Grassland management intensification weakens the associations among the diversities of multiple plant and animal taxa

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Abstract. Land-use intensification is a key driver of biodiversity change. However, little is known about how it alters relationships between the diversities of different taxonomic groups, which are often correlated due to shared environmental drivers and trophic interactions. Using data from 150 grassland sites, we examined how land-use intensification (increased fertilization, higher livestock densities, and increased mowing frequency) altered correlations between the species richness of 15 plant, invertebrate, and vertebrate taxa. We found that 54% of pairwise correlations between taxonomic groups were significant and positive among all grasslands, while only one was negative. Higher land-use intensity substantially weakened these correlations (35% decrease in r and 43% fewer significant pairwise correlations at high intensity), a pattern which may emerge as a result of biodiversity declines and the breakdown of specialized relationships in these conditions. Nevertheless, some groups (Coleoptera, Heteroptera, Hymenoptera and Orthoptera) were consistently correlated with multidiversity, an aggregate measure of total biodiversity comprised of the standardized diversities of multiple taxa, at both high and low land-use intensity. The form of intensification was also important; increased fertilization and mowing frequency typically weakened plant–plant and plant–primary consumer correlations, whereas grazing intensification did not. This may reflect decreased habitat heterogeneity under mowing and fertilization and increased habitat heterogeneity under grazing. While these results urge caution in using certain taxonomic groups to monitor impacts of agricultural management on biodiversity, they also suggest that the diversities of some groups are reasonably robust indicators of total biodiversity across a range of conditions.

Key words: Biodiversity indicators; correlation; fertilization; grassland management; grazing; land-use change; land-use intensity; mowing; multidiversity; multitrophic interactions.

Introduction

Land-use change is a major driver of biodiversity loss (Sala et al. 2000), and an important component of this

change is land-use intensification (Foley et al. 2005, Flynn et al. 2009). For instance, intensification in European grasslands involves increased fertilization, higher livestock densities and increased mowing frequency (see Plate 1); this reduces the biodiversity of many plant, vertebrate, and invertebrate taxa (Hendrickx et al. 2007, Billeter et al. 2008, Allan et al. 2014). Although many previous studies have investigated the effects of land-use intensification on the abundances of particular species and the biodiversity of individual taxonomic or functional groups, there are still significant gaps in our understanding of the ecological consequences of land-use intensification. For example, little is known regarding how land-use intensity differentially affects a range of taxonomic groups and the consequences that this has for the relationships between taxa and trophic guilds (Allan et al. 2014, Weiner et al. 2014). Understanding these relationships is also of practical importance in conservation biology, as indicator taxa are commonly used to estimate wider biodiversity (Howard et al. 1998, Andelman and Fagan 2000, Schulze et al. 2004). These estimates are then often used in conservation planning (e.g., reserve selection) and in the assessment of management actions (Andelman and Fagan 2000, Schulze et al. 2004, Kessler et al. 2011). Use of inappropriate indicators could therefore lead to poor management decisions. Conversely, improved biodiversity indicators can help to ensure that management resources are allocated efficiently and effectively. An implicit assumption of this approach is that the relationships between the diversity of taxa are consistent across broad environmental gradients (e.g., Sauberer et al. 2004, Larsen et al. 2012). However, this assumption has only been tested for a limited range of taxa (Schulze et al. 2004, Beck et al. 2013, Gossner et al. 2014), and has not been investigated at all for grasslands differing in their land-use intensity.

Relationships between the biodiversities of different taxa can be generated by a range of underlying causes. In some cases they reflect ecological interdependence, such as plant–herbivore or predator–prey interactions. If taxonomic groups are trophically or functionally interdependent and interactions are specialized, then a higher diversity of one group should support a higher diversity of another group (resource specialization hypothesis; Hutchinson 1959). In contrast, where taxa are trophically diverse (e.g., a mix of secondary consumers, herbivores, and omnivores) and interactions are general, their diversity will be weakly correlated (Scherber et al. 2010, Weiner et al. 2014). Another possible cause for correlation between the diversities of different taxonomic groups is shared environmental drivers. If the diversities of different groups of organisms respond similarly to environmental factors (e.g., climate, soil fertility, or habitat heterogeneity), positive associations will emerge (Wolters et al. 2006, Qian and Ricklefs 2008).

Here, we explored associations among the diversities of 15 different taxonomic groups of plants (mostly clades), invertebrates (mostly orders), and vertebrates (birds and bats) across 150 Central European grasslands spanning a large range of land-use intensities. Previous work in these grasslands has found that land-use intensification reduced the diversity of most plant and animal taxa (Allan et al. 2014), and that declines in pollinator richness were driven by changes in the availability of the plant species visited by pollinators (Weiner et al. 2014). Here, we build upon these studies by examining the relationships between taxa more broadly and asking: (1) How the direction and strength of correlations between biodiversities differs between different pairs of taxa? (2) How land-use intensification and trophic status affect these relationships? (3) Which groups are the best indicators of the diversity of other taxa and of the overall biodiversity of the ecosystem? This was achieved by assessing the degree of correlation between the species richness of individual taxa, and between the diversity of coarse trophic groupings of taxa. We then divided grasslands into smaller groups based upon their land-use intensity and examined how land-use intensity altered these relationships. Finally, we assessed the correlation of the biodiversity of each taxa with a new metric of total ecosystem diversity, multidiversity (Allan et al. 2014).

Methods

Data

The biodiversity and land-use data used in this study were collected within the framework of the German Biodiversity Exploratories Project (Fischer et al. 2010). This project maintains 150 study plots in grasslands of different land-use intensities within three regions of Germany, the Schorfheide-Chorin (northeast), Hainich-Dün (central) and Schwäbische Alb (southwest; Appendix A: Table A1). For each region, we obtained data on the biodiversity of 15 abundant and species-rich taxonomic groups found within grasslands that are regularly surveyed in the monitoring of agroecosystem biodiversity. Data were collected using standard methods (e.g., sweep netting, transect walks, and quadrat surveys) between 2008 and 2010 (Appendix A, Table A2). The 15 taxa collected were: bryophytes, lichens, and vascular plants (Monocots, Ranunculales, Rosids, and Asterids); birds (Aves) and bats (Chiroptera); and eight orders of invertebrates (Hemiptera [sub-divided into Heteroptera and Homoptera], Lepidoptera, Hymenoptera, Orthoptera, Diptera, Coleoptera, and Araneae; Table A2). These taxa were chosen to represent all trophic levels and a large proportion of aboveground diversity. Plants were subdivided into several groups (mostly monophyletic clades) based upon the latest angiosperm phylogeny (Angiosperm Phylogeny Group 2009); this was appropriate due to their large biomass, important basal position within the ecosystem, and to prevent multidiversity measures from being dominated

by arthropod taxa. As we aimed to identify taxonomic groups that could predict the biodiversity of other groups, as well as to explore whether relationships were influenced by the nature of their trophic interactions, we used taxonomic rather than functional groups in our analysis and assigned taxa to broad trophic classes: primary producers, primary consumers (including pollinators) and secondary consumers (including predators and omnivores; Table A2). In many cases, trophic status was fully consistent within a group (e.g., bats, Araneae, and Lepidoptera are all primary producers). Where trophic status was not consistent within a group, the taxa were assigned to a trophic class based on the expert knowledge of those sampling the species (Table A2). Omnivores were classified as secondary consumers. The species and associated trophic classes sampled were often dependent on sampling method; for example, Diptera and Hymenoptera were recorded from flower visitation, which made primary consumer species far more likely to be sampled, and Coleoptera were recorded from sweep netting, which captured far fewer carnivorous species than pitfall traps (Standen 2000). In addition to single taxon measures, we also calculated a measure of total biodiversity: multidiversity. This measure is calculated as the average scaled species richness per taxonomic group, where the species richness of each group is scaled to its maximum across all plots. Therefore, taxa were weighted equally (Allan et al. 2014). An advantage of the multidiversity metric over total species richness or diversity indices is that speciose taxa (e.g., Coleoptera) do not drown the signal of species-poor groups when gaining a measure of the overall diversity of the ecosystem.

Land use in the studied grasslands comprised combinations of mowing, grazing, and fertilization at different intensities. Using questionnaires submitted annually to farmers and landowners, estimates of the intensity of each factor were obtained for each plot for the years 2006–2008 (Appendix A; Fischer et al. 2010). Fertilization intensity was quantified as the amount of nitrogen added (both organic and inorganic forms), grazing intensity as livestock density (numbers and type of grazing animals per unit area and grazing duration), and mowing intensity as the number of cuts per year (one to four). To make all plots comparable through a common land-use metric and due to high correlation between them, the three land-use factors were aggregated into a compound land-use intensity index (LUI; Blüthgen et al. 2012) that summed the three land-use components, each standardized by its mean value within each region (Appendix A). This index has been found to be a better predictor of biodiversity responses in these grasslands than its individual components (Blüthgen et al. 2012, Allan et al. 2014).

Analysis

The three regions of the study differed in their species richness. As we focused on the effect of land-use intensity on among-plot relationships, we corrected for these regional differences by fitting a linear model with region as a fixed factor to the species richness of each taxon. Residuals were then used in subsequent analyses of a matrix of Pearson correlations for all pairwise combinations of the 15 taxa. This gave a total of 105 pairwise species richness correlations. A pairwise correlation was considered significant if its 95% confidence interval excluded zero. For the matrix we calculated average and matrix-wide Pearson correlation coefficient (r) values. Additionally, we divided the matrix into six sub-matrices representing interactions between different trophic levels (plant–plant, plant–primary consumer, primary consumer–primary consumer, plant–secondary consumer, primary consumer–secondary consumer, and secondary consumer–secondary consumer), and repeated calculations for each of these.

To examine the influence of land-use intensification on correlations between the species richnesses of different taxa, we ranked all 150 plots by their LUI and divided them into two groups, the bottom 50% (mean LUI = 1.05; range 0.49–1.53) and top 50% (mean LUI = 2.15; range 1.54–3.21). For each subset of 75 plots, we calculated summary statistics as above, and quantified changes in correlation in two ways. First we assessed whether there was a significant difference between individual pairwise correlations at high and low LUI by testing for homogeneity among correlation coefficients (Sokal and Rohlf 1995). Secondly, we calculated the average difference in correlation between low and high LUI, for the entire matrix, and for the six sub-matrices described above. We then assessed the significance of these differences with permutation tests for which we created a null distribution of correlation differences by randomizing individual correlations across matrices 10 000 times and recalculated the mean difference in correlation. Differences were considered significant if they were within the top or bottom 2.5% probability tails of this distribution. We also performed analogous analyses in which the highest 50% and lowest 50% of sites were analyzed separately for the individual components of the LUI: mowing, grazing and fertilization intensity. This allowed us to compare the effects of these individual factors with overall LUI effects. It should be noted, however, that due to agricultural practices, these three factors are strongly correlated (fertilization and mowing, $r = 0.61$, $P < 0.0001$; mowing and grazing, $r = -0.46$, $P < 0.0001$; and grazing and fertilization, $r = -0.14$, $P < 0.08$). These correlations indicate that frequently mown sites are usually fertilized but are usually ungrazed; thus, the effects of each cannot be considered independently (Blüthgen et al. 2012). Additionally, we explored changes in correlation strength across the LUI gradient by dividing the sites into low (0.49–1.26), medium (1.27–1.91), and high (1.91 to 3.21) LUI classes.
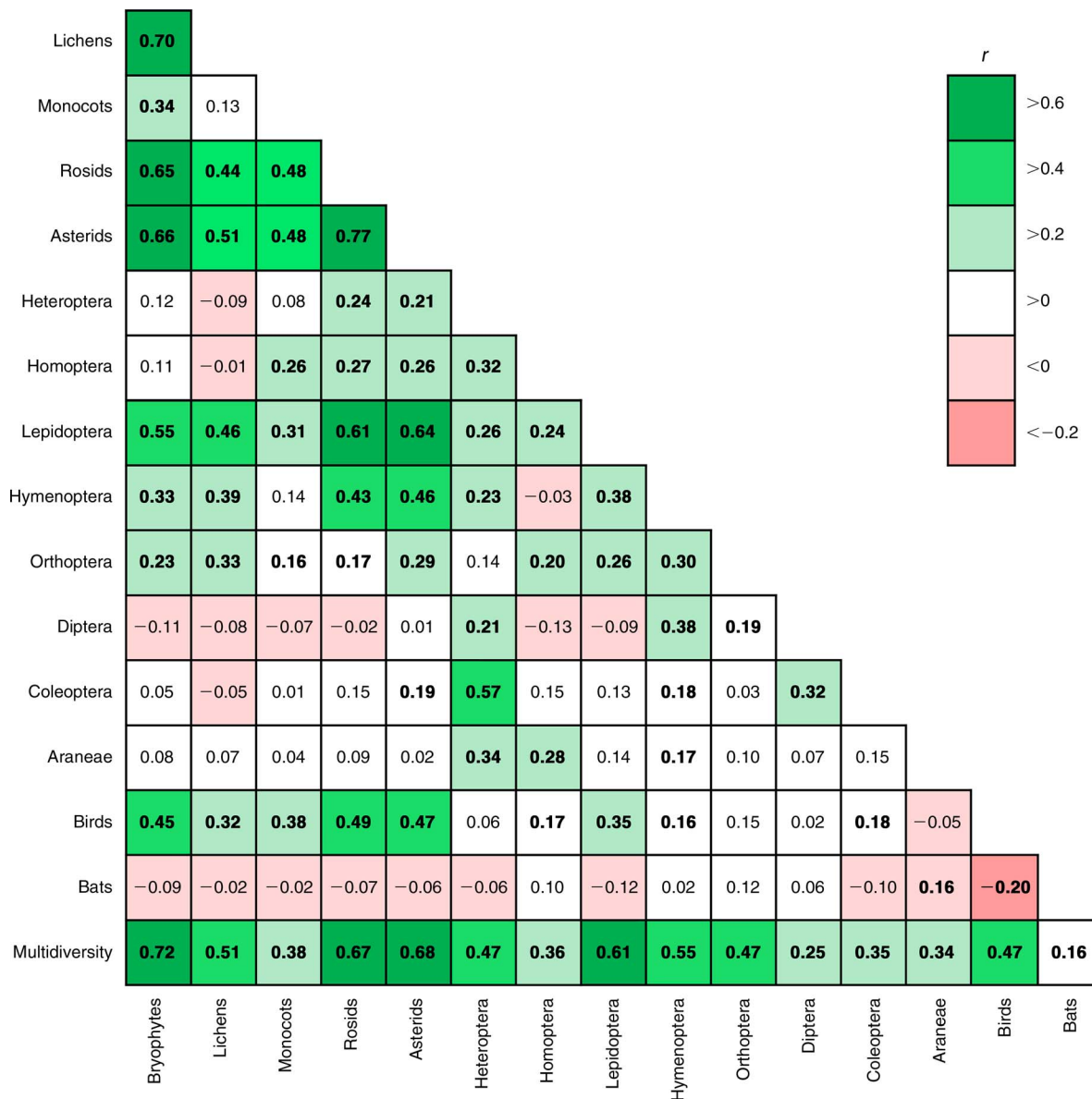
FIG. 1. Correlations between the species richnesses of 15 taxonomic groups in 150 central European grasslands. Green squares indicate positive correlations between the species richness of two taxa, and red squares indicate negative correlations between the species richness of two taxa. Significant correlation coefficients (r, $P < 0.05$) are highlighted in bold.

To identify which taxa were the best potential indicators of overall diversity, we calculated the average correlation between the diversity of each taxonomic group and all other groups and the diversity of each taxonomic group with multidiversity. We measured the consistency of these correlations across the LUI gradient by calculating the average correlation for each taxa at both high and low LUI. We also tested for the sensitivity of our analyses to correlation test and diversity metric to ensure our conclusions were robust (Appendix A). All analyses were performed in R version 3.0.2 (R Development Core Team 2013).

RESULTS

Across all 150 grassland plots, 57 of the 105 pairwise species-richness correlations among taxa were significantly positive (mean $r = 0.20$; Fig. 1, Table 1) and only one was significantly negative, the one between birds and bats ($r = -0.20$). The strongest associations were between the five plant groups, where 90% of correlations were significant and all were positive (mean $r = 0.51$). Significant positive associations were also frequent between plants and plant-feeding invertebrates (20 out of 35 correlations, mean $r = 0.20$) and common between groups of plant-feeding invertebrates, where 14 out of

Table 1. Correlations between the species richness of taxa classified into trophic groups (PP, primary producers; PC, primary consumers; and SC, secondary consumers), and differences between high and low land-use intensity (LUI) overall and by use category.

Relationship class by plot intensity	All plots		LUI overall		Fertilization		Grazing		Mowing	
	r	Corr	r	Corr	r	Corr	r	Corr	r	Corr
All relationships ($n = 105$)	0.197	57-1								
Low			0.196	45-1	0.194	46-1	0.23	57-2	0.186	43-2
High			0.128	25-0	0.143	29-0	0.164	43-4	0.123	31-1
Diff.			−0.068**	↓11 ↑1	−0.051	↓4	−0.065*	↓10 ↑1	−0.063*	↓9 ↑9
PP–PC ($n = 35$)	0.197	20-0								
Low			0.212	17-0	0.217	18-0	0.231	19-1	0.235	19-0
High			0.106	7-0	0.123	8-0	0.177	15-1	0.065	6-1
Diff.			−0.106*	↓4	−0.094*	1↓	−0.054	↓3 ↑1	−0.170***	↓2 ↑1
PP–SC ($n = 15$)	0.142	5-0								
Low			0.137	5-0	0.119	5-0	0.204	7-0	0.088	5-0
High			0.063	0-0	0.075	4-0	0.049	5-1	0.045	1-0
Diff.			−0.078	↓1	−0.044		−0.155*	↓3	−0.043	↓2
PC–SC ($n = 21$)	0.112	8-0								
Low			0.111	5-0	0.096	3-0	0.144	9-1	0.092	3-0
High			0.092	3-0	0.11	4-0	0.071	3-1	0.09	4-0
Diff.			0.019		0.014		−0.073	↓2	−0.002	
PP–PP ($n = 10$)	0.515	9-0								
Low			0.485	9-0	0.494	9-0	0.506	9-0	0.49	9-0
High			0.186	4-0	0.221	5-0	0.468	9-0	0.182	5-0
Diff.			−0.300**	↓6	−0.272**	3↓	−0.039	↓1	−0.307**	↓5
PC–PC ($n = 21$)	0.204	14-0								
Low			0.195	9-0	0.203	11-0	0.224	13-0	0.17	7-1
High			0.242	11-0	0.247	11-0	0.219	11-0	0.3	15-0
Diff.			0.047	↑1	0.045		−0.005		0.131*	↑8
SC–SC ($n = 3$)	−0.028	1-1								
Low			−0.056	0-0	−0.061	0-1	0.061	0-0	−0.119	0-1
High			−0.028	0-0	−0.044	0-0	−0.141	0-1	−0.004	0-1
Diff.			0.028		0.017		−0.202	↓1	0.115	

Notes: The average correlation coefficient (r) and the number and direction of significant ($P < 0.05$) individual correlations (Corr, positive-negative) are given for relationship classes across all plots and by plots of low or high land use intensity, by type of use. Average differences (Diff.) between high- and low-intensity plots are given; bold values indicate significant differences. Arrows show the number of relationships that significantly decrease (down arrow) and increase (up arrow) between low and high land use intensity.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

the 21 correlations were significantly positive (mean $r =$ 0.20, Fig. 1). Correlations were generally weaker between plant and secondary consumer taxa (mean $r =$ 0.11), between primary and secondary consumer groups (mean $r = 0.14$), and among secondary consumer taxa (mean $r = -0.03$).

The diversity of no single taxa was strongly correlated with the diversities of all other taxa. The strongest predictors in this respect were Asterids, Rosids, Lepidoptera, and Bryophytes (mean r of 0.29–0.34, Fig. 1). In contrast, the diversities of Diptera (mean $r = 0.05$), Araneae (mean $r = 0.12$), and bats (mean $r = -0.02$) were generally very weakly correlated with the diversities of other groups. Correlations with multidiversity were generally stronger than those between the diversities of individual taxa (mean $r = 0.46$, Fig. 1), with the strongest predictors being Asterids, Bryophytes, and Rosids ($r =$ 0.68, 0.71, and 0.67 respectively). Bats, Aranae, and Diptera were relatively poor predictors of taxa diversities (all $r < 0.35$).

When comparing plots of low vs. high LUI, we found that correlations were generally weaker at high LUI (Fig. 2). The number of significant correlations between taxa also decreased from 45 to 25 of the 105 pairwise species-richness correlations. The matrix-wide average correlation coefficient was 35% lower at high LUI (mean $r = 0.20$) than at low LUI (mean $r = 0.13$), and permutation tests indicated this change was significant ($P < 0.01$, Table 1). The correlation between the diversity of individual taxa and multidiversity was also lower at high LUI than at low LUI (mean r reduced from 0.48 to 0.36). Changes to individual pairwise correlations were significant in 12 of the 105 cases; coefficients of 11 correlations decreased, and the coefficient of only one (Diptera and Heteroptera) increased (Table 1, Fig. 2).

Strong weakening of association in response to land-use intensification occurred in plant–plant (r reduced from 0.48 to 0.19), plant–primary consumer (r reduced from 0.20 to 0.11) and plant–secondary consumer
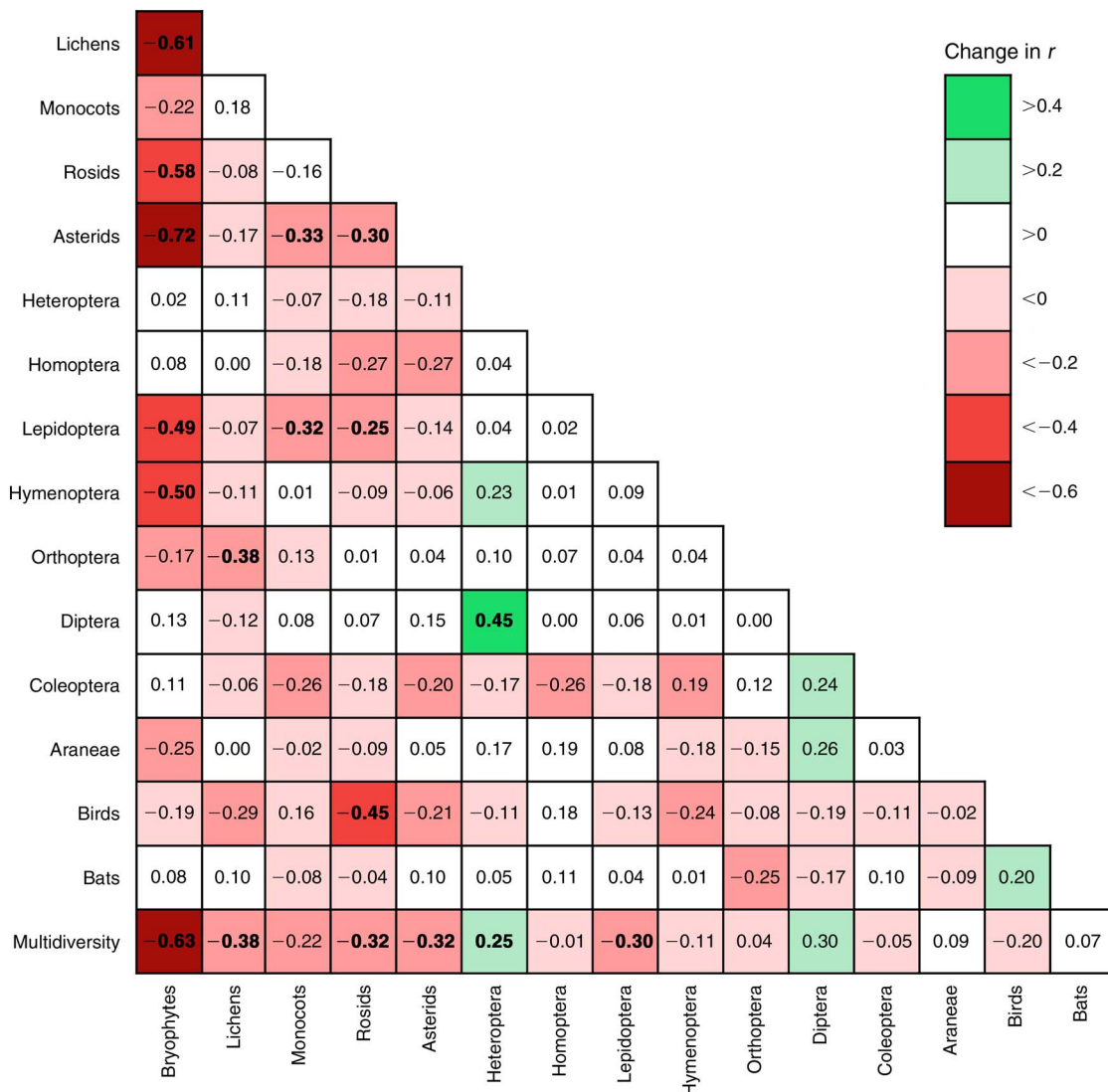
FIG. 2. Differences in the strengths of correlations (change in *r*) between the species richness of 15 taxa at low and high land-use intensity (LUI) in 150 central European grasslands. Green squares indicate increases in correlation strengths between the species richness of two taxa at high LUI, and red squares indicate decreases in correlation strengths between the species richness of two taxa at high LUI. Values in bold highlight correlation coefficients that differ significantly between high and low LUI (r, $P < 0.05$).

relationships (r reduced from 0.14 to 0.06; Table 1, Fig. 2). At high LUI, the significance of more than half of the significant correlations between plants and primary consumers disappeared, as did all significant plant–secondary consumer correlations. In contrast, diversity correlations between primary and secondary consumers remained stable (mean change in $r = 0.02$; Table 1).

The average pairwise diversity correlation between each group and all other groups was also lower at high LUI. The degree of change varied considerably between the groups (average change in r ranged from −0.26 to 0.08), and taxa whose diversity had been strongly correlated across all plots. For example, Bryophytes (reduced from mean r of 0.32 at low LUI to 0.09 at high LUI) tended to show the largest decreases in correlation

strength between low LUI and high LUI (Fig. 2). Groups that showed relatively little difference in the strength of their relationship with other taxa between high and low LUI included the Homoptera, Hymenoptera, Orthoptera, Coleoptera, and Araneae, which also showed a mean change in r of less than 0.05. The diversities of Orthoptera, Heteroptera, Coleoptera, and Hymenoptera were also strong and robust predictors of multidiversity ($r > 0.39$ for all groups at both high and low LUI).

The species richness of many taxa was lower at high LUI (Table 1) and those that declined most strongly with increasing LUI tended to be those that displayed strong correlations with the richness of other groups across the whole LUI gradient. This is demonstrated by

PLATE 1.   Increased mowing frequency is an important component of grassland management intensification in central European grasslands. Photo credit: V. H. Klaus.

a negative correlation ($r = -0.52$) between the percentage difference in richness between high and low LUI and the average correlation strength with other taxa. Observed changes in the correlations between taxa were also strongly correlated with the magnitude of difference in species richness ($r = -0.78$) and the difference in the standard deviation in richness between high and low LUI ($r = -0.62$; Table 1); this suggests that the correlation change at high LUI was also driven by biodiversity declines.

When we analyzed the effects of the individual land-use components: mowing, grazing and fertilization, instead of the composite LUI index, we found very similar overall patterns of correlation changes (Table 1). However, the individual land-use components differed in their effects on diversity correlations between particular groups: when we compared plots with low vs. high intensities of fertilization or mowing, we found strong and sometimes significant decreases of plant–plant and plant–primary consumer correlations (mean r reduced by -0.30, and 0.11 respectively). In contrast, the strength of diversity correlations hardly changed between plots of low and high grazing intensity for these groups (r reduced by 0.04 for plant–primary consumer and 0.05 for plant–plant relationships (Table 1). Also notable was that the correlation between primary consumer groups, in contrast to others, increased significantly under high mowing intensity (r ranged from 0.17 to 0.30, Table 1).

Dividing the data into three classes of LUI demonstrated that the overall decline in correlation strength between high and low land-use intensity is likely to be strongest between low and medium levels of land-use intensity (mean $r = 0.227$ at low LUI, $r = 0.130$ at medium LUI, and $r = 0.126$ at high LUI; Table A3). However, the correlation between some groups (e.g., primary producers and secondary consumers) declined most strongly between low and medium LUI (r reduction of 0.12), while others (e.g., between primary producers) declined more steadily across the LUI gradient (Table B1).

DISCUSSION

Our results not only confirm that land-use intensification reduces the biodiversity of most individual plant and animal taxonomic groups in grasslands (Allan et al. 2014), but in addition provide clear evidence that land-use intensification changes the relationships between the diversities of different taxonomic groups. Although correlations were strong in some cases, the diversities of most taxa were weakly positively correlated with each other. This pattern is consistent with previous studies where similarly moderate levels of correlation have been observed across a wide range of ecosystems and spatial scales (Howard et al. 1998, Schulze et al. 2004, Wolters et al. 2006, Kessler et al. 2011, Beck et al. 2013).

While most correlations were relatively weak, there were consistent patterns in their strength with the

strongest associations observed between plant groups and between plants and primary consumers. It is likely that these associations result from a combination of shared environmental drivers and ecological interactions. Associations between plant groups are likely to be primarily driven by shared environmental drivers, as land-use intensity has similar effects on all of the plant groups studied here (Allan et al. 2014); other environmental drivers such as soil conditions, along with regional processes such as dispersal limitation, can also affect different plant clades in similar ways (Löbel et al. 2006). In contrast, close associations between plant and primary consumer diversity (e.g., Haddad et al. 2009, Scherber et al. 2010) are more likely to be driven by trophic interactions, with stronger associations occurring between taxa with more specialized interactions (Hutchinson 1959). This is exemplified by a detailed analysis of plant–pollinator interactions in the same grasslands studied here (Weiner et al. 2014), in which pollinator species abundance was explained by the availability of plant species used as food. Furthermore, the strongest plant–invertebrate diversity correlations in our data were between higher plants and butterflies, which are tightly linked through host–plant specialization (Ehrlich and Raven 1964, Pellisier 2013). Our results are also consistent with patterns observed in fertilized grasslands, where plant diversity losses appeared to have stronger effects on the richness of herbivores than on that of higher trophic levels (Hurd and Wolf 1974).

Strong associations between primary consumer taxa may be explained by a common response to shared trophic drivers, and the abundance and diversity of plant resources (Hutchinson 1959). Stronger correlations between plants and primary consumers than between plants and secondary consumers also suggest that interactions between groups are responsible for the patterns observed, and not simply shared direct responses to drivers such as land-use intensity. The weak relationship between plants and secondary consumers is likely to reflect trophic distance, i.e., a lack of direct interaction (Scherber et al. 2010), while the weak correlation between primary consumer and secondary consumer diversities may reflect greater generalism in the feeding habits of secondary consumers than in herbivores. The groups that showed the weakest correlations with the diversity of other taxa also tended to be those typified by generalist feeding habits: bats, Diptera, and Araneae. Weak correlations between secondary consumers and other taxa may also result from their greater mobility and larger range size, such that their diversity may be driven by landscape factors rather than local factors, e.g., the abundance of semi-natural habitat in the wider landscape (Billeter et al. 2008).

Another important and consistent finding of this study was that diversity correlations were weaker and less significant at high land-use intensity (Fig. 2, Table 1). The loss of specialists under intensive management may largely explain this pattern. Several studies have shown that rare and specialist species decline most strongly with increasing land-use intensity in agro-ecosystems (Filippi-Codaccioni et al. 2010, Allan et al. 2014), that butterfly communities contain fewer specialist species at high land-use intensity (Börschig et al. 2013), and that specialist pollinators become less abundant at high land-use intensity (Weiner et al. 2014). These results indicate that many rare and vulnerable species exhibit specialization in both biotic interactions and habitat requirements, and that high management intensity creates a homogenized environment where only common specialists (e.g., the herbivores of dominant nitrophilous plants) and a few generalist species are found. Contrasting responses of different groups to more intensive management may further contribute to weakened diversity associations under more intense land use. A third potential and more statistical explanation could be that the diversity of most taxa is lower at high land-use intensity (Allan et al. 2014). This would imply that variation in species richness may also be lower, thus creating a shorter diversity gradient at high land-use intensity. Variation in species richness was lower at high land-use intensity for some taxa (Table A2). Moreover, changes in diversity and its variation (as measured by the standard deviation in species richness) were also related to observed changes in correlation strengths between low and high land-use intensity. This suggests that lower diversity and variation in diversity at high management intensity can also explain some of the weakening of associations at higher land-use intensity. We therefore conclude that weaker biodiversity correlations under more intensive management are likely to be driven by several mechanisms: declines in diversity, increases in the proportion of generalist species, and diverging responses to land-use intensity. Further studies should address this hypothesis and assess the relative importance of shared environmental drivers and biotic interactions in shaping the observed levels of association, e.g., by seeing whether species co-occurrence patterns are best explained by environmental factors or the functional traits of interacting organisms. This mechanistic understanding could help improve management strategies that aim to conserve biodiversity within farmed landscapes and the efficiency of schemes that monitor this biodiversity.

Intensification of fertilization and mowing reduced the association between the diversities of both plant–plant and plant–primary consumer taxa. In contrast, grazing intensification, which tended to occur on sites that were not mown, had little effect on associations between the diversities of taxa. Grazing, via trampling, selective browsing, and livestock droppings, may increase grassland habitat heterogeneity and create diverse niches for both plants and invertebrates (Dennis et al. 1998, Bakker et al. 2003). In contrast, the combination

of mowing and fertilization typically seen in these grasslands tends to homogenize grassland habitats, thus selecting for generalists and species that specialize in this narrow range of conditions. Fertilization is well known to reduce plant species richness, while increasing community productivity (Suding et al. 2005). This reduction in species richness may have an impact on specialized herbivores, as has been seen in diversity experiments (Haddad et al. 2009, Scherber et al. 2010). However, productivity gains in structural complexity and productivity may increase invertebrate species richness and the net effect of fertilization of the species richness on higher trophic levels can be both positive and negative (Sedlacek et al. 1988, Haddad et al. 2000). In our grasslands, fertilization is strongly correlated with higher mowing frequencies; this disturbance and removal of additional biomass results in a negative overall effect on the diversity of both plant and primary consumer taxa. This result is consistent with previous findings showing that increased mowing frequency and fertilization rates are more detrimental for biodiversity than increased grazing intensity (Ausden 2007, Socher et al. 2012).

In addition to indicating fundamental changes to ecosystem structure, the breakdown of associations between the richness of taxonomic groups at high land-use intensity also raises concerns about the general utility of some indicator taxa in biodiversity monitoring. Our results show that the relationships between taxa depend on the environmental context and that candidate indicators should be validated across a wide range of conditions (Gossner et al. 2014). Single taxon correlations suggest that some commonly used indicator groups, e.g., birds and Lepidoptera, (e.g., Sauberer et al. 2004, Schulze et al. 2004, Kessler et al. 2011, Larsen et al. 2012), are not good indicators of multidiversity at high land-use intensity. Plant diversity (e.g., of Rosids and Asterids) was also only a good biodiversity indicator at low land-use intensity. At high land-use intensity, associations between plant diversities and those of other taxa and multidiversity were greatly weakened. The most robust multidiversity indicators in terms of land use were Heteroptera, Orthoptera, Coleoptera and Hymenoptera. This concurs with an investigation of several taxa within an agricultural landscape, which had lower replication and a smaller geographical extent, but also found the best predictors of total species numbers to be Heteroptera, Coleoptera and Hymenoptera (Duelli and Obrist 1998). While some taxa were reasonable predictors of multidiversity, our results show that no single group is correlated strongly with all taxa, thus supporting recent suggestions that low-intensity sampling of a carefully selected subset of taxa may be the most accurate and cost-effective means of predicting overall biodiversity (Kessler et al. 2011, Larsen et al. 2012).

In conclusion, our study demonstrates that land-use intensification not only affects the biodiversity of individual plant and animal taxa, but also the relationships between the diversities of these taxa. This finding indicates that overall ecosystem structure may differ at high land-use intensity and implies a cautionary message for the biodiversity monitoring community by revealing that using some indicator groups can give misleading results about the effects of management practices on overall biodiversity. Future users of biodiversity indicators should acknowledge that some widely used indicator groups may be poor indicators of total biodiversity at high land-use intensity, and that more robust indicators are required when surveying sites that cover a wide range of land-use intensities.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: http://dx.doi.org/10.1890/14-1307.1.sm