



Mobile species' responses to surrounding land use generate trade-offs and synergies among nature's contributions to people

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Agricultural landscapes provide material, nonmaterial, and regulating contributions that affect human well-being (nature's contributions to people, NCP). The responses of these NCP to land-use patterns depend on supporting biota with different habitat requirements, generating trade-offs and synergies. Predictions from spatially explicit modeling of NCP trade-offs and synergies could inform land-use decisions, but these do not typically account for the effects of land-use patterns on the movement of NCP-providing species, nor for interactions among NCP providers. To explore spatial trade-offs and synergies in eight indicators of NCP, we used Bayesian models that allow for interactions among land uses and among NCP using data from 150 grassland sites across rural Germany. We found that spatial arrangements of forest and open habitat influenced many beneficial NCP: acoustic diversity, birdwatching potential, natural enemy abundance, and pollination. In particular, the amount and proximity of land uses in the surrounding landscape, especially forest and open habitat, drove the supply of most NCP. However, detrimental NCP provided by smaller-bodied taxa (herbivory and pathogen infection) responded weakly to landscape factors. Multiple NCP provided by a given taxon responded differently to their surrounding landscape (e.g., bird-provided beneficial caterpillar predation and detrimental seed predation), leading to trade-offs and synergies among NCP over short distances. These were caused by different rates and directions of response to amount and location of land uses. Resulting spatial predictions revealed that the ratio of beneficial to detrimental NCP was maximized in areas with a high ($\geq 95\%$) area of grassland or mixed forest-grassland (70:30%), rather than purely forest-dominated areas. This suggests promoting seminatural vegetation in agricultural landscapes to provide greater-than-additive benefits to net NCP supply.

ecosystem services | multifunctionality | biotic interactions | trade-offs | mobile species

Global environmental change alters the ability of landscapes to supply nature's contributions to people (NCP), "all the contributions, both positive and negative, of living nature to people's quality of life" (1). Nature's contributions extend upon the ecosystem services framework by better incorporating nonmaterial values and allowing for the influence of culture and worldview on human-nature connections (2). Globally, two-thirds of human-modified landscapes lack the natural and seminatural habitat required for the supply of multiple NCP (3). In efforts to reverse this global trend, many countries and regions are adopting policies for increasing seminatural vegetation cover and decreasing land-use intensity (4). However, depending on its intensity, land use has contrasting influences on co-occurring NCP (NCP bundles), such as pollination and crop production (5, 6). This generates trade-offs and synergies among NCP in mixed-use, mixed-intensity landscapes (7). Moreover, because landscape processes influence the capacity of natural areas to provide NCP (8), predictions of the supply of NCP bundles for use in land-use decisions must account for landscape context (9). Yet, three outstanding gaps limit such predictions.

First, many NCP are provided by particular species, whose presence and abundance is determined by a combination of local- and landscape-level abiotic and biotic environmental conditions (10). It is therefore challenging to predict spatial variation in NCP trade-offs and synergies when species movement across land uses or lateral physical processes determine NCP flow across landscapes (11–13), relative to NCP provided by ecosystems rather than particular species [e.g., water filtration; (10)]. Substantial work has demonstrated how species-provided NCP respond to surrounding landscape composition (14–16), but such approaches do not account for the spatial arrangement of multiple habitats and therefore cannot predict well into new landscapes. Analyzing how species and associated NCP change across the edges of a focal land use (17) can capture distance

Significance

Land use affects nature's contributions to people (NCP), including those provided by mobile species, in complex ways. Variation in species responses to the amount and location of land uses results in NCP trade-offs and synergies across landscapes, but decision-makers lack the capacity to target them spatially. We predict how the supply of beneficial and detrimental NCP and associated trade-offs and synergies vary across diverse rural landscapes. We find that the arrangements of open habitats and forest drive NCP supply, though the responses of NCP provided by arthropods were weaker and less consistent than NCP from larger-bodied species. Our findings support policies for promoting seminatural vegetation cover in agricultural landscapes, as these may provide greater-than-additive benefits for net NCP supply.

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decay of NCP from a source habitat. However, such designs do not account for multiple patches of multiple land uses, which can act as both sources and sinks of NCP-providing organisms. Moreover, the ways in which different NCP are affected by the surrounding land uses may also depend on the taxa that contribute to each NCP. For example, larger taxa (e.g., birds) may disperse further than smaller taxa [e.g., arthropods; (18)], thereby exhibiting weaker distance decay from preferred habitat.

Second, a range of mechanisms may cause interactions between the effects of different land uses on NCP supply. For example, species may use complementary resources from multiple land uses in which their relative abundance differs (16) or adjacent land uses may distract mobile species, such as when pollinating arthropods or mammals are distracted by neighboring resource-rich patches (15). Drawing from movement ecology and landscape ecology, the movement of mobile species depends on both their characteristics [e.g., potential mobility, degree of generalism, and feeding guild; (12, 19)] and their fine-scale movement decisions within increasingly fragmented and modified landscapes (20). The differing tendencies of different NCP-providing organisms to move among land uses changes the relative balance of NCP at given points, therefore generating trade-offs and synergies among NCP.

Third, there are trade-offs and synergies among beneficial and detrimental NCP (1). Even a given taxon can concurrently provide beneficial and detrimental NCP, for example small rodents consume weed seeds but also damage crops (21). Yet, our ability to predict the net supply of NCP at a given point in space [netNCP; (22)] is presently limited because most previous work does not integrate detrimental NCP (6, 23).

We fill these three gaps with a spatially explicit approach for predicting NCP trade-offs and synergies that accounts for the amount, location, and identity of land-use patches across landscapes, while allowing for interactive effects between land uses and between different NCP. We explore how the supply of five beneficial (pollination, natural enemy abundance, birdwatching potential, caterpillar predation and acoustic diversity) and three detrimental (seed predation, herbivory, and pathogen infection) NCP indicators (hereafter, “NCP”), provided in grasslands by mobile species, vary spatially with the distribution of land uses in the surrounding landscape, across three European agricultural regions. We test four hypotheses: (H_1) Different NCP are favored by different land uses, and NCP that share a providing species will respond similarly to similar landscape patterns (e.g., all bird-provided NCP will respond to the availability of the same land uses; Fig. 1 and *SI Appendix, Table S1*); (H_2) the combined effect of multiple land uses on NCP provided by mobile species will be synergistic, because adjacent land uses may distract mobile species (15) or because species with a broad diet may benefit from the resources provided by multiple land uses (16) (e.g., merged arrows to arthropod-provided pollination in Fig. 1); (H_3) the supply of multiple NCP will vary spatially, generating trade-offs and synergies caused by differences in the direction and/or magnitude of NCP responses to different land uses (and their arrangement); and (H_4) NCP provided by larger-bodied taxa, such as birds, will exhibit flatter spatial decay from a source land use due to their larger movement ranges.

We test these hypotheses using comprehensive NCP and land-use datasets for 150 agricultural grassland plots of the German Biodiversity Exploratories project (24). We extend existing spatial modeling techniques (13, 17, 25) to illustrate how point-based measures of multiple NCP can be used to generate a high-resolution prediction surface of netNCP supply that accounts for the direct and indirect effects (via another NCP; Fig. 1 and *SI Appendix, Table S1*) of multiple land uses. We apply a stepwise

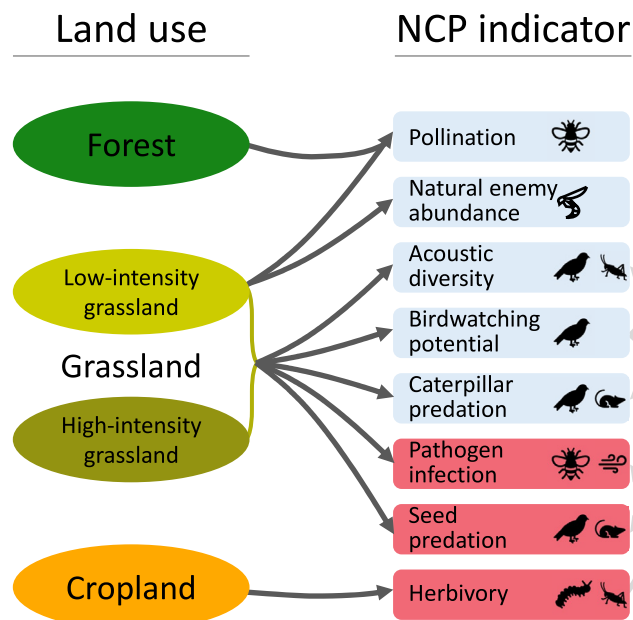


Fig. 1. Conceptual summary of the NCP indicators modeled. Dark gray arrows show the land uses in the surrounding landscape expected to be the strongest positive drivers of each NCP (based on existing literature; *SI Appendix, Table S1*) in a measured grassland plot. Light gray curved arrows show the hypothesized directional effects between NCP. We expect both low-intensity grassland and forest to strongly drive NCP supply of pollination (merging dark gray arrow), and we test whether these effects are additive or interactive in model selection (*Statistical Analysis and Model Selection*). The mobile providers of each NCP are represented as icons in NCP boxes, where the larger left-most icon represents the primary provider of that NCP if multiple providers are shown. The NCP deemed beneficial are presented in blue boxes, and those deemed detrimental in red boxes. The indicators measured for each NCP are as follows: pollination (number of flower visitors); natural enemy abundance (number of brood cells recorded in trap nests attacked by parasitoids of pest arthropods); acoustic diversity (the distribution of acoustic energy among frequency bands during diurnal recordings); birdwatching potential (bird species richness); caterpillar predation (probability of dummy caterpillar predation by birds after 48 h); pathogen infection (total cover of foliar fungal pathogens); seed predation (probability of sunflower seed removal after 48 h); and herbivory (total proportion of leaf area damaged by invertebrate herbivores).

model selection approach to determine the relative importance of the distance-weighted amount of four land uses (forest, cropland, low-intensity grassland, and high-intensity grassland), all two-way land-use interactions, environmental covariates, and other NCP. Our focal land-use effect ($LUE_{i,j}$) metrics therefore combine effects of both landscape configuration and composition, rather than attempting to disentangle these effects. Across all models, we fit NCP-specific distance-decay parameters to test for between-NCP differences in the spatial range of influence. The eight NCP, considered as beneficial or detrimental in these European agricultural landscapes, and their hypothesized responses to land use and to other NCP are summarized in Fig. 1.

Results

Differing Responses of NCP to the Amount and Proximity of Land Uses Generate Trade-Offs and Synergies. Overall, the supply of most NCP in grasslands was driven to some extent by the amount and proximity of different land use types in the surrounding landscape, but differences in specific NCP responses generated trade-offs and synergies (Fig. 2 and *SI Appendix, Table S2*). All four land-use main effects and two-way interactions were removed in model selection except for those described below and presented in Fig. 2 (*Statistical Analysis and Model Selection*). The control variable TWI_i (topographic wetness index) was retained in the

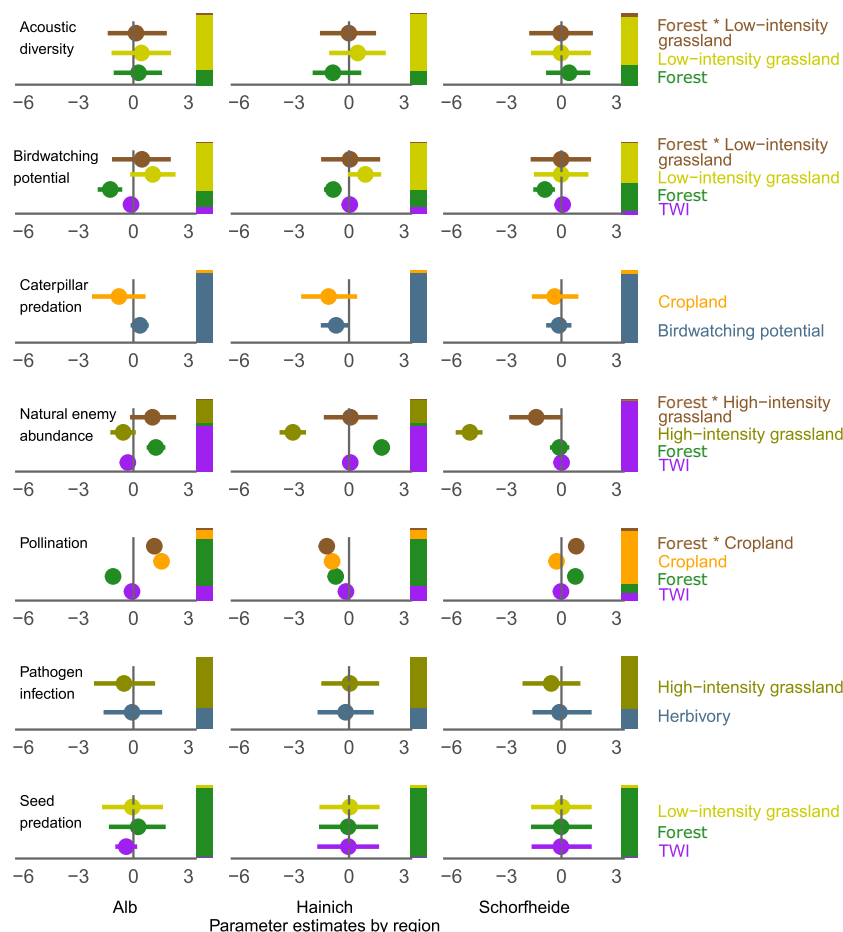


Fig. 2. Parameter estimates (points and error bars) and variance explained (vertical bars) from the best-fit models of each NCP, separated by region. Parameters for forest, cropland, and low- and high-intensity grassland are shown in green, orange, yellow, and dark yellow, respectively. Purple points and bars correspond to topographic wetness index (TWI); which has been shown previously to be an important predictor of multiple NCP in the region), and blue points and bars to NCP covariates when retained in the best-fit model of the focal NCP. All two-way land-use effect interactions are shown in brown. Points and error bars are posterior median and 90% credible intervals, respectively. Credible intervals around the coefficient estimates that overlap with zero indicate uncertainty about the direction of the effect, although the variable's retention in model selection suggests its inclusion did improve model fit. Vertical bars to the right of each region column show the NCP-specific proportions of explained variance attributable to each predictor, by region. The NCP herbivory is omitted from this figure because the best-fit model retained only the intercept term (not presented here).

best-fitting models for birdwatching potential, natural enemy abundance, pollination, and seed predation; secondary NCP variables were retained in the best-fitting models for pathogen infection (herbivory) and caterpillar predation (birdwatching potential; *SI Appendix, Table S2*).

Of the land uses we tested, the amount of forest surrounding grassland was a prevalent driver retained in model selection for most NCP (Fig. 2 and *SI Appendix, Table S2*). These results were robust to the scale at which land use main effects were calculated (*SI Appendix, Fig. S1*). However, the strength and direction of forest effects varied between NCP. For example, birdwatching potential was strongly negatively associated with high forest area in the surrounding landscape in all regions, while natural enemy abundance responded positively to forest cover in regions with large forest patches (Alb and Hainich; Fig. 3 and *SI Appendix, Fig. S2*).

NCP provided primarily by birds, which we hypothesized would exhibit flatter spatial decay from a source land use than arthropods [large fitted values of γ in Eq. 1; (18)], in fact showed the strongest and most consistent responses to the amount and location of land uses in the surrounding landscape. Specifically, bird-provided NCP appeared to respond to forest and low-intensity grassland, both directly (acoustic diversity, birdwatching potential and seed predation) and indirectly via another NCP (caterpillar predation via birdwatching potential; Fig. 2 and *SI Appendix, Table S3*).

The amount and location of low-intensity grassland was more important for acoustic diversity and birdwatching potential, with positive effects in most regions. In contrast, most variation in seed predation was explained by the amount of forest surrounding the grasslands, with lower supply in more forested areas in most regions (Fig. 2 and *SI Appendix, Tables S2 and S3*).

Strongly opposing responses of pollination and natural enemy abundance to the surrounding landscape caused trade-offs and synergies among NCP provided by arthropods. For example, a grassland with greater surrounding forest area supported significantly higher natural enemy abundance but significantly lower pollination supply (Fig. 3 *B* and *C* and *SI Appendix, Fig. S2*). In contrast, pollination was more strongly driven by surrounding cropland area, though the direction of this effect differed across regions (Fig. 2 and *SI Appendix, Tables S2 and S3*). These differences could be attributable to regional differences in landscape composition; i.e. the lowest overall forest cover and smallest forest patch size in the Schorfheide region aligned with a relatively high proportion of explained variance attributable to cropland [Fig. 2*B*, (26)].

Even when multiple NCP responded in the same direction to a given land use, differing strengths of their response generated trade-offs and synergies by changing the relative balance of NCP at different distances from source patches. The supply of

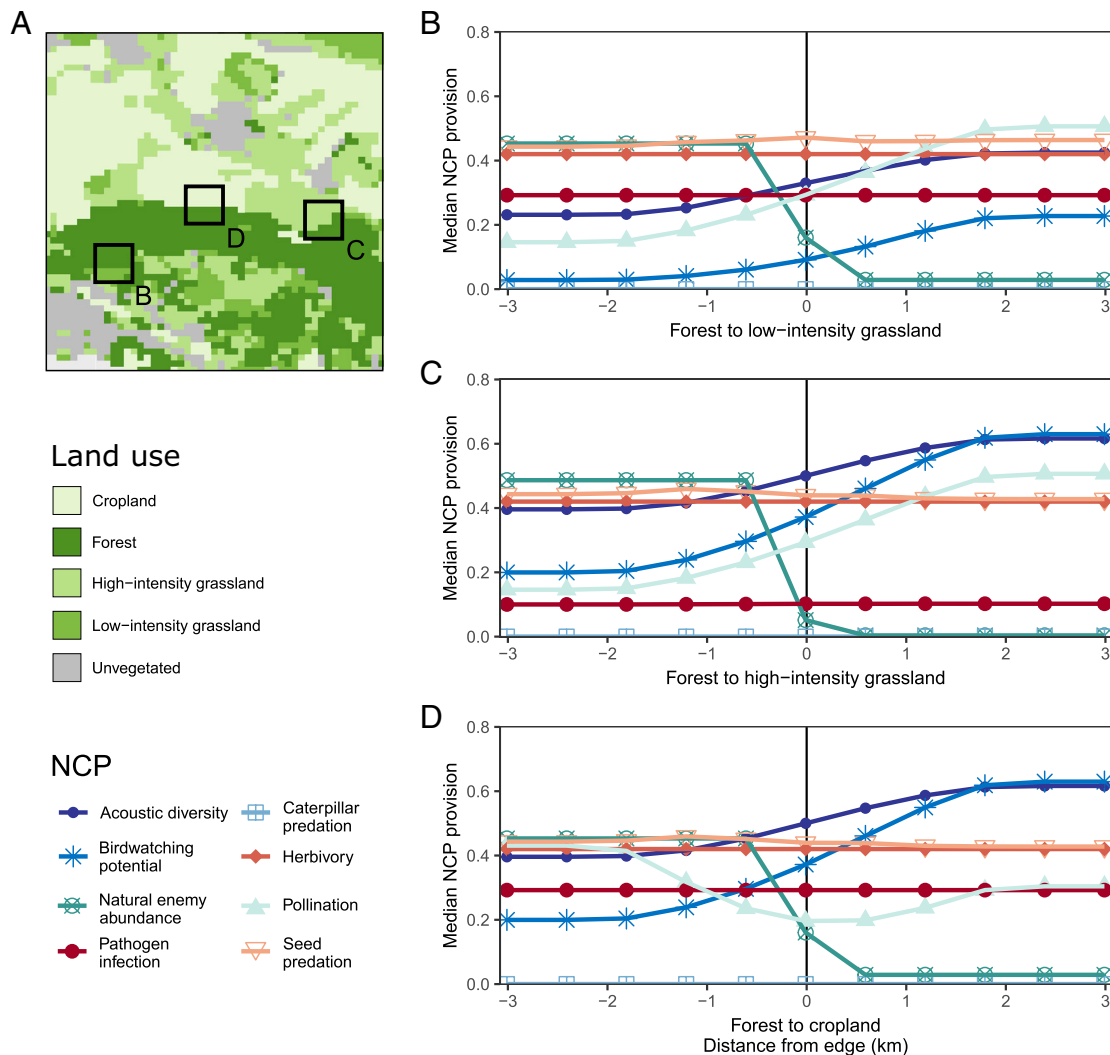


Fig. 3. Predicted supply of eight NCP, displayed for a subset of the Hainich-Dün region (Panel A). Panels B–D show fitted values for the normalized median supply of each NCP in a grassland plot surrounded by different landscape contexts. Landscape contexts represent moving from a landscape of pure forest (negative x-axis values) across the boundary into pure (B) low-intensity grassland, (C) high-intensity grassland, and (D) cropland, predicted using the best-fitting models for each NCP in *SI Appendix, Table S2* and coefficient estimates from the Hainich-Dün region. These between-land-use boundaries correspond to the areas marked B–D in Panel A. Spatial base data: © GeoBasis-DE/BKG (2018); Terms of use: http://sg.geodatenzentrum.de/web_public/nutzungsbedingungen.pdf.

most NCP decayed steeply with distance from a source land-use patch, indicating that local flows of NCP-providing species are key to supply. Conversely, pollination showed a flatter decay (*SI Appendix, Table S3*). This generated trade-offs and synergies, for example, because increasing the total amount of forest area in Schorfheide grasslands rapidly maximized acoustic diversity, while more was needed to maximize pollination (mean γ of 2.1 and 20.2, respectively; *SI Appendix, Table S3*), though this pattern was absent in the other regions. Contrary to expectations, NCP provided by birds (which are larger-bodied) were not influenced by land use at greater distances than NCP provided by arthropods (hypothesis H_4). That is, we found no evidence of taxon-specific differences in the distance decay of NCP supply (*SI Appendix, Table S3*).

Effects of Land-Use Interactions on NCP Supply. We detected positive interactions between neighboring land uses for some NCP, suggesting synergistic effects of multiple land uses on NCP (hypothesis H_2). However, negative interactions arose for other NCP, suggesting trade-off effects of multiple land uses. Nevertheless, interactions only ever accounted for a small

proportion of explained variance (Fig. 2B and *SI Appendix, Table S3*). For example, surrounding forest more strongly affected birdwatching potential and acoustic diversity if the landscape also contained grassland managed at high- rather than low-intensity (Fig. 3B and C and *SI Appendix, Fig. S2 B and C*).

Predictability Among Regions Varies Across NCP. The responses of bird-provided NCP to the surrounding landscape did not significantly differ across regions (acoustic diversity, birdwatching potential and seed predation; Fig. 2 and *SI Appendix, Table S3*). Conversely, NCP provided mostly by arthropods (herbivory, pollination, natural enemy abundance) responded less consistently (Fig. 2), contrary to hypothesis H_1 . This is represented by among-region variation in the direction and magnitude of the predictor variables in their best-fit models, which likely reflects different landscape contexts (*SI Appendix, Table S3*). However, the NCP–NCP interactions captured by covariates in the best-fit models (birdwatching potential in the caterpillar predation model and herbivory in the pathogen infection model) were consistent across regions (Fig. 2). Overall, these findings suggest that both bird-provided NCP and NCP–NCP relationships are generalizable,

while those provided by arthropods are less predictable and more specific to regional context.

Different Directions and Magnitudes of Land-use Responses Between NCP Create Trade-Offs and Synergies Across Landscapes.

Accounting for the direct effects of land use on NCP supply and the interactions between land uses and between NCP allowed us to predict individual NCP supply within each study region. We combine these surfaces of individual predicted NCP to predict a landscape-wide surface of netNCP (Fig. 4 *A* and *C*). As hypothesized, we find that the differing directions and magnitudes of NCP responses to different surrounding land uses (Fig. 2) result in spatial variation in the supply of multiple NCP. In the Schwäbische Alb region, the ratio of beneficial to detrimental NCP was maximized in areas with a high ($\geq 95\%$) area of grassland or mixed forest-grassland (70:30%), rather than forest-dominated areas (Fig. 4 *A* vs. *C* and *SI Appendix*, Fig. S2*B*). We also find that locations with larger patches of several land uses, rather than a greater number of smaller patches, support higher netNCP, relative to the region's mean patch size of 19.7 ha [(27); Fig. 4 *A* vs. *C*]. Although we are unable to state whether these findings are generalizable beyond our study system, these differences do show that there can be stark trade-offs and synergies between the landscape structures that promote beneficial and detrimental NCP.

Discussion

Extensive research has demonstrated how NCP supply at a given location is affected by surrounding landscape composition (7, 14, 17). However, NCP trade-off and synergy analysis and prediction urgently need to move beyond spatial association and correlation to incorporate a more mechanistic understanding of drivers (28). Specifically, understanding how causal among-NCP and NCP-land use relationships depend on associated biota and their characteristics could better inform land management (29).

We drew upon seminal methods for estimating seed dispersal functions (25) and recent advances in modeling mobile NCP provider responses to land use (13) to generate high-resolution spatial predictions of NCP trade-offs and synergies that more accurately account for the spatial dynamics of multiple providers and for complex interactive effects of land uses. Importantly, we explored which trade-off and synergy predictions were transferable across landscapes based on generalities and context dependencies we identified; the absence of such validation is a persistent weakness of many approaches (10, 23). Our results reveal that the amount and identity of land uses in the landscape surrounding grasslands drive the supply of most NCP, both directly and indirectly (via another NCP). Importantly, the NCP interaction effects we found are driven by the biology of NCP-providing taxa, thereby moving beyond broad-scale patterns of correlation or



Fig. 4. Land use across the Schwäbische Alb region, with heatmaps of median predicted netNCP supply (Insets A and C) in grasslands, given the surrounding landscape, for two subsets of the region (Insets B and D). Heat maps in Insets A and C correspond to the land-use configurations in Insets B and D, respectively. Here, darker blue areas represent higher values of netNCP, resulting from relatively higher supply of beneficial NCP or relatively lower supply of detrimental NCP relative to pixels in paler areas. Unfilled pixels in Insets A and C correspond to pixels without grassland cover (the land use for which projections were made). Each NCP was predicted individually for each 100 m pixel using best-fitting models from *SI Appendix*, Table S2, accounting for direct and indirect effects of habitat (i.e. predicted pathogen infection accounts for indirect land-use effects via predicted herbivory supply, and predicted caterpillar predation via predicted birdwatching potential; *SI Appendix*, Table S3). NCP were weighted such that beneficial and detrimental NCP were equally weighted by dividing by the total number of beneficial (five) or detrimental (three) NCP, respectively. Spatial base data: © GeoBasis-DE/BKG (2018); Terms of use: http://sg.geodatenzentrum.de/web_public/nutzungsbedingungen.pdf.

co-occurrence (28, 29). Additionally, we revealed interactions among land uses, with the responses of most mobile NCP-providing taxa to a given land use being modified by neighboring land use types.

Contrary to expectations, NCP provided by the same taxa did not respond consistently to their surrounding landscape (hypothesis H_1). For example, birdwatching potential consistently responded negatively to the amount of forested area in all regions. This finding aligns with the general pattern of European bird diversity being better supported by mixed and semiopen habitats than extensive forest (30). Conversely, other NCP provided by birds through trophic interactions (caterpillar predation and seed predation) were insensitive to surrounding land use (Figs. 2 and 3 *B–D*), possibly because species which feed heavily upon caterpillars and seeds have movement ranges larger than the grain of landscape variation at the three study sites, making them less sensitive to local composition. Favorable land uses for arthropod-provided NCP also varied considerably (Figs. 2 and 3 *B–D*). These inconsistencies align with trait differences among taxa that contribute to different ecosystem functions and NCP. For example, arthropods in higher trophic levels tend to be more generalist and therefore more likely to disperse into nearby habitats (12). This may explain why surrounding land uses played a more important role for pollination than for herbivory or pathogen infection. Similarly, although birdwatching potential, caterpillar predation and seed predation are all provided by birds, it is known that birds with different diets vary in their dispersal traits (19).

When we categorize the indicators of our focal NCP as either diversity-driven (acoustic diversity, birdwatching potential, natural enemy abundance, pollination) or interaction-driven (seed predation, caterpillar predation, herbivory, and pathogen infection), interaction-driven NCP consistently show weaker responses to land use in the surrounding landscape (Fig. 3 *B–D* and *SI Appendix, Figs. S2 B–D and S3 B–D*). In contrast, inclusion of candidate mechanistic linkages among NCP improved model fit for interaction-driven (caterpillar predation and pathogen infection) but not diversity-driven (acoustic diversity) NCP. This supports recent calls for building species interactions into NCP trade-off and synergy predictions to improve accuracy and realism (10), especially when the indicators used as proxies for NCP measure interactions, not diversity.

Surprisingly, we did not find the hypothesized taxonomic differences in the distance decay among the NCP tested. We expected larger-bodied taxa to have the flattest distance decay (hypothesis H_4), and NCP involving specialist interactions to be restricted to a single land use and thus show steep distance decay (12). Instead, we found consistently steep distance decay for all NCP except pollination (γ values in *SI Appendix, Table S3*). The flatter distance decay of pollination means that its supply responds to land-use changes over a wider area than the other NCP. Such differences in distance decays create spatial variability in trade-offs and synergies. The lack of taxa-specific differences echoes a recent finding that, against expectations based on body size and movement range, bird-provided NCP were not affected at broader scales than arthropod-provided NCP (14). Overall, the lack of common response of NCP provided by arthropods to land use suggests that management decisions about arthropod-provided NCP need to consider the spatial processes underlying specific NCP (31).

We tested the extent to which interactions among adjacent land uses result in interactions among NCP (hypothesis H_2). Here, trade-offs and synergies were generated by differing NCP responses to surrounding landscape composition (Fig. 3 *B–D*). Trade-offs can emerge if a land-use change increases the supply of one beneficial NCP while reducing another, for example where increasing

the forest area surrounding a grassland increases natural enemy abundance but decreases pollination (Fig. 3 *B–D*). However, trade-offs can also emerge when a beneficial and a detrimental NCP respond in the same direction to a land-use type. For example, seed predation and natural enemy abundance both responded positively to surrounding forest area in the Alb region (*SI Appendix, Fig. S2D and Table S3*). The different slopes of those responses will change the balance of that trade-off as surrounding forest increases. Moreover, we find that initial increases in surrounding forest cover will rapidly increase natural enemy abundance more than seed predation, but further increases will keep increasing seed predation relative to a stabilized level of natural enemy abundance (Fig. 3C). Synergies emerge when the responses to a land-use type of multiple beneficial or multiple detrimental NCP differ in slope but not direction, such as both acoustic diversity and birdwatching potential responding negatively to surrounding forest area in the Hainich region, but the latter more steeply (Fig. 3C and D). We therefore add to previous studies quantifying trade-offs and synergies among beneficial NCP (7, 23) by incorporating a range of beneficial and detrimental NCP into our high-resolution spatial predictions of the surface of spatial NCP trade-offs and synergies.

Our findings are subject to several caveats. First, our approach summed the area of land use weighted by each pixel's distance from a focal point, but did not account for land-use patch shape or the potential for connectivity and edge effects (32). Future work that accounts for this additional nuance could improve model predictions and generalizability across landscapes. Second, future work could also consider more specific land-use categories than those used in our study, which could allow comparisons of forests of different types and management intensities. Third, our approach was neutral to stakeholder preferences; we assigned weightings to NCP such that total beneficial NCP and total detrimental NCP were equally weighted when visualizing trade-offs (Fig. 4). However, the perception of a NCP as beneficial or detrimental, and their relative importance, depends on a given stakeholder's cultural and socioeconomic context (1). Indeed, it is the inclusion of diverse worldviews and knowledge systems that enhances the NCP concept beyond the ecosystem services framework (1). Additionally, our approach would be strengthened in future work by weighting NCP according to spatial preferences, for example using spatial multicriteria decision analysis (33), as well as incorporating the level of uncertainty around the netNCP estimates (Fig. 4). Fourth, our findings of the land-use arrangements that maximize particular NCP (and netNCP) should be interpreted with caution, in part because the predictability of NCP supply (i.e. the consistency of responses across our three study regions) varied among NCP, especially among those provided by arthropods. Furthermore, these same findings are relevant only to the particular NCP analyzed in our netNCP measure; for example, NCP provided by forest specialists are unlikely to be maximized in mixed forest-grassland areas (32). Nevertheless, our results demonstrate the potential of our approach to provide insights into how multiple NCP covary across diverse landscapes, and the factors that drive this covariation.

Land-use change and its interactions with other global change drivers necessitate predictive mapping of NCP provided by mobile species (7, 11). Accordingly, we present several recommendations based on our findings. First, our finding that the beneficial NCP varied more within landscapes than detrimental NCP suggests that the net balance of NCP supply will be highest close to hot-spots of beneficial NCP providers, and thus with a landscape composition that promotes these biota. This finding could be used to guide management that seeks to maximize netNCP (23).

Second, the lack of taxa-specific commonalities in land-use responses indicates that managing bundles of NCP requires more in-depth consideration of the functional mechanisms underlying NCP responses to land use. Third, we suggest that the relevance of diversity-based indicators for NCP that are underpinned by species interactions (e.g., the plant-arthropod mutualism of pollination) needs further scrutiny. More broadly, our findings demonstrate that promoting conservation and restoration of semi-natural vegetation cover within fields and at field edges, and the conservation of larger forest patches in agricultural landscapes, may provide greater-than-additive benefits to netNCP supply (Fig. 4), and management must carefully consider the differing responses of multiple NCP to land-use changes to successfully foster the multifunctionality upon which rural communities rely (14).

Materials and Methods

Study Regions and Land Cover Data. We studied 150 agricultural grassland plots (50 × 50 m) evenly divided among three regions of Germany: Schwäbische Alb (Alb), Hainich-Dün (Hainich), and Schorfheide-Chorin (Schorfheide). These regions vary by land cover, soil type, and topography, and the plots are part of a long-term research project Biodiversity Exploratories [(24); www.biodiversity-exploratories.de]. All plots had been grassland for at least 10 years prior to project commencement. Of the regions, Alb has greatest grassland area (Alb: 35.8%; Hainich: 17.6%; Schorfheide: 17.1%), Hainich the highest proportion of croplands (Alb: 17.2%; Hainich: 52.1%; Schorfheide: 23.6%), and Schorfheide the greatest forest area (Alb: 44.0%; Hainich: 26.3%; Schorfheide: 50.9%) (SI Appendix, Table S4). The regions also varied in spatial configuration. Alb has the highest density of forest and grassland edges, and smallest mean patch size for croplands (7.8 ha vs. 36 ha in other regions). Hainich has the least fragmented landscape overall, and mean patch sizes of 16.7 and 20.3 ha for grasslands and forests, respectively (26). Schorfheide has the smallest mean patch size for forests (8.4 ha) but the largest for grasslands when main highways, but not minor roads, are used to define patch boundaries [36.6 ha; (26)].

To proxy for land use, we used land cover data from the Federal Agency of Cartography and Geodesy (34), grouped into four broad categories: forest (including forest and scrub), grassland, cropland, and unvegetated (including water bodies, roads, urban areas and rock) (SI Appendix, Table S4). Unvegetated areas were not considered in our analyses as these act as barriers to, rather than sources of, NCP. Because management type is known to have considerable effects on NCP supply in grasslands (5), we further classified grassland as either low-intensity or intermediate/high-intensity (hereafter, high-intensity) using a secondary remote-sensed land-use intensity (LUI) dataset that takes into account grazing intensity, mowing frequency, and fertilizer application (35). We classified each 20 m grid cell of grassland for the whole region as high intensity if the LUI value > 1.2, or low intensity if LUI value ≤ 1.2 (4). For the 8% of land that was classified as grassland according to our primary dataset but not considered grassland in our secondary dataset, we took the LUI value from the nearest grassland pixel with a LUI value.

Landscape Explanatory Variables. We first constructed a land-use effect ($LUE_{i,j}$) variable each for cropland, low-intensity grassland, high-intensity grassland, and forest. These variables captured the distance-weighted contribution of each focal land use, accounting for the area of a land use l and its proximity d to a given plot i . To calculate $LUE_{i,j}$ for each plot, we first gridded the landscapes and assigned to each 20 × 20 m cell the majority land use within. We positioned plots in this landscape based on their GPS coordinates. Because species respond at different scales, for each focal NCP we calculated the $LUE_{i,j}$ variables at the scale previously demonstrated to best explain the response of the primary trophic group that provides that focal NCP, either 500, 1,000, or 2,000 m; (SI Appendix, Table S5). Here, we constructed a circular buffer with a radius around each plot according to that response scale described in SI Appendix, Table S5. For each plot, we measured the distance to all cell centroids that fell within its buffer [median number of cells: 31,414 (2,000 m), 7,854 (1,000 m), 1,962 (500 m)]. We modeled the potential effect of each cell of each land use within this buffer, weighted by their distance from a plot. Then we calculated $LUE_{i,j}$ as

$$LUE_{i,j} = \begin{cases} 0, & \text{if } N_l = 0 \\ \sum_{j=1}^{N_l} \left(\frac{d_{i,j}^2}{2\gamma^2} \right), & \text{if } N_l \geq 1 \end{cases} \quad [1]$$

where $d_{i,j}^2$ is the Euclidean distance from focal plot i to the centroid of cell j of land use l , γ is a distance-decay parameter that reduced the effect of cell j with increasing distance to plot i , and N_l is the total number of plots of land use l surrounding plot i . We used a half-normal distance-decay function to allow for a cell's effect to diminish with increasing distance from a plot (Eq. 1). One γ was estimated for all land uses for each NCP to reduce parameterization and because we assumed that species' mobility is equal across land-use types [although see (36)].

In addition to the $LUE_{i,j}$ variables and the two-way interactions among them, we controlled for study region (a categorical variable with three levels) and the topographic wetness index (37) of plot i , an index that accounts for relevant spatial hydrological processes and was demonstrated to be an important factor influencing species in other studies of these grasslands (7).

NCP Data. We follow Le Provost et al. (7) and explored the six cultural and aboveground regulating indicators of NCP ("services and disservices" in their study, "NCP" hereafter) that are delivered by mobile species. We also included data for two additional NCP delivered by mobile species (seed predation and caterpillar predation) in the same grassland plots. All NCP were measured and data collected at the plot level (SI Appendix, Table S6), therefore covering a subset of the study regions' total environments. We assigned each NCP as either beneficial or detrimental in the context of the German agricultural landscapes in which they were measured, acknowledging that this assignment is stakeholder- and context-specific [(13); SI Appendix, Table S1]. Overall, our analyses included five beneficial NCP: acoustic diversity (the distribution of acoustic energy among frequency bands during diurnal recordings); birdwatching potential (bird species richness); natural enemy abundance (number of brood cells recorded in trap nests attacked by parasitoids of pest arthropods); pollination (number of flower visitors); and caterpillar predation (probability of dummy caterpillar predation by birds after 48 h). We also included three detrimental NCP: pathogen infection (total cover of foliar fungal pathogens); herbivory (total proportion of leaf area damaged by invertebrate herbivores); and seed predation (probability of sunflower seed removal after 48 h). Further details of sampling methods are provided in SI Appendix, Table S6.

Recent reviews of NCP prediction have called for better integration of interactions among species that provide NCP (10). Therefore, we explored ecologically mechanistic potential linkages among NCP according to existing literature. Specifically, we tested for the effects of birdwatching potential (bird species richness) on NCP that are known to respond to bird diversity: caterpillar predation (38), acoustic diversity (39), and seed predation (40). We also tested for effects of herbivory on plant pathogen infection, as herbivores can be important vectors of plant pathogens [(41); see SI Appendix, Table S1].

Statistical Analysis and Model Selection. Conceptually, our modeling approach predicted the supply of an NCP at a particular plot i by accounting for the surrounding landscape ($LUE_{i,j}$; Eq. 1), between-NCP linkages (NCP data) and other environmental controls (Landscape Explanatory Variables). Specifically, we modeled NCP supply y_i using a basic model structure with the set of predictors presented in SI Appendix, Table S7 for each NCP. At its core, the expected value $E[y_i]$ is

$$g(E[y_i]) = \beta_{0,region} + \beta_{1,region} TWI_i + \beta_{2,region} NCP_i + \beta_{3,region} LUE_{i,j} \quad [2]$$

where $g(\cdot)$ represents the link function for the corresponding data distribution (SI Appendix, Table S7), TWI_i is the topographic wetness index of plot i that accounts for spatial hydrological processes (42), NCP_i is another NCP with which y_i may vary, and $LUE_{i,j}$ is the cumulative spatial land-use effect of land use l . We allowed for intercepts and slopes to vary by region (i.e., each β has a region subscript). Other components that were added to this basic structure in subsequent models are detailed below.

We applied a model selection approach to determine which model components were important for predicting the supply of each NCP individually (SI Appendix, Table S2). To do this, we explored various combinations of predictor

variables according to our specific hypotheses and assessed model fit using the leave-one-out information criterion (LOOIC) [loo package v2.5.1; (43)]. First, we compared models 1 to 4 in *SI Appendix, Table S2* to determine whether topographic wetness index (TWI_i) and/or relevant other NCP were important for predicting NCP supply and therefore should be included in all subsequent models that explored land-use effects. For each NCP, we then compared models 5 to 8 with the best-fitting control model in *SI Appendix, Table S2*, determining the importance of each land use individually (forest, high-intensity grassland, low-intensity grassland, and cropland). Finally, we ran models that included main effects of land use for pairs of land uses, with all combinations of two-way interactions to test for nonadditivity, and compared models with and without interaction terms (models 9 to 20 in *SI Appendix, Table S2*). We then reran the overall best-fitting models for each NCP with LUE_{ij} terms recalculated at all buffer sizes we considered (500, 1000, and 2000 m); comparing parameter estimates confirmed that the choice of buffer size did not qualitatively change our main results (*SI Appendix, Fig. S1*).

Models were fitted with Bayesian inference using the greta package v0.4.3 (44) in R v4.0.4 (45). We scaled LUE_{ij} by dividing it by the maximum effective number of cells (e.g., for a 2,000 m buffer, $\frac{\text{buffer area}}{\text{grid area}} = \frac{2000^2 \times \pi}{20^2}$). We used Hamiltonian Monte Carlo sampling across four parallel chains, each with 3,000 warm-up (which were discarded) and 1,000 post-warm-up samples, which resulted in a total of 4,000 posterior samples. All models achieved convergence based on visual assessment of trace plots and the potential scale reduction factor ($\hat{R} < 1.05$) calculated using the coda package v0.19.4 (46). We diagnosed the residuals with Dunn-Smyth randomized quantile residuals (47) and quantile-quantile plots. Our data were processed using the sf package v1.0.5 (48) and visualized using the ggplot2 v3.4.1 (49) and bayesplot v1.10.0 packages (50).

Calculation of netNCP. We hypothesized that the supply of multiple NCP will vary spatially and generate trade-offs due to varying responses of NCP to different land uses in the surrounding landscape. We visualized these trade-offs as the weighted sum of beneficial and detrimental NCP [netNCP; (22)]. In this calculation, NCP were weighted such that beneficial and detrimental NCP were equally weighted by dividing by the total number of beneficial (five) or detrimental (three) NCP, respectively.

Data, Materials, and Software Availability. Most datasets and associated metadata (IDs: 21447, 27568, 27569, 27570, 25806, and 24966) are publicly available on the Biodiversity Exploratories Information System (51). The remaining datasets (IDs: 27087, 27727, and 31018) are subject to an embargo period of three years and will be made available at the same data repository at the conclusion of the respective embargo period. Correspondence for specific datasets should be directed to the respective data owners listed in *SI Appendix, Table S6*. Code used to prepare data and conduct analyses will be made available in the same repository.

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