The supply of multiple ecosystem services requires biodiversity across spatial scales

Gaëtane Le Provost, Noëlle Schenk, Caterina Penone, Jan Thiele, Catrin Westphal, Eric Allan, Manfred Ayasse, Nico Blüthgen, Runa Boeddinghaus, Andrea Larissa Boesing, et al.

Postprint of published version to be found at the journal's website (Nature Ecology and Evolution): https://doi.org/10.1038/s41559-022-01918-5 (Non-commercial use only

Title: The supply of multiple ecosystem services requires biodiversity across spatial scales

Author list

Gaëtane Le Provost[1,2,*], Noëlle V. Schenk[3], Caterina Penone[3], Jan Thiele[4], Catrin Westphal[5], Eric Allan[3], Manfred Ayasse[6], Nico Blüthgen[7], Runa S. Boeddinghaus[8,9], Andrea Larissa Boesing[1], Ralph Bolliger[3], Verena Busch[10], Markus Fischer[1,3], Martin M. Gossner[11,12], Norbert Hölzel[13], Kirsten Jung[6], Ellen Kandeler[14], Valentin H. Klaus[15], Till Kleinebecker[10], Sophia Leimer[16], Sven Marhan[8], Kathryn Morris[17], Sandra Müller[18], Felix Neff[11,19], Margot Neyret[1], Yvonne Oelmann[20], David J. Perović[21], Sophie Peter[1,22], Daniel Prati[3], Matthias C. Rillig[23,24], Hugo Saiz[3,25], Deborah Schäfer[26], Michael Scherer-Lorenzen[18], Michael Schloter[27,28], Ingo Schöning[29], Marion Schrumpf[29], Juliane Steckel[30], Ingolf Steffan-Dewenter[30], Marco Tschapka[6], Juliane Vogt[31], Christiane Weiner[7], Wolfgang Weisser[32], Konstans Wells[33], Michael Werner[30], Wolfgang Wilcke[34], Peter Manning[1,35]

Affiliations

[1]Senckenberg Biodiversity and Climate Research Centre (SBIK-F), Senckenberg Gesellschaft für Naturforschung, Senckenberganlage 25, 60325 Frankfurt, Germany.

[2]INRAE, Bordeaux Sciences Agro, ISVV, SAVE, F-33140, Villenave d'Ornon, France.

[3]Institute of Plant Sciences, University of Bern, Altenbergrain 21, 3013 Bern, Switzerland.

[4]Thünen Institute of Biodiversity, Bundesallee 65, 38116 Braunschweig, Germany.

[5]Functional Agrobiodiversity, Department of Crop Sciences, University of Göttingen, Göttingen, Germany.

[6]Institute of Evolutionary Ecology and Conservations Genomics, University of Ulm, Albert-Einstein-Allee 11, 89081 Ulm, Germany.

[7]Ecological Networks, Biology, Technische Universität Darmstadt, Schnittspahnstr. 3, 64287 Darmstadt, Germany.

[8]Institute of Soil Science and Land Evalution, Department of Soil Biology, University of Hohenheim, Emil-Wolff-Str. 27, 70599 Stuttgart, Germany.

[9]Center for Agricultural Technology Augustenberg (LTZ), Section Agroecology, Neßlerstr. 25, 76227 Karlsruhe, Germany.

[10]Department of Landscape Ecology and Resources Management, Justus Liebig University Giessen, Heinrich-Buff-Ring 26-32, 35392 Gießen, Germany.

[11]Forest Entomology, WSL Swiss Federal Research Institute, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland.

[12]Department of Environmental Systems Science, Institute of Terrestrial Ecosystems, ETH Zürich, Universitätstr. 16, 8092 Zürich, Switzerland

[13]Institute of Landscape Ecology, University of Münster, Heisenbergstr. 2, 48149 Münster, Germany.

[14]Institute of Soil Science and Land Evaluation, University of Hohenheim, Stuttgart, Germany.

[15]Institute of Agricultural Sciences, ETH Zürich, Universitätstr. 2, 8092 Zürich, Switzerland.

[16]Research Data Services, University Library, University of Duisburg-Essen, Lotharstr. 65, 47057 Duisburg, Germany.

[17]Department of Biology, Xavier University, 3800 Victory Parkway, Cincinnati, OH, 45207, USA.

[18]University of Freiburg, Faculty of Biology, Geobotany, Schaenzlestr. 1, D-79104 Freiburg, Germany.

[19]Agroecology and Environment, Agroscope, Reckenholzstrasse 191, CH-8046 Zurich, Switzerland.

[20]Geoecology, University of Tübingen, Rümelinstr. 19-23, 72070 Tübingen, Germany.

[21]School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia.

[22]ISOE – Institute for Social-Ecological Research, Biodiversity and People, Frankfurt am Main, Germany

[23]Institut für Biologie, Plant Ecology, Freie Universität Berlin, Berlin, D-14195 Germany.

[24]Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, D-14195 Germany.

[25]Departamento de Ciencias Agrarias y Medio Natural, Escuela Politécnica Superior, Instituto Universitario de Investigación en Ciencias Ambientales de Aragón (IUCA), Universidad de Zaragoza, 22071 Huesca, Spain.

[26]Botanical Garden of the University of Bern, Altenbergrain 21, 3013 Bern, Switzerland.

[27]Helmholtz Munich, Research Unit for Comparative Microbiome Analysis, Ingolstaedter Landstr. 1, 85758 Oberschleissheim, Germany.

[28]Chair for Soil Science, Technical University of Munich, Emil-Ramann-Straße 2, 85354 Freising, Germany.
[29]Max-Planck Institute for Biogeochemistry, Hans-Knoell-Str. 10, 07745 Jena, Germany.
[30]Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Am Hubland, D-97074 Würzburg, Germany.
[31]Natura 2000-Station „Unstrut-Hainich/Eichsfeld“, Wildtierland Hainich gGmbH, Schlossstr. 4, 99820 Hörselberg-Hainich, Germany.
[32]Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, Technical University of Munich, Freising, Germany.
[33]Department of Biosciences, Swansea University, Swansea SA28PP, United Kingdom.
[34]Institute of Geography and Geoecology, Karlsruhe Institute of Technology (KIT), Reinhard-Baumeister-Platz 1, 76131 Karlsruhe, Germany.
[35]Department of Biological Sciences, University of Bergen, Bergen, Norway.
***corresponding author**: gaetane.le-provost@inrae.fr

Abstract

The impact of local biodiversity loss on ecosystem functioning is well-established but the role of larger-scale biodiversity dynamics in the delivery of ecosystem services remains poorly understood. We address this gap using a comprehensive dataset describing the supply of 16 cultural, regulating and provisioning ecosystem services in 150 European agricultural grassland plots, and detailed multi-scale data on land use and plant diversity. After controlling for land-use and abiotic factors, we show that both plot-level and surrounding plant diversity play an important

role in the supply of cultural and aboveground regulating ecosystem services. In contrast, provisioning and belowground regulating ecosystem services are more strongly driven by field-level management and abiotic factors. Structural equation models revealed that surrounding plant diversity promotes ecosystem services both directly, likely by fostering the spill-over of ecosystem service providers from surrounding areas, and indirectly, by maintaining plot-level diversity. By influencing the ecosystem services that local stakeholders prioritized, biodiversity at different scales was also shown to positively influence a wide range of stakeholder groups. These results provide a comprehensive picture of which ecosystem services rely most strongly on biodiversity, and the respective scales of biodiversity that drives these services. This key information is required for the upscaling of biodiversity-ecosystem service relationships, and the informed management of biodiversity within agricultural landscapes.

Main text

Introduction

Global threats to biodiversity have motivated much research into the relationship between biodiversity and ecosystem functioning[1–3]. This work has provided substantial evidence that plot-level (typically <1000m²) biodiversity drives multiple ecosystem functions and services, in both experimental communities[2,4] and in natural ecosystems[5–12]. However, most of these studies have focused on the effects of biodiversity on ecosystem processes at these relatively small spatial scales, rather than on the impact of larger-scale biodiversity on ecosystem services[13–15]. This gap is significant as biodiversity change occurs at all spatial scales, and sometimes in contrasting directions, e.g. local enrichment but homogenization and loss at larger spatial scales[16,17]. The lack of a mechanistic understanding of how biodiversity at larger spatial scales affects the delivery of multiple ecosystem services also precludes the upscaling of biodiversity-ecosystem service relationships to the large spatial scales relevant to policy and management[14,15].

Considering the multiscale nature of biodiversity is essential to understand how biodiversity underpins ecosystem services[14,15]. At the plot level, higher plant species richness (i.e. α-diversity) enhances ecosystem functioning due to complementarity between co-occurring species[1,18] and because diverse plant communities are more likely to contain species that strongly affect ecosystem functioning (i.e. the selection effect[19,20]; Fig. 1, arrow 1). However, plant diversity and the associated diversity of other taxa at larger scales could also influence local ecosystem functioning[7,10,15,21]. The plant diversity of the overall surrounding species pool (i.e. γ-diversity) can directly affect ecosystem services by fostering the spill-over of a diverse pool of associated ecosystem service providers from surrounding areas[22] (Fig. 1, arrow 2), and indirectly by enhancing local plant diversity through dispersal processes (Fig. 1, arrows 1 & 3). Alongside the effects of γ-diversity, heterogeneity in species identities and abundances between local communities (i.e. β-diversity) can affect local ecosystem services directly and positively, by creating diverse habitat niches for ecosystem service providers with complex life-histories. These will in turn promote ecosystem services in surrounding areas[23]. However, β-diversity could also have negative direct effects if ecosystem service providers require large amounts of contiguous habitat. Finally, β-diversity can have indirect effects, as the presence of functionally distinct species in the surrounding areas can maintain plant α-diversity in the face of environmental change[20,24,25] (Fig. 1, arrows 2 and 3).

Following the pathways described above, we predict that ecosystem services provided by mobile animal species that use the whole landscape to meet their feeding and habitat requirements[23], such as aboveground regulating ecosystem services relying on arthropods (e.g. pollination, pest control) or cultural ecosystem services (e.g. bird watching) will be most strongly influenced by the direct 'spill-over' of these organisms[26–28] (Fig. 1, arrow 2), but that the direction of these effects will vary depending on the ecology of ecosystem service providers. By contrast, ecosystem services provided by less mobile species, such as provisioning ecosystem services linked to plants or regulating belowground ecosystem services that rely on soil biodiversity, will be more affected by local biodiversity, and thus the indirect 'dispersal' effects of a diverse surrounding species pool (Fig. 1, arrows 1 & 3).

Within agricultural landscapes, which cover a large proportion of the Earth's surface[29], biodiversity effects on ecosystem services operate within the context of land-use factors, which influence ecosystem services directly, and indirectly by affecting biodiversity[15,30]. Therefore, to understand the role of biodiversity in the supply of agroecosystem services, the relative importance of these many pathways and influences should be determined. At the agricultural field level, intensive land use typically promotes a small set of provisioning ecosystem services directly (e.g. fertilization and pesticide use that promote biomass production; Fig. 1, arrow 4) but causes changes to biodiversity and functional composition that indirectly impact other ecosystem services[2,5] (Fig. 1, arrows 5 and 6). Land-use effects at local scales can also operate via long time lags, such as lasting effects of tillage on soil biodiversity and structure[31,32]. At the landscape level, the conversion of natural or semi-natural habitats such as forests or grassland into cropland can have both immediate and legacy effects on biodiversity[31,33] and ecological processes[34]. For example, the presence and permanency of semi-natural habitats in the surrounding landscape can significantly affect local ecosystem service provision directly, by affecting cross-habitat exchanges of material and energy[35,36] (Fig. 1, arrow 7), and indirectly by influencing the dispersal and colonization of plant species[23,31,37,38] (Fig. 1, arrows 8 and 9). In addition, the landscape context can determine local land-use decisions due to physical constraints (e.g. via farmer decisions to specialize or diversify in land use, Fig. 1, arrow 10) and therefore indirectly affect ecosystem services[23,39]. While there has been a substantial effort to identify how landscape-level factors in agroecosystems affect biodiversity and ecosystem services[23,40], these studies tend to focus on a small number of regulating ecosystem services provided by aboveground species, such as pollination and pest control[23,41,42]. How spatial processes influence a broader set of ecosystem services, particularly cultural and belowground regulating ecosystem services, is far less understood.

In this study, we addressed the gaps highlighted above by investigating how plant diversity at different spatial scales affect the supply of a wide range of ecosystem services, while controlling for and evaluating the effects of land-use factors. We did this by using a comprehensive dataset from the German Biodiversity Exploratories project[43] on indicators for the supply of 16 cultural, regulating, and provisioning ecosystem services (hereafter 'ecosystem services') in 150 agricultural grassland plots, and detailed multi-scale data on land use, plant diversity and the ecosystem service priorities of different stakeholder groups. These measures were taken in agricultural grassland fields that vary strongly in their land-use intensity[44,45], and which were situated in landscapes of varying complexity[46] and management history (see Methods).

Ecosystem services were classified into four types: (i) cultural ecosystem services: acoustic diversity, bird watching potential and total flower cover; (ii) aboveground regulating ecosystem services: pollination, natural enemy abundance, lack of pathogen infection, lack of herbivory, dung decomposition; (iii) aboveground provisioning ecosystem services: shoot biomass and forage quality; (iv) belowground regulating ecosystem services: soil aggregation, phosphorus retention index, nitrogen retention index, soil carbon stocks, potential nitrification and groundwater recharge (Supplementary Data Table 1). The capacity of ecosystems to provide these bundles was captured by calculating separate multifunctionality metrics[49] for each ecosystem service type. We also calculated grassland ecosystem service multifunctionality, a measure of overall ecosystem service supply relative to demand[47], from the perspective of the main grassland stakeholder groups in the studied areas: local residents, nature conservation associations, agriculture and tourism sectors. These measures were based upon the relative priority given to the four grassland ecosystem services most valued by local stakeholders: aesthetic value, biodiversity conservation, fodder production, and carbon sequestration (see Methods).

We used structural equation models (SEM) to estimate the direct and indirect effects of different factors on the local supply of grassland ecosystem services, according to the pathways of influence described above (Fig. 1). These factors belong to five main classes: plant diversity measured at the plot level (here defined as 50 m × 50 m) and field level (here defined as the plot surroundings in a 75-m radius, a scale selected to coincide with the dispersal kernel of most plant species[48]), environmental factors, and land-use components encompassing field-level and landscape-level (here defined within a 1000-m radius) factors. The specific variables considered represent drivers of the local supply of ecosystem services. At the plot level, plant diversity (i.e.

α-diversity, measured as plot-level plant species richness) was considered a proxy for the diversity of multiple taxa (hereafter defined as ‘plant diversity’), because plant species richness is closely correlated with whole aboveground ecosystem biodiversity in these grasslands[49]. At the field level, we test for the effects of the overall surrounding plant species pool (i.e. plant γ-diversity, measured as field-level plant species richness, which also represents the γ-diversity of other taxa) and of the surrounding habitat heterogeneity[15] (i.e. β-diversity, measured as the Sørensen dissimilarities between field-level plant communities).

To more accurately estimate the role of plant diversity across scales in driving ecosystem services, we statistically controlled for and estimated the effects of environmental and land-use factors known to affect plant species richness and ecosystem processes. Environmental factors considered were soil pH, soil thickness and topographic wetness index[30,33]. Field-level land-use intensity was measured as a compound index of grazing, mowing and fertilization intensities[44,45]. In addition, we consider the effect of the grassland permanency (i.e. the number of times the field was recorded as being grassland in four survey dates spanning 200 years), as tillage in grasslands can have lasting negative effects on biodiversity and ecosystem functioning[31,32]. Finally, at the landscape level, the presence of stable natural or semi-natural habitats, such as grasslands, can positively affect biodiversity and ecosystem services[23,31,33,50]. We therefore consider the effects of the quantity (i.e. grassland cover) and stability (i.e. historical grassland cover) of semi-natural habitats, and the presence of a diversity of habitats (i.e. land-cover diversity) in the surrounding landscape, which can act as a proxy for landscape-level biodiversity. We interpret the associations between the drivers described above and local levels of ecosystem services as evidence of biodiversity and land-use effects, and for simplicity use terms such as ‘effects’ and ‘drivers’ hereafter. While we acknowledge the correlational and static nature of our study, we believe our interpretation is supported by existing knowledge and the nature of our study design, which minimizes confounding factors (Fig. 1).

Results and discussion

Overall drivers of ecosystem services

The supply of many ecosystem services was strongly affected by the surrounding plant diversity and landscape factors, and these classes of effect were of equal importance to plot-level plant diversity and field-level land use (Fig. 2). This suggests that spatial biodiversity dynamics are a major driver of local ecosystem service supply. Although plant diversity showed many positive effects, the strength and direction of these effects varied between the four ecosystem service types (Fig. 3, see also Extended Data Fig. 1 and Fig. 2). Both plot- and field-level plant diversity played a positive and important role in the supply of cultural and aboveground regulating ecosystem services. In contrast, provisioning and belowground regulating ecosystem services were more strongly driven by field-level land use and environmental factors (Fig. 2). After accounting for inherent regional differences, the total remaining explained variance in ecosystem service supply varied greatly between ecosystem services. On average, our structural equation models explained 26% ± 9.0 s.e.m (average ± standard error of the mean total effect size across all ecosystem services of this category) of the variance for cultural ecosystem services, 11% ± 0.9 s.e.m for aboveground regulating ecosystem services, 46% ± 10.5 s.e.m for aboveground provisioning ecosystem services and 27% ± 7.6 s.e.m for belowground ecosystem services (Fig. 2). Below, we detail which ecosystem services were most reliant on biodiversity and the scale of biodiversity that drives these services.

Cultural ecosystem services

Cultural ecosystem services were promoted by independent effects of both plot- and field-level plant diversity (Fig. 3 and Extended Data Fig. 2), meaning that, as hypothesized, cultural ecosystem services, including acoustic diversity, flower cover and birdwatching potential, were higher in diverse grassland plots surrounded by diverse plant communities. Plot-level plant diversity accounted for 12.2% ± 4.6 s.e.m of the total effects for cultural ecosystem services (Fig. 2), with a total standardized effect (hereafter 'total effect') of plant α-diversity = 0.06 on cultural ecosystem service multifunctionality index (Fig. 3, Supplementary Data Table 2). Field-level plant diversity accounted for 30.3% ± 7.0 s.e.m of the total effects (Fig. 2), with a total effect of plant γ-diversity = 0.33 (Fig. 3). Cultural ecosystem services were also negatively affected by field-level land-use intensity (25.9% ± 2.0 s.e.m, Fig. 2), with a total effect of land-use intensity = -0.17 (Fig. 3). In general, the effects of field-level plant diversity were as strong as those of field-level land use (Fig. 2). In addition, field-level grassland permanency positively affected cultural ecosystem services (total effect = 0.17). Grassland permanency can enhance the local abundance and the diversity of cultural ecosystem service providers, such as birds[31] (Extended Data Fig. 1). However, these organisms often need diverse habitats to meet their nesting and feeding requirements[51–53], potentially explaining the negative relationship with a high cover of permanent grasslands at the landscape level (total effect of historical grassland cover = -0.15, Fig. 3). This hypothesis is supported by the net positive effect of land-cover diversity within the landscape on cultural ecosystem services (total effect of land-cover diversity = 0.09, Fig. 3) and particularly on the individual service of bird watching potential (total effect of land-cover diversity = 0.18, Extended Data Fig. 1).

Aboveground regulating ecosystem services

Similar to cultural ecosystem services, aboveground regulating ecosystem services were positively affected by both plot- and field-level plant diversity (total effects of plant α-diversity = 0.23, and of plant γ-diversity = 0.13, Fig. 3). This was particularly true for pollination and natural enemy abundance (Extended Data Fig. 1). The strength of positive effects of plant γ-diversity increased when considering multifunctionality indices calculated as the percentage of measured services that exceeded 75% of their maximum observed level across all study plots instead of 50% (Extended Data Fig. 3), meaning the supply of aboveground regulating ecosystem services was highest in plots with biodiverse surroundings. These results, along with those presented for cultural ecosystem services, suggest that promoting a large species pool in agricultural landscapes could offset the negative effects of land-use practices on cultural and aboveground regulating ecosystem services. The effects of β-diversity however, contrasted with those on cultural ecosystem services, as they were negative (total effects of plant β-diversity = -0.09, Fig. 3), indicating that local habitat heterogeneity benefits cultural ecosystem service providers but not the arthropod providers of regulating ecosystem services.

Alongside the effects of plant diversity, aboveground regulating ecosystem services were strongly influenced by both field-level (accounting for 20.1% ± 2.8 s.e.m of the total effects) and landscape-level land use (26.4% ± 1.7 s.e.m of the total effects, Fig. 2). Field-level land-use intensity reduced the local supply of aboveground regulating ecosystem services (total effect = -0.04, Fig. 3). The effect of landscape-level land use was largely due to positive effects of historical grassland cover on aboveground regulating ecosystem services (total effects = 0.10, Fig. 3). The stability of favorable and resource-rich grasslands at the landscape level can thus strongly benefit the mobile organisms that provide aboveground regulating services[31,54,55], such as pollinators (Extended Data Fig. 1).

Aboveground provisioning ecosystem services

Unlike cultural and aboveground regulating ecosystem services, aboveground provisioning ecosystem services were primarily driven by field-level land use (accounting for 32.9% ± 1.0 s.e.m of the total effects, Fig. 2), in that land-use intensity strongly and positively increases aboveground provisioning services (total effect = 0.49), including fodder production (Extended Data Fig. 1). Landscape-level land use played little role in driving this type of services, and only accounted for 13.6% ± 3.0 s.e.m of the total effects (Fig. 2). We also found a negative effect of plot-level plant diversity (total effect of the plant α-diversity = -0.29) and of the field-level plant diversity on these services (total effects of plant β-diversity = -0.05, plant γ-diversity = -0.08, Fig. 3). These effects are likely related to high fodder production and quality in fertilized ecosystems[56] and the shifts towards higher plant tissue quality that accompany fertilization-induced plant functional composition changes and diversity loss[30].

Belowground regulating ecosystem services

Belowground regulating ecosystem services, such as those related to carbon storage and nutrient cycling, were most strongly driven by environmental factors (Fig. 2). These services were positively related to topographic wetness (total effect of topographic wetness index = 0.20) and soil pH (total effect = 0.08, Fig. 3). This relates to tighter cycling of nutrients and higher topsoil carbon stocks in moist and pH-neutral soils (Extended Data Fig. 1). We also found a strong positive effect of field-level grassland permanency on belowground regulating ecosystem services (total effect = 0.23, Fig. 3), reflecting that soil processes were faster, nutrient cycling tighter and carbon stocks higher in fields that have not been ploughed and remained as grasslands for a long time (Extended Data Fig. 1). This is likely due to the accumulation of soil organic matter, after local tillage has stopped[57] but may also include the positive effects of soil biodiversity on soil processes[34,58,59] as more diverse soil communities develop following the cessation of agricultural practices such as tillage[33]. Such effects of soil biodiversity are unlikely to be captured by our plant diversity measures as belowground diversity is weakly associated with aboveground biodiversity in these grasslands[5].

Direct and indirect effects of field-level plant diversity

We assessed whether the effects of plant γ-diversity and β-diversity on ecosystem services operate directly, or indirectly, according to the mechanisms described in the introduction. This was achieved by focusing on a subset of our SEM, specifically direct paths from plant γ-diversity and β-diversity to ecosystem services, and indirect paths of plant γ-diversity and β-diversity through changing plant α-diversity (Fig. 4, see also Extended Data Fig. 4). These analyses revealed that plant γ-diversity and β-diversity affected the supply of multiple ecosystem services via different mechanisms (Fig. 4). As hypothesized, cultural ecosystem services, which rely upon highly mobile animal species, were mainly affected by positive and independent direct effects of both plant γ-diversity and β-diversity (Fig. 4b). This indicates that higher plant diversity in the surroundings promoted a large regional species pool that provided ecosystem services, and that high habitat heterogeneity provides diverse resources and habitats for these ecosystem service providers. In contrast, above- and belowground regulating ecosystem services were mostly affected by an indirect positive effect of plant γ-diversity (Fig. 4b). This suggests that the surrounding field-plant diversity enhances these services by maintaining plot-level plant diversity. Conversely, we found weakly negative direct and indirect β-diversity effects on aboveground regulating ecosystem services, indicating negative effects of heterogeneity on ecosystem service providers that require large amounts of contiguous habitat. For aboveground provisioning ecosystem services, the surrounding field-plant diversity had negative effects, operating via both direct and indirect pathways (Fig. 4b). An exception to this trend was that plant γ-diversity had a strong direct and positive effect on aboveground provisioning services (Fig. 4b), mostly driven by its positive effect on forage quality (Extended Data Fig. 1). While the underlying mechanism is difficult to discern in this case, higher biodiversity in the surroundings could help secure a sustainable supply of provisioning ecosystem services such as forage quality, e.g. via dilution effects on pathogen spread[60].

Linking biodiversity to stakeholders

To estimate the impact of biodiversity across scales on ecosystem services that directly benefit local people in the study regions, we fitted our structural equation models to measures of the grassland ecosystem services, at the final benefits level[61], most prioritized by local stakeholders, as identified in a social survey[62] (see Methods). This showed that both aesthetic value and biodiversity conservation were strongly promoted by plant γ-diversity, with total effects = 0.18 on aesthetic value, and 0.28 on biodiversity conservation (Extended Data Fig. 6). By contrast, fodder production and carbon sequestration were mostly driven by land-use and environmental factors (Extended Data Fig. 6). Field-level land-use intensity positively affected fodder production, with a total effect of land-use intensity = 0.50. Grassland permanency and historical grassland cover also had strong positive effects on carbon sequestration, with total effects of 0.43 and= 0.22, respectively (Extended Data Fig. 6).

When considering multifunctionality measures calculated for local residents, nature conservation associations, and the agriculture and tourism sectors, we found that biodiversity across scales positively influenced all four stakeholder groups (Fig. 5). Plant α-diversity had a total effect of 0.32 on multifunctionality for local residents, 0.34 for conservationists, 0.11 for the agriculture sector, and 0.35 for the tourism sector (Fig. 5). Similarly, plant γ-diversity had strong positive effects on multifunctionality for each stakeholder group (total effect = 0.54 for local residents, 0.50 for conservationists, 0.29 for the agriculture sector, and 0.58 for the tourism sector), with differences reflecting their relative prioritization of cultural and provisioning services. Alongside biodiversity effects, land-use intensity promoted multifunctionality across stakeholder groups due to the relatively high priority given by all groups to fodder production (Fig. 5, see also Supplementary Table 1). Thus, by influencing the ecosystem services that different local stakeholder prioritized, biodiversity at a range of scales positively influences all major grassland stakeholder groups in these study regions.

These results indicate that management strategies focusing on the delivery of few aboveground provisioning ecosystem services may be detrimental to other prioritized cultural ecosystem services, as they are driven in opposing directions by the same factors. However, our results also indicate that such trade-offs may be weakened by conserving both high and low intensity patches within agricultural landscapes, as biodiverse low intensity areas promoted multiple services when present in the immediate landscape. It remains to be seen if a spatially interwoven mosaic of permanent and biodiverse habitats and intensive patches (i.e. 'land-sparing' strategy[63]) is the best means of delivering landscape multifunctionality to multiple stakeholder groups, i.e. landscapes that simultaneously provide high levels of multiple ecosystem services to people[64].

Wider implications

The results presented here show that a focus on local diversity when investigating the relationships between biodiversity and ecosystem services is not sufficient, as biodiversity change across a range of scales has consequences for ecosystem functions and services[15,20,65]. Many theoretical studies have highlighted the potential importance of β- and γ-diversity for ecosystem functioning (e.g. [15,65,66]), but to date very little empirical evidence has been provided (but see[12]). By decomposing the direct and indirect effects of surrounding biodiversity on local ecosystem service supply, we reveal that both a biodiverse species pool (i.e. plant γ-diversity) and habitat heterogeneity (i.e. plant β-diversity) can promote many ecosystem services, likely via different mechanisms, i.e. by fostering the spill-over of a diverse array of ecosystem service providers, by maintaining plot-level biodiversity (Fig. 4), and by creating habitat niches for ecosystem service providers with complex life-histories. These surrounding biodiversity effects were strongest for cultural and aboveground regulating ecosystem services (Fig. 2). Loss of diversity within the overall species pool and loss of habitat heterogeneity may therefore affect cultural and aboveground regulating ecosystem services just as strongly as local species losses (i.e. loss in plant α-diversity)[66].

Alongside the effects of biodiversity, cultural and belowground regulating ecosystem services were higher in grasslands that were not converted regularly (i.e. a high field-level grassland permanency). We also found that aboveground regulating ecosystem services were positively impacted by the presence and the permanency of grasslands at the landscape-level (Fig. 3). There is now substantial evidence that permanent grasslands are important in maintaining the biodiversity of ecosystem service providers in agricultural landscapes[23,31,33,50]. However, these studies focused almost exclusively on a small number of aboveground regulating services, such as pollination or pest control[37,41,63]. By considering multiple ecosystem services, our results indicate that reducing grassland field conversion, coupled with the strategic arrangement of permanent grasslands within agricultural landscapes can both help to maintain a biodiverse species pool, and enhance the supply of above- and belowground ecosystem services that are essential to sustainable agriculture.

To date, biodiversity-ecosystem functioning research has concentrated on the impact of biodiversity loss at small spatial scales on ecosystem functions, rather than on the impact of large-scale biodiversity change on ecosystem services[13,14,65]. However, it is at larger spatial scales that most management and policy decisions affecting biodiversity and ecosystem functioning are taken. Since all stakeholder groups considered in this study prioritized ecosystem services driven by biodiversity, we show that biodiversity across spatial scales benefits the whole local community, and therefore that landscape-level biodiversity conservation would benefit these rural communities. The role of biodiversity in driving stakeholder multifunctionality might even be underestimated in our metrics as we did not consider the role of regulating ecosystem services in underpinning final benefits, and these were heavily dependent on spatial biodiversity (Fig. 3). However, despite a general dependency on biodiversity, the relative importance of biodiversity differs across stakeholders, depending on their ecosystem service priorities, and this may in part explain relative differences in attitudes towards nature and conservation between these groups[62].

While this study demonstrates a general reliance of local-level ecosystem services on surrounding biodiversity and other studies have investigated the correlation between larger scale biodiversity and landscape multifunctionality[67,68], a fully mechanistic understanding of how spatial biodiversity dynamics affect the landscape-level supply of ecosystem services is still largely missing[14,69,70]. Larger scale, interdisciplinary and mechanistic approaches, that are spatially explicit in terms of both ecosystem service supply and demand, are therefore needed to fully understand the link between biodiversity and ecosystem services, and the impact of landscape management actions on the needs of multiple stakeholder groups[71,72].

Conclusion

By employing a comprehensive study setup and using structural equation models, we revealed that the supply of multiple ecosystem services requires biodiversity across spatial scales, and that surrounding biodiversity promotes local ecosystem services through a range of mechanisms. Future assessment of ecosystem service delivery must therefore consider spatial biodiversity dynamics, e.g. when mapping ecosystem services[68], to accurately assess the status and drivers of ecosystem services, and to evaluate the consequences of biodiversity change on ecosystem services. Another key message of this work is that the local-level supply of many important ecosystem services is enhanced in landscapes containing biodiverse and permanent grasslands. Preserving large species pools within permanent habitats in agricultural landscapes can promote a wider range of the vital ecosystem benefits, especially the cultural and aboveground regulating ecosystem services, upon which many rural people ultimately depend[73].

Figures

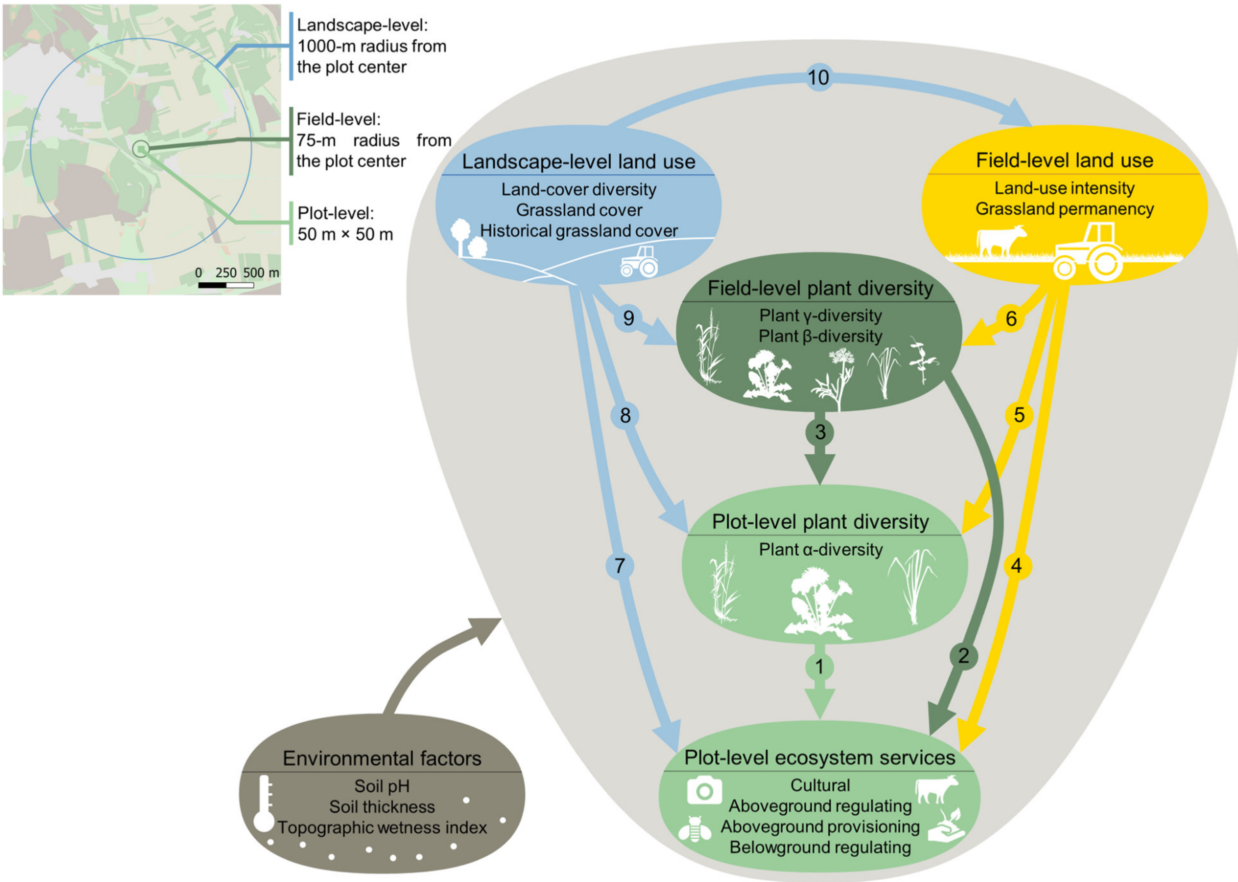


Figure 1. Conceptual framework of the relationship between landscape- and field-level land use, field- and plot-level plant diversity and plot-level ecosystem services. Landscape-level (1000-m radius from the plot center) land use is represented in blue, field-level (75-m radius from the plot center) plant diversity and land use are represented in dark green and in yellow respectively, and plot-level (50 m × 50 m plot) factors are represented in light green. Note that this framework is a simplification of the full structural equation model used in this study, and for simplicity multiple paths between environmental factors and the other variables are not shown. All individual paths considered are presented in Table S2. Each plant icon represents a different

species in the species pool. Arrows illustrate causal links between plot-level plant diversity and ecosystem services, field-level plant diversity and land use, and landscape-level land use. See introduction for a full explanation of these relationships and associated hypotheses.

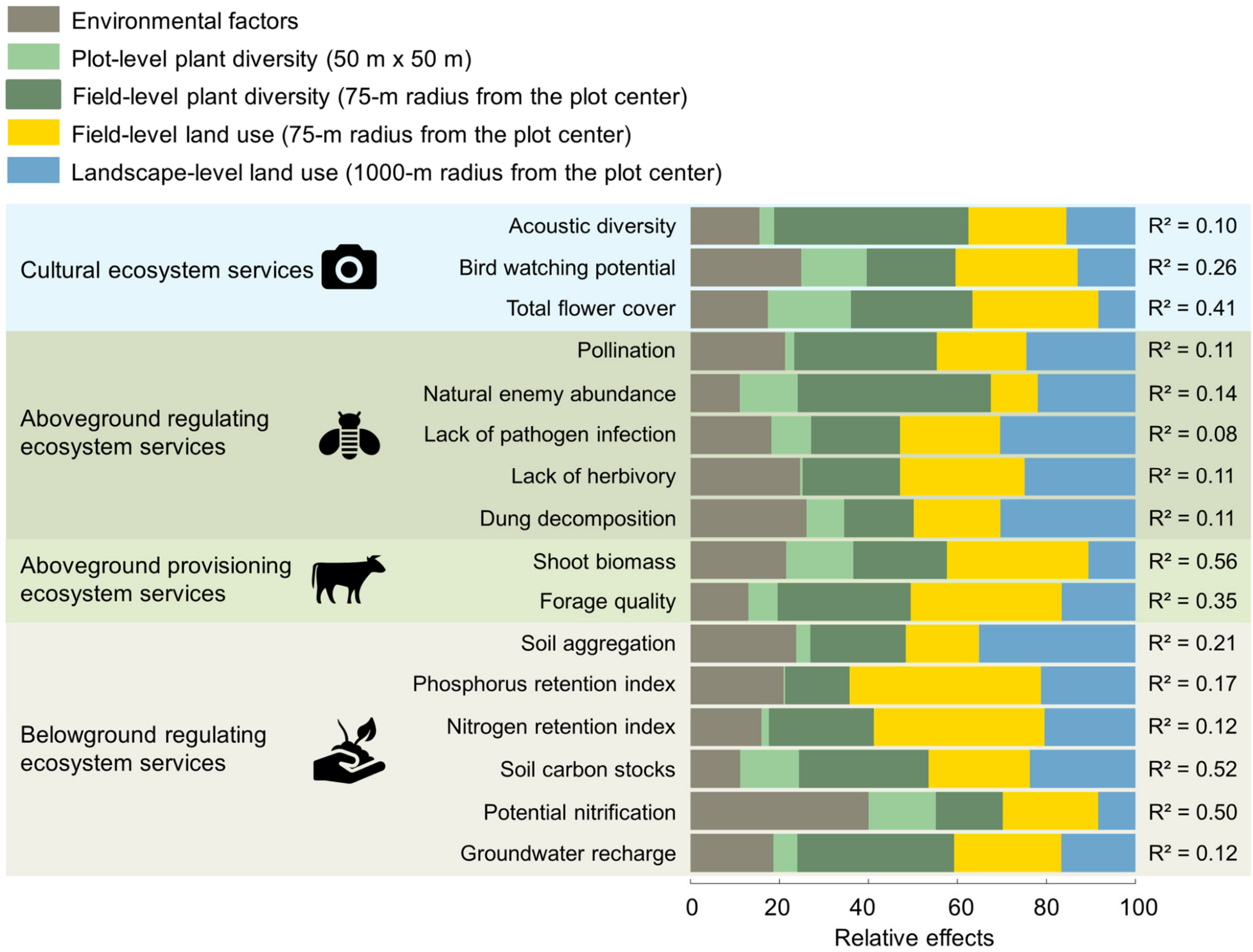
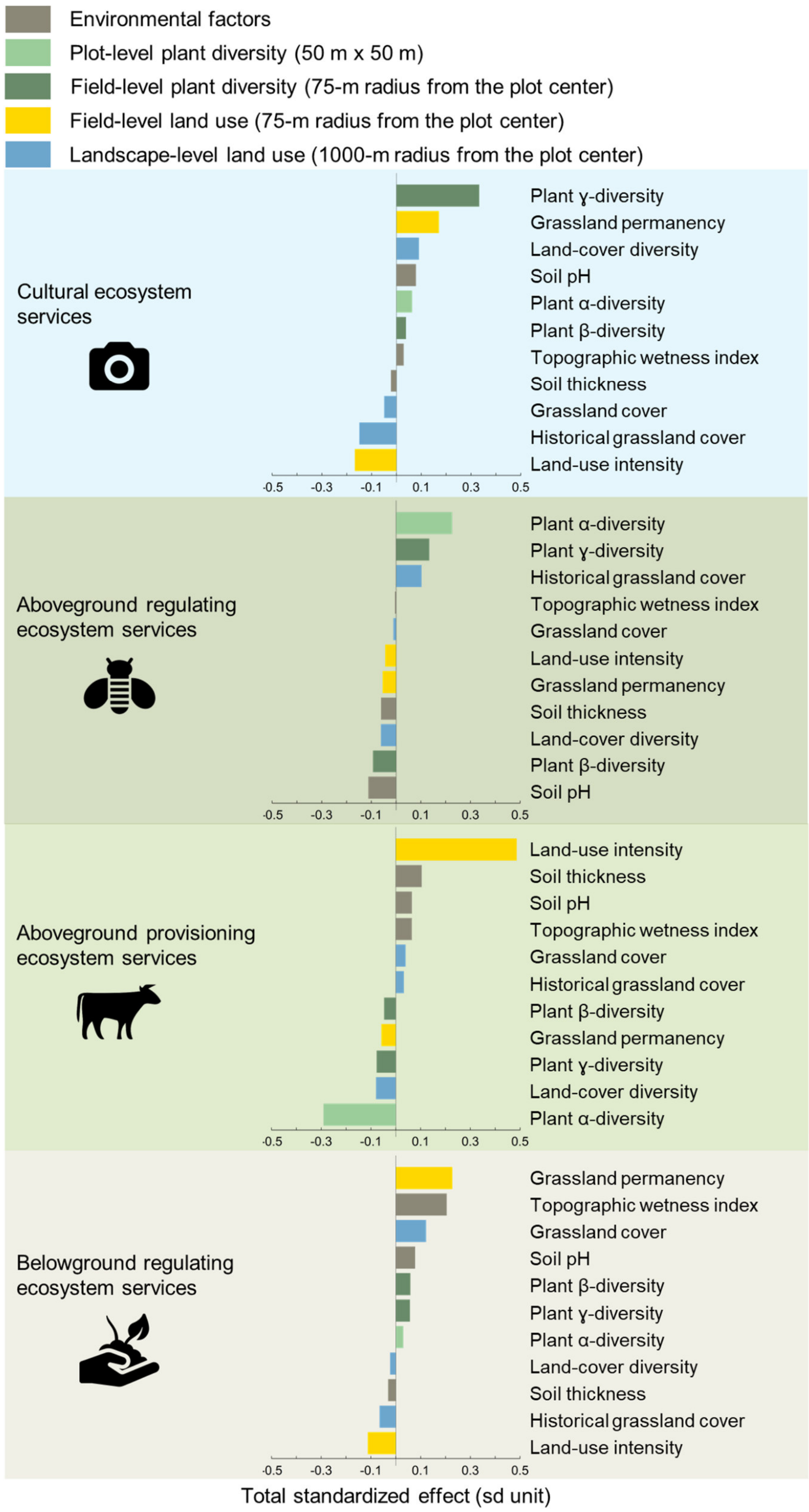


Figure 2. Relative importance of plant diversity and land-use predictors on cultural, aboveground regulating and provisioning, and belowground regulating ecosystem services. The effects of the predictors were calculated considering both direct and indirect relationships (total effects) between the predictors and the response variables. We then expressed the importance of each group of predictors as the percentage of total effects they explained, based on the comparison between the absolute values of their standardized path coefficients and the sum of the absolute value of all standardized path coefficients from the SEM. Relative effects were calculated for each group of predictors: environmental factors, plot-level (50 m × 50 m) plant diversity, field-

level (75-m radius from the plot center) plant diversity, field-level (75-m radius from the plot center) land use, and landscape-level (1000-m from the plot center) land use. R^2 for each ecosystem service is calculated based on the full structural equation model (see Table S2 for the individual path coefficients). All predictors and response variables were scaled to interpret parameter estimates on a comparable scale. See also Fig. S1 for the total standardized effects of each predictor. The number of biologically independent samples for each ecosystem service was n = 150 for bird watching potential, forage quality, nitrogen retention index, potential nitrification, groundwater recharge; n = 147 for lack of herbivory; n = 146 for soil carbon stocks; n = 142 for dung decomposition, lack of pathogen infection and shoot biomass; n = 136 for phosphorus retention index; n = 119 for pollination; n = 114 for acoustic diversity; n = 93 for soil aggregation; n = 83 for the natural enemy abundance; n = 70 for the total flower cover.



459 **Figure 3. The multiple drivers of cultural, aboveground regulating and provisioning, and**

belowground regulating ecosystem services in grasslands. Total standardized effects (sd unit) were calculated based on the results of structural equation models (considering both direct and indirect effects of the predictors) for each predictor: environmental factors, plot-level (50 m × 50 m) plant diversity, field-level (75-m radius from the plot center) plant diversity, field-level (75-m radius from the plot center) land use, and landscape-level (1000-m radius from the plot center) land use. Models were fitted to four multifunctionality measures: cultural, aboveground regulating and provisioning, and belowground regulating ecosystem service multifunctionality. The total standardized effects correspond to the sum of standardized direct effects (i.e. individual paths) and indirect effects (i.e. the multiplied paths). For each multifunctionality measure, total standardized effects of the different predictors are ordered from the highest positive effect to the lowest negative effect. All predictors were scaled to allow interpretation of parameter estimates on a comparable scale. Plot-level and landscape-level predictors were log-transformed. See Table S2 for the individual path coefficients and Fig. S1 for the effects of predictors on each individual ecosystem service. n = 150 biologically independent samples.

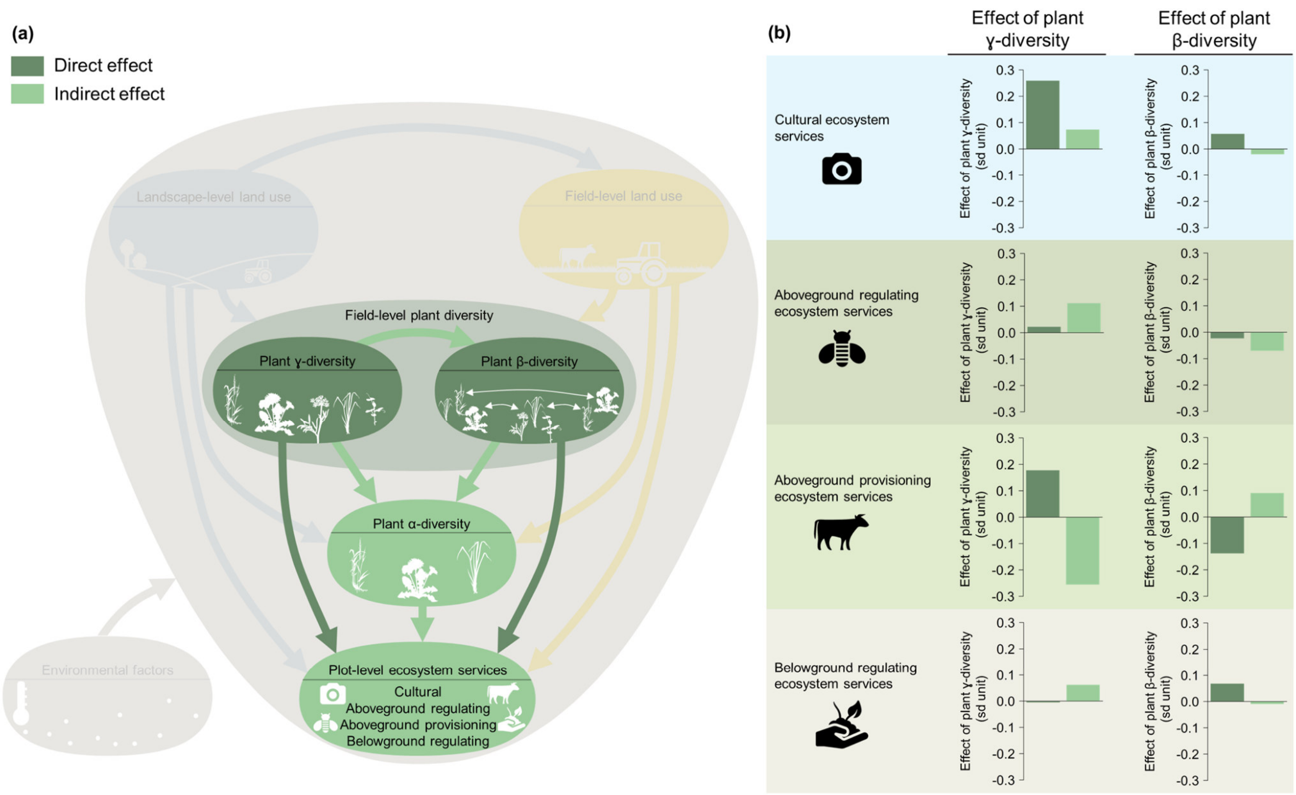
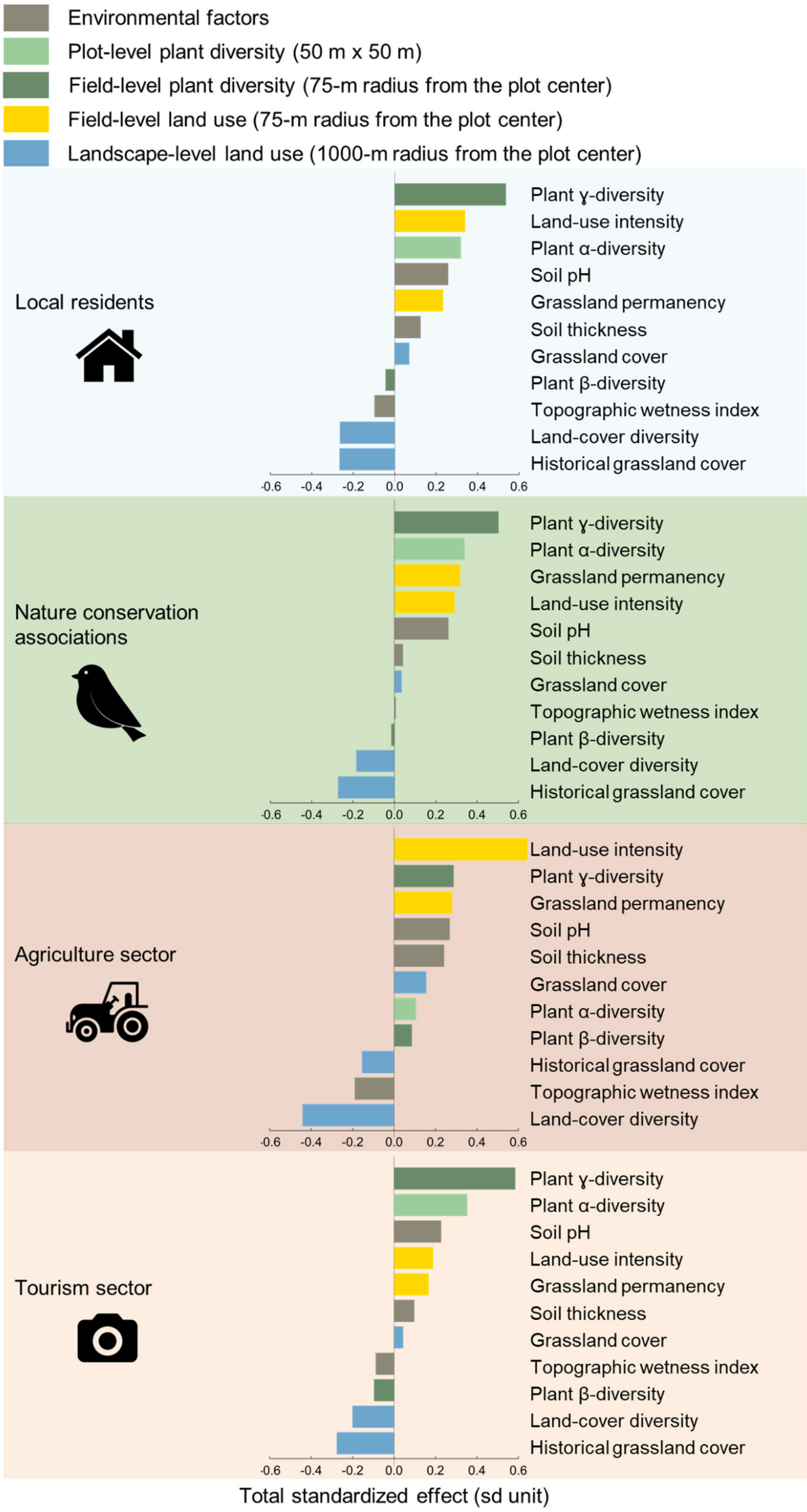


Figure 4. The strength of direct and indirect effects of field-level plant diversity on plot-level ecosystem services. A subset of the full structural equation model (a) was used to calculate the indirect effects of field-level plant γ-diversity and plant β-diversity, through changing plot-level plant α-diversity. Direct and indirect effects of field-level plant γ-diversity and plant β-diversity (b) were calculated based on the full structural equation models, i.e. also including the components shown as faded in (a), for cultural, aboveground regulating and provisioning, and belowground regulating ecosystem services separately. All individual paths considered are presented in Table S2. n = 150 biologically independent samples.



482 **Figure 5. Effect of multiple drivers on the multifunctionality of grassland ecosystem services**

prioritized by four local stakeholder groups. Total standardized effects (sd unit) were calculated based on the results of structural equation models (considering both direct and indirect effects of the predictors) for each predictor: environmental factors, plot-level (50 m × 50 m) plant diversity, field-level (75-m radius from the plot center) plant diversity, field-level (75-m radius from the plot center) land use, and landscape-level (1000-m radius from the plot center) land use. Models were fitted to four multifunctionality measures calculated for each stakeholder group. These measure the combined supply of the four most prioritized grassland ecosystem services (i.e. aesthetic value, biodiversity conservation, fodder production, carbon sequestration) relative to their demand (see methods for details). The total standardized effects correspond to the sum of standardized direct effects (i.e. individual paths) and indirect effects (i.e. the multiplied paths). For each multifunctionality measure, total standardized effects of the different predictors are ordered from the highest positive effect to the lowest negative effect. All predictors were scaled to allow interpretation of parameter estimates on a comparable scale. Plot-level and landscape-level predictors were log-transformed. See Table S5 for the priority scores given by each stakeholder groups to each ecosystem service and Fig. S5 for the effects of predictors on each individual prioritized ecosystem service. n = 52 independent samples.

Methods

Study design

The studied grassland plots are part of the large-scale and long-term Biodiversity Exploratories project[43] (www.biodiversity-exploratories.de) and are located in three German regions: (i) the Schwäbische Alb region in the low mountain range of south-western Germany; (ii) the Hainich-

Dün region in hilly central Germany; and (iii) the Schorfheide-Chorin region in the post-glacial lowlands of north-eastern Germany. The three regions differ in climate, geology and topography, but each is characterized by a gradient of grassland land-use intensity that is typical for large parts of temperate Europe[43]. In each region, fifty plots (50 m × 50 m) were chosen in mesic grasslands by stratified random sampling from a total of 500 candidate plots on which initial vegetation, soil and land-use surveys were conducted. This ensured that the plots covered the whole range of land-use intensities and management types, while minimizing confounding factors such as spatial position or soil type. All plots were grasslands for at least 10 years before the start of the project in 2006[45].

Ecosystem service indicators

In each of the 150 grassland plots, data on 16 indicators of ecosystem services were collected[74–79]. These services included (i) three cultural ecosystem services: acoustic diversity (the distribution of acoustic energy among frequency bands during diurnal recordings), bird watching potential (bird species richness), aesthetic value (measured as the total flower cover[80,81]); (ii) five aboveground regulating ecosystem services: pollination (number of flower visitors), the abundance of natural enemies that regulate crop pests in neighboring arable fields (measured as the number of brood cells recorded in trap nest attacked by parasitoids of pest insects), lack of pathogen infection (inverse of the total cover of foliar fungal pathogens), lack of herbivory (inverse of the total proportion of leaf area damaged by invertebrate herbivores), dung decomposition (proportion of dung dry mass removed); (iii) two aboveground provisioning ecosystem services: shoot biomass (peak standing biomass), forage quality (index based on crude protein concentration and relative forage value); (iv) six belowground regulating ecosystem services: soil aggregation (proportion of water stable soil aggregates), phosphorus retention index (calculated as a ratio between shoot and microbial phosphorus stocks and that of soil extractable phosphorus), nitrogen retention index (calculated as a ratio between shoot and microbial nitrogen stocks and that of soil extractable nitrogen), soil carbon stocks (soil organic carbon stocks in the top 10 cm), potential nitrification (ammonia oxidation under lab conditions), groundwater recharge (annual net downward water fluxes to below 0.15 m soil depth). To classify ecosystem services, we used the Common International Classification of Ecosystem Services (CICES[82]) and the Intergovernmental Platform for Biodiversity and Ecosystem Services (IPBES; which includes ecosystem services in the broader concept of nature's contributions to people[73]) classifications. See also Supplementary Data Table 1 for further details.

Measures of overall ecosystem service supply can be useful for addressing general trends (e.g. for management purposes) in addition to the study of responses of individual ecosystem services. We therefore calculated the overall ecosystem capacity to maintain ecosystem services simultaneously (i.e. multifunctionality[6,64,83]). To do so, we first scaled values of each ecosystem service. We then calculated multifunctionality measures for cultural, aboveground regulating, aboveground provisioning and belowground regulating ecosystem services separately. Multifunctionality was calculated as the percentage of measured services that exceeded a given threshold of their maximum observed level across all study plots[83]. To reduce the influence of outliers, we calculated the maximum observed level as the average of the top five sites[83]. Given that any threshold is likely to be arbitrary, the use of multiple thresholds is recommended to better understand the role that biodiversity and land use play in affecting ecosystem multifunctionality and to account for tradeoffs between services[83]. Therefore, we used three different thresholds

(25%, 50% and 75%) to represent a wide spectrum in the analyses performed. Our results focus on the 50% threshold, while results for the 25% and 75% threshold are presented in Extended Data Fig. 3. As an alternative approach, we also calculated average-based indices by calculating the average across all services[83]. In these metrics, all ecosystem services are weighted equally, thus preventing the measure from being driven by specific services (Extended Data Fig. 2). We further calculated overall multifunctionality measures, considering all ecosystem services simultaneously. Because the different types of ecosystem services considered in this study show contrasting responses, the use of an overall multifunctionality measure provides little insights (see results for overall ecosystem multifunctionality measures in Extended Data Fig. 5).

Ecosystem service prioritized by local stakeholders

As part of a wider study, expert workshops were conducted in 2018 in the same three German regions, with representatives of numerous pre-selected stakeholder groups. Based on these workshops, lists of stakeholder groups and ecosystem services that are prioritized regionally were established[62]. We only considered ecosystem services with direct links to final benefits, thus excluding regulating ecosystem services (e.g. pollination), which underpin the supply of other services (e.g. food production) but do not directly benefit humans. A larger survey was then conducted across 14 stakeholder groups in 2019[62], in which 321 respondents were requested to distribute a maximum of 20 points across all ecosystem services to quantify the priorities of their group. As the survey considered the whole study region, including other land-use types and services delivered at larger scales, survey results were subsetted to include only the most prioritized ecosystem services provided by grasslands (e.g. removing timber and food crop production), resulting in four ecosystem services: aesthetic value, biodiversity conservation, livestock production and carbon sequestration[62,84]. Priority scores for each ecosystem service were normalized by the total number of points attributed to grassland ecosystem services by each respondent. We focused on four stakeholder groups, who placed high priority on grassland services, but with contrasting priorities to different services: local residents, nature conservation associations, the agriculture and the tourism sectors (126 respondents in total). The priority scores for each group did not vary significantly across regions so we used overall scores. Senckenberg Gesellschaft für Naturforschung employed the researchers who conducted this study. They did not have an ethics committee for social science research at the time when the data were collected. However, the standards and recommendations of the German Data Forum (2017) were followed and employed. This includes that a written consent for the collection and processing of the anonymized personal survey data was obtained before starting the survey. Participation in the survey was voluntary. At any time, the participants were able to cancel the survey or withdraw their consent.

We estimated the supply for prioritized ecosystem services from several indicators. For aesthetic value, we integrated direct measures of acoustic diversity and total flower cover (sum of scaled indicators). Acoustic diversity was used as experience of nature sounds, and specifically bird songs that have positive effects on human well-being[85]. We also considered flower cover to characterize aesthetic value as people value flower-rich landscapes[86]. Biodiversity conservation was based on bird species richness, the main focus of conservation efforts in these regions, for instance for the delimitation of Natura 2000 sites based on the Birds and Habitat Directives. For fodder production, we integrated both the shoot biomass and the forage quality (sum of scaled indicators), which are strongly linked to yield output[56]. Finally, climate regulation via carbon sequestration was quantified as soil organic carbon stocks in the top 10 cm, which is where most carbon is stored in these systems. We then used these measures to calculate ecosystem service multifunctionality for each of the four stakeholder groups[64]. To do so, we scaled the ecosystem service values between 0 and 1, and weighted these values by the relative priority scores of each service to the stakeholder group[64]. These weighted values where then summed for each stakeholder group. Measures therefore quantify the overall supply of all prioritized grassland ecosystem services, relative to stakeholder demand[47,63], when priority is defined as the relative importance of an ecosystem service to a stakeholder[87] and demand is 'the amount of a service required or desired by society'[88]. While demand is a dynamic property, it is represented as a fixed value in ecosystem service multifunctionality measures. In these, the service level demanded is represented by two separate components. The first of these is the priority score, in that any service with a priority score of zero is not demanded at all. The second component is the supply–benefit relationship. This can take a variety of forms and describes the relationship between ecosystem service supply and the benefit received. Here we assumed the relationship was linear, and thus that demand is not saturated at the levels of supply measured. As values for individual indicators were missing for some plots, we focus on a subset of the data, considering plots with all indicators available, to calculate ecosystem service multifunctionality measures (n = 52).

Plant diversity

At the plot level (i.e. 50 m × 50 m grassland plot), we annually sampled vascular plants in an area of 4 m × 4 m on each plot between mid-May and mid-June, and estimated the percentage cover of each occurring species[89]. For our local plant α-diversity measure, we used mean plant species richness between 2009 and 2018.

To assess the field-level plant diversity of each grassland plot, we surveyed the vegetation within the major surrounding homogeneous vegetation zones in a 75-m radius of each plot in 2017 and 2018[90]. Each of these zones represented visually distinct habitats and were mostly situated within the same grassland-field as the focal plot, but we occasionally surveyed other habitat types (c. 20% were situated in hedgerows, margins or forests). In each of these zones, we selected a single, representative area of 2 m × 2 m in which the cover of all vascular plant species was estimated. We surveyed at least four zones for each grassland plot. If less than four different homogeneous zones were identified, we surveyed the vegetation twice or more within a large homogeneous zone. We characterized the overall surrounding species pool (i.e. field-level plant γ-diversity) by calculating the total species richness recorded in these surrounding zones. In addition, to characterize the overall changes in species composition between these surrounding plant communities (i.e. field-level plant β-diversity), we calculated dissimilarities between plant communities based on Sørensen dissimilarity index using the *betapart* package[91,92]. A high β-diversity is often associated with the presence of distinct habitats in the surroundings of the grassland plot (e.g. ditches, hedgerows, wetlands, scrub, and forest). These are not always species-rich habitats, hence field-level plant γ-diversity and β-diversity were not highly correlated (r = 0.40). These two metrics therefore represent distinct aspects of the surrounding diversity, i.e. overall surrounding biodiversity and habitat heterogeneity, respectively.

Field-level land use

Land-use intensity was assessed annually for the field within which each plot, and most associated field-level plant diversity plots, was located. This was done via questionnaires sent to land managers in which they reported the level of fertilization (N total kg ha^{-1} year^{-1}), the number of mowing events per year (from one to three cuts), and the number and type of livestock and their duration of grazing (number of livestock units × grazing days ha^{-1} $year^{-1}$). We used this information to calculate three indices for fertilization, mowing and grazing intensity respectively, standardized by their mean value across all three regions overall the years 2006-2018[44,45]. We then quantified the land-use intensity (LUI) as the square-root of the sum of these three indices according to 44, using the LUI calculation tool[93] implemented in BExIS (http://doi.org/10.17616/R32P9Q). We used this compound index as fertilization and mowing are positively correlated (r = 0.68), and grazing and mowing negatively correlated (r = -0.62). At the minimum LUI of 0.5–0.7, grasslands are typically unfertilized, and grazed by one cow (>2 year old) per hectare for 30 days (or one sheep per hectare for the whole year). At an intermediate LUI of 1.5, grasslands are usually unfertilized (or fertilized with less than 30 kg N ha^{-1} $year^{-1}$), and are either mown twice a year or grazed by one cow per hectare for most of the year (300 days). At a high LUI of 3, grasslands are typically fertilized at a rate of 60–120 kg N ha^{-1} y^{-1}, are mown 2–3 times a year or grazed by three cows per hectare for most of the year (300 days), or are managed by a combination of grazing and mowing.

Additionally, we used historical land-use maps to calculate the permanency of field-level land use[94]. Historical maps from the Schwäbische Alb are digitized cadastral maps from 1820, topographic maps (map scale = 1:25000) from the German Empire from 1910, and topographic maps (map scale = 1:25000) from the Federal Republic of Germany from 1960. Historical maps from the Hainich are digitized old topographic maps (map scale = 1:25000) from 1850, topographic maps (map scale = 1:25000) from the German Republic from 1930, and topographic maps (map scale = 1:10000) from the German Democratic Republic from 1960. Historical maps from Schorfheide-Chorin are digitized old topographic maps (map scale = 1:25000) of 1850, topographic maps (map scale = 1:25000) from the German Republic from 1930, and topographic maps (map scale = 1:25000) from the German Democratic Republic from 1960. Field-level land use permanency was calculated as the number of times the field was recorded as being grassland within four survey dates between 1820/50 and 2008, and varied between 4 (the field was always recorded as a grassland in all time points) and 1 (the land use recorded at the field level was different between all subsequent time points).

Landscape-level land use

At the landscape level (i.e. 1000-m radius of the center of the grassland plot), land use was recorded in 2008 within a 1000-m radius of each grassland plot[95,96], and mapped in a Geographical Information System (GIS) database running on QGIS v3.24. This scale has been chosen as it approximates the dispersal distance of different taxa. Land use was classified into six broad categories: croplands, grasslands, forests, water bodies, roads and urban areas (see Supplementary Table 2). To describe the current landscape-level land use, we first calculated the proportion of the landscape covered by grasslands. Grasslands represent relatively undisturbed habitats in temperate agricultural landscapes and are likely to act as favorable habitats and dispersal corridors for some ecosystem service providers[31,50,97]. We also calculated the diversity of land-cover types in the landscape (i.e. the Shannon diversity of land-cover types), which is positively related to biodiversity in agricultural landscapes and been shown to positively affect associated ecosystem services[41,46,98,99]. Note that the Shannon diversity index contains an evenness component, meaning low abundance land-cover types have little weighting in the three regions. Within the 1000-radii, water bodies, roads and urban areas generally covered a small proportion (0.55–6.39%) of the landscape (Supplementary Table 2). Therefore, the land-cover diversity metric was not sensitive to the presence of these rare land-cover types. A second landscape land-use survey was done in a 250-m radius of the plots in 2017 and we found that grassland cover (r = 0.81), forest cover (r = 0.80) and total land-cover diversity (r = 0.71) recorded in 2017 were highly correlated with data calculated in the same 250-m radius of each grassland plot in 2008, suggesting that over the last 10 years landscape composition was largely unchanged.

Additionally, we used the historical land-use maps to quantify the landscape-level historical grassland cover, between 1820/50 and 2008. To do so, we calculated the ratio of the mean to the standard deviation of grassland cover recorded in the landscape from 1820/50 to 2008. Historical grassland cover values were high when there was a higher grassland cover and this cover did not fluctuate over time.

Environmental factors

In each grassland plot, we measured important environmental covariates known to affect plant species richness[100–105] and ecosystem processes[30]. Soil thickness was measured as the combined thickness of all topsoil and subsoil horizons. We determined soil thickness by sampling a soil core in the center of the study plots. We used a motor driven soil column cylinder with a diameter of 8.3 cm for the soil sampling (Eijkelkamp, Giesbeek, The Netherlands). To determine soil pH, a composite sample representing the soil of the whole plot was prepared by mixing 14 mineral topsoil samples (0–10 cm, using a manual soil corer with 5.3 cm diameter) from the same plot[106]. Soil samples were air dried and sieved (< 2 mm), and we then measured the soil pH in the supernatant of a 1:2.5 mixture of soil and 0.01 M $CaCl_2$. Finally, for each plot we calculated the Topographic Wetness Index (TWI), defined as ln(a/tanB) where a is the specific catchment area (cumulative upslope area which drains through a Digital Elevation Model (DEM, http://www.bkg.bund.de) cell, divided by per unit contour length) and tanB is the slope gradient in radians calculated over a local region surrounding the cell of interest[100,107]. TWI therefore combines both upslope contributing area (determining the amount of water received from upslope areas) and slope (determining the loss of water from the site to downslope areas). TWI was calculated from raster DEM data with a cell size of 25 m for all plots, using ArcGIS tools (flow direction and flow accumulation tools of the hydrology toolset and raster calculator)[108]. The TWI measure used was the average value for a 4 × 4 window in the center of the plot, i.e. 16 DEM cells corresponding to an area of 100 m ×100 m. Initial analyses found that this was a stronger predictor than more local measures, thus indicating it is representative of the 50 m × 50 m plot area and its surroundings.

Data analysis

All analyses were performed using R version 4.1.2[109]. To assess the relative importance of plot-, field- and landscape-level factors in driving cultural, aboveground regulating, aboveground provisioning and belowground regulating ecosystem services, we used structural equation models (SEM)[110]. Structural equation modeling is a statistical framework that uses a combination of scientific theory and statistical control of co-varying factors to help determine causal relationships in observational datasets[111]. This approach therefore allows for the quantification of independent direct and indirect effects of multiple variables. We defined five groups of predictors, spanning a range of spatial scales: (i) environmental factors that may drive plant species richness[100–105] and also directly affect ecosystem services[30]: soil pH, soil thickness, and the TWI; (ii) the plot-level plant diversity, corresponding to plant α-diversity; (iii) the field-level plant diversity, which included plant β-diversity and plant γ-diversity; (iv) the field-level land-use factors, which included land-use intensity and field-level grassland permanency; (v) the landscape-level land-use factors, which included the land-cover diversity, the grassland cover, and the historical grassland cover. We formulated a hypothetical causal model (Fig. 1) based on *a priori* knowledge of grassland agroecosystem landscapes and used this to test the fit of the model to the data. We detailed in the Introduction a full explanation of the paths included in this model, and associated hypotheses, but note that this hypothetical causal model is based on a large body of theoretical and empirical studies beyond those cited in this study. Covariances between variables were added to the initial model if they significantly improved model fit using modification indices ($P < 0.05$). We fitted separate SEM for each ecosystem service measure individually, and for the different multifunctionality measures (i.e. cultural, aboveground regulating, aboveground provisioning and belowground regulating ecosystem services, and overall multifunctionality), using the *lavaan* package[112]. To account for inherent regional differences in environmental factors, plant diversity, land use and ecosystem services, we calculated the residuals for all our variables from linear models including region as a predictor, and then used these residual values in all SEM analyses. In order to allow comparison between the responses of the different ecosystem services, we always use the same SEM structure, without running any model simplification.

We estimated direct and indirect effects as standardized path coefficients, thus allowing for comparisons between ecosystem services. We calculated the fit of each SEM to the data using a Chi-squared test (Supplementary Table 3). Response variables and predictors were log-transformed if necessary before analysis to meet linear model assumptions. To evaluate the relative importance of (i) environmental factors, (ii) the plot-level plant diversity, (iii) the field-level plant diversity, (iv) the field-level land use, and (v) the landscape-level land use as drivers of ecosystem services, we expressed the importance of each group of predictors as the percentage of the total effect they explained, based on the comparison between the absolute values of their standardized path coefficients and the sum of all absolute values of standardized path coefficients from the SEM[6,31,99,113]. Before running our SEM, we fitted separately linear models contained in the SEM (Supplementary Data Table 2) to test for residual spatial autocorrelation using Moran's I tests. We did not find any evidence of residual spatial autocorrelation (P-values > 0.10). In order to establish the link between biodiversity at a range of spatial scales and the ecosystem services prioritized by a range of stakeholders within our study regions, we used a similar approach and fitted our SEM separately to each prioritized ecosystem service measure, and to the different multifunctionality measures calculated for each stakeholder group.

Data availability

This work is based on data from several projects of the Biodiversity Exploratories program (DFG Priority Program 1374). The data used for analyses are publicly available from the Biodiversity Exploratories Information System (https://doi.org/10.17616/R32P9Q), or will become publicly available after an embargo period of three years from the end of data assembly to give the owners and collectors of the data time to perform their analysis. Any other relevant data are available from the corresponding author upon reasonable request.

Acknowledgements

We thank the managers of the three Exploratories, Iris Steitz, Sandra Weithmann, Florian Staub, Sonja Gockel, Kerstin Wiesner, Katrin Lorenzen, Andreas Hemp, Martin Gorke, Miriam Teuscher and all former managers for their work in maintaining the plot and project infrastructure; Simone Pfeiffer, Maren Gleisberg, Christiane Fischer and Jule Mangels for giving support through the central office, Jens Nieschulze, Michael Owonibi and Andreas Ostrowski for managing the central data base, and Eduard Linsenmair, Dominik Hessenmöller, François Buscot, Ernst-Detlef Schulze and the late Elisabeth Kalko for their role in setting up the Biodiversity Exploratories project. We thank the administration of the Hainich national park, the UNESCO Biosphere Reserve Swabian Alb and the UNESCO Biosphere Reserve Schorfheide-Chorin as well as all landowners for the excellent collaboration. The work was partly funded by the DFG Priority Program 1374 "Biodiversity-Exploratories" and by the Senckenberg Gesellschaft für Naturforschung. C.W. is grateful for being funded by the German Research Foundation (DFG, Project number 493487387). E.K. is supported by the German Research Foundation (DFG, KA1590/8-5). H.S. is supported by a María Zambrano fellowship funded by the Ministry of Universities and European Union-Next Generation plan. M.M.G. acknowledges support from the Swiss National Science Foundation (Grant number 310030E-173542). S.M. is supported by the German Research Foundation (DFG, MA4436/1-5). P.M. acknowledges support from the German Research Foundation (DFG; MA 7144/1-1). Field work permits were issued by the state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg from 2008 to 2021.

Author Contributions

G.L.P. and P.M. conceived the study, designed and performed the analyses; G.L.P. and P.M. wrote the manuscript with significant inputs from all authors. Data were contributed by G.L.P., N.V.S., C.P., J.T., C.W., E.A., M.A., N.B., R.S.B., R.B., V.B., M.F., M.M.G., N.H., K.J., E.K., V.H.K., T.K., S.L., S.M., K.M., S.M., F.N., Y.O., D.P., S.P., D.J.P., M.C.R., D.S., M.S.L., M.S., I.S., M.S., J.S., I.S.D., M.T., J.V., C.W., W.W., K.W., M.W., W.W., P.M. Authorship order was determined as follows: (1) core authors; (2) other authors contributing data and inputs on the manuscript (alphabetical); (4) senior author.

Competing Interests

The authors declare no competing interests.

References

1. Hooper, D. U. *et al.* Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* **75**, 3–35 (2005).
2. Cardinale, B. J. *et al.* Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67 (2012).
3. Tilman, D., Isbell, F. & Cowles, J. M. Biodiversity and ecosystem functioning. *Annu. Rev. Ecol. Evol. Syst.* **45**, 471–493 (2014).
4. Hector, A. *et al.* Plant Diversity and Productivity Experiments in European Grasslands. *Science* **286**, 1123–1127 (1999).
5. Soliveres, S. *et al.* Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. *Nature* **536**, 456–459 (2016).
6. Gross, N. *et al.* Functional trait diversity maximizes ecosystem multifunctionality. *Nat. Ecol. Evol.* **1**, 0132 (2017).
7. van der Plas, F. *et al.* Towards the development of general rules describing landscape heterogeneity–multifunctionality relationships. *J. Appl. Ecol.* **56**, 168–179 (2019).
8. Jochum, M. *et al.* The results of biodiversity–ecosystem functioning experiments are realistic. *Nat. Ecol. Evol.* **4**, 1485–1494 (2020).
9. Duffy, J. E., Godwin, C. M. & Cardinale, B. J. Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature* **549**, 261–264 (2017).
10. van der Plas, F. *et al.* Biotic homogenization can decrease landscape-scale forest multifunctionality. *Proc. Natl. Acad. Sci. U. S. A.* **113**, E2549–E2549 (2016).
11. Isbell, F. *et al.* High plant diversity is needed to maintain ecosystem services. *Nature* **477**, 199–202 (2011).

12. Hautier, Y. *et al.* Local loss and spatial homogenization of plant diversity reduce ecosystem multifunctionality. *Nat. Ecol. Evol.* **2**, 50–56 (2018).

13. Srivastava, D. S. & Vellend, M. Biodiversity-ecosystem function research: is it relevant to conservation? *Annu. Rev. Ecol. Evol. Syst.* **36**, 267–294 (2005).

14. Isbell, F. *et al.* Linking the influence and dependence of people on biodiversity across scales. *Nature* **546**, 65–72 (2017).

15. Mori, A. S., Isbell, F. & Seidl, R. β-Diversity, Community Assembly, and Ecosystem Functioning. *Trends Ecol. Evol.* **33**, 549–564 (2018).

16. Chase, J. M. & Knight, T. M. Scale-dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. *Ecol. Lett.* **16**, 17–26 (2013).

17. Chase, J. M. *et al.* Embracing scale-dependence to achieve a deeper understanding of biodiversity and its change across communities. *Ecol. Lett.* **21**, 1737–1751 (2018).

18. Barry, K. E. *et al.* The Future of Complementarity: Disentangling Causes from Consequences. *Trends Ecol. Evol.* **34**, 167–180 (2019).

19. Loreau, M. & Hector, A. Partitioning selection and complementarity in biodiversity experiments. *Nature* **412**, 72–76 (2001).

20. Hagan, J. G., Vanschoenwinkel, B. & Gamfeldt, L. We should not necessarily expect positive relationships between biodiversity and ecosystem functioning in observational field data. *Ecol. Lett.* **24**, 2537–2548 (2021).

21. Brose, U. & Hillebrand, H. Biodiversity and ecosystem functioning in dynamic landscapes. *Philos. Trans. R. Soc. B Biol. Sci.* **371**, 20150267 (2016).

22. Isbell, F. *et al.* Benefits of increasing plant diversity in sustainable agroecosystems. *J. Ecol.* **105**, 871–879 (2017).

23. Tscharntke, T. *et al.* Landscape moderation of biodiversity patterns and processes-eight hypotheses. *Biol. Rev.* **87**, 661–685 (2012).

24. Ricotta, C. On beta diversity decomposition: trouble shared is not trouble halved. *Ecology* **91**, 1981–1983 (2010).

25. Kraft, N. J. B. *et al.* Disentangling the Drivers of β Diversity Along Latitudinal and Elevational Gradients. *Science* **333**, 1755–1758 (2011).

26. Gonthier, D. J. *et al.* Biodiversity conservation in agriculture requires a multi-scale approach. *Proc. R. Soc. Lond. B Biol. Sci.* **281**, 20141358 (2014).

27. Flynn, D. F. *et al.* Loss of functional diversity under land use intensification across multiple taxa. *Ecol. Lett.* **12**, 22–33 (2009).

28. Seibold, S. *et al.* Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* **574**, 671–674 (2019).

29. Foley, J. A. *et al.* Solutions for a cultivated planet. *Nature* **478**, 337–342 (2011).

30. Allan, E. *et al.* Land use intensification alters ecosystem multifunctionality via loss of biodiversity and changes to functional composition. *Ecol. Lett.* **18**, 834–843 (2015).

31. Le Provost, G. *et al.* Land-use history impacts functional diversity across multiple trophic groups. *Proc. Natl. Acad. Sci.* **117**, 1573–1579 (2020).

32. Adl, S. M., Coleman, D. C. & Read, F. Slow recovery of soil biodiversity in sandy loam soils of Georgia after 25 years of no-tillage management. *Agric. Ecosyst. Environ.* **114**, 323–334 (2006).

33. Le Provost, G. *et al.* Contrasting responses of above- and belowground diversity to multiple components of land-use intensity. *Nat. Commun.* **12**, 3918 (2021).

34. James, L. A. (2015). Legacy effects. Oxford Bibliographies in Environmental Science. 720 729 https://doi.org/10.1093/OBO/97801 99363445-0019

35. Lamy, T., Liss, K. N., Gonzalez, A. & Bennett, E. M. Landscape structure affects the provision of multiple ecosystem services. *Environ. Res. Lett.* **11**, 124017 (2016).

36. Alsterberg, C. *et al.* Habitat diversity and ecosystem multifunctionality—The importance of direct and indirect effects. *Sci. Adv.* **3**, e1601475 (2017).

37. Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I. & Thies, C. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecol. Lett.* **8**, 857–874 (2005).

38. Gámez-Virués, S. *et al.* Landscape simplification filters species traits and drives biotic homogenization. *Nat. Commun.* **6**, 8568 (2015).

39. Benton, T. G., Vickery, J. A. & Wilson, J. D. Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* **18**, 182–188 (2003).

40. Bullock, J. M., Aronson, J., Newton, A. C., Pywell, R. F. & Rey-Benayas, J. M. Restoration of ecosystem services and biodiversity: conflicts and opportunities. *Trends Ecol. Evol.* **26**, 541–549 (2011).

41. Dainese, M. *et al.* A global synthesis reveals biodiversity-mediated benefits for crop production. *Sci. Adv.* **5**, eaax0121 (2019).

42. Mitchell, M. G. E., Bennett, E. M. & Gonzalez, A. Linking Landscape Connectivity and Ecosystem Service Provision: Current Knowledge and Research Gaps. *Ecosystems* **16**, 894–908 (2013).

43. Fischer, M. *et al.* Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. *Basic Appl. Ecol.* **11**, 473–485 (2010).

44. Blüthgen, N. *et al.* A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and fertilization. *Basic Appl. Ecol.* **13**, 207–220 (2012).

45. Vogt, J. *et al.* Eleven years' data of grassland management in Germany. *Biodivers. Data J.* **7**, e36387 (2019).

46. Gámez-Virués, S. *et al.* Landscape simplification filters species traits and drives biotic homogenization. *Nat. Commun.* **6**, (2015).

47. Linders, T. E. W. *et al.* Stakeholder priorities determine the impact of an alien tree invasion on ecosystem multifunctionality. *People Nat.* **3**, 658–672 (2021).

48. Nathan, R. Long-distance dispersal of plants. *Science* **313**, 786–788 (2006).

49. Manning, P. *et al.* Grassland management intensification weakens the associations among the diversities of multiple plant and animal taxa. *Ecology* **96**, 1492–1501 (2015).

50. Clough, Y. *et al.* Density of insect-pollinated grassland plants decreases with increasing surrounding land-use intensity. *Ecol. Lett.* **17**, 1168–1177 (2014).

51. Vickery, J. A. *et al.* The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *J. Appl. Ecol.* **38**, 647–664 (2001).

52. López-Jamar, J., Casas, F., Díaz, M. & Morales, M. B. Local differences in habitat selection by Great Bustards Otis tarda in changing agricultural landscapes: implications for farmland bird conservation. *Bird Conserv. Int.* **21**, 328–341 (2011).

53. Wells, K., Böhm, S. M., Boch, S., Fischer, M. & Kalko, E. K. Local and landscape-scale forest attributes differ in their impact on bird assemblages across years in forest production landscapes. *Basic Appl. Ecol.* **12**, 97–106 (2011).

54. Bommarco, R., Lindborg, R., Marini, L. & Öckinger, E. Extinction debt for plants and flower-visiting insects in landscapes with contrasting land use history. *Divers. Distrib.* **20**, 591–599 (2014).

55. Kuussaari, M. *et al.* Extinction debt: a challenge for biodiversity conservation. *Trends Ecol. Evol.* **24**, 564–571 (2009).

56. Lee, M., Manning, P., Rist, J., Power, S. A. & Marsh, C. A global comparison of grassland biomass responses to CO2 and nitrogen enrichment. *Philos. Trans. R. Soc. B Biol. Sci.* **365**, 2047–2056 (2010).

57. Smith, P. Do grasslands act as a perpetual sink for carbon? *Glob. Change Biol.* **20**, 2708–2711 (2014).

58. Wagg, C., Bender, S. F., Widmer, F. & Heijden, M. G. A. van der. Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proc. Natl. Acad. Sci.* **111**, 5266–5270 (2014).

59. Bradford, M. A. *et al.* Discontinuity in the responses of ecosystem processes and multifunctionality to altered soil community composition. *Proc. Natl. Acad. Sci.* **111**, 14478–14483 (2014).

60. Schaub, S. *et al.* Plant diversity effects on forage quality, yield and revenues of semi-natural grasslands. *Nat. Commun.* **11**, 768 (2020).

61. Mace, G. M., Norris, K. & Fitter, A. H. Biodiversity and ecosystem services: a multilayered relationship. *Trends Ecol. Evol.* **27**, 19–26 (2012).

62. Peter, S., Le Provost, G., Mehring, M., Müller, T. & Manning, P. Cultural worldviews consistently explain bundles of ecosystem service prioritisation across rural Germany. *People Nat.* **4**, 218–230 (2022).

63. Emmerson, M. *et al.* How Agricultural Intensification Affects Biodiversity and Ecosystem Services. *Adv. Ecol. Res.* **55**, 43–97 (2016).

64. Manning, P. *et al.* Redefining ecosystem multifunctionality. *Nat. Ecol. Evol.* **2**, 427–436 (2018).

65. Gonzalez, A. *et al.* Scaling-up biodiversity-ecosystem functioning research. *Ecol. Lett.* **23**, 757–776 (2020).

66. Loreau, M., Mouquet, N. & Gonzalez, A. Biodiversity as spatial insurance in heterogeneous landscapes. *Proc. Natl. Acad. Sci.* **100**, 12765–12770 (2003).

67. Anderson, B. J. *et al.* Spatial covariance between biodiversity and other ecosystem service priorities. *J. Appl. Ecol.* **46**, 888–896 (2009).

68. Maes, J. *et al.* Mapping ecosystem services for policy support and decision making in the European Union. *Ecosyst. Serv.* **1**, 31–39 (2012).

69. Mace, G. M., Norris, K. & Fitter, A. H. Biodiversity and ecosystem services: a multilayered relationship. *Trends Ecol. Evol.* **27**, 19–26 (2012).

70. Metzger, J. P. *et al.* Considering landscape-level processes in ecosystem service assessments. *Sci. Total Environ.* **796**, 149028 (2021).
71. Costanza, R. *et al.* Twenty years of ecosystem services: how far have we come and how far do we still need to go? *Ecosyst. Serv.* **28**, 1–16 (2017).
72. DeFries, R. & Nagendra, H. Ecosystem management as a wicked problem. *Science* **356**, 265–270 (2017).
73. Díaz, S. *et al.* Assessing nature's contributions to people. *Science* **359**, 270–272 (2018).
74. Schenk, N. *et al.* Assembled ecosystem measures from grassland EPs (2008-2018) for multifunctionality synthesis - June 2020. Version 40. Biodiversity Exploratories Information System. Dataset. (2022) https://www.bexis.uni-jena.de/ddm/data/Showdata/27087
75. Michael Scherer-Lorenzen, M. & Mueller, S. Acoustic diversity index based on environmental sound recordings on all forest EPs, HAI, 2016. Version 2. Biodiversity Exploratories Information System. Dataset. (2020) https://www.bexis.uni-jena.de/ddm/data/Showdata/27568
76. Michael Scherer-Lorenzen, M. & Mueller, S. Acoustic diversity index based on environmental sound recordings on all forest EPs, Alb, 2016. Version 2. Biodiversity Exploratories Information System. Dataset. (2020) https://www.bexis.uni-jena.de/ddm/data/Showdata/27569
77. Michael Scherer-Lorenzen, M. & Mueller, S. Acoustic diversity index based on environmental sound recordings on all forest EPs, SCH, 2016. Version 2. Biodiversity Exploratories Information System. Dataset. (2020) https://www.bexis.uni-jena.de/ddm/data/Showdata/27570

78. Penone, C. *et al.* Assembled RAW diversity from grassland EPs (2008-2020) for multidiversity synthesis - November 2020. Version 2. Biodiversity Exploratories Information System. Dataset. (2021) https://www.bexis.uni-jena.de/ddm/data/Showdata/27707

79. Penone, C. *et al.* Assembled species information from grassland EPs (2008-2020) for multidiversity synthesis - November 2020. Version 3. Biodiversity Exploratories Information System. Dataset. (2021) https://www.bexis.uni-jena.de/ddm/data/Showdata/27706

80. Junge, X., Schüpbach, B., Walter, T., Schmid, B. & Lindemann-Matthies, P. Aesthetic quality of agricultural landscape elements in different seasonal stages in Switzerland. *Landsc. Urban Plan.* **133**, 67–77 (2015).

81. Lindemann-Matthies, P., Junge, X. & Matthies, D. The influence of plant diversity on people's perception and aesthetic appreciation of grassland vegetation. *Biol. Conserv.* **143**, 195–202 (2010).

82. Haines-Young, R. & Potschin, M. *CICES-Towards a common classification of ecosystem services*. (2016).

83. Byrnes, J. E. *et al.* Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. *Methods Ecol. Evol.* **5**, 111–124 (2014).

84. Neyret, M. *et al.* Assessing the impact of grassland management on landscape multifunctionality. *Ecosyst. Serv.* **52**, 101366 (2021).

85. Ferraro, D. M. *et al.* The phantom chorus: birdsong boosts human well-being in protected areas. *Proc. R. Soc. B Biol. Sci.* **287**, 20201811 (2020).

86. Graves, R. A., Pearson, S. M. & Turner, M. G. Species richness alone does not predict cultural ecosystem service value. *Proc. Natl. Acad. Sci.* **114**, 3774–3779 (2017).

87. Chan, K. M. A., Satterfield, T. & Goldstein, J. Rethinking ecosystem services to better address and navigate cultural values. *Ecol. Econ.* **74**, 8–18 (2012).
88. Villamagna, A. M., Angermeier, P. L. & Bennett, E. M. Capacity, pressure, demand, and flow: A conceptual framework for analyzing ecosystem service provision and delivery. *Ecol. Complex.* **15**, 114–121 (2013).
89. Bolliger, R., Prati, D., Fischer, M., Hoelzel, N. & Busch, V. Vegetation Records for Grassland EPs, 2008 - 2018. Version 2. Biodiversity Exploratories Information System. Dataset. (2020) https://www.bexis.uni-jena.de/ddm/data/Showdata/24247
90. Le Provost, G. & Manning, P. Cover of all vascular plant species in representative 2x2 quadrats of the major surrounding homogeneous vegetation zones in a 75-m radius of the 150 grassland EPs, 2017-2018. Version 4. Biodiversity Exploratories Information System. Dataset. (2021) https://www.bexis.uni-jena.de/ddm/data/Showdata/27846
91. Koleff, P., Gaston, K. J. & Lennon, J. J. Measuring beta diversity for presence–absence data. *J. Anim. Ecol.* **72**, 367–382 (2003).
92. Baselga, A. Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.* **19**, 134–143 (2010).
93. Andreas Ostrowski, Katrin Lorenzen, Eleonora Petzold & Sirko Schindler. *Land use intensity index (LUI) calculation tool of the Biodiversity Exploratories project for grassland survey data from three different regions in Germany since 2006, BEXIS 2 module*. (Zenodo, 2020). doi:10.5281/zenodo.3865579.

94. Thiele, J., Weisser, W. & Scherreiks, P. Historical land use and landscape metrics of grassland EP. Version 2. Biodiversity Exploratories Information System. Dataset. (2020) https://www.bexis.uni-jena.de/ddm/data/Showdata/25747

95. Steckel, J. *et al.* Landscape composition and configuration differently affect trap-nesting bees, wasps and their antagonists. *Biol. Conserv.* **172**, 56–64 (2014).

96. Westphal, C., Steckel, J. & Rothenwöhrer, C. InsectScale / LANDSCAPES - Landscape heterogeneity metrics (grassland EPs, radii 500m-2000m, 2009) - shape files. Version 2. Biodiversity Exploratories Information System. Dataset. (2019) https://www.bexis.uni-jena.de/ddm/data/Showdata/24046

97. Shoffner, A., Wilson, A. M., Tang, W. & Gagné, S. A. The relative effects of forest amount, forest configuration, and urban matrix quality on forest breeding birds. *Sci. Rep.* **8**, 1–12 (2018).

98. Fahrig, L. *et al.* Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecol. Lett.* **14**, 101–112 (2011).

99. Sirami, C. *et al.* Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proc. Natl. Acad. Sci.* **116**, 16442–16447 (2019).

100. Gessler, P. E., Moore, I. D., McKENZIE, N. J. & Ryan, P. J. Soil-landscape modelling and spatial prediction of soil attributes. *Int. J. Geogr. Inf. Syst.* **9**, 421–432.

101. Zinko, U., Seibert, J., Dynesius, M. & Nilsson, C. Plant species numbers predicted by a topography-based groundwater flow index. *Ecosystems* **8**, 430–441 (2005).

102. Moeslund, J. E. *et al.* Topographically controlled soil moisture drives plant diversity patterns within grasslands. *Biodivers. Conserv.* **22**, 2151–2166 (2013).

103. Keddy, P. A. Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.* **3**, 157–164 (1992).

104. Myers, M. C., Mason, J. T., Hoksch, B. J., Cambardella, C. A. & Pfrimmer, J. D. Birds and butterflies respond to soil-induced habitat heterogeneity in experimental plantings of tallgrass prairie species managed as agroenergy crops in Iowa, USA. *J. Appl. Ecol.* **52**, 1176–1187 (2015).

105. Carvalheiro, L. G. *et al.* Soil eutrophication shaped the composition of pollinator assemblages during the past century. *Ecography* **43**, 209–221 (2020).

106. Schöning, I., Klötzing, T., Schrumpf, M., Solly, E. & Trumbore, S. Mineral soil pH values of all experimental plots (EP) of the Biodiversity Exploratories project from 2011, Soil (core project). Version 8. Biodiversity Exploratories Information System. Dataset. (2021) https://www.bexis.uni-jena.de/ddm/data/Showdata/14447

107. Sørensen, R., Zinko, U. & Seibert, J. On the calculation of the topographic wetness index: evaluation of different methods based on field observations. *Hydrol. Earth Syst. Sci.* **10**, 101–112 (2006).

108. Le Provost, G. *et al.* Aggregated environmental and land-use covariates of the 150 grassland EPs used in "Contrasting responses of above- and belowground diversity to multiple components of land-use intensity". Version 5. Biodiversity Exploratories Information System. Dataset. (2021) https://www.bexis.uni-jena.de/ddm/data/Showdata/31018

109. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (2020).

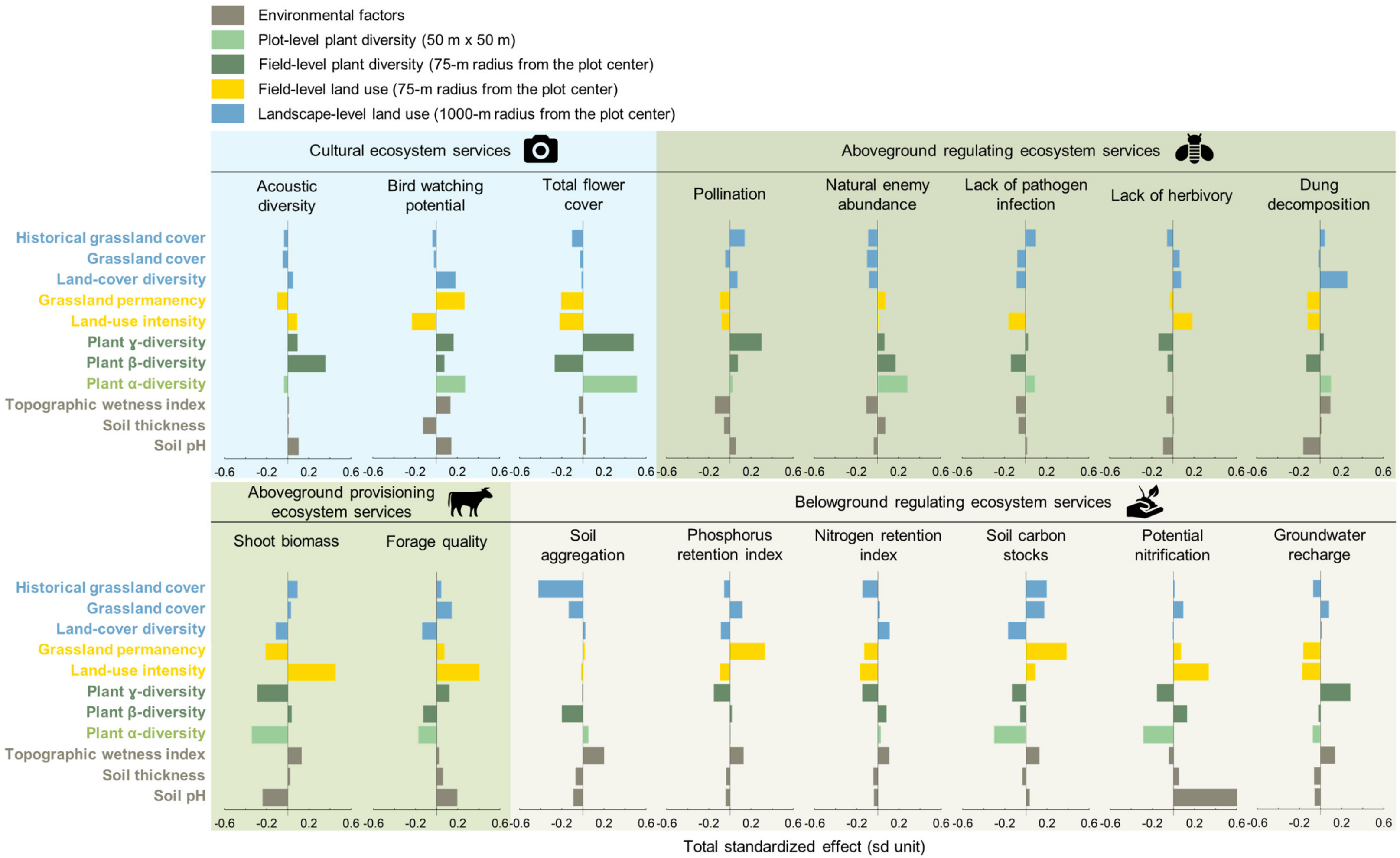
110. Grace, J. B. Structural equation modeling for observational studies. *J. Wildl. Manag.* **72**, 14–22 (2008).

111. Grace, J. B. *Structural equation modeling and natural systems*. (Cambridge University Press, 2006).

112. Rosseel, Y. Lavaan: An R package for structural equation modeling and more. Version 0.5–12 (BETA). *J. Stat. Softw.* **48**, 1–36 (2012).

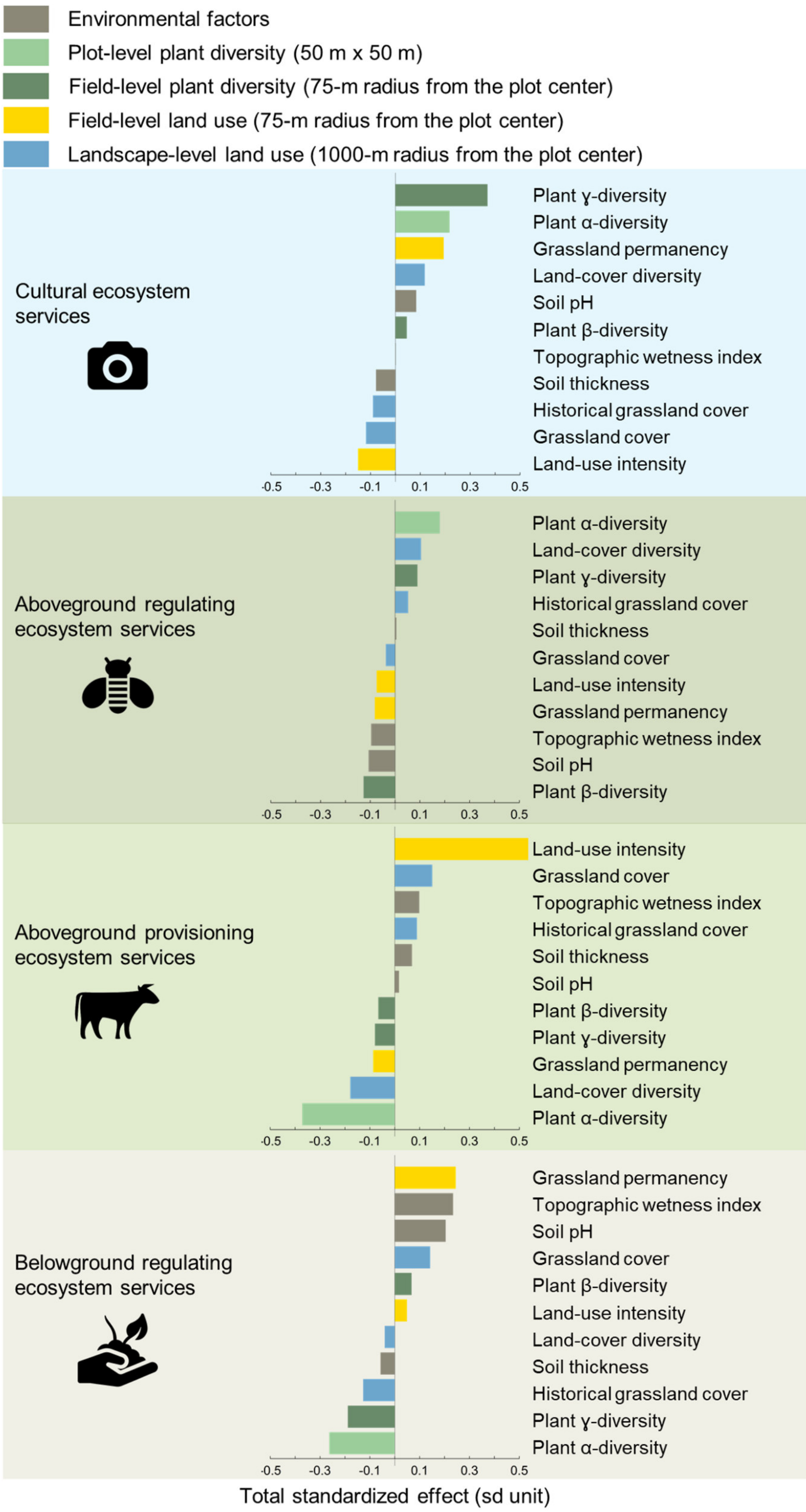
113. Le Bagousse-Pinguet, Y. *et al.* Phylogenetic, functional, and taxonomic richness have both positive and negative effects on ecosystem multifunctionality. *Proc. Natl. Acad. Sci.* **116**, 8419–8424 (2019).

1058 **Supplementary Information**



1059 **Figure S1. Drivers of individual cultural, aboveground regulating and provisioning, and belowground regulating ecosystem**
1060 **services in grasslands.** Total standardized effects (sd unit) were calculated based on the results of structural equation models

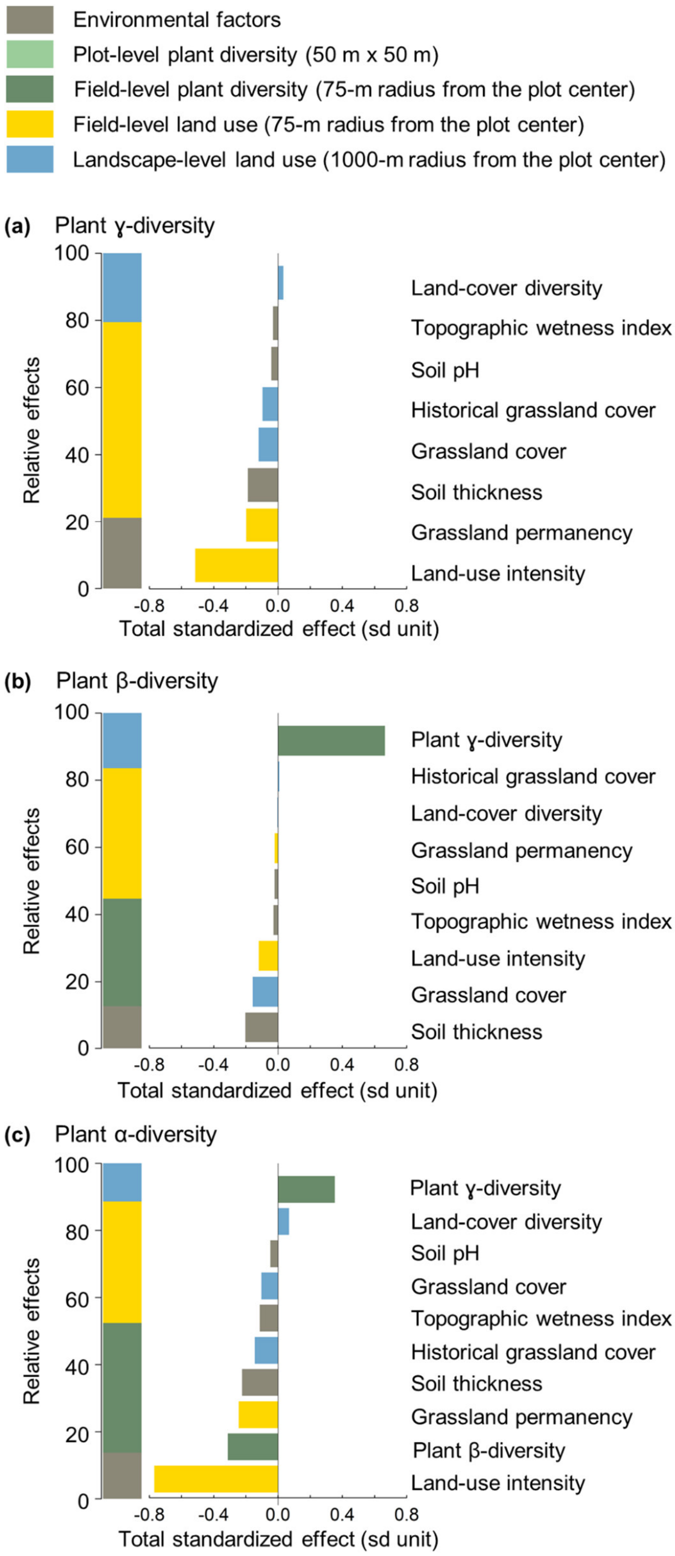
(considering both direct and indirect effects of the predictors) for each predictor: environmental factors, plot-level (50 m × 50 m) plant diversity, field-level (75-m radius from the plot center) plant diversity, field-level (75-m radius from the plot center) land use, and landscape-level (1000-m radius from the plot center) land use. The total standardized effects correspond to the sum of standardized direct effects (i.e. individual paths) and indirect effects (i.e. the multiplied paths). All predictors were scaled to allow interpretation of parameter estimates on a comparable scale. Plot-level and landscape-level predictors were log-transformed. n = 150 biologically independent samples for bird watching potential, forage quality, nitrogen retention index, potential nitrification, groundwater recharge; n = 147 biologically independent samples for lack of herbivory; n = 146 biologically independent samples for soil carbon stocks; n = 142 biologically independent samples for dung decomposition , lack of pathogen infection and shoot biomass; n = 136 biologically independent samples for phosphorus retention index; n = 119 biologically independent samples for pollination; n = 114 biologically independent samples for acoustic diversity; n = 93 biologically independent samples for soil aggregation; n = 83 biologically independent samples for the natural enemy abundance; n = 70 biologically independent samples for the total flower cover.



1072 **Figure S2. The multiple drivers of cultural, aboveground regulating and provisioning, and**

belowground regulating ecosystem services in grasslands *considering average-based multifunctionality indices*. Total standardized effects (sd unit) were calculated based on the results of structural equation models (considering both direct and indirect effects of the predictors) for each predictor: environmental factors, plot-level (50 m × 50 m) plant diversity, field-level (75-m radius from the plot center) plant diversity, field-level (75-m radius from the plot center) land use, and landscape-level (1000-m radius from the plot center) land use. Models were fitted to four multifunctionality measures: cultural, aboveground regulating and provisioning, and belowground regulating ecosystem service multifunctionality. The total standardized effects correspond to the sum of standardized direct effects (i.e. individual paths) and indirect effects (i.e. the multiplied paths). For each multifunctionality measure, total standardized effects of the different predictors are ordered from the highest positive effect to the lowest negative effect. All predictors were scaled to allow interpretation of parameter estimates on a comparable scale. Plot-level and landscape-level predictors were log-transformed. n = 150 biologically independent samples.

Figure S3. The multiple drivers of cultural, aboveground regulating and provisioning, and belowground regulating ecosystem services in grasslands *considering multifunctionality indices calculated at the 25% (panel on the left) and 75% (panel on the right) thresholds.* Total standardized effects (sd unit) were calculated based on the results of structural equation models (considering both direct and indirect effects of the predictors) for each predictor: environmental factors, plot-level (50 m × 50 m) plant diversity, field-level (75-m radius from the plot center) plant diversity, field-level (75-m radius from the plot center) land use, and landscape-level (1000-m radius from the plot center) land use. Models were fitted to four multifunctionality measures: cultural, aboveground regulating and provisioning, and belowground regulating ecosystem service multifunctionality. The total standardized effects correspond to the sum of standardized direct effects (i.e. individual paths) and indirect effects (i.e. the multiplied paths). For each multifunctionality measure, total standardized effects of the different predictors are ordered from the highest positive effect to the lowest negative effect. All predictors were scaled to allow interpretation of parameter estimates on a comparable scale. Plot-level and landscape-level predictors were log-transformed. n = 150 biologically independent samples.



1101 **Figure S4. Drivers of plot-level plant α-diversity, and field-level plant β-diversity and γ-**
1102 **diversity.** To assess the surrounding field-level plant diversity of each grassland plot, we surveyed

the vegetation within the major surrounding homogeneous vegetation zones in a 75-m radius of each plot (i.e. field level). These zones were mostly situated within the same grassland-field as the focal plot but we occasionally surveyed other habitat types (c. 20% were situated in hedgerows, margins or forests). We surveyed at least four quadrats in the surroundings of each grassland plot. Total standardized effects (sd unit) were calculated based on the results of structural equation models (considering both direct and indirect effects of the predictors) for each predictor: environmental factors, plot-level (50 m × 50 m) plant diversity, field-level (75-m radius from the plot center) plant diversity, field-level (75-m radius from the plot center) land use, and landscape-level (1000-m radius from the plot center) land use. The total standardized effects correspond to the sum of standardized direct effects (i.e. individual paths) and indirect effects (i.e. the multiplied paths). Total standardized effects of the different predictors are ordered from the highest positive effect to the lowest negative effect. All predictors were scaled to allow interpretation of parameter estimates on a comparable scale. Plot-level and landscape-level predictors were log-transformed. See Table S2 for the individual path coefficients. n = 150 biologically independent samples.

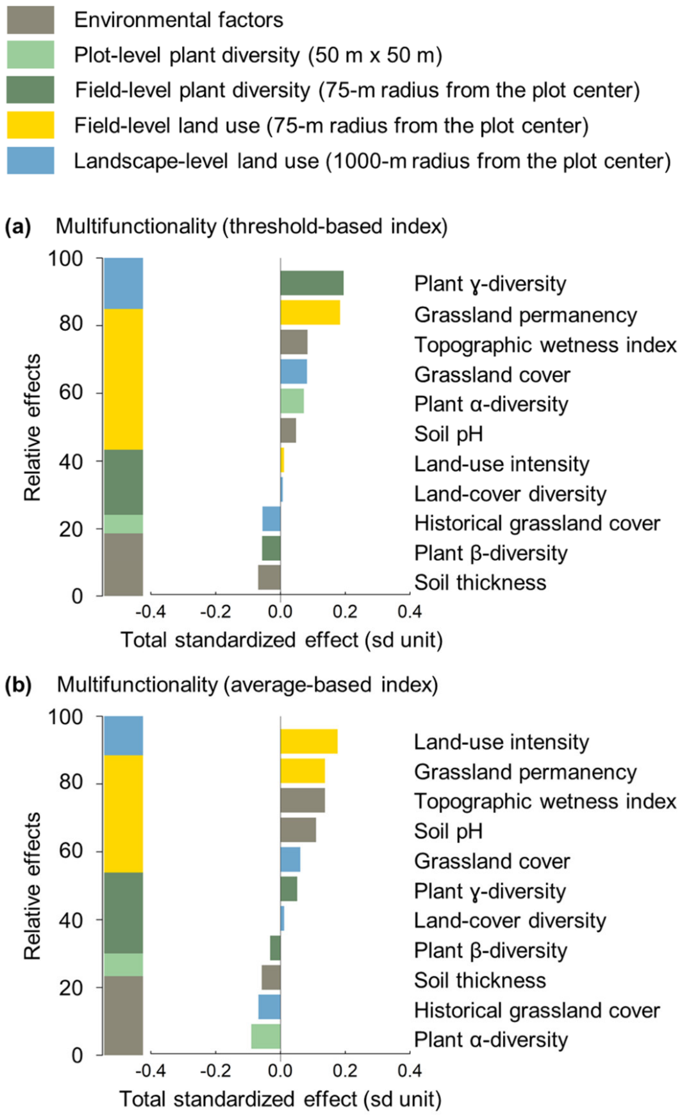
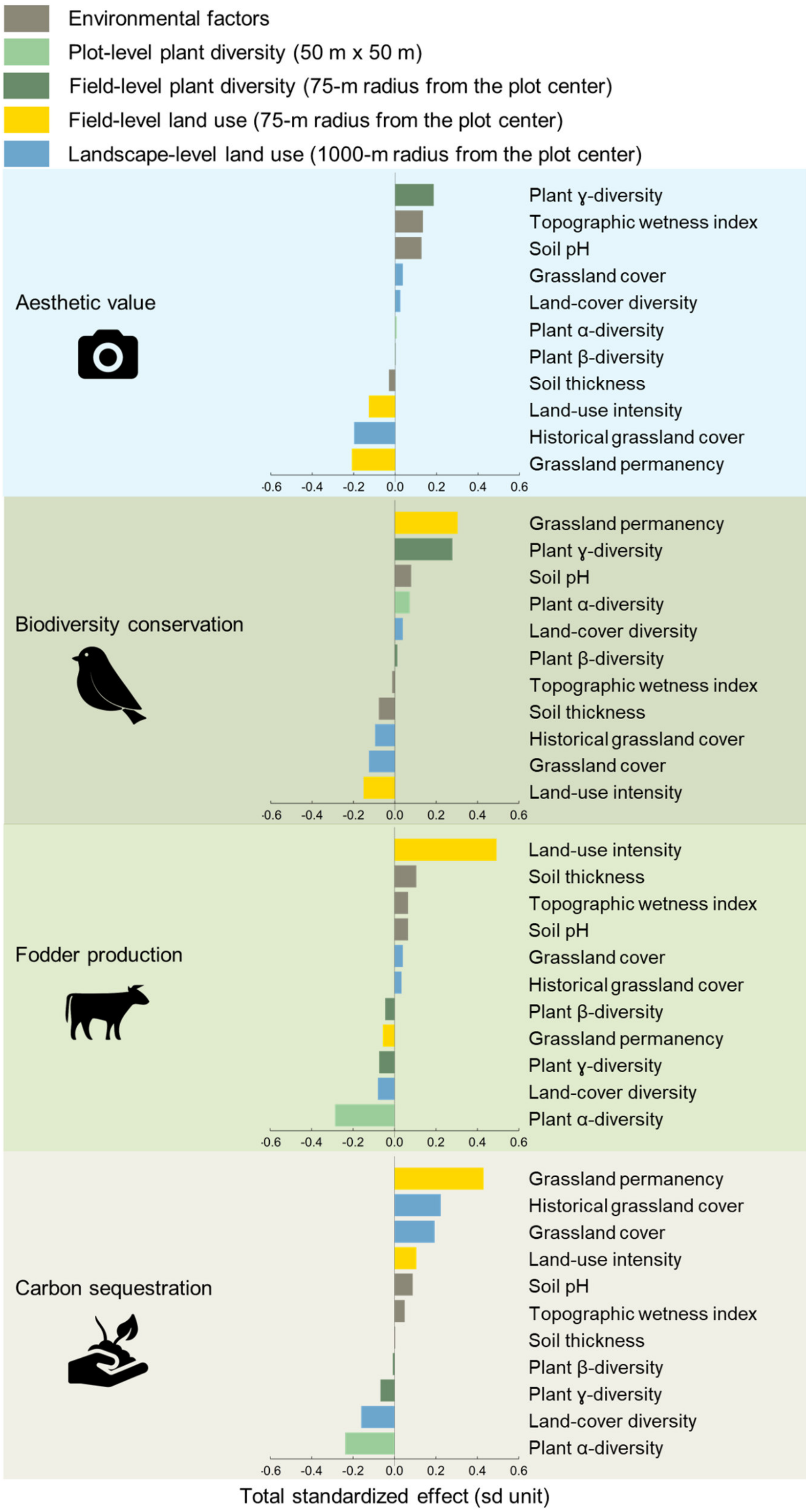


Figure S5. Drivers of overall ecosystem service multifunctionality, considering (a) a 50% threshold-based index or (b) an average-based index. Total standardized effects (sd unit) were calculated based on the results of structural equation models (considering both direct and indirect effects of the predictors) for each predictor: environmental factors, plot-level (50 m × 50 m) plant diversity, field-level (75-m radius from the plot center) plant diversity, field-level (75-m radius from the plot center) land use, and landscape-level (1000-m radius from the plot center) land use. The total standardized effects correspond to the sum of standardized direct effects (i.e. individual paths) and indirect effects (i.e. the multiplied paths). For each multifunctionality measure, total standardized effects of the different predictors are ordered from the highest positive effect to the lowest negative effect. All predictors were scaled to allow interpretation of parameter estimates on a comparable scale. Plot-level and landscape-level predictors were log-transformed. n = 150 biologically independent samples.



1129 **Figure S5. The multiple drivers of the most prioritized ecosystem services in grasslands by**

1130 **local stakeholders: aesthetic value, biodiversity conservation, fodder production, carbon**

sequestration. Total standardized effects (sd unit) were calculated based on the results of structural equation models (considering both direct and indirect effects of the predictors) for each predictor: environmental factors, plot-level (50 m × 50 m) plant diversity, field-level (75-m radius from the plot center) plant diversity, field-level (75-m radius from the plot center) land use, and landscape-level (1000-m radius from the plot center) land use. Models were fitted to four ecosystem service supply variables: aesthetic value (i.e. acoustic diversity and total flower cover, n = 129 independent samples), fodder production (i.e. shoot biomass and forage quality, n = 150 independent samples), biodiversity conservation (i.e. bird watching potential, n = 150 independent samples) and carbon sequestration (i.e. soil carbon stocks, n = 146 independent samples). The total standardized effects correspond to the sum of standardized direct effects (i.e. individual paths) and indirect effects (i.e. the multiplied paths). For each ecosystem service supply variable, total standardized effects of the different predictors are ordered from the highest positive effect to the lowest negative effect. All predictors were scaled to allow interpretation of parameter estimates on a comparable scale. Plot-level and landscape-level predictors were log-transformed.

Table S1. Details of the sampling methods for each ecosystem service considered in the analysis. For each ecosystem service, we used a specific indicator measured for one or multiple years. Note that different services were measured on different areas within a given 50 m × 50 m plot. Most data available at https://doi.org/10.17616/R32P9Q.

Ecosystem service type	Ecosystem service	Indicator	Year	Number of plots	Data owners	Methods description
Cultural ecosystem services	Acoustic diversity	Distribution of acoustic energy among frequency bands	2016	114	S. Müller M. Scherer-Lorenzen	Sounds were recorded 1 minute every 10 minutes each day in April and May 2016, from 7am to 7pm, using an autonomous recording system (Soundscape Explorer T, Lunilettronics) placed at 2-m height in the center of the grassland plot. The acoustic diversity (ADI)[1,2] was calculated across the frequency range of 0–24 kHz using 1 kHz steps and a decibel threshold of −50.
	Bird watching potential	Bird species richness	Sum between 2008 and 2012	150	K. Jung S. Renner M. Tschapka	Birds were surveyed during the breeding season (March-June) by standardized audio-visual point-counts between 2008-2012. We used fixed-radius point counts and recorded all individuals, seen or heard during a five-minute count during the morning chorus (sunrise-11:00h) were registered. In exceptional cases, observations were made during the evening chorus (last 3 hours before sunset). Each plot was visited five times each year.
	Total flower cover	% flower cover	2009	70	J. Binkenstein M. Schäfer	Between May and September 2009 we counted flowering units, i.e. single flowers or aggregations of flowers that touched each other, of all flowering plant species (excluding grasses and sedges) on transects along the four edges of each plot (50 m x 4 x 3 m = 600 m^2). Flowering units were counted before and after the

						first mowing event. For very abundant plant species we extrapolated the number of flowering units from an area of 112 m^2 homogeneously distributed across the transect area on each plot. Total blossom cover of each species was calculated by multiplying the number of flowering units by the area of a single flowering unit. We obtained data on sizes of flowering units from the literature[3,4]. In case of very variably sized flowering units (e.g. in some Apiaceae) we estimated the area of each flowering unit individually. The total blossom cover of each plot was calculated as the sum of the individual blossom cover of all plant species[5].
Abovegrou nd regulating ecosystem services	Pollination	Total abundance of flower visitors	2008	119	C. Weiner M. Werner N. Blüthgen	On a transect of 200 x 3 m along the plot edge, all individual flower visitors were recorded and identified during three transect walks (total 6 h) on a single day between April and August 2008. The total number of individuals of the orders Diptera, Hymenoptera, Lepidoptera and Coleoptera (excluding Nitidulidae) defined the total abundance used here.
	Natural enemy abundance	Number of parasitoid predating pest insects recorded in trap-nesting wasps	2008	83	J. Steckel C. Westphal I. Steffan-Dewenter	Four wooden poles were placed 4-m apart on each plot and two trap nests were mounted 1.5 m high on each pole[6]. Trap nests were constructed using PVC tubes 10.5 cm in diameter, filled with reed internodes of *Phragmites australis*. To sample the entire community of cavity-nesting species, we used reed of internodes differing in diameter (0.2–1.2 cm). Trap nests were installed between the middle of April and the middle of

						May 2008 and were collected at the end of September and beginning of October 2008. The traps were stored until hatching and the wasps emerging were counted and identified to species. Here we include only those wasps feeding on pest insects. This was the total number of wasp individuals belonging to the families Crabonidae (excluding Trypoxylon species, which feed on spiders) and Vespidae.
	Lack of pathogen infection	Inverse of the total cover of foliar fungal pathogens	2011	142	S. Blaser D. Prati M. Fischer	On four transects of 25 x 1 m per plot all plant species were scanned for pathogens infection, including rust, powdery mildew, downy mildew and smut fungi between May and June 2011. The percentage of infected plants was multiplied with the severity per pathogen species (divided by 1000 to get a number between 0 and 1). The infection of all pathogens per plant species was combined, because one plant species can be infected by various pathogens at the same time. The infection severity per plant species was multiplied with the according plant species cover on each plot separately. For each plot, we then calculated the lack of pathogen infection as 1 - the total cover of foliar fungal pathogens.
	Lack of herbivory	Inverse of the total proportion of leaf area damaged by herbivores	2017 and 2018 (depending on	147	F. Neff M. Gossner	Based on vegetation records from the previous year, we collected leaf material of the 10 most abundant plant species at the margins of each 50 m × 50 m plot to reduce impact on other experiments in May 2017 or 2018. Plant material was collected before the first mowing event. For each plant, we visually estimated the

			the region)			area damaged by invertebrate herbivores on 12 to 200 leaves (depending on leaf size) and measured total leaf area using a leaf area meter. The deduced herbivory rates (% damaged area) per plant species were then summarised to community-level herbivory rates based on the respective plant cover values in vegetation records of the sampling year (2017 or 2018). For each plot, we then calculated the lack of herbivory as 1 - the herbivory rate.
	Dung decomposition	Average percentage of dung dry mass removed	2014 and 2015	142	K. Frank N. Blüthgen	Dung beetle communities contribute to the rapid decomposition of fecal deposits from both wild mammals and domestic livestock, representing a key ecosystem service[7]. We installed five dung piles (cow, sheep, horse, wild boar, red deer) on each 150 plots and collected the remaining dung after 48 hours, between May and July. The average percentage of scaled (per dung type) dung dry mass removed (mostly by tunnelling dung beetles) was used as indicator of dung removal rates.
Aboveground provisioning ecosystem services	Shoot biomass	Shoot biomass (mean biomass 2009-2017)	Mean 2009-2017	142	B. Schmitt D. Prati M. Fischer V. Klaus T. Kleinebecker N. Hölzel	Between mid-May and mid-June each year, peak-standing aboveground biomass was harvested by clipping the vegetation 2 - 3 cm above ground in four randomly placed quadrates of 0.5 m × 0.5 m in each subplot. Dead standing biomass was removed as far as possible form the samples. Plant biomass was dried at 80°C for 48 hours and weighed. Temporary fences

						prevented biomass removal by livestock or cutting before sampling.
	Forage quality	Mean of scaled crude protein concentration* and scaled relative forage value†	Mean 2009-2013	150	V. Klaus N. Hölzel T. Kleinebecker	Total nitrogen concentrations in ground samples of aboveground biomass were determined using an elemental auto-analyzer (NA1500, CarloErba, Milan, Italy). Neutral detergent fibre (NDF) and acid detergent fibre (ADF) contents were measured gravimetrically[8]. *6.25×shoot nitrogen concentration †[[88.9-(0.779×shoot acid detergent fibre)]×[120/Shoot neutral detergent fibre]]/1.29[9]
Belowground regulating ecosystem services	Soil aggregation	Proportion of water stable soil aggregates	2011	93	E. K. Morris M. Rillig	Five perforated plastic cups filled with crushed sterile soil and wrapped with 35 µm mesh were buried in each plot from April to October 2011. After collection, one combined soil sample for each site was prepared by combining the contents of all recovered cups from each site. A subsample of this soil was passed through a 250 µm sieve under water to determine the percentage of water stable macroaggregates.
	Phosphorus retention index	Ratio between plant shoot and microbial phosphorus stock and soil extractable phosphorus	2014	136	E. Sorkau Y. Oelmann R. Boeddinghaus S. Marhan D. Schäfer	Phosphorus (P) retention index was calculated as the ratio between the sum of P in aboveground vascular plants and microbes related to the sum of plant-available P in soil, P in vascular plants and P in microbes[10] as follow: PRI = $(P_b + P_m) / (P_b + P_m + P_s)$, where P_b = P in plants × Plant biomass, P_m = P in microbes × Bulk density, and P_s = Olsen P_i × Bulk density Plant samples were digested with concentrated HNO_3 in a microwave oven. In the extracts, P_i concentrations

						were determined with a continuous flow analyzer (Bran+Luebbe, Norderstedt, Germany) using the molybdenum blue method. To determine the microbial biomass P, we used a combination of methods[11]. We used hexanol instead of chloroform as fumigation agent. Plant-available P concentrations in soil were determined using a slightly modified $NaHCO_3$ method[12]. 0.5 g of air-dried soil was extracted with 0.2 l of a 0.5 M $NaHCO_3$ solution (adjusted to pH 8.5 with 1M NaOH).
	Nitrogen retention index	Ratio between plant shoot and microbial nitrogen stock and soil extractable nitrogen	2014	150	D. Berner R. Boeddinghaus E. Kandeler S. Marhan B. Stempfhuber M. Schloter D. Schäfer M. Fischer	Nitrogen (N) retention index was calculated as the ratio between N in aboveground vascular plants and microbes related to the sum of N in soil, N in vascular plants and N in microbes as follow: NRI = $(N_b + N_m) / (N_b + N_m + N_s)$, where N_b = N in plants × Plant biomass, N_m = N in microbes × Bulk density, and $N_s = (NH_4 + NO_3)$ × Bulk density Plant samples were dried at 80 C for 48 h, weighed and pulverized using a cyclone mill. Samples of 2–3 g were analyzed with a NIR spectrometer. The reflectance spectrum of each pulverized biomass sample was recorded between 1250 and 2350 nm at 1 nm intervals; with each scan consisting of 24 single measurements averaged to one spectrum. Calibration models that were used to predict N, P and K concentrations were derived from previously established calibration models; accuracy of model prediction was checked by applying an external validation process[13]. Chloroform-

						fumigation-extraction method[14] was used to determine microbial biomass nitrogen. N was extracted from each fumigated and non-fumigated replicate (5 g) with 40 ml 0.5 M M K_2SO_4. The suspension was horizontally shaken (30 Min, 150 rpm) and centrifuged (30 Min, 4400 x g). Fumigated sample replicates were incubated with $CHCl_3$ for 24 hours. N concentrations in dissolved (1:4, extract:deion. H_2O) extracts were measured with a TOC/TN analyzer (Multi N/C 2100S, Analytik Jena AG, Jena, Germany). Ammonium (NH_4) and nitrate (NO_3) analyzed in the 2011 soil campaign (see Methods) were used to estimate N in soil. After extraction of soil samples with 0.01 M $CaCl_2$ at a soil-to-liquid ratio of 1:3, ammonium and nitrate concentrations were determined by continuous flow analysis with a photometric autoanalyzer (CFA-SAN Plus; Skalar Analytik, Germany).
	Soil carbon stocks	Soil carbon stocks in the top 10 cm	2011	146	I. Schöning M. Schrumpf	Soil samples were collected in 2011 within the plots and each composite soil sample was weighed, air-dried, sieved (<2 mm) and a subsample homogenized and ground with a ball mill (RETSCH MM200, Retsch, Haan, Germany). Total carbon (TC) contents were analyzed on ground subsamples by dry combustion in a CN analyzer "Vario Max" (Elementar Analysensysteme GmbH, Hanau, Germany). Inorganic carbon (IC) was determined after combustion of organic carbon in a muffle furnace (450°C for 16 h). The soil organic carbon

						(SOC) equals the difference between TC and IC. The total soil mass was calculated based on the weight of the dry fine-soil (105°C) and its volume. Organic carbon stocks were determined by multiplying SOC concentrations with the total soil mass (<2 mm, 0-10 cm) per m^2 for each plot.
	Potential nitrification	Potential nitrification rates	2011	150	B. Stempfhuber M. Schloter	Following [15], 10 mM ammonium sulphate solution was supplied as substrate to 2.5g of soil composite samples, from the 2011 soil sampling campaign (see Methods). 1.5M sodium chlorate was added to prevent the turnover of nitrite to nitrate. After incubation for 5h at 25°C, 2M potassium chloride was used to stop the reaction, followed by 20 min incubation and a centrifugation step. After addition of ammonium chloride buffer and a reagent for nitrite determination to the supernatant, the colour reaction was spectrometrically detected. Potential nitrification rates were calculated as the production of nitrite per g of dry soil per hour[16].
	Groundwater recharge	Annual net downward water fluxes to below 0.15 m soil depth, i.e. downward minus upward water fluxes by capillary rise	Mean between 2010-2016	150	S. Leimer W. Wilcke	We used a soil water balance model, developed to calculate vertical soil water fluxes (in mm) from the 0–0.15 m soil layer in grassland[17,18]. The model is based on the soil water balance equation: $P + UF = DF + ETa + \Delta S$; where P is precipitation, UF is upward flux (via capillary rise), DF is downward flux, ETa is actual evapotranspiration, and ΔS is the change in soil water storage between two subsequent observation dates ($\Delta S = S_{t2} - S_{t1}$). As input data for the model, we used

						biweekly precipitation, and climate data (soil moisture, air temperature, relative humidity) per plot. The model output comprised biweekly actual evapotranspiration, downward water flux and upward water flux. The net flux from the 0–0.15 m soil layer to deeper soil was calculated as the difference between downward water flux and upward water flux in 14-day resolution and then aggregated to annual resolution for the years 2010 to 2016[17]. Then, we used the average values of the net flux per plot; i.e. the net flux between the 0–0.15 m soil layer and deeper soil in mm as an estimate of the water flux to deeper soil layers and finally into groundwater.

Table S2. Path coefficients for the different structural equation models fitted to the four multifunctionality measures: cultural, aboveground regulating and provisioning, and belowground regulating ecosystem service multifunctionality. All estimates are standardized path coefficients. Single headed arrows → indicate directional relationships between variables, double headed arrows ↔ indicate covariances between variables. Direct effects correspond to the individual paths (e.g. Plant γ-diversity → Cultural ecosystem services) and indirect effects are the multiplied paths, e.g. (Plant γ-diversity → Plant α-diversity) × (Plant α-diversity → Cultural ecosystem services). n = 150 biologically independent samples.

Models with plant α-diversity				
	Path	**Estimate**	**Standard error**	**p value**
Cultural ecosystem services	Soil pH → Cultural ecosystem services	0.09	0.08	0.28
	Soil thickness → Cultural ecosystem services	-0.01	0.08	0.92
	Topographic wetness index → Cultural ecosystem services	0.04	0.09	0.61
	Plant α-diversity → Cultural ecosystem services	0.06	0.13	0.63
	Plant β-diversity → Cultural ecosystem services	0.12	0.10	0.21
	Plant γ-diversity → Cultural ecosystem services	0.06	0.10	0.57
	Land-use intensity → Cultural ecosystem services	-0.02	0.11	0.85
	Grassland permanency → Cultural ecosystem services	0.22	0.09	0.02

	Land-cover diversity → Cultural ecosystem services	0.08	0.08	0.30
	Grassland cover → Cultural ecosystem services	-0.01	0.08	0.90
	Historical grassland cover → Cultural ecosystem services	-0.13	0.09	0.17
	Soil pH → Plant α-diversity	-0.02	0.05	0.65
	Soil thickness → Plant α-diversity	-0.14	0.05	0.00
	Topographic wetness index → Plant α-diversity	-0.10	0.05	0.07
	Plant β-diversity → Plant α-diversity	-0.31	0.06	0.00
	Plant γ-diversity → Plant α-diversity	0.56	0.07	0.00
	Land-use intensity → Plant α-diversity	-0.41	0.06	0.00
	Grassland permanency → Plant α-diversity	-0.10	0.06	0.09
	Land-cover diversity → Plant α-diversity	0.04	0.05	0.38
	Grassland cover → Plant α-diversity	-0.06	0.05	0.21
	Historical grassland cover → Plant α-diversity	-0.07	0.06	0.23
	Soil pH → Plant β-diversity	0.01	0.07	0.94
	Soil thickness → Plant β-diversity	-0.08	0.07	0.25
	Topographic wetness index → Plant β-diversity	-0.01	0.08	0.93

	Plant γ-diversity → Plant β-diversity	0.67	0.08	0.00
	Land-use intensity → Plant β-diversity	0.22	0.08	0.01
	Grassland permanency → Plant β-diversity	0.11	0.08	0.17
	Land-cover diversity → Plant β-diversity	-0.02	0.07	0.70
	Grassland cover → Plant β-diversity	-0.08	0.07	0.25
	Historical grassland cover → Plant β-diversity	0.07	0.08	0.36
	Soil pH → Plant γ-diversity	-0.04	0.07	0.58
	Soil thickness → Plant γ-diversity	-0.19	0.07	0.01
	Topographic wetness index → Plant γ-diversity	-0.03	0.08	0.69
	Land-use intensity → Plant γ-diversity	-0.52	0.07	0.00
	Grassland permanency → Plant γ-diversity	-0.20	0.08	0.01
	Land-cover diversity → Plant γ-diversity	0.03	0.07	0.63
	Grassland cover → Plant γ-diversity	-0.12	0.07	0.07
	Historical grassland cover → Plant γ-diversity	-0.10	0.08	0.23
	Soil pH ↔ Land-use intensity	-0.19	0.08	0.01
	Soil pH ↔ Topographic wetness index	0.35	0.08	0.00

	Soil pH ↔ Grassland permanency	0.30	0.08	0.00
	Soil pH ↔ Historical grassland cover	0.26	0.08	0.00
	Soil thickness ↔ Topographic wetness index	0.23	0.08	0.00
	Topographic wetness index ↔ Historical grassland cover	0.35	0.08	0.00
	Topographic wetness index ↔ Grassland permanency	0.27	0.08	0.00
	Land-use intensity ↔ Grassland permanency	-0.21	0.07	0.00
	Land-use intensity ↔ Land-cover diversity	0.18	0.08	0.02
	Grassland permanency ↔ Historical grassland cover	0.51	0.09	0.00
	Land-cover diversity ↔ Grassland cover	0.19	0.08	0.02
Aboveground regulating ecosystem services	Soil pH → Aboveground provisioning ecosystem services	-0.11	0.09	0.23
	Soil thickness → Aboveground provisioning ecosystem services	-0.03	0.09	0.76
	Topographic wetness index → Aboveground provisioning ecosystem services	0.02	0.09	0.85
	Plant α-diversity → Aboveground provisioning ecosystem services	0.23	0.14	0.10
	Soil pH → Aboveground provisioning ecosystem services	-0.11	0.09	0.23
	Soil thickness → Aboveground provisioning ecosystem services	-0.03	0.09	0.76

	Land-use intensity → Aboveground regulating ecosystem services	0.07	0.17	0.57
	Grassland permanency → Aboveground regulating ecosystem services	-0.03	0.17	0.81
	Land-cover diversity → Aboveground regulating ecosystem services	-0.07	0.19	0.39
	Grassland cover → Aboveground regulating ecosystem services	0.00	0.16	0.98
	Historical grassland cover → Aboveground regulating ecosystem services	0.12	0.19	0.21
	Soil pH → Plant α-diversity	-0.02	0.05	0.65
	Soil thickness → Plant α-diversity	-0.14	0.05	0.00
	Topographic wetness index → Plant α-diversity	-0.10	0.05	0.07
	Plant β-diversity → Plant α-diversity	-0.31	0.06	0.00
	Plant γ-diversity → Plant α-diversity	0.56	0.07	0.00
	Land-use intensity → Plant α-diversity	-0.41	0.06	0.00
	Grassland permanency → Plant α-diversity	-0.10	0.06	0.09
	Land-cover diversity → Plant α-diversity	0.04	0.05	0.38
	Grassland cover → Plant α-diversity	-0.06	0.05	0.21
	Historical grassland cover → Plant α-diversity	-0.07	0.06	0.23
	Soil pH → Plant β-diversity	0.01	0.07	0.94

	Soil thickness → Plant β-diversity	-0.08	0.07	0.25
	Topographic wetness index → Plant β-diversity	-0.01	0.08	0.93
	Plant γ-diversity → Plant β-diversity	0.67	0.08	0.00
	Land-use intensity → Plant β-diversity	0.22	0.08	0.01
	Grassland permanency → Plant β-diversity	0.11	0.08	0.17
	Land-cover diversity → Plant β-diversity	-0.02	0.07	0.70
	Grassland cover → Plant β-diversity	-0.08	0.07	0.25
	Historical grassland cover → Plant β-diversity	0.07	0.08	0.36
	Soil pH → Plant γ-diversity	-0.04	0.07	0.58
	Soil thickness → Plant γ-diversity	-0.19	0.07	0.01
	Topographic wetness index → Plant γ-diversity	-0.03	0.08	0.69
	Land-use intensity → Plant γ-diversity	-0.52	0.07	0.00
	Grassland permanency → Plant γ-diversity	-0.20	0.08	0.01
	Land-cover diversity → Plant γ-diversity	0.03	0.07	0.63
	Grassland cover → Plant γ-diversity	-0.12	0.07	0.07
	Historical grassland cover → Plant γ-diversity	-0.10	0.08	0.23

	Soil pH ↔ Land-use intensity	-0.19	0.08	0.01
	Soil pH ↔ Topographic wetness index	0.35	0.08	0.00
	Soil pH ↔ Grassland permanency	0.30	0.08	0.00
	Soil pH ↔ Historical grassland cover	0.26	0.08	0.00
	Soil thickness ↔ Topographic wetness index	0.23	0.08	0.00
	Topographic wetness index ↔ Historical grassland cover	0.35	0.08	0.00
	Topographic wetness index ↔ Grassland permanency	0.27	0.08	0.00
	Land-use intensity ↔ Grassland permanency	-0.21	0.07	0.00
	Land-use intensity ↔ Land-cover diversity	0.18	0.08	0.02
	Grassland permanency ↔ Historical grassland cover	0.51	0.09	0.00
	Land-cover diversity ↔ Grassland cover	0.19	0.08	0.02
Aboveground provisioning ecosystem services	Soil pH → Aboveground provisioning ecosystem services	0.07	0.07	0.35
	Soil thickness → Aboveground provisioning ecosystem services	0.09	0.07	0.21
	Topographic wetness index → Aboveground provisioning ecosystem services	0.04	0.07	0.58
	Plant α-diversity → Aboveground provisioning ecosystem services	-0.29	0.11	0.01

	Plant β-diversity → Aboveground provisioning ecosystem services	-0.14	0.09	0.11
	Plant γ-diversity → Aboveground provisioning ecosystem services	0.18	0.11	0.11
	Land-use intensity → Aboveground provisioning ecosystem services	0.49	0.09	0.00
	Grassland permanency → Aboveground provisioning ecosystem services	-0.04	0.08	0.64
	Land-cover diversity → Aboveground provisioning ecosystem services	-0.08	0.07	0.24
	Grassland cover → Aboveground provisioning ecosystem services	0.03	0.07	0.61
	Historical grassland cover → Aboveground provisioning ecosystem services	0.04	0.08	0.60
	Soil pH → Plant α-diversity	-0.02	0.05	0.65
	Soil thickness → Plant α-diversity	-0.14	0.05	0.00
	Topographic wetness index → Plant α-diversity	-0.10	0.05	0.07
	Plant β-diversity → Plant α-diversity	-0.31	0.06	0.00
	Plant γ-diversity → Plant α-diversity	0.56	0.07	0.00
	Land-use intensity → Plant α-diversity	-0.41	0.06	0.00
	Grassland permanency → Plant α-diversity	-0.10	0.06	0.09
	Land-cover diversity → Plant α-diversity	0.04	0.05	0.38
	Grassland cover → Plant α-diversity	-0.06	0.05	0.21

	Historical grassland cover → Plant α-diversity	-0.07	0.06	0.23
	Soil pH → Plant β-diversity	0.01	0.07	0.94
	Soil thickness → Plant β-diversity	-0.08	0.07	0.25
	Topographic wetness index → Plant β-diversity	-0.01	0.08	0.93
	Plant γ-diversity → Plant β-diversity	0.67	0.08	0.00
	Land-use intensity → Plant β-diversity	0.22	0.08	0.01
	Grassland permanency → Plant β-diversity	0.11	0.08	0.17
	Land-cover diversity → Plant β-diversity	-0.02	0.07	0.70
	Grassland cover → Plant β-diversity	-0.08	0.07	0.25
	Historical grassland cover → Plant β-diversity	0.07	0.08	0.36
	Soil pH → Plant γ-diversity	-0.04	0.07	0.58
	Soil thickness → Plant γ-diversity	-0.19	0.07	0.01
	Topographic wetness index → Plant γ-diversity	-0.03	0.08	0.69
	Land-use intensity → Plant γ-diversity	-0.52	0.07	0.00
	Grassland permanency → Plant γ-diversity	-0.20	0.08	0.01
	Land-cover diversity → Plant γ-diversity	0.03	0.07	0.63

	Grassland cover → Plant γ-diversity	-0.12	0.07	0.07
	Historical grassland cover → Plant γ-diversity	-0.10	0.08	0.23
	Soil pH ↔ Land-use intensity	-0.19	0.08	0.01
	Soil pH ↔ Topographic wetness index	0.35	0.08	0.00
	Soil pH ↔ Grassland permanency	0.30	0.08	0.00
	Soil pH ↔ Historical grassland cover	0.26	0.08	0.00
	Soil thickness ↔ Topographic wetness index	0.23	0.08	0.00
	Topographic wetness index ↔ Historical grassland cover	0.35	0.08	0.00
	Topographic wetness index ↔ Grassland permanency	0.27	0.08	0.00
	Land-use intensity ↔ Grassland permanency	-0.21	0.07	0.00
	Land-use intensity ↔ Land-cover diversity	0.18	0.08	0.02
	Grassland permanency ↔ Historical grassland cover	0.51	0.09	0.00
	Land-cover diversity ↔ Grassland cover	0.19	0.08	0.02
Belowground regulating ecosystem services	Soil pH → Belowground regulating ecosystem services	0.08	0.08	0.35
	Soil thickness → Belowground regulating ecosystem services	-0.02	0.08	0.79

	Topographic wetness index → Belowground regulating ecosystem services	0.20	0.09	0.02
	Plant α-diversity → Belowground regulating ecosystem services	0.03	0.13	0.82
	Plant β-diversity → Belowground regulating ecosystem services	0.07	0.10	0.51
	Plant γ-diversity → Belowground regulating ecosystem services	-0.01	0.13	0.97
	Land-use intensity → Belowground regulating ecosystem services	-0.12	0.11	0.28
	Grassland permanency → Belowground regulating ecosystem services	0.22	0.10	0.02
	Land-cover diversity → Belowground regulating ecosystem services	-0.02	0.08	0.78
	Grassland cover → Belowground regulating ecosystem services	0.13	0.08	0.09
	Historical grassland cover → Belowground regulating ecosystem services	-0.07	0.09	0.45
	Soil pH → Plant α-diversity	-0.02	0.05	0.65
	Soil thickness → Plant α-diversity	-0.14	0.05	0.00
	Topographic wetness index → Plant α-diversity	-0.10	0.05	0.07
	Plant β-diversity → Plant α-diversity	-0.31	0.06	0.00
	Plant γ-diversity → Plant α-diversity	0.56	0.07	0.00
	Land-use intensity → Plant α-diversity	-0.41	0.06	0.00
	Grassland permanency → Plant α-diversity	-0.10	0.06	0.09

	Land-cover diversity → Plant α-diversity	0.04	0.05	0.38
	Grassland cover → Plant α-diversity	-0.06	0.05	0.21
	Historical grassland cover → Plant α-diversity	-0.07	0.06	0.23
	Soil pH → Plant β-diversity	0.01	0.07	0.94
	Soil thickness → Plant β-diversity	-0.08	0.07	0.25
	Topographic wetness index → Plant β-diversity	-0.01	0.08	0.93
	Plant γ-diversity → Plant β-diversity	0.67	0.08	0.00
	Land-use intensity → Plant β-diversity	0.22	0.08	0.01
	Grassland permanency → Plant β-diversity	0.11	0.08	0.17
	Land-cover diversity → Plant β-diversity	-0.02	0.07	0.70
	Grassland cover → Plant β-diversity	-0.08	0.07	0.25
	Historical grassland cover → Plant β-diversity	0.07	0.08	0.36
	Soil pH → Plant γ-diversity	-0.04	0.07	0.58
	Soil thickness → Plant γ-diversity	-0.19	0.07	0.01
	Topographic wetness index → Plant γ-diversity	-0.03	0.08	0.69
	Land-use intensity → Plant γ-diversity	-0.52	0.07	0.00

	Grassland permanency → Plant γ-diversity	-0.20	0.08	0.01
	Land-cover diversity → Plant γ-diversity	0.03	0.07	0.63
	Grassland cover → Plant γ-diversity	-0.12	0.07	0.07
	Historical grassland cover → Plant γ-diversity	-0.10	0.08	0.23
	Soil pH ↔ Land-use intensity	-0.19	0.08	0.01
	Soil pH ↔ Topographic wetness index	0.35	0.08	0.00
	Soil pH ↔ Grassland permanency	0.30	0.08	0.00
	Soil pH ↔ Historical grassland cover	0.26	0.08	0.00
	Soil thickness ↔ Topographic wetness index	0.23	0.08	0.00
	Topographic wetness index ↔ Historical grassland cover	0.35	0.08	0.00
	Topographic wetness index ↔ Grassland permanency	0.27	0.08	0.00
	Land-use intensity ↔ Grassland permanency	-0.21	0.07	0.00
	Land-use intensity ↔ Land-cover diversity	0.18	0.08	0.02
	Grassland permanency ↔ Historical grassland cover	0.51	0.09	0.00
	Land-cover diversity ↔ Grassland cover	0.19	0.08	0.02

Table S3. The values of χ^2 and R^2 for the different structural equation models. Models were fitted to four multifunctionality measures: cultural, aboveground regulating and provisioning, and belowground regulating ecosystem service multifunctionality. The χ^2 and P-values indicate whether the model covariance significantly differs from the observed one (non-significant P-values indicate good model fits). The R^2 indicates the amount of variance in the cultural, aboveground regulating and provisioning, and belowground regulating ecosystem service multifunctionality explained by the model. n = 150 biologically independent samples.

Multifunctionality measure	χ^2	P-value	R^2
Cultural ecosystem services	**22.44**	**0.17**	**0.17**
Aboveground regulating ecosystem services	**22.44**	**0.17**	**0.06**
Aboveground provisioning ecosystem services	**22.44**	**0.17**	**0.42**
Belowground regulating ecosystem services	**22.44**	**0.17**	**0.17**

Table S4. Current average proportion of the different land-cover types, and past average proportion of grasslands within a 1000-m landscape of each grassland plot in the three Biodiversity Exploratories region.

			Schwäbische Alb	**Hainich-Dün**	**Schorfheide-Chorin**
Current landscape-level land use	% croplands		14.98	34.29	24.70
	% grasslands		36.66	30.03	45.85
	% forests		41.41	30.68	21.24
	% roads		0.55	0.62	0.73
	% urban areas		6.39	4.35	4.60
	% water bodies		0.01	0.03	2.88
Past landscape-level land use	% grasslands	year 1820/50	30.34	8.60	27.36
		year 1910/30	26.56	5.97	25.50
		year 1960	30.82	7.64	22.45

Table S5. Relative ecosystem service (ES) priority for each stakeholder group (local residents, nature conservation associations, agriculture and tourism sectors) for the four major ecosystem services supplied by grasslands within the study regions: aesthetic value (indicated by acoustic diversity and total flower cover), fodder production (shoot biomass and forage quality), biodiversity conservation (bird species richness) and carbon sequestration (i.e. soil carbon stocks). ES priority was calculated as the proportion of the total priority points allocated to the service within a social survey, averaged across the individual responses within each stakeholder group.

Ecosystem service	Indicators	Weightings for each stakeholder group			
		Local residents	Nature conservation associations	Agriculture	Tourism
Aesthetic value	Acoustic diversity + Total flower cover	0.26	0.18	0.15	0.32
Fodder production	Shoot biomass + Forage quality	0.22	0.15	0.49	0.16
Biodiversity conservation	Bird species richness	0.35	0.45	0.26	0.34
Carbon sequestration	Soil carbon stocks	0.17	0.22	0.11	0.18

References

1. Villanueva-Rivera, L. J., Pijanowski, B. C., Doucette, J. & Pekin, B. A primer of acoustic analysis for landscape ecologists. *Landsc. Ecol.* **26**, 1233–1246 (2011).
2. Shaw, T., Müller, S. & Scherer-Lorenzen, M. Slope does not affect autonomous recorder detection shape: considerations for acoustic monitoring in forested landscapes. *Bioacoustics* **0**, 1–22 (2021).
3. Jäger E.J. & Werner K (2007). Gefässpflanzen Atlasband, 11th edn.n. Spektrum, Heidelberg.
4. Schauer T. & Caspari C. (2005). Der grosse BLV-Pflanzenführer, 9th edn. Blv, Munich.
5. Binkenstein, J., Renoult, J. P. & Schaefer, H. M. Increasing land-use intensity decreases floral colour diversity of plant communities in temperate grasslands. *Oecologia* **173**, 461–471 (2013).
6. Steckel, J. *et al.* Landscape composition and configuration differently affect trap-nesting bees, wasps and their antagonists. *Biol. Conserv.* **172**, 56–64 (2014).
7. Frank, K., Hülsmann, M., Assmann, T., Schmitt, T. & Blüthgen, N. Land use affects dung beetle communities and their ecosystem service in forests and grasslands. *Agric. Ecosyst. Environ.* **243**, 114–122 (2017).
8. Klaus, V. H. *et al.* Nutrient concentrations and fibre contents of plant community biomass reflect species richness patterns along a broad range of land-use intensities among agricultural grasslands. *Perspect. Plant Ecol. Evol. Syst.* **13**, 287–295 (2011).
9. Rohweder, D., Barnes, R. F. & Jorgensen, N. Proposed hay grading standards based on laboratory analyses for evaluating quality. *J. Anim. Sci.* **47**, 747–759 (1978).
10. Oelmann, Y. *et al.* Above- and belowground biodiversity jointly tighten the P cycle in agricultural grasslands. *Nat. Commun.* **12**, 4431 (2021).

11. Sorkau, E. *et al.* The role of soil chemical properties, land use and plant diversity for microbial phosphorus in forest and grassland soils. *J. Plant Nutr. Soil Sci.* **181**, 185–197 (2018).

12. Olsen, S. R. *Estimation of available phosphorus in soils by extraction with sodium bicarbonate*. (US Department of Agriculture, 1954).

13. Kleinebecker, T., Klaus, V. H. & Hölzel, N. Reducing sample quantity and maintaining high prediction quality of grassland biomass properties with near infrared reflectance spectroscopy. *J. Infrared Spectrosc.* **19**, 495–505 (2011).

14. Vance, E. D., Brookes, P. C. & Jenkinson, D. S. An extraction method for measuring soil microbial biomass C. *Soil Biol. Biochem.* **19**, 703–707 (1987).

15. Hoffmann, H., Schloter, M. & Wilke, B.-M. Microscale-scale measurement of potential nitrification rates of soil aggregates. *Biol. Fertil. Soils* **44**, 411–413 (2007).

16. Stempfhuber, B. *et al.* Drivers for ammonia-oxidation along a land-use gradient in grassland soils. *Soil Biol. Biochem.* **69**, 179–186 (2014).

17. Leimer, S. *et al.* Does plant diversity affect the water balance of established grassland systems? *Ecohydrology* **11**, e1945 (2018).

18. Leimer, S. *et al.* Plant diversity effects on the water balance of an experimental grassland. *Ecohydrology* **7**, 1378–1391 (2014).