Cross-scale effects of land use on the functional composition of herbivorous insect communities

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Abstract

Context Insect herbivores comprise the majority of macroinvertebrate communities of temperate grasslands and act as drivers for important ecosystem functions. Landscape- and local-level land use may alter species pools and dispersal possibilities and act as local environmental filters, affecting insect trait composition.

Objectives While environmental filtering by local land use has repeatedly been shown to affect insect community assembly, less is known about the role of land-use intensity at the landscape level. We studied the relative importance of both local- and landscape-level land use in shaping the functional diversity and composition as well as the functional β-diversity among herbivore communities.

Methods We used abundance data of three main herbivorous insect groups from grasslands across three regions in Germany and combined it with data on nine morphometric traits related to functions such as dispersal abilities to analyse the effects of different land-use components on community assembly.

Results Land use at both the local and landscape level affected the functional composition of insect

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communities. Some trait combinations were particularly sensitive to changes in management intensity, whereas others reacted strongly to the availability of suitable habitats in the surrounding area. Simultaneously, functional diversity was not affected by land use at either spatial level. However, increasing local management intensity reduced functional β-diversity. *Conclusions* We conclude that both local- and landscape-level land use shape the functional composition of insect communities. Our results highlight the importance of considering land use across multiple spatial scales to understand its effects on the functional integrity of herbivore communities in temperate grasslands.

Introduction

Biodiversity has been declining at an alarming rate in the recent past and is expected to decline further in the coming century (Pereira et al. 2010). The reasons for this ongoing loss of biodiversity are manifold, however land-use change and intensification have been identified as main drivers (Sala et al. 2000). While land-use change comprises of more obvious processes, such as the conversion of forests into agricultural land, effects of land-use intensification might be less obvious, however they are not less prevalent. Semi-natural grasslands cover a large proportion of terrestrial ecosystems in the temperate zone and are subjected to increasing land-use intensity, such as higher nutrient input and mowing intensities (e.g. Temme and Verburg 2011). They harbour a great diversity of insects, which have been shown in several studies to diminish as a result of land-use intensification (e.g. Di Giulio et al. 2001).

Land-use intensification takes place at different spatial levels and thus affects community assembly processes differently. These processes can be categorised into deterministic processes such as environmental filtering and competitive sorting, as well as stochastic processes such as ecological drift (Weiher et al. 2011). In grasslands, local-level management practices such as mowing, fertilization and grazing

have been shown to act as important environmental filters, changing the functional composition of arthropod communities (Rader et al. 2014; Birkhofer et al. 2017; Mangels et al. 2017) Grassland management consists of disturbances, which filter for traits related to disturbance tolerance (e.g. jumping ability) (Mouillot et al. 2013); and alterations of habitat and microclimatic conditions, which affect traits related to habitat preference (e.g. body shape) as well as feeding (e.g. mouthpart constitution) (Ibanez et al. 2013). While many studies have addressed the effects of local management on functional aspects of grassland communities, much less is known about the role of land use at the landscape level in shaping community assembly (Tscharntke et al. 2012; but see Gámez-Virués et al. 2015). Previous studies indicate the importance of landscape-level processes in shaping the trait composition of grassland insect communities (Gámez-Virués et al. 2015; Perović et al. 2015; Papanikolaou et al. 2017). Land use at the landscape level can be characterized by management intensity and landscape composition (i.e. the amount of suitable habitat, or habitat diversity), which can all act as filters shaping the landscape species pool (cf. Tscharntke et al. 2012). Additionally, landscape composition might affect dispersal in the landscape; with more suitable and less diverse and thus less fragmented landscapes enabling more grassland species with restricted dispersal abilities to arrive at local sites and persist in the landscape. Apart from knowing the effects of individual components of landscape-level land-use intensity, it is also important to estimate its relative contribution compared to local-level processes, and thus its potential to compensate local land-use intensification.

By taking a functional perspective and investigating the trait-based community composition, we gain a better understanding of the effects of human drivers such as land-use intensification on community assembly (Lavorel and Garnier 2002). Strong filtering would result in trait convergence within a community towards land-use adapted characteristics, which can be counteracted by competitive species sorting at small spatial scales (Weiher et al. 2011). However, responses to land-use intensification are not solely defined by single traits, but may be determined by a combination of traits. Species which occupy similar positions in multidimensional functional space can be similarly affected by environmental filters (Mouillot

et al. 2013), either as a result of multiple traits determining the response to such filters or because environmental filters can comprise of several different aspects, which select for different traits. Additionally, different traits might be linked by trade-offs or phylogenetic linkage. This should allow the identification of trait syndromes, i.e. sets of traits, which react similarly to environmental filters.

In addition to imposing filters and changing dispersal in the landscape, anthropogenic influences can also reduce the influence of neutral processes such as ecological drift by reducing the size of species pools and changing their abundance distribution. In combination, those processes would result in more similar communities (Mori et al. 2018). Thus, we would expect to find biotic homogenization of communities with increasing land-use intensity. Gossner et al. (2016) showed homogenization among grassland communities of high local land-use intensity. While their study was based on taxonomic data, it remains unclear how land-use intensity affects functional β-diversity, i.e. the functional dissimilarity among communities (Ricotta and Burrascano 2008). Functional diversity measures may, however, be better predictors for the functional consequences of land-use intensification than taxonomic measures (Laureto et al. 2015). Furthermore, nothing is known about the effect of landscape-level land use on functional β-diversity, which may be driven by altered dispersal in the landscape. Investigating how land use at both the local and landscape level affects functional β-diversity is therefore crucial to improve our understanding of how land-use affects the community assembly of grassland insects.

In this study we focus on herbivorous insect groups, which are at the base of many terrestrial food webs and have an essential role in the cycling of energy and nutrients in terrestrial ecosystems. We focus on three taxonomic groups (Auchenorrhyncha, Heteroptera, Orthoptera), which comprise a large portion of the total aboveground insect herbivore community. Such multi-taxa approaches are important for the generalization of community responses to drivers such as land-use intensification (Aubin et al. 2013). Trait-based studies of insects normally use literature-based data, which has two caveats. First, such data is usually discrete, resulting in a loss of information compared with traits measured on continuous scales (McGill et al. 2006). Secondly, literature-based traits are often derived from the observation of natural communities under certain environmental conditions (e.g. micro-habitat use). However, such 'traits' reflect an outcome of the interplay between a set of (measurable) traits and the abiotic and biotic environment (Violle et al. 2007), and thus are not ideal for analysing the effects of abiotic environmental filters on functional community composition. In this study, we used morphometric measurements, which are continuous measures of traits taken directly from individual specimens. We used traits potentially involved in species responses to land-use pressures. To reflect the multiple aspects of land use, we included traits related to dispersal (e.g. wing length), disturbance tolerance (e.g. jumping ability), microhabitat use (e.g. eye width) and resource acquisition (e.g. constitution of mouth parts) and consumption (e.g. body volume). Using nine morphometric traits we tested the influence of different land-use intensity components (management intensity, habitat suitability and diversity) across two spatial levels (local and landscape level) on the functional composition and diversity of herbivores. With this approach, we aimed to investigate the following questions:

(1) How does land-use intensity at both the local and landscape level affect community assembly in terms of changes in the functional composition (i.e. mean trait values) and diversity of herbivore communities?

(2) Is there evidence of trait syndromes, which describe species that react similarly to land-use intensity?

(3) How does land-use intensity affect functional β-diversity among communities?

(4) Do functional responses at local and landscape level differ between taxa?

Materials and methods

Study system

This study was conducted within the framework of the Biodiversity Exploratories project (Fischer et al. 2010), which is a long-term, large-scale project covering three regions in Germany: The UNESCO Biosphere Reserve Schwäbische Alb in south-western Germany (48°20′28″–48°32′02″N, 9°10′49″–

09°35′54″E), the National Park Hainich and its surroundings in central Germany (50°56′14″–51°22′43″N, 10°10′24″–10°46′45″E) and the UNESCO Biosphere Reserve Schorfheide-Chorin in north-eastern Germany (52°47′25″–53°13′26″N, 13°23′27″–14°08′53″E). The three regions differ in many aspects such as their climate, geology and land-use history and thus are suitable for testing the generalizability of observed patterns. In each of these regions, 50 experimental plots, each 50×50 m^2, were selected by stratified random sampling from a total of 500 candidate plots in managed grasslands, on which initial vegetation, soil and land-use surveys had been conducted. This ensured that the plots covered the regional gradient of local land-use intensity, under comparable site conditions. Details on plot selection are given by Fischer et al. (2010).

Land-use variables

Local management practices were recorded for each plot on a yearly basis from 2006 to 2016 with standardized questionnaires (Fischer et al. 2010). Intensity values for each management component (mowing, fertilization and grazing) were averaged across years, thus representing long-term conditions shaping the local communities, and standardized relative to the means over all three regions. To calculate the combined local management intensity index (hereafter *local management intensity*), the sum of the standardized intensity values for each of the three components was square root transformed (see Blüthgen et al. 2012 for details).

To assess the effects of land use at landscape level, eight land-use types were mapped using data from field campaigns and aerial photographs from 2008 and 2009, covering an area of 2000 m radius around each plot (see Steckel et al. 2014 for details). The following land-use types were identified: arable land, grasslands, semi-natural habitats, woodlands, forests, roads, settlements and water bodies. Landscape metrics characterizing the land use around the plots were calculated for five radii (250 m, 500 m, 1000 m, 1500 m and 2000 m). Based on the percentage cover of these land-use types, we calculated Shannon's diversity index for each plot and radius as a representation of habitat diversity in the plot surroundings (hereafter *landscape diversity*) using the package 'vegan' (Oksanen et al. 2018) in R 3.4.4 (R Core

Team 2018). Additionally, we used the sum of the percentage cover of grassland (including intensively managed grassland) and semi-natural habitat (including extensively managed grassland) as an indicator for the suitability of the surrounding habitats (hereafter *landscape suitability*) and the proportion of grasslands (i.e. intensively managed grasslands) therein as an indicator for landscape-level management intensity (hereafter *landscape management intensity*). All landscape metrics were standardized relative to the means over all three regions.

Insect sampling

Three main groups of herbivorous insects in temperate grasslands were assessed in this study: Hemiptera: Auchenorrhyncha, Hemiptera: Heteroptera, and Orthoptera. Collectively, these cover 56% of all herbivorous insects (Auchenorrhyncha 28%, Heteroptera 26%, Orthoptera 2%) encountered in our study. Of the remaining groups (Sternorrhyncha 22%, Thysanoptera 13%, Coleoptera 6%, holometabolic larvae 3%, Hymenoptera: Symphyta 0.1%; data based on sweep netting samples), the two most abundant groups can hardly be identified to species level without knowing their host plants.

We used two sampling types on all 150 plots to account for differences in method suitability for the different insect groups. On the one hand, insects were sampled by sweep netting through the vegetation twice a year, in early summer (June/July) and in late summer (August/September), on a yearly basis between 2008 and 2016. On the other hand, a biocenometer approach was used. In August 2014 (Orthoptera) and during July and August 2015 (Auchenorrhyncha, Heteroptera), insects were collected from 1×1 m^2 squares randomly placed on the plots. In contrast to sweep netting, the biocenometer approach also collects insect species living on the ground (e.g. species feeding at the base of the plants) and not only species living in the herb layer (for more details on sampling procedures, see Online Resource 1). Specimens were then identified to species level by taxonomic experts (cf. Acknowledgements).

Previous work has shown that biocenometer sampling with vacuuming is better for sampling Auchenorrhyncha (Holzinger et al. 2003; Brook et al. 2008) and Orthoptera (Gardiner and Hill 2006) in comparison to sweep netting. For Heteroptera, vacuuming

does not perform better than sweep netting (Brook et al. 2008). Thus, the main focus of the analyses is laid on biocenometer data for Auchenorrhyncha and Orthoptera, while sweep netting data is used for Heteroptera (better coverage across years). All additional results based on the other sampling types are reported in Online Resource 2.

For all analyses, we excluded juveniles, species which only occurred up to two times in a data set and specimens not identifiable to species level (Heteroptera, Orthoptera) or genus level (Auchenorrhyncha) (Table S1). In Auchenorrhyncha, identification to species level is not possible for female specimen in several genera. To prevent a bias, genus-level specimens were assigned to the species of the genus that were found on particular plots according to their relative abundances in these locations. If no species of this genus was found on a plot, the genus-level specimens were kept in the data set with genus-level allocation.

Morphometric trait measurements

Morphometric measurements were performed on specimens of all species including at least one female and one male per species. Additionally, specimens with different wing development morphs were measured in both sexes for species known to have frequent wing dimorphism, adding to 923 specimens measured in total (3.27 ± 1.75 specimens per species). Based on these measurements, we calculated nine morphometric traits, which cover different functions: body volume (1), which is related to dispersal ability, microhabitat use, disturbance tolerance and resource consumption (e.g. Peters 1983; Fountain-Jones et al. 2015); wing length (2), which is related to dispersal and disturbance avoidance (e.g. Rose 1972); leg length (3), which is related to dispersal and microhabitat use (e.g. Kaspari and Weiser 1999); hind femur shape (4), which is a good indicator for jumping ability and thus disturbance avoidance in Orthoptera (Chapman 2013) and Heteroptera (Schuh and Slater 1995); hind/front leg ratio (5), which is a better indicator for jumping ability in Auchenorrhyncha (Burrows and Sutton 2008); body shape (6), which is associated with microhabitat use (e.g. Barton et al. 2011); antenna length (7) and eye width (8), which indicate the relative importance of tactile and visual orientation, indicating microhabitat use (e.g. Bauer and Kredler

1993); rostrum length (9a) for sucking insects (Auchenorrhyncha, Heteroptera) as a proxy for penetration depth and thus food resource use; mandibular incisive strength (9b) for Orthoptera, which determines the strength of the biting mouthparts and thus defines available food resources (Ibanez et al. 2013). Traits that are related to body size were scaled relative to body length. From these measurements species averages were determined for all nine traits weighting the two sexes equally. Details on trait calculations and species averaging are given in Online Resource 1. Body volume was log-transformed prior to analysis.

Statistical analyses

All analyses were performed in R 3.4.4 (R Core Team 2018). Separate analyses were conducted for each group (Auchenorrhyncha, Heteroptera, Orthoptera) and both sampling types (biocenometer, sweep netting).

Functional composition and diversity

For all morphometric traits, we calculated community-weighted means (CWMs), which indicate changes in the functional composition of a community, potentially driven by environmental filtering of certain trait values and species sorting within the community. If environmental filtering not just shifts the available trait space but actually excludes species with particular traits, it is expected to be accompanied by a reduction in functional diversity, whereas species sorting should increase functional diversity. Based on the nine morphometric traits, we determined Rao's quadratic entropy as a measure of functional diversity (FD), which enables the detection of environmental filtering and also species sorting (Botta-Dukát 2005; Botta-Dukát and Czúcz 2016). Both CWMs and FD were calculated with the package 'FD' (Laliberté et al. 2014). As FD is not independent from species richness, results should be compared to null expectations to allow the detection of environmental filtering (FD lower than expected) and species sorting (FD higher than expected) (Petchey et al. 2007). Thus, we used a null model approach. The complete trait matrix was permuted by randomly swapping species names (Botta-Dukát and Czúcz 2016). Rao's quadratic entropy was calculated for 9999 permutations and standardized effect sizes for each plot (FD_{SES}) were

determined by dividing the difference between observed FD and mean FD of the permutated matrices by the standard deviation of the permutated FD values (Gotelli and McCabe 2002). Communities which only contained one species (biocenometer: 22 Heteroptera communities (17.6%), 23 Orthoptera communities (17.6%); sweep netting: 11 Orthoptera communities (7.6%)) were excluded from the null models. In order to interpret the differences between FD and FD_{SES}, we also analysed species richness (SR) and the Shannon diversity index (SD). SD was calculated using the package 'vegan' (Oksanen et al. 2018).

CWMs, SR, SD, FD and FD_{SES} were analysed with linear mixed effects models with local management intensity, landscape management intensity, landscape suitability and landscape diversity as explanatory variables. Based on a multi-model inference approach (Burnham and Anderson 2004), landscape metrics calculated from a radius of 2000 m around plots were used in all analyses (see Online Resource 1 for details). To identify the drivers of local management intensity, additional models were run with the components mowing, fertilization and grazing separate, rather than as a combined index. All response variables and fixed factors were scaled to a mean of 0 and a standard deviation of 1 prior to analysis. Models included region as random factor, a random slope with respect to region for each fixed factor and spatial autocorrelation for residuals. Models were run with the package 'nlme' (Pinheiro et al. 2017). Details on the models are given in Online Resource 1.

Trait syndromes

To identify sets of species sharing similar traits, which react similarly to land use (trait syndromes), we used RLQ analysis (Dolédec et al. 1996). We included local management intensity, landscape management intensity, landscape suitability and landscape diversity as environmental variables and the nine morphometric traits as trait variables. The abundance matrix was Hellinger transformed prior to analysis, which is recommended for ordination of abundance data (Legendre and Gallagher 2001). RLQ analysis was performed with the package 'ade4' (Dray et al. 2018). Based on ordination axes 1 and 2, we identified species clusters using Euclidean distances and Ward's hierarchical clustering. We restricted the analysis to three resulting clusters to improve comparability

among groups. Subsequently, we calculated correlation ratios between trait dispersion within clusters and trait dispersion within the whole community as a measure of the strength of relationships between clusters and traits. Both clustering and correlation ratios were implemented following Kleyer et al. (2012).

Functional β-diversity

To test for functional homogenization among the communities as a result of increasing land-use intensity at both the local and landscape level, we analysed functional dissimilarity among plots, which was calculated based on the trait probability density framework (Carmona et al. 2016), using a generalised dissimilarity modelling (GDM) approach (Ferrier et al. 2007). As an extension of matrix regression, GDM allows the incorporation of several explanatory variables whilst simultaneously allowing for nonlinearity in the effect of environmental distances on community dissimilarity. We used local management intensity, the three landscape-level variables and geographic distances between plots as explanatory variables. The effect of each explanatory variable can then be plotted over its range, leaving all other variables constant to identify effect size (absolute height of the curve) and nonlinearity of the effect (shape of the curve). However, GDM results only contain information on effect sizes but not the direction of effects. Thus, we additionally used linear models to analyse the direction of the effects. Details on the analyses of functional β-diversity are given in Online Resource 1.

Results

Analyses of biocenometer data were based on 30,232 Auchenorrhyncha individuals from 98 species (plot average: 211.4 ± 18.2 individuals; 13.10 ± 0.32 species), 1721 Heteroptera individuals from 59 species (13.8 ± 1.8; 4.66 ± 0.29) and 2021 Orthoptera individuals from 21 species (15.4 ± 1.4; 2.88 ± 0.13). Sweep netting data comprised a total of 99,456 Auchenorrhyncha individuals from 113 species (672.0 ± 46.8; 20.98 ± 0.42), 40,611 Heteroptera individuals from 126 species (274.4 ± 16.3;

19.97 ± 0.47 species) and 2694 Orthoptera individuals from 18 species (18.47 ± 1.3; 3.51 ± 0.14).

Functional composition and diversity

Local management intensity strongly affected the CWM of several functional traits in all groups and landscape-level land-use components had equally strong effects for Auchenorrhyncha (Fig. 1, Fig. S1). High local management intensity showed a reduction in mean body volume (Auchenorrhyncha, Heteroptera) and favoured thinner body shapes (Orthoptera), longer wings (Auchenorrhyncha, Heteroptera), thinner and longer hind femora (Heteroptera), longer antennae (Auchenorrhyncha) and larger eyes (Orthoptera). Effects of local management intensity on CWMs were mainly driven by mowing and to a lesser degree by grazing intensity (Fig. S2). Auchenorrhyncha were found to have: thinner hind femora and longer hind legs with increasing landscape management intensity; smaller bodies, longer wings and legs, relatively shorter hind legs and thicker bodies with decreasing landscape suitability; and smaller bodies, shorter hind legs and longer rostra with decreasing landscape diversity. Significant effects of landscape-level land-use components were rarely identified for the two other groups.

High local management intensity and landscape management intensity equally showed a strong reduction in SR (Fig. 2, Fig. S3). For Orthoptera, this was also followed by a reduction of SD. FD was not associated with land use at the local or at the landscape level. Similarly, for FD$_{SES}$, no consistent effects of land-use intensity were found. When dividing local management into its separate components, mowing and to a lesser degree grazing were most strongly related to low SR and partly to low SD, however no consistent effects on FD or FD$_{SES}$ were observed (Fig. S4).

Trait syndromes

RLQ analysis revealed two mostly orthogonal environmental axes for Auchenorrhyncha and Heteroptera, which were driving differences in trait combinations within the groups (Fig. 3, Figs S5 and S6). The first was a management axis comprised of local and landscape management intensity, the second was a composition axis comprised of landscape suitability

and diversity (the latter only for Auchenorrhyncha). For Auchenorrhyncha, higher management intensity was associated with longer wings and thinner hind femora (cluster C), whereas less suitable and less diverse landscapes were associated with shorter hind legs, thicker bodies, larger eyes and longer rostra (cluster A). Species associated with low management and high landscape suitability and diversity were characterized by larger bodies, shorter wings, shorter legs and shorter antennae (cluster B). For Heteroptera, high management intensity was associated with species having longer wings, longer legs and relatively longer hind legs (cluster C). High landscape suitability was related to thinner hind femora, thinner bodies and shorter rostra (cluster B), whereas a combination of low management intensity and low suitability favoured short legs and antennae, thinner bodies and longer rostra (cluster A). For Orthoptera, results were ambiguous due to the small number of species (Fig. S7).

Functional β-diversity

GDM showed strong effects of both local and landscape variables on functional dissimilarity among communities (Fig. 4, Figs S8 and S9). Increasing local management intensity significantly reduced functional β-diversity in all groups. This association was non-linear, with functional β-diversity decreasing strongly at low management intensity. In contrast, increasing landscape management intensity was related to higher functional β-diversity with the main changes occurring at high intensity levels. This relationship was however generally weaker. In addition to local management intensity, landscape suitability strongly affected functional β-diversity in all three groups. Both the shape and direction of this association varied amongst groups and even within groups among sampling types. For Heteroptera (sweep netting) and Auchenorrhyncha (biocenometer), we found a negative effect of increasing landscape suitability on functional β-diversity, which only occurred at low suitability levels (saturating curves). Nonetheless, for the other groups and sampling types, we found positive effects of increasing landscape suitability, which were most pronounced at high suitability levels (exponential curves). No strong effects were found for landscape diversity.
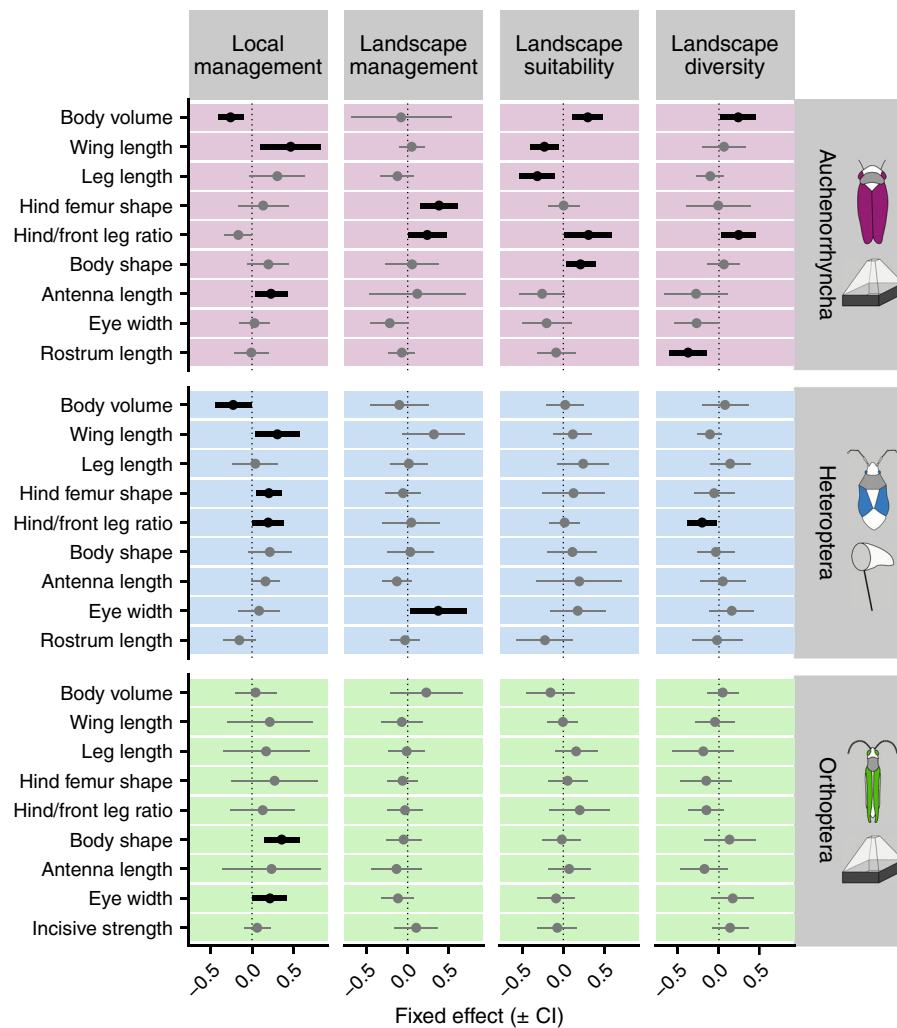
Fig. 1 Model coefficients with confidence intervals of fixed effects from linear mixed effects models testing for local- and landscape-level land-use intensity effects on trait community weighted means. Significant effects are indicated in bold and black, non-significant effects are grey. Auchenorrhyncha and Orthoptera data originate from biocenometer sampling and Heteroptera data from sweep netting

Discussion

We found that the community assembly of herbivorous insects in temperate grasslands was strongly affected by land use both at the local and landscape level, indicated by shifts in CWMs of various traits. Increasing local management intensity filtered for higher disturbance tolerance (longer wings, smaller bodies) in Auchenorrhyncha and Heteroptera. In Orthoptera, only traits related to microhabitat use (e.g. body shape) were affected by local management intensity. At the landscape level auchenorrhynchan communities in particular responded strongly, with

traits related to microhabitat use being most responsive, indicating substantial landscape-level environmental filtering. This filtering resulted in well-defined trait syndromes of species reacting similarly to land use for Auchenorrhyncha and Heteroptera. However, although SR was lower under high local management intensity and landscape management intensity, this did not result in a reduction in FD, which was not related to land-use intensity at either scale. Functional β-diversity was strongly reduced with increasing local management intensity across all groups indicating functional homogenization, which was strongest at low levels of local management intensity. Similarly,

Fig. 2 Model coefficients with confidence intervals of fixed effects from linear mixed effects models testing for local- and landscape-level land-use intensity effects on species richness (SR), species Shannon diversity (SD), functional diversity (FD) and null model effect sizes for functional diversity (FD$_{SES}$). Significant effects are indicated in bold and black, non-significant effects are grey. Auchenorrhyncha and Orthoptera data originate from biocenometer sampling and Heteroptera data from sweep netting
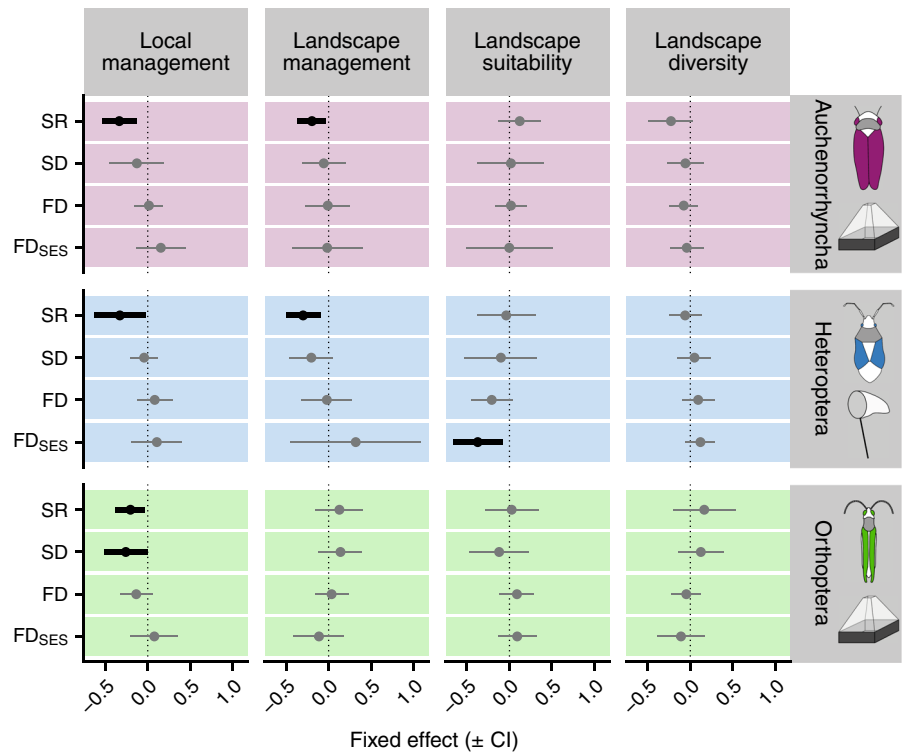
we found strong effects of landscape suitability on functional β-diversity, which differed between groups and sampling types. Generally, Auchenorrhyncha were found to be more affected by landscape-level land use compared to the other groups, indicating taxon specificity due to differences in dispersal capabilities between groups.

Functional composition and diversity

The considerable effects of land-use intensity at both spatial levels on mean functional composition indicates that environmental filtering affects community assembly across spatial scales. These results are in line with previous studies showing effects of local- (Simons et al. 2016; Birkhofer et al. 2017; Mangels et al. 2017) and landscape-level (Perović et al. 2015; Papanikolaou et al. 2017) land-use intensity on the functional composition of grassland arthropod communities. In our study we show that filters at the landscape level are as strong as those at the local level in shaping functional community composition, which has previously only been suggested by Gámez-Virués et al. (2015). At the same time, we did not observe effects of land-use intensity on FD, although SR was

lower at high local and landscape management intensity, a finding that was consistent after a null-model correction of FD. This indicates that changes in CWMs are mainly due to shifts in the abundance distribution in trait space and loss of primarily rare species, as a loss of common species would result in a decrease of the occupied trait space and thus lower FD. This is supported by the results for abundance-weighted Shannon diversity, which was affected by land-use intensity only in Orthoptera. Still, our results show that we need to consider land-use drivers across different spatial levels to improve our understanding of the consequences of land-use intensification for community assembly at broader scales.

Different traits were associated with land-use intensity at the two spatial levels. Interestingly, landscape-level land-use components not only affected traits related to dispersal (e.g. wing length), but mainly related to microhabitat use. This suggests that landscape land-use intensity primarily shapes the landscape species pool by providing suitable and diverse habitats (Tscharntke et al. 2012). Several relationships between CWMs and different landscape-level land-use components can be explained by changes in the proportion of the auchenorrhynchan
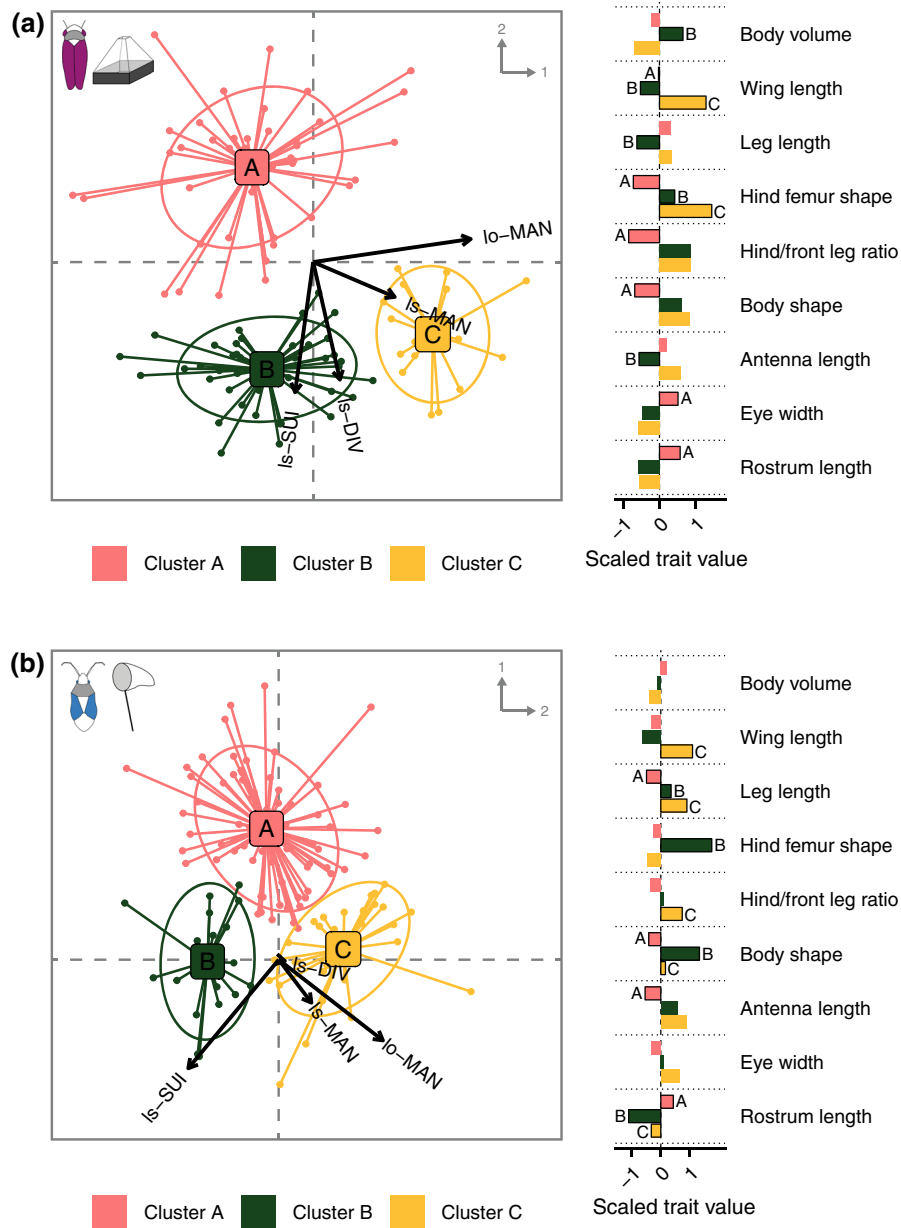
Fig. 3 Results of the RLQ analysis for **a** Auchenorrhyncha (biocenometer) and **b** Heteroptera (sweep netting). Graphs on the left: Ordination biplots with points representing species and colours referring to the three clusters, derived from hierarchical cluster analysis. The associated ellipses show cluster allocations assuming a multivariate normal distribution for a confidence level of 0.66. The black arrows represent the strength and direction of the environmental effects (lo-MAN: local management intensity; ls-MAN: landscape management intensity; ls-SUI: landscape suitability; ls-DIV: landscape diversity). Arrows have been rescaled for illustration and the orientation of the biplot was turned for Heteroptera for better comparability between the groups. Original axis orientation is indicated with the grey arrows and numbers. Graphs on the right: Means of the scaled trait values for the three clusters. Bars of traits that significantly distinguish one cluster from the other two (Anova, Tukey-HSD) have solid outlines and are indicated with the cluster letters. (Extended information on trait values and correlation ratios as well as results for Orthoptera and other sampling data are shown in Figs S5, S6 and S7)

community of the suborder Fulgoromorpha. This suborder is characterized by smaller animals with longer legs but relatively shorter hind legs, thicker hind femora, thicker bodies and longer rostra (see Figs
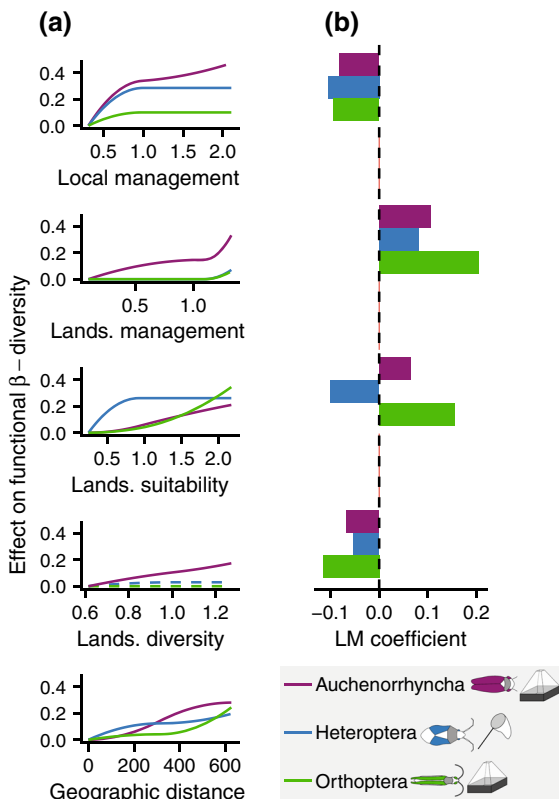
Fig. 4 Effects of four land-use variables on functional β-diversity of all three insect groups investigated. **a** Results of generalised dissimilarity models. Curve shapes indicate the effect of each land-use variable and geographic distance along its gradient on functional community dissimilarity. Absolute curve height indicates the strength of these effects. Significant effects are indicated with solid lines, non-significant effects with dashed lines. **b** Results of linear models for functional dissimilarity. The bars show size and direction of the model coefficients for the mean of each land-use variable between plot pairs, not including geographic distance. Auchenorrhyncha and Orthoptera data originate from biocenometer sampling and Heteroptera data from sweep netting

S10 and S11). Fulgoromorpha differ from Cicado-morpha, the other suborder covered in this study, in ecological characteristics such as microhabitat use and feeding preference. For example, Fulgoromorpha in our study region generally live closer to the ground and feed more on grass species (Holzinger et al. 2003). This could mean that they are less affected by decreasing landscape suitability and diversity, which would explain why they account for a larger proportion of the communities at low landscape suitability and diversity.

High management intensity at the local level was correlated to longer wings in both Auchenorrhyncha and Heteroptera, a finding consistent with previous studies investigating management effects on wing length or development (Ribera et al. 2001; Börschig et al. 2013; Simons et al. 2016; Birkhofer et al. 2017). The fact that wing length was not consistently related to landscape land-use intensity indicates its importance for disturbance avoidance (e.g. escape from mowing) and not just dispersal. Not surprisingly, body volume, which is related to many different processes such as dispersal and microhabitat use, was affected by management intensity as well as landscape suitability and diversity. While the landscape components only affected Auchenorrhyncha, which is probably explained by the shift in the abundance of the two suborders, high local management intensity favoured smaller animals in both Auchenorrhyncha and Heteroptera, which concurs with findings from previous studies on arthropods (Ribera et al. 2001; Rader et al. 2014; Simons et al. 2016; Birkhofer et al. 2017). Small-bodied insects are expected to have higher disturbance tolerance because they are more likely to escape mechanical disturbances and have shorter generation times.

Trait syndromes

The multivariate RLQ analysis revealed that the separation between management and composition (landscape suitability and diversity) as opposed to the separation between local- and landscape-level variables is essential for defining trait syndromes. Due to the limited number of species in the data for Orthoptera, trait syndromes will only be discussed further for Auchenorrhyncha and Heteroptera. Species related to high management intensity were characterised by longer wings in both groups, supporting the role of wing length in disturbance avoidance. Species in landscapes with low suitability (and diversity) and low local management intensity were mainly compact insects (i.e. thicker bodies; short appendices in Heteroptera) with poor jumping ability and long rostra. This indicates that they are ground associated species, which might explain why they are sensitive to local management intensity but less susceptible to a decreasing availability of suitable habitats. In landscapes with high suitability (and diversity) and low local management intensity (the third cluster),

Auchenorrhyncha and Heteroptera species were characterised by two different morphs. Auchenorrhynchan species comprised of large insects with short wings and legs. While body size may be primarily related to local management, shorter wings and legs indicate both lower disturbance avoidance capacity and dispersal ability, which are less disadvantageous at low local management sites in highly suitable landscapes. Heteropteran species in those landscapes were characterized by thin bodies and hind femora as well as short rostra indicating grass-associated species, which may profit from the higher proportion of grassland in the landscape. These findings inform more accurate estimations of the risk of endangerment for a large set of species and help predict outcomes under different management scenarios.

Functional β-diversity

We found strong negative effects of local management intensity on functional β-diversity in all three groups. Our results suggest that the taxonomic homogenization previously observed in the same study system (Gossner et al. 2016) translates into functional homogenization among communities. Similar to taxonomic β-diversity, effects of local management intensity on functional β-diversity were confined to low levels of local management intensity, indicating a major shift towards functionally homogenous communities between low and intermediate local management intensity. Additionally, we found strong effects of landscape suitability on functional β-diversity. However, results differed among groups and sampling types. Two differing results can be distinguished. In the first instance, we found a decrease in functional β-diversity at low levels of landscape suitability. In landscapes with low suitability, the dispersal potential is low, making different community assembly outcomes more probable. This might explain the elevated levels of β-diversity at low landscape suitability. In the second instance, we found an increase in functional β-diversity at high levels of landscape suitability. This might indicate the potential of highly suitable landscapes to support a larger landscape species pool, promoting neutral processes and consequently functional diversification among communities (Mori et al. 2018). Thus, functional β-diversity among grassland communities is most likely shaped by a combination of both local and landscape processes.

Taxon specificity in functional responses

While the overall observed patterns were similar for the three groups investigated, we still found substantial variation in their responses. The landscape-level effects were strongest for Auchenorrhyncha, while Heteroptera and Orthoptera reacted primarily to local land use, indicating differing dispersal capabilities of the three groups. As mobility generally increases with body size (Peters 1983), Heteroptera and Orthoptera are likely more mobile than Auchenorrhyncha (mean body volume of 33.21 ± 6.29 mm^3 for Heteroptera and 487 ± 144 mm^3 for Orthoptera compared to 7.11 ± 1.03 mm^3 for Auchenorrhyncha across all study species). Thus, they are potentially better in actively dispersing to suitable habitats even in landscapes impeding dispersal. Additionally, their landscape species pool likely comprises an area larger than the one covered in this study, which may be one reason why no significant effects were identified. In contrast, Auchenorrhyncha rely more on passive, wind-driven dispersal, which is prevalent in small-bodied insects (Compton 2002). As such the auchenorrhynchan landscape species pool is key in deciding what arrives at a site. This may be why landscape-level environmental filters, in particular those related to microhabitat use, were found to be more important in this group. Further studies are required to investigate how dispersal capabilities differ among insect groups, and how they are related to sensitivity to landscape-level processes. Our results highlight the importance of multi-taxa approaches for questions concerning the effects of land use on community assembly.

Conclusions

Our results demonstrate strong effects of land-use intensity, at both the local and landscape level, on the assembly of insect communities. Although the observed changes in functional composition of insect communities were not accompanied by changes in functional diversity, we found strong functional homogenization among communities. This is probably a consequence of filtering mechanisms acting at different spatial levels and on different taxonomic groups of herbivorous insects. Our study highlights the importance of incorporating land use at different spatial levels when investigating the assembly of

grassland communities. Additionally, it emphasizes the importance of multi-taxa approaches, as we found substantial differences between insect taxa in their response to land use. Further research should investigate how the observed shifts in functional community composition are related to ecosystem functions such as herbivory and productivity. The strong homogenization effects of local management and landscape composition on the functional composition of insect communities highlight the potential role of both local and landscape-level land-use intensity in determining landscape-wide ecosystem multi-functionality.

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