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

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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 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.

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, in real-world ecosystems, plant diversity and the associated diversity of other taxa at larger scales could also influence local ecosystem functioning[7,10,15,21]. The 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 the overall surrounding species pool, 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, that 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 highly 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 the permanency of semi-natural habitats in the surrounding landscape can significantly affect local ecosystem service provision directly, via 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 might 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, including understudied services such as cultural 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 (Table S1). 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 (see Methods): aesthetic value, biodiversity conservation, fodder production, and carbon sequestration.

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 in our models 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 we 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

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 studied ecosystem service types (Fig. 3, see also Figs. S1 and S2). 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 (Figs. 3 and S2), 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 of plant α-diversity = 0.06 on cultural ecosystem service multifunctionality index (Fig. 3, Table S2). Field-level plant diversity accounted for 30.3% ± 7.0 s.e.m of the total effects (Fig. 2), with a total standardized 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 standardized 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 standardized effect = 0.17). Grassland permanency can enhance the local abundance and the diversity of cultural ecosystem service providers, such as birds[31] (Fig. S1). 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 standardized 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 standardized effect of land-cover diversity = 0.09, Fig. 3) and particularly on the individual service of bird watching potential (total standardized effect of land-cover diversity = 0.18, Fig. S1).

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 standardized 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 (Fig. S1). 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% (Fig. S3), meaning levels of aboveground regulating ecosystem services were at their 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 standardized 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 standardized effect = -0.04, Fig. 3). The effect of landscape-level land use was largely due to a positive effect of historical grassland cover on aboveground regulating ecosystem services (total standardized 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 (Fig. S1).

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 standardized effect = 0.49), including fodder production (Fig. S1). 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 standardized effect of the plant α-diversity = -0.29) and of the field-level plant diversity on these services (total standardized 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 standardized effect of topographic wetness index = 0.20) and soil pH (total standardized effect = 0.08, Fig. 3). This relates to tighter cycling of nutrients and higher topsoil carbon stocks in moist and pH-neutral soils (Fig. S1). We also found a strong positive effect of field-level grassland permanency on belowground regulating ecosystem services (total standardized 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 (Fig. S1). 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 on ecosystem services

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 Fig. S4). 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 (Fig. S1). 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 stakeholder prioritized ecosystem services

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 standardized effects = 0.18 on aesthetic value, and 0.28 on biodiversity conservation (Fig. S5). By contrast, fodder production and carbon sequestration were mostly driven by land-use and environmental factors (Fig. S5). Field-level land-use intensity positively affected fodder production, with a total standardized effect of land-use intensity = 0.50. Grassland permanency and historical grassland cover also had strong positive effects on carbon sequestration, with total standardized effects of 0.43 and= 0.22, respectively (Fig. S5).

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 standardized 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 standardized 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 Table S5). 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 drivers. 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 preserving 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 will have 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 not only help to maintain a biodiverse species pool, but can also 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 seen to be 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

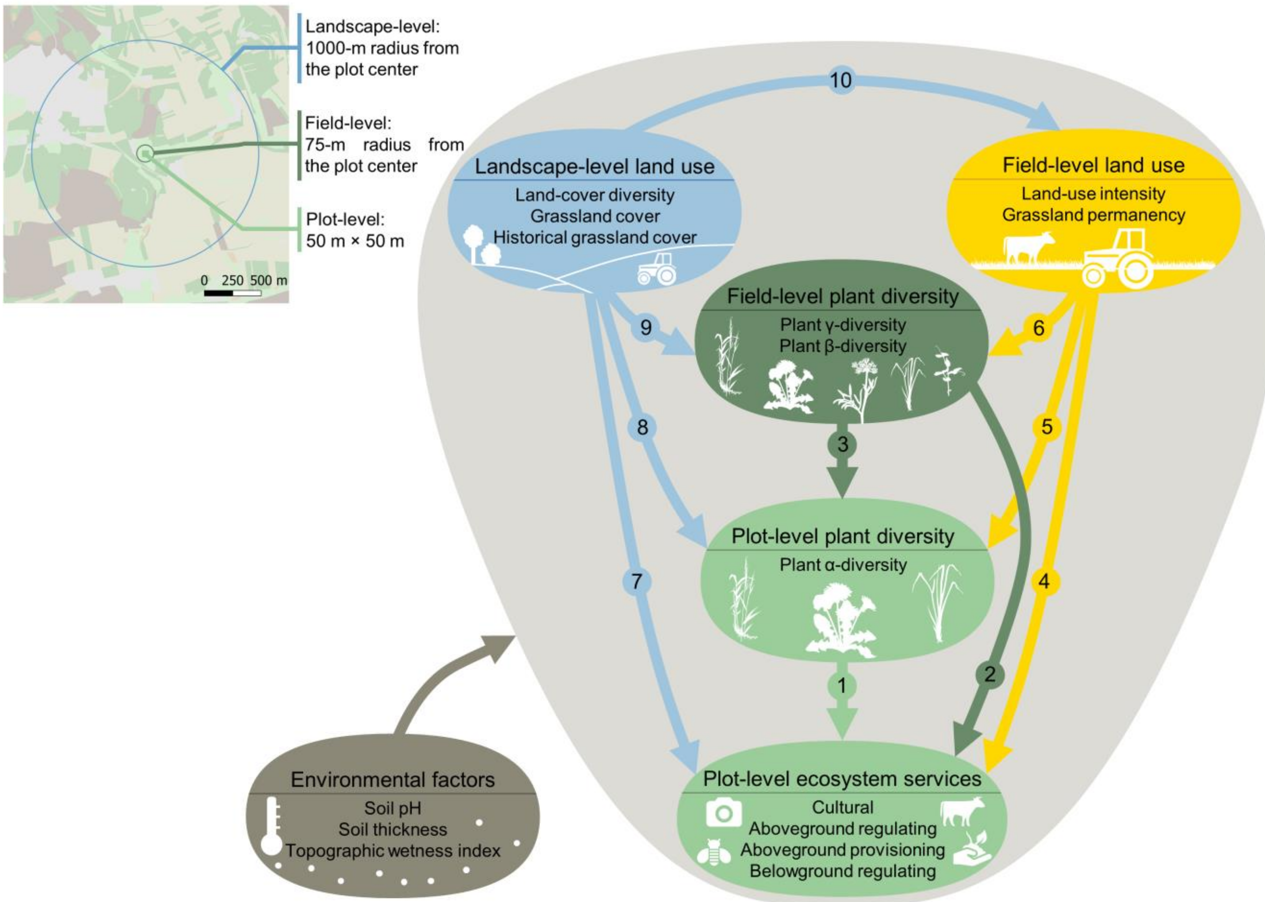


Figure 1. Conceptual framework of the relationship between landscape- and field-level land use, field- and plot-level plant diversity and plot-level ecosystem services. Landscape-level (1000-m radius from the plot center) land use is represented in blue, field-level (75-m radius from the plot center) 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.

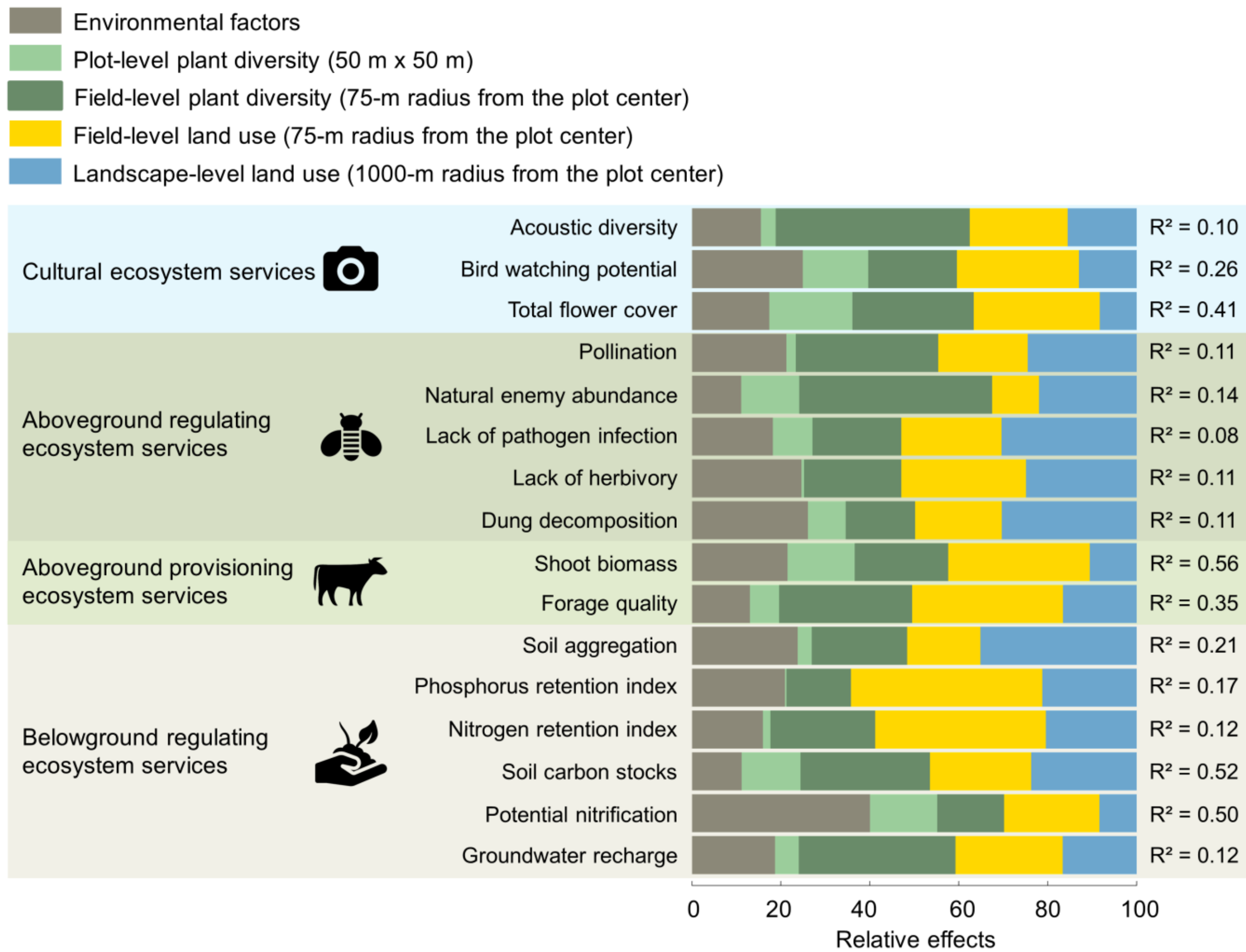
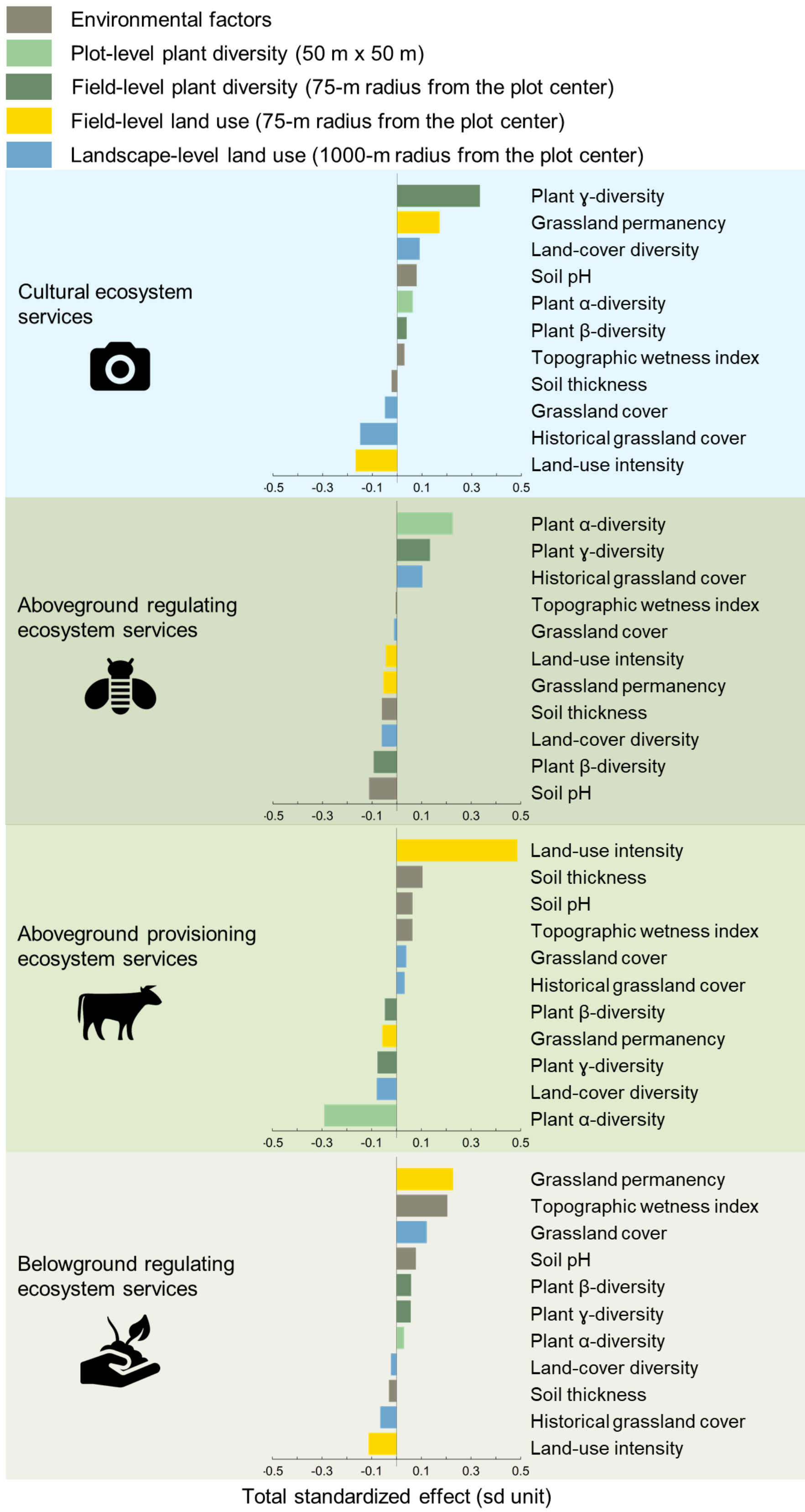


Figure 2. Relative importance of plant diversity and land-use predictors on cultural, aboveground regulating and provisioning, and belowground regulating ecosystem services. The effects of the predictors were calculated considering both direct and indirect relationships (total effects) between the predictors 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.



467 **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.

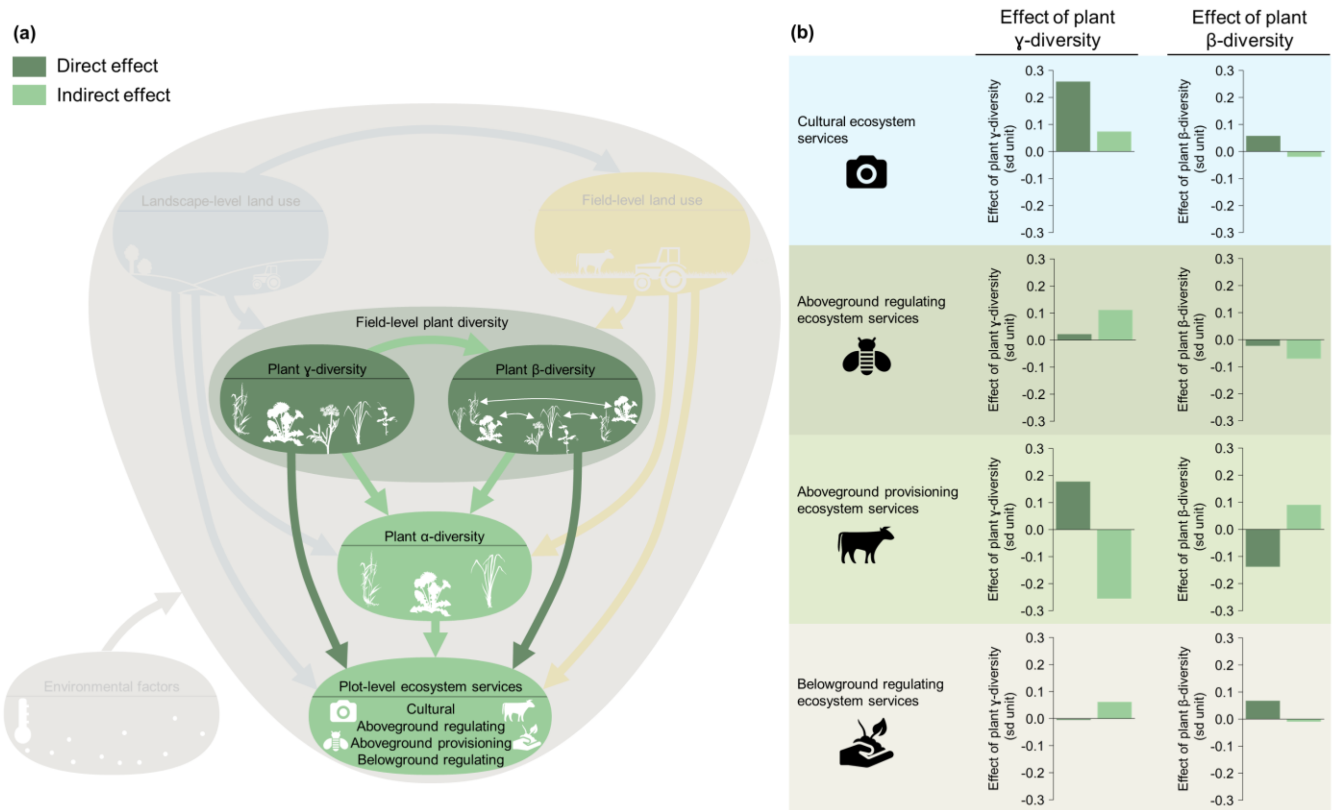
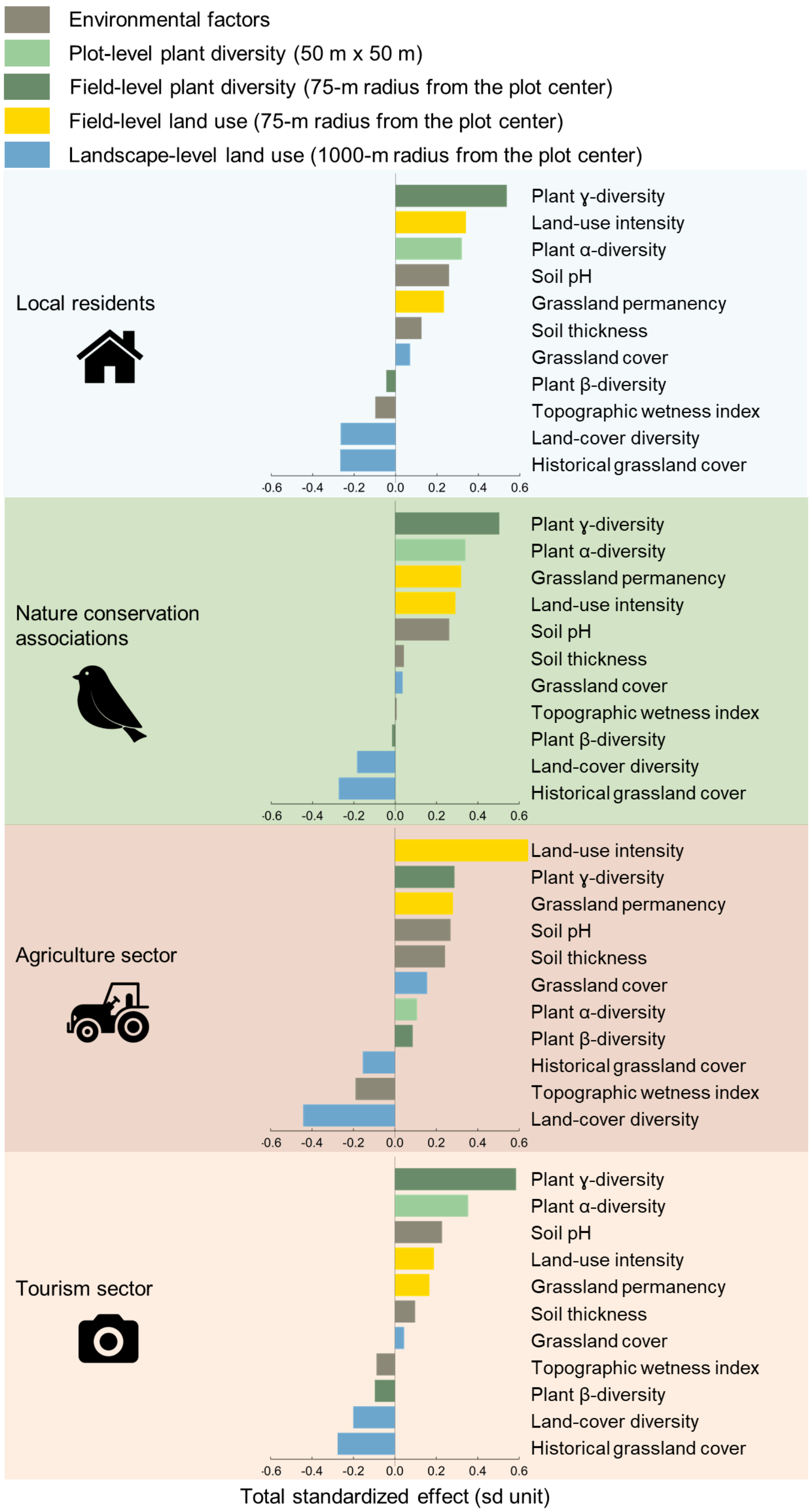


Figure 4. The strength of direct and indirect effects of field-level plant diversity on plot-level ecosystem services. To disentangle the direct and indirect effects of field-level plant γ-diversity and plant β-diversity, through changing plot-level plant α-diversity, a subset of the full structural equation model was considered (a). Direct and indirect effects of field-level plant γ-diversity and plant β-diversity 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.



490 **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 Table S1 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 Fig. S3. 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 (Fig. S2). 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 Fig. S5).

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 of 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 Table S4). 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 (Table S4). 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 (Table S3). 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 (Table S2) 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.

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