Land-use type and intensity differentially filter traits in above- and belowground arthropod communities

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Running title: Land use filters traits in arthropod communities

Abstract

1. Along with the global decline of species richness goes a loss of ecological traits. Associated biotic homogenization of animal communities and narrowing of trait diversity threaten ecosystem functioning and human well-being. High management intensity is regarded as an important ecological filter, eliminating species that lack suitable adaptations. Belowground arthropods are assumed to be less sensitive to such effects than aboveground arthropods.

2. Here, we compared the impact of management intensity between (grassland vs. forest) and within land-use types (local management intensity) on the trait diversity and composition in below- and aboveground arthropod communities.

3. We used data on 722 arthropod species living above ground (Auchenorrhyncha and Heteroptera), primarily in soil (Chilopoda and Oribatida) or at the interface (Araneae and Carabidae).

4. Our results show that trait diversity of arthropod communities is not primarily reduced by intense local land use, but is rather affected by differences between land-use types. Communities of Auchenorrhyncha and Chilopoda had significantly lower trait diversity in grassland habitats as compared to forests. Carabidae showed the opposite pattern with higher trait diversity in grasslands. Grasslands had a lower proportion of large Auchenorrhyncha and Carabidae individuals, whereas Chilopoda and Heteroptera individuals were larger in grasslands. Body size decreased with land-use intensity across taxa, but only in grasslands. The proportion of individuals with low mobility declined with land-use intensity in Araneae and Auchenorrhyncha, but increased in Chilopoda and grassland Heteroptera. The proportion of carnivorous individuals increased with land-use intensity in Heteroptera in forests and in Oribatida and Carabidae in grasslands.

5. Our results suggest that gradients in management intensity across land-use types will not generally reduce trait diversity in multiple taxa, but will exert strong trait filtering within individual taxa. The observed patterns for trait filtering in individual taxa are not related to major classifications into above- and belowground species. Instead, ecologically different taxa resembled each other in their trait diversity and compositional responses to land-use differences. These previously undescribed patterns offer an opportunity to develop management strategies for the conservation of trait diversity across taxonomic groups in permanent grassland and forest habitats.

Key words

Biodiversity Exploratories, Biotic homogenization, **Ecological filters**, Ecosystem functioning, Environmental filtering, Forest, Grassland, Soil animals, Trait composition, Trait diversity

Introduction

Biodiversity is threatened by land-use change, including the conversion from one major land-use type to another (e.g. afforestation or deforestation) and the local intensification of management (e.g. fertilization) (Hooper et al. 2012). Afforestation for example is an active policy instrument in Germany (e.g. German Forest Strategy 2020, BMELV 2011). Lienhoop and Brouwer (2014) discuss this strategy and highlight that both agricultural land with low soil fertility and non-agricultural land are targeted by this instrument. Comparable patterns are also evident for neighbouring countries such as France or Poland (Mean annual total new forest creation in EEA-23 countries; EEA database). Both land classes include a range of permanent grasslands with different management intensity (see also Lautenbach et al. 2017). In the European Union, 8.2 billion have been allocated to measures that support forests under the recent Common Agricultural Policy (CAP), including afforestation practices (Ragonnaud 2016). Deforestation and subsequent conversion to grassland is primarily a local land-use pattern in Germany, as it is often a response to severe forest pest outbreaks or windfall. The consequences of these and other anthropogenic activities for species diversity have been evaluated globally and predictions suggest an ongoing loss of biodiversity under a "business-as-usual" scenario (Newbold et al. 2015). Besides this global decline of species richness the associated loss of species traits ("trait filtering", Duffy et al. 2008) and the associated biotic homogenization of communities (Gámez-Virués et al. 2015) are of major concern. Here, we aim at understanding how large scale differences between land-use types

and local management intensity within land-use types affect the trait diversity and trait distribution in below- and above-ground arthropod communities.

Traits are attributes of individuals or species that are linked to their long-term fitness or short-term performance and include morphological, ecological, physiological or life-history characteristics (Violle et al. 2007). A loss of traits often reflects the response of local communities to environmental change ("response traits", Lavorel & Garnier 2002) and can affect ecosystem functions ("effect traits", Lavorel & Garnier 2002) via changes in trait composition (Mlambo 2014, Warzecha et al. 2016). Trait-based studies therefore offer a unique framework to understand mechanisms through which land-use change and intensification affects biodiversity and potentially alters associated ecosystem functions (Verberk et al. 2013, Fournier et al. 2015). While effects of land-use change and intensity on community composition and trait diversity have been studied at the landscape scale (Schweiger et al. 2005), local effects of land-use change and intensification on trait diversity and composition are understudied in arthropod communities (but see Wood et al. 2015).

Recently it has been shown that trait composition in aboveground arthropod communities is vulnerable to changes in landscape composition and land-use intensity (Gámez-Virués et al. 2015). The transient nature of major structural features in arable fields for example contributes to a low trait diversity of arthropod communities compared to communities in forest habitats (Birkhofer et al. 2015). Species that lack suitable adaptations to high management intensity and frequency (for example a high mobility, Gavish-Regev et al. 2008 or small body size, Postma-Blaauw et al. 2010) are often eliminated from intensively managed habitats (Webb et al. 2010, Simons et al. 2016). Such management practices are therefore considered to act as ecological filters (Tscharntke et al. 2005) that alter the diversity

and composition of traits in local communities. The generality of this filtering effect across land-use types and above- and belowground taxonomic groups, however, remains unknown.

In contrast to aboveground arthropod communities, belowground arthropod communities are assumed to be less sensitive to land-use change and intensification (Allan et al. 2014). The underlying assumptions are that soils protect belowground animals from disturbances (Haimi et al. 2000) or generally offer fewer niches and thus are characterized by a high proportion of generalist species (Wolters 2001). However, anthropogenic disturbances to soils such as liming in forests or fertilization in grasslands directly alter major soil properties, with severe consequences for soil communities (Auclerc et al. 2012, Birkhofer et al. 2012). Limitations in niche space or dimensionality due to such management practices may even further constrain the number of traits in belowground arthropod communities (Franzén 2004, Statzner and Moss 2004). These proposed constraints in trait space due to soil management and the high proportion of generalist species may lead to a higher level of functional redundancy between belowground compared to aboveground arthropod species (Jackson et al. 2007).

Considering the predicted changes in land-use with ever growing food demands, it is increasingly important to understand effects of land use on community attributes that change independent of species richness (Stuart-Smith et al. 2013), across taxonomic groups (Podgaiski et al. 2013, Fournier et al. 2015) and in systems in which trait-based studies are still rare, such as soils (Pey et al. 2014). Here, we studied the effects of two major land-use types (grassland and forest) and land-use intensity within these types on the trait diversity and composition in arthropod communities including species that are living aboveground (Auchenorrhyncha and Heteroptera), primarily in soil (Chilopoda and Oribatida) or at the

interface (Araneae and Carabidae). We hypothesized that increasing local land-use intensity and more frequent management in grasslands compared to forests negatively affect trait diversity. We expected that these negative effects on trait diversity are stronger in above- compared to belowground arthropod taxa. Concerning trait composition, we hypothesized that large, less mobile and vegetation-living individuals suffer most from increasing land-use intensity and more frequent management in grasslands, and that such trait filtering effects are weaker in below- than in aboveground arthropod taxa.

Material and methods

Site selection and sampling

Communities of six arthropod taxa (Araneae, Coleoptera: Carabidae, Chilopoda, Hemiptera: Auchenorrhyncha, Hemiptera: Heteroptera and Sarcoptiformes: Oribatida) were sampled in the same 12 grasslands (meadows and pastures of at least 20 years age) and 12 forests (deciduous and coniferous forests of at least 80 years age) in each of three regions in Germany (total: 72 sites; Tab. 1). These three regions are part of the Biodiversity Exploratories Project in Germany (Schwäbische Alb, AEP; Hainich-Dün, HEP and Schorfheide-Chorin, SEP) which spans a latitudinal range of approximately 600 km (Fischer et al. 2010). Sites were selected to cover a long land-use intensity gradient with an almost even distribution of sites along the gradient within each region (Fig. S1). In grassland, the land-use intensity gradient ranged from extensive pastures to up to four-times mown and heavily fertilized meadows. It was defined by a composite index that is the sum of the standardized intensities of grazing (duration and livestock type), mowing (number of cuts per year), and fertilization (kilograms of nitrogen (N) per hectare) averaged over all sites and a period from 2007-2009 (LUI; Blüthgen et al. 2012). In forests, the gradient ranged from beech forests that were unmanaged for 20-70 years to conifer plantation with a rotation

period of <100 years. It was defined by an index of silvicultural management intensity which reflects the risk of stand loss (based on tree species composition and stand age) and stand density (SMI; Schall & Ammer 2013). Both indices were developed to provide a standardized measure of land-use intensity in the Biodiversity Exploratories. Note that the intensity gradient for forests in the Schwäbische-Alb is longest since no forest plots with SMIs > 0.51 (HEP) or >0.39 (SEP) existed in the other two model regions (Fig. S1). Land-use intensity indices for grasslands and forests were individually standardized by dividing each value by the overall highest value (setting the highest value to 1 for each index). This was done to create a shared scale before combining land-use indices in grasslands and forests to a single index for further analyses (Fig. 1c). At each site, animals were collected using standard methods (for details see Appendix S1 in Supporting Information). Adult individuals were identified to species level resulting in 722 arthropod species with juveniles being excluded from our analyses.

The differences in sampling methods and intensity between land-use types may introduce a bias. We took two pre-cautionary measures to address this potential source of error. First, we did not use raw abundance data, but transferred all data to dominances (see section *Trait analyses*). Raw abundances would certainly be affected by differences in sample methods or intensity. Second, we standardized all plot-level values by the number of sampled species in the respective plot (see Fig. 1). This step was needed as species richness was expected to be biased by differences in sample methods or intensity. All data comes from identical grassland and forest plots in each region with at least partial overlap of sample periods within taxonomic groups but different land-use types.

Trait analyses

In a first step, community data at each site were standardized by dividing the abundance of each species at a site by the total abundance of all individuals in that taxonomic group at that site (Fig. 1a). Multiplying these values with 100 resulted in a dominance matrix of species at each site (theoretically ranging from 0% = species not present at the site to 100% = only this species present at the site). Using dominance values is a compromise between introducing a bias due to potential differences in sample intensity between land-use types and oversimplification by transforming data to presence/absence records (Beck et al. 2013). To create species × traits tables we selected four trait categories describing the body size, mobility, foraging characteristics and stratum preferences for each of the 722 species based on 2-3 individual variables in each category that were binary coded for all species (Tab. 1, for details see Appendix S2 in Supporting Information). The number of trait variables in each category implies a weighting of the importance of each category and we accounted for this potential bias by only including 2-3 variables for each trait category (Somerfield et al. 2008). One advantage of trait coding using categories is that a species can score for more than one trait variable within each category. A Chilopoda species with a size range provided in the literature (usually not providing mean body size) could score for two size categories or an omnivorous Carabidae species could score for the carnivorous and herbivorous category. Next, we used the simple matching coefficient to calculate resemblances between species within the same community based on the species × traits matrices (Fig. 1b). This resemblance measure provides a value between 0 and 100 % for the average pairwise similarity between species based on the trait information. A value of zero indicates that two species have no shared 0's or 1's for any trait variable and are therefore as different in trait composition as possible. A value of 100 indicates that two species share all 0's and 1's at the same trait variables (Somerfield et al. 2008). The average trait diversity (X in Fig. 1) of each

community was then calculated for the six arthropod taxa as the average pairwise similarity between all species in a community (Somerfield et al. 2008, see also Ruhí et al. 2013, Birkhofer et al. 2015). We then divided the average trait diversity of each community by the observed species richness to control for potential effects of local species richness (X^o in Fig. 1). This index was then log (x+1) transformed to fulfil assumptions of parametric tests. Lower X^o values characterize communities that are functionally less diverse per observed species compared to communities with higher trait diversity values.

Statistical analyses

General linear mixed models with region (Schwäbische Alb; Hainich-Dün and Schorfheide-Chorin) as random factor, land-use type (grassland vs. forest) and taxon (Araneae, Carabidae, Heteroptera, Auchenorrhyncha, Chilopoda, Oribatida) as fixed factors and the standardized land-use intensity index as continuous predictor were used to test for effects on the log(x+1) transformed average trait diversity (Fig. 1). Interaction terms were calculated for all combinations of fixed factors and continuous predictors. The same model structure was also used to analyse trait composition based on the arcsine-transformed proportion of soil-living, carnivorous, less mobile and small individuals in communities (Tab. S1 for the proportion of species). All means in figures are least square means calculated at the mean value of the land-use intensity covariate to provide a valid comparison of responses in the unbalanced design with covariate. The design is slightly unbalanced because a few sites did not provide adult individuals from all analysed taxa (Tab. 1 footnote). General linear mixed models were performed in Statistica 12 (StatSoft, Inc. 2014) based on type 3 sums of squares and F ratio tests.

Results

Trait diversity

The average trait diversity per species increased across taxa in the order Araneae ($X^o = 1.1$), Carabidae (1.6), Heteroptera (1.8), Oribatida (2.0), Auchenorrhyncha (2.8) and Chilopoda (3.96) and was higher in forests (2.6) compared to grasslands (1.7). The average trait diversity per species differed significantly between land-use types depending on taxonomic group (land-use type × taxonomic group interaction: $F_{5,392}=2.94$, P=0.013), but not between land-use types in general ($F_{1,392}=0.60$, P=0.439). Auchenorrhyncha and Chilopoda communities had a significantly higher trait diversity in forests (Fig. 2b&d), whereas Carabidae communities had a significantly higher trait diversity in grasslands (Fig. 2c). Trait diversity of Heteroptera and Oribatida communities did not differ significantly between land-use types (Fig. 2e&f). Trait diversity was not significantly affected by land-use intensity or taxonomic group and all interaction terms apart from land-use type × land-use intensity were non-significant.

Araneae and Carabidae were sampled with the same method (pitfall traps), but for a longer period in forests compared to grasslands. However, trait diversity in both taxa shows opposite patterns in response to land use (Fig. 2a&c). Auchenorrhyncha and Heteroptera were sampled over identical periods but with different methods in grasslands and forests (Fig. 2b&e). Trait diversity in these taxa does not show a systematic bias towards one land-use type.

Trait composition

The proportion of individuals in the smallest size class was significantly affected by land-use type, but this effect varied between taxonomic groups (Tab. 2a; for effects on the proportion of species Tab. S1). Auchenorrhyncha and Carabidae communities had significantly higher proportions of smaller individuals in grassland compared to forest communities (Fig. 3b-c),

while Chilopoda and Heteroptera communities showed the opposite pattern (Fig. 3d&e). The proportion of individuals in the smallest size class was significantly affected by land-use intensity depending on land-use type. The effect of land-use intensity on the proportion of small individuals was not significant in forests ($F_{1,213}$=0.07, P=0.791), but significantly negative in grasslands ($F_{1,201}$=3.93, P=0.048).

The proportion of individuals with low mobility significantly differed between land-use types, but this effect varied across taxonomic groups (Tab. 2b). The proportion of individuals with low mobility did not differ significantly between land-use types in Araneae and Auchenorrhyncha communities (Fig. 4a&b). Carabidae communities had significantly higher proportions of individuals with low mobility in forests (Fig. 4c), while Chilopoda, Heteroptera and Oribatida showed the opposite pattern (Fig. 4d-f). Concerning the effects of management on this trait, the proportion of individuals with low mobility decreased with land-use intensity in Araneae and Auchenorrhyncha communities (Fig. 4a&b), but increased in Chilopoda and grassland Heteroptera communities (Fig. 4d&e).

The proportion of carnivorous individuals differed significantly between land-use types, but this effect varied between taxonomic groups (Tab. 2c). The proportion was lower for Carabidae in grasslands and for Oribatida in forests (Fig. 5a&c), with no difference between land-use types for Heteroptera (Fig. 5b). It increased with land-use intensity in forest Heteroptera and grassland Oribatida communities (Fig. 5b&c).

The proportion of soil-living individuals across taxa was significantly higher in grasslands than in forests (27.7±2.8 vs. 23.4±2.7; Tab. 2d) and increased in the order Araneae (2.4±0.3), Carabidae (12.4±2.5), Oribatida (27.3±2.4) and Chilopoda (66.4±4.7; Tab. 2d). The proportion of soil-living individuals was not significantly affected by land-use intensity.

Similar to trait diversity, differences in sampling methods between land-use types may bias trait composition results within taxonomic groups. The proportion of small

Auchenorrhyncha and Heteroptera individuals shows opposite patterns (Fig. 3b&e) comparing forests (flight interception traps) and grasslands (sweep netting). This result does not support the assumption of a systematic bias.

Discussion

Higher local land-use intensity in grasslands and forests did not generally reduce trait diversity across above- and belowground arthropod communities. However a single below- (Chilopoda) and aboveground (Auchenorrhyncha) taxon had significantly lower trait diversity in grassland habitats compared to forests. Trait diversity in aboveground arthropod taxa was not generally more affected by land-use intensity or differences between land-use types compared to belowground taxa. Trait composition changed significantly in response to land-use type and –intensity, but responses to disturbance regarding body size and mobility traits were contrasting between taxa. The result that primarily land-use type, rather than intensity affected the trait diversity of arthropod communities would suggest that management intensification in permanent grasslands and forests may not exert a strong trait filtering across arthropod taxonomic groups. The strong effects of land-use type and intensity on the trait composition, however, suggest that conversion of forest to grassland and management intensification within land-use types will lead to filtering of traits in several above- and belowground arthropod taxa. These results underline that it is crucial to address both, trait richness and composition to fully understand land use effects on trait properties in arthropod communities (see also Mouillot et al. 2013). These losses of traits are not predictable based on simple classifications into above- or belowground arthropod taxa or according to major trophic groups. Instead, the identified joint responses of ecologically very different arthropod groups offer a chance to predict future responses to land-use change and

intensification in above- and belowground arthropod communities of permanent grasslands and forests.

Trait diversity

Similar to our finding of differences in trait diversity between forests and grasslands, a change in trait diversity between land-use types was previously observed in plant (Carmona et al. 2012), bird (Meynard et al. 2011), aquatic invertebrate (Larsen and Ormerod 2010) and belowground arthropod (Vandewalle et al. 2010) communities. In our study, trait diversity was significantly higher in forest communities than in grasslands for two of the arthropod groups (Auchenorrhyncha and Chilopoda). This is in line with the observed decrease in trait diversity of plant, bird and mammal communities along a gradient from natural to agricultural land-use types shown by Flynn et al. (2009). While the gradient in our study only included managed ecosystems it is still likely that the less transient and structurally more complex nature of forests contributed to the higher trait diversity in Auchenorrhyncha and Chilopoda communities in forest habitats. The annual removal of vegetation and mechanical disturbance in grassland habitats compared to forests more frequently exerts stress on arthropod populations. Environmental stress leads to a reduction of available niche-space (Díaz et al. 2013) and the associated environmental filtering resulted in the lower trait diversity in the studied grasslands. Carabidae showed the opposite pattern of higher trait diversity in grasslands, supporting previous results in a study that compared the functional distinctness of carabid species in forest, grassland and crop field communities (Birkhofer et al. 2015). Carabidae are known to be well adapted to conditions in intensively managed arable fields and are often winners of land-use intensification compared to other arthropod taxa (Birkhofer et al. 2014a). The national German Forest Strategy 2020 states that "within the frame-work of regional possibilities, new forest sites, offering particularly advantageous climate benefits and

positive effects on nature and the landscape, should be planted" (BMELV 2011)." On a European scale a total area of approximately 519.350 ha of predominantly permanent grassland (60% of the total area for EU15, ca. 35% in Germany) were converted to forest between 1993 and 1997 (EUROSTAT). These policy instruments and land-use changes together with our results highlight the potential of anthropogenic impact on trait diversity in below- and aboveground arthropods.

In contrast to our expectation, land-use intensity did not significantly affect the trait diversity in above-and belowground arthropod taxa. Given the geographic extent of the study regions, the number of species, as well as the range of above- and belowground taxa we expected pronounced effects of land-use intensity on trait diversity in above-, and to a lower extent in belowground taxa. However, our study focused on rather short intensity gradients within land-use types and this may explain why trait diversity was not generally affected by local land-use intensity. Previous studies in the German Biodiversity Exploratories also suggest limited effects of land-use intensity within grasslands on measures of trait diversity for foliage-living (Liu et al. 2014) and ground beetle (Birkhofer et al. 2015) communities and generally emphasize the importance of landscape-scale filters on arthropod traits (Gámez-Virués et al. 2015). We conclude that differences between the two studied land-use types (forest and grassland) were consistently stronger drivers of trait diversity than gradients of land-use intensity within the two land-use types. This result was equally observed in above- and belowground arthropod communities and should raise the awareness for potential consequences of future land-use conversion (e.g. afforestation or deforestation) in the study regions.

Trait composition

The identification of traits that are vulnerable to land-use change in our study provides insights about patterns of trait filtering in above- and belowground arthropod taxa. Chilopoda and Heteroptera communities had a higher proportion of individuals that were small in grasslands compared to forests. This result resembles previous comparisons of Heteroptera body size distributions in less frequently (field margins) versus frequently (arable fields) disturbed habitats (Birkhofer et al. 2014b). It supports our hypothesis that smaller species and individuals are less vulnerable to frequent disturbances in grasslands compared to larger species (see also Blake et al. 1994). Tsiafouli et al. (2015) similarly showed that larger soil animals are more vulnerable to management practices compared to smaller species along a gradient of land-use types that included arable fields and grasslands. These results suggest that large species in some arthropod taxa may avoid more frequently disturbed habitats and prefer temporally more stable habitats. Larger species are also more affected by frequent management due to longer development times and may generally suffer from a higher mortality through disturbance than smaller species.

   In contrast, Auchenorrhyncha and Carabidae communities had a higher proportion of small individuals in forests compared to grasslands. Differences between land-use types that are not directly related to management may have contributed to this pattern. Major predators of the studied arthropod taxa for example differ between land-use types and these differences may affect the observed size range. The effect of land-use type on body size patterns highlights that environmental filtering is not a unifying mechanism to explain trait composition across multiple above-and belowground taxa in arthropod communities. This result has crucial implications for ecosystem functions that arthropod species provide and highlights the need to design studies that address and identify potential grouping patterns across a range of taxonomic groups. Body size distributions in Araneae and Carabidae

communities are for example important predictors of biological pest control services (Rusch et al. 2015).

Grasslands had higher proportions of mobile Carabidae individuals, but lower proportions of mobile Chilopoda, Heteroptera and Oribatida individuals compared to forests. Limited mobility is a key constraint for the ability of arthropods to survive agronomic disturbances in grasslands and to recolonize fields after disturbances (Simons et al. 2016). Brachypterous Carabidae species cannot easily recolonize grasslands after mowing (Ribera et al. 2001) and suffer from high mortality due to mechanic disturbance (Thorbek & Bilde 2004). Grasslands had lower proportions of carnivorous Oribatida, but higher proportions of granivorous Carabidae. At least in the case of Carabidae, this pattern is related to resource availability. Seeds of grasses and grassland weeds are among the most important resources for granivorous Carabidae species (Lundgren 2009).

Increasing land-use intensity within grassland habitats has recently been shown to cause consistent shifts in aboveground arthropod trait composition (Simons et al. 2016). Our study of a comprehensive range of above- and belowground arthropod taxa comes to the same conclusion of decreasing body size with increasing management intensity in grassland habitats (see also Ribera et al. 2001, Braun et al. 2004). However, this pattern was not observed across all above- and belowground taxa in forest habitats. Araneae and Auchenorrhyncha communities further showed the expected decrease of individuals with low mobility with increasing land-use intensity in forests and grasslands (see also Birkhofer et al. 2014b, Simons et al. 2016). In contrast, the proportion of individuals with low mobility in Chilopoda and grassland Heteroptera communities even increased with land-use intensity. Intense land use led to forest Heteroptera and grassland Oribatida communities with a higher proportion of carnivorous individuals. These results are in line with previous studies that suggested that management effects on plant communities cascade up to reduce the dominance

of herbivores in arthropod communities (Scherber et al. 2010, Scohier and Dumont 2012). Several traits however were not affected by land-use intensity in our study, as for example the mobility trait in Carabidae and Oribatida, the feeding trait in Carabidae or the stratum trait in all taxa.

Conclusions

Our multi-taxon study of arthropod traits allows addressing land-use intensity within and between land-use types for above- and belowground arthropods. The different responses of trait diversity and composition to land use in arthropod taxa suggest that a simple "one size fits all" approach that focuses on reducing land-use intensity will not generally achieve the conservation of trait diversity and trait composition across grassland and forest arthropod communities. A simple classification into above- and belowground arthropods or major trophic groups will not provide a more general framework to understand these relationships between land use and trait diversity. However, our results also document that some arthropod taxa show comparable patterns for trait filtering independent of simple a priori classifications. This results suggests that some general rules for the relationship between land use and trait diversity exist across above- and belowground arthropod taxa. A better understanding of these rules will lead to an improved conservation of arthropod functional diversity in permanent grasslands and forests.

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Data accessibility

All data is archived in the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.c186k (Birkhofer et al. 2017).

Author contribution

KB, MMG and HGS developed the idea for the analyses and the conceptual framework. KB, VW, AZ and TD were responsible for the grassland studies on Araneae, Carabidae, Oribatida and Chilopoda. MMG and WWW were responsible for the grassland and forest studies on Hemiptera. SS, MM & OF were responsible for the forest studies on Chilopoda and Oribatida. CD provided support for trait collection in Carabidae. OF assembled traits for Chilopoda. MM & AZ assembled traits for Oribatida. All authors contributed to the interpretation of results and writing of the manuscript.

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Table 1 Arthropod groups analysed in this study with trait categories (number of individual trait variables per category in parentheses), the number of sites with individuals and overall number of species. For details on sampling method for each land-use type and trait information refer to Appendix S1 and S2 in the supporting information.

	Araneae	Auchenorrhyncha	Carabidae
Body size (3)	1-6/6-11/>11mm	1-3/3-6/>6mm	1-12/12-24/>24mm
Mobility (2)	ballooning (yes/no)	adults brachypterous/macropterous	brachypterous/macropterous
Feeding (2)	cursorial/web-building	phloem & xylem/mesophyll	predaceous/herbivorous
Stratum (3)	soil/surface/vegetation	epigeic/herb/shrub & tree layer	soil/surface/vegetation
Sites with individuals[a]	72	71	71
Species	192	107	127
	Chilopoda	Heteroptera	Oribatida
Body size (3)	6-19/19-32/>32mm	0-5/5-10/>10mm	100-500/500-900/>900µm
Mobility (2)	high/low movement category	adults brachypterous/macropterous	cuticule mineralisation (yes/no)
Feeding (2)	arthropod/annelid prey	predaceous/herbivorous	predaceous/saprophagous
Stratum (3)	soil–(2-5cm)/soil-(0-2cm)/litter	epigeic/herb/shrub&tree layer	soil/surface/litter
Sites with individuals[a]	60	72	72
Species	24	159	113

[a] Some of the 72 sites did not have adult individuals from all taxonomic groups, e.g. several grassland sites in Schorfheide-Chorin did not have adult (identifiable) Chilopoda.

Table 2 Results of general linear mixed effects models for the arcsine-transformed proportions of individuals that were a) small, b) less mobile, c) carnivorous or d) soil living in local arthropod communities. Araneae or Chilopoda communities exclusively had carnivorous species and Auchenorrhyncha communities had no carnivorous species, Auchenorrhyncha and Heteroptera communities had no soil-living species. These taxa were therefore excluded from the analysis of the respective trait category. Significant effects are in bold.

	a) Small body size			b) Low mobility		
	DF	F	P	DF	F	P
Region	2	0.47	0.628	2	0.51	0.602
Land-use (LU) type	1	3.84	0.051	1	**7.15**	**0.008**
Taxonomic group	5	**9.62**	**<0.001**	5	**16.28**	**<0.001**
Land-use intensity	1	**4.14**	**0.043**	1	0.27	0.605
LU type × Taxon	5	**3.33**	**0.006**	5	**7.18**	**<0.001**
LU type × LU intensity	1	**7.51**	**0.006**	1	0.83	0.362
Taxon × LU intensity	5	0.31	0.909	5	**3.68**	**0.003**
LU type × Taxon × LU intensity	5	0.47	0.802	5	**2.39**	**0.037**
Residuals	392			392		
	c) Carnivorous diet			d) Soil living		
	DF	F	P	DF	F	P
Region	2	2.88	0.058	2	**6.52**	**0.002**
Land-use (LU) type	1	0.06	0.803	1	**6.07**	**0.014**
Taxonomic group	2	**13.04**	**<0.001**	3	**15.37**	**<0.001**
Land-use intensity	1	0.11	0.736	1	1.35	0.246
LU type × Taxon	2	**15.14**	**<0.001**	3	2.49	0.061
LU type × LU intensity	1	0.03	0.864	1	2.68	0.103
Taxon × LU intensity	2	1.35	0.263	3	0.85	0.470
LU type × Taxon × LU intensity	2	**7.73**	**0.001**	3	1.52	0.209
Residuals	201			257		

Figure 1 Overview of the procedures to analyse the effect of land-use type (grassland vs. forest), land-use intensity and taxonomic group on the average trait diversity per species (X^o) in communities (for details refer to sections *Trait analysis* and *Statistical analysis* in the Material and Methods part).

Figure 2 The log-transformed (x+1) average trait diversity per species (X^o, least square means ± 95% confidence intervals; see Figure 1 and section *Trait analyses* in Material and Methods for details on X^o) for a) Araneae, b) Auchenorrhyncha (P<0.05), c) Carabidae (P<0.05), d) Chilopoda (P<0.05) , e) Heteroptera and f) Oribatida communities in grasslands (●) and forests (○).

Figure 3 Proportion of individuals with small size (least square means ± 95% confidence intervals) in a) Araneae, b) Auchenorrhyncha, c) Carabidae, d) Chilopoda, e) Heteroptera (all P<0.05) and f) Oribatida communities in grasslands (●) and forests (○).

Figure 4 The relationship between land-use intensity and the proportion of individuals with low mobility (with 95% confidence intervals) in a) Araneae, b) Auchenorrhyncha, c) Carabidae, d) Chilopoda, e) Heteroptera and f) Oribatida communities in grasslands (solid line) and forests (dashed line).

Figure 5 The relationship between land-use intensity and the proportion of individuals with carnivorous diets (with 95% confidence intervals) in a) Carabidae, b) Heteroptera and c) Oribatida communities in grasslands (solid line) and forests (dashed line). Araneae and Chilopoda communities exclusively had carnivorous species and Auchenorrhyncha communities had no carnivorous species.