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Landscape management strategies for multifunctionality and social equity

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Increasing pressure on land resources necessitates landscape management strategies that simultaneously deliver multiple benefts to numerous stakeholder groups with competing interests. Accordingly, we developed an approach that combines ecological data on all types of ecosystem services with information describing the ecosystem service priorities of multiple stakeholder groups. We identifed landscape scenarios that maximize the overall ecosystem service supply relative to demand (multifunctionality) for the whole stakeholder community, while maintaining equitable distribution of ecosystem benefts across groups. For rural Germany, we show that the current landscape composition is close to optimal, and that most scenarios that maximize one or a few services increase inequities. This indicates that most major land-use changes proposed for Europe (for example, large-scale tree planting or agricultural intensifcation) could lead to social conficts and reduced multifunctionality. However, moderate gains in multifunctionality (4%) and equity (1%) can be achieved by expanding and diversifying forests and de-intensifying grasslands. More broadly, our approach provides a tool for quantifying the social impact of land-use changes and could be applied widely to identify sustainable land-use transformations.

Growing demand for ecosystem goods and services throughout the globe is placing increased pressure on land resources to provide mul-tiple benefits, simultaneously and at high levels^{[1,](#page-10-0)[2](#page-10-1)}. These changing demands have also resulted in major shifts in land use, which, by altering the balance of ecosystem services provided, can lead to conflicts between stakeholder groups. Conflicts often emerge because land-use changes typically promote only a few ecosystem services³, especially those related to provisioning. However, due to biophysical trade-offs among services^{[4](#page-10-3)}, this often comes at the expense of other services, including the protection of biodiversity^{[5](#page-10-4)}. Because stakeholder groups differ in their demands, these changes result in 'winners', 'losers' and inequities regarding distribution and access^{[6](#page-10-5)[,7](#page-10-6)}.

To understand how landscapes can be managed to best supply multiple ecosystem services and to minimize conflicts between land users, a range of modelling approaches have been applied $8-12$ $8-12$. These typically focus on the impact of land-use changes on ecosystem service supply, but without quantifying their impact on stakeholders. Meanwhile, the assessment of the societal impact of land-use change has been largely conducted within social–ecological and landscape man-agement research, via interviews, scenario workshops or surveys^{[13,](#page-10-9)[14](#page-10-10)}.

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While insightful, these assessments rarely provide quantitative outputs that can be used in decision-making—for example, specific land-use proportions that minimize conflicts (but see ref. [15\)](#page-10-18). Clearly, quantitative tools are needed that can guide decision-making and help structure the participatory approaches that aim to resolve such conflicts¹⁶. Such quantitative tools should consider not only the supply of ecosystem services but also the equity of this supply across society, as equity in the access to, supply of and management of ecosystem services is increasingly recognized as an essential aspect of successful and sustainable land management 17 .

Recently, interest in quantifying the supply of multiple ecosystem services has led to the development of multifunctionality metrics^{[18,](#page-10-21)19}. One of these metrics, ecosystem service multifunctionality (hereafter multifunctionality), quantifies the simultaneous supply of multiple ecosystem services, relative to their human demand^{9,20}. It advances previous approaches, such as the identification of supply-and-demand bundles 21 , by combining biophysical indicators of ecosystem service supply with measures of demand for multiple stakeholder groups. While economic valuation approaches often ignore or underestimate the importance of cultural ecosystem services 22 22 22 , with the risk of overlooking resulting trade-offs, the multifunctionality approach values services on the basis of their relative priority to stakeholders. This use of standardized priority scores helps overcome some of the difficulties of integrating material and non-material values within a single metric²³. Also, as multifunctionality scores contain measures of the supply of all prioritized services, the overall impact of changes in ecosystem service supply on stakeholder groups can be assessed, as can the equity of this supply across society.

In this study, we compare multifunctionality scores among stakeholder groups to assess both the overall impact of land-use strategies on a stakeholder community and how changes to ecosystem service supply affect social equity. As our measure of equity, we focus on distribution equity, defined as the equitable access of multiple stakeholder groups to ecosystem service supply¹⁷, which we measure as the homogeneity of multifunctionality across groups. Hereafter, for simplicity, we refer to this as equity. Our assessment was conducted using data from three regions of rural Germany in which we quantified the societal impacts of landscape change by simulating changes in the proportions of land-use types and measuring their impact on multifunctionality and equity. We based our metrics of multifunctionality on the 11 terrestrial services that are most prioritized by local stakeholders in these regions^{[24](#page-10-28)} (Fig. [1](#page-2-0)). All of these are directly linked to final benefits (sensu the cascade model²⁵). The supply measure of each service was based on multiple indicators collected at 150 forest and 150 grassland sites that vary greatly in their management²⁶. These were augmented by literature-based estimates of arable cropland services. In addition, data on ecosystem service priorities were collected from 321 respondents belonging to 14 stakeholder groups in a social survey in the same regions 24 24 24 . To assess the impact of landscape composition on ecosystem service supply, we assembled artificial landscapes with varying proportions of grasslands, forests and different management types within them, by randomly picking plots of each considered land use and management type, and then measuring their aggregated ecosystem service supply. Standardized ecosystem service supply values were multiplied by stakeholder priority scores to give multifunctionality values for each stakeholder group. The resulting multifunctionality and equity scores were then compared with the baseline landscape (that is, the current landscape composition, averaged across the three study regions) to identify land-use strategies that are broadly applicable to rural Germany.

Results

Current landscape

We first explored the societal impact of >6,000 landscape scenarios that cover the full range of landscape compositions (Methods), by varying the proportions of forests and grasslands under different management types and measuring the multifunctionality and equity of each landscape. Arable crop cover was kept constant, primarily due to limited data on cropland ecosystem services, but also because it is likely to be affected by drivers external to the local community, such as national and global food consumption (Supplementary Information). This scenario ensemble revealed that the baseline landscape composition is close to optimum, in that 87% of the possible landscape compositions had a lower community-level multifunctionality (calculated as the average multifunctionality across groups) or a lower equity score, or both, than the baseline composition (Fig. [2b,c](#page-3-0)), and only 13% improved both, with potential gains marginal compared with potential losses (few scenarios in the high-multifunctionality–high-equity area; top-right corner in Fig. [2a](#page-3-0)).

Service contributions to baseline multifunctionality

The failure of most potential landscape compositions to improve multifunctionality and equity relative to the baseline landscape can be understood by examining the multifunctionality scores of each stakeholder group and the relative contributions of different services to these scores. The baseline landscape composition consists on average of 38% cropland, 20% grassland and 42% forest (Fig. [3a](#page-4-0)) and is thus close to the national average (relative proportions of 43%, 21% and 37%, respectively, based on national-level Corine land-cover data). This baseline landscape provides moderate to high levels of most ecosystem services. This results in relatively similar and high multifunctionality levels across stakeholder groups (Fig. [3f\)](#page-4-0). Because most stakeholder groups prioritized a wide range of services, and due to inherent synchronies and trade-offs among services (Supplementary Fig. 3), current supply meets the demand of all groups approximately equally well, with overall multifunctionality ranging between 0.5 and 0.55 between stakeholder groups, where 1 means that all prioritized services are provided at the maximum level (Fig. [3f](#page-4-0)). Despite this, the relative contributions of different services to the multifunctionality of each group differed substantially. For example, more than half of the multifunctionality of the tourism, nature conservation and economic sectors is related to cultural services, while the overall demand of landowners, agricultural and forestry sectors is mostly met through provisioning services (Fig. [3f\)](#page-4-0).

Specific land-use change scenarios

There have been numerous calls for land-use strategies to meet specific goals, including greatly increased area dedicated to biodiversity conservation (for example, "half-Earth"[27\)](#page-10-11), large-scale tree planting to mitigate climate change²⁸, increased local food production to sup-port food security^{[29,](#page-10-13)30} and agri-environmental schemes to de-intensify landscapes^{[31](#page-10-15),32}. These strategies are widely debated and often contro-versial^{[33](#page-10-17)}. To gain a more detailed understanding of how such land-use strategies would affect the stakeholder community, we explored several specific land-use change scenarios (detailed in Supplementary Table 9). All scenarios involving deforestation (see scenario 1 in Fig. [2b,c](#page-3-0)), forest homogenization (scenarios 2–4 and 7) or grassland intensification (scenarios 5 and 6) decreased community multifunctionality and were often also associated with a decrease in equity (Fig. [2b,c](#page-3-0)). However, some scenarios led to marginal increases in both multifunctionality and equity (for example, scenarios 8–10). In these scenarios, there was usually moderate conversion of grasslands to forests, with multifunctionality and equity increasing gradually from a current forest cover of 42% up to about 48% before steadily decreasing beyond this point (Extended Data Fig. 1). This increase in multifunctionality was probably due to some services being predominantly or exclusively provided by forests, such as hunting and timber production (Supplementary Fig. 1). Unsurprisingly, increased forest cover increases multifunctionality for groups that favour forest services, such as hunters and foresters. As these groups currently have relatively low multifunctionality scores (Fig. [3f](#page-4-0)), afforestation simultaneously increases equity.

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Fig. 1 | Eleven ecosystem services included in the multifunctionality metric and their indicators. The symbols indicate the land-use types that provide each service (forests, grasslands and croplands). The arrow widths pointing to multifunctionality are proportional to the mean priority score given to each service across all stakeholder groups. Multifunctionality is calculated as the sum of the standardized landscape-level supply of each service, weighted by

stakeholder priority, as measured in a social survey²⁴. Orange-to-brown colours, shades of blue and teal are used throughout the manuscript to represent provisioning, cultural and regulating services, respectively. NDSI, normalized difference soundscape index (the ratio between biological sounds and anthropogenic sounds). Credit: grass icon, Jhonatan, the Noun Project.

Impact of optimizing landscapes for individual services

As certain land-use strategies aim to maximize the supply of specific services, such as carbon storage or biodiversity conservation $27,34,35$ $27,34,35$ $27,34,35$, we also explored the impact of maximizing a landscape for a particular ecosystem service on the provision of other ecosystem services and the stakeholder community. We did this first for biodiversity conservation. We identified the 15 landscape compositions with the highest biodiversity scores and calculated their average proportions of land uses and the changes in ecosystem service supply, multifunctionality and equity relative to the baseline landscape. High-biodiversity landscapes increased low-intensity grassland area while reducing forest and intensive grassland cover compared with the baseline landscape (Fig. [3b](#page-4-0)). This sharply decreased the supply of all ecosystem services, except livestock production and foraging (Fig. [3d\)](#page-4-0), and in turn reduced multifunctionality for all groups (Fig. [3g\)](#page-4-0) and led to community inequity (highlighted in green in Fig. [2b,c](#page-3-0)) compared with the baseline landscape. We also investigated the impact of optimizing a landscape for carbon storage, by identifying the landscape composition in which this service was highest, using the same method. This carbon-rich landscape composition was forest-dominated (only 1% grasslands on average); had low levels of many services, including livestock production, biodiversity conservation, aesthetic value and foraging; and led to low community-level multifunctionality and high inequity (11 of 14 groups significantly losing multifunctionality; Extended Data Fig. 2). These results indicate that any land-use strategy that prioritizes a single service without considering the diversity of land-user demands could have severe impacts on other services^{[36](#page-10-33)} and therefore on the whole community, potentially increasing conflict between stakeholder groups.

Optimizing land use for entire stakeholder communities

In further analyses, we identified the optimum landscape composition—that which delivers the highest possible community-level multifunctionality and equity. To do so, we selected the 15 landscape compositions that simultaneously maximized both equity and multifunctionality and averaged their compositions (highlighted in blue in Fig. [2b,c\)](#page-3-0). Relative to current conditions, these landscapes are characterized by grassland extensification, an increase in the proportion of forests by approximately 8% and an increased proportion of mixed forests (Fig. [3c\)](#page-4-0). These changes would increase the supply of most services (except biodiversity conservation, aesthetic value and livestock production; Fig. [3e](#page-4-0)), leading to increases in multifunctionality for all stakeholders of up to 9% for individual groups and 3.7% on average (Fig. [3h\)](#page-4-0).

Do-no-harm scenario

Although certain landscape compositions are optimal for community multifunctionality and equity, their adoption could lead to decreases in the supply of already vulnerable services, such as biodiversity

multifunctionality (overall ecosystem service supply) and higher equity (measured as equitable access to ecosystem services) than the baseline (that is, current) landscape composition. The sizes of the stakeholder icons represent the landscape multifunctionality for each stakeholder group. **b**, Empirical estimation in simulated German landscapes. The changes in multifunctionality (*x* axis) and equity (*y* axis) are compared with the baseline landscape composition in predefined scenarios of land-use change (large coloured dots; each dot shows

possible simulated landscape compositions (small black dots; each shows the mean of 200 replicates for each composition). Clusters of highlighted dots and the corresponding shaded polygons show the landscape compositions that were used to calculate the results shown in Figs. [3](#page-4-0) and [4.](#page-5-0) **c**, Subset of **b** for the highestscoring landscapes. For descriptions of the full range of scenarios and their associated changes in multifunctionality and equity, see Extended Data Fig. 4 and Supplementary Table 9.

conservation, and in decreased multifunctionality for particular stakeholder groups. To address these issues, we further identified a do-no-harm scenario, in which no stakeholder group loses multifunctionality and which would cause no loss of vulnerable services (purple areas in Figs. [2b,c](#page-3-0) and [4\)](#page-5-0). Vulnerable services were identified during the stakeholder survey as those whose supply was deemed 'threatened' or 'insufficient' by most (>65%) stakeholders—namely, biodiversity conservation, foraging, climate change mitigation and regional identity. We then identified landscape compositions in which the supply of those services and the multifunctionality for all groups was at least

as high as in the baseline landscape (that is, zero groups losing multifunctionality (Fig. [4a](#page-5-0)) and zero vulnerable services with decreased supply (Fig. [4b](#page-5-0))). The landscape composition identified was consistent with the optimal scenario in that it involved increased forest cover and grassland extensification, although with more moderate changes. It led to small but still significant multifunctionality gains of up to 5.6% (2.6% on average; Extended Data Fig. 3).

Finally, to assess the sensitivity of our results to a range of factors, we conducted additional sensitivity analyses. The results were not sensitive to the weighting of equity and multifunctionality by stakeholder

Fig. 3 | The impacts of three land-use change scenarios on ecosystem service supply and multifunctionality relative to the baseline (current) landscape composition. a–**c**, Landscape composition under selected scenarios. The area of each land use is proportional to its area in the considered scenario. **d**,**e**, Average difference in the supply of each service compared with the baseline landscape composition, as a percentage of the current supply. **f**, Relative contribution of each service (current service supply × stakeholder group priority) to total multifunctionality (total bar length) for each stakeholder group in the baseline landscape. **g**,**h**, Average difference in multifunctionality for each stakeholder group compared with the baseline landscape, as a percentage of baseline multifunctionality. The data in **d**,**e**,**g** and **h** are presented as means and 95% confidence intervals, calculated on *n* = 15 landscape compositions, each averaged across 200 replicated simulations. Credit: grass icon, Jhonatan, the Noun Project; pine tree icon, Roger Cline, the Noun Project; tractor icon, parkjisun, the Noun Project; cow icon, Andreas Preuss, PhyloPic.

groups' perceived power (Supplementary Figs. 8 and 9) or to correction for environmental covariates (Supplementary Figs. 10 and 11). The classification of forests into even- or uneven-aged forests, instead of

by tree type, did not change the finding that increased forest cover and grassland extensification was the optimal scenario (Supplementary Figs. 12 and 13). The introduction of service-specific 'supply-benefit'

a, Identification of landscape compositions in which no group sees a reduction in multifunctionality. **b**, Identification of landscape compositions in which no ecosystem services deemed vulnerable (biodiversity conservation, foraging, climate change mitigation and regional identity) are lost. In both cases, the optimal landscape composition, if present, would be in the top right corner. Change in multifunctionality (*x* axis) and number of losing groups or services (*y* axis) are shown compared with the baseline (current) landscape composition,

in predefined scenarios of land-use change (large coloured dots) and in all simulated landscape compositions (small black dots; each represents the mean of 200 replicates for the given composition). The coloured dots and the corresponding shaded polygons show the positions of the optimal landscape compositions that were used to calculate the results shown in Fig. [3.](#page-4-0) For presentation, only a subset of landscape compositions is shown, the rest extending beyond the bottom left corner of the plot (see Extended Data Fig. 4 for the full range).

relationships (Supplementary Figs. 14 and 15) or changes in cropland cover changed the optimal land-use proportions (Supplementary Figs. 16 and 17), but the optimum in these cases also involved increased forest cover and grassland de-intensification. Region-specific optimization (Supplementary Figs. 18–23) showed that the outcomes of land-use change scenarios were partly dependent on regional specificities. For instance, optimizing for biodiversity in the Central region could be achieved via a more moderate increase in grassland cover than in other regions and so led to concurrent increases in landscape aesthetic and foraging values.

Discussion

By combining natural and social science data with a landscape simulation approach, we show that the baseline landscape composition of our German study regions is close to optimal with respect to both the overall supply of demanded ecosystem services (multifunctionality) and equity. While small increases in these properties are achievable with de-intensification, most land-use change scenarios would reduce community-wide ecosystem service supply and lead to unequal service provision, potentially triggering conflicts between stakeholder groups. As our baseline was close to the national average, demand patterns do not differ between regions²⁴, and the three regions are broadly representative of northern, central and southern Germany²⁶, we expect our results to be broadly applicable for rural Germany.

The fact that the baseline landscape is close to optimal may reflect the history of the study regions and the policy and governance within them. Governance in all three regions has historically aimed to balance the conservation of biodiversity with support for a diverse local economy that includes tourism, forestry and agriculture. This may explain the breadth of services requested by all groups, who are aware of the need for multiple services and might mediate their priorities to acknowledge those of others 24 24 24 . This is furthered in two of the regions, Schwäbische Alb and Schorfheide-Chorin, by their designation as UNESCO Biosphere Reserves, which aim "to balance human responsibility for maintaining nature and the human need to use natural resources to enhance social and economic well-being"[37](#page-10-34). The studied regions are also cultural landscapes³⁸ that have been shaped by centuries of interactions between humans and nature. We thus hypothesize that people living in these areas have shaped the landscape to meet their needs, while also adapting their demand to what these managed ecosystems supply. This coevolution process is also constrained by biophysical factors that might limit the expansion of some land uses as well as external drivers such as national policies. We hypothesize that very different results will be found in areas where rapid changes in land use have occurred recently, as this leads to a mismatch between demand and supply for most stakeholder groups⁹. Also, in systems where demand is more polarized, it may be more difficult to find an optimum in which all groups are supplied with their demanded ecosystem services⁹.

The finding that most major land-use changes will lead to inequalities in ecosystem service supply to the stakeholder community is an important one, as it provides quantitative evidence that landscape planning that focuses on one or few selected services can be

detrimental to rural communities. Indeed, while previous studies have shown that focusing on biodiversity can maximize several other services^{[39](#page-10-36)}, these studies mostly focused on cultural and regulating services, without considering their relative importance to stakeholders. By including all terrestrial final benefits valued by local stakeholders and by weighting their relative priority to stakeholders, a more complete picture emerges. These results demonstrate that while large-scale strategies to protect biodiversity and increase carbon storage are clearly needed¹, these must carefully account for the existing needs of the local communities⁴⁰. For large-scale land-use changes to be acceptable, in our study regions at least, there are only two solutions. First, the supply of ecosystem services on existing land must be increased—for example, via the development of innovative land-use options that allow for higher-than-current agricultural production or a restoration to higher local biodiversity levels than are currently observed. The other, and less explored, alternative is to alter priorities and demand^{[13](#page-10-9)}. In our study, stakeholders prioritized a wide range of services. If priorities and demand shifted—for example, due to changes in awareness, consumption patterns or policies (subsidies or payments for ecosystem services)—then land-use changes may be implemented without loss of multifunctionality or equity. For instance, a shift towards a higher priority for cultural than for provisioning services would allow a de-intensification or nature-first strategy to become more acceptable. While the management and alteration of societal demand presents substantial challenges, we propose that it may be more successful in finding sustainable land strategies than finding optimal land-use transformations, especially where biophysical trade-offs in ecosystem service supply limit ecosystem service co-supply $8,41$ $8,41$.

Although large increases in multifunctionality and equity were not possible under current levels of supply and demand, our results indicate that the de-intensification of land use could offer moderate benefits to local communities. The scenarios that outperformed the baseline landscape composition had two main characteristics: an increase in forest cover, associated with an increase in the proportion of mixed forests; and a simultaneous extensification of grasslands. Our results indicate that moderate afforestation, especially with mixed forests 42 , which is one of the major land-use trends in Germany⁴³, could provide many benefits to local communities. This finding also corresponds to the identification of forests as multifunctional hotspots in other European $landscapes¹³$ $landscapes¹³$ $landscapes¹³$. In this regard, our optimal de-intensification scenario is consistent with the objectives of both European Union and national policies that aim to decrease land-use intensity (LUI) and increase forest cover (European Union Biodiversity Strategy, Green Deal, new European Union Forest Strategy, National Biodiversity Strategy, Action Programme Insect Protection, Bund-Länder-Gemeinschaftsaufgabe Agrarstruktur und Küstenschutz and Forest Strategy 2050). Such changes would reduce livestock production and grassland biodiversity, but this would be compensated by gains in most other services (that is, a 'small loss, big gain' situation¹²), though clearly certain stakeholder groups would gain more than others. However, while this scenario is optimal at the level of local communities, the loss of livestock production could have external impacts in a globalized world. For example, if demand for food remained constant, de-intensification in Europe could lead to agricultural expansion and biodiversity loss in other areas of the world 44 .

The modelling approach employed here allowed us to investigate the impact of a wide range of landscape composition changes on both the supply of ecosystem services and the stakeholder communities who use these services. This was achieved by integrating supply and demand data for more services than are usually included—meaning that all the trade-offs are better represented and the picture is more complete, as we include non-material benefits that are not captured by monetary valuation approaches 22 . Because stakeholder groups prioritize multiple but different ecosystem services $13,24$ $13,24$ $13,24$, such a comprehensive approach is important if we are to understand the direct implications of landscape strategies for the well-being of stakeholder communities⁴⁵ and the causes of rural conflicts.

While our current approach is powerful and potentially applicable to a wide range of social–ecological systems, some aspects that would refine model predictions are missing. First, the inclusion of ecosystem services from a wider range of land-use types, including unmanaged land, urban and peri-urban areas, and water bodies, would better represent the services provided by a landscape, including water-based services. In particular, croplands (whose area was large but fixed here due to the lack of reliable data) provide important services and should be more accurately characterized in future studies. Second, the simple equity measure used here could be expanded on by accounting for the population sizes of the different groups, their degree of dependency on the considered services or other factors deemed important by policymakers. Third, the current model allows the investigation of the effect of a landscape's composition on multifunctionality but not its configuration. Future models should aim to integrate aspects of landscape configuration, as they are known to affect ecosystem service supply⁴⁶. This means that spatial interactions between landscape units (for example, the runoff of agricultural pollutants and the movement of matter or organisms across the landscape 47) should be accounted for^{[48](#page-11-1)}. Furthermore, we recommend the inclusion of local biophysical constraints into spatially explicit models (for example, limits on which soil types can support certain land uses) as well as path dependency-limits on converting one land use to another⁴⁹ (for example, it is difficult to rapidly restore fertilized intensive grasslands to a species-rich state). These measures would ensure that only realistic scenarios were considered. Our scenarios did not incorporate feasibility, and it is possible that some of the land-use change scenarios we explored may be challenging to implement (for example, large-scale grassland de-intensification, which would require many years to implement due to nutrient retention⁵⁰). Future models could also connect regional demand to global and interregional supply—for instance, by using telecoupling methods^{[44](#page-10-41)}. Finally, the integration of long-term ecosystem dynamics in both supply and demand would allow future studies to assess the sustainability of land-use strategies and the time lags before new outcomes are realized. On the demand side, the modelling of demographic changes as well as changes in consumption patterns (for example, a switch to more plant-based diets) could also be considered.

The approach presented here provides detailed information on the potential impacts of land-use changes on local communities. However, because of the aforementioned uncertainties and the unrepresented complexity of the social system, we advise that it should be viewed as a decision support tool that is best used to identify and plan land-use strategies within a participatory approach, though it may also be presented in the form of online tools^{[8](#page-10-7)}. Participatory approaches are increasingly seen as beneficial for assessing and discussing the choice and social impact of land-use change, one example being the "land-scape approach^{["16](#page-10-19)}, which aims to balance competing land-use priorities to promote environmental conservation and human well-being (for example, the African Forest Landscape Restoration Initiative⁵¹). The quantitative tool presented here can also help government and corporate policymakers assess strategies for improved land use and identify means of implementing them—for example, via agri-environment schemes that encourage different land-use types or land-use intensities within certain parts of the landscape 52 .

When our approach is applied at different spatial scales, it can provide different types of information and recommendation. For example, the approach adopted here (that is, using results averaged across three regions that are broadly representative of rural Germany) can provide information that can inform national or regional-level guidelines and policies (for example, to encourage moderate increases in forest cover and grassland de-intensification nationally). However, the best places in which to implement these strategies should be identified at the local level, where local conditions may require the modification of general guidelines⁵³. For example, across our study regions, stakeholder demand is consistent²⁴ but initial land-use proportions are very different, and the relationship between LUI and service supply also differs^{[8](#page-10-7)}. By tailoring and parameterizing our model for local conditions, one can apply our approach within specific regions to determine the optimal land use in these areas and prevent the application of land-use strategies that may be locally inappropriate (Supplementary Figs. 18–23).

At even larger scales, the approach presented here can potentially be used to explore the societal impacts of the major land-use changes that are currently advocated, including large-scale tree planting^{[28](#page-10-12)} or half-Earth²⁷ policies. While we note that reliable results are contingent on the availability of high-quality and region-specific supply-and-demand data, we also believe that outputs of this approach can inform landscape-level decision-making. By doing so, it can help identify land-use strategies that are sustainable and equitable and that can lead to more harmonious relationships between local stakeholders.

Methods

Ethics

Senckenberg Gesellschaft für Naturforschung employed the researchers who conducted the social survey in this study and its subsequent use. 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 Forum⁵⁴ were followed and employed. This includes obtaining written consent for the collection and processing of the anonymized personal survey data 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. Field work permits were issued by the state environmental offices of Baden-Württemberg, Thüringen and Brandenburg.

Study area

We used data from 150 grassland and 150 forest sites (hereafter plots) studied within the large-scale and long-term Biodiversity Exploratories project in Germany[26](#page-10-30) [\(https://www.biodiversity-exploratories.de/](https://www.biodiversity-exploratories.de/)). The plots are located in three regions, including two hilly regions with calcareous bedrock: the UNESCO Biosphere Reserve Schwäbische Alb and its surroundings (Southwest region) and the Hainich-Dün region comprising the National Park Hainich and its surroundings (Central region), as well as the flat area of the UNESCO Biosphere Reserve Schorfheide-Chorin with sandy and organic soils (Northern region). The plots measured 50 m × 50 m for grasslands and 100 m × 100 m for forests and were selected to span the full range of LUI in grassland and forest management within the regions, while minimizing variation in potentially confounding environmental factors.

Population density ranges from 39 km−2 in Schorfheide-Chorin (Uckermark) to 106 km−2 in Hainich (Unstrut-Hainich-Kreis) and 262 km⁻² in the Schwäbische Alb (Reutlingen County) (2017)⁵⁵⁻⁵⁷. All three regions are historically mostly agricultural with contrasting historical legacies—for example, large-scale agriculture persists from the former German Democratic Republic era in the Schorfheide-Chorin and Hainich-Dün, while smaller farms of the former West Germany dominate in Schwäbische Alb. The population directly involved in the forestry and agricultural sectors have steadily declined in the past few decades as the activities of other interest groups, such as tourists and nature conservation associations, have become more economically important.

Land use

Grassland sites were classified according to a LUI index on the basis of grazing, mowing and fertilization intensity data collected annually from site owners using a questionnaire between 2008 and 2015 (refs. [58,](#page-11-10)[59\)](#page-11-11). These three land-use factors were summed after standardization by

their mean values across all three regions in the same period. LUI was then calculated as the square root of the sum. We classified all grasslands as low, medium or high intensity on the basis of whether their LUI index (averaged over time) belonged to the 0–33%, 33–66% or 66–100% quantiles of all LUI indices⁸.

The forests of all regions are dominated by European beech (*Fagus sylvatica*), but Scots pine (*Pinus sylvestris*) and oak (*Quercus* spp.) are relatively common in Schorfheide-Chorin, and Norway spruce (*Picea abies*) in Schwäbische Alb⁶⁰. Forest plots were classified as deciduous or coniferous if >80% of the basal area belonged to deciduous or coniferous trees, or as mixed otherwise.

Ecosystem service priority

We conducted one expert workshop in each region in 2018, with representatives of some preselected stakeholder groups. These led to the identification of 14 stakeholder groups and a list of all terrestrial ecosystem services of importance to this community²⁴. We restricted the list to services with direct links to final benefits (sensu the cascade model²⁵), thus excluding regulating services (such as pollination) that underpin the supply of other services (such as food production) but do not provide direct benefits to humans. This prevents the double-counting of ecosystem service benefits in the multifunctionality metric. We also excluded water-based services and the production of energy from technology, which were outside the scope of this study²⁴. The final list consisted of 11 ecosystem services (Fig. [1\)](#page-2-0).

Following the workshops, we conducted an online and postal survey across all 14 stakeholder groups in 2019 and received 321 responses. When respondents belonged to multiple stakeholder groups, they were asked to identify their main one and answer the survey as a representative of this group. In the survey, the respondents were requested to distribute a maximum of 20 points across the 11 pre-identified services to quantify their personal priorities. The number of points given for each service was then normalized by the total number of points given by the respondent. The respondents were also requested to indicate whether they considered the supply of a service to be sufficient, barely sufficient or insufficient, for services to which they assigned more than two points. Services for which 65% or more of the respondents (among those who attributed at least two points to the service) answered 'barely sufficient' or 'insufficient' were characterized as vulnerable: foraging (65%), regional identity (74%), carbon storage (88%) and biodiversity (89%). The details and socio-demographic data on this survey can be found in ref. [24,](#page-10-28) and the relative priority scores of each group for the 11 services considered can be found in Supplementary Fig. 2.

All participants took part in the workshops and the survey voluntarily. Their anonymity is guaranteed in all subsequent research steps. The participants could withdraw at any time, and the traceability to individuals is made impossible by the data analysis, following the standards of ref. [54.](#page-11-7)

Ecosystem service supply

In grasslands and forests, ecosystem service supply was quantified on the basis of plot-level indicators collected in all plots between 2008 and 2015 (with the actual year and measurement frequency depending on the service). For cropland, artificial 'plots' were created in which indicator values were derived from literature sources (Supplementary Information). Plot-level indicators were then corrected for the environment (see below) and aggregated to the landscape level to quantify the landscape-level service supply. Unless stated otherwise, the plot-level indicators were scaled between 0 and 1 and averaged to obtain ecosystem service supply (in some cases, indicators were not directly comparable across land uses and so were scaled between 0 and 1 within each land use), and landscape-level service supply was calculated as the sum of plot-level supply values. The details on the measurement of each indicator can be found in Supplementary Methods and in Supplementary Table 1.

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Provisioning services included food, fodder, timber and energy production, as well as hunting and foraging opportunities. Cropland plots were randomly assigned a crop type on the basis of the proportion of crop types in each region^{[61](#page-11-13)}. Food production was then quantified as the product of national yield averages and market values for each crop type[61](#page-11-13) (Supplementary Table 2). We estimated fodder production in grasslands as the average grassland productivity (plant biomass collected in spring, and corrected for the number of cuts and livestock units—assuming that the full field biomass production is used by the owners⁶² – multiplied by the average hay market value in Germany (123 ϵ per ton $^{(3)}$). Fodder production in croplands was quantified as crop yield (acquired from yearly biomass measurements and mowing and grazing data from farmer survey⁵⁸; Supplementary Methods) multiplied by market values of the main crops used as fodder (for example, alfalfa and silo maize) and square-transformed for further use. For timber production, the indicators were the total wood volume and the annual increment of all marketable species from selected European timber companies^{64[,65](#page-11-17)}. Increment and volume were then split into proportions of wood used respectively for timber, firewood and energy wood on the basis of national statistics⁶⁶, and then multiplied by each species' timber and energy wood market values in Germany. Timber production in grasslands and croplands was set to zero. Energy production was calculated in forests and croplands as the production of firewood or energy crops, respectively. Firewood production was calculated as the annual volume increment dedicated to firewood (see above) and multiplied by firewood market value. Energy crop value was calculated as described above. Hunting opportunity was estimated as the habitat suitability of the landscape for the most commonly hunted species in Germany: wild boar and roe deer 67 . Both are generalist and adaptable species, so we used broad indicators representing the suitability of forest habitats (forest type and square-transformed shrub cover 68) and the availability of other habitats (the availability of cropland or grassland in the landscape). The landscape-level hunting service was averaged across both species. Foraging opportunity was quantified as the abundance of edible wild plant species (square-transformed) and the richness of edible mushrooms (the species lists are in Supplementary Tables 6 and 7). In both cases, the most-harvested species were double-weighted. The landscape-level supply was calculated as the sum of the total cover of edible plant species and the gamma diversity of edible mushrooms across the landscape, both scaled between 0 and 1.

We considered only one regulating service, carbon storage. Carbon storage in grasslands was calculated as the total soil organic carbon stock in the 0–10 cm layer, which is the layer most responsive to management. In forests, total carbon storage was calculated as the sum of soil carbon stocks (0–10 cm layer) and the above-ground tree carbon stock. Crop plots were given fixed values for carbon stocks, corresponding to 72% of the regional average of carbon stocks in grasslands 69 .

Cultural services included aesthetic value, biodiversity conservation, regional identity and recreational value. The indicators for cultural services were chosen on the basis of existing literature and from semi-structured interviews with stakeholders conducted in the regions²⁴ (Supplementary Methods). Aesthetic value was divided into two subcomponents, naturalness and diversity, in line with the landscape aesthetic quality framework^{70,71}. In forests, naturalness was quantified on the basis of equally weighted measures of bryophyte cover and forest openness⁷². In grasslands, naturalness was quantified from flower cover, butterfly abundance (both square-root-transformed) and the normalized difference soundscape index $7³$. In both forests and grasslands, the diversity component was quantified from measures of plot-level acoustic diversity index and landscape-level land-use diversity (calculated as the Shannon diversity of the land-use types). Crops were assigned the lowest observed score of grassland naturalness and acoustic diversity. Biodiversity conservation value was quantified as the sum of the gamma diversity of bird and plant species at the landscape level (both scaled between 0 and 1 beforehand). Plant species richness and abundance were recorded in annual botanical surveys of grassland and forest plots between 2009 and 2015. Bird species richness was based on annual point-count surveys in grassland and forest plots between 2008 and 2012. Artificial plant and bird communities were simulated for crops, on the basis of known frequencies of the different species in German croplands $74,75$ (Supplementary Methods). Regional identity was considered to be related to the uniqueness of a given environment. For both grasslands and forests, it was quantified as the average of a plot-level 'historical or cultural habitat' score (grasslands with *Juniperus communis*; *Carpinus* and *Fagus* cover in forests), and a 'cultural species' score, on the basis of the abundance (square-transformed) and richness of culturally important plants and birds (Supplementary Tables 4 and 5). As the area surveyed was different in forests and grasslands (Supplementary Table 1), plant cover was not directly comparable across land uses and was independently scaled in each land use. The recreational/leisure value of a landscape depends on large-scale factors such as infrastructure and accessibility, which could not be assessed within this study. However, European studies on recreational preference have also identified site-level drivers, with visitors preferring natural, low-intensity open land and forests to anthropized land uses^{[76](#page-11-28)} while also favouring land-use diversity⁷⁷. The suitability of each landscape for outdoor activities was thus calculated as the proportion of low- and medium-intensity grasslands (saturating at 50%) plus the proportion of forests (also saturating at 50%)—that is, maximum suitability was reached for landscapes composed of 50% low- and medium-intensity grasslands and 50% forests.

Landscape simulations

All steps of data preparation and analyses were conducted using R v.4.2.1 (ref. [78\)](#page-11-30). Landscape simulations were conducted using the Rust programming language 79 , which provided a faster environment for data-intensive simulations. Simulations were run using data from all three regions simultaneously, which allowed us to identify general strategies that improve either one service or community-level multifunctionality, relative to the baseline landscape (the average current landscape composition of the three regions).

In our landscape simulations, we initially considered landscape compositions spanning the whole range of landscape compositions (from 100% crops to 100% forests and 100% grasslands, with varying proportions of land management within grasslands and forests). These results can be found in Supplementary Figs. 16 and 17. We focus in the main text on a subset of combinations with a fixed proportion of crops corresponding to the baseline landscape composition (see below), including around 6,000 possible landscape compositions (the small black dots in Fig. [2](#page-3-0)). For each of the considered landscape compositions, we simulated 200 artificial landscapes by randomly drawing, without repetition, the corresponding proportion of existing plots (of a total of 20 plots) in each of the land-use categories. Landscape-scale services were then scaled between 0 and 1 by subtracting the minimum and dividing by the range (the 97.5% quantile to avoid the outliers, minus the minimum) across all landscapes. This scaling was required for the standardized weighting of each service within the multifunctionality metric (see below and Fig. [1\)](#page-2-0). Among the 6,000 landscape compositions, we also identified a range of predefined land-use change scenarios (the large coloured dots in Fig. [2\)](#page-3-0), such as increasing forest cover by 50% or converting all grasslands to high intensity. A description of the scenarios is shown in Supplementary Table 9.

To characterize the baseline landscape composition, we averaged the relative proportions of crops, grasslands and forests, as well as proportions of forest types (coniferous, deciduous or mixed), obtained from local CORINE land-use land-cover maps (Corine Land Cover 2018, excluding settlement areas) across the three study regions. For comparison, we also calculated the relative proportions of croplands, grasslands and forests from German-level Corine Land Cover maps.

To estimate the current proportions of grassland intensity classes, we used grassland management data obtained in 1,000 plots in each region in 2007. These data (estimates of grazing units, fertilization and cuts each year) were used to calculate an index similar to the LUI used for the 150 intensively studied grasslands. We then calibrated the LUI with this new index on all 150 intensively studied grasslands (correlation = 0.73, *P* < 10−6) and used the LUI thresholds for low-, medium- and high-intensity classes to estimate the proportion of these 1,000 plots that fell in each LUI class.

Correction for environmental conditions and area

To ensure that the observed variation in multifunctionality was due to differences in the land use and land management of landscapes, rather than other factors (for example, differences in soil types), we conducted an environmental correction of all service indicators. Plot-level indicators (that is, all except plant, bird and fungus diversities, land-use type diversity, and proportions of forests or low-intensity grasslands) were corrected at the plot level to account for environmental drivers of services unrelated to land use. This was done for all three regions at once but separately for forests and grasslands, by running linear models of each indicator with mean annual temperature, precipitation, soil pH, soil depth, topographic wetness index (a good proxy for soil humidity 80 80 80) and soil texture (clay content) as the explanatory variables, using stepwise selection to select only relevant variables and avoid overfitting. The residuals were then extracted and added to the predicted mean of the variable to keep the data in the same range as the raw data, so that cross-land-use comparisons remained possible where applicable, before use in further analyses.

For plant diversity, the area sampled in forests was larger than that in grasslands (Supplementary Table 1). This meant that forest diversities were initially overestimated compared with grasslands, leading to incompatible plant diversities in landscapes composed of different sizes (that is, the diversity sampling area in a landscape composed of 20 forest plots would comprise 20 \times 400 m², while a landscape composed of 20 grassland plots would sample 20 \times 16 m²). To correct for this, we first modelled species–area curves by randomly drawing a variable number of forest and grassland plots and assigning size as the sum of sampled areas in all plots. The diversities of the landscapes simulated as described above were then corrected by the predicted diversity of a landscape of similar size, as per the species–area curve (Supplementary Fig. 7).

Finally, bird and fungus diversities and area-corrected plant diversity were corrected using the same method as for other services, but at the landscape level. Gamma diversities (area-corrected as described above for plants) were first calculated at the landscape level and then regressed on landscape conditions, using as explanatory variables the landscape mean of the aforementioned environmental variables, as well as landscape heterogeneity. Landscape heterogeneity was calculated as the volume of the convex hull of the selected sites in a principal component analysis that included all environmental variables.

Landscape-level ecosystem multifunctionality and identification of optimal scenarios

Ecosystem service multifunctionality is a measure of the simultaneous supply of multiple prioritized ecosystem services, relative to their human demand^{[9](#page-10-23),[20](#page-10-24)}. Here we use it to quantify how well the demand of a stakeholder group is met by the service supply. For each replicate landscape, multifunctionality was calculated for each stakeholder group as the average of the considered services, weighted by the group's priority scores.

We then identified optimal landscape compositions on the basis of different sets of criteria (Supplementary Table 9):

(a) Optimization of individual services: the identifcation of landscape compositions that maximize one service.

(b) Optimization of multifunctionality and equity. Community-level multifunctionality was calculated as the average of the stakeholder multifunctionality scores, weighted by the relative power of each group. For community-level equity, we focus here on distribution equity^{[17](#page-10-20)}, which we calculated as the negative index of the Gini index of multifunctionality values across groups, weighted by each group's power (ranging from −1, maximal inequity, to 0, perfect equity). The Gini index is a measure of statistical dispersion, which was originally designed as a measure of wealth inequality 81 .

To identify the landscape composition that maximizes these properties, we selected the 15 landscape compositions (each with 200 landscape replicates) that maximized the supply of the considered service or the sum of equity and multifunctionality (both scaled and square-root-transformed beforehand). The number 15 was chosen to provide a sufficient range of the composition space while also ensuring that the selection was restricted to only high-scoring landscapes.

(c) Do-no-harm scenario: no loss of vulnerable service supply and no loser groups.

Groups were considered to lose multifunctionality if there was a signifcant decrease in their multifunctionality score compared with the baseline landscape—that is, if the upper limit of the confdence interval of the groups' multifunctionality change in the new scenario compared with the baseline was under 0.

There was a loss in vulnerable services ('Ecosystem service priority') if there was a signifcant decrease in their supply compared with the baseline landscape—that is, if the upper limit of the confdence interval of the service supply change in the new scenario compared with the baseline was under 0.

All landscape compositions that had both no group losing multifunctionality and no loss in vulnerable services were selected. If more than 15 fit these criteria, the 15 with the highest multifunctionality were selected. In both cases, we then calculated the average landscape composition (the average proportion of each land-use type) across these landscapes, as well as the average change in service supply (from values scaled between 0 and 1) and group-specific multifunctionality, compared with the baseline landscape composition, by subtracting the average baseline value from the average composition value and dividing by the average baseline value.

Reporting summary

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

Data availability

This work is based on data collected by several projects of the Biodiversity Exploratories programme (DFG Priority Program 1374). Most datasets are publicly available in the Biodiversity Exploratories Information System [\(https://doi.org/10.17616/R32P9Q](https://doi.org/10.17616/R32P9Q)). However, to give data owners and collectors time to perform their analyses, the Biodiversity Exploratories' data and publication policy includes by default an embargo period of three years from the end of data collection/data assembly, which applies to the remaining datasets. These datasets will be made publicly available via the same data repository. All datasets and their current status (publicly available or not) are listed in Supplementary Table 1 and corresponding references. All correspondence and requests should be addressed to the corresponding author, or, when concerning a specific dataset, to the data owners (see the dataset references).

Code availability

The full code to replicate the analyses can be found on GitHub [\(https://](https://doi.org/10.5281/zenodo.7019909) doi.org/10.5281/zenodo.7019909 or [https://github.com/mneyret/](https://github.com/mneyret/landscape-equity) [landscape-equity\)](https://github.com/mneyret/landscape-equity).

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Author contributions

M.N., S.P., G.L.P. and P.M. conceived the study and designed and performed the analyses. M.N., S.P., G.L.P. and P.M. wrote the manuscript with significant inputs from A.L.B, S.B., J.M.B., N.H., V.H.K, T.K., J.K., J.M. and S.M., and contributions from all authors. The data were contributed by S.P., G.L.P., S.B., N.H., V.H.K., J.K., S.M., C.A., F.B., M.E., M.F., K.G., K.J., S.C.R., P.S., M.S.-L., C.W., T.W. and P.M. Authorship order was determined as follows: (1) core authors; (2) other major contributors (alphabetical); (3) other contributors, including data contributors (alphabetical); and (4) senior author.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at [https://doi.org/10.1038/](https://doi.org/10.1038/s41893-022-01045-w) [s41893-022-01045-w.](https://doi.org/10.1038/s41893-022-01045-w)

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Extended Data Fig. 1 | Variation of multifunctionality (a) and equity (b) at the landscape level with increasing proportion of forests. Each dot is one simulated landscape composition. The green line shows the fitted loess model. The dashed vertical line shows the current proportion of forests, while the

solid line shows the optimal forest cover for the corresponding score (top row: multifunctionality; bottom row: equity). The analysis was completed only on landscapes with a crop cover equal to the baseline landscape composition, hence a maximum forest proportion of 60%.

Extended Data Fig. 2 | Changes in landscape composition (a), service supply (b) and multifunctionality (c) when maximising carbon storage compared to the baseline landscape composition. Data are presented as mean and 95% confidence intervals, calculated on n = 15 landscape compositions, each averaged across 200 replicated simulations.

Extended Data Fig. 3 | Changes in landscape composition (a), service supply (b) and multifunctionality (c) in the 'do-no-harm' scenario (that is, when maintaining the supply of threatened services and preventing loss of multifunctionality by any stakeholder group) compared to the baseline

landscape composition. Data are presented as mean and 95% confidence intervals, calculated on n = 15 landscape compositions, each averaged across 200 replicated simulations.

equity, (middle) number of stakeholder groups losing multifunctionality and (right) vulnerable service scores in multiple landscape compositions compared to the baseline landscape composition. This figure shows the full range of landscape compositions, of which a subset is shown in the main figures Fig. [2](#page-3-0)c and [4.](#page-5-0) Large coloured dots show a few predefined scenarios while small black dots represent all the other scenarios that were simulated; they show the mean of all the 200 replicates for each given scenario.

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Reporting Summary

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Statistics

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) 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 Analyses were run using R v4.2.1. The main packages used during the simulation and analysis of the results were data.table (v. 1.14.2), readxl (v. 1.4.1), sp (v. 1.5.0), rgdal (v. 1.6.2), raster (v. 3.5.29), lubridate (v. 1.8.0), hms (v. 1.1.2), vegan (v. 2.6.2), ggplot2 (v. 3.3.6), ggnewscale (v. 0.4.7), Hmisc (v. 4.7.1), boot (v. 1.3.28), R.utils (v. 2.12.0), Rmisc (v. 1.5.1), cowplot (v. 1.1.1), DescTools (v. 0.99.47), tidyr (v. 1.2.1), ade4 (v. 1.7.19), geometry (v. 0.4.6.1), mice (v. 3.14.0), zoo (v. 1.8.10), plyr (v. 1.8.7). The full code to replicate the analyses can be found on GitHub (DOI: 10.5281/zenodo.7019909, https://github.com/mneyret/landscapeequity).

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This work is based on data collected by several projects of the Biodiversity Exploratories program (DFG Priority Program 1374). Most datasets are publicly available in the Biodiversity Exploratories Information System (http://doi.org/10.17616/R32P9Q). However, to give data owners and collectors time to perform their analyses the Biodiversity Exploratories' data and publication policy includes by default an embargo period of three years from the end of data collection/data assembly, which applies to the remaining datasets. These datasets will be made publicly available via the same data repository. All datasets and their current status (publicly available or not) are listed in Table S1 and corresponding references.

Human research participants

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

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Field-specific reporting

Life sciences Behavioural & social sciences \boxtimes Ecological, evolutionary & environmental sciences

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Sampling strategy diversity of management practices and they were all pooled together, resulting in 150 individual plots which is commonly accepted as sufficient sample size for most statistical tests. In our case, this was sufficient to simulate independent landscapes without excessive overlap.

Data collection Data collection followed standard protocols appropriate for each considered variable.

Bird diversity: Birds were surveyed by standardized audio-visual point-counts and all birds exhibiting territorial displays (singing and calling) were recorded. We used fixed-radius point counts and recorded all males of each bird species during a five-minute interval per plot. Each plot was visited five times between 15 March and 15 June between 2008 and 2012.

Plant abundance and diversity: Sampling of all vascular plant species and estimation of the % cover of each species in a 4 m x 4 m subplot (grasslands) or 20m x 20m plot (forests), done in 2009-2015.

Bryophytes: In 2007 and 2008, we recorded the cover of all moss and liverwort species and estimated for each species their abundance on a 20m x 20m area in each plot. We distinguished between 4 substrate layers: terricolous (on soil); lignicolous (on dead wood); corticolous (on bark) and saxicolous (on rock). Low abundant species with scarce cover got cover values of 0.5%.

Canopy openness: Canopy openness is quantified as percentage of sky pixels of a simulated hemispherical image for an opening angle of 60°.Canopy openness values are based on nine systematically distributed single terrestrial laser scans per plot that were made centre between June to September 2014. We used a Faro Focus 3D 120 (Faro Technologies Inc., Lake Mary, USA) laser scanner that operates based on the phase-shift technology, which we set to scan a field of view of 305° vertically and 360° horizontally with a step width of 0.14065°. Maximum scan distance was defined by the instrument's limit by 120m. The simulated hemispherical image was computed based on the three-dimensional point cloud data obtained through the laser scans. Canopy openness values were aggregated to plot means for further analyses.

Flower cover: Flowering units were counted between May and September 2009 for all flowering plant species (excluding grasses and sedges) on transects along the four edges of each plot, in a total area of 600m2. For abundant species, the number of flowering units was extrapolated to the whole plot from a smaller area of 112m2. The total flower cover was calculated at the plot scale as the sum of the individual flower cover of all plant species.

Lepidoptera: Butterfly and day-active moths (hereafter termed as Lepidoptera) abundance was measured in 2008 and averaged among sites within each landscape. We conducted surveys of Lepidoptera from early May to mid-August. We sampled Lepidoptera during 3 surveys, each along one fixed 300m transect of 30nnin in each site. Each transect was divided in 50m sections of 5min intervals and we recorded all Lepidoptera within a 5m corridor.

NDSI and acoustic diversity: From March to July 2016 an autonomous recording unit (Soundscape Explorer T recorder, by Lunilettronics), was placed at 2m height on each plot. The autonomous recorders were equipped with omnidirectional microphone capsule (EMY-63M/P, sensitivity (0 dB=1 V/Pa. 1 kHz): dB -38 +/- 3, signal to noise ratio: > 60 dB, input voltage of the ADC: 0.75 Vrms (personal communication with Lunilettronik Coop.). The microphone gain was manually set to +25 dB. The signals were sampled at 48 kHz with a 16 bits digitization, recording for one-minute every tenth minute during 24 hours a day. We calculated the normalized difference soundscape index (NDSI) using the "multiple sounds" function in the soundecology package in R. NDSI was calculated as the ratio ([biophony — anthrophony]/[biophony + anthrophony]) of the normalised power spectral density values (W/kHz) for the frequency intervals corresponding to anthrophony (1-2 kHz) and biophony (2-24 kHz). The acoustic diversity (ADI) was calculated across the frequency range of 0-24 kHz using 1 kHz steps and a decibel threshold of -50

Culturally important species list: The list of culturally important bird species was obtained from an online survey among 57 German respondents who were asked to say whether each species was unimportant (0 points), slightly important (1 point) or very important (5 points) species, based on whether the species "were part of German cultural identity or that of the study regions, e.g. by regularly appearing in German folklore, iconography, or popular entertainment". We then retained the 25% species with highest average scores, and used the survey data described above to calculate species richness. The list of culturally important vascular plant species also followed the same definition ("part of German cultural identity or that of the study regions, e.g. by regularly appearing in German folklore, iconography, or popular entertainment") but was created by experts with botanical knowledge of the species in the three Exploratories. We then used the survey data described above to calculate total cover of culturally important vascular plant species.

Soil C stocks: In 2011 and 2014, we sampled composite samples for each plot, prepared by mixing 14 mineral surface soil samples per plot. Soil samples were taken along two 18 m transects in each plot using a split tube auger, 40 cm long and 5 cm wide (Eijkelkamp, Giesbeek, The Netherlands). Composite samples were weighed, homogenized, air-dried and sieved (<2 mm). We then measured total carbon (TC) contents by dry combustion in a CN analyser "Vario Max" (Elementar Analysensysteme GmbH, Hanau, Germany) on ground subsamples. We determined inorganic carbon (IC) contents after combustion of organic carbon in a muffle furnace (450°C for 16 h). We then calculated the soil organic carbon (SOC) content as the difference between TC and IC, and the SOC concentration based on the weight of the dry fine-earth (105°C) and its volume. SOC concentration was then multiplied by soil bulk density to obtain plot-level soil carbon stock values. Values for 2011 and 2014 were then averaged for each plot.

Tree C stocks: To assess the amount of carbon stored in trees in each of the 150 plots, we estimated the living tree volume of each plot. Biomass was estimated by multiplying the volume by species-specific wood densities. The carbon stored in above ground trees is approximately 50% of its dry biomass.

Hay production: We quantified hay production as total biomass production in the grasslands. Between mid-May and mid-June each year, aboveground biomass was harvested by clipping the vegetation 2-3 cm above ground in four randomly placed quadrats of 0.5m x 0.5m in each subplot. The plant biomass was dried at 80°C for 48 hours, weighed and summed over the four quadrats. Biomass was then averaged between 2008 and 2012. In order to convert this one-time biomass measurements into estimates of annual field productivity, we used the information on the number of cuts and the number of livestock units at a site to estimate the total annual biomass production harvested by farming activities, i.e. converted into fodder or consumed directly by livestock. Timber volume: Species, diameter at breast height and geographical location of all trees (calliper limit dbh >7cm) growing in the forest plots (EPs) were surveyed between 2014 and 2018. Tree height was measured for a subsample of trees across the observed

diameter range (per species and EP). Using stand height curves the height of all trees was estimated. Wood volume was estimated using diameter and height. Wood volume was then multiplied for each species by the proportion of wood used for timber ad industry wood based on national statistics

Fungi: From each plot, in May 2011, a pooled soil sample was collected and stored by -80°C. DNA was extracted twice from a 0.5g subsample of each soil sample.

We then used a PCR approach to amplify fungal rDNA (Primers: ITS1F and ITS4), purified and cleaned the products and sequenced by using 454 pyrosequencing. The sequences were additionally clustered at 97% sequence identity using cd-hit-2d. The shared OTUs were compared and sequence abundances combined. Finally, a taxonomic assignment of the resulting representative sequences of each OTU was performed using the classify.seq command of MOTHUR applied to the UNITE fungal ITS reference database version 7. Finally, for landscape we calculated the gamma diversity of edible fungi species.

pH, texture: Composite samples were taken in 2011 and 2014 in all plots, by mixing 14 mineral topsoil samples (0-10 cm, using a manual soil corer with 5.3 cm diameter). Soil samples were air dried and sieved (<2mm) and we then measured the soil pH in the supernatant of a 1:2.5 mixture of soil and 0.01 M CaCl2

TWI: The topographic Wetness Index (TWI) combines measures of 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), and has been shown in previous analyses to be a better predictor than local humidity measures. It is defined as In(a/tanB), where a is the specific catchment area (cumulative upslope area which drains through a Digital Elevation Model (DEM, http://www.bkg.bund.de) cell, divided by per unit contour length) and tanB is the slope gradient in radians calculated over a local region surrounding the cell of interest. TWI was calculated from raster DEM data with a cell size of 25m for all plots, using GIS tools (flow direction and flow accumulation tools of the hydrology toolset and raster calculator). The TWI measure used was the average value for a 4 x 4 window centred on the plot, i.e. 16 DEM cells corresponding to an area of 100m x 100m.

Soil depth: Soil depth was measured as the combined thickness of all topsoil and subsoil horizons, determined 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).

Mean annual temperature: Temperature measured 2m above ground level in each plot, then aggregated at the year level and averaged between 2008 and 2015.

Precipitation: Precipitation measures based on the RADOLAN product, aggregated at the year level then averaged between 2008 and 2015

Grasslands cover: Based on Corine landcover data

Field work, collection and transport

Field conditions Specific field conditions depending on the variable and year considered (see methods).

Location With a size of about 422 km2 the Exploratory 'Schwabische Alb' is the smallest of the Exploratories and is characterised by calcareous bedrock with karst formations. It is located 460-860 m above sea level, with an average annual temperature of 6-7 °C and an annual precipitation with 700-1000 mm (Fischer et al., 2010).

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