ECOLOGY

Changes in plant-herbivore network structure and robustness along land-use intensity gradients in grasslands and forests

Felix Neff[1,2]*, Martin Brändle[3], Didem Ambarlı[4,5], Christian Ammer[6], Jürgen Bauhus[7], Steffen Boch[8], Norbert Hölzel[9], Valentin H. Klaus[10], Till Kleinebecker[9,11], Daniel Prati[12], Peter Schall[6], Deborah Schäfer[13], Ernst-Detlef Schulze[14], Sebastian Seibold[4,15], Nadja K. Simons[16], Wolfgang W. Weisser[4], Loïc Pellissier[2,17], Martin M. Gossner[1,4,18]

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Land-use intensification poses major threats to biodiversity, such as to insect herbivore communities. The stability of these communities depends on interactions linking herbivores and host plants. How interaction network structure begets robustness, and thus stability, in different ecosystems and how network structure and robustness are altered along land-use intensity gradients are unclear. We analyzed plant-herbivore networks based on literature-derived interactions and long-term sampling from 289 grasslands and forests in three regions of Germany. Network size and nestedness were the most important determinants of network robustness in both ecosystems. Along land-use intensity gradients, networks in moderately grazed grasslands were more robust than in those managed by frequent mowing or fertilization. In forests, changes of network robustness along land-use intensity gradients relied on changes in plant species richness. Our results expand our knowledge of the stability of plant-herbivore networks and indicate options for management aimed at stabilizing herbivore communities.

INTRODUCTION

Global change poses a threat to ecological communities around the globe (*1*), with land-use change and intensification being the most important drivers (*2*). In temperate regions, historical land-use change has resulted in the conversion of forests to arable land and seminatural grasslands, with the latter being important biodiversity hot spots nowadays (*3*). While forest management in Central Europe is currently becoming increasingly extensified toward close-to-nature management (*4*), legacies of preceding intensive management on forest communities still prevail (*5*). At the same time, seminatural grasslands are being abandoned in marginal areas, whereas land use is intensifying in grasslands with high production potential (*6*), posing a growing threat to biodiversity and the proliferation of ecosystem functions and services (*7*). Land-use intensification has repeatedly been shown to affect the diversity and composition of both plant and insect communities (*8*–*11*), in particular, herbivores, which are associated with many ecosystem functions (*12*). Through consumption of biomass from primary producers, insect herbivores ensure the cycling of energy and nutrients and are thus central to many food webs (*13*, *14*). To persist in a community, herbivores depend on the trophic interactions with their food plants. Still, these interactions between herbivorous insects and plants have rarely been addressed in a comprehensive way in the context of changing land-use intensity. Land-use intensification is expected to change the structure of networks, i.e., the arrangement of interactions in these communities (*15*), and thus the stability of these systems (Fig. 1). The study of networks along gradients of land-use intensity is a promising field of research that helps to gain insight into how multitrophic communities are assembled and how they are affected by shifting environmental conditions in the face of global change (*16*).

Ecological interaction networks are structured in a modular or a nested way or in a combination of both (*17*, *18*). Highly modular networks tend to be organized into modules of species, with the species within a module interacting strongly with each other, whereas interactions between modules are scarce (Fig. 2A) (*19*). In strongly nested networks, interaction specialists, i.e., species interacting with only a few species, tend to interact with a subset of the species that an interaction generalist interacts with (Fig. 2B) (*20*). Land-use pressures that reduce species richness are generally expected to decrease modularity because of a reduction of overall network size (*21*). The same is true for nestedness if rare and specialized species first get lost under increasing pressures (*22*). Also, land-use pressures

[1]Forest Entomology, Swiss Federal Institute for Forest, Snow, and Landscape Research WSL, Zürcherstr. 111, 8903 Birmensdorf, Switzerland. [2]Landscape Ecology, Institute of Terrestrial Ecosystems, ETH Zürich, Universitätstr. 16, 8092 Zürich, Switzerland. [3]Division of Animal Ecology, Department of Ecology, Philipps-Universität Marburg, Karl-von-Frisch-Str. 8, 35043 Marburg, Germany. [4]Terrestrial Ecology, Department of Ecology and Ecosystem Management, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany. [5]Department of Agricultural Biotechnology, Faculty of Agriculture, Düzce University, 81620 Düzce, Turkey. [6]Silviculture and Forest Ecology of the Temperate Zones, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany. [7]Chair of Silviculture, Faculty of Environment and Natural Resources, Albert-Ludwigs-Universität Freiburg, Tennenbacherstr. 4, 79085 Freiburg, Germany. [8]Ecosystem Dynamics, Swiss Federal Institute for Forest, Snow, and Landscape Research WSL, Zürcherstr. 111, 8903 Birmensdorf, Switzerland. [9]Biodiversity and Ecosystem Research, Institute of Landscape Ecology, University Münster, Heisenbergstr. 2, 48149 Münster, Germany. [10]Institute of Agricultural Sciences, ETH Zürich, Universitätstr. 2, 8092 Zürich, Switzerland. [11]Landscape Ecology and Landscape Planning, Institute of Landscape Ecology and Resource Management, Justus-Liebig-University Giessen, Heinrich-Buff-Ring 26-32, 35392 Giessen, Germany. [12]Plant Ecology, Institute of Plant Sciences, University of Bern, Altenbergrain 21, 3013 Bern, Switzerland. [13]Botanical Garden of the University of Bern, Altenbergrain 21, 3013 Bern, Switzerland. [14]Max Planck Institute for Biogeochemistry, Hans-Knöll-Str. 10, 07745 Jena, Germany. [15]Ecosystem Dynamics and Forest Management in Mountain Landscapes, Department of Ecology and Ecosystem Management, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany. [16]Ecological Networks, Technical University of Darmstadt, Schnittspahnstr. 3, 64287 Darmstadt, Germany. [17]Landscape Ecology, Swiss Federal Institute for Forest, Snow, and Landscape Research WSL, Zürcherstr. 111, 8903 Birmensdorf, Switzerland. [18]Department of Environmental Systems Science, Institute of Terrestrial Ecosystems, ETH Zürich, Universitätstr. 16, 8092 Zürich, Switzerland.
*Corresponding author. Email: felix.neff@wsl.ch

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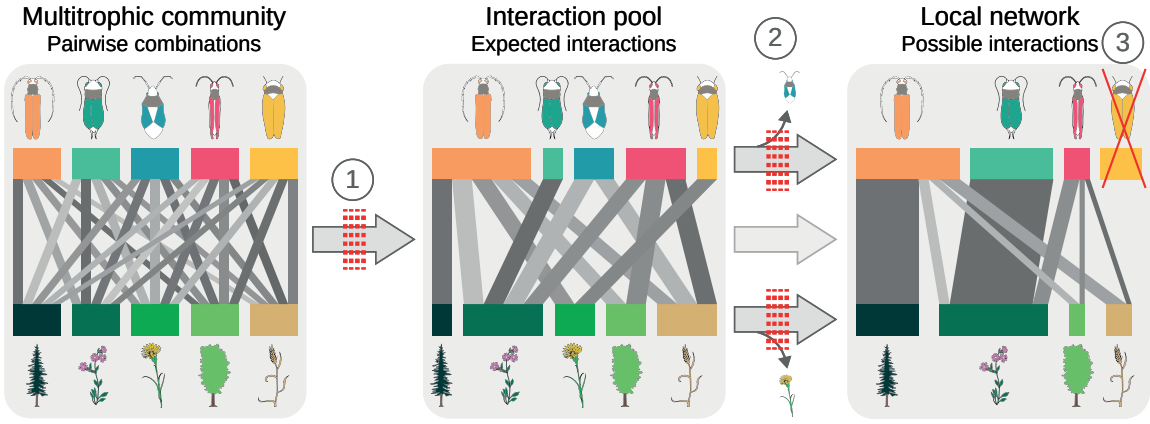


Fig. 1. Conceptual diagram of the multistep procedure determining the structure of a local interaction network. Starting from a regional pool of plant and herbivore species with all pairwise interaction combinations, (1) interactions are excluded because of ecological constraints (indicated by red dots on the arrow), such as mismatches between herbivore feeding traits and plant structural traits or mismatches between phenologies. This defines a pool of interactions that can be observed in nature between pairs of herbivores and plants. (2) Each local community contains only a subset of plant and herbivore species and thus interactions from the regional pool, as a result of local environmental filters such as those imposed by land use (indicated by red dots). In addition to changes in presence and absence, abundances of species differ between communities, changing the local network structure. Furthermore, environmental conditions can exclude or weaken certain interactions, but this filtering step was not addressed in the present study. (3) Some herbivore species that would find the environmental conditions suitable are excluded (or reduced in abundance) from these networks because of the absence (or rarity) of suitable food plants.

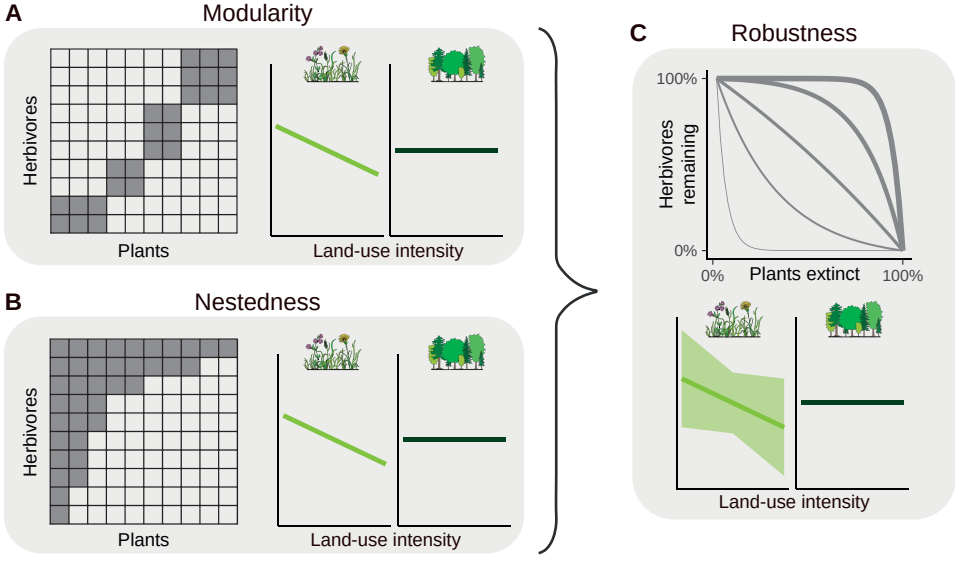


Fig. 2. Illustration of network metrics and hypotheses. The network metrics (**A**) modularity, (**B**) nestedness, and (**C**) robustness are schematically illustrated. The line graphs show the hypotheses of how weighted networks change along land-use intensity gradients in the two ecosystems. For modularity and nestedness, the schematic figures show the arrangement of interactions (gray shading) in a plant-herbivore network. For robustness, the schematic figure shows the course of herbivore extinctions following plant extinctions for different robustness scenarios. Thicker lines indicate more robust networks. In the hypothesis graphs, the lines represent the hypothesized pattern of the network metrics along the land-use intensity gradient in grasslands (light green) and forests (dark green). The effect of modularity on robustness is not well resolved, and there could be a positive, negative, or no association between modularity and robustness. In combination, this results in a range of possible scenarios for grassland network robustness, which are indicated with the shaded area. The solid line for grassland robustness shows the case when there is only a nestedness but no modularity effect on robustness. We do not expect an effect of land-use intensity on robustness in forests because disturbances happen at longer temporal scales.

can change the proportion of interaction generalists in a community (*23*). Generalists are expected to blur boundaries between modules (*21*) and increase network connectance (i.e., the proportion of realized interactions out of all possible pairwise combinations), which is often positively linked to nestedness (*24*). Thus, changes in the balance of specialists and generalists due to land-use pressures should also manifest in changes in network structure. Evidence from studies on land-use effects on both mutualistic and antagonistic interaction networks in different ecosystems is not consistent. It may comprise negative but also neutral or positive effects of land-use drivers, such as habitat degradation or agricultural intensification, on modularity and nestedness (*22*, *25*–*29*). Our large-scale assessment of plant-herbivore network structure along well-defined gradients of land-use intensity across two major temperate ecosystems (i.e., grasslands and forests)

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could help to clarify the impact of land use on the structure of trophic interaction networks.

Modularity and nestedness in combination are used to describe network structure (*21*, *30*) and to understand how network structure and stability are linked in different systems (*25*, *30*–*35*). A particularly important component of stability is the robustness of interaction networks to species extinctions (*36*). In a bipartite network, i.e., a network involving two interacting groups of organisms, robustness quantifies the extent of extinctions in one group following extinctions in the other (i.e., secondary extinctions; Fig. 2C). In the context of this study, it quantifies the tolerance of herbivore communities to extinctions of host plants. Robustness of different systems is affected by land-use intensity (*26*, *28*, *29*, *37*), but the kind and direction of the effect seem to depend on the underlying network structure shaped by nestedness and modularity. On the one hand, robustness proved to be positively affected by nestedness. In a nested network, the presence of interaction generalists at one level (e.g., widely used food plants) buffers the extinction risk for interaction specialists at the other level (e.g., herbivores specialized on few host plant species), particularly if these generalist food plants are less likely to get extinct (*33*). These positive associations between nestedness and robustness have been found for different systems including both mutualistic and antagonistic networks (*29*, *33*–*35*) [but see (*28*)]. On the other hand, the relationship between modularity and robustness is less clear. The internal organization of networks into modules can prevent the effect of a perturbation on a single species to cascade through a system, and it has been shown that the dynamic stability of antagonistic networks can be increased by modularity (*30*, *32*). However, studies on the association between network robustness and modularity show inconclusive results (*28*, *29*), and this relationship needs a further in-depth analysis.

Here, we aim to identify the role of plant-herbivore network structure for network robustness across ecosystems and to assess the impact of land-use intensity on these relationships. This will help to better understand the stability of herbivorous insect communities. To circumvent the difficulties in obtaining reliable plant-herbivore interaction data from field observations at large spatial and temporal scales, we used (i) abundance data of vascular plant and herbivore insect communities from 10 years of sampling in 150 permanent grasslands and from 7 years of sampling in 139 temperate forests (*38*) and (ii) a literature-based database of recorded plant-herbivore feeding interactions to construct networks of possible interactions. This approach has recently been used to infer networks in an experimental setup (*39*) but has never been applied to plant–insect herbivore systems at larger scales. From these plant-herbivore networks covering gradients of land-use intensity commonly found in Central European grasslands and forests, we determined modularity, nestedness, and robustness as well as network size and connectance, which are both known to be correlated with other network metrics (*24*), to understand how the different structural attributes affect network robustness in the two studied ecosystems. Furthermore, we assessed changes in network measures along land-use intensity gradients and compared them to null-model expectations based on network size and connectance. Thus, null models reflected the differences between networks that would be expected if the number of interacting species and the number of interactions differ, but no fundamental (directed) restructuring of interactions takes place. For grasslands, we hypothesized a decrease in both modularity and nestedness with increasing land-use intensity. This is because grasslands are increasingly disturbed by mowing and grazing. This should result in a net negative effect on robustness if the effect of nestedness on robustness outweighs the more inconclusive effect of modularity (hypothesis 1; Fig. 2). This hypothesis applies, in particular, to mowing frequency, which has well-documented strong effects on plant and insect communities (*8*, *11*, *40*). For forests, we hypothesized no substantial changes in network structure and robustness along the land-use intensity gradient (hypothesis 2; Fig. 2) because these ecosystems are formed by long-lived trees and experience infrequent anthropogenic disturbances.

RESULTS

Grassland networks were constructed from 184,528 herbivore individuals (1230 ± 701; means ± SD per plot) belonging to 773 species (82 ± 18) and from 352 vascular plant taxa (49 ± 16). Forest networks were constructed from a total of 48,934 insect herbivore individuals (352 ± 146) belonging to 552 species (44 ± 12) and from 326 vascular plant taxa (49 ± 28) (see table S1 and figs. S1 and S2 for details).

Network structure and robustness in grasslands and forests

While mean plant species richness was comparable between grasslands and forests, herbivore species richness and thus network size were higher in grasslands (fig. S3). At the same time, forest herbivore communities were characterized by a higher share of polyphagous species (fig. S2), resulting in higher average connectance and nestedness of forest networks (fig. S3). To determine the relationships between structural attributes of networks and robustness in the two studied ecosystems, we used structural equation modeling (SEM) (Fig. 3A). Pathways were summarized to assess the contribution of both direct and indirect pathways. Particularly in forests, but also in grasslands, network size was strongly positively associated with network robustness, mainly through a direct effect (Fig. 3B and table S2). In addition, nestedness was strongly positively related to network robustness, which was particularly evident in grasslands but also in forests (Fig. 3B). Modularity was not associated with robustness in grasslands and negatively associated with robustness in forests (Fig. 3B). The observed patterns were found to be generally consistent in sensitivity analyses (fig. S4 and table S2). Largest deviations were found for presence-absence networks, but the positive association of robustness with network size in forests and with nestedness in grasslands was confirmed even if abundance was not accounted for.

Network changes along the land-use intensity gradient in grasslands

In grasslands, land-use intensity was characterized by the land-use intensity index (LUI), which combines intensities of mowing, grazing, and fertilization. We found profound changes in network measures along LUI that differed significantly from null-model expectations (Fig. 4). High LUI was strongly associated with reduced network modularity (Fig. 4A). This effect was mainly driven by grazing intensity, but also by fertilization intensity, and was not related to changes in network size or connectance (Fig. 4C) and thus not anticipated by the null models. Simultaneously, robustness was directly increased by increasing grazing intensity but was not directly affected by mowing or fertilization (Fig. 4C). In contrast to the null models that predicted no change (grazing) or a slight decrease (mowing and fertilization) in robustness due to declining network size, none of the land-use

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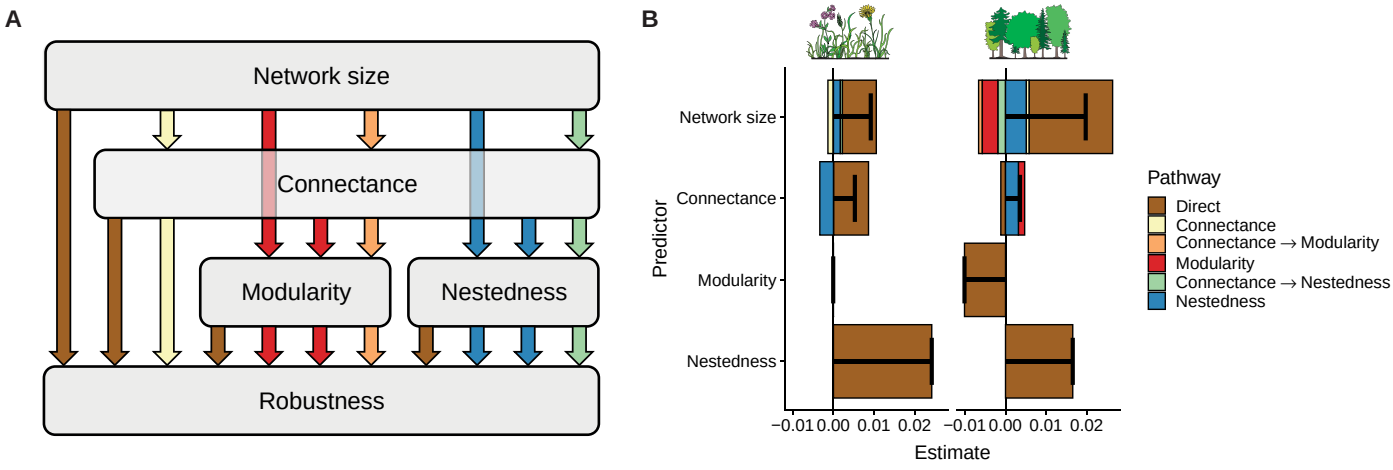


Fig. 3. Network structure and robustness in grasslands and forests. (**A**) All potential direct and indirect pathways linking different attributes of network structure (network size, connectance, modularity, and nestedness) to network robustness. These pathways were quantified on the basis of SEM. (**B**) Summarized pathway estimates from SEM for all direct and indirect pathways linking network structure to network robustness in grasslands (left) and forests (right), arranged by the different network structure metrics. The intermediate variables linking predictors and robustness as well as direct pathways are indicated by the different colors. The overall effect of a predictor on robustness (i.e., sum of all direct and indirect pathways) is shown with the black bars. Note that all predictor variables were scaled to SD 1 (across both ecosystems) before analyses to make pathway estimates comparable. Detailed results from SEM are given in table S2.

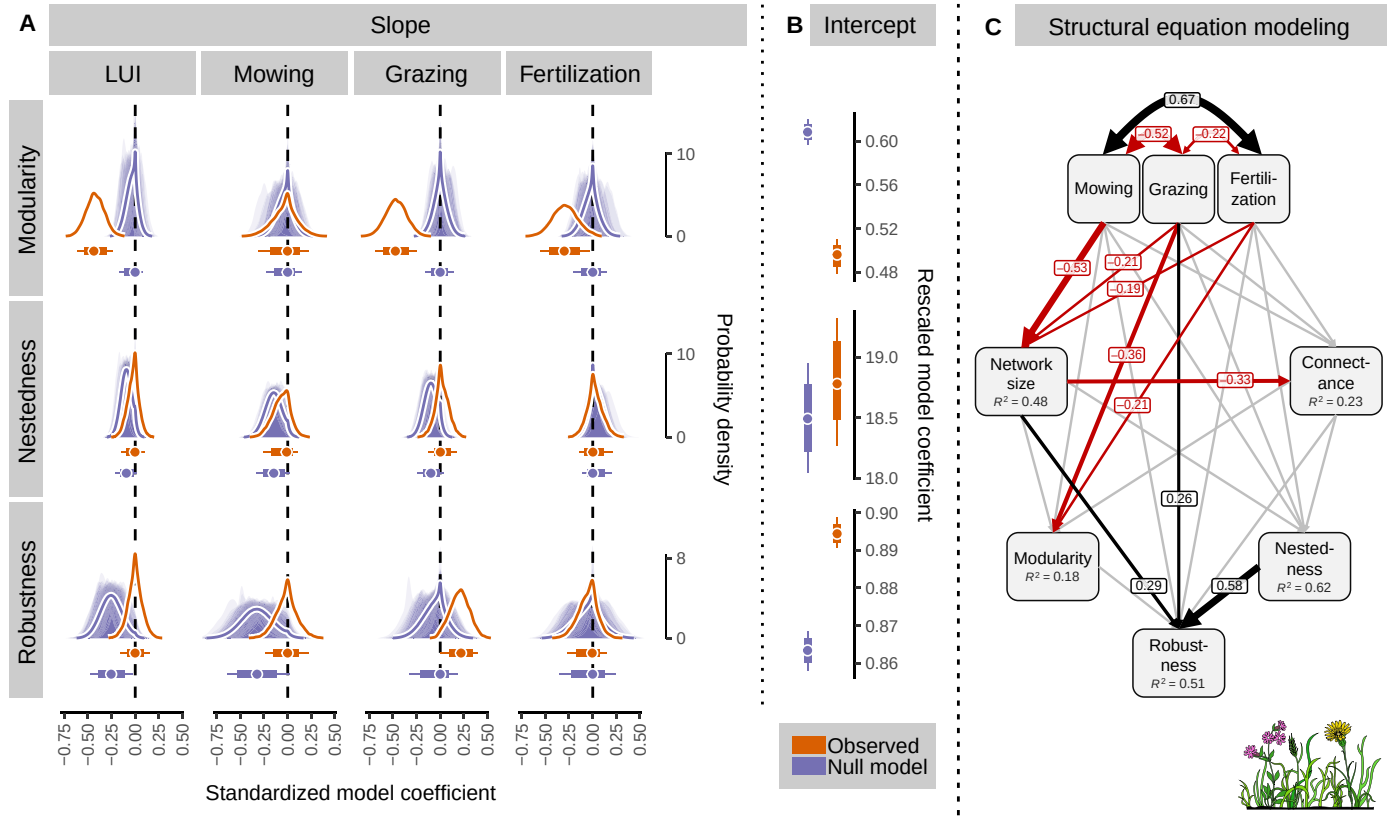


Fig. 4. Changes in network structure and robustness along land-use intensity gradients in grasslands. Posterior distributions of (**A**) slope estimates and (**B**) intercept estimates from models testing the effects of land-use intensity on network metrics in observed networks (orange) and null-model networks (purple). Slopes are shown for models on combined land-use intensity and on the single components of land-use intensity. Intercepts correspond to overall means on the original scale of the metric. Curves, probability densities of the posterior distributions; thin lines, 95% highest density interval (HDI); bold lines, 77.6% HDI (no overlap indicates a significant difference on the 5% level); points, highest maximum a posteriori estimates; shaded purple areas, posterior distributions for 100 of 999 null-model realizations. (**C**) Results from piecewise SEM on the relations of land-use intensity components, network size, connectance, modularity, nestedness, and robustness. Numbers show standardized path coefficients for significant pathways. Positive paths in black, negative in red, and nonsignificant in gray. Conditional R^2 values in the boxes. Fisher's $C = 0.81$, $P = 0.665$.

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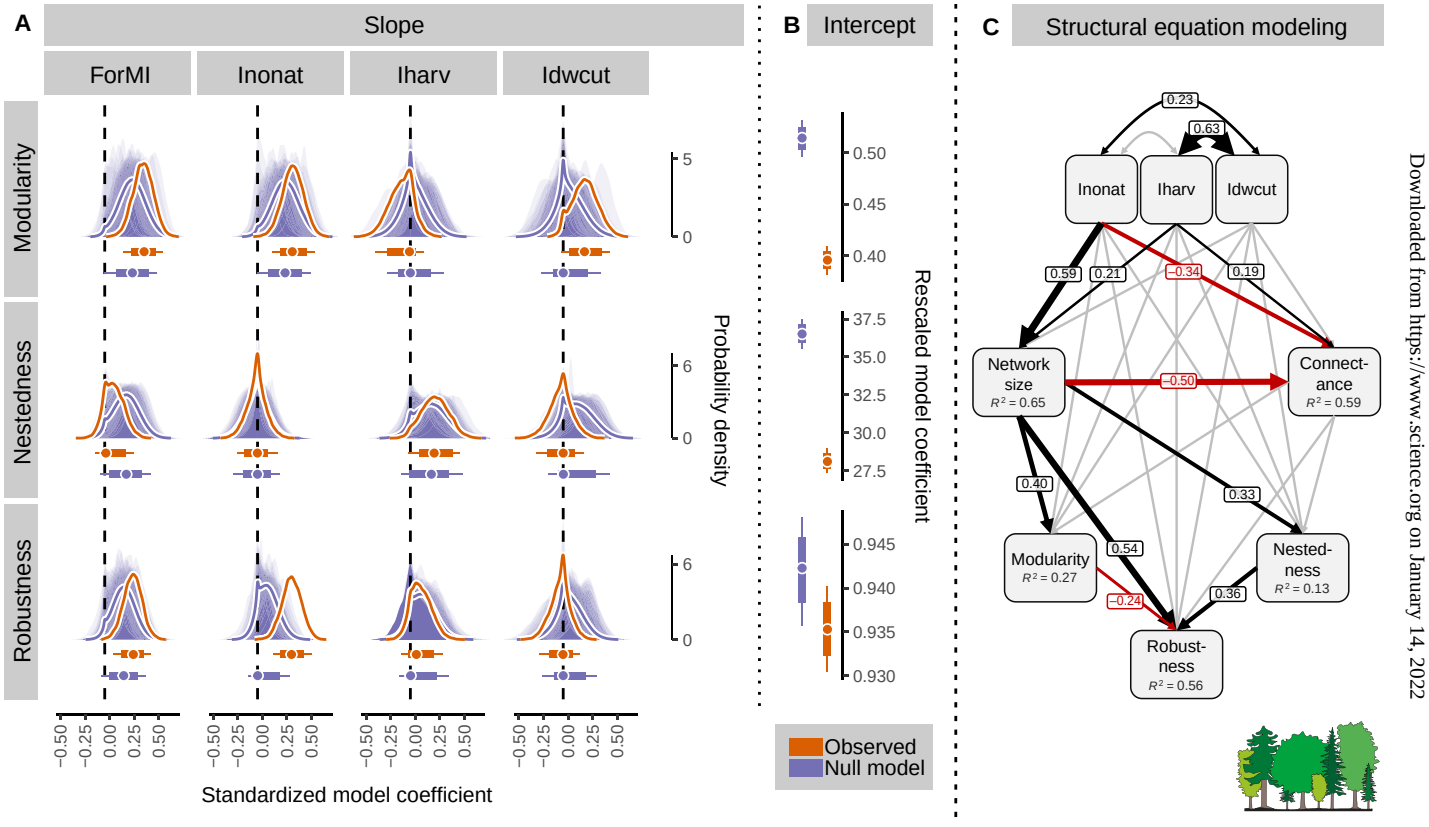
components was found to decrease robustness, and grazing was even found to be associated with an increase in robustness (Fig. 4A). Nestedness had a positive relationship with network robustness, but differences in nestedness were not explained by differences in land-use intensity (Fig. 4C). The conditional R^2 of 0.62 for nestedness in SEM (marginal R^2 = 0.02) showed that the variability of nestedness was, however, substantially explained by the random term of the models, i.e., the regional differences. Land-use effects were found to be consistent in most of the sensitivity analyses (figs. S5 to S10). Main deviations were observed for presence-absence networks, for which no effect on modularity was found, indicating the role of species abundances in shaping this pattern.

Network changes along the land-use intensity gradient in forests

In forests, land-use intensity was characterized by the forest management intensity index (ForMI), which is calculated from the proportion of tree species that are not part of the natural forest community (henceforth, Inonat), the proportion of harvested wood volume (henceforth, Iharv), and the proportion of deadwood with saw cuts (henceforth, Idwcut). We observed no changes in network measures that differed from null-model expectations along the ForMI gradient (Fig. 5A). Modularity and nestedness but not robustness of the observed forest networks were always lower than what would be expected on the basis of networks randomly assembled from the regional interaction pool (Fig. 5B). Although modularity significantly increased with increasing ForMI (mainly driven by Inonat), this increase was not significantly different from null-model expectations but was a consequence of increased network size due to higher plant species richness at high Inonat and Iharv levels (Fig. 5C and fig. S3). We also observed an increase in robustness with increasing ForMI (Fig. 5A), which was again mainly linked to an increase in Inonat and the resulting increase in network size (Fig. 5C and table S3). Apart from the direct positive effect of network size on robustness, we found indirect negative effects of network size on robustness through modularity and indirect positive effects through nestedness (Fig. 5C). Both relationships, increasing modularity and robustness with higher Inonat, were found to be consistent in sensitivity analyses (figs. S11 to S17).

DISCUSSION

In this study, we combined species abundance data across trophic levels with a literature-based interaction database to construct plant-herbivore networks of 150 grasslands and 139 forests along gradients



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Fig. 5. Changes in network structure and robustness along land-use intensity gradients in forests. Posterior distributions of (**A**) slope estimates and (**B**) intercept estimates from models testing the effects of land-use intensity on network metrics in observed networks (orange) and null-model networks (purple). Slopes are shown for models on combined land-use intensity (ForMI) and on the single components of land-use intensity (Inonat, proportion of tree species that are not part of the natural community; Iharv, proportion of harvested wood volume; Idwcut, proportion of deadwood with saw cuts). Intercepts correspond to overall means on the original scale of the metric. Curves, probability densities of the posterior distributions; thin lines, 95% HDI; bold lines, 77.6% HDI (no overlap indicates a significant difference on the 5% level); points, highest maximum a posteriori estimates; shaded purple areas, posterior distributions for 100 of 999 null-model realizations. (**C**) Results from piecewise SEM on the relations of land-use intensity components, network size, connectance, modularity, nestedness, and robustness. Numbers show standardized path coefficients for significant pathways. Positive paths in black, negative in red, and nonsignificant in gray. Conditional R^2 values in the boxes. Fisher's C = 0.84, P = 0.657.

of land-use intensity. We observed larger networks in grasslands but more nested networks in forests. Although the assembled networks in the two ecosystems differed considerably in their underlying structure, our results show a generally positive effect of nestedness on the robustness of networks in both ecosystems. Thus, a nested network structure not only stabilizes mutualistic networks (*33*, *34*) but also plays a major role for the stability of antagonistic networks such as plant-herbivore networks, as has been shown previously for hybrid networks (*29*). The effects of modularity on robustness have rarely been studied, and those few studies yielded inconsistent results (*28*, *29*). In our work, we found no effect of modularity on robustness in grasslands and only a weak negative effect in forests. The latter might indicate the presence of modules with herbivores specialized on rare food plants, making modular networks more prone to secondary extinctions. Besides the effects mediated by nestedness and modularity, network size was positively associated with network robustness in both ecosystems. This underlines the potential of species-rich systems to enhance community stability. The relation of network size and robustness was particularly strong in forests and might reflect the presence of very small networks, which are more susceptible to species extinctions. Small network size was particularly evident in unmanaged forests. In our study, these sites were generally very poor in plant species because of species-poor tree layers dominated by beech and very sparse understory vegetation. Sparse understory vegetation is mostly caused by the very shady conditions in stands where management has recently been abandoned and more gap-rich old-growth forest structures are still lacking (*41*, *42*). In sum, the consistent positive relations of robustness to network size and nestedness across ecosystems indicate their general role in determining the stability of plant-herbivore communities.

In accordance with hypothesis 1, land-use intensity in grasslands was associated with changes in network structure and robustness that clearly differed from null-model expectations. This finding implies that the frequent disturbances imposed by land use in grasslands perturb plant-herbivore networks through species turnover of plants and herbivores (*43*). In particular, we found a decrease in network modularity with increasing grassland land-use intensity, which is in line with recent findings on the effects of agricultural intensification (*29*). At the same time, variability of nestedness, which was strongly linked to robustness, was poorly explained by land-use intensity. Nestedness seemed to be more affected by other factors, which were linked to differences between the study regions, such as climate or land-use history (*44*). We expected the largest changes in network structure to occur with high mowing frequency, as mowing showed the most distinct effects on plant and insect communities in previous grassland studies (*8*, *11*, *40*). Contrary to our expectations, we found no significant effect of mowing frequency on any of the focal network metrics. Although mowing frequency was negatively associated with network size and thus indirectly with robustness, there was no overall effect of mowing frequency on robustness. This might indicate that mainly rare, host plant–specialized insect species, which are more prone to secondary extinction, got lost at high mowing frequency, keeping network robustness constant (*37*). This is supported by previous findings from grasslands, showing that both specialist and rare species are most vulnerable to high land-use intensities (*23*, *45*).

In contrast to mowing, we found clear effects of grazing intensity on network modularity and robustness. The strong decrease in modularity with high grazing intensity was due to changes in the relative proportion of different modules. Highly specialized, self-contained modules based on grasses tended to decrease with increasing grazing pressure, while more diverse modules based on different plant lineages increased (figs. S18 and S19). Thus, networks were found to decrease in modularity at high grazing intensity. Lower modularity was not related to the observed change in network robustness, but robustness was directly positively associated with grazing intensity. As for the mowing effect, we might attribute this increase in robustness to specialists first getting lost from the system (*37*). However, the proportion of specialized herbivores did not decrease with increasing grazing but even increased at low grazing intensity compared to ungrazed plots (fig. S20). This indicates that regular disturbances imposed by grazing positively affect the resistance of these systems. Grazing occurs locally and results in spatially more heterogeneous habitats (*46*), which may enhance the persistence of undisturbed patches that harbor certain plants and their specialized herbivores. At the same time, the absence of grazing in these managed grasslands means that mowing frequency and also fertilization intensity are higher (fig. S20), which could explain the lower specialization and network robustness that were observed in ungrazed plots. Thus, in grasslands where some sort of management is needed to prevent shrub and tree encroachment, we might expect a hump-shaped relationship with the highest robustness occurring at low to moderate grazing intensities, as found in grazing-related disturbance-diversity patterns (*47*). In accordance with predictions made by the hump-backed model of species diversity (*48*), both very low and also high disturbance levels by grazing may result in impoverished, unstable communities. This is indicated by the sharp increase of robustness in moderately grazed compared to ungrazed plots (fig. S20). Unfortunately, our study lacks sufficient sampling at the high end of the grazing intensity gradient to foster this hypothesis.

We expected land-use intensity in forests to have little effect on network structure and robustness (hypothesis 2). In support of this hypothesis, we found no effects of land-use intensity on forest network structure that were significantly different from null-model expectations. Still, there was an increase in modularity and robustness in intensively used forests, which was driven mainly by Inonat (i.e., the proportion of tree species that are not part of the natural forest community) and Iharv (i.e., the proportion of harvested wood volume). Both forest management components increased plant species richness, directly by adding more tree species but also indirectly through topsoil disturbances and increased light penetration to the forest floor (*42*), which, in turn, provided additional niches for insect herbivores (*49*). This resulted in larger networks, which supported higher modularity and robustness. At the same time, changes in land-use intensity in forests were not directly related to changes in modularity, nestedness, or robustness, suggesting that no fundamental restructuring of the networks occurred along forest land-use intensity gradients. This finding may indicate that plant-herbivore communities in forests are relatively stable against anthropogenic disturbances, at least within the range of land-use intensities encountered here. In addition, it could be a consequence of long time spans between anthropogenic disturbances in forests. Most of the forest communities did not experience any proximate interference with strong impact on forest structure and tree species composition such as windthrow or clear-cut recently.

Because changes in network structure along land-use intensity gradients in forests were only driven by changes in network size, whereas changes in grasslands included more fundamental restructuring

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of networks, we conclude that land-use intensity in grasslands is more apparent than in forests. This implies that more regular and intense disturbances such as mowing have stronger effects on networks than the subtler management practices in forests without heavy recent management interventions such as clear-cuts. Although we did not compare effect sizes for land-use intensity between grasslands and forests, differences in the length of the land-use intensity gradient between the two ecosystems could affect the comparison. Clear-cuts are generally avoided in current German forestry, owing to legal restrictions and prevailing management concepts. Moreover, natural regeneration is favored and stand replacement is done over two to three decades by single-tree selection, group selection, or gap cuttings. Thus, the forest management intensity gradient of our study may be too short to cause substantial changes in community stability compared to the gradient in grassland land-use intensity. We, however, argue that forest and grassland gradients both reflect a range of land-use intensities typical of most regions in Central Europe. Also, the length of the gradients is comparable between both habitat types because we also miss the high end of the land-use intensity gradient in grasslands. For example, the maximum mowing frequency on our plots was three cuts per year (with sporadic exceptions), while up to five, sometimes even six, cuts per year are applied in German grasslands elsewhere (*50*). Thus, we are quite confident that the differences in effects of land-use intensity between forests and grasslands are not based on different gradient lengths but differences inherent to the ecosystems and their respective land-use practices.

In this study, we inferred interaction networks from species abundances and a literature interaction database. This merging of data made it possible to include robust data, which was based on large-scale and long-term monitoring data of vascular plants and insect herbivores. Our approach proved to be useful for unraveling interactions that are hard to sample directly or prone to sampling bias (*51*). However, the applied procedure does not rely on interactions directly observed in the field, which might be influenced by environmental conditions at the plot level (Fig. 1), and it cannot be used to address differences in feeding preferences within species, as interaction strength is solely conditional on plant abundance. Furthermore, different sampling methods used in grasslands and forests, although optimized for the respective circumstances, might differently record herbivore communities. Especially in forests, herbivore communities in the canopies can differ from understory-associated communities (*49*). While these limitations cannot be completely overcome in the current study, a variety of sensitivity analyses including additional data from forest canopies and presence-absence networks confirmed the main results. Thus, we are confident that our results provide valid, new insight into general changes in the organization of plant-herbivore networks in response to land use.

Our analyses clearly showed that the robustness of plant-herbivore networks is mainly determined by network size and nestedness and that land-use intensification directly (grasslands) or indirectly (forests) affects robustness. This should be considered when managing landscapes to slow down biodiversity loss in general and insect decline in particular (*52*). Furthermore, as plant-herbivore interactions drive important ecosystem processes, the observed shifts in robustness of plant-herbivore networks along land-use intensity gradients likely translate into differences in the stability of ecosystem function provisioning. Our study indicates that different approaches should be applied when managing grasslands and forests for stable plant-herbivore communities. In forests, high plant species richness was found to be the main determinant of network robustness. Higher plant species richness can be reached by managing forests as mixed stands rich in tree species rather than as pure beech stands, which normally establish if unmanaged. As a side effect, these mixed stands might also prove more stable in the face of ongoing climate change (*53*). Furthermore, higher understory plant diversity can be reached by regularly opening the tree canopy to allow for more light to penetrate to the forest floor. In grasslands, management by moderate grazing rather than mowing could increase network robustness. Nestedness, however, which showed to be an important determinant of the robustness of plant-herbivore networks, was, at best, weakly related to land use in the studied ecosystems and should be further investigated to foster our understanding of the stability of herbivore communities.

MATERIALS AND METHODS

Study system and land-use intensity

The study was performed in three regions of Germany, which are part of the Biodiversity Exploratories framework (*38*). The UNESCO Biosphere Reserve Schorfheide-Chorin is situated in the lowlands of northern Germany and is a postglacial moraine landscape [52°47′25′′N to 53°13′26′′N, 13°23′27′′E to 14°08′53′′E; 10 to 140 m above sea level (a.s.l.)]. The Hainich-Dün region is an undulating landscape located in central Germany, comprising the Hainich National Park and its surroundings (50°56′14′′N to 51°22′43′′N, 10°10′24′′E to 10°46′45′′E; 285 to 550 m a.s.l.). The UNESCO Biosphere Reserve Schwäbische Alb is a calcareous mountain range of medium elevation located in southwestern Germany (48°20′28′′N to 48°32′02′′N, 09°10′49′′E to 09°35′54′′E; 462 to 858 m a.s.l.). In each of the three regions, 50 plots were selected both in permanent grasslands (50 m by 50 m) and in forests (100 m by 100 m). Different plot sizes are aimed to cover a coherent, representative area for the respective ecosystem. Plot selection followed a stratified random sampling framework of 1000 plots in each region based on information about land-use intensity, vegetation, and soil characteristics (*38*). Eleven forest plots (1 in Schwäbische Alb and 10 in Schorfheide) had to be excluded from the analyses because of missing sampling years, resulting in a total of 139 forest plots (see fig. S21 for a map of all study plots).

All grasslands included in this study were managed, and management types covered meadows, pastures, and mown pastures with different intensities of mowing, fertilization, and grazing. The level of intensity of these three individual practices was recorded annually for each plot from 2006 to 2017 with standardized farmers' questionnaires (*38*) and, afterward, averaged across years and standardized relative to the overall means. The intensity gradient ranged from pastures being grazed a few days a year (less than 50 livestock unit days/ha) to pastures being heavily grazed (up to over 1500 livestock unit days/ha in some years) or meadows being mown three times a year (four times in very few cases) and simultaneously fertilized (up to over 400 kg N/ha in some years). While mowing and fertilization intensity were strongly positively correlated ($r = 0.67$, $P < 10^{-21}$), grazing intensity was negatively correlated with both mowing ($r = -0.52$, $P < 10^{-11}$) and fertilization intensity ($r = -0.22$, $P < 0.01$). The combined grassland LUI was calculated as the square root–transformed sum of the standardized intensity values of mowing, fertilization, and grazing (*54*).

The forests in the three study regions were managed differently, ranging from unmanaged forests dominated by European beech

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(*Fagus sylvatica*), to managed beech forests, to intensively managed coniferous forests comprising Norway spruce (*Picea abies*) in Alb and Hainich and Scots pine (*Pinus sylvestris*) in Schorfheide. To quantify the land-use intensity in forests, inventories of living trees were first carried out in all plots between 2008 and 2014 and a second time between 2015 and 2018. In addition, inventories of stumps and deadwood were made once in 2012 and a second time between 2017 and 2018. From these inventories, three basic measures were obtained: (i) the proportion of wood volume of non-natural tree species, i.e., species that are not part of the natural forest community, to the wood volume of all tree species (Inonat); (ii) the proportion of harvested wood volume to the total wood volume (Iharv); and (iii) the proportion of deadwood volume with saw cuts to the total deadwood volume (Idwcut), as an indicator for non-naturally occurring deadwood. For Inonat and Iharv, the wood volumes considered were the sum of standing, harvested, and deadwood volume, with harvested volume being estimated from stumps. All three measures are proportions ranging between 0 and 1, with 1 denoting maximum management intensity and 0 indicating no apparent management, and were averaged across the two sampling campaigns. Idwcut was positively correlated with both Inonat ($r = 0.23$, $P < 0.01$) and Iharv ($r = 0.63$, $P < 10^{-15}$). The combined ForMI was then calculated as the sum of the three component measures (*55*). The theoretical maximum value of 3 would indicate a clear-cut stand of non-native species such as Norway spruce and Scots pine with deadwood composed only of harvest residuals, while a similar clear-cut of a native species would reach a value of 2. In this study, ForMI ranged between 0 (beech forest unmanaged for several decades) and 2.28 (immature, thinned, monospecific spruce forest). On average, ForMI increased with management intensity and non-natives share from unmanaged (0.23 ± 0.22; means ± SD) and managed (0.98 ± 0.36) beech forests to mixed pine/beech (1.49 ± 0.15), pure pine (1.55 ± 0.26), and pure spruce (1.88 ± 0.29) managed forests. ForMI is closely correlated with another silvicultural management intensity index (SMI), which is derived using a completely different approach (*56*) but yields comparable figures for management intensity on the stand level.

Plant data

To construct plant-herbivore interaction networks for each plot, an abundance measure was used for both insects and plants, collected across several years. In grasslands, all vascular plant species were recorded and their cover estimated visually within a subplot of 4 m by 4 m on an annual basis between 2008 and 2017 (*8*). In forests, vascular plants up to 5-m height were recorded twice a year in spring and summer of the same year and their cover estimated (spring and summer records were combined, always using the higher cover value for each species) in a subplot within each plot (20 m by 20 m) on a yearly basis (2009–2014) (*42*). Larger subplots were chosen in forests to cover higher small-scale variability in plant community composition compared to grasslands. Temporal trends in grassland and forest plant community composition as recorded in annual surveys were not or only weakly directional and did not vary between different land-use intensities (figs. S22 and S23). Thus, mean cover values across years were used for subsequent statistical analyses. Because tree species composition was poorly recorded with the subplot surveys, tree species composition was characterized using data from two inventories of large trees, which were carried out on the whole plots (100 m by 100 m) during two periods (2008–2014 for the first inventory; 2014–2018 for the second inventory) (*57*), and data from an inventory of tree regeneration, which was carried out in 25 circles of 2.5-m radius on all plots (2014–2016). From these inventories, data from all trees higher than 5 m were used to estimate their cover in the tree layer. On the basis of diameter at breast height, crown projection area (CPA) was estimated for all trees with a set of allometric equations (*58*). CPA was then related to sampling area to calculate percentage cover values, which were first standardized to have a maximum value of 100% and then corrected for canopy cover recorded on each plot. The maximum cover value for each plant taxon and plot reported in the subplot survey data or plot inventory data was ultimately used for analyses.

Insect data

Insect herbivores were recorded across several years with different sampling methods for the two ecosystems. Methods were chosen to representatively sample the vegetation-associated insects in the respective ecosystem. In grasslands, insects were sampled by sweep netting twice a year (early and late summer) from 2008 to 2017. A total of 60 double sweeps with a net 30 cm in diameter were conducted along three sides of the plot borders. In forests, flight-interception traps were installed in three randomly selected corners of the plots (1.5 m above ground) in 3 years (2008, 2011, and 2014). In 2008, three additional traps per plot were installed in the outer crown area at the height of the vertical center of the canopy layer (*59*) to cover vertical differences in insect community composition. The traps were built from a crossed pair of transparent plastic shields (60 cm by 40 cm), framed by funnels opening into sampling jars at both the top and the bottom (*60*). A solution of 3% $CuSO_4$, with a drop of detergent added to reduce surface tension, was used as sampling fluid. All traps were emptied monthly between May and October, and two of the three traps in each plot and layer were randomly selected each month for further processing. All insect samples were preserved in 70% ethanol, sorted to higher taxonomic levels, and later identified to the species level by taxonomic experts (cf. Acknowledgements). Because sampling of the canopy layer in forests was only done in 1 year, these samples were only used for sensitivity analyses (see below) but were not included in the main analyses.

This study was focused on four main groups of herbivores: Coleoptera, Hemiptera: Auchenorrhyncha, Hemiptera: Heteroptera, and Orthoptera. Together, they made up 61% of all groups with herbivorous species sampled in the studied grasslands (Auchenorrhyncha, 26%; Heteroptera, 25%; Coleoptera, 7%; and Orthoptera, 2%) and 33% in the studied forests (Coleoptera, 30%; Heteroptera, 2%; Auchenorrhyncha, 1%; and Orthoptera, 0.03%). The remaining groups (Sternorrhyncha, 22% in grasslands/11% in forests; Thysanoptera, 13/27%; holometabolic larvae, 3/28%; Lepidoptera, 0.68/2%; and Hymenoptera: Symphyta, 0.1/0.02%) were rare or are difficult to identify to the species level without knowing the host plant. For forest samples, Orthoptera and Auchenorrhyncha were not identified in 2014. However, because both groups were very rare in forest samples, the missing herbivorous specimens made up only 0.02% (Orthoptera) and 0.94% (Auchenorrhyncha) of the overall sample (estimation based on the proportions of these groups in the previous year's samples), and we expect no effect on the study outcomes. Because herbivore communities tend to show strong interannual fluctuations, yearly samples might be weak representations of the long-term community established on a plot. Also, because sampling techniques were chosen to not disturb local insect communities, samples of single years tended to be very small in several plots, making the inference of networks unreliable. Thus,

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all samples were pooled per plot across the sampling years to ensure good coverage. There were some directional trends in community composition across years, which were, however, not different between land-use intensities (figs. S22 and S23). Thus, these trends potentially represent among-year fluctuations, which were not the objective of this study and were thus leveled out by the pooling approach. Also, network metrics of temporally resolved networks followed the trend of the pooled data (fig. S24). Inconsistencies found for nestedness are probably based on less reliable metric estimation at small network sizes, which further indicates that pooling of years better represents the long-term patterns prevailing in the studied ecosystems. Pooling is also consistent with the way interactions were inferred, as they are also based on pooled information from literature and do not include year-to-year fluctuations (see below).

From both grassland and forest samples, all specimens not identifiable to the genus level and all juveniles were excluded. Because species identification was not possible for female specimens in several genera (particularly, Auchenorrhyncha), genus-level specimens were assigned to species of the respective genus in a two-step procedure to prevent a bias. First, if species of that genus were found on the same plot, then specimens were assigned to those species according to their relative abundances. If no species of that genus were found on the same plot, then those specimens were assigned to the species of that genus according to relative abundances of those species in the regional species pool of the particular ecosystem (see table S1 for details on sampling numbers).

Interaction database

Data on plant cover and insect abundance were combined with a literature-based interaction database to construct networks of probable plant-herbivore interactions. Information on food plants at the lowest possible taxonomic level was extracted for all herbivore insect species encountered in our study from the relevant literature sources covering the studied insect groups for our study region (see table S4 for details). All feeding interactions with living plant tissue were considered. Wherever possible, precise information on food plant species, genera, or families was used. For species for which precise information was missing, which mainly concerned highly polyphagous species, potential food plants were restricted to polyphyletic categories such as forbs, trees, and shrubs if reported in the literature. For species that have different feeding habits as juveniles and adults, this information was collected separately for the two life stages.

Network construction

All the following analyses were run in R v.3.5.2 (*61*), and all relevant R codes are available from the repository located at https://github.com/nefff1/fcntnw. To construct interaction networks for each plot, it was assumed that feeding interactions only occurred between herbivores and plants that are known to interact from the interaction database. Interaction strength per insect species for each plant species was then determined by plant cover on the basis of the simplifying assumption that herbivore food choice is solely determined by encounter probability, i.e., there is no preference within the spectrum of possible food plants. Thus, for each plot p, an interaction matrix was constructed with interaction strength S_{ijp} between herbivore species i and plant species j defined as

$$S_{ijp} = a_{ij} \times N_{ip} \times \frac{C_{jp}}{\sum_k a_{ik} \times C_{kp}} \quad (1)$$

where a_{ij} (a_{ik}) is a value derived from the interaction database, equaling 1 for a reported interaction between species i and species j (k) and 0 for no reported interaction; N_{ip} is the total abundance of herbivore species i in plot p; and C_{jp} (C_{kp}) is the mean cover of plant species j (k). The fracture term determines the relative cover value of a plant among all plants that an herbivore species interacts with in a particular plot (indexed with k). For species with differences in food plants between the juvenile and adult stages, abundance was split evenly into a juvenile and an adult stage, and the two stages were treated as separate species in Eq. 1 and then reassembled for subsequent analyses. To address the sensitivity of our methods to certain assumptions, Eq. 1 was corrected for species differences in feeding type, accuracy of literature information, differences in metabolic rates between insects (i.e., size), and differences in biomass between plants (see the Supplementary Materials).

The same analyses were performed for networks with specific characteristics changed to test the sensitivity of our method and to get a better understanding of the processes explaining our results. First, because herbivore communities in forests are vertically structured and our main analyses only included samplings close to the ground, analyses were performed including the herbivores sampled in both vertical layers in forests. Canopy sampling was only conducted in 1 year (2008); thus, all herbivore data were restricted to this year. Also, plant community data were restricted to the year 2009, which was the closest sampling year in forests. Second, networks excluding imprecise interaction information, i.e., on interactions of species assumed to be highly polyphagous, were constructed. To this end, all interactions that were specified at taxonomic levels higher than the family level or were not specific to any taxonomic unit were excluded from the analyses (7.1 ± 2.8% of species in grasslands and 24.9 ± 7.5% of species in forests were completely excluded). Third, because of the way networks were constructed from co-occurrences, specialist herbivore species might have ended up without interacting partners and thus would not be included in the final network. This was only the case for 1.9% [3590 individuals; 2.1 ± 2.3% (means ± SD per plot)] of the total number of herbivore records in grasslands and 2.5% (1216 individuals; 2.6 ± 2.2%) in forests. Still, these herbivores might be part of the local community if their food plants occur only outside of the plant survey subplots. Thus, the impact of missing food plants was analyzed by adding all plant species recorded in any of the surveys at very low cover values to all plots to prevent the exclusion of some specialist herbivore species. From these additional interactions, only those involving herbivore species that were previously excluded from the analyses were kept in the final network. Fourth, the basic networks were converted to presence-absence networks to determine the contribution of abundance-driven processes. Results for all sensitivity analyses, which support the robustness of our findings, are reported in figs. S4 to S17.

Network metrics

For all plot-based interaction networks, the three network metrics describing network structure and robustness were calculated with the R package "bipartite" (*62*): (i) Modularity was calculated with Becket's implementation of Newman's modularity measure; (ii) nestedness was determined by using the method "weighted NODF" (except for presence-absence networks, where "NODF2" was used); and (iii) robustness was calculated following the secondary extinction curve approach (*33*). Only secondary extinctions of herbivores

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following extinctions of plants were considered. To represent the most realistic extinction scenario, the extinction order of plants was chosen to follow increasing abundance. To apply the same procedure for extinction order in the null models, plant cover values could not be used directly, and instead, plant abundance was determined by the interaction sum per plant species. To test for the effects of covariates in network structure on modularity, nestedness, and robustness, we additionally determined plant species richness, herbivore species richness, network size (i.e., number of plant species × number of herbivore species), and connectance (i.e., proportion of realized interactions out of all possible pairwise interactions) for each network.

Null models

Comparability of network metrics between different networks can be limited because of correlations with network size (i.e., number of interacting species) and network connectance (*24*). To rule out the possibility that observed patterns in modularity, nestedness, and robustness along land-use intensity gradients were solely caused by differences in species richness at both trophic levels and in network connectance, a null modeling approach was used. For both ecosystems, regional interaction pools containing all interactions observed within a region were assembled, including the strength of those interactions. This approach allowed us to keep not only species richness and connectance constant but also some global linkage patterns between herbivores and plants, such as the overall proportions of specialists and generalists. Thus, it increased the validity of the null models and yielded more realistic predictions along the land-use intensity gradients. From this interaction pool, interaction networks for all plots were randomly assembled, while keeping the number of plants, insects, and interactions the same as in the observed network for each plot. Sampling probability of interactions was thereby proportional to total standardized abundance of the herbivore species to avoid oversampling interactions of more generalist herbivore species. Nine hundred ninety-nine random draws were run for the results presented in the main text and 100 random draws for the different sensitivity analyses presented in the Supplementary Materials. The networks generated by null models were then analyzed using the same metrics and statistical models that were used to analyze the observed networks (see below).

Statistical analysis

To test the relationships among basic network metrics (network size and connectance), modularity, nestedness, and robustness, piecewise SEM (*63*) on linear mixed-effects models including region as a random factor was used. Separate models were run for the two ecosystems. Pathways were summarized to understand which structural attributes determine network robustness in grasslands and forests. Linear mixed-effects models were run with the R package "nlme" (*64*), and SEM was implemented with the package "piecewiseSEM" (*65*).

To test how network structure and robustness change along land-use intensity gradients, Bayesian hierarchical models were used, following the approach in (*66*), and results for the observed networks were compared to results of the same hierarchical models used for data generated by null models. Before analyses, all network metrics and predictor variables were standardized to have a mean of 0 and SD of 1. To make results between observed data and null-model data comparable, mean and SD of the observed data were used for all standardizations. For both ecosystems, models were run for the combined land-use intensity (LUI/ForMI) and for the separate land-use components. The hierarchical models had the form

$$\hat{y}_i = \alpha_i + \boldsymbol{l_i} \cdot \boldsymbol{\beta} \quad (2)$$

$$\alpha \sim \mathcal{N}(\mu_\alpha, \sigma_\alpha^2) \quad (3)$$

$$\beta_j \sim \mathcal{N}(0, \sigma_{\beta_j}^2) \quad (4)$$

$$y \sim \mathcal{N}(\hat{y}, \sigma_{\hat{y}}^2) \quad (5)$$

where y is the standardized network metric, α is the random intercept for the study region, and $\boldsymbol{\beta}$ is a vector that contains the fixed effect parameters β_j for the land-use variables l_j. All parameters and the response variable were assumed to be randomly distributed with different SDs σ, for which a set of weakly informative priors was used (table S5) (*66*). All hierarchical models were run in Stan through the R interface "rstan" (Markov chain Monte Carlo settings: four chains with 5500 iterations each, including 500 warm-up iterations) (*67*). In addition, the SEM used to analyze the relationships among network metrics was expanded to also include the different land-use components of the two ecosystems as additional explanatory variables. This allowed to assess how the land-use intensity gradients affect the relationships among structural network attributes and, particularly, network robustness.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/7/20/eabf3985/DC1

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Felix NeffMartin BrändleDidem Ambarl#Christian AmmerJürgen BauhusSteffen BochNorbert HölzelValentin H. KlausTill KleinebeckerDaniel PratiPeter SchallDeborah SchäferErnst-Detlef SchulzeSebastian SeiboldNadja K. SimonsWolfgang W. WeisserLoïc PellissierMartin M. Gossner

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