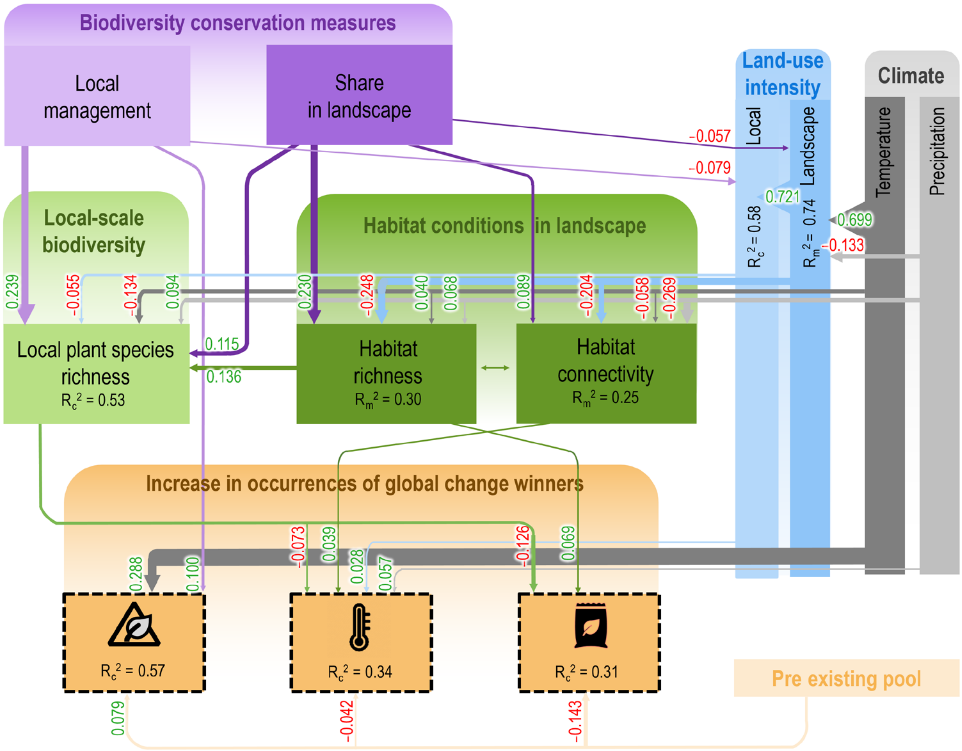

Fig. 4. SEM for the increase in occurrences of global change winners. Results of the SEM to test for direct and indirect effects of biodiversity conservation measures on the increase in occurrences of global change winners (left. invasive neophytes; middle, thermophytes; right, nutriophytes) while controlling for land-use intensity and climate. The magnitude of the standardized coefficients is indicated beside the respective arrows, and the thickness of the paths is proportional to the magnitude of the standardized coefficient. See table S1 for more details on the results and fig. S1 for bivariate plots of direct effects.

conservation areas in the landscape and a high habitat richness in the landscape that partly depends on these, were associated with an increased local-scale biodiversity (Fig. 3 and table S4). In turn, local-scale biodiversity increased the biotic resistance, indicated by a lower increase in cover of all global change winners (Fig. 3 and table S4). Similarly, global change winners were less likely to increase their occurrences: Although higher local-scale biodiversity was not associated with a lower probability of an increased invasive neophytes occurrence, it was associated with a lower probability of an increased occurrence of thermophytes and nutriophytes (Fig. 4 and table S4).

Facilitative landscape effects

Biodiversity conservation measures that lead to lower land-use intensity and more biodiversity-friendly habitat conditions in the landscape, and thereby contribute to biodiversity-friendly landscapes, directly facilitated the increase in global change winners. More specifically, a high share of biodiversity conservation measures in the landscape was associated, via habitat connectivity, with an increased probability of the additional occurrence of thermophytes (Fig. 4 and table S4) and an increased cover of nutriophytes (Fig. 3 and table S4). Furthermore, a high share of biodiversity conservation measures in the landscape was associated, via habitat richness, with an increased probability of an additional occurrence of nutriophytes (Fig. 4 and table S4). Furthermore, for nutriophytes, there was an inhibitory effect of a high share of biodiversity conservation measures in the landscape, i.e., a decreased land-use intensity in the landscape was associated with a lower increase in cover (Fig. 3 and table S4). Last, there was no effect of the share of biodiversity measures in the landscape on the cover or the probability of an additional occurrence of invasive neophytes. In contrast, there were local management effects of biodiversity conservation measures on invasive neophytes (Figs. 3 and 4 and table S4). For example, a reduction in local land-use intensity through the local management with biodiversity measures was associated with an increase in cover (Fig. 3 and table S4), whereas the local management with biodiversity measures was associated with an increased probability of additional occurrences (Fig. 4 and table S4).

Effects of climate and preexisting pools

In addition to the two counteracting processes associated with biodiversity-friendly landscapes affecting the increase in global change winners, climate was also associated with the increase in different global change winners (Figs. 3 and 4 and table S4). For example, a higher average temperature was associated with an increase in the additional occurrence of invasive neophytes (Fig. 4 and table S4) and with an increase in the cover of thermophytes (Fig. 3 and table S4).

The preexisting pool of global change winners was also associated with the increase in different global change winners: They increased less in cover when their cover was already higher (Fig. 3 and table S4). Similarly, thermophytes and nutriophytes were less likely to occur additionally in previously unoccupied patches of the landscape if they had an increased frequency of occurrence in the landscape (Fig. 4 and table S4). In contrast, an additional occurrence of invasive neophytes was positively associated with the preexisting pool (Fig. 4 and table S4).

Overall inhibitory effects

The overall effect of biodiversity conservation measures targeting biodiversity-friendly landscapes (Fig. 5 and table S5) was calculated by multiplying the standardized coefficients of the pathways in the SEMs (Figs. 3 and 4) that were influenced by biodiversity conservation measures (i.e., by their local management or by their share in the landscape) and adding up all the products of the different pathways (*46*). Similarly, separate effects were calculated, e.g., for biodiversity conservation measures via biotic resistance on establishment (i.e., the effects of biodiversity conservation measures through local-scale biodiversity on the increase in global change winners) and for biodiversity conservation measures via habitat conditions on dispersal (i.e., the effects of biodiversity conservation measures through habitat richness and connectivity on the increase in global change winners).

Overall, biodiversity conservation measures targeting biodiversity-friendly landscapes had an inhibiting effect on the increase in global change winners (Fig. 5 and table S5): An increase in local-scale biodiversity due to the biodiversity conservation measures was related to a reduced increase in global change winners (Fig. 5 and table S5). This effect of biodiversity conservation measures on biotic resistance (Fig. 5 and table S5) was much stronger than their promoting effect on the increase in global change winners by improving habitat conditions at landscape scale that facilitated their dispersal (Fig. 5 and table S5).

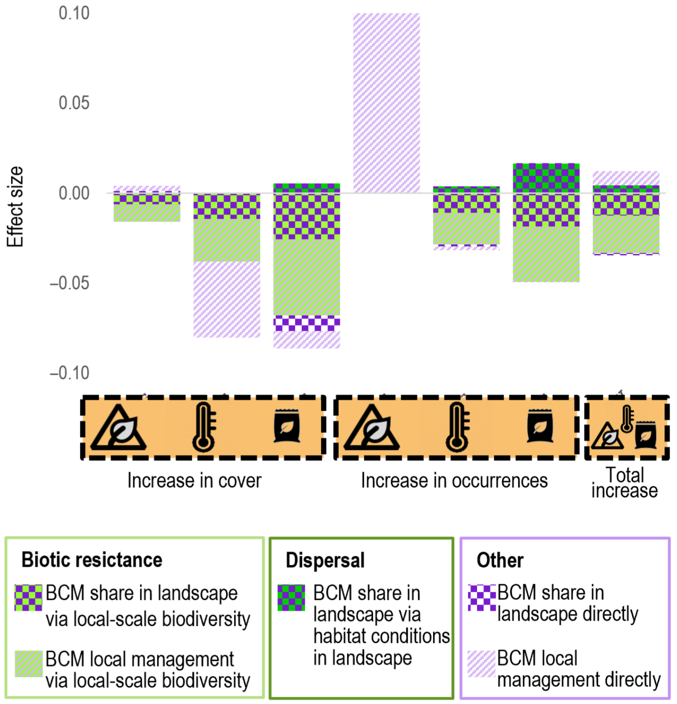

Fig. 5. Overall effects of biodiversity conservation measures. Overall effects of biodiversity conservation measures (BCMs) on the increase in global change winners (left, invasive neophytes; middle, thermophytes; right, nutriophytes), while controlling for effects of climate, land-use intensity, and the preexisting pool of the global change winners. The increase in global change winners was measured by the increase in cover of global change winners and their additional occurrence. The total increase represents the mean of the effects on the increase in cover of global change winners and the effects on the additional occurrence of all global change winners. The overall effects of conservation measures on the increase in global change winners were calculated by multiplying the standardized coefficients of the paths influenced by biodiversity conservation measures from table S4 and adding all resulting products. This estimation was performed separately for biotic resistance effects to establishment (i.e., biodiversity conservation effects through local-scale biodiversity), for dispersal effects from biodiversity-friendly habitat conditions (i.e., biodiversity conservation effects through habitat richness and connectivity), and for other biodiversity conservation measure effects.

DISCUSSION

Biotic resistance effects

Biodiversity conservation measures, especially those aiming at biodiversity-friendly landscapes, were associated with higher local-scale biodiversity, which, in turn, increased biotic resistance to global change winners. Specifically, higher local-scale biodiversity was associated with a lower increase in cover of all global change winners and a lower probability of an additional occurrence of thermophytes and nutriophytes. The fact that, in the case of invasive neophytes, only the increase in cover was decreased by biotic resistance, but not the probability of additional occurrence, is in line with the findings of a recent study (*59*) and suggests that, although they may invade another patch, e.g., small areas of open ground in disturbed habitats, they do not increase their cover, probably due to the high biotic resistance in the rest of the patch.

Our results provide one of the rare examples in which the biotic resistance hypothesis appears to be ubiquitous not only for invasive alien species (*60*, *61*) but also for other global change winners. This might become increasingly relevant given the accelerated increase in temperature, land-use change, and global trading. In addition, we were able to show that local-scale biodiversity provides increased resistance to both measures of increase in global change winners, possibly because lower cover of global change winners indirectly inhibits their dispersal across the landscape by reducing the number of available propagules (*62*). In maximizing biotic resistance to global change winners, biodiversity-friendly landscapes that increase local-scale biodiversity and thus biotic resistance appear to offer a valuable contribution.

Facilitative landscape effects

Biodiversity conservation measures that promote lower land-use intensity and more biodiversity-friendly habitat conditions in the landscape, all of which contribute to biodiversity-friendly landscapes, have directly facilitated the increase in global change winners. More specifically, an increased habitat connectivity was associated with an increased probability of additional occurrence of thermophytes and an increased cover of nutriophytes, as well as an increased habitat richness with an increased probability of additional occurrence of nutriophytes. For nutriophytes, however, we found the only inhibitory effect of a high share of biodiversity conservation measures in the landscape, i.e., a thereby decreased land-use intensity in the landscape was associated with a lower increase in cover. This was probably because a lower land-use intensity is associated with a lower nutrient supply in the agricultural soil. Last, for invasive neophytes, no effects of the share of biodiversity measures in the landscape could be identified, but only local management effects of biodiversity conservation measures could be identified. For example, a reduction in local land-use intensity through the local management of biodiversity measures was associated with an increase in cover, whereas the local management of biodiversity measures was associated with an increased probability of additional occurrences. The lack of effect of implementing biodiversity conservation measures in the landscape on the dispersal of invasive neophytes may be because invasive neophytes still have a rather low cover in Swiss farmlands (table S2); therefore, the size of their propagule source, which is the basis for additional occurrences in the landscape, is currently influenced mainly by local biotic resistance. Alternatively, their dispersal might be sufficiently effective even without biodiversity conservation measures, such that these measures do not substantially increase dispersal further.

Thus, although rarely reported, biodiversity conservation measures, especially those targeting biodiversity-friendly landscapes, not only support native biodiversity by increasing habitat richness and connectivity (*32*, *33*) but also facilitate the dispersal of species that benefit from global change, such as invasive alien species (*63*) and temperature- and nutrient-tolerant species. Furthermore, our results show that biodiversity-friendly landscapes enhance both measures of the increase in global change winners, possibly because their wider dispersal in the landscape also increases their chances of establishing locally.

Effects of climate and preexisting species pools

In addition to the two counteracting processes associated with biodiversity-friendly landscapes affecting the increase in global change winners, climate was also associated with the increase in different global change winners. For example, a higher average temperature was associated with an increase in the additional occurrence of invasive neophytes and with an increase in the cover of thermophytes, possibly due to their physiological adaptation to heat (*64*, *65*).

Furthermore, contrary to our expectation that the size of the preexisting pool of global change winners would be positively associated with their further increase (*66*, *67*), all global change winners increased less in cover when their cover was already higher. This could be because, for example, nutriophytes on sites with high initial cover already had such a high cover that it could hardly increase further (table S2). Similarly, thermophytes and nutriophytes were less likely to occur additionally in previously unoccupied patches of the landscape if they had an increased frequency of occurrence in the landscape, possibly because thermophytes and nutriophytes were already present at most sites in these landscapes (table S2), leaving fewer unoccupied areas available. In contrast, the additional occurrence of invasive neophytes was likely positively associated with the preexisting pool, as invasive neophytes were not widespread in the landscape (table S2).

Together, these findings suggest that both climate and the preexisting pool of global change winners do influence the distribution patterns of global change winners in biodiversity-friendly landscapes. Biotic resistance and facilitated dispersal, however, appear to exert more uniform effects across all groups of global change winners.

Overall inhibitory effects

Biodiversity-friendly landscapes entail a paradox in biodiversity conservation. While they increase biotic resistance to global change winners at the local scale by enhancing local-scale biodiversity, they simultaneously promote the dispersal of the global change winners by creating biodiversity-friendly habitat conditions in the landscape. This dual effect creates a complex dynamic in conservation efforts.

Despite the potential of biodiversity-friendly landscapes to increase global change winners, the inhibitory effects of biodiversity-friendly landscapes appear to outweigh the facilitative effects. This means that the positive effects of increased local-scale biodiversity on the biotic resistance of global change winners are greater than the negative effects of improved habitat connectivity for global change winners.

Given the high share of agriculture in global land use, implementing biodiversity-friendly landscapes in farmlands and the adoption of biodiversity-friendly practices on farmland could be keys to halting global biodiversity loss. Moving from small-scale biodiversity conservation measures to landscape-scale strategies, such as the creation of biodiversity-friendly landscapes, could be a promising way to mitigate the ongoing loss of biodiversity and halt the sixth mass extinction.

MATERIALS AND METHODS

Study area

Reaching from the low plateau to the Alps, Switzerland has a large climatic and thus land-use gradient, which leads to different constraints on biodiversity. The study area was the Swiss farmland (45°81′N to 47°81′N, 5°57′E to 10°49′E; ~15,000 km^2; Fig. 2), which accounts for approximately one-third of the Swiss land area and has recorded considerable species losses in recent decades (*14*). Meadows and pastures (~40%), summer pastures (~30%), and arable land (~30%) made up the largest part of the farmland, while orchards, vineyards, and other uses made up a minor part (*68*). The proof of ecological performance that farmers must provide to receive direct payments requires a minimum dedication of 7% of the land to ecological focus areas (see description below) per farm: The average for the farmland was ~18% (*68*). We investigated 125 landscapes (squares of 1 km^2) (Fig. 2), within which we surveyed farmland only [i.e., excluding buildings, settlements, traffic routes, forests, water bodies, glaciers, and rocks (Fig. 2); minimum = 0.25 km^2, maximum = 1.00 km^2, and means ± SD = 0.71 ± 0.19 km^2 of farmland per landscape].

Data

We investigated the effects of the preexisting species pool, local-scale biodiversity, habitat conditions in the landscape, biodiversity conservation measures, land-use intensity, and climate on the increase in global change winners (Fig. 1). An overview of all the variables is given in table S1. The variables were processed using R version 4.2.2 (*69*).

In terms of measures for the increase in global change winners, we considered two aspects separately: on one hand, the increase in cover, which may be mainly determined by the suitability of the local habitat in terms of resources; and, on the other hand, the additonal occurrence, which may be mainly determined by the suitability of the landscape for movement (*57*). Ultimately, however, the two measures may be interdependent. Metrics on the increase in global change winners were derived from data on vascular plant species from the "Swiss farmland biodiversity monitoring program" (www.allema.ch). In each of the 125 landscapes (squares of 1 km^2), first, vegetation types were surveyed within 10-m^2 circular plots on a 50 m–by–50 m sampling grid within the farmland (Fig. 2), and then ~20 of these vegetation type plots per landscape (Fig. 2) were selected to cover as many different vegetation types as possible (*47*). In those selected plots (further referred to as vegetation survey plots), all vascular plant species and their cover percentages were determined once at or near the peak of flowering in the year of survey. In total, 2050 vegetation survey plots were surveyed for the first time between

2015 and 2018 (in the following "t_0") and were resurveyed 5 years later (in the following "t_1"). From these vegetation surveys, we derived measures for invasive neophytes, thermophytes, and nutriophytes. Invasive neophytes are plant species alien to Switzerland and classified as invasive by experts (*70*). The thermophytes are plant species of the lowlands and considered as indicators of locally warm conditions within Switzerland [T4 (heat indicator) and T5 (strong heat indicator) according to (*71*)]. Last, nutriophytes are plant species that are indicators of nutrient-rich and overfertilized soils in Switzerland [N4 (nutrient indicator) and N5 (strong nutrient indicator) according to (*71*)]. For each group of global change winners, in terms of increase in cover, we estimated the change in their cover (i.e., their cover relative to the total cover of plant species in a vegetation survey plot) by subtracting the t_0 values from t_1. In terms of additional occurrence, we checked whether individuals in a group of global change winners were present at time t_1 on vegetation survey plots where no individuals in a group of global change winners were present at time t_0 (yes = 1 and no = 0); plots where individuals of a group of global change winners were already present at time t_0 were assigned the value 0. The preexisting pool for the increase in global change winners was also derived from vegetation surveys. On one hand, with respect to the preexisting local pool for the increase in cover, we estimated their cover (i.e., their cover relative to the total cover of plant species in a vegetation survey plot) at time t_0. On the other hand, with respect to the preexisting landscape pool for additional occurrence, we estimated their frequency of occurrence in the vegetation survey plots of a landscape at time t_0. In general, invasive neophytes and thermophytes had lower cover at t_0 than did nutriophytes (table S2), while invasive species had a lower frequency of occurrence in the 1-km^2 landscapes at t_0 than did thermophytes and nutriophytes (table S2). Within 5 years, thermophytes showed the greatest increase in cover and in frequency of occurrence in the landscapes (table S2).

Furthermore, for local-scale biodiversity, we used the local plant species richness at time t_0, which was also derived from the vegetation survey plots. Species richness is a commonly used metric in biodiversity studies, but it has limitations, as it does not capture the full complexity of biodiversity. For example, it does not account for species identity, ecological roles, or evolutionary relationships (*72*), which potentially limits its explanatory power. Other metrics, such as phylogenetic, functional, and genomic diversity, provide complementary insights (*73*–*75*). Furthermore, species richness is sensitive to sampling effort and spatial scale, which may affect comparability across studies (*76*). Despite these limitations, we chose species richness due to its key role in ecological processes and widespread application in conservation management and policy (*77*).

In terms of habitat conditions at the landscape scale, we included two metrics. First, as a measure of habitat richness, we used land-cover richness. Land-cover richness was defined at t_0 as the number of different vegetation types in the vegetation-type surveys of a landscape. Second, as a measure of habitat connectivity, we used land-cover interspersion. Land-cover interspersion quantifies the degree to which different vegetation types are mixed within a landscape. Higher index values indicate more heterogeneous landscapes with interspersed habitats, while lower values indicate more homogenous landscapes. More heterogeneous landscapes with interspersed habitats provide more different habitat types in a smaller area, facilitating seed dispersal by wind, water, or animals. In contrast, more homogeneous landscapes with large, continuous patches of habitat may limit dispersal by confining species to specific environmental conditions and creating higher structural barriers to dispersal. We defined the interspersion index at t_0 based on the vegetation types from the vegetation-type surveys of a landscape [function "lsm_l_iji" from the R package "landscapemetrics" version 1.5.7 (*78*)].

Biodiversity conservation measures in agricultural landscapes consist of only a small extent of natural protection areas; rather, they are subject to agri-environmental schemes with specific conservation measures for farmland, such as ecological focus areas. These areas are the primary biodiversity conservation element on Swiss farmland. Depending on the ecological focus area type, they can be either unproductive set-aside areas or fields that yield less biomass due to later cutting dates and lower nutrient inputs. These management restrictions lead to higher biodiversity within these areas compared to conventionally managed areas (*53*–*56*) and thereby support biodiversity at local and landscape scales (*34*, *36*). Here, we assessed local management by the biodiversity conservation measures, i.e., the local presence of an ecological focus area at t_0, and the share of biodiversity conservation measures in the landscape, i.e., the area with ecological focus areas in each landscape at t_0 divided by the total farmland area in each landscape at t_0. We derived data on ecological focus areas and the size of the farmland from polygon data of the authorities.

Land-use intensity was described by the local land-use intensity index at t_0 and by the mean local land-use intensity index per landscape at t_0. The vegetation types from the vegetation-type survey were classified into a land-use intensity index, from which both metrics were derived. We parametrized the index by rating vegetation types according to fertilizer and pesticide use, ploughing, grazing, mowing, and harvesting. The resulting ratings were then standardized and summed to generate a single land-use intensity value, ranging from 0 (no land use) to 1 (maximum intensity). For details, see (*79*).

Last, we obtained climate data for each landscape by calculating the means of the average temperature and yearly precipitation sum fitting t_0 (i.e., 2010–2019) with a grid size of 100 m by 100 m, derived from interpolated daily values from MeteoSwiss weather stations using Daymet software (*80*).

Statistical analyses

To quantify the direct, indirect, and overall effects of the different factors on the increase in global change winners, we first developed a hypothetical SEM (*46*). We expected climate to influence all the other factors without a specific direction. We also expected that biodiversity conservation measures and low land-use intensity would increase local-scale biodiversity, thereby increasing biotic resistance to global change winners and thus reducing their increase. We further expected biodiversity conservation measures and low land-use intensity to improve habitat conditions in the landscape (i.e., increase habitat richness and connectivity), thereby facilitating the dispersal of global change winners and thus enhancing their increase. Last, we expected that the preexisting pool of global change winners would increase their increase. Our expectations are shown in Fig. 1, and an overview of all variables per factor can be found in table S1.

Second, we formulated a statistical model for each endogenous variable [i.e., variable explained by other variables in the SEM (*46*)] according to its distribution and spatial scale. If the endogenous variable was normally distributed and based on plot measures, then we used a linear mixed model [function "lmer" with the landscape as a random factor; R package "lme4" version 1.1-31 (*81*)], i.e., for explaining local land-use intensity, local plant species richness, and increase in cover of global change winners. Furthermore, if the endogenous variable was binomially distributed and was based on plot measures, then we used a generalized linear mixed model [function "glmer" with binomial distribution and the landscape as a random factor; R package lme4 version 1.1-31 (*81*)], i.e., for explaining the additional occurrence of global change winners. Last, when the endogenous variable was normally distributed and based on landscape measures, we used a linear model, i.e., for land-use intensity in the landscape, habitat richness, and habitat connectivity. The variation inflation factors of the predictors in the models were all less than 5, indicating low multicollinearity.

Last, we combined the models for the endogenous variables in two empirical SEMs (i.e., one for the increase in cover of global change winners and one for their additional occurrence), optimized the SEMs, and estimated the direct, indirect, and overall effects of all variables remaining in the final SEMs. Therefore, we first converted all covariates into comparable scales by Z-transforming all variables. Then, to fit the SEMs, we used the R package "piecewiseSEM" version 2.3.0 (*82*). To optimize the SEMs, we investigated whether any important paths between variables were missing or whether any paths could be omitted. Missing paths were identified by high modification indices and large residual correlations between pairs of variables and were subsequently incorporated into the model. Paths that did not explain patterns were identified by omitting them from the model and assessing whether the model fit was decreased compared to the model with the variable included. As the model fit improves with increasing model size but decreases with increasing sample size, as a measure of model fit**,** we used the ratio of the chi-square statistic to the respective degrees of freedom (χ^2/df) (*83*). In addition to the comparative aspect, $\chi^2/\mathrm{df} \leq 5$ indicates a very good fit between the hypothesized model and the sample data (*84*). Last, on the basis of the final SEMs, we estimated the direct, indirect, and overall effects of variables by multiplying the standardized coefficients of the involved paths and summing all resulting products (*46*) using the R package "semEff" version 0.6.1 (*82*). All analyses were performed with R version 4.2.2 (*69*).

Supplementary Materials

The PDF file includes:
Fig. S1
Tables S1 to S6
Legend for data S1

Other Supplementary Material for this manuscript includes the following:
Data S1

REFERENCES AND NOTES

1. D. Leclère, M. Obersteiner, M. Barrett, S. H. M. Butchart, A. Chaudhary, A. De Palma, F. A. J. DeClerck, M. Di Marco, J. C. Doelman, M. Dürauer, R. Freeman, M. Harfoot, T. Hasegawa, S. Hellweg, J. P. Hilbers, S. L. L. Hill, F. Humpenöder, N. Jennings, T. Krisztin, G. M. Mace, H. Ohashi, A. Popp, A. Purvis, A. M. Schipper, A. Tabeau, H. Valin, H. van Meijl, W.-J. van Zeist, P. Visconti, R. Alkemade, R. Almond, G. Bunting, N. D. Burgess, S. E. Cornell, F. Di Fulvio, S. Ferrier, S. Fritz, S. Fujimori, M. Grooten, T. Harwood, P. Havlík, M. Herrero, A. J. Hoskins, M. Jung, T. Kram, H. Lotze-Campen, T. Matsui, C. Meyer, D. Nel, T. Newbold, G. Schmidt-Traub, E. Stehfest, B. B. N. Strassburg, D. P. van Vuuren, C. Ware, J. E. M. Watson, W. Wu, L. Young, Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature* **585**, 551–556 (2020).
2. A. D. Barnosky, N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, J. L. McGuire, E. L. Lindsey, K. C. Maguire, B. Mersey, E. A. Ferrer, Has the Earth's sixth mass extinction already arrived? *Nature* **471**, 51–57 (2011).
3. C. Bellard, C. Marino, F. Courchamp, Ranking threats to biodiversity and why it doesn't matter. *Nat. Commun.* **13**, 2616 (2022).
4. IPBES, *Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services* (IPBES, 2019).
5. M. Dornelas, N. J. Gotelli, H. Shimadzu, F. Moyes, A. E. Magurran, B. J. McGill, A balance of winners and losers in the Anthropocene. *Ecol. Lett.* **22**, 847–854 (2019).
6. T. Finderup Nielsen, K. Sand-Jensen, M. Dornelas, H. H. Bruun, More is less: Net gain in species richness, but biotic homogenization over 140 years. *Ecol. Lett.* **22**, 1650–1657 (2019).
7. J. M. Alexander, J. M. Diez, J. M. Levine, Novel competitors shape species' responses to climate change. *Nature* **525**, 515–518 (2015).
8. M. M. Gossner, T. M. Lewinsohn, T. Kahl, F. Grassein, S. Boch, D. Prati, K. Birkhofer, S. C. Renner, J. Sikorski, T. Wubet, H. Arndt, V. Baumgartner, S. Blaser, N. Blüthgen, C. Börschig, F. Buscot, T. Diekötter, L. R. Jorge, K. Jung, A. C. Keyel, A. M. Klein, S. Klemmer, J. Krauss, M. Lange, J. Müller, J. Overmann, E. Pašali, C. Penone, D. J. Perovic, O. Purschke, P. Schall, S. A. Socher, I. Sonnemann, M. Tschapka, T. Tscharntke, M. Türke, P. C. Venter, C. N. Weiner, M. Werner, V. Wolters, S. Wurst, C. Westphal, M. Fischer, W. W. Weisser, E. Allan, Land-use intensification causes multitrophic homogenization of grassland communities. *Nature* **540**, 266–269 (2016).
9. J. M. M. Lewthwaite, A. Ø. Mooers, Geographical homogenization but little net change in the local richness of Canadian butterflies. *Glob. Ecol. Biogeogr.* **31**, 266–279 (2022).
10. J. M. Pandolfi, T. L. Staples, W. Kiessling, Increased extinction in the emergence of novel ecological communities. *Science* **370**, 220–222 (2020).
11. J. Lenoir, J. C. Svenning, Climate-related range shifts - A global multidimensional synthesis and new research directions. *Ecography* **38**, 15–28 (2015).
12. J. C. Habel, W. Ulrich, P. Gros, M. Teucher, T. Schmitt, Butterfly species respond differently to climate warming and land use change in the northern Alps. *Sci. Total Environ.* **890**, 164268 (2023).
13. J. M. Alexander, L. Chalmandrier, J. Lenoir, T. I. Burgess, F. Essl, S. Haider, C. Kueffer, K. McDougall, A. Milbau, M. A. Nuñez, A. Pauchard, W. Rabitsch, L. J. Rew, N. J. Sanders, L. Pellissier, Lags in the response of mountain plant communities to climate change. *Glob. Chang. Biol.* **24**, 563–579 (2018).
14. C. Bühler, T. Roth, Spread of common species results in local-scale floristic homogenization in grassland of Switzerland. *Divers Distrib.* **17**, 1089–1098 (2011).
15. E. Iseli, C. Chisholm, J. Lenoir, S. Haider, T. Seipel, A. Barros, A. L. Hargreaves, P. Kardol, J. J. Lembrechts, K. McDougall, I. Rashid, S. B. Rumpf, J. R. Arévalo, L. Cavieres, C. Daehler, P. A. Dar, B. Endress, G. Jakobs, A. Jiménez, C. Küffer, M. Mihoc, A. Milbau, J. W. Morgan, B. J. Naylor, A. Pauchard, A. Ratier Backes, Z. A. Reshi, L. J. Rew, D. Righetti, J. M. Shannon, G. Valencia, N. Walsh, G. T. Wright, J. M. Alexander, Rapid upwards spread of non-native plants in mountains across continents. *Nat. Ecol. Evol.* **7**, 405–413 (2023).
16. B. E. Lopez, J. M. Allen, J. S. Dukes, J. Lenoir, M. Vilà, D. M. Blumenthal, E. M. Beaury, E. J. Fusco, B. B. Laginhas, T. L. Morelli, M. W. O'Neill, C. J. B. Sorte, A. Maceda-Veiga, R. Whitlock, B. A. Bradley, Global environmental changes more frequently offset than intensify detrimental effects of biological invasions. *Proc. Natl. Acad. Sci.* **119**, e2117389119 (2022).
17. F. Neff, F. Korner-Nievergelt, E. Rey, M. Albrecht, K. Bollmann, F. Cahenzli, Y. Chittaro, M. M. Gossner, C. Martínez-Núñez, E. S. Meier, C. Monnerat, M. Moretti, T. Roth, F. Herzog, E. Knop, Different roles of concurring climate and regional land-use changes in past 40 years' insect trends. *Nat. Commun.* **13**, 7611 (2022).
18. M. Díaz, Dealing with global threats to biodiversity: A pressing but realistic challenge. *Front. Conserv. Sci.* **4**, 1147470 (2023).
19. S. Taheri, B. Naimi, C. Rahbek, M. B. Araújo, Improvements in reports of species redistribution under climate change are required. *Sci. Adv.* **7**, eabe1110 (2021).
20. L. Comte, J. D. Olden, P. A. Tedesco, A. Ruhi, X. Giam, Climate and land-use changes interact to drive long-term reorganization of riverine fish communities globally. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2011639118 (2021).
21. K. J. Komatsu, M. L. Avolio, N. P. Lemoine, F. Isbell, E. Grman, G. R. Houseman, S. E. Koerner, D. S. Johnson, K. R. Wilcox, J. M. Alatalo, J. P. Anderson, R. Aerts, S. G. Baer, A. H. Baldwin, J. Bates, C. Beierkuhnlein, R. T. Belote, J. Blair, J. M. G. Bloor, P. J. Bohlen, E. W. Bork, E. H. Boughton, W. D. Bowman, A. J. Britton, J. F. Cahill, E. Chaneton, N. R. Chiariello, J. Cheng, S. L. Collins, J. H. C. Cornelissen, G. Du, A. Eskelinen, J. Firn, B. Foster, L. Gough, K. Gross, L. M. Hallett, X. Han, H. Harmens, M. J. Hovenden, A. Jagerbrand, A. Jentsch, C. Kern, K. Klanderud, A. K. Knapp, J. Kreyling, W. Li, Y. Luo, R. L. McCulley, J. R. McLaren, J. P. Megonigal, J. W. Morgan, V. Onipchenko, S. C. Pennings, J. S. Prevéy, J. N. Price, P. B. Reich, C. H. Robinson, F. L. Russell, O. E. Sala, E. W. Seabloom, M. D. Smith, N. A. Soudzilovskaia, L. Souza, K. Suding, K. B. Suttle, T. Svejcar, D. Tilman, P. Tognetti, R. Turkington, S. White, Z. Xu, L. Yahdjian, Q. Yu, P. Zhang, Y. Zhang, Global change effects on plant communities are magnified by time and the number of global change factors imposed. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 17867–17873 (2019).
22. D. Lindenmayer, Small patches make critical contributions to biodiversity conservation. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 717–719 (2019).
23. M. G. Anderson, M. Clark, A. P. Olivero, A. R. Barnett, K. R. Hall, M. W. Cornett, M. Ahlering, M. Schindel, B. Unnasch, C. Schloss, D. R. Cameron, A resilient and connected network of

sites to sustain biodiversity under a changing climate. *Proc. Natl. Acad. Sci.* **120**, e2204434119 (2023).
24. J. M. Chase, A. Jeliazkov, E. Ladouceur, D. S. Viana, Biodiversity conservation through the lens of metacommunity ecology. *Ann. N. Y. Acad. Sci.* **1469**, 86–104 (2020).
25. J. B. Heffernan, P. A. Soranno, M. J. Angilletta, L. B. Buckley, D. S. Gruner, T. H. Keitt, J. R. Kellner, J. S. Kominoski, A. V. Rocha, J. Xiao, T. K. Harms, S. J. Goring, L. E. Koenig, W. H. McDowell, H. Powell, A. D. Richardson, C. A. Stow, R. Vargas, K. C. Weathers, Macrosystems ecology: Understanding ecological patterns and processes at continental scales. *Front. Ecol. Environ.* **12**, 5–14 (2014).
26. Y. Chauvier-Mendes, L. J. Pollock, P. H. Verburg, D. N. Karger, L. Pellissier, S. Lavergne, N. E. Zimmermann, W. Thuiller, Transnational conservation to anticipate future plant shifts in Europe. *Nat. Ecol. Evol.* **8**, 454–466 (2024).
27. J. L. McGuire, A. M. Lawing, S. Díaz, N. C. Stenseth, The past as a lens for biodiversity conservation on a dynamically changing planet. *Proc. Natl. Acad. Sci. U.S.A.* **120**, e2201950120 (2023).
28. T. Tscharntke, I. Grass, T. C. Wanger, C. Westphal, P. Batáry, Beyond organic farming – Harnessing biodiversity-friendly landscapes. *Trends Ecol. Evol.* **36**, 919–930 (2021).
29. V. Arroyo-Rodríguez, L. Fahrig, M. Tabarelli, J. I. Watling, L. Tischendorf, M. Benchimol, E. Cazetta, D. Faria, I. R. Leal, F. P. L. Melo, J. C. Morante-Filho, B. A. Santos, R. Arasa-Gisbert, N. Arce-Peña, M. J. Cervantes-López, S. Cudney-Valenzuela, C. Galán-Acedo, M. San-José, I. C. G. Vieira, J. W. F. Slik, A. J. Nowakowski, T. Tscharntke, Designing optimal human-modified landscapes for forest biodiversity conservation. *Ecol. Lett.* **23**, 1404–1420 (2020).
30. N. Estrada-Carmona, A. C. Sánchez, R. Remans, S. K. Jones, Complex agricultural landscapes host more biodiversity than simple ones: A global meta-analysis. *Proc. Natl. Acad. Sci. U.S.A.* **119**, e2203385119 (2022).
31. G. L. W. Perry, K. A. Moloney, T. R. Etherington, Using network connectivity to prioritise sites for the control of invasive species. *J. Appl. Ecol.* **54**, 1238–1250 (2017).
32. L. Fahrig, Ecological responses to habitat fragmentation per se. *Annu. Rev. Ecol. Evol. Syst.* **48**, 1–23 (2017).
33. L. Fahrig, J. I. Watling, C. A. Arnillas, V. Arroyo-Rodríguez, T. Jörger-Hickfang, J. Müller, H. M. Pereira, F. Riva, V. Rösch, S. Seibold, T. Tscharntke, F. May, Resolving the SLOSS dilemma for biodiversity conservation: A research agenda. *Biol. Rev.* **97**, 99–114 (2022).
34. E. S. Meier, G. Lüscher, E. Knop, Disentangling direct and indirect drivers of farmland biodiversity at landscape scale. *Ecol. Lett.* **25**, 2422–2434 (2022).
35. E. F. Connor, E. D. McCoy, The statistics and biology of the species-area relationship. *Am. Nat.* **113**, 791–833 (1979).
36. E. S. Meier, G. Lüscher, F. Herzog, E. Knop, Collaborative approaches at the landscape scale increase the benefits of agri-environmental measures for farmland biodiversity. *Agric. Ecosyst. Environ.* **367**, 108948 (2024).
37. C. Kremen, A. M. Merenlender, Landscapes that work for biodiversity and people. *Science* **362**, eaau6020 (2018).
38. C. S. Elton, *The Ecology of Invasions by Animals and Plants* (Springer US, 1958).
39. N. M. Levine, K. Zhang, M. Longo, A. Baccini, O. L. Phillips, S. L. Lewis, E. Alvarez-Dávila, A. C. Segalin de Andrade, R. J. W. Brienen, T. L. Erwin, T. R. Feldpausch, A. L. Monteagudo Mendoza, P. Nuñez Vargas, A. Prieto, J. E. Silva-Espejo, Y. Malhi, P. R. Moorcroft, Ecosystem heterogeneity determines the ecological resilience of the Amazon to climate change. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 793–797 (2016).
40. J. M. Levine, P. B. Adler, S. G. Yelenik, A meta-analysis of biotic resistance to exotic plant invasions. *Ecol. Lett.* **7**, 975–989 (2004).
41. J. D. van Elsas, M. Chiurazzi, C. A. Mallon, D. Elhottovā, V. Krištůfek, J. F. Salles, Microbial diversity determines the invasion of soil by a bacterial pathogen. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 1159–1164 (2012).
42. J. D. Fridley, J. J. Stachowicz, S. Naeem, D. Sax, E. Seabloom, M. Smith, T. Stohlgren, D. Tilman, B. Von Holle, The invasion paradox: Reconciling pattern and process in species invasions. *Ecology* **88**, 3–17 (2007).
43. K. Guo, P. Pyšek, M. Chytrý, J. Divíšek, M. Sychrová, Z. Lososová, M. van Kleunen, S. Pierce, W.-Y. Guo, Stage dependence of Elton's biotic resistance hypothesis of biological invasions. *Nat. Plants* **10**, 1484–1492 (2024).
44. S. Naeem, J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy, S. Gale, Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* **91**, 97–108 (2000).
45. D. A. Wardle, Experimental demonstration that plant diversity reduces invasibility: Evidence of a biological mechanism or a consequence of sampling effect? *Oikos* **95**, 161–170 (2001).
46. J. B. Grace, *Structural Equation Modeling and Natural Systems* (Cambridge Univ. Press, 2009); https://doi.org/10.1017/CBO9780511617799.
47. K. T. Ecker, E. S. Meier, Y. Tillé, Integrating spatial and ecological information into comprehensive biodiversity monitoring on agricultural land. *Environ. Monit. Assess.* **195**, 1161 (2023).
48. L. Fahrig, Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **34**, 487–515 (2003).
49. N. M. Haddad, L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, W. M. Cook, E. I. Damschen, R. M. Ewers, B. L. Foster, C. N. Jenkins, A. J. King, W. F. Laurance, D. J. Levey, C. R. Margules, B. A. Melbourne, A. O. Nicholls, J. L. Orrock, D.-X. Song, J. R. Townshend, Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* **1**, e1500052 (2015).
50. T. Tscharntke, A. M. Klein, A. Kruess, I. Steffan-Dewenter, C. Thies, Landscape perspectives on agricultural intensification and biodiversity–Ecosystem service management. *Ecol. Lett.* **8**, 857–874 (2005).
51. L. Lecoq, C. Mony, H. Saiz, M. Marsot, A. Ernoult, Investigating the effect of habitat amount and landscape heterogeneity on the gamma functional diversity of grassland and hedgerow plants. *J. Ecol.* **110**, 1871–1882 (2022).
52. FAO, *World Food and Agriculture – Statistical Yearbook 2023* (FAO, 2023); www.fao.org/documents/card/en/c/cc8166en.
53. P. Batáry, L. V. Dicks, D. Kleijn, W. J. Sutherland, The role of agri-environment schemes in conservation and environmental management. *Conserv. Biol.* **29**, 1006–1016 (2015).
54. F. A. Boetzl, J. Krauss, J. Heinze, H. Hoffmann, J. Juffa, S. König, E. Krimmer, M. Prante, E. A. Martin, A. Holzschuh, I. Steffan-Dewenter, A multitaxa assessment of the effectiveness of agri-environmental schemes for biodiversity management. *Proc. Natl. Acad. Sci. U.S.A.* **118**, 1–9 (2021).
55. D. Kleijn, R. A. Baquero, Y. Clough, M. Díaz, J. Esteban, F. Fernández, D. Gabriel, F. Herzog, A. Holzschuh, R. Jöhl, E. Knop, A. Kruess, E. J. P. Marshall, I. Steffan-Dewenter, T. Tscharntke, J. Verhulst, T. M. West, J. L. Yela, Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecol. Lett.* **9**, 243–254 (2006).
56. E. Knop, D. Kleijn, F. Herzog, B. Schmid, Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. *J. Appl. Ecol.* **43**, 120–127 (2006).
57. S. Unnithan Kumar, J. Turnbull, O. Hartman Davies, T. Hodgetts, S. A. Cushman, Moving beyond landscape resistance: Considerations for the future of connectivity modelling and conservation science. *Landsc. Ecol.* **37**, 2465–2480 (2022).
58. T. Montràs-Janer, A. J. Suggitt, R. Fox, M. Jönsson, B. Martay, D. B. Roy, K. J. Walker, A. G. Auffret, Anthropogenic climate and land-use change drive short- and long-term biodiversity shifts across taxa. *Nat. Ecol. Evol.* **8**, 739–751 (2024).
59. A. Petruzzella, T. A. da S. S. R. Rodrigues, C. H. A. van Leeuwen, F. de Assis Esteves, M. P. Figueiredo-Barros, E. S. Bakker, Species identity and diversity effects on invasion resistance of tropical freshwater plant communities. *Sci. Rep.* **10**, 5626 (2020).
60. E. M. Beaury, J. T. Finn, J. D. Corbin, V. Barr, B. A. Bradley, Biotic resistance to invasion is ubiquitous across ecosystems of the United States. *Ecol. Lett.* **23**, 476–482 (2020).
61. C. Cheng, Z. Liu, W. Song, X. Chen, Z. Zhang, B. Li, M. van Kleunen, J. Wu, Biodiversity increases resistance of grasslands against plant invasions under multiple environmental changes. *Nat. Commun.* **15**, 4506 (2024).
62. D. Simberloff, The role of propagule pressure in biological invasions. *Annu. Rev. Ecol. Evol. Syst.* **40**, 81–102 (2009).
63. A. Lázaro-Lobo, K. O. Evans, G. N. Ervin, Evaluating landscape characteristics of predicted hotspots for plant invasions. *Invasive Plant Sci. Manag.* **13**, 163–175 (2020).
64. D. Scherrer, M. Bürgi, A. Gessler, M. Kessler, M. P. Nobis, T. Wohlgemuth, Abundance changes of neophytes and native species indicate a thermophilisation and eutrophisation of the Swiss flora during the 20th century. *Ecol. Indic.* **135**, 108558 (2022).
65. Y. Liu, A. M. O. Oduor, Z. Zhang, A. Manea, I. M. Tooth, M. R. Leishman, X. Xu, M. van Kleunen, Do invasive alien plants benefit more from global environmental change than native plants? *Glob. Chang. Biol.* **23**, 3363–3370 (2017).
66. D. W. Carstensen, J.-P. Lessard, B. G. Holt, M. Krabbe Borregaard, C. Rahbek, Introducing the biogeographic species pool. *Ecography* **36**, 1310–1318 (2013).
67. R. E. Ricklefs, Community diversity: Relative roles of local and regional processes. *Science* **235**, 167–171 (1987).
68. Federal Office for Agriculture, Agrarbericht (2022); www.agrarbericht.ch.
69. R Core Team, "R: A language and environment for statistical computing" (R Foundation for Statistical Computing, 2024); www.r-project.org.
70. BAFU, "Gebietsfremde Arten in der Schweiz. Übersicht über die gebietsfremden Arten und ihre Auswirkungen. 1. aktualisierte Auflage 2022. Erstausgabe 2006." (Bern, 2022).
71. E. Landolt, B. Bäumler, A. Erhardt, O. Hegg, F. Klötzli, W. Lämmler, M. Nobis, K. Rudmann-Maurer, F. H. Schweingruber, J. P. Theurillat, Flora indicativa - Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen. *Haupt. Bern* **7**, 378 (2010).
72. N. Mouquet, V. Devictor, C. N. Meynard, F. Munoz, L. Bersier, J. Chave, P. Couteron, A. Dalecky, C. Fontaine, D. Gravel, O. J. Hardy, F. Jabot, S. Lavergne, M. Leibold, D. Mouillot, T. Münkemüller, S. Pavoine, A. Prinzing, A. S. L. Rodrigues, R. P. Rohr, E. Thébault, W. Thuiller, Ecophylogenetics: Advances and perspectives. *Biol. Rev.* **87**, 769–785 (2012).
73. D. P. Faith, Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* **61**, 1–10 (1992).
74. O. L. Petchey, K. J. Gaston, Functional diversity (FD), species richness and community composition. *Ecol. Lett.* **5**, 402–411 (2002).
75. G. M. Mace, J. L. Gittleman, A. Purvis, Preserving the tree of life. *Science* **300**, 1707–1709 (2003).

76. N. J. Gotelli, R. K. Colwell, Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* **4**, 379–391 (2001).
77. C. R. Margules, R. L. Pressey, Systematic conservation planning. *Nature* **405**, 243–253 (2000).
78. M. H. K. Hesselbarth, M. Sciaini, K. A. With, K. Wiegand, J. Nowosad, landscapemetrics: An open-source R tool to calculate landscape metrics. *Ecography* **42**, 1648–1657 (2019).
79. E. S. Meier, A. Indermaur, C. Ginzler, A. Psomas, An effective way to map land-use intensity with a high spatial resolution based on habitat type and environmental data. *Remote Sens. (Basel)* **12**, 1–22 (2020).
80. P. E. Thornton, S. W. Running, M. A. White, Generating surfaces of daily meteorological variables over large regions of complex terrain. *J. Hydrol. (Amst)* **190**, 214–251 (1997).
81. D. Bates, M. Mächler, B. Bolker, S. Walker, Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
82. J. S. Lefcheck, piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* **7**, 573–579 (2016).
83. B. Wheaton, B. Muthen, D. F. Alwin, G. F. Summers, Assessing reliability and stability in panel models. *Sociol. Methodol.* **8**, 84 (1977).
84. D. A. Cole, Utility of confirmatory factor analysis in test validation research. *J. Consult. Clin. Psychol.* **55**, 584–594 (1987).

Acknowledgments: We thank G. Lüscher for providing feedback on the analyses. **Funding:** This research was conducted as part of the Swiss farmland biodiversity monitoring program ALL-EMA (www.allema.ch), funded by the Swiss Federal Office for the Environment (FOEN) and the Swiss Federal Office for Agriculture (FOAG). **Author contributions:** Conceptualization: E.S.M. and E.K. Methodology: E.S.M., E.K., and A.I. Software: E.S.M. Validation: E.S.M., E.K., and A.I. Formal analysis: E.S.M. and E.K. Investigation: A.I., E.S.M., and E.K. Resources: E.S.M. and A.I. Data curation: E.S.M. and A.I. Writing—original draft: E.S.M. and E.K. Writing—review and editing: E.S.M., E.K., and A.I. Visualization: E.S.M. and E.K. Supervision: E.S.M. and E.K. Project administration: E.K. and E.S.M. Funding acquisition: E.K. and E.S.M. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All processed data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. The raw data, including exact locations, are restricted to protect endangered species and are available upon request from the Swiss farmland biodiversity monitoring program ALL-EMA (www.allema.ch) by contacting G. Lüscher at gisela.luescher@agroscope.admin.ch.

Submitted 17 October 2024
Accepted 25 June 2025
Published 23 July 2025
10.1126/sciadv.adt9564