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# Agricultural intensification without biodiversity loss is possible in grassland landscapes

Nadja K. Simons* and Wolfgang W. Weisser

**Grassland biodiversity in managed landscapes is threatened by land-use intensification, but is also dependent on low-intensity management. Solutions that allow for both agricultural production and species conservation may be realized either on individual grasslands, by adjusting management intensity, or at the landscape level, when grasslands are managed at different intensities. Here we use a dataset of more than 1,000 arthropod species collected in more than 100 grasslands along gradients of productivity, to assess the reaction of individual species to changes in productivity. We defined a range of land-use strategies and evaluated their effects on overall production and on species abundances. We show that conservation of arthropods can be improved without reducing overall production. We also find that production can be increased without jeopardizing conservation. Conservation and production could, however, not be maximized simultaneously at the landscape level, emphasizing that management goals need to be clearly defined.**

Conversion of habitats for human use is a major driver of biodiversity loss globally and locally. Additionally, conflicts between production and conservation arise when biodiversity is threatened by land-use intensification. In regions of the world where most available land is cultivated, century-long management has led to selection of the most suitable sites for specific land uses, such as forestry, pastures or arable fields[1]. In those regions, conversion of habitats is less likely to occur, in some cases it is strictly regulated (for example, the European Common Agricultural Policy[2]) or simply not possible due to limiting abiotic factors. Here, an increase in management intensity is a larger threat to biodiversity than conversion of habitats. One example is grasslands in central Europe, where land-use intensification decreases biodiversity both locally and regionally[3,4]. At the same time, many species are adapted to managed systems, and a particular fauna and flora is associated with grasslands under low-intensity management such as occasional mowing or low-intensity grazing[5]. This biodiversity is lost when management is abandoned and the grassland undergoes succession, making management a tool for conservation[6]. Thus, the conflict between production and conservation does not take place between two different land uses, such as crops versus grasslands, but rather within the grassland habitats. This has consequences for the design of strategies for biodiversity conservation, as both abandoning management and management intensification can lead to biodiversity loss. Hence, conservation measures (for example, 'high nature value grasslands' in central Europe) take into account the beneficial effects of low-intensity management and include management at very low intensity to maintain biodiversity, even in protected areas[7].

On the scale of individual grasslands, the trade-off between biodiversity conservation and production can be easily evaluated from species' abundances across land-use intensity or productivity gradients. On a landscape or regional scale, the trade-off between production and conservation is, however, more complex, as the grasslands contribute differently to production or conservation, based on the level of management intensity. Management strategies that include multiple levels of productivity might therefore be needed to allow for a coexistence of production and conservation within the same habitat, but at the landscape level.

We use a dataset of 1,005 grassland arthropod species sampled along gradients in productivity in three regions of Germany to test how individual species react to different levels of productivity, and how landscapes can be managed to maintain or increase overall production and at the same time protect species. First, we define a range of strategies based on one or two levels of productivity and compare the best strategy for different production and conservation goals. Second, we evaluate strategies with multiple levels of productivity that either maximize productivity at the landscape level, or maximize the number of species with a certain population size. All analyses were conducted separately for the three regions to assess the consistency of results.

## Results

All analyses are based on arthropod species' abundances along the gradient of grassland productivity within each of the three regions (for an overview of terms and definitions see Supplementary Table 1). We calculated abundance–productivity curves to estimate abundance of each species at any level of productivity (Fig. 1a) for common arthropods, defined as species sampled on at least six plots and with at least ten individuals per region. All other species, that is, rare species, were used in an additional analysis. Most arthropod species (between 54 and 76% in the different regions) showed hump-shaped or more complex abundance–productivity curves (Table 1; Supplementary Figure Set 1–3), which is in contrast to other studies where most species showed simple convex or concave curves[8–10].

The estimated abundance–productivity curves were used to calculate the landscape-level population size of each species under different land-use strategies (Fig. 1b,c; Supplementary Methods 3). We first defined a landscape-level target production, that is, the level of production that needs to be reached at the landscape level (cf. ref. [10]). Under the constraint that the total grassland area remains unchanged at the landscape level, a particular landscape-level target

Terrestrial Ecology Research Group, Department for Ecology and Ecosystem Management, School of Life Sciences Weihenstephan, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354, Freising, Germany. *e-mail: nadja.simons@tum.de

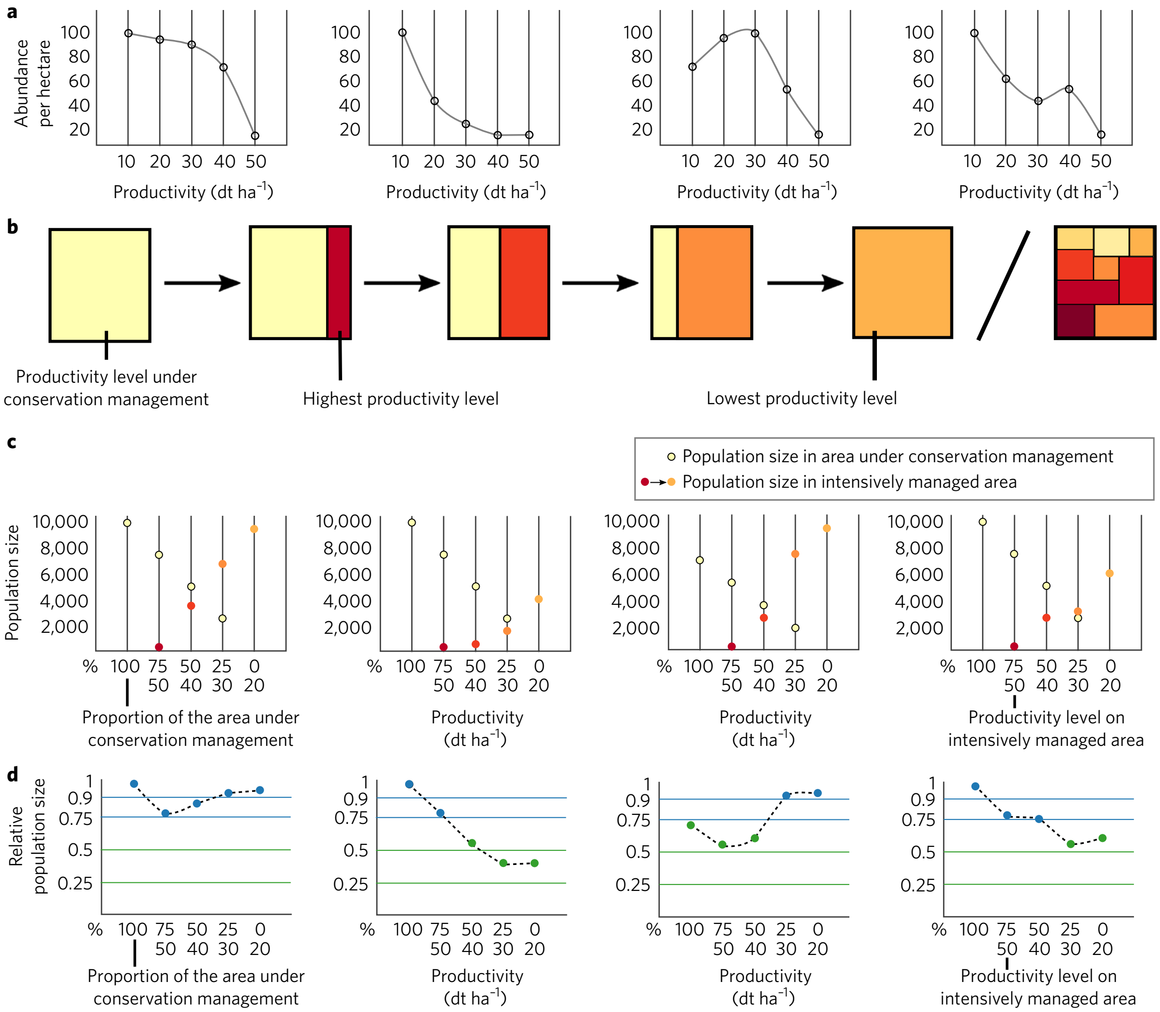

**Figure 1 | Selection of optimal land-use strategies based on abundance–productivity curves. a**, Abundance–productivity curves (grey lines) are estimated for each species based on its abundance per hectare along the productivity gradient. In this example, the productivity of 10 dt ha$^{-1}$ is the productivity under conservation management. The four graphs show typical forms of abundance–productivity curves; note that all species in this example are loser species (their abundance at highest productivity is lower than at lowest productivity) but winner species were equally or more common among the sampled arthropods (see Table 1). **b**, Land-use strategies are defined by assigning a specific proportion of the available area (here 100 ha) for conservation management. The productivity level on the remaining area is then given by the landscape-level target production, that is, the higher the proportion under conservation management, the higher the productivity level in the remaining area. Arrows indicate an increasing proportion of the area under high productivity. Plot-level strategies (first and fifth box) consider only one level of productivity across the whole area (see also Supplementary Fig. 1). More complex landscape-level strategies (sixth box) assign one specific level of productivity to each grassland. As there are too many possible options for such strategies to calculate by hand, those are assessed through multi-criteria optimization. **c**, For each strategy, the species' population size is calculated for the area under conservation management (yellow points with black border) and for the intensively managed area (coloured points). **d**, The landscape-level population size is calculated as the sum of the population sizes from both the area under conservation management and from the intensively managed area for each strategy. Acceptable strategies for each species are those under which the species' landscape-level population size is above the target threshold (points above the respective horizontal line). The thresholds are defined as population sizes relative to the maximum potential population size (that is, the species' population size if the whole area were managed at the productivity level under which it has the highest abundance per hectare). The optimal strategy for the whole community is defined as the strategy that is acceptable for the most species.

production can be reached by different strategies. One possibility is to manage all grasslands for the same productivity, henceforth referred to as 'plot-level strategy'. Alternatively, one part of the landscape is managed at maximum possible productivity, while the remaining plots in the landscape are managed less intensively for conservation (Fig. 1b). Within such 'landscape-level strategies', the level of productivity under intensive management will depend on the proportion of land used for conservation. We defined landscape-level strategies ranging from all land under intensive management (in effect a plot-level strategy) to the lowest possible proportion under intensive management to meet the observed landscape-level target production (Fig. 1b; Supplementary Fig. 1).

To select the best strategy for each species, we defined a target population size at the landscape level that the species has to reach (Fig. 1d). Previous publications[9,11–13] chose the maximum possible population size, that is, the estimated population size if the entire area was managed at the optimal productivity level for this species. However, species differ strongly in their abundance–productivity curves (Supplementary Figure Set 1–3), and therefore differ in the level of productivity that maximizes their abundance. We thus

**Table 1 | Observed range of productivity and landscape-level production in the 109 grasslands used for the analysis.**

| | Schwäbische Alb | Hainich-Dün | Schorfheide-Chorin |
|---|---|---|---|
| **Characteristics of the regions** | | | |
| Number of plots in analysis | 38 | 37 | 34 |
| Area of grasslands around plots (ha) | 226.02 | 1283.6 | 961.2925 |
| Landscape-level production (dt) | 16,893.33 | 35,978.73 | 98,975.81 |
| Minimum observed productivity (dt ha$^{-1}$) | 5.27 | 8.17 | 38.45 |
| Maximum observed productivity (dt ha$^{-1}$) | 173.07 | 143.39 | 176.73 |
| **Arthropod communities** | | | |
| Number of species sampled | 501 | 529 | 539 |
| Number of common species | 120 | 133 | 128 |
| Number of rare species | 381 | 396 | 411 |
| Higher abundance at highest productivity | 68 | 106 | 93 |
| Higher abundance at lowest productivity | 52 | 27 | 35 |
| **Abundance–productivity curves** | | | |
| Convex or concave | 27 (21/6) | 54 (38/16) | 56 (47/9) |
| Hump-shaped | 86 (43/43) | 70 (60/10) | 64 (41/23) |
| Polynomial | 5 (4/1) | 7 (6/1) | 6 (4/2) |
| Linear | 2 (0/2) | 2 (2/0) | 2 (1/1) |

Number of species in each region, and number of common and rare species within the community are shown. For the common species, the number of species that have higher abundances under highest/lowest productivity are given. Number of common species that show best fit with one of four abundance–productivity models are shown. Numbers in parentheses indicate the number of winner/loser species (that is, higher abundance at highest/lowest productivity).

analysed which strategies are acceptable for a species, based on a population target of 90% (75%, 50%, 25%) of the maximum possible population size (see ref. [14] for a similar approach). As the higher thresholds will be reached by only a small number of species under each strategy, these reflect conservation targets that in effect aim at large population sizes for a few species. The lower thresholds reflect conservation targets that in effect aim at a large number of species being present with a minimum population size. We then calculated under which strategies the number of species reaching the respective population target is highest and defined those as the best strategies for the entire community.

As a baseline, we counted the number of species that currently reach the different thresholds in the three regions. Under current management, less than 20% of species reach at least 90% of their maximum possible population size, and less than 40% of species reach at least 75% of the maximum possible population size (dashed vertical lines in Supplementary Fig. 2). Nevertheless, a number of alternative strategies can be found under which the number of species reaching the population targets is higher than under the current situation, at the same landscape-level production (Supplementary Fig. 2). Thus, it is possible to improve species conservation without reducing landscape-level production. At thresholds of 50% and 25%, most species already meet these population targets under current conditions, and the number cannot be further increased through alternative strategies (Supplementary Fig. 2).

We showed that it is possible to define strategies that improve conservation without reducing production. Can we also define strategies that have a higher landscape-level production and still reach the population targets with the same or even higher number of species? To answer this question, we defined a range of possible landscape-level production targets, ranging from all grasslands being managed for conservation to all grasslands managed with the highest observed productivity. At each landscape-level production target, we again chose the optimal strategy for the entire community based on the maximum number of species reaching the respective population target. For the 90% threshold, the best landscape-level strategies for the entire community had a higher number of species above the threshold compared with the current situation (asterisks in Fig. 2), across the whole range of production targets in two out of three regions (blue points above horizontal lines in Fig. 2a). Hence, production and conservation could be increased simultaneously in those regions. In the third region (Schorfheide-Chorin), the best strategies for the entire community under higher landscape-level production were only slightly better or worse than the current situation with respect to conservation (Fig. 2). For the 25% threshold, the number of species reaching the population target under the best strategy was higher than the current situation in only two regions, and only in Hainich-Dün did those include the best strategies under increased production (green points in Fig. 2a). Hence, strategies under which landscape-level production and conservation of many species could be increased at the same time were rarely found. Under both the 75% and the 50% thresholds, only a few strategies under increased production were found that also increased conservation (Supplementary Fig. 3).

For each landscape-level production target, we found more than one strategy that could be defined as the best strategy for the entire community, that is, where the maximum number of species reached the respective population target (points in Fig. 2b). However, only a few strategies were best for the entire community at both the 90% and the 25% threshold (overlapping points in Fig. 2b, compare with Supplementary Fig. 4). This means that the best strategies for one population target are not necessarily the best strategies for other population targets, indicating a trade-off between optimizing landscapes for conservation of a few species with a large population and optimizing for conservation of many species.

One could argue that an ideal strategy will not only be considered a best strategy for both the 25% and 90% thresholds, but also increase the number of species reaching the respective threshold compared with the current situation. However, none of the landscape-level strategies, which could be defined as best for the entire community at both thresholds, did lead to an improvement compared with the current situation (compare number of species in Fig. 2a and strategies with overlapping points in Fig. 2b). The same holds true for the two other thresholds (75% and 50%): while some strategies increase

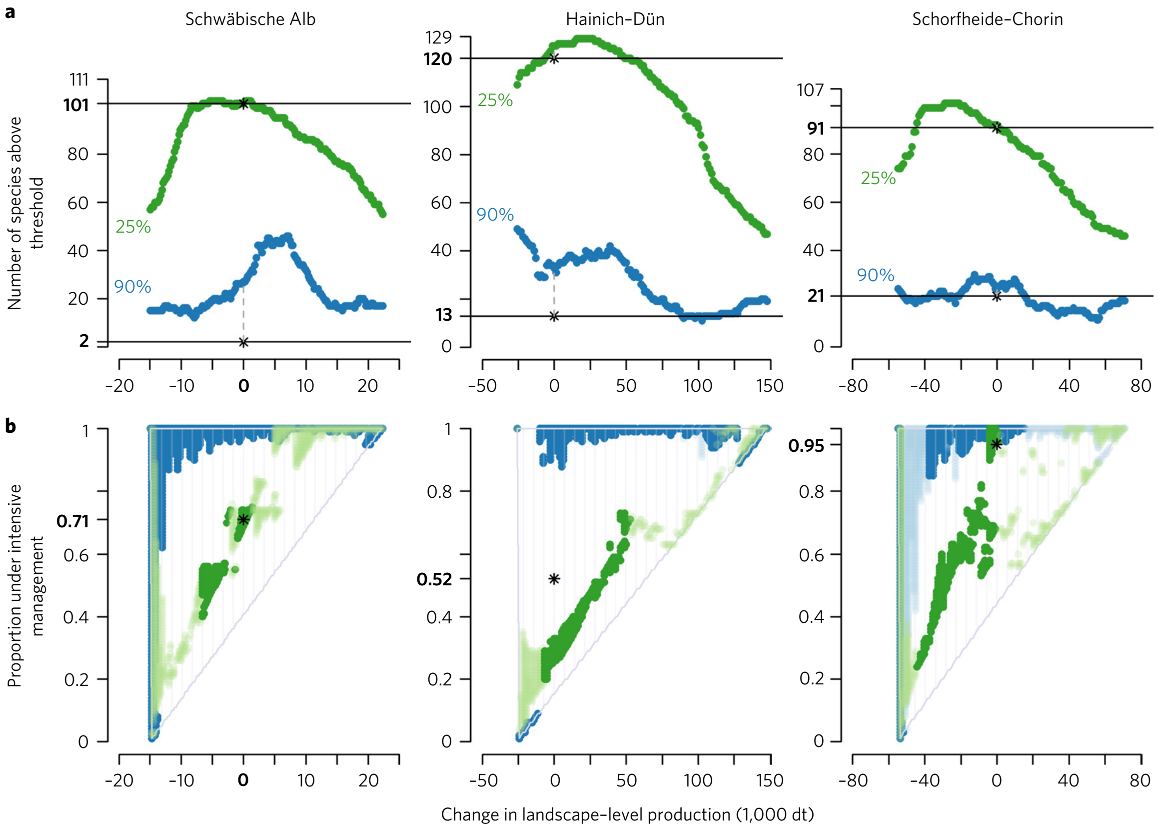

**Figure 2 | Optimal strategies across the range of possible landscape-level production targets.** The current landscape-level production and the corresponding number of arthropod species at both the 90% and 25% threshold as well as the current strategy are indicated by black asterisks. The different landscape-level production targets are indicated on the horizontal axes as difference to the observed landscape-level production. Bold numbers on the *y* axes indicate the observed number of species that reach the respective population size and the observed proportion of grasslands under intensive management, that is, not under conservation management. **a**, Number of species for which the population size is at least as high as 90% (blue points) or 25% (green points) of the maximum possible population size under the optimal strategy for each landscape-level production. **b**, Triangles indicate the range of possible strategies across the range of landscape-level productions. The *y* axis ranges from all grassland to only 1% of the grasslands being managed intensively. The *x* axis ranges from lowest (all grasslands managed for conservation) to highest landscape-level production (all grasslands managed under the highest productivity possible). The higher the landscape-level production, the lower the number of possible strategies. Coloured points indicate optimal strategies for the respective population size thresholds. Darker colours indicate strategies under which the number of species at the threshold is equal or larger to the current number of species, lighter colours indicate strategies with fewer species at the thresholds. Separate graphs for each threshold are given in Supplementary Fig. 4.

the number of species at one of the thresholds compared with the current situation, none do so for both a high and a low threshold (Supplementary Fig. 4). Hence, if we increase landscape-level production by implementing a landscape-level strategy that considers both production and conservation, we can improve conservation outcomes, that is, increase the number of species that reach a set population size compared with the current situation. However, we can only achieve this for either a large number of species with a small population size (strategies where all common species reach the 25% threshold were found for Hainich-Dün, Fig. 2a) or for fewer species with a population size close to the maximum possible.

So far, the landscape-level strategies were constrained to two levels of productivity, the productivity under conservation management and the productivity level on the remaining grasslands. However, more complex landscape-level strategies are conceivable where grasslands are free to vary in productivity under the constraint that a particular landscape-level target production is reached. We evaluated those strategies and their effect on population sizes with multi-criteria optimization algorithms[15]. The first algorithm maximizes landscape-level production under the constraint that all species have the same or more individuals than currently observed in the whole region. Under the optimal solution, most grasslands are managed at the highest possible productivity, and only one or two grasslands are managed under lower productivity (left-hand graphs in Fig. 3). The second algorithm maximizes conservation (that is, the number of species reaching at least 90% of their maximum possible population size) under the constraint that landscape-level production is not lower than the observed production and that all species are found with at least five individuals across the whole region. Here, the resulting optimal solutions have almost all grasslands managed at an intermediate level of productivity, with a single grassland managed under lowest productivity in one region (right-hand graphs in Fig. 3). As the optimization algorithms do not take into account the observed productivity levels, the final levels within the optimal multi-level strategies are quite different from the currently observed productivity levels (asterisks in Supplementary Fig. 5).

The differences in the optimal solutions for the two approaches (maximized production or maximized conservation) show that the optimization goal needs to be clearly defined and that there is no solution that maximizes both production and conservation. Nevertheless, the optimal solutions for conservation also resulted in a higher landscape-level production than the observed

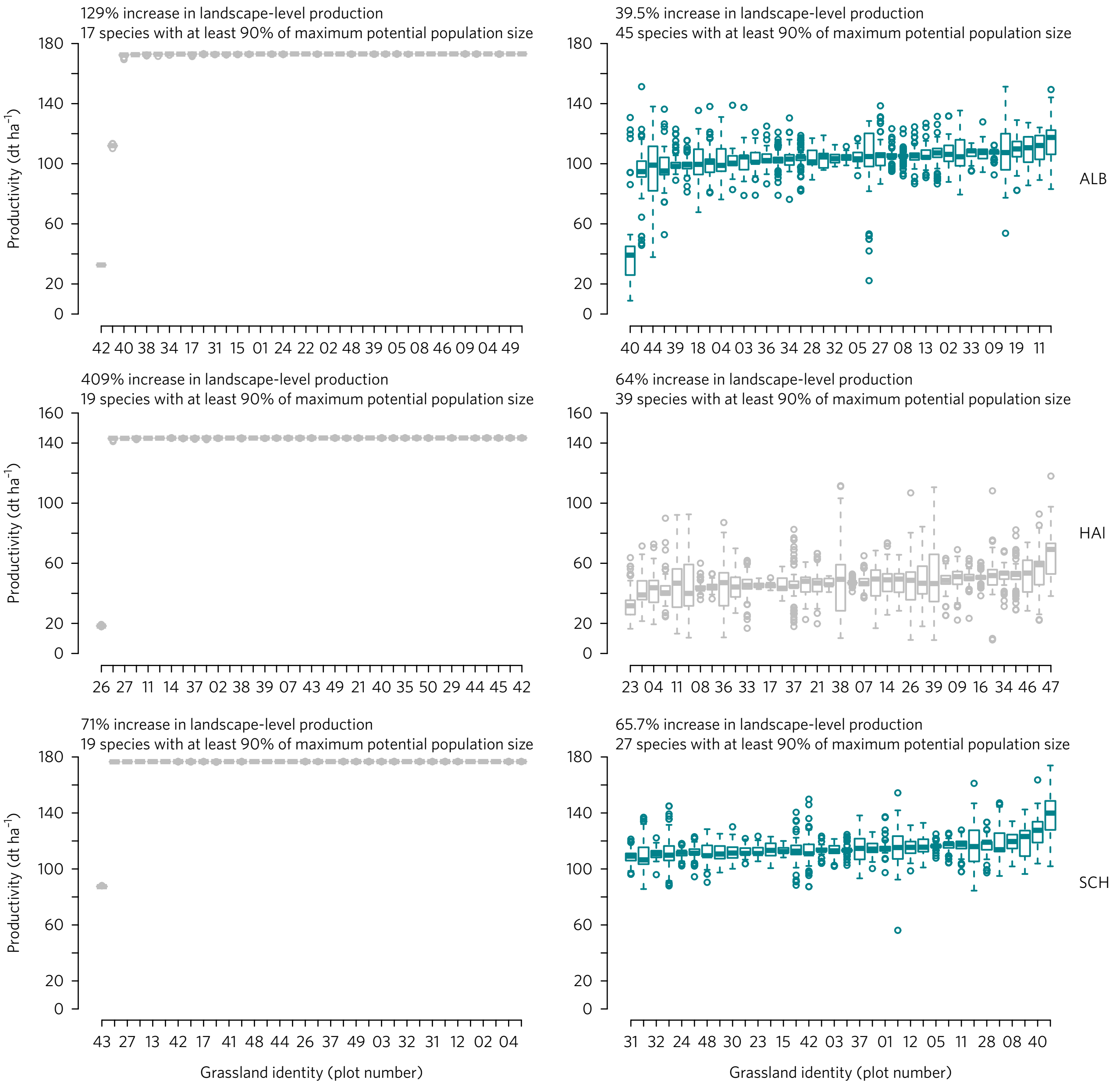

**Figure 3 | Productivity in grassland biomass on each grassland assigned by the optimization algorithms.** The left-hand graphs show assigned productivity for the optimization that maximizes landscape-level production under the constraint that the overall abundance of each species is not lower than currently observed. The right-hand graphs show assigned productivity for the optimization that maximized the number of species that reach at least 90% of the maximum potential population size under the constraint that landscape-level production is not lower than observed and that all species have to be present with at least five individuals over the whole region. Each optimization (for each optimization goal and region) was run 100 times with 500 iterations each; the best result for all 100 optimizations is shown (error bars on boxplots show standard errors). Grey boxplots indicate optimizations without pareto-optimal solutions. Coloured points show optimizations with pareto-optimal solutions. Coloured boxplots indicate that all 100 optimizations were pareto-optimal. ALB, Schwäbische Alb; HAI, Hainich-Dün; SCH, Schorfheide-Chorin.

landscape-level production (Fig. 3). While only one optimal solution was found when landscape-level production was maximized, multiple optimal solutions were found when conservation was maximized (coloured points in Fig. 3). Surprisingly, the same species reached the 90% threshold under each of the optimal solutions for maximized conservation (see Supplementary Methods 3 for an example); future studies would be needed to evaluate which traits characterize these species and can explain their consistent reaction across solutions.

All approaches based on common species ignore those that are found with only few individuals. Those rare species can make up a substantial portion of grassland arthropod communities (about 75% in our three regions; Table 1). To estimate the impact of changes in productivity on rare species, we defined two critical levels of productivity. The critical level for extinction was defined as the productivity level above which a species does not occur anymore in the grasslands. The critical productivity for vulnerability was defined as the productivity level above which a species is found with fewer than three individuals per grassland. In two out of three regions, 75% of rare species had their critical productivity for vulnerability already at the lowest productivity level (left border of the grey area in Fig. 4). About half of the rare species had their

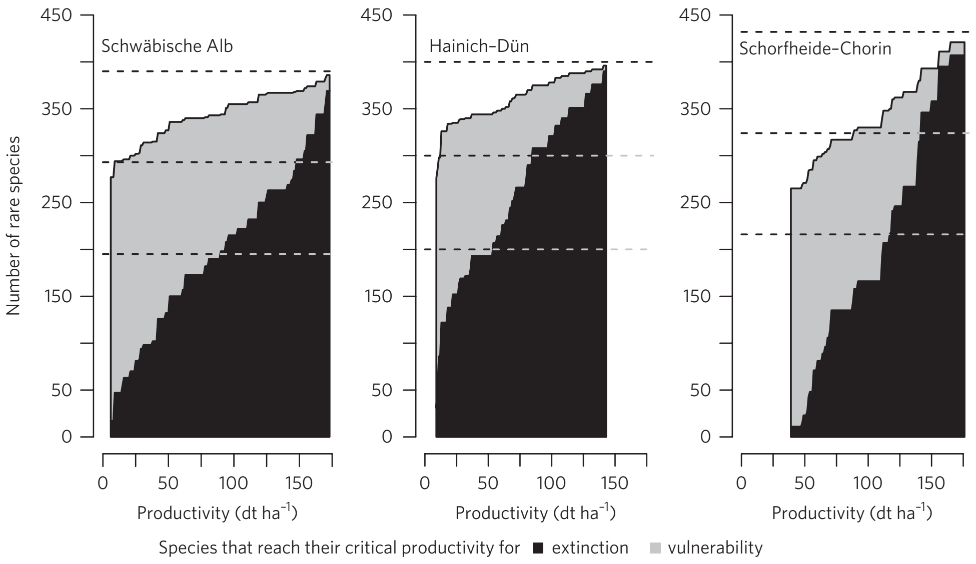

**Figure 4 | Rare species that reach their critical productivity for vulnerability or extinction at different levels of productivity.** The number of rare arthropod species with a maximum of two individuals (vulnerability) or no occurrence (extinction) on any grassland above the respective productivity level (steps of 1 dt ha$^{-1}$) is counted. The lowest level of productivity is 1 dt ha$^{-1}$ above the observed minimum productivity in each region. The highest level of productivity is 1 dt ha$^{-1}$ below the maximum observed productivity. Dashed lines show 50%, 75% and 100% of rare species per region. Lines are stacked, hence the upper line shows the sum of both categories. Total number of rare species per region: Schwäbische Alb = 390; Hainich-Dün = 400; Schorfheide-Chorin = 432.

critical productivity for extinction at intermediate productivity levels, that is, they were never encountered in grasslands with higher than average productivity (black area in Fig. 4). On average across the three regions, for every increase in productivity by 1 decitonne (dt, 100 kg) per hectare (dt ha$^{-1}$), an additional 2.3 rare species reached their critical level for extinction. Hence, rare species need a large proportion of the landscape at lowest or some intermediate productivity. Rare species would cope better under strategies that include two productivity levels than under strategies that include only one level, because the former always include management for conservation. Thus, plot-level strategies would be suitable for rare species only if the level of productivity was very low. Depending on the area necessary, a number of landscape-level strategies could support rare species as long as the minimum required amount of grassland was managed for conservation. The optimal landscape-level strategies for the common species under increased landscape-level production are, however, similar to a plot-level strategy (Fig. 2b), indicating that landscapes in which both common and rare species profit from landscape optimization are hard to find. The optimal solutions under the conservation objective and under the increased production objective always included grasslands with the lowest level of productivity. Depending on the size of those grasslands and the requirements of rare species, those solutions could accommodate both rare and common species.

## Discussion

One major conclusion from our analysis is that the current distribution of grassland-use intensities is not optimal with respect to either conservation or production. Landscape-level strategies with a low proportion of grasslands under conservation management (and subsequently low productivity levels on the remaining grasslands) resulted in highest numbers of species, including the rarest species. Thus, current landscape-level production could support more species if land management was distributed optimally within the landscape. Similarly, landscape-level production could be increased without reducing species numbers. It is perhaps not surprising that the current situation optimizes neither conservation nor production, because decisions are made locally by farmers on the farm scale, and there is at present no mechanism to allow for landscape-level decisions on the allocation of different grassland-use intensities. Our analysis shows, however, that landscape-level strategies may be key to lessen the trade-off between land-use intensification and biodiversity conservation within one habitat type.

Landscape-level strategies to find compromises between production and conservation have been discussed before; the most prominent proposition is the land sharing–land sparing paradigm[8–10,16–19], which has been discussed for regions where biodiversity-rich habitats are threatened by conversion into agricultural areas[9–13]. Land sharing is, in effect, a plot-level strategy with the entire landscape managed at the same intensity, whereas land sparing implies that part of the landscape is not converted to production, that is, 'spared' for conservation. The land sharing–land sparing dichotomy has been criticized because only two extreme solutions are considered[14], and because it concentrates only on food production and conservation[18,20]. Furthermore, most studies on land sharing and land sparing[8–10,21] have found that not all species show simple convex or concave abundance–productivity curves, but still focus only on land sharing or land sparing, assigning species with more complex curves to an undefined intermediate strategy[8–10,21]. Species with simple abundance–productivity curves will indeed always profit from the same strategy, independent of the average productivity level or target production (Supplementary Fig. 6a). However, this is not the case for species with complex abundance–productivity curves as, under the land sparing–land sharing dichotomy, the best strategy for those species depends on the average productivity considered (Supplementary Fig. 6b). We can visualize this effect by comparing the number of species assigned to land sharing or land sparing for the whole range of observed productivity levels in each of the three regions. For species with a complex abundance–productivity curve, the optimal solution will switch between land sharing and land sparing, sometimes several times, along the range of productivity. This results in varying numbers of species assigned to either strategy along the productivity gradient (Supplementary Fig. 6c). As most of the arthropod species sampled in our grasslands do in fact show complex abundance–productivity curves, strategies other than the extremes need to be considered. Here, we extended the concept of land sharing and sparing to include all theoretically possible combinations of management approaches across the landscape and show that intermediate solutions are often superior to the extremes. As complex abundance–productivity curves are probably not found only among grassland arthropods, we call for future studies on trade-offs between conservation and agricultural production to use approaches that adequately accommodate species with complex abundance–productivity relationships.

Our results also emphasize that the conservation aim needs to be clearly defined, with respect both to common species and to the weight given to rare species. For example, if a strategy is chosen that supports the highest number of species close to their maximum possible population size, fewer species will reach at least a small population size than under the current situation. Additional considerations can further complicate the choice for or against a certain optimization strategy. While our analyses focus on species richness and species abundances, they could be extended to also include other conservation targets such as functional or phylogenetic diversity[22,23]. Previous analyses have shown that intensification of grassland management affects certain functional groups more strongly than others[24–27], hence additional conservation aims that target specific functional groups or a high functional diversity are conceivable. Solutions where species need to occur in a minimum number of sites are also a useful extension, similar to optimization strategies for finding an optimal network of protected areas (for example, as in spatial prioritization software[28]). In fact, landscape-level optimization of land use for both production and conservation is similar to selecting optimal sites for conservation, and both approaches could benefit each other.

We have shown that landscapes that cover the whole gradient of productivity provide the best benefit both for production and for conservation. This is a clear contrast to the dichotomy of land sharing versus land sparing. However, optimization techniques have to be adapted to specific situations and involve more constraints than in our example. Areas already under conservation management are most likely not available for intensification; and soil quality or other abiotic factors such as slope or accessibility might reduce the available management options. Certain species might also not be able to disperse if suitable conditions are moved within the landscape. Additionally, large-scale management plans including several stakeholders—as in our example—are difficult to implement, especially if the optimal strategy would impose different productivity limits on different stakeholders. Nevertheless, optimization approaches are the best choice if changes to productivity are not limited, for example if all grasslands considered belong to the same stakeholder.

Even though the landscape-level strategies with multiple levels of productivity led to the best outcomes with respect to the conservation goal, simpler landscape-level strategies can be useful if the implementation of multi-level strategies is not feasible, or when part of the landscape is to be set aside for conservation and the optimal size of this area is to be determined. Both the simple and multi-level strategies can potentially be refined, for example, based on economic considerations or estimations of sustainability. They are also not limited to the trade-off between production and conservation but could, for example, be used to optimize the provisioning of ecosystem services. Our results suggest that the analysis of landscape-level strategies should inform and guide agricultural policies, for example by incorporating strategies at the landscape level into the already existing system of subsidies (cf. ref. [29]). More generally, landscape-level approaches rather than the focus on local productivity can pave the way for sustainable management or intensification.

## Methods

**Study system and arthropod data.** We used a five-year dataset of arthropods[25], which was collected on managed grasslands within the Biodiversity Exploratories project in Germany. For this project, 50 experimental plots of 50 × 50 m in size were selected in managed grasslands along the gradient of land-use intensity within grasslands in each of three regions in Germany[30]: (1) the United Nations Educational, Scientific and Cultural Organization (UNESCO) biosphere reserve Schorfheide-Chorin in the northeast (53° 02′ N, 13° 83′ E, about 1,300 km$^2$ in size, 3–140 m above sea level (a.s.l.)); (2) the national park Hainich and its surrounding areas in central Germany (51° 20′ N, 10° 41′ E, about 1,300 km$^2$, 285–550 m a.s.l.); and (3) the UNESCO biosphere reserve Schwäbische Alb in the Swabian Jura in the southwest (48° 43′ N, 9° 37′ E, about 422 km$^2$, 460–860 m a.s.l.).

Arthropods were sampled yearly from 2008 to 2012, once in early and once in late summer, by sweep-netting at each visit with a total of 60 double-sweeps along three plot border transects (150 m in total). Specimens were sorted to taxonomic order by student helpers and identified to species level by taxonomic experts. Araneae, Hemiptera: Auchenorrhyncha, Hemiptera: Heteroptera, Coleoptera and Orthoptera were chosen as target taxa[25]. Only adult individuals and data from plots that were sampled two times in all years were included in the analysis. The final arthropod dataset included 42 plots in Schwäbische Alb, 46 plots in Hainich-Dün and 36 plots in Schorfheide-Chorin, for which all 10 samples (2 months × 5 years) were pooled (total 124 plots). Abundances per hectare were calculated by multiplying the pooled abundance per plot by 33 as the sweep-net sample covers an area of about 150 × 2 m = 300 m$^2$ (the mathematically correct multiplication would be with 33.33, but the model fitting and the optimization algorithms cannot use floating numbers for abundances).

**Calculation of productivity.** The grassland plots are managed by farmers as meadows (only mown), pastures (only grazed) or mown pastures (mown and grazed), and are fertilized or unfertilized, all at various intensities, for example with different numbers of cattle per hectare. Management of the grasslands is assessed yearly through standardized questionnaires with land owners and managers[30]. Mowing intensity is represented by the number of cuts per year, varying from one to three cuts. Grazing intensity is calculated as the number of individuals of sheep, cows and/or horses multiplied by the length of the grazing period. Fertilization intensity is assessed as amount of nitrogen from chemical fertilizer, manure or slurry. In the Biodiversity Exploratories project, this information is often combined into a standardized index of land-use intensity (LUI)[31]. However, LUI is not a measure of grassland productivity and it is not very informative to calculate a landscape-level land-use intensity.

To estimate productivity, we additionally used data on plant biomass, which was sampled in spring 2008 and 2009 at a height of 2 to 3 cm above ground and dried for 48 h at 80 °C before weighing[32,33]. The biomass samples were averaged across the two years and converted to decitonnes per hectare, representing the grassland's productivity in spring. Although plant biomass in spring is closely linked to management intensity[32], it does not reflect the productivity over the whole year. This is especially the case under conservation management, where only part of the plant biomass is converted into an agricultural product. Therefore, plant biomass in spring is used as a baseline for the potential productivity of each grassland (indirectly incorporating other factors that affect productivity, such as previous management or abiotic factors). We used the information on mowing and grazing in combination with the productivity in spring to estimate the productivity (dt ha$^{-1}$ dry plant biomass) of the grasslands over the whole year (Supplementary Methods 1 and Supplementary Data 1). On pastures, productivity was calculated following ref. [34] as:

$$\text{Dry plant biomass} = (\text{livestock units} \times \text{grazing days} \times 0.147)/\text{grazed area}$$

with dry plant biomass in units of dt ha$^{-1}$ and one livestock unit equalling an adult cow of 500 kg body mass (for conversion of other grazers to livestock units, see Supplementary Methods 1). The calculation of productivity on pastures follows the assumption that a farmer will not have more grazers on a pasture than can be sustained by the growth of plant biomass. In cases where additional fodder (mostly as hay) was provided for the grazers, the amount of hay was subtracted from the grassland's productivity. On meadows with one mowing event, productivity equals the productivity in spring; on meadows with more than one mowing event, the productivity in spring was multiplied by 2.5 following ref. [35]. This calculation is based on the assumption that the plant biomass sampling in spring took place at a similar time as the first mowing event, and that the first of several mowing events is not done at peak plant biomass but at peak quality. On mown pastures, productivity estimates based on grazing and plant biomass samples were combined. By correcting the productivity in spring with the management information, we make sure that our measure of productivity includes only the proportion of plant biomass that is used as fodder for livestock (either directly through grazing or indirectly as hay). Plant biomass that remains on the grassland, for example after a low-intensity grazing period, is not included in the productivity measure. For each plot, we calculated the average productivity over the years 2006 to 2012. As information on plant biomass was incomplete for some plots, we could calculate productivity for only 109 of the 124 plots (38 plots in Schwäbische Alb, 37 in Hainich-Dün, 34 in Schorfheide-Chorin).

The productivity under conservation management was set to the median productivity of less-intensively grazed grasslands within natural reserves in each region, which represented the lowest management intensity in our grasslands. The resulting productivity under conservation management is 8.4 dt ha$^{-1}$ for

Schwäbische Alb and Hainich-Dün, and 46.2 dt ha$^{-1}$ for Schorfheide-Chorin. All abundances and productivities were calculated per hectare.

**Modelling of abundance–productivity curves.** Abundance–productivity curves can be calculated only for species that were sampled on multiple plots and with a minimum number of individuals. We chose a minimum of six plots and ten individuals per region as criteria for the selection of species. Those species are henceforth referred to as 'common' species, all other species as 'rare' species. Different species were common in each region and not all species were common in all regions. For each common species in each region, we fitted univariate parametric regression models with population density (abundance per hectare) as the dependent variable and productivity (decitonnes per hectare) as the independent variable, following ref. [9]. We used four alternative models:

$$y = \exp(b_0 + b_1 \times (x^a)) \qquad \text{(convex/concave)}$$

$$y = b_0 \times \exp(-0.5 \times ((x - b_1)/b_2)\hat{}\,2) \qquad \text{(hump - shaped)}$$

$$y = \exp(b_0 + b_1 \times (x^a) + b_2 \times (x^{2a})) \qquad \text{(polynomial)}$$

$$y = b_0 \times x + b_1 \qquad \text{(linear)}$$

where $y$ represents the sampled population density of the target species, $x$ represents productivity, and $b_0$, $b_1$, $b_2$ and $a$ are constants. The first model fits convex or concave distributions, the second fits hump-shaped distributions and the third model fits more complex polynomial distributions. The last model fits linear distributions. We fitted the models using a maximum-likelihood approach with the optim function in R v3.3.0 (ref. [36]). For each common species, we selected the best model fit based on the differences in residual deviance, following the assumption that a more complex model is to be favoured over a simpler model, if its residual deviance is more than 3.84 ($\chi^2$ with 1 d.f. for $P = 0.05$) lower. First, the most complex polynomial model was compared with the hump-shaped model; the 'better' model was then compared with the convex/concave model, of which the 'better' model was finally compared with the linear model (more details are given in Supplementary Methods 2).

After the best model was selected for each species based on the residual deviances, we used the lme function from the 'bbmle' package[37] in R to calculate standard errors and significance levels for the model parameters (Supplementary Data 2–4). Significance levels are based on the $z$-values of a maximum likelihood test. Those common species that showed only non-significant ($P$ value > 0.05) parameters within their selected best model were removed from the main analyses and included in the analysis with rare species. This was the case for 9 species in Schwäbische Alb, 4 species in Hainich-Dün and 21 species in Schorfheide-Chorin. To check if the removal of those common species affects our results, we repeated the analyses (except the multi-level optimization) with the complete set of common species (results are presented in Supplementary Figs 7–12).

Based on the fitted abundance–productivity curves, we estimated whether a species profits ('winner') or suffers ('loser') from increasing productivity. To assess winners and losers, a straight line (the threshold line) connecting the (model-estimated) abundances at the lowest and highest observed productivity is defined. A species is assigned to be a 'winner' of productivity if the slope of the threshold line is larger than zero, that is, positive, and assigned a 'loser' if the slope is smaller than zero, that is, negative (Supplementary Methods 2).

**Definition of land-use strategies.** A given landscape-level production target can be reached by different combinations of low and high productivity (Supplementary Fig. 1). This range of possibilities covers all possible landscape configurations between all land being used at an intermediate level of productivity (plot-level strategy) and the smallest proportion of land being used for production (landscape-level strategy). With an increasing proportion of land under conservation management, productivity in the remaining grasslands increases. The set of possible strategies can hence be defined either by increasing the proportion of land under conservation management in steps of, say, 1%, or by increasing the productivity on the land under intensive management in steps of, say, 1 dt ha$^{-1}$. The calculation of all possible strategies is straightforward for landscapes where unmanaged land does not contribute to landscape-level production, for example when forests are compared with agricultural land. In our case, where 'unmanaged' implies conservation management of grasslands, the area under conservation does contribute to landscape-level production. It is, however, important to notice that the level of productivity under conservation management is the same in all possible landscape-level strategies. This conservation management corresponds to the median level of productivity observed in the protected grasslands of the three regions. Those grasslands are, for example, grazed by about 30 sheep and goats per hectare for less than 20 days per year and not mown. For each landscape-level strategy, we calculated the landscape-level population size for each species based on the estimated population densities under conservation management or intensive productivity, multiplied by the size of the respective areas (Supplementary Methods 3).

We calculated all possible strategies for all possible landscape-level production targets, which range from the whole area being managed for conservation (1,898.57 dt in Schwäbische Alb, 10,782.24 dt in Hainich-Dün and 44,411.71 dt in Schorfheide-Chorin) to the whole area being managed under the highest observed productivity (39,124.06 dt in Schwäbische Alb, 184,068.2 dt in Hainich-Dün and 169,860.4 dt in Schorfheide-Chorin). For every step in this range we calculate the next highest landscape-level production target by adding a production of 1dt for each hectare in the area (226.02 dt in Schwäbische Alb, 1,283.6 dt in Hainich-Dün and 961.29 dt in Schorfheide-Chorin). The range of possible strategies for each landscape-level production target is defined by the landscape-level production target and the highest observed productivity in a grassland as a starting point. We assumed that all studied grasslands in the region can, given intensification, be equally productive as the most productive grassland, that is, the grassland with the highest observed productivity (average over 2006–2010) in each region. This assumption is valid in our case because soil types of the selected grasslands are very similar within each of the regions and only grasslands on shallow slopes were selected[30]. This is an important constraint for this approach and future studies that implement this approach in other regions or ecosystems have to make sure that the constraint is met or that the possible strategies account for differences in potential productivity. Strategies range from the lowest possible proportion of the landscape under intensive management to 100% of the landscape under intensive management. The lowest possible proportion was calculated through an iterative process that considers first a landscape with 99% of the area under conservation management, and then calculates the productivity on the remaining area (1%) needed to reach the landscape-level production target. As the productivity level of the land under intensive management cannot exceed the highest observed productivity, the proportion of the area under conservation management is decreased in steps of 1% until the productivity level of the land under intensive management is equal or lower than the highest observed productivity (Supplementary Methods 3). The other possible strategies cover all proportions of land under intensive management from the lowest possible proportion to 100% in steps of 1%. The lowest possible proportion of land under intensive management increases with each increase in landscape-level production: while the lowest landscape-level production target can be reached with only 1% under intensive management, the highest possible landscape-level production target can only be reached with 100% of the area under intensive management.

**Landscape-level population size under different strategies.** For each combination of target production and strategy, the landscape-level population size of each species can be calculated based on the size (ha) of the area under intensive management, the remaining area under conservation management and the estimated population density of the species at both levels of productivity. The optimal strategy for each species is normally identified as the strategy where the species has its highest possible population size. However, as we look at different sets of strategies across the range of landscape-level production targets, the highest possible population size changes for each landscape-level production target. To make the suitability of all strategies comparable, we defined the highest possible population size as the maximum population density of a species (from their abundance–productivity curve) multiplied by the area of grasslands in the region. This equals the population size that the species could achieve if all grasslands were managed at the productivity under which the species has its highest population density. It is unlikely that this highest possible population size is achieved by a species and it might not be required for its conservation, as long as the population size remains above a threshold. Hence, we defined thresholds for the landscape-level population size of a species that will make a certain strategy 'acceptable' for this species. We used thresholds of 90%, 75%, 50% and 25% of the highest possible population size. For each strategy we then counted the number of species that reach each of those target population sizes.

**Optimization of productivity across the landscape.** In the basic set of strategies, only two levels of productivity are considered: the productivity under conservation management and the productivity that is needed to reach the landscape-level production target under the given proportion of land not under conservation management. To simulate a more flexible distribution of productivity levels across all grasslands, we used an optimization approach that maximizes the output of a function under the constraint of another function. These simulations produce a set of pareto-optimal solutions, that is, solutions for which the main function cannot be increased further without violating the constraint[38]. Two optimization approaches were implemented: (1) the landscape-level production is maximized under the constraint that the estimated number of individuals for all species is the same or higher than this species' observed number of individuals; and (2) the number of species that reach at least 90% of their maximum possible population size is maximized under the constraint that landscape-level production is the same as the observed landscape-level production and under the constraint that all species are found with at least five individuals across the whole region.

For both approaches, the productivity (dt ha$^{-1}$) on each individual grassland can be assigned freely from the range of observed productivity levels. At each step in the optimization procedure, the size (ha) of each grassland is multiplied by the selected level of productivity and the sum of those products is taken as the landscape-level production. For each arthropod species, the number of individuals is estimated based on the fitted abundance–productivity curves and the selected productivity level on each grassland. The overall number of individuals is calculated over all grasslands. For the first approach, the estimated overall number of individuals is compared with the observed overall number of individuals for each species. The number of species with at least the same number of estimated and observed number of individuals is counted. If this number of species is the same as the observed number of species (that is, all species have a least the same or a higher number of individuals estimated than observed), the constraint is not violated and the current set of productivity levels is considered for the next optimization step. For the second approach, the constraint is not violated if the optimized landscape-level production is the same or higher as the observed landscape-level production and if all species are found with at least five individuals. The value to be maximized in the second approach is the number of species that reach at least 90% of their maximum possible population size.

Both approaches were implemented in R v3.3.0[36] with the nsga2() function from the 'mco' package v15.1 (ref. [39]). The nsga2() function uses the NSGA-II algorithm[40], which finds the pareto-optimal set of parameters (that is, set of productivity levels) by successive sampling (each sample is a population) of the search space. For each population, a set number of generations is calculated, from which the best individuals are selected to start a new population. The function was run with 100 populations and 500 generations resulting in 50,100 function evaluations. The best individual of each population is reported by the function and is used to create boxplots with the average and variance of the pareto-optimal levels of productivity (dt ha$^{-1}$) for each grassland.

**Rare species under different levels of productivity.** As described above, abundance–productivity curves were not estimated for rare species that were found on fewer than six plots and with fewer than ten individuals per region. To estimate the effect of productivity on those rare species and on the common species for which abundance–productivity curves were not reliable (see above), we counted the number of species that were not observed in plots above a certain level of productivity. For each level of observed productivity (in steps of 1 dt ha$^{-1}$), we checked if a species occurs in any of the grasslands of this or a higher level of productivity. If yes, we increased productivity and tested for the presence of the species in grasslands at the next highest level of productivity, and so on, until the species did not occur in any of the remaining grasslands. This defined the 'critical productivity for extinction' for this species. We then counted for each level of productivity the number of species for which this productivity corresponded to the critical level for extinction. We repeated this exercise to define not only the critical productivity for extinction, but also the 'critical productivity for vulnerability', defined here as the level of productivity at which species occur with, at maximum, only two individuals in any of the grasslands of this or a higher level of productivity.

**Code availability.** Commented R code is provided in markdown format in the Supplementary Material. Original R code is available from the corresponding author upon reasonable request.

**Data availability.** The dataset on species abundance data analysed during the current study is available from the Supplementary Information in ref. [25]. File: ecy1243-sup-0004-DataS1.zip under http://onlinelibrary.wiley.com/doi/10.1890/15-0616.1/full.

The dataset on plant biomass from the years 2008 and 2009 analysed during the current study is available on Dryad. Doi: 10.5061/dryad.f3b77 under http://datadryad.org/resource/doi:10.5061/dryad.f3b77.

The dataset on average productivity values for the grasslands that was generated and analysed during the current study is included in this published article as Supplementary Data 1.

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## References

1. Hejcman, M., Hejcmanová, P., Pavlů, V. & Beneš, J. Origin and history of grasslands in central Europe - a review. *Grass Forage Sci.* **68**, 345–363 (2013).
2. *Greening* (European Commission, 2016); http://ec.europa.eu/agriculture/direct-support/greening/index_en.htm
3. Gossner, M. M. *et al.* Land-use intensification causes multitrophic homogenization of grassland communities. *Nature* **540**, 266–269 (2016).
4. Allan, E. *et al.* Interannual variation in land-use intensity enhances grassland multidiversity. *Proc. Natl Acad. Sci. USA* **111**, 308–313 (2014).
5. Hopkins, A. & Wilkins, R. J. Temperate grassland: key developments in the last century and future perspectives. *J. Agr. Sci.* **144**, 503–523 (2006).
6. Kleijn, D. & Sutherland, W. J. How effective are European agri-environment schemes in conserving and promoting biodiversity? *J. Appl. Ecol.* **40**, 947–969 (2003).
7. Veen, P., Jefferson, R., de Smidt, J. & van derStraaten, J. (eds) *Grasslands in Europe of High Nature Value* 320 (KNNV, 2009).
8. Phalan, B., Onial, M., Balmford, A. & Green, R. E. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science* **333**, 1289–1291 (2011).
9. Hulme, M. F. *et al.* Conserving the birds of Uganda's banana-coffee arc: land sparing and land sharing compared. *PLoS ONE* **8**, e54597 (2013).
10. Kamp, J. *et al.* Agricultural development and the conservation of avian biodiversity on the Eurasian steppes: a comparison of land-sparing and land-sharing approaches. *J. Appl. Ecol.* **52**, 1578–1587 (2015).
11. Green, R. E., Cornell, S. J., Scharlemann, J. P. & Balmford, A. Farming and the fate of wild nature. *Science* **307**, 550–555 (2005).
12. Gabriel, D., Sait, S. M., Kunin, W. E., Benton, T. G. & Steffan-Dewenter, I. Food production vs. biodiversity: comparing organic and conventional agriculture. *J. Appl. Ecol.* **50**, 355–364 (2013).
13. Lamb, A., Balmford, A., Green, R. E. & Phalan, B. To what extent could edge effects and habitat fragmentation diminish the potential benefits of land sparing? *Biol. Conserv.* **195**, 264–271 (2016).
14. Butsic, V. & Kuemmerle, T. Using optimization methods to align food production and biodiversity conservation beyond land sharing and land sparing. *Ecol. Appl.* **25**, 589–595 (2015).
15. Miettinen, K. *Nonlinear Multiobjective Optimization* (Springer, 1998).
16. Edwards, D. P. *et al.* Land-sharing versus land-sparing logging: reconciling timber extraction with biodiversity conservation. *Glob. Change Biol.* **20**, 183–191 (2014).
17. Tscharntke, T. *et al.* Global food security, biodiversity conservation and the future of agricultural intensification. *Biol. Conserv.* **151**, 53–59 (2012).
18. Fischer, J. *et al.* Land sparing versus land sharing: moving forward. *Conserv. Lett.* **7**, 149–157 (2014).
19. Tilman, D., Cassman, K. G., Matson, P. A., Naylor, R. & Polasky, S. Agricultural sustainability and intensive production practices. *Nature* **418**, 671–677 (2002).
20. Bennett, E. M. Changing the agriculture and environment conversation. *Nat. Ecol. Evol.* **1**, 0018 (2017).
21. Dotta, G., Phalan, B., Silva, T. W., Green, R. & Balmford, A. Assessing strategies to reconcile agriculture and bird conservation in the temperate grasslands of South America. *Conserv. Biol.* **30**, 618–627 (2016).
22. Bennett, J. R. *et al.* Balancing phylogenetic diversity and species numbers in conservation prioritization, using a case study of threatened species in New Zealand. *Biol. Conserv.* **174**, 47–54 (2014).
23. Cadotte, M. W. & Jonathan Davies, T. Rarest of the rare: advances in combining evolutionary distinctiveness and scarcity to inform conservation at biogeographical scales. *Divers. Distrib.* **16**, 376–385 (2010).
24. Simons, N. K. *et al.* Contrasting effects of grassland management modes on species-abundance distributions of multiple groups. *Agr. Ecosyst. Environ.* **237**, 143–153 (2017).
25. Simons, N. K., Weisser, W. W. & Gossner, M. M. Multi-taxa approach shows consistent shifts in arthropod functional traits along grassland land-use intensity gradient. *Ecology* **97**, 754–764 (2016).
26. Allan, E. *et al.* Land use intensification alters ecosystem multifunctionality via loss of biodiversity and changes to functional composition. *Ecol. Lett.* **18**, 834–843 (2015).
27. Batáry, P. *et al.* Responses of grassland specialist and generalist beetles to management and landscape complexity. *Divers. Distrib.* **13**, 196–202 (2007).
28. Ball, I. R., Possingham, H. P. & Watts, M. in *Spatial Conservation Prioritisation: Quantitative Methods and Computational Tools* (eds Moilanen, A., Wilson, K. A. & Possingham, H. P.) Ch. 14, 185–195 (Oxford Univ. Press, 2009).
29. Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I. & Thies, C. Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecol. Lett.* **8**, 857–874 (2005).
30. Fischer, M. *et al.* Implementing large-scale and long-term functional biodiversity research: the biodiversity exploratories. *Basic Appl. Ecol.* **11**, 473–485 (2010).
31. Blüthgen, N. *et al.* A quantitative index of land-use intensity in grasslands: integrating mowing, grazing and fertilization. *Basic Appl. Ecol.* **13**, 207–220 (2012).
32. Simons, N. K. *et al.* Resource-mediated indirect effects of grassland management on arthropod diversity. *PLoS ONE* **9**, e107033 (2014).
33. Socher, S. A. *et al.* Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. *J. Ecol.* **100**, 1391–1399 (2012).
34. Riehl, G. *Ermittlung von Erträgen auf dem Grünland* (Sächsisches Landesamt für Umwelt, Landwirtschaft und Geologie, 2001).
35. Mewes, M. *Agrarökonomische Kostenberechnungen für Biodiversitätsschutzmaßnahmen* Report No. 1436-140X (Helmholtz-Zentrum für Umweltforschung GmbH - UFZ, 2010).
36. R Core Team *R: A Language and Environment for Statistical Computing v3.3.0* (R Foundation for Statistical Computing, 2016).

37. Bolker, B. & R Core Team *Tools for General Maximum Likelihood Estimation Version 1.0.18* (2016).
38. Marler, R. T. & Arora, J. S. Survey of multi-objective optimization methods for engineering. *Struct. Multidiscip. O.* **26**, 369–395 (2004).
39. Mersmann, O. *mco: Multiple Criteria Optimization Algorithms and Related Functions* (2014).
40. Deb, K., Pratap, A. & Agarwal, S. A fast and elitist multiobjective genetic algorithm: NSGAII. *IEEE T. Evolut. Comput.* **6**, 182–197 (2002).

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## Author contributions

N.K.S. and W.W.W. conceived the idea for the manuscript and defined the final outline. N.K.S. analysed the data and wrote the first manuscript draft. W.W.W. commented on all manuscript versions.

## Competing interests

The authors declare no competing financial interests.

## Additional information

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