Multi-taxa approach shows consistent shifts in arthropod functional traits along grassland land-use intensity gradient

Nadja K. Simons,[1] Wolfgang W. Weisser, and Martin M. Gossner

Terrestrial Ecology Research Group, Department for Ecology and Ecosystem Management, Center for Life and Food Sciences Weihenstephan, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, Freising, D-85354, Germany

Abstract. Intensification of land use reduces biodiversity but may also shift the trait composition of communities. Understanding how land use affects single traits and community trait composition, helps to understand why some species are more affected by land use than others. Trait-based analyses are common for plants, but rare for arthropods. We collected literature-based traits for nearly 1000 insect and spider species to test how land-use intensity (including mowing, fertilization, and grazing) across 124 grasslands in three regions of Germany affects community-weighted mean traits across taxa and in single taxa. We additionally measured morphometric traits for more than 150 Heteroptera species and tested whether the weighted mean morphometric traits change with increasing land-use intensity. Community average body size decreased and community average dispersal ability increased from low to high land-use intensity. Furthermore, the relative abundance of herbivores and of specialists among herbivores decreased and the relative abundance of species using the herb layer increased with increasing land-use intensity. Community-weighted means of the morphometric traits in Heteroptera also changed from low to high land-use intensity toward longer and thinner shapes as well as longer appendices (legs, wings, and antenna). While changes in traits with increasing mowing and fertilization intensity were consistent with the combined land-use intensity, community average traits did often not change or with opposite direction under increasing grazing intensity. We conclude that high land-use intensity acts as an environmental filter selecting for on average smaller, more mobile, and less specialized species across taxa. Although trait collection across multiple arthropod taxa is laborious and needs clear trait definitions, it is essential for understanding the functional consequences of biodiversity loss due to land-use intensification.

Key words: beetles; body volume; cutting; feeding guild; grasshopper; leafhopper; management; planthopper; stratum; trophic group; true bug.

Introduction

Among the major drivers of global biodiversity loss, land-use change and intensification has the strongest negative effect on biodiversity in terrestrial habitats (Sala et al. 2000). This loss in biodiversity often comes along with a loss in functional diversity or change in trait composition of communities, which is well-studied in plants (e.g., Laliberté et al. 2010), birds (e.g., Flynn et al. 2009, Luck et al. 2013), and vertebrates (e.g., Blaum et al. 2011). However, similar studies on invertebrates, such as insects, are only recently becoming more common (e.g., Ribera et al. 2001, Dziock et al. 2011, Börschig et al. 2013, Rader et al. 2014, Uchida and Ushimaru 2014, Birkhofer et al. 2015). The majority of studies on functional traits in invertebrates compared the trait composition of communities between arable land (e.g., cereal fields) and grassland (Ribera et al. 2001, Cole et al. 2002, Rader et al. 2014), or compared different management types within arable fields and grasslands (Uchida and Ushimaru 2014, Birkhofer et al. 2015). However, grassland management often includes a combination of different modes (e.g., mowing, grazing, and fertilization) of which each can have different selective effects on communities. Only very few studies analyzed changes in community trait composition along continuous intensity gradients of mowing, grazing, fertilization or a combination of those (Dziock et al. 2011, Börschig et al. 2013) and if they did, they often considered only gradients of one mode (e.g., grazing or mowing).

We studied arthropod communities in a large set of grasslands that cover the whole range of land-use intensities in three regions in Germany. Previous studies in these grasslands have shown that the diversity of multiple taxa decreases from low to high land-use intensity (Allan et al. 2014) and that, in particular, rare arthropod species are threatened (Simons et al. 2015). It is, however, largely unknown if these changes in arthropod diversity and abundance structure are accompanied by a shift in trait composition.

There has been some debate in the literature on the definition of "traits" or "functional traits" (e.g., Violle et al. 2007, Mlambo 2014, Fountain-Jones et al. 2015). Here, we adopt the definition that traits are "…any morphological, physiological, phenological or behavioral characteristic that can be measured on an individual and that affects its fitness" (Violle et al. 2007) to also include characteristics that might not affect a species' fitness but are correlated to ecological variables. An example for such an "ecomorphological trait" is a morphological characteristic that is related to microhabitat use (Fountain-Jones et al. 2015). While efforts are undertaken to set up trait databases for arthropods world-wide (e.g., carabids.org; araneae. unibe.ch; Statzner et al. 2008), the scope of trait information is still limited. In addition, existing databases mostly focus on a single taxon and use incomparable trait definitions. While some recent studies did compare traits across taxa, they included only two taxa (e.g., Gossner and Müller 2011, Schirmel and Buchholz 2012) or defined traits in each taxon differently (e.g., Aubin et al. 2013).

We developed a comparable classification across five arthropod (sub-)orders: beetles (Coleoptera), true bugs (Heteroptera), leaf- and planthoppers (Auchenorrhyncha), grasshoppers (Orthoptera), and spiders (Araneae) to enable an analysis of the majority of the grassland arthropod community (Gossner et al. 2015a). For each arthropod species that we sampled over 5 yr across 150 grassland plots, we collected trait information from the literature (including textbooks, identification keys, and expert knowledge). We chose traits for which there are a priori expectations about how they may respond to increasing land-use intensity (body size, dispersal ability) and traits that are important descriptors of trophic structure (feeding mode, specialization, stratum use). Many studies in open habitat (i.e., grassland or arable land) found that average body length decreases with higher levels of disturbance (e.g., Cole et al. 2002, Uchida and Ushimaru 2014), hence we expect average body size to decrease with increasing land-use intensity, especially mowing and grazing intensity (H1). We further expect dispersal ability to increase from low to high land-use intensity, in particular with increasing mowing and grazing intensity (H2), because a high dispersal ability increases the potential for recolonization after disturbance (e.g., Ribera et al. 2001, Dziock et al. 2011). Several studies analyzed the effect of management on feeding guild or trophic groups mostly within beetles (e.g., Cole et al. 2002, Scohier and Dumont 2012, Liu et al. 2014, Winqvist et al. 2014), but their findings were inconclusive. For the whole arthropod community, we expect a decrease in the proportion of herbivores from low to high land-use intensity (H3) because herbivores react more strongly than higher trophic levels to changes in plant diversity (Scherber et al. 2010) and grassland plant diversity has been shown to decrease with increasing land-use intensity (Socher et al. 2012). We further expect to find a decrease in the proportion

of specialists within herbivores for the whole arthropod community (H4). Specialization in resource use, for example among pollinators, has been shown to decrease both along land-use types of increasing intensity (Rader et al. 2014) and with increasing land-use intensity within grasslands (Weiner et al. 2011). We also expect the proportion of species related to the herb layer to decrease from low to high land-use intensity (H5) because the community composition differs between strata (Morris 1971) and because frequency of herb-layer removal increases with increasing land-use intensity, in particular with mowing. For all hypotheses we test whether effects within the community are driven by changes in one taxonomic group.

The number of traits for which information across taxa is available in the literature is, however, necessarily limited. Furthermore, many literature-based traits are defined in categories (e.g., trophic group) that mask variation within the defined groups (e.g., mouth parts). Ideal traits should hence "preferably be measured on continuous scales" (McGill et al. 2006). We thus additionally considered nine morphometric traits derived from morphometric measurements that we took on sampled Heteroptera species (Gossner et al. 2015b). For those morphometric traits, we ask whether traits change in their average value from high to low land-use intensity and whether this depends on the land-use mode (mowing, grazing, and fertilization). We believe that morphometric traits can provide a useful starting point for further studies by pointing to traits that might provide new insights on responses to land use for other taxa.

The average trait in a community should be strongly influenced by the traits in those species that show a strong change in abundance over the land-use intensity gradient. Therefore, we selected species that decrease (losers) or increase (winners) strongly in abundance with increasing land-use intensity and compared their average trait values in order to see whether loser or winner species drive the changes in average traits.

MATERIAL AND METHODS

Study system and land use

The study was conducted within the large-scale and long-term Biodiversity Exploratory project (Fischer et al. 2010), which covers three regions in Germany: (1) UNESCO Biosphere Reserve Schorfheide-Chorin in the northeast (52°47′25″–53°13′26″ N, 13°23′27″–14°08′53″ E; about 1300 km² in size, 3–140 m above sea level), (2) Hainich National Park and its surrounding areas in central Germany (50°56′14″–51°22′43″ N, 10°10′24″–10°46′45″ E; about 1300 km², 285–550 m above sea level), and (3) UNESCO Biosphere Reserve Schwäbische Alb in the Swabian Jura in the southwest (48°20′28″–48°32′02″ N, 9°10′49″–09°35′54″ E; about 422 km², 460–860 m above sea level). In each of the three regions, 50 experimental plots of 50 × 50 m size

had been selected on managed grasslands to cover the whole regional gradient of land-use intensity and land-use modes. Plot selection followed a stratified random design in order to minimize confounding effects of differences in soil type, depth, and other abiotic factors (Fischer et al. 2010). The grasslands surrounding the plots as well as the plots themselves are continually managed by farmers. The management on each plot was assessed yearly through standardized questionnaires from 2006 to 2010 (see Fischer et al. [2010] for a detailed description of management assessment). The assessed intensity of mowing, grazing, and fertilization on each plot was divided by the mean intensity from the respective region. Those values were combined into a standardized index of land-use intensity (LUI) for each year and experimental plot by summing them and applying a square-root transformation to achieve more evenly distributed data (Blüthgen et al. 2012). We used the mean LUI and the mean intensity of the single land-use modes over 5 yr (2006–2010) to better reflect the long-term land use.

Arthropod sampling

Arthropods were sampled yearly from 2008 to 2012 in early summer (June/July) and late summer (August/September) by sweep netting with a round sweep net of 30 cm diameter. A total of 60 double-sweeps was conducted while walking along three sides of the plots (150 m total length) and arthropods were pooled into one sample per plot. With this sampling intensity of 10 samples per plot (5 yr × 2 seasons), we cover the within- and among-year variability in species' occurrences. Sampling in all three regions was conducted within several days per region and within a maximum of 2 weeks across regions during favorable weather conditions (no rain, temperature above 15°C). The sampled arthropods were killed and preserved in 70% ethanol and target taxa were identified to species level by taxonomic experts. Araneae, Hemiptera: Auchenorrhyncha, Hemiptera: Heteroptera, Coleoptera, and Orthoptera were chosen as target taxa due to their numerical importance in temperate grasslands. Only adult individuals were included in the analysis. In total, 124 plots (42 plots in the Schwäbische Alb, 46 plots in the Hainich-Dün, and 36 plots in the Schorfheide-Chorin) were analyzed, for which all 10 samples were pooled. Of those plots, 30 were never grazed, 34 plots were never mown (the remaining 60 plots were mown and grazed at least once between 2006 and 2010), and 62 plots were never fertilized.

Trait definition and measurement

We extracted trait information for all sampled species within our five target taxa from a published trait database that includes trait information from literature and expert knowledge (Gossner et al. 2015a). Selected

traits were body size, dispersal ability, feeding mode, specialization, and stratum use. Body size was defined as the averaged body length (mm) over males and females. Dispersal ability was based on the level of wing dimorphism between males and females, descriptions of flying ability or dispersal strategies. Feeding mode includes herbivores, carnivores, detritivores, fungivores, and omnivores. Specialization was only assigned within herbivores, monophages (i.e., specialists) were defined as feeding only on one plant genus and oligophages/polyphages were defined as feeding on one or several higher plant lineage(s). For a detailed description of trait definitions see Appendix S1 and Gossner et al. (2015a). The morphometric traits for Heteroptera were derived from measurements on 415 male and female Heteroptera individuals that were selected to be representative specimen for the 158 Heteroptera species sampled in our grasslands (Gossner et al. 2015b). For each species, between one and four male and female individuals were measured and at least one brachypterous and one macropterous specimen was measured if the species is known to display wing dimorphism. For each species, the mean value from all measured specimen was used. From the 23 morphometric measurements taken in total, we selected and calculated nine morphometric traits. Body volume was calculated from body length, width, and thickness following Siemann et al. (1999). Body shape was calculated by dividing body length by body width. Leg length, wing length, rostrum length, and antenna length were defined relative to body length. Hind femur shape was calculated by dividing the hind femur length by its width and the shape of the front femur was calculated by dividing its length by its width. Eye width was defined relative to head width.

Statistical analyses

All analyses were conducted in R v.3.0.2 (R Core Team 2014). For all continuous traits (literature-based body size and dispersal ability as well as all morphometric traits), we calculated community-weighted means (CWM, weighted by the relative abundance of each species) using the package FD (Laliberté et al. 2014). Here, a community refers to all species in all taxonomic groups or to all species within one of the taxonomic groups that were sampled on one plot within the 10 sampling events. For categorical traits (feeding mode, specialization, and stratum use), we calculated the relative abundance of species within the category for which we formulated our hypotheses (herbivores, monophagous species, and species associated with the herb layer) in relation to the other categories.

To explore possible confounding effects between the traits, which would lead to an increased type I error, we used ANOVA to compare the average of body length and dispersal ability between taxa and between the different levels within the categorical traits (e.g.,

average body length was compared between species with different feeding modes) and we calculated Pearson's correlation coefficient between all morphometric traits. By comparing the relationship of traits with land use and the relationships among traits, we assessed whether changes in one trait (e.g., feeding mode) with increasing land use might be driven by a strong correlation with another trait (e.g., body size) and this trait's relationship with land use.

Another factor that might lead to increased type I error is spatial autocorrelation of the response variables (e.g., through abiotic gradients within the regions that also affect land-use intensity). Hence, we first tested for spatial autocorrelation of the residuals from ordinary linear regressions between the traits and the combined land-use intensity. We used Moran's I as a measure of autocorrelation and tested for its significance using Monte Carlo tests within the package ade4 in R (Dray and Dufour 2007). As the residuals of several traits showed significant autocorrelation (Appendix S2: Table S1), we used spatial generalized linear mixed effect models (GLMM; Venables and Ripley 2002) to account for the spatial autocorrelation. GLMMs can include autocorrelation structures that are nested within regions. This nested structure is defined by including a random effect and allows autocorrelation distances to be different between regions (Dormann et al. 2007). The spatial autocorrelation was included as an exponential covariance structure between the Euclidean distances of the plots (based on the midpoint coordinates). We selected the exponential covariance structure over a Gaussian or spherical structure based on the log-likelihood values of the three model versions. Models with exponential covariance structure had higher or equally high log-likelihood values compared to the other two structures for all response variables. While log-likelihood variables of GLMMs are not reliable for model simplification, they are reliable for comparison of different covariance structures (C. F. Dormann, *personal communication*).

Besides the covariance structure and the random effect of region, models included land-use intensity and region as explanatory variables. Land-use intensity was either the combined intensity from mowing, grazing, and fertilization or the intensity of only one of those modes. As we only study three regions and include region as fixed and random effect in the model, there is no degree of freedom available to calculate the significance of differences between regions. The model family in the GLMM was set to "gaussian" as the response variables are neither binomial nor count data. However, some variables were left or right skewed and hence transformed by logarithmic or cubic functions (transformations are given in the footnote of Appendix S1: Table S1 for literature-based traits and in the footnote of Appendix S3: Table S1 for the morphometric traits).

To test if one taxonomic group is driving the effects in the entire community, models were also calculated for the different taxa separately. To assess whether the traits of loser species or of winner species drive the changes in average traits, we defined loser and winner species by calculating the correlation between each species' abundance and the combined land-use intensity across plots (Spearman's correlation coefficient; Spearman's rho). The mean and standard deviation of rho were used to set cut-off points for the definition. Winner species have a correlation coefficient >0.09 and loser species have a correlation coefficient <−0.15. We then compared the trait values of losers and winners using ANOVA for the average values of numerical traits and using chi-square tests (Pearson) for categorical traits.

Results

We sampled 102 265 adult arthropod individuals from a total of 986 species. The number of individuals sampled per plot and year was 165 ± 10 (mean ± SE) individuals from 26 ± 1 species. Abundances per region ranged from 604 ± 47 in Hainich-Dün over 842 ± 45 in Schorfheide-Chorin to 1053 ± 119 in Schwäbische Alb. Of our five target taxa, Coleoptera were sampled with the highest number of species (541 species), followed by Heteroptera (158 species), Auchenorrhyncha (133 species), Araneae (130), and Orthoptera (24 species). Auchenorrhyncha were sampled with the highest number of individuals (53 829 individuals), followed by Heteroptera (25 783 individuals), Coleoptera (18 866 individuals), Araneae (2513), and Orthoptera (1274).

Response of literature-based traits to land use

The community's average body size significantly decreased and the average dispersal ability significantly increased from low to high land-use intensity in all three regions (Fig. 1, Appendix S1: Table S1). Average body size and average dispersal ability were significantly affected only by increasing mowing intensity but not by increasing fertilization or grazing intensity. The change in the community's average body size and in average dispersal ability was driven by Araneae and Auchenorrhyncha, which were the only two taxa showing a significant response of body size or dispersal ability to changes in land-use intensity in taxon-specific analyses (Appendix S1: Fig. S1, Table S2). While winner and loser species did not differ in their average body size ($F_{1,286} = 0.06$, $P = 0.80$) they differed significantly in their average dispersal ability ($F_{1,286} = 5.89$, $P = 0.016$) with only four of 146 winner species being not assigned to the highest dispersal category.

The relative abundance of herbivores (in relation to predators and omnivores) and the relative abundance of monophagous herbivores (compared to oligo- and polyphagous herbivores) decreased significantly from low to high land-use intensity (Fig. 1, Appendix S1: Table S1). For the relative abundance of herbivores, the effect strength depended on region (decrease in
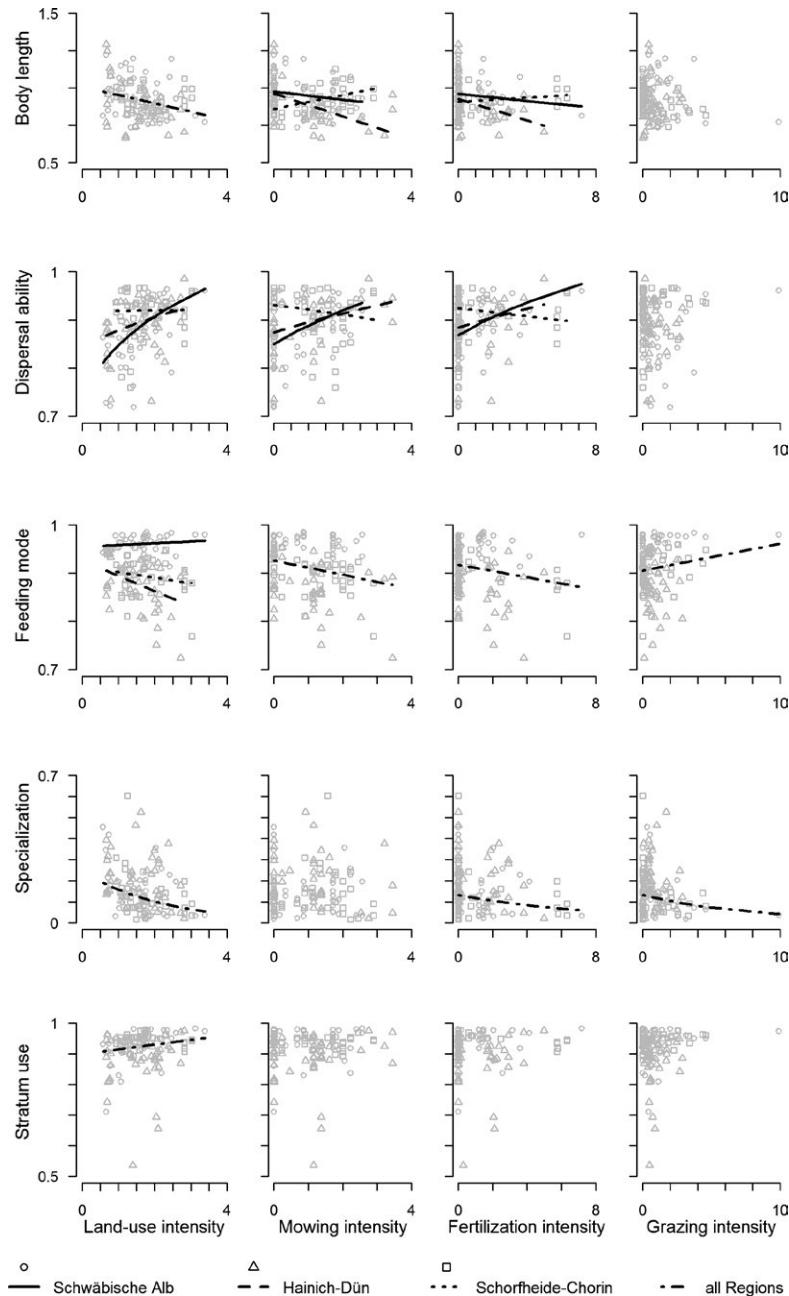
Fig. 1. Response of community body length, dispersal ability, feeding mode, specialization, and stratum use to combined land use, mowing, fertilization, and grazing intensity. Body length and dispersal ability were defined as community-weighted means. Feeding mode was defined as relative abundance of herbivores; specialization was defined as relative abundance of monophagous herbivores; stratum use was defined as relative abundance of herb-layer species. The community includes Araneae, Auchenorrhyncha, Coleoptera, Heteroptera, and Orthoptera. The three study regions are indicated by different symbols. Regression lines indicate significant relationships with land-use intensity ($P < 0.05$). Three regression lines indicate a significant ($P < 0.05$) interaction between region and land use. Statistics are given in Appendix S1: Table S1. Results for single taxa are shown in Appendix S1: Fig. S1 and Table S2. The results were consistent when excluding the one extreme value of grazing intensity (Appendix S2: Table S3).

Hainich-Dün and Schorfheide-Chorin but no effect in Schwäbische Alb). The relative abundance of monophagous herbivores decreased in all three regions and with increasing grazing and fertilization intensity, but not with mowing intensity (Fig. 1, Appendix S1: Table S1). In the single-taxon approach, relative abundance of herbivores decreased significantly with increasing combined land-use intensity for Coleoptera and Orthoptera with more or less strong differences between regions. Changes in the relative abundance of

monophagous herbivores were driven by Auchenorrhyncha (Appendix S1: Fig. S1, Table S2). The number of species with different feeding modes and the number of species with different specialization levels was significantly (χ^2 = 16.88, P < 0.01; χ^2 = 21.33, P < 0.001) different between winner and loser species with more herbivores and less omnivores as well as more monophagous and oligophagous herbivores and less polyphagous herbivores among loser compared to winner species (Appendix S1: Table S3).

The relative abundance of species associated with the herb layer (in comparison to ground-dwelling species and species associated with shrubs and trees) increased with increasing combined land-use intensity in all three regions, but not with increasing intensity of single land-use modes (Fig. 1, Appendix S1: Table S1). The increase in relative abundance of species associated with the herb layer was driven by Auchenorrhyncha, whereas Orthoptera showed a significant decrease in relative abundance of herb-layer species with increasing land-use intensity (Appendix S1: Fig. S1, Table S2). The number of species using different strata differed significantly between winner and loser species (χ^2 = 13.97, P < 0.01), with more herb-layer species and less ground- and soil-dwelling species found among loser species (Appendix S1: Table S3).

We did find significant differences in average body size and dispersal ability between categories of other traits (Appendix S2: Fig. S1). However, none of the shifts in traits with increasing land-use intensity was caused by similar responses of linked traits to land-use intensity. For example, the decrease in herbivores was not driven by a significantly smaller body size or dispersal ability among herbivores in comparison to other feeding categories.

Response of morphometric traits in Heteroptera to land use

Community-weighted mean body volume and rostrum length decreased from low to high land-use intensity (Fig. 2, Appendix S3: Table S1), hence Heteroptera under high land-use intensity were dominated by on average smaller species with an on average shorter rostrum. All other measures increased from low to high land-use intensity (Fig. 2, Appendix S3: Table S1), hence the Heteroptera community under high land-use intensity was dominated by long and thin species with on average longer appendices relative to their body length. Heteroptera species under high land-use intensity were also dominated by species with on average bigger eyes relative to their head width. The relationships between the morphometric traits and mowing and fertilization intensity were consistent with the combined land-use intensity for all morphometric traits, except for eye width (Appendix S3: Figs. S1, S2). Responses to grazing intensity showed the exact opposite pattern for all morphometric traits, except eye width (Appendix S3: Fig. S3). We found no significant difference between winner and loser species for any of the nine morphometric traits (Appendix S3: Table S2).

DISCUSSION

We found that the trait composition of arthropod communities shifted strongly from low to high land-use intensity. Communities under high land-use intensity had on average a smaller body size (supporting H1) and higher dispersal ability (supporting H2) and had an overall lower relative abundance of herbivores (supporting H3), in particular of specialists (supporting H4). In contrast to H5, the proportion of herb-layer species increased with increasing land-use intensity. Additionally, Heteroptera communities shifted toward longer and thinner species with longer appendices. We are aware that some limitations exist for using traits from textbooks or identification keys (as we did for our literature-based traits) as values such as body size are averaged across unknown geographic ranges and do often not include a measure of the variability within a species. Other traits, such as feeding guild, are often based on occasional observations and rarely on systematic assessments. However, we can assume that the variation of a trait within a species is sufficiently smaller than the variation across all our sampled species (as was shown for leaf traits in plants; Garnier et al. 2001). The rapid method of taxon-specific assessment of traits also allows us to include more species and more plots compared to measuring traits on individuals across plots (Lavorel et al. 2008).

Land use and traits across taxa

The shift toward smaller community average body size under intensive land use is in line with our first hypothesis and confirms observations made on carabid beetle communities (Ribera et al. 2001, Cole et al. 2002, Birkhofer et al. 2015), on butterflies (Uchida and Ushimaru 2014) and on bees and flies (Rader et al. 2014). Body size is among the most fundamental traits of organisms and is related to several physiological and ecological characteristics (Peters 1983, Brändle et al. 2000, Brown et al. 2004, Brose et al. 2006). For example, larger species tend to have longer life cycles, build up smaller populations, and have higher mobility than smaller species. A longer life cycle in larger species can explain the negative effect of higher mowing intensity on body size, as a higher frequency of disturbances with removal of the vegetation increases the chances of disrupting the development or reproduction cycle of larger species. Although larger species would have an advantage over small species under high land-use intensity because they tend to be more mobile, low mobility might not be a general rule in small-bodied arthropods. As den Boer (1990) pointed out, very small arthropod species often disperse over long distances as aerial plankton and will then be able to recolonize habitats very fast after disturbances. Such wind dispersal is common in spiders (Samu et al. 1999), which could explain the stronger decrease in average body size with land-use intensity
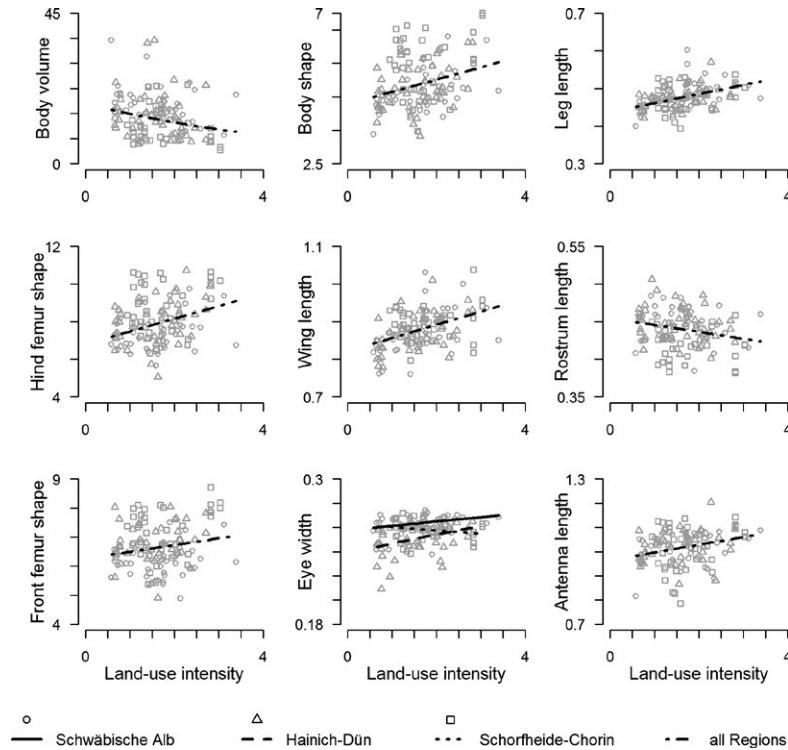
FIG. 2. Response of morphometric measures taken on Heteroptera species to increasing land-use intensity. All measures were taken on at least two individuals (male and female) per species and community-weighted means were calculated. Shape values were calculated as length/width. Leg, wing, rostrum, and antenna length were measured relative to body length; eye size was measured relative to head width. The three study regions are indicated by symbols. Regression lines indicate significant relationships with land-use intensity ($P < 0.05$). Three regression lines indicate a significant ($P < 0.05$) interaction between region and land use. Responses to mowing, fertilization, and grazing intensity are shown in Appendix S3: Figs. S1–S3. Statistics are given in Appendix S3: Table S1.

in this taxon compared to the other taxa. A decrease in average body size likely leads to a decrease in overall arthropod biomass and decelerated ecosystem processes such as herbivory and nutrient cycling because smaller species consume lower amounts of plant or animal tissue. This is supported in a study by Gossner et al. (2014), which showed a decrease in insect herbivory with increasing land-use intensity on our studied grasslands. A loss of large-bodied arthropod species also changes the resource availability for higher trophic levels (e.g., birds). Dennis et al. (2007), e.g., showed that grazing intensity reduces the overall biomass of arthropods that are important in the diet of bird species that have been declining in agricultural areas.

In line with our second hypothesis, average dispersal ability across taxa increased from low to high land-use intensity. Higher dispersal ability under intensive management has also been found in butterflies (Börschig et al. 2013), grasshoppers (Dziock et al. 2011), spiders, and true bugs (Birkhofer et al. 2015) as well as in carabid beetles (Ribera et al. 2001, Birkhofer et al. 2015). Species with high dispersal ability have an advantage in the recolonization of habitats after disturbances (Tscharntke et al. 2005, Burrows and Sutton 2008), which are generally more frequent under intensive

management. Grazing probably did not affect average dispersal ability because it does not induce a disturbance on the whole grassland at once. Although differences in average dispersal ability were only small between losers and winners of increasing land-use intensity, more low-dispersal species were found among loser species, which indicates that low-dispersal species are more likely to be threatened by high land-use intensity. The loss of species with low dispersal ability emphasizes the need for conservation schemes to incorporate a landscape-level perspective. While a reduction in management intensity can lead to an increase in arthropod diversity at one site, the most vulnerable species will only profit if they have the possibility to recolonize the site from surrounding habitats. In order to find an optimal landscape configuration, more information is needed on the possible range and speed of dispersal among species with low dispersal ability.

The relative abundance of herbivores across all taxa decreased from low to high land-use intensity, which is in accordance with our third hypothesis and with observations made in experimental grasslands (Scherber et al. 2010); the higher the trophic level, the weaker the effects of plant species richness, which decreases

with increasing land-use intensity (Socher et al. 2012). Other studies that analyzed changes in feeding guilds with land-use intensity in grasslands found similar results (Rothenwöhrer 2012, Scohier and Dumont 2012). The reduced dominance of herbivores also supports the finding of a decreasing herbivory rate under intensified land use (Gossner et al. 2014).

The decrease in relative abundance of herbivores was accompanied by a decrease in the relative abundance of monophagous species among herbivores, confirming our fourth hypothesis. We additionally found a higher proportion of monophagous herbivores among loser species, indicating that specialist herbivores are most strongly affected by land-use intensification. This is in accordance with other studies in grasslands that found a loss of specialized species (pollinators, leaf-beetles) with increasing land-use intensity (Batáry et al. 2007, Weiner et al. 2011). It has been shown for butterflies (Börschig et al. 2013) and for Heteroptera (Torma and Császár 2013) that shifts in specialization are related to shifts in plant community composition. We thus conclude that the negative effect of land-use intensity on specialist herbivores in our study is a consequence of a decrease in plant diversity. Including plant species that are host plants for specialist herbivores into seed mixtures for pollinators (e.g., wildflower strips in the framework of agri-environmental schemes) could therefore be an easy and efficient measure to also increase non-pollinator diversity (e.g., Anderson et al. 2013). The breakdown of specialized interactions under land-use intensification is also critical for ecosystem functions such as nutrient cycling due to changes in trophic cascades (Schmitz 2008).

The relative abundance of species associated with the herb layer increased from low to high land-use intensity. This is in contrast to our fifth hypothesis that herb-layer species are affected most strongly due to the removal of their habitat. However, the relative abundance of herb-layer species was generally very high and effects were driven by a decrease in the relative abundance of shrub- and tree-dependent species with increasing land-use intensity (Appendix S1: Fig. S2). As shrubs and trees are basically absent on our grassland plots and as all plots have a minimum distance of 30 m to forests (Fischer et al. 2010), species associated with those structures are naturally not very likely to occur in our samples. Exceptions are extensively grazed grasslands, in particular, in the Schwäbische Alb and Hainich-Dün, where small shrubs (mostly *Juniperus* spp. and *Crataegus* spp.) are a typical element of the landscape. The higher relative abundance of shrub- and tree-dependent arthropod species on extensively managed grasslands and the decrease in abundance of those species with increasing land-use intensity thus explains the increase in the relative abundance of herb-layer species with increasing land-use intensity. This suggests that biodiversity in agricultural landscapes can be effectively increased by

conservation measures that add structural elements in the landscape, supporting previous studies (Schneider et al. 2014). The higher number of loser species than winner species among herb-layer species suggests that some herb-layer species are sensitive to high land-use intensity. The lower number of ground-dwelling species among loser species indicates that they are less strongly affected by land-use intensity compared to herb-layer species, which has also been shown for Coleoptera and Orthoptera in grasslands of Kansas, USA (Jonas et al. 2002).

Land use and morphometric traits in Heteroptera

The community-weighted means of all morphometric traits changed significantly from low to high land-use intensity. While we found a number of morphometric traits to be significantly correlated with each other (Appendix S2: Table S2), none of the morphometric traits was correlated with all other traits (which would increase the chances of detecting false positive effects of land-use intensity). We can, however, identify one group of morphometric traits that are positively correlated among each other and react similarly to increasing land-use intensity.

This group includes body shape and front and hind femur shape, which all three increased from low to high land-use intensity. The change in those three traits can be explained by two possible mechanisms. First, land-use intensity increases the proportion of grass species (Socher et al. 2012) and thus selects for grass-associated Heteroptera species, which typically have a long and thin body shape (Wachmann et al. 2004–2012). Such grass-associated species are, e.g., species of the Stenodemini (family Miridae), which indeed increase in relative abundance with increasing land-use intensity in our grasslands. Secondly, the availability of seeds can be scarce in frequently disturbed grasslands and thus lead to a lower abundance of seed-feeding specialists, which typically have a thick front femur (Wachmann et al. 2004–2012). The observed change in hind femur shape indicates different responses to different land-use modes. While the change with increasing mowing and fertilization intensity is likely due to the strong correlation with body shape, the shift toward short and thick hind femurs with increasing grazing intensity might be driven by higher jumping ability (Burrows and Sutton 2008, Barton et al. 2011).

A loss of seed-feeding specialists under high land-use intensity can also explain the decrease in average relative rostrum length from low to high land use: the species with the longest relative rostrum in our samples are described in the literature as species feeding on flowers and seeds of only a small number of plant species (Appendix S3: Table S3) and herbivores (0.414 ± 0.007 [mean $\pm$ SE]) in our samples tended to have a longer rostrum than carnivores (0.377 ± 0.016; Welch two-sample t test, $t = 2.013$, df $= 39.578$, $P = 0.05$). The

increase in average relative eye size with increasing land-use intensity is also indicative of an increase in the relative abundance of carnivorous species (Bauer et al. 1998, Talarico et al. 2007). Front femur shape, rostrum length, and relative eye size are, however, not correlated, indicating that similar mechanisms affect different traits in different species.

Higher disturbance frequency under high land-use intensity can explain the increase in both relative leg and wing length, as both traits are considered proxies for dispersal ability. An increase in walking speed (related to longer legs) was found to be an important factor for colonization ability in beetles and leafhoppers (Burrows and Sutton 2008, Barton et al. 2011). A strong correlation between relative leg length and relative antenna length might explain the change in antenna length with land-use intensity. Such a correlation has also been found for beetles (Barton et al. 2011).

While most of the morphometric traits increased from low to high dispersal ability, one trait decreased strongly from low to high land-use intensity, i.e., body volume. As the average literature-based body length did not change from low to high land-use intensity in the analysis considering only Heteroptera (Appendix S1: Fig. S1), the average measured body volume might be a more informative measure of body size also in other taxa (e.g., Coleoptera or Orthoptera, which also did not show a change in literature-based body length). In addition, body volume seems to be a good candidate for an across-taxon trait because it is not strongly correlated with the other morphometric traits (Appendix S2: Table S2).

All morphometric traits showed opposite shifts for an increase in grazing intensity compared to an increase in mowing or fertilization intensity. This means that the community composition not only differs between extensively used grasslands and grasslands of high management intensity but that the land-use mode strongly influences response patterns, depending on which species can cope with an increase in intensity or is threatened by it.

CONCLUSION

Our results suggest that land-use intensity acts as a strong environmental filter shifting trait composition of arthropod communities. Identifying traits that make species susceptible to increasing land-use intensity gives important indications for possible countermeasures, e.g., sowing host plants for monophagous herbivores or providing less disturbed habitat for species with low dispersal ability. Those measures will then also support the occurrence of other species that were not sampled or identified but exhibit the same traits. The observed filtering effects of land-use intensity on nine morphometric traits in Heteroptera suggests that this is a promising approach for generating hypotheses on the mechanisms behind changes in community composition and diversity loss through land-use intensification.

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Supporting Information