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The supply of multiple ecosystem services requires biodiversity across spatial scales

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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. Here 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, probably 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 drive these services. This key information is required for the upscaling of biodiversity–ecosystem service relationships, and the informed management of biodiversity within agricultural landscapes.

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 <1,000 m^2) 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 substantial as biodiversity change occurs at all spatial scales, and sometimes in contrasting directions, for example 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 multi-scale nature of biodiversity is essential to understanding how biodiversity underpins ecosystem services[14,15]. At the plot level, higher plant species richness (that is, 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 (that is, 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 overall

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plant diversity of the surrounding species pool (that is, 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 and 3). Alongside the effects of γ-diversity, heterogeneity in species identities and abundances between local communities (that is, 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 (for example, pollination and pest control) or cultural ecosystem services (for example, birdwatching), 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 and 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 (for example, fertilization and pesticide use that promotes 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 (for example, 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 Article, we addressed the gaps highlighted above by investigating how plant diversity at different spatial scales affects 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 (LUI)[44,45], and that were situated in landscapes of varying complexity[38] and management history (Methods).

Ecosystem services were classified into four types: (1) cultural ecosystem services: acoustic diversity, birdwatching potential and total flower cover; (2) aboveground regulating ecosystem services: pollination, natural enemy abundance, lack of pathogen infection, lack of herbivory and dung decomposition; (3) aboveground provisioning ecosystem services: shoot biomass and forage quality; (4) 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[46] 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 (Methods).

We used structural equation models (SEMs) 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 (defined as within a 1,000 m radius) factors. The specific variables considered represent drivers of the local supply of ecosystem services. At the plot level, plant diversity (that is, 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 (that is, 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] (that is, 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 control for and estimate 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 (TWI)[30,33]. Field-level LUI was measured as a compound index of grazing, mowing and fertilization intensities[44,45]. In addition, we consider the effect of the grassland permanency (that is, 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 (that is, grassland cover) and stability (that is, historical grassland cover) of semi-natural habitats, and the presence of a diversity of habitats (that

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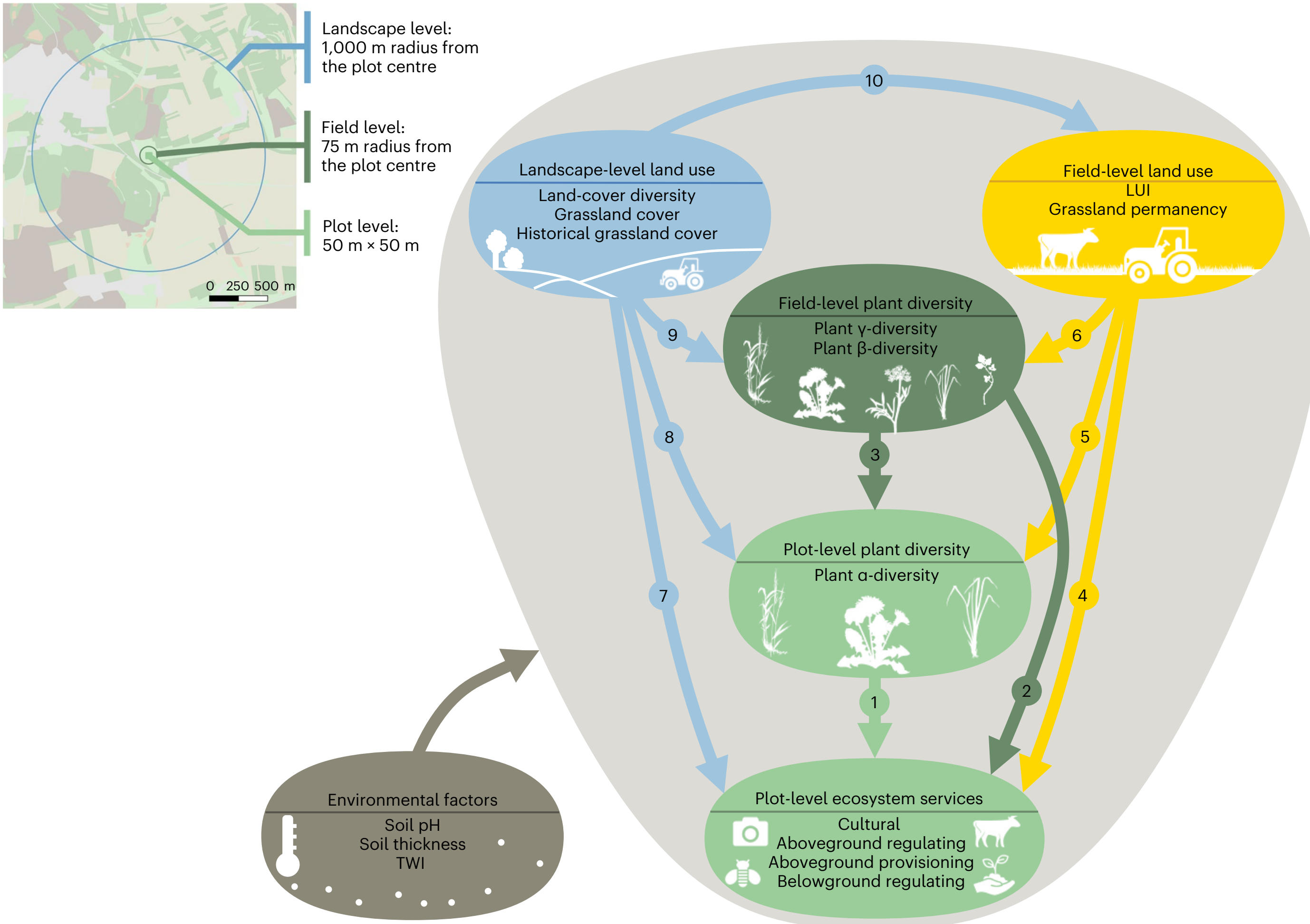

Fig. 1 | Conceptual framework of the relationship between landscape- and field-level land use, field- and plot-level plant diversity and plot-level ecosystem services. Landscape-level (1,000 m radius from the plot centre) land use is represented in blue, field-level (75 m radius from the plot centre) 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 SEM 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 Supplementary Data Table 2. Each plant icon represents a different species in the species pool. Arrows illustrate causal links between plot-level plant diversity, field-level plant diversity and land use, landscape-level land use and ecosystem services. For a full explanation of these relationships and associated hypotheses, see introduction.

is, 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 effects 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 Figs. 1 and 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 SEMs 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 of

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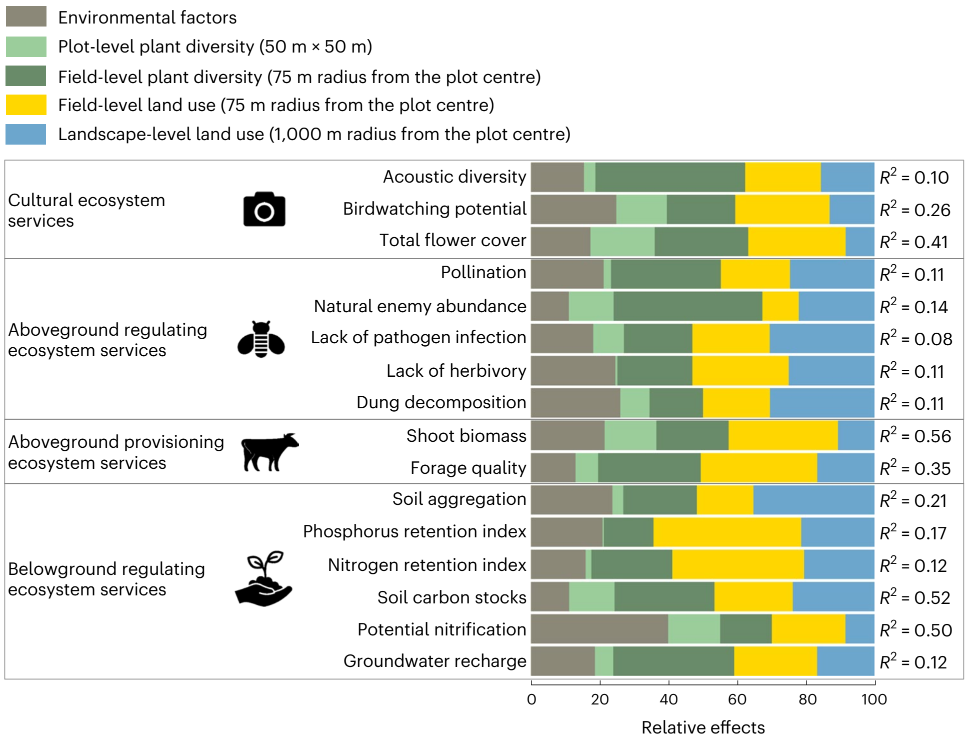

Fig. 2 | Relative importance of plant diversity and land-use predictors on cultural, aboveground regulating and provisioning, and belowground regulating ecosystem services. The effects of the predictors were calculated considering both direct and indirect relationships (total effects) between the predictors 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 centre) plant diversity, field-level (75 m radius from the plot centre) land use, and landscape-level (1,000 m from the plot centre) land use. R^2 for each ecosystem service is calculated on the basis of the full SEM (for the individual path coefficients, see Supplementary Data Table 2). All predictors and response variables were scaled to interpret parameter estimates on a comparable scale. For the total standardized effects of each predictor, see also Extended Data Fig. 1. The number of biologically independent samples for each ecosystem service was $n = 150$ for birdwatching potential, forage quality, nitrogen retention index, potential nitrification and 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 natural enemy abundance; $n = 70$ for total flower cover.

0.06 on cultural ecosystem service multifunctionality index (Fig. 3 and 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 of 0.33 (Fig. 3). Cultural ecosystem services were also negatively affected by field-level LUI (25.9 ± 2.0% s.e.m.; Fig. 2), with a total effect of LUI of −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 birdwatching 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 LUI 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 favourable and resource-rich grasslands at the landscape level can thus strongly benefit the mobile organisms that

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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 LUI 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 accounted for only 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 probably related to high fodder production and quality in fertilized ecosystems[56] and the shift towards higher plant tissue quality that accompanies 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 TWI 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 probaby 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[49].

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 and 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 affected mainly 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-level 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

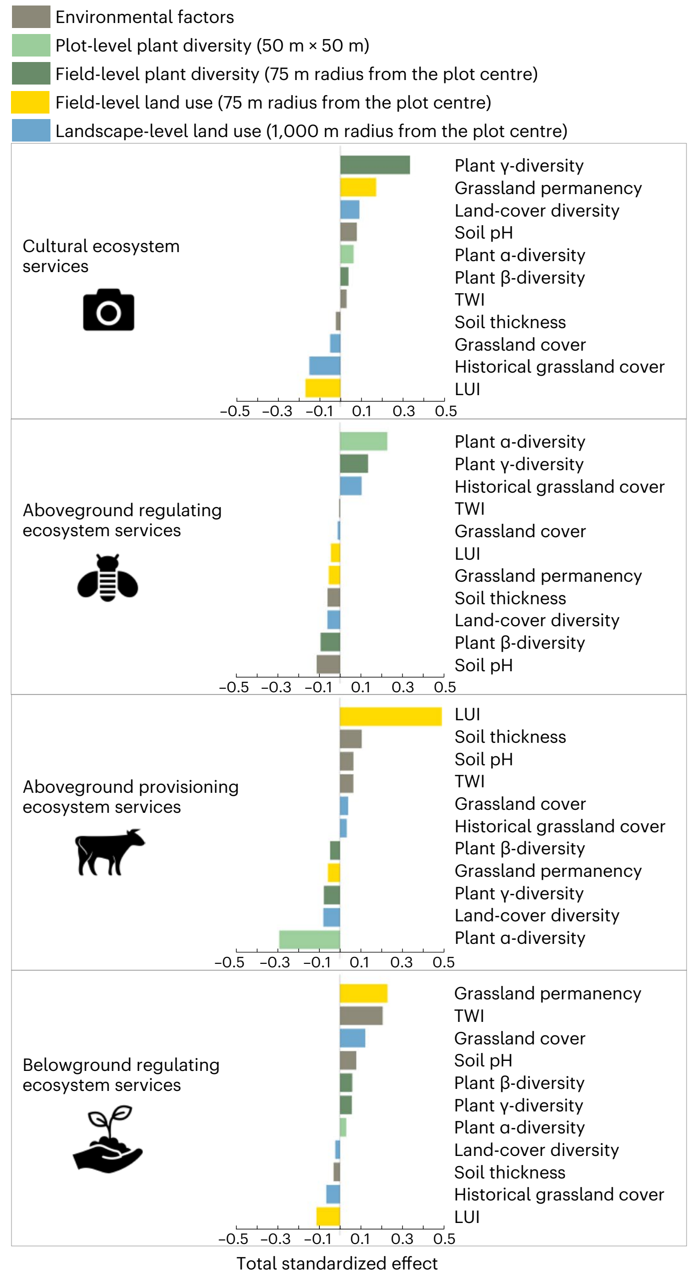

Fig. 3 | The multiple drivers of cultural, aboveground regulating and provisioning, and belowground regulating ecosystem services in grasslands. Total standardized effects were calculated on the basis of the results of SEMs (considering both direct and indirect effects of the predictors) for each predictor: environmental factors, plot-level (50 m × 50 m) plant diversity, field-level (75 m radius from the plot centre) plant diversity, field-level (75 m radius from the plot centre) land use, and landscape-level (1,000 m radius from the plot centre) 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 (that is, individual paths) and indirect effects (that is, 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. For the individual path coefficients, see Supplementary Data Table 2, and for the effects of predictors on each individual ecosystem service, see Extended Data Fig. 1. $n = 150$ biologically independent samples.

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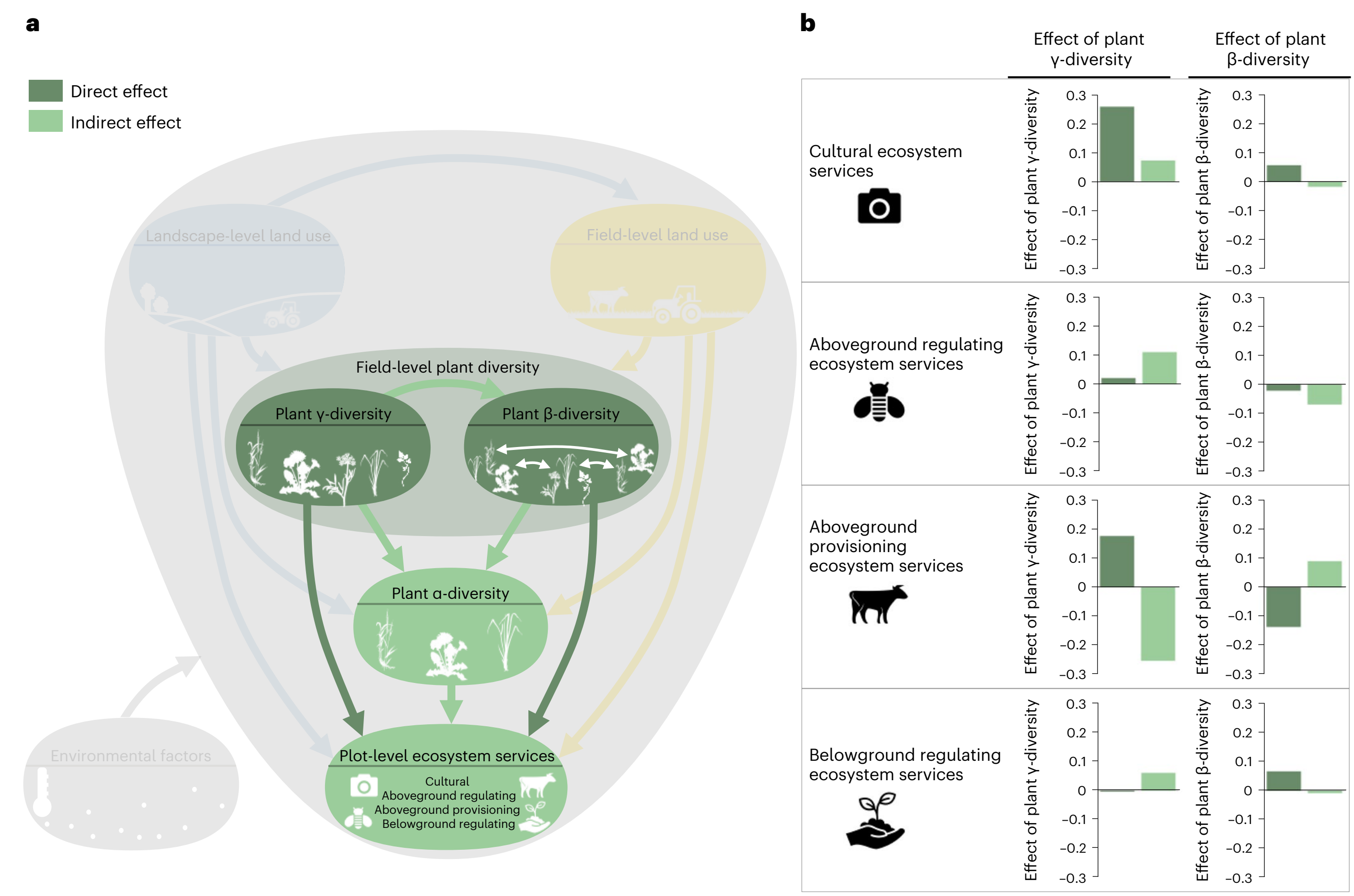

Fig. 4 | The strength of direct and indirect effects of field-level plant diversity on plot-level ecosystem services. a, To disentangle the direct and indirect effects of field-level plant γ-diversity and plant β-diversity, through changing plot-level plant α-diversity, a subset of the full SEM was considered. **b**, Direct and indirect effects of field-level plant γ-diversity and plant β-diversity were calculated on the basis of the full SEMs, that is, 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 Supplementary Data Table 2. $n = 150$ biologically independent samples.

provisioning ecosystem services, the surrounding field-level 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), driven mostly 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, for example, 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 SEMs 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] (Methods). This showed that both aesthetic value and biodiversity conservation were strongly promoted by plant γ-diversity, with total effects of 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 LUI positively affected fodder production, with a total effect of LUI of 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 from the perspective of 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, LUI promoted multifunctionality across stakeholder groups owing to the relatively high priority given by all groups to fodder production (Fig. 5 and Supplementary Table 1). Thus, by influencing the ecosystem services that different local stakeholders 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 whether a spatially interwoven mosaic of permanent and biodiverse habitats and intensive patches (that is, 'land-sparing' strategy[63]) is the best means of delivering landscape multifunctionality to multiple stakeholder groups, that is, landscapes that simultaneously provide high levels of multiple ecosystem services to people[46].

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[15,20,64]. Many theoretical studies have highlighted the potential importance of β- and γ-diversity for ecosystem functioning (for example, refs. [15,64,65]), but so far very little empirical evidence has been provided (but see ref. [12]). By decomposing the direct and indirect effects of surrounding biodiversity on local ecosystem service supply, we reveal that both a biodiverse species pool (plant γ-diversity) and habitat heterogeneity (plant β-diversity) can promote many ecosystem services, probably via different mechanisms. These are fostering the spill-over of a diverse array of ecosystem service providers, maintaining plot-level biodiversity (Fig. 4), and 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 (loss in plant α-diversity).

Alongside the effects of biodiversity, cultural and belowground regulating ecosystem services were higher in grasslands that were not converted regularly (characterized by 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.

So far, 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[14,15,64]. However, it is at larger spatial scales that most management and policy decisions affecting biodiversity and ecosystem functioning are taken. As 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

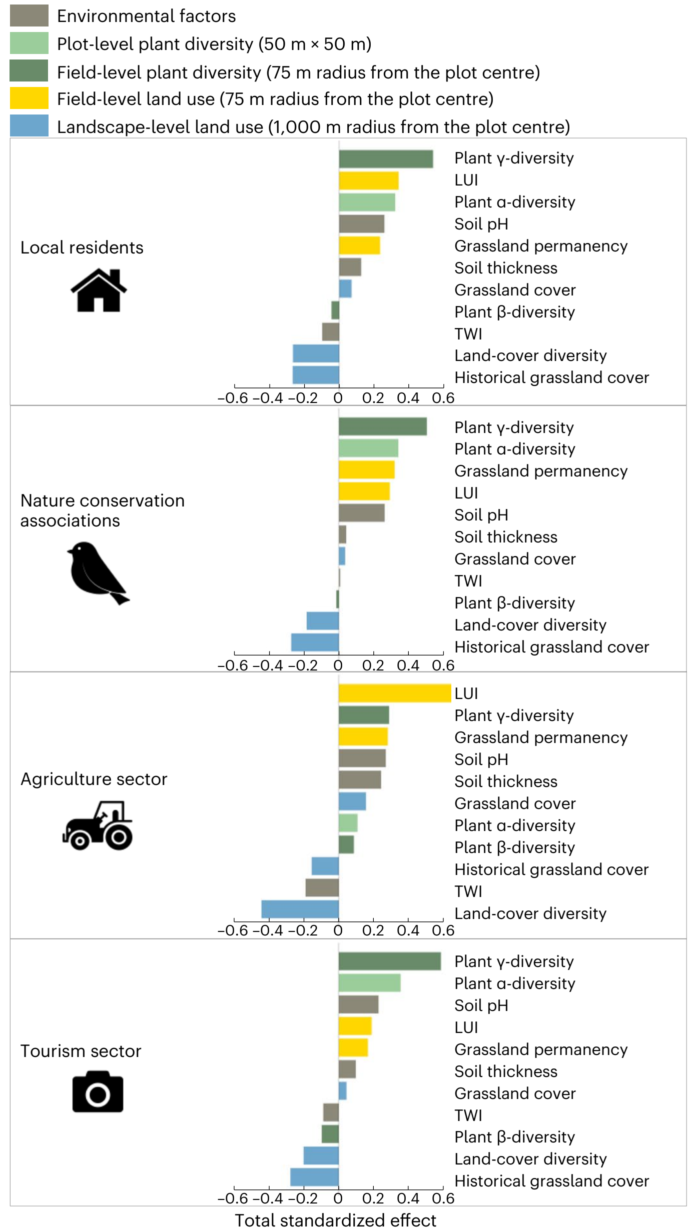

Fig. 5 | Effect of multiple drivers on the multifunctionality of grassland ecosystem services prioritized by four local stakeholder groups. Total standardized effects were calculated on the basis of the results of SEMs (considering both direct and indirect effects of the predictors) for each predictor: environmental factors, plot-level (50 m × 50 m) plant diversity, field-level (75 m radius from the plot centre) plant diversity, field-level (75 m radius from the plot centre) land use, and landscape-level (1,000 m radius from the plot centre) 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 (that is, aesthetic value, biodiversity conservation, fodder production and carbon sequestration) relative to their demand (for details, see Methods). The total standardized effects correspond to the sum of standardized direct effects (that is, individual paths) and indirect effects (that is, 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. For the priority scores given by each stakeholder groups to each ecosystem service, see Supplementary Table 4, and for the effects of predictors on each individual prioritized ecosystem service, see Extended Data Fig. 6. $n = 52$ independent samples.

have investigated the correlation between larger-scale biodiversity and landscape multifunctionality[66,67], a fully mechanistic understanding of how spatial biodiversity dynamics affect the landscape-level supply of ecosystem services is still largely missing[14,61,68]. 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[69,70].

Conclusion

By employing a comprehensive study setup and using SEMs, 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, for example when mapping ecosystem services[67], to accurately assess the status and drivers of ecosystem services, and to evaluate the consequences of biodiversity change. 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[71].

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: (1) the Schwäbische Alb region in the low mountain range of south-western Germany; (2) the Hainich-Dün region in hilly central Germany; and (3) 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 LUI that is typical for large parts of temperate Europe[43]. In each region, 50 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 LUIs 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 (ref. [45]).

Ecosystem service indicators

In each of the 150 grassland plots, data on 16 indicators of ecosystem services were collected[72–77]. These services included (1) three cultural ecosystem services: acoustic diversity (the distribution of acoustic energy among frequency bands during diurnal recordings), birdwatching potential (bird species richness) and aesthetic value (measured as the total flower cover[78,79]); (2) five aboveground regulating ecosystem services: pollination (number of flower visitors), the abundance of natural enemies that regulate crop pests in neighbouring arable fields (measured as the number of brood cells recorded in trap nests 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) and dung decomposition (proportion of dung dry mass removed); (3) two aboveground provisioning ecosystem services: shoot biomass (peak standing biomass), forage quality (index based on crude protein concentration and relative forage value); (4) 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) and 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[80] and the Intergovernmental Platform for Biodiversity and Ecosystem Services (which includes ecosystem services in the broader concept of nature's contributions to people[71]) classifications. For further details, see also Supplementary Data Table 1.

Measures of overall ecosystem service supply can be useful for addressing general trends (for example, 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 (that is, multifunctionality[6,46,81]). 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[81]. To reduce the influence of outliers, we calculated the maximum observed level as the average of the top five sites[81]. 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 trade-offs between services[81]. 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% thresholds are presented in Extended Data Fig. 3. As an alternative approach, we also calculated average-based indices by calculating the average across all services[81]. 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. As the different types of ecosystem services considered in this study show contrasting responses, the use of an overall multifunctionality measure provides little insights (for results for overall ecosystem multifunctionality measures, see 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. On the basis of these workshops, lists of stakeholder groups and ecosystem services that are prioritized regionally were established[62]. We considered only ecosystem services with direct links to final benefits, thus excluding regulating ecosystem services (for example, pollination), which underpin the supply of other services (for example, food production) but do not directly benefit humans. A larger survey was then conducted across 14 stakeholder groups in 2019 (ref. [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 (for example, removing timber and food crop production), resulting in four ecosystem services: aesthetic value, biodiversity conservation, livestock production and carbon sequestration[62,82]. 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, and 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 wellbeing[83]. We also considered flower cover to characterize aesthetic value as people value flower-rich landscapes[84]. 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[46]. 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[46]. These weighted values were then summed for each stakeholder group. Measures therefore quantify the overall supply of all prioritized grassland ecosystem services, relative to stakeholder demand[47,62], when priority is defined as the relative importance of an ecosystem service to a stakeholder[85] and demand is 'the amount of a service required or desired by society'[86]. 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 (that is, 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[87]. 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 (ref. [88]). 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 (approximately 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 (that is, 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 (that is, field-level plant β-diversity), we calculated dissimilarities between plant communities based on Sørensen dissimilarity index using the betapart package[89,90]. A high β-diversity is often associated with the presence of distinct habitats in the surroundings of the grassland plot (for example, 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: overall surrounding biodiversity and habitat heterogeneity, respectively.

Field-level land use

LUI 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 (refs. [44,45]). We then quantified the LUI as the square root of the sum of these three indices according to ref. [44], using the LUI calculation tool[91] implemented in BExIS (https://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 years 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} year^{-1}, are mown two to three 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[92]. Historical maps from the Schwäbische Alb are digitized cadastral maps from 1820, topographic maps (map scale 1:25,000) from the German Empire from 1910, and topographic maps (map scale 1:25,000) from the Federal Republic of Germany from 1960. Historical maps from the Hainich are digitized old topographic maps (map scale 1:25,000) from 1850, topographic maps (map scale 1:25,000) from the German Republic from 1930, and topographic maps (map scale 1:10,000) from the German Democratic Republic from 1960. Historical maps from Schorfheide-Chorin are digitized old topographic maps (map scale 1:25,000) of 1850, topographic maps (map scale 1:25,000) from the German Republic from 1930, and topographic maps (map scale 1:25,000) 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 timepoints) and 1 (the land use recorded at the field level was different between all subsequent timepoints).

Landscape-level land use

At the landscape level (that is, 1,000 m radius of the centre of the grassland plot), land use was recorded in 2008 within a 1,000 m radius of each grassland plot[93,94], and mapped in a geographical information system 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 (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 favourable habitats and dispersal corridors for some ecosystem service providers[31,50]. We also calculated the diversity of land-cover types in the landscape (that is, 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[38,41,95,96]. 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 1,000 m 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 high 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[97–102] 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 centre 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[103]. 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 TWI, defined as $\ln(a/\tan B)$ where a is the specific catchment area (cumulative upslope area that 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[97,104]. 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)[105]. The TWI measure used was the average value for a 4 × 4 window in the centre of the plot, that is, 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 (ref. [106]). 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 SEMs[107]. Structural equation modelling 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[108]. 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: (1) environmental factors that may drive plant species richness[97–102] and also directly affect ecosystem services[30]: soil pH, soil thickness and the TWI; (2) the plot-level plant diversity, corresponding to plant α-diversity; (3) the field-level plant diversity, which included plant β-diversity and plant γ-diversity; (4) the field-level land-use factors, which included LUI and field-level grassland permanency; (5) 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. Co-variances 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 (that is, cultural, aboveground regulating, aboveground provisioning and belowground regulating ecosystem services, and overall multifunctionality), using the lavaan package[109]. 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. 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 (1) environmental factors, (2) the plot-level plant diversity, (3) the field-level plant diversity, (4) the field-level land use and (5) 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[6,31,96,110]. 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). 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.

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

This work is based on data from several projects of the Biodiversity Exploratories programme (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 3 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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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. Marhan, K.M., S. Müller, F.N., Y.O., D.P., S.P., D.J.P., M.C.R., D.S., M.S.-L., M. Schloter, I.S., M. Schrumpf, J.S., I.S.-D., M.T., J.V., C.W., W. Weisser, K.W., M.W., W. Wilcke and P.M. Authorship order was determined as follows: (1) core authors; (2) other authors contributing data and inputs on the manuscript (alphabetical); (3) senior author.

Competing interests

The authors declare no competing interests.

Additional information

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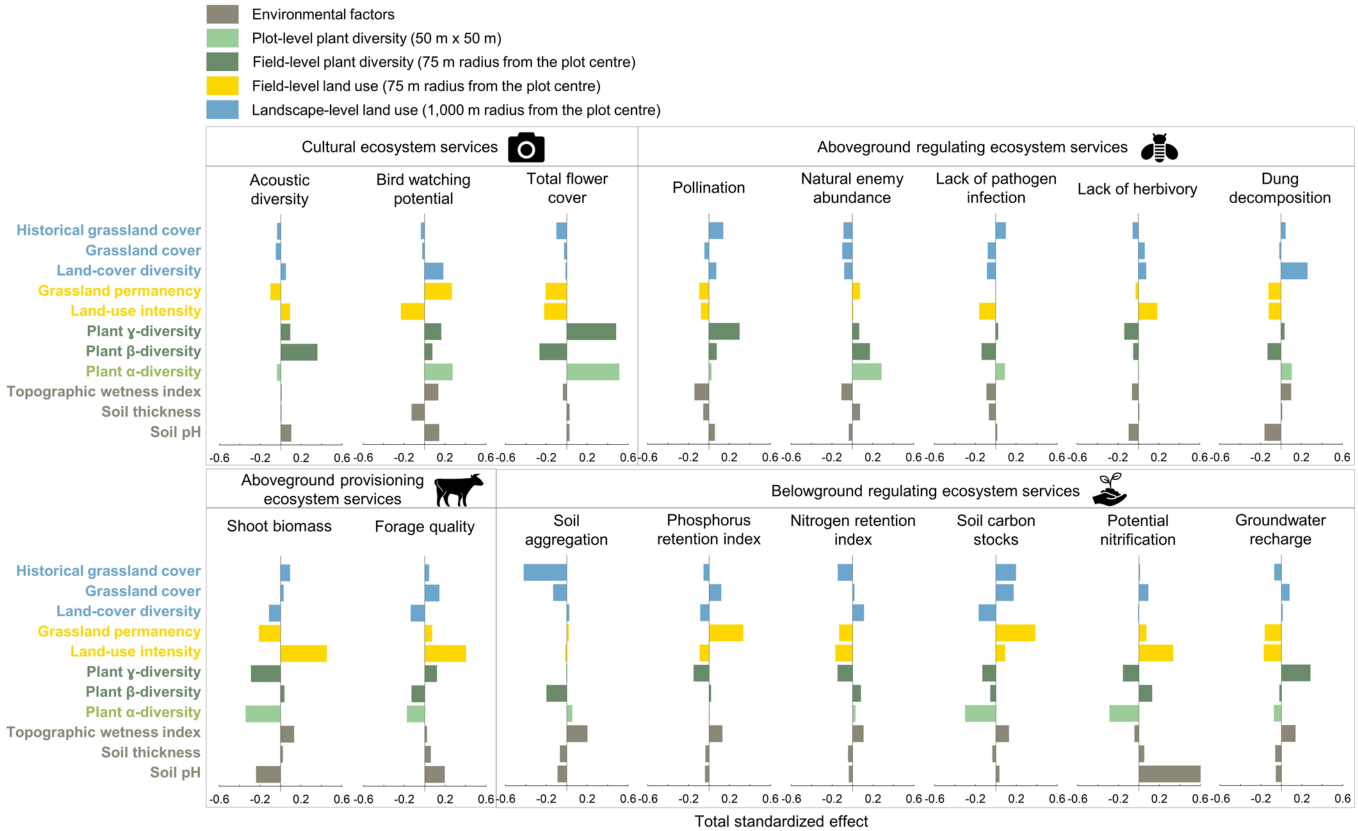

Extended Data Fig. 1 | Drivers of individual cultural, aboveground regulating and provisioning, and belowground regulating ecosystem services in grasslands. Total standardized effects were calculated based on the results of structural equation models (considering both direct and indirect effects of the predictors) for each predictor: environmental factors, plot-level (50 m × 50 m) plant diversity, field-level (75 m radius from the plot centre) plant diversity, field-level (75 m radius from the plot centre) land use, and landscape-level (1,000 m radius from the plot centre) land use. The total standardized effects correspond to the sum of standardized direct effects (that is individual paths) and indirect effects (that is 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 birdwatching 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.

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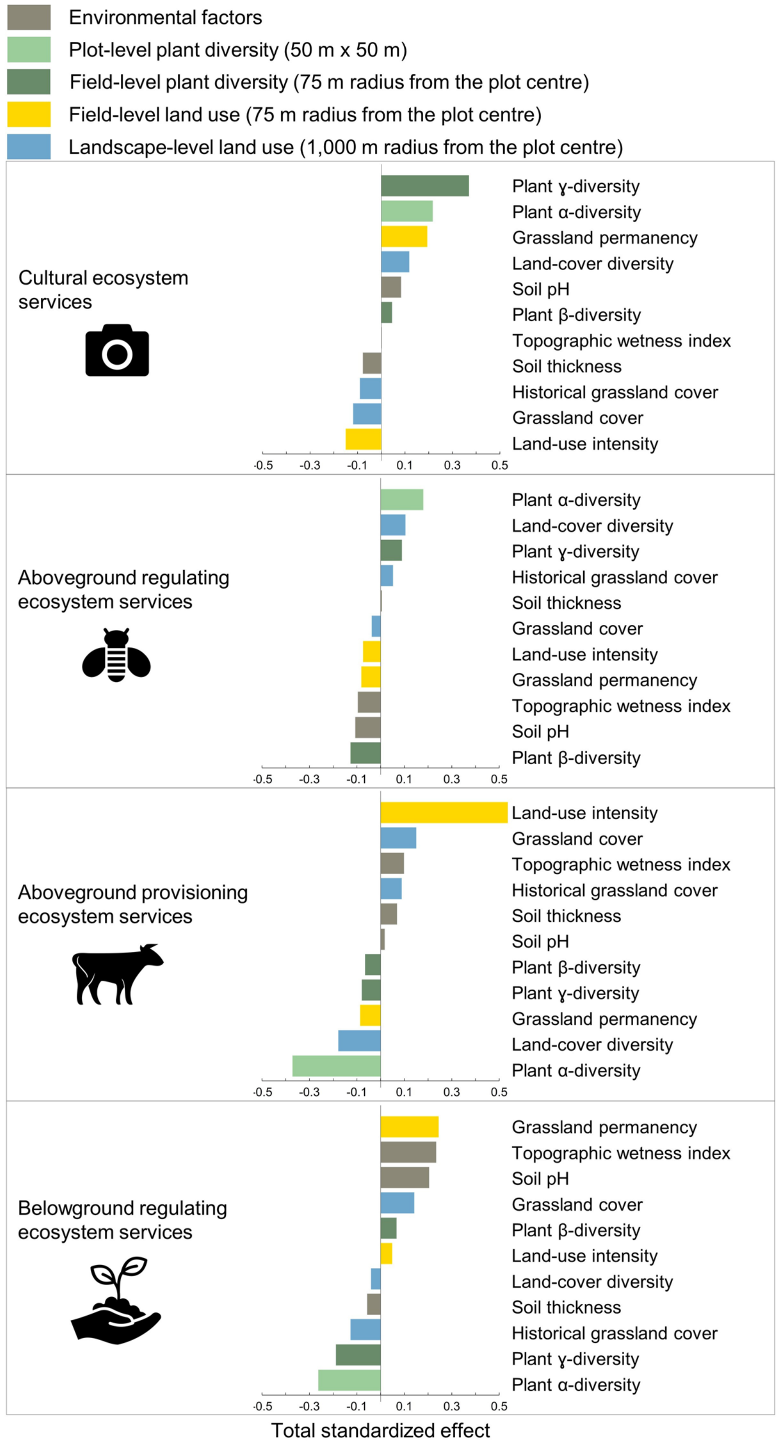

Extended Data Fig. 2 | The multiple drivers of cultural, aboveground regulating and provisioning, and belowground regulating ecosystem services in grasslands *considering average-based multifunctionality indices*. Total standardized effects were calculated based on the results of structural equation 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 centre) plant diversity, field-level (75 m radius from the plot centre) land use, and landscape-level (1,000 m radius from the plot centre) 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 (that is individual paths) and indirect effects (that is 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.

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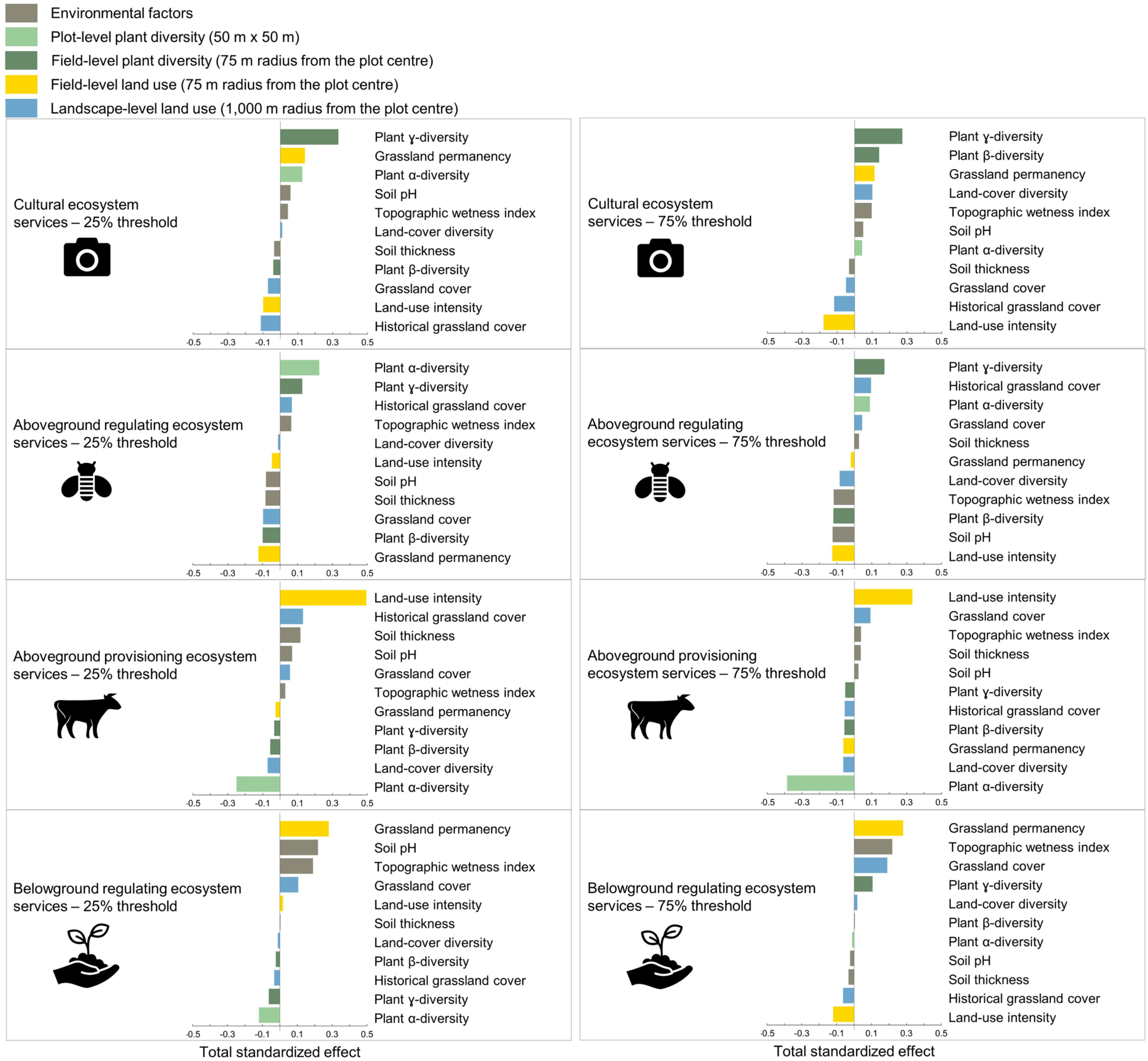

Extended Data Fig. 3 | The multiple drivers of cultural, aboveground regulating and provisioning, and belowground regulating ecosystem services in grasslands *considering multifunctionality indices calculated at the 25% (panel on the left) and 75% (panel on the right) thresholds.* Total standardized effects 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 centre) plant diversity, field-level (75 m radius from the plot centre) land use, and landscape-level (1,000 m radius from the plot centre) 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 (that is individual paths) and indirect effects (that is 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.

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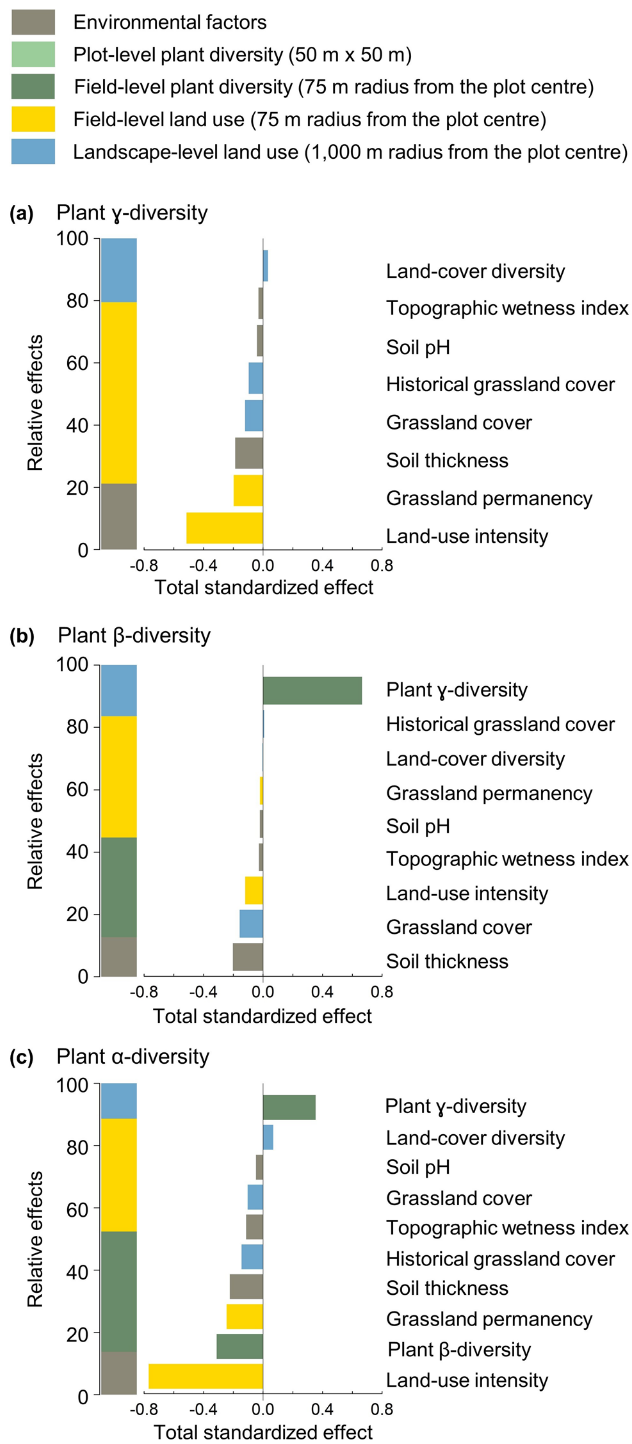

Extended Data Fig. 4 | Drivers of plot-level plant α-diversity, and field-level plant β-diversity and γ-diversity. To assess the surrounding field-level plant diversity of each grassland plot, we surveyed the vegetation within the major surrounding homogeneous vegetation zones in a 75 m radius of each plot (that is 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 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 centre) plant diversity, field-level (75 m radius from the plot centre) land use, and landscape-level (1,000 m radius from the plot centre) land use. The total standardized effects correspond to the sum of standardized direct effects (that is individual paths) and indirect effects (that is 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 Supplementary Data Table 2 for the individual path coefficients. $n = 150$ biologically independent samples.

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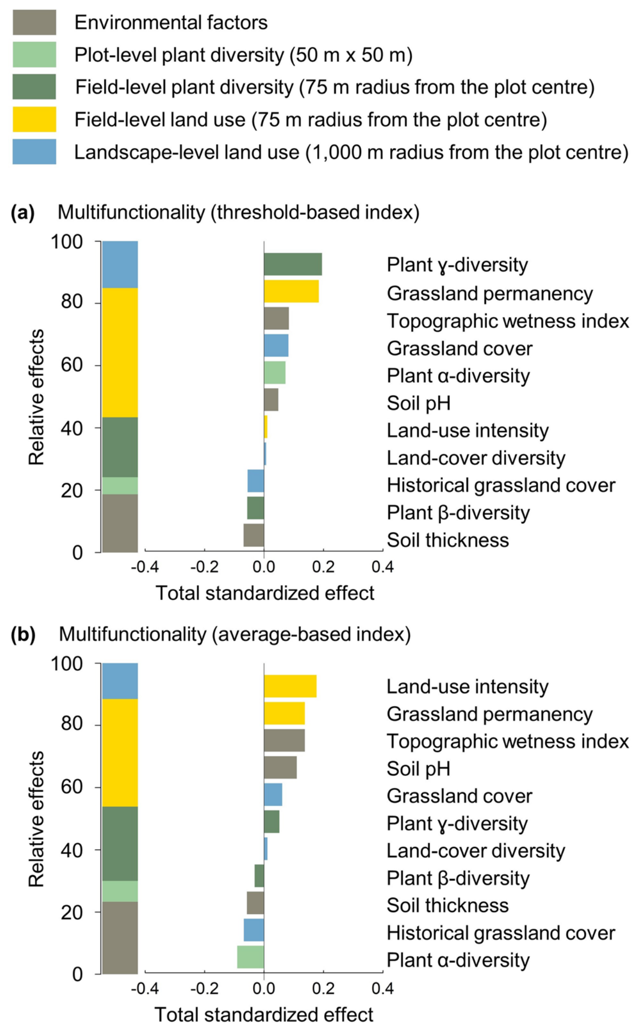

Extended Data Fig. 5 | Drivers of overall ecosystem service multifunctionality, considering (a) a 50% threshold-based index or (b) an average-based index. Total standardized effects were calculated based on the results of structural equation models (considering both direct and indirect effects of the predictors) for each predictor: environmental factors, plot-level (50 m × 50 m) plant diversity, field-level (75 m radius from the plot centre) plant diversity, field-level (75 m radius from the plot centre) land use, and landscape-level (1,000 m radius from the plot centre) land use. The total standardized effects correspond to the sum of standardized direct effects (that is individual paths) and indirect effects (that is 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.

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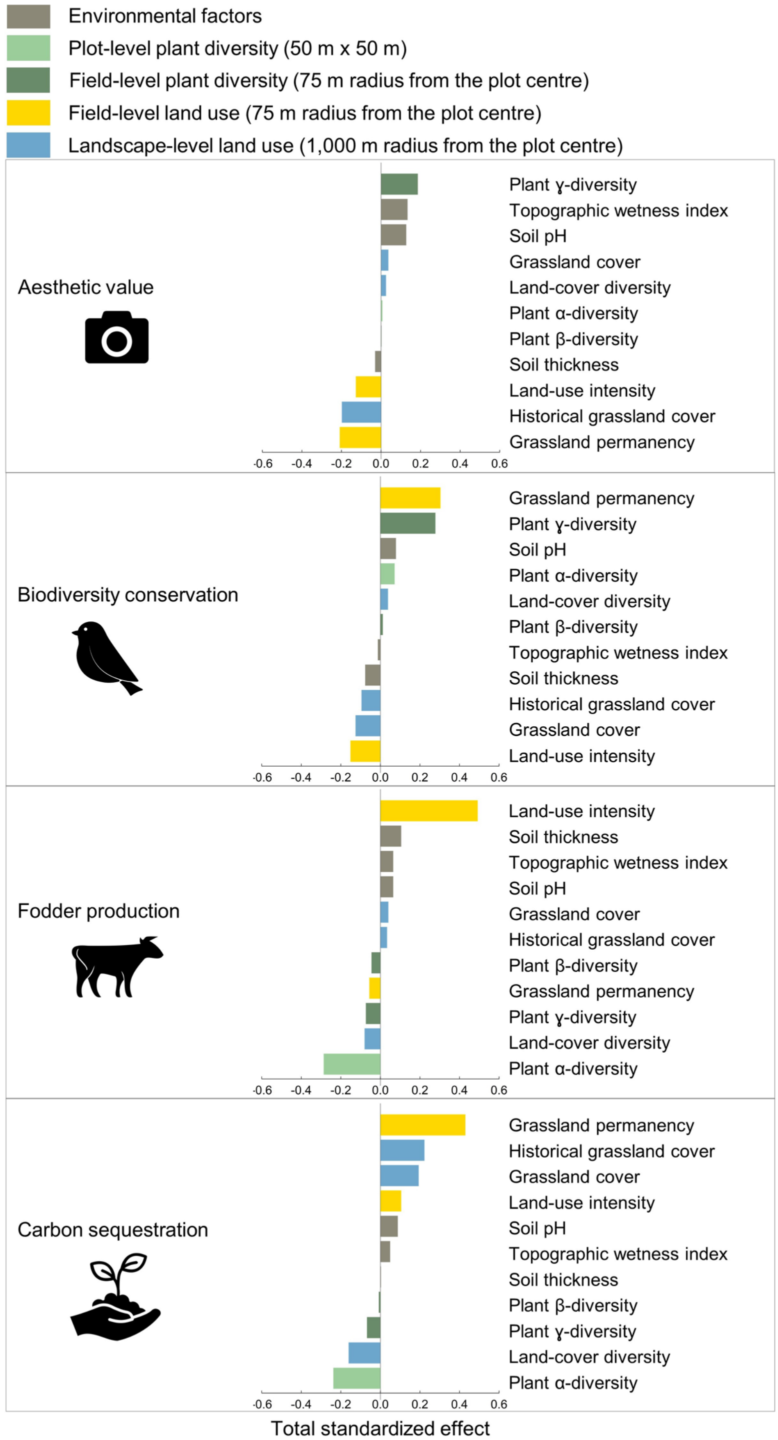

Extended Data Fig. 6 | The multiple drivers of the most prioritized ecosystem services in grasslands by local stakeholders: aesthetic value, biodiversity conservation, fodder production, carbon sequestration. Total standardized effects were calculated based on the results of structural equation models (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 centre) plant diversity, field-level (75 m radius from the plot centre) land use, and landscape-level (1,000 m radius from the plot centre) land use. Models were fitted to four ecosystem service supply variables: aesthetic value (that is acoustic diversity and total flower cover, $n = 129$ independent samples), fodder production (that is shoot biomass and forage quality, $n = 150$ independent samples), biodiversity conservation (that is birdwatching potential, $n = 150$ independent samples) and carbon sequestration (that is soil carbon stocks, $n = 146$ independent samples). The total standardized effects correspond to the sum of standardized direct effects (that is individual paths) and indirect effects (that is 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.

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Software and code

Policy information about availability of computer code

Data collection

Acoustic diversity was recorded using an autonomous recording system (Soundscape Explorer T, Lunilettronics).

Total nitrogen concentrations in ground samples of aboveground biomass were determined using an elemental auto-analyzer (NA1500, CarloErba, Milan, Italy).

To estimate Phosphorus concentrations for the phosphorus retention index, we used a continuous flow analyzer (Bran+Luebbe, Norderstedt, Germany) with the molybdenum blue method.

Ammonium and nitrate concentrations were determined by continuous flow analysis with a photometric autoanalyzer (CFA-SAN Plus; Skalar Analytik, Germany).

To prepare samples for estimation of soil carbon stocks, we used a 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).

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 thickness and soil pH.

Data analysis	Data analyses were conducted using R version 4.1.2 and QGIS version 3.24.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

This work is based on data from several projects of the Biodiversity Exploratories programme (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.

Human research participants

Policy information about studies involving human research participants and Sex and Gender in Research.

Reporting on sex and gender	Sex and gender information were not considered in our analyses as it was not relevant to our research questions.
Population characteristics	See above.
Recruitment	Expert workshops were conducted in 2018 in three German regions, with representatives of numerous pre-selected stakeholder groups. Based on these workshops, lists of stakeholder groups were established. A large survey was then conducted across 14 stakeholder groups in 2019, in which 321 voluntary respondents were invited to complete the survey and requested to quantify the priorities for ecosystem services of their respective group. At the beginning of the survey, written consent was requested for the collection and processing of anonymous personal data. All participants of the survey and workshops could withdraw at any time and we have complied with all relevant ethical regulations. 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). For further details on survey methodology see Peter et al. (2022) People and Nature 4, 218-230.
Ethics oversight	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 anonymised 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.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	The studied grassland plots are part of the large-scale and long-term Biodiversity Exploratories project (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. 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. In summary, there are 150 replicates, nested within three regions, each containing 50 replicates.
Research sample	The sample unit is a 50 m x 50 m grassland plot, in which we took measures of biodiversity and 16 ecosystem services (cultural

Research sample

ecosystem services: acoustic diversity, bird watching potential and total flower cover; aboveground regulating ecosystem services: pollination, natural enemy abundance, lack of pathogen infection, lack of herbivory, dung decomposition; aboveground provisioning ecosystem services: shoot biomass and forage quality; belowground regulating ecosystem services: soil aggregation, phosphorus retention index, nitrogen retention index, soil carbon stocks, potential nitrification, groundwater recharge). Data from different years and samples were pooled per plot. Measures were also taken in the surroundings of each plot (see sampling strategy section).

Sampling strategy

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. 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. 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 changes in species composition between these surrounding plant communities (i.e. field-level plant β-diversity) by calculating the average of all pairwise dissimilarities between plant communities based on Sørensen dissimilarity index. In addition, to characterize the overall surrounding species pool (i.e. plant γ-diversity), we calculated the total species richness recorded in these surrounding zones.

In each of the 150 grassland plots, data on 16 indicators of ecosystem services were collected. 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 diversity), aesthetic value (total flower cover); (ii) five aboveground regulating ecosystem services: pollination (number of flower visitors), natural enemy abundance (number of attacked brood cells by parasitoid predating pest insects recorded in trap-nesting wasps), 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).

No statistical methods were used to predetermine sample size.

Data collection

The percentage cover of each vascular plant species was visually estimated and recorded on sheets of paper.

Acoustic diversity was estimated by recording sounds 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) was calculated across the frequency range of 0–24 kHz using 1 kHz steps and a decibel threshold of −50.

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.

Flower cover was estimated by counting 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 m2). 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 m2 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. 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.

Pollination was estimated on a transect of 200 x 3 m along the plot edge where all individual flower visitors were recorded and identified during three transect walks (total 6 h) on a single day. The total number of individuals of the orders Diptera, Hymenoptera, Lepidoptera and Coleoptera (excluding Nitidulidae) defined the total abundance used here.

Natural enemy abundance was estimated using four wooden poles placed 4-m apart on each plot and two trap nests and mounted 1.5 m high on each pole. 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.

Pathogen infection was estimated 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. 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.

Herbivory was estimated by collecting 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. Plant material was collected before the first mowing event. For each plant, we visually estimated the 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 was estimated by installing five dung piles (cow, sheep, horse, wild boar, red deer) on each 150 plots and collected the remaining dung after 48 hours. The average percentage of scaled (per dung type) dung dry mass removed (mostly by tunneling dung beetles) was used as indicator of dung removal rates.

Shoot biomass was estimated 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 was estimated as the mean of scaled crude protein concentration and scaled relative forage value. 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.

Soil aggregation was estimated as the proportion of water stable soil aggregates. 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 (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 as follow: PRI = (Pb + Pm) / (Pb + Pm + Ps), where Pb = P in plants × Plant biomass, Pm = P in microbes × Bulk density, and Ps = Olsen Pi × Bulk density. Plant samples were digested with concentrated HNO3 in a microwave oven. In the extracts, Pi 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. We used hexanol instead of chloroform as fumigation agent. Plant-available P concentrations in soil were determined using a slightly modified NaHCO3 method. 0.5 g of air-dried soil was extracted with 0.2 l of a 0.5 M NaHCO3 solution (adjusted to pH 8.5 with 1M NaOH).

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 = (Nb + Nm) / (Nb + Nm + Ns), where Nb = N in plants × Plant biomass, Nm = N in microbes × Bulk density, and Ns = (NH4 + NO3) × 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. Chloroform-fumigation-extraction method 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 K2SO4. The suspension was horizontally shaken (30 Min, 150 rpm) and centrifuged (30 Min, 4400 x g). Fumigated sample replicates were incubated with CHCl3 for 24 hours. N concentrations in dissolved (1:4, extract:deion. H2O) extracts were measured with a TOC/TN analyzer (Multi N/C 2100S, Analytik Jena AG, Jena, Germany). Ammonium (NH4) and nitrate (NO3) analyzed in the 2011 soil campaign (see Methods) were used to estimate N in soil. After extraction of soil samples with 0.01 M CaCl2 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 were estimated using composite soil samples weighed, air-dried, sieved (<2 mm), 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 m2 for each plot.

Potential nitrification was estimated as potential nitrification rates. 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.

Groundwater recharge was calculated as annual net downward water fluxes to below 0.15 m soil depth, i.e. downward minus upward water fluxes by capillary rise. 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. The model is based on the soil water balance equation: P + UF = DF + ETa + ΔS; 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 (ΔS = St2 − St1). 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. 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.

Soil thickness was measured as the combined thickness of all topsoil and subsoil horizons. We determined soil depth 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). For 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. 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 $CaCl_2$.

Samples were operated in the field and sorted in the lab by trained technicians. All identification was done by expert taxonomists. All people involved in data collection are listed in the acknowledgments section.

Timing and spatial scale

Within the Biodiversity Exploratories project, some ecosystem services are sampled regularly by 'core' projects (e.g. biomass production), while the sampling and data gathering on other services depend on the funding of more temporary 'contributing' projects. Therefore, all services have not been sampled annually.

The timing of the sampling was selected to coincide with the annual peak of biological activity:
- Plants were sampled annually from mid-May to mid-June, from 2008 to 2018.
- Acoustic diversity was recorded in April and May, in 2016.
- Birds were observed annually from March to June, from 2008 to 2012.
- Total flower cover was estimated between May and September, in 2009.
- Pollination was estimated between April and August, in 2008.
- Natural enemy abundance was estimated between April and October, in 2008.
- Pathogen infection was estimated between May and June, in 2011.
- Herbivory was estimated in May 2017 or 2018.
- Dung decomposition was estimated between May and July, in 2014 or 2015.
- Shoot plant biomass was estimated between mid-May and mid-June, each year from 2009 to 2017.
- Forage quality was estimated between May and June, each year from 2009 to 2013.
- Soil aggregation was estimated using soil samples collected from April to October, in 2011.
- Phosphorus and Nitrogen retention indices were estimated using samples collected in 2014.
- Soil carbon stocks were estimated using soil samples collected from April to October, in 2011.
- Potential nitrification was estimated using soil samples collected from April to October, in 2011.
- Groundwater recharge was estimated between 2010 and 2016.

All these data were collected within a 50 m x 50 m area, in 150 grassland plots. These grassland plots were chosen to cover a wide gradient of land-use intensity.

To assess the surrounding plant diversity of each grassland plot, we have also surveyed the vegetation within the major surrounding homogeneous vegetation zones in a 75-m radius of each plot from May to July (during the growing season) in 2017 and 2018. 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).

Data exclusions

No data was excluded from the analyses.

Reproducibility

There are no experiments in the study. Our data were collected as part of a monitoring over several years and which cannot be repeated.

Randomization

Study plots were selected from 3000 candidate plots. Surveys of initial vegetation and land use were conducted on candidate plots by stratified random sampling to ensured that the selected plots covered the whole range of land-use intensity in each region, and to minimize confounding effects of spatial position or soil type.

Blinding

Investigators were not aware of the land-use intensity of the plot were they worked, but they could not otherwise be blinded during data collection and analyses for example with respect to the year a sample came from.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions

For ecosystem services relying on observation on arthropods (i.e. pollination, natural enemy abundance), the sampling was carried out during the day, when the vegetation was dry (no rainfall) and wind speed was low.

For birds, the sampling was carried out during the morning chorus (sunrise-11:00h) when the wind speed was low. In exceptional cases, observations were made during the evening chorus (last 3 hours before sunset).

For all other measures, the sampling was operated at all weather conditions.

Location

Our data were collected in three German regions: (1) Schwäbische Alb in south-western Germany (420 km^2, 460–860 m above sea level (a.s.l.), Latitude: 48.413, Longitude: 9.4912); (2) Hainich-Dün in central Germany (1560 km^2, 285–550 m a.s.l., Latitude: 51.1186, Longitude: 10.5056); and (3) Schorfheide-Chorin in northeastern Germany (1300 km^2, 3–140 m a.s.l., Latitude: 53.0178, Longitude: 14.0042). Exact plot locations cannot be disclosed due to a legal agreement with landowners.

Access & import/export

Fieldwork permits were issued from 2008 to 2021 by the responsible state environmental offices of Baden-Württemberg (Regierungspräsidium Tübingen), Thüringen (Thüringer Landesverwaltungsamt) and Brandenburg (Landesumweltamt Brandenburg).

Disturbance	Activity of investigators was spatially limited to the 50 m x 50 m grassland plots. We used small paths to access the plots and carefully ensure to avoid any damage to the habitat. Destructive sampling was minimized by using protocols described in the Methods section.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☐	☒ Palaeontology and archaeology
☐	☒ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Palaeontology and Archaeology

Specimen provenance	Geological samples were collected in three German regions: (1) Schwäbische Alb in south-western Germany (420 km², 460–860 m above sea level (a.s.l.), Latitude: 48.413, Longitude: 9.4912); (2) Hainich-Dün in central Germany (1560 km², 285–550 m a.s.l., Latitude: 51.1186, Longitude: 10.5056); and (3) Schorfheide-Chorin in northeastern Germany (1300 km², 3–140 m a.s.l., Latitude: 53.0178, Longitude: 14.0042). Exact plot locations cannot be disclosed due to a legal agreement with landowners. Soil samples were collected and exported in a responsible manner and in accordance with relevant permits and local laws. Fieldwork permits were issued from 2008 to 2021 by the responsible state environmental offices of Baden-Württemberg (Regierungspräsidium Tübingen), Thüringen (Thüringer Landesverwaltungsamt) and Brandenburg (Landesumweltamt Brandenburg).
Specimen deposition	Geological samples were collected by original data providers from different institutions in Germany, who are listed as co-authors on our manuscript. Geological samples are deposited in the respective institution of data providers, and data provider names are listed in Supplementary Data Table 1.
Dating methods	No new dates are provided.

☒ Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information.

Ethics oversight	The responsible state environmental offices of Baden-Württemberg (Regierungspräsidium Tübingen), Thüringen (Thüringer Landesverwaltungsamt) and Brandenburg (Landesumweltamt Brandenburg) approved the study protocol.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Animals and other research organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research, and Sex and Gender in Research

Laboratory animals	No laboratory animals were involved in the study.
Wild animals	Arthropods were collected in the field and killed using ethanol. Identification of arthropods requires killing and transport to the lab were microscopes can be used. Bird species were assessed by remote observation only (see Methods section for details).
Reporting on sex	Sex was not considered in the study design as it was not relevant to our research questions.
Field-collected samples	Aboveground arthropod samples were stored in 93% ethanol at 7°C except for short time periods during transport, sorting and identification.
Ethics oversight	It could not be ruled out that threatened or protected species would be collected and killed. Thus, permission was required from the authorities which was granted for scientific reasons. These permits were issued by the responsible state environmental offices of Baden-Württemberg (Regierungspräsidium Tübingen), Thüringen (Thüringer Landesverwaltungsamt) and Brandenburg (Landesumweltamt Brandenburg).

Note that full information on the approval of the study protocol must also be provided in the manuscript.