Contrasting effects of grassland management modes on species- abundance distributions of multiple groups

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Summary

Intensive land use is a major cause of biodiversity loss, but most studies comparing the response of multiple taxa rely on simple diversity measures while analyses of other community attributes are only recently gaining attention. Species-abundance distributions (SADs) are a community attribute that can be used to study changes in the overall abundance structure of species groups, and whether these changes are driven by abundant or rare species.

We evaluated the effect of grassland management intensity for three land-use modes (fertilization, mowing, grazing) and their combination on species richness and SADs for three belowground (arbuscular mycorrhizal fungi, prokaryotes and insect larvae) and seven aboveground groups (vascular plants, bryophytes and lichens; arthropod herbivores; arthropod pollinators; bats and birds). Three descriptors of SADs were evaluated: general shape (abundance decay rate), proportion of rare species (rarity) and proportional abundance of the commonest species (dominance).

Across groups, taxonomic richness was largely unaffected by land-use intensity and only decreased with increasing mowing intensity. Of the three SAD descriptors, abundance decay rate became steeper with increasing combined land-use intensity across groups. This reflected a decrease in rarity among plants, herbivores and vertebrates. Effects of fertilization on the three descriptors were similar to the combined land-use intensity effects. Mowing intensity only affected the SAD descriptors of insect larvae and vertebrates, while grazing intensity produced a range of effects on different descriptors in distinct groups. Overall, belowground groups had more even abundance distributions than aboveground groups. Strong differences among aboveground groups and between above- and belowground groups indicate that no single taxonomic group can serve as an indicator for effects in other groups.

In the past, the use of SADs has been hampered by concerns over theoretical models underlying specific forms of SADs. Our study shows that SAD descriptors that are not

74 connected to a particular model are suitable to assess the effect of land use on community
75 structure.

1. Introduction

Biodiversity is declining globally at an unprecedented rate across a wide range of taxonomic groups (Ceballos *et al.*, 2015). Many studies which investigate the loss of biodiversity across groups and large scales rely however on simple diversity measures, such as species richness, or on abundance-weighted indices, such as Shannon or Simpson (e.g. Murphy and Romanuk, 2014; Newbold *et al.*, 2015). While synthetic indices such as Shannon or Simpson are clearly useful, they are often used as indicators of changes in diversity without an interpretation of the underlying changes in species abundance patterns.

Diversity measures alone may also obscure taxonomical or functional homogenization, because two communities with identical index values can differ markedly in their species composition, functional diversity or abundance structure. Much progress has been made in recent years in our understanding of changes in species composition for example by analyzing beta diversity to distinguish species turnover from nestedness (Baselga, 2010; Solar *et al.*, 2015; Gossner *et al.*, in press). Mean functional traits and functional diversity indices have long been used for plant communities (e.g. Laliberté *et al.*, 2010) and are increasingly used for animal communities (e.g. Birkhofer *et al.*, 2015; Simons *et al.*, 2016). Similarly, changes in community structure can be assessed in more depth by analyzing species-abundance distribution (SADs). However, SADs have mostly been used to describe single communities and only rarely to assess changes between several communities (McGill *et al.*, 2007). This is surprising, given that the typical abundance structure of species communities with few dominant and many rare species has been being recognized as a general pattern in ecology at least since the 1930s (Motomura, 1932).

Most studies on the SAD of a single community have evaluated the fit of the observed SAD to a particular pre-chosen model - especially the log-series or log-normal model (Tokeshi, 1993) - or to a variety of distributions, choosing whichever has a better fit to each dataset. The

a priori choice of a given model and the statistical assessment of fit are however beset by problems (Williamson and J. Gaston, 2005). Alternatively, differences in SAD characteristics between communities can be quantified by using descriptors which are not tied to a particular SAD model. One such descriptor is the slope of a regression between the logarithm of species abundances and species ranks (Figure 1). Variations in this slope among communities reflect differences in the numerical hierarchy of species in a community, which in turn reflect their competitive ranking (i.e. the presence of a highly competitive species often leads to steep slopes). A further step is to distinguish between two main processes that can produce changes in SAD's slope: a change in the dominance structure and a change in the proportion of rare species. Changes in the dominance structure can be estimated by calculating the relative abundance of the most abundant species (Figure 1); if this increases, the SAD's slope will become steeper, even if the total number of species or the proportion of rare species remains unchanged. The proportion of rare species is estimated from the length of the SAD tail (Figure 1) and a reduction in rare species will also lead to an increase in the SAD's slope. With only these three descriptors, one can hence first quantify the overall change in the abundance structure of communities (by changes in the SAD's steepness) and then disentangle two possible processes behind the overall change by testing if changes in the SAD's slope are driven by changes in dominance or by changes in the proportion of rare species. Those descriptors can be calculated for multiple communities and then compared statistically to differences in the environments in which the communities were sampled. This approach has been used to describe effects of environmental changes on SADs in aquatic systems, but similar studies including terrestrial communities are still very rare (McGill *et al.*, 2007).

Biodiversity in terrestrial systems is most threatened by intensification of land use, especially in grasslands (Vitousek, 1994; Sala *et al.*, 2000; Newbold *et al.*, 2015). Previous studies have shown that grassland management intensity has more pronounced effects on rare

than on common species (Allan *et al.*, 2014), indicating that land-use intensity can have variable effects on different sections of an SAD.

Additionally, different land-use modes have been found to affect different parts of SADs in arthropod communities differently (Simons *et al.*, 2015) with effects on dominance being mainly driven by fertilization. Other land-use modes, i.e. grazing and mowing, affected the number of rare species. It is important to disentangle the effects of single land-use modes on diversity and abundance structures in order to better understand the mechanisms behind the loss of biodiversity in managed landscapes. By disentangling the effects of different land-use modes on abundance structures and by comparing the two mechanisms behind changes in SADs, Simons *et al.* (2015) showed that intensive land use increases dominance within grassland arthropod communities, which was mainly driven by fertilization intensity. While arthropods are the most species-rich group in temperate grasslands (Groombridge and Jenkins, 2002), other groups may respond differently to changes in land-use intensity (e.g. Allan *et al.*, 2014). In this respect, SADs prove to be advantageous: while diversity indices are difficult to compare directly between communities that differ markedly in richness, descriptors of SADs are comparable among species-rich and species-poor assemblages. Comparing the effect of land-use intensity on SADs across groups can reveal similarities in responses between groups, based on which one can identify indicator groups for land-use change. Alternatively, differences in SADs between groups can also suggest mechanisms accounting for their differential response to changes in land-use intensity.

In this paper, we analyze species-abundance data from a wide array of groups, which were sampled along a gradient of grassland land-use intensity, to assess how SAD descriptors of multiple groups change in response to environmental management regimes. Specifically, we address the following questions:

1. Does land-use intensity increase the steepness of the species-abundance distribution equally in all groups?

- 152 2. Are changes in steepness driven mostly by changes in the dominance of the most
153 abundant species or by changes in the number of rare species?
- 154 3. Do land-use intensity effects and the mechanisms behind the observed changes differ
155 between groups?
- 156 4. Do different land-use modes have similar or divergent effects on species-abundance
157 distributions?

2. Material and Methods

2.1 Study system and land use

The study was conducted within the large-scale and long-term Biodiversity Exploratory project (Fischer *et al.*, 2010), which comprises three regions in Germany: (1) the UNESCO Biosphere Reserve Schorfheide-Chorin in the North-East (53°02' N 13°83' E, 3–140 m a.s.l.), (2) the National Park Hainich and its surrounding areas in Central Germany (51°20' N 10°41' E, 285–550 m a.s.l.), and (3) the central Schwäbische Alb plateau, which is partly included in the UNESCO Biosphere Reserve Schwäbische Alb in South-West Germany (48°43' N 9°37' E, 460–860 m a.s.l.). The study regions Schorfheide-Chorin and Hainich-Dün have a similar size (about 1300 km²), while the study region Schwäbische Alb is considerably smaller (about 422 km²). In each of the three regions, 50 managed grasslands were selected by a stratified random design from a regular grid of 500 candidate plots across the region to cover the entire range of land-use intensity and land-use modes representative for these regions (see Fischer *et al.*, 2010 for details). The grasslands are between 0.49 ha and 187.1 ha in size (mean $\pm$ standard deviation: 17.94 ha $\pm$ 27.32 ha). All grasslands are continually managed by farmers as meadows (only mown), pastures (only grazed) or mown pastures (mown and grazed), which are either unfertilized or fertilized. Management decisions are made only by the farmers and might vary between years for the same grasslands.

Management regimes and changes to those are assessed yearly through standardized questionnaires with the land owners and managers since 2006 for each grassland. Mowing intensity is expressed as the number of cutting events per year. Grazing intensity is represented by the standardized number of grazer individuals (cattle, sheep and/or horses) per hectare times the number of days the plots were grazed per year. Fertilization intensity includes nitrogen amounts from chemical fertilizer, manure or slurry per hectare (see Blüthgen *et al.*, 2012 for a more detailed description). While mowing, fertilization and grazing intensity are correlated

with each other (Blüthgen *et al.*, 2012), only mowing and fertilization intensity are positively correlated; meaning that the overall management intensity cannot be inferred from only one of the land-use modes. Intensities of the three land-use modes were standardized by dividing the values by the corresponding mean from the respective region and then combined into a standardized index of land-use intensity (LUI) by summing the resulting values for the three modes and taking the square-root 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 three years (2006-2008) to better represent long-term land use.

2.2 Biodiversity sampling

One each of the 150 grasslands, survey plots of 50 m × 50 m size were established in 2007. These plots are located with a minimum distance of 200 m from each other and at a minimum distance of 30 m from the nearest forest edge (Fischer *et al.*, 2010). We compiled biodiversity data from ten taxonomic and/or functional groups (henceforth groups) for which richness and abundance data was available, comprising three belowground groups (soil prokaryotes, arbuscular mycorrhizal fungi and insect larvae) and seven aboveground groups (vascular plants, bryophytes, lichens, herbivorous arthropods, pollinators, bats and birds). All taxa within each group were sampled within the same assessment, i.e. with the same method and at the same time. On about half of the mown grasslands, sampling for most groups took place after the first mowing event of 2008 including grasslands with one, two or three mowing events in total, sampling was equally likely to occur after a disturbance on grasslands with different mowing intensities. The individual groups were sampled on different subplots within the 50 m × 50 m plots.

Vascular plants, bryophytes and lichens were assessed in 4 m × 4 m temporarily fenced subplots in early summer 2008. Species abundances were estimated as percentage of ground cover. For details on vascular plant sampling see Socher *et al.* (2012), for bryophyte sampling

Müller *et al.* (2012) and for lichen sampling Boch *et al.* (2016). Vascular plants, bryophytes and lichen were combined as one group (hereafter referred to as “plants”), because of low species richness of bryophytes and lichens in some plots. *Herbivorous arthropods* were sampled twice, in June and August 2008, by sweep-netting with a total of 60 double-sweeps in transects along three plot borders (Simons *et al.*, 2014). Only twice-sampled plots were analyzed and data from the two samples were pooled. Hemiptera: Auchenorrhyncha (Cicadomorpha, Fulgoromorpha), Hemiptera: Heteroptera, Coleoptera and Orthoptera were determined to species level. Only adult individuals and herbivorous species were included in the analysis. The assignment of feeding guilds followed Gossner *et al.* (2015). *Pollinator* species and their abundances were assessed in 2008 during peak flowering (May to August). On 31 plots, no flowering plants were observed at the time of visit, mainly due to grazing or mowing. On the remaining plots, 162 surveys were conducted in total (Schwäbische Alb: 63; Hainich-Dün: 51; Schorfheide-Chorin: 48), sampling 29 plots up to four times as pollinator composition changes during the flowering period. Each survey covered a transect area of 200 m × 3 m three times during six hours of morning and afternoon sampling. Only insects posed directly in the center of the flowers while seemingly feeding on pollen or nectar were caught with an insect net or with help of an exhaustor. These insects were regarded as pollinators as their behavior may lead to pollination. Insects resting on petals were not taken into consideration. *Bird* species and their abundances were scored by standardized audio-visual point-counts for five periods of 5 minutes per point count, locality and season (Renner *et al.*, 2014). Since abundances in each year were very low, we combined counts from the years 2008 to 2012. *Bats* were assessed with standardized acoustic surveys (Jung *et al.*, 2012) between June and September in the years 2008 to 2012. Acoustic monitoring does not allow the identification of individuals, therefore we used the cumulative number of species presence records per plot within the five year study period as a measure of abundance. Bats and birds were analyzed together because of low species richness of the individual groups in some plots.

Belowground groups were sampled from soil cores. *Prokaryotes* and *arbuscular mycorrhizal fungi (AMF)* were sampled from 14 soil cores (40 cm length, 5 cm diameter) per plot, taken in May 2011. All soil cores per plot were homogenized and combined into one sample per plot (see also Solly *et al.*, 2014). Total microbial DNA was isolated from soils using a MoBio PowerSoil DNA isolation kit. Operational taxonomic units (OTUs) of prokaryotes were determined at species level (3% genetic divergence) based on pyro-sequenced amplicons covering the V3-V5 region of the 16S rRNA gene using the QIIME software package version 1.8 (Caporaso *et al.*, 2010). The NS31-AM1 fragment of the fungal 18S rDNA was amplified using arbuscular mycorrhizal fungal specific primers (Morris *et al.*, 2013) and sequenced using a Genome Sequencer FLX+ 454 System. The reads were quality filtered using MOTHUR (Schloss *et al.*, 2009) and classified using the MaarjaM AMF reference database (Opik *et al.*, 2010). When interpreting data based on DNA analyses, one has to take into account that those methods also detect DNA in dormant and dead cells or outside of cells. Detailed description of the data processing is presented in the Supplementary Information (Appendix S1). *Insect larvae* were extracted from an additional soil core per plot (5 cm depth, 20 cm diameter) sampled in April 2011, by means of a heat/moisture gradient in the cores (Kempson *et al.*, 1963) over a period of eight days. Extracted larvae were stored in 70% ethanol until identification to family level (Stehr, 1991, 2005). Although belowground taxa were sampled two years after the aboveground taxa and are likely affected by the land use in the years 2009 and 2010, we used the 2006-2008 index for the entire dataset. Given that the land-use intensity index LUI over this triennium is highly correlated with the LUI from 2009 to 2011 ($F_{1,148}=746.26$, $p<0.001$; $R^2=0.83$; slope= 0.99 ± 0.04) the choice of index should not affect the results.

We used different levels of taxonomic resolution (species, family or operational taxonomic unit) depending on the group. Hence, we use taxonomic richness instead of species richness to describe effects on diversity. Individuals which could not be identified to species

(plants, aboveground arthropods) or family level (belowground insect larvae) were excluded from the analysis.

2.3 Calculation of SAD descriptors

As species-abundance distributions (SADs) can only be calculated above a minimum number of species and individuals, we excluded plots with fewer than three taxonomic units (species, families, OTUs) or fewer than five counts overall (5 individuals or 5% cover) per group. Six plots were excluded for insect larvae, three plots for birds plus bats, two plots for AMF and one plot for pollinators. All other groups were sampled with at least five counts and at least three taxonomic units on all plots. For each group and plot, we counted the overall number and abundance of taxonomic units and fitted species-abundance distributions (SADs). All analyses were conducted in R v.3.1.2 (R Core Team, 2014).

Three descriptors were extracted from the SADs: abundance decay rate to describe the overall shape of the SAD, the Berger-Parker index to describe dominance, and the standardized value of Fisher's alpha to describe rarity. The abundance decay rate was calculated from the geometric series, or niche pre-emption model (Motomura, 1932), in which the expected abundance n of a species i is defined by the total number of individuals N of all species, the estimated abundance decay rate r per rank and by a constant factor C (defined by r and the number of species S) (McGill, 2011):

$$n = N C r (1-r)^{i-1} \text{ with } C = [1 - (1-r)S]^{-1}$$

Although the above model includes two parameters (r and C), it can be treated as a one-parameter model, because C is defined by r (Oksanen *et al.*, 2012). The abundance decay rate r is the fitted parameter and represents the slope of the model. We extracted the abundance decay rate r from the niche pre-emption model using the R package 'vegan' (Oksanen *et al.*, 2012). The dominance d (May, 1975) and Fisher's alpha were extracted from the log-series distribution (Fisher *et al.*, 1943) fitted with the R package 'sads' (Inacio Prado and Dantas

Miranda, 2013). Dominance d , or Berger-Parker Index (May, 1975), is calculated as the count of the most abundant taxonomic unit (N1) divided by the total count over all taxonomic units (N). The value for Fisher's alpha was corrected by the number of taxonomic units (alpha/S). Restriction to plots for which SAD descriptors could be obtained for all groups would have almost halved the number of observations (to 87 of 150 plots), therefore missing data from individual groups were coded as NA (not available) in the dataset. The number of plots with data for each group are shown in Table 1.

2.4 Statistical analysis

The effect of land-use intensity was analyzed using the R package 'lmerTest' v2.0-32 (Kuznetsova *et al.*, 2014). Linear mixed effect models were build using the function lmer() provided within 'lmerTest'. Each model included an interaction between land-use intensity (one of the three modes or the land-use intensity index LUI) and the groups as fixed effects. Before testing effects on the three SAD descriptors, we tested if land-use intensity affected species richness and if species richness was correlated with any of the descriptors. Both the abundance decay rate and dominance were positively correlated with the number of taxonomic units (richness). Thus, in our analyses, we used the residuals from linear models between richness and abundance decay rate or dominance, respectively. We were not interested in estimating the differences in effects between regions, instead we allowed random variation of slopes and intercepts between regions within the groups. Therefore, we included two random effects in the model:

descriptor ~Land use*Group+ (1|Group:Region)+(0+Land use|Group:Region)

Including two random effects in the model ensured that the variation in slopes and variation in intercepts were uncorrelated. If one of the two random effects did show zero variation, it was excluded from the model. The overall effects of land-use intensity, group, and their interaction on the three descriptors were tested for significance using F-values from

ANOVA with Satterthwaite approximation for degrees of freedom. For the overall effect of land-use intensity, the different groups are ignored, hence one intercept and one slope across all data points is calculated. A significant effect of group indicates that intercepts differ between groups. The interaction term between land-use intensity and group tests if slopes differ between groups, but it does not show which of the groups differ from each other.

Differences in intercepts and slopes between the groups were hence tested for significance using t-Tests with the same approximation for degrees of freedom. Note, however, that differences are only tested against a reference group (in other cases, this would be a control group). All tests were performed with soil prokaryotes as reference group, because we expect this group to show the weakest reaction to land-use intensity, in which case it is most similar to a control group. While the choice of the reference group does not influence the estimates for intercepts and slopes, p-values from t-tests may differ slightly if effects are weak (see Table C.1 for an example). A significant t-Test for one group, e.g. plants, would show that the intercept of plants differs significantly from the intercept of soil prokaryotes. Equivalently, a significant t-Test for the interaction between land-use intensity and plants would show that the slope for plants is significantly different from the slope for soil prokaryotes. If intercept or slope of soil prokaryotes differ significantly from zero and none of the t-Tests with the other groups is significant, one could infer that intercepts and slopes are significantly different from zero in all groups. However, slopes or intercept could be intermediate and therefore neither different from soil prokaryotes nor from zero. Therefore, we will consider only significant effects for which the estimate and standard errors for intercepts or slopes do not include zero. Similarly, we will also identify non-significant effects for individual groups if the estimate and standard errors are clearly different from zero. Both F-tests and t-tests were run in the R package ‘lmerTest’ (Kuznetsova *et al.*, 2014).

3. Results

Across all groups and all 150 plots, 84,565 individuals of insects (below-and aboveground) and 4,193 occurrences of vertebrates were recorded. The 841,037 recorded sequences of soil prokaryotes and arbuscular mycorrhizal fungi (AMF) DNA were recorded, which represent 7,287 operational taxonomic units of prokaryotes and AMF (at the species level). We found 31 families of insect larvae, 1,121 species of insects and 94 vertebrate species. Additionally, 382 taxa of vascular plants, bryophytes and lichens were recorded (Table 1). The taxonomic richness across groups and within individual groups was not affected by the combined land-use intensity index LUI (Table 2), i.e. the number of species or their equivalent did not change with land-use intensity (Figure B.1 & Table D.1). Taxonomic richness within groups was negatively affected by mowing intensity (Figure B.1, Table D.2) but not by fertilization or grazing intensity (Figure B.1 & Table D.3-D.4).

3.1 Land-use intensity effects on SAD descriptors

The LUI index had a weak though significant positive overall effect on abundance decay rate, i.e. SADs across all groups became steeper with increasing land-use intensity (Table 2, Table D.5). Among the individual groups, we found a significant increase in abundance-decay rate for plants. Herbivores and vertebrates showed similar effect sizes as plants, though non-significant (Figure 2A, Table D.5). The intercepts differed strongly among groups, with the estimate for insect larvae being significantly higher and those of plants significantly lower than the estimate for soil prokaryotes (Figure 2A & Table D.5). Hence, insect larvae showed on average a much steeper SAD than soil prokaryotes or plants.

The effect of LUI on rarity (Fisher's alpha) differed among groups (Table 2). This interaction was driven by a significant decrease in rarity (i.e. a lower proportion of rare species under intensive land use) for plants, a slightly weaker decrease for insect larvae and an increase in rarity for bats and birds (Figure 2B & Table D.6). Hence, effects on abundance decay-rate in

plants were driven by a decrease in the proportion of rare species. For dominance, we found no overall effect of LUI and no effect in individual groups (Figure 2C & Table D.7).

3.2 Effects of land-use mode on SAD descriptors

Fertilization intensity showed a significant but weak positive overall effect on abundance decay rate across groups (Table 2, Table D.8) and weak positive effects for plants and insect larvae, i.e. their SADs increased in steepness with increasing fertilization (Figure 2D & Table D.8). The effect of fertilization on rarity differed significantly between groups, driven by a significant decrease in vertebrate rarity (i.e. lower proportion of rare species) and a weaker decrease in AMF rarity (Figure 2E & Table D.9). Fertilization showed a weak positive overall effect on dominance, i.e. the relative abundance of the most abundant species increases across all groups. Among individual groups, only insect larvae showed a slight increase in dominance with increasing fertilization intensity (Figure 2F & Table D.10). Overall, the effects of fertilization on the SAD descriptors resembles the effects of the LUI index.

Mowing intensity did not have an overall effect for any of the SAD descriptors across groups (Table 2). However, abundance decay rate and dominance of insect larvae increased significantly with increasing mowing intensity, while the other groups showed no effects (Figure 3A&C, Table D.11 & D.13). Mowing intensity had no significant effect on rarity for the individual groups, but insect larvae as well as bats and birds showed weak, though non-significant, decreases in rarity (Figure 3B & Table D.12). Taken together, SADs of insect larvae became steeper under frequent mowing, driven by both an increase in dominance and a loss of rare species.

The effect of grazing on abundance decay rate differed significantly among groups (Table 2), with a significant decrease in the abundance decay rate of insect larvae (an effect of similar size was found for AMF) and a significant increase in the abundance decay rate of herbivorous arthropods (Figure 3D & Table D.14). Only vertebrate rarity increased

383 significantly with increasing grazing intensity (Figure 3E & Table D.15). As for abundance
384 decay rate, the effect of grazing intensity on dominance differed among groups (Table 2), driven
385 by a significant increase in herbivorous arthropods and a decrease in insect larvae (Figure 3F
386 & Table D.16). In effect, above-and belowground arthropods showed changes in SADs under
387 intensive grazing, driven by changes in dominance. The effect of grazing intensity on
388 abundance decay rate and dominance of insect larvae and herbivorous arthropods was
389 influenced by a single plot with a very high grazing intensity, as effects became non-significant
390 after removing this plot (Table E.1-Table E.4).

4. Discussion

The combined land-use intensity (LUI) affected taxonomic richness only in plants and herbivores, while mowing intensity affected taxonomic richness in all groups. The absence of an overall effect of land-use intensity on taxonomic richness is at first surprising, given that Allan *et al.* (2014) found clear effects of LUI and its variability on the diversity of multiple groups on the same grasslands. However, the authors found that effects were non-linear and only few groups showed linear effects (see their Supplementary Information). Additionally, Allan *et al.* (2014) used slightly different datasets for the belowground groups and when they calculated effects of land-use intensity separately for below- and aboveground groups, they found no effect of LUI on the belowground groups. In our study, idiosyncratic changes in the shape of species-abundance distributions under increasing land-use intensity across groups are the most important finding.

4.1 Differences between groups

Belowground taxa that are often excluded from multi-group biodiversity studies due to difficulties in sampling, despite their important role for many ecosystem processes (Blossey and Hunt-Joshi, 2003). In our study, they were sufficiently well represented to allow the comparative assessment of responses between above and belowground groups. One notable difference between above- and belowground groups was that the average abundance decay rate and dominance differed more strongly among belowground groups than among aboveground groups. This effect is not an artefact of greater span in taxonomic richness in the belowground groups. Even though the taxonomic diversity of prokaryotes and arbuscular mycorrhizal fungi was much higher than the diversity of insect larvae, this does not account for the differences within the belowground groups, as both values were corrected for taxonomic richness.

Among belowground groups, arbuscular mycorrhizal fungi (AMF) showed the lowest dominance and shallow, i.e. even, abundance distributions. While we are not aware of other

studies which compared SADs between AMF and other groups, we can search other studies on AMF for similar abundance-distributions in other studies on AMF. Several studies found that the SADs of arbuscular mycorrhizal fungi fit better to lognormal or broken stick models than to geometric models (Dumbrell *et al.*, 2010; Unterseher *et al.*, 2011; Moebius-Clune *et al.*, 2013). Lognormal distributions are described as being relatively even with no strong dominant and many rare species, which is in line with our findings. One notable exception is the study by Moebius-Clune *et al.* (2013), who found a very pronounced dominance of the top ranked taxon in AMF communities associated to an annual monoculture (maize). As our grasslands are perennial and commonly more than 50 years old, AMF community structure seems to be driven by changes in agricultural practices rather than changes in intensity within the same management (cf. Jansa *et al.*, 2014). The generality of even distributions in belowground groups, particularly in the prokaryotes and arbuscular mycorrhizal fungi across our plots, with no detectable effect of land-use mode or intensity, might also be due to the ubiquitous distribution of the majority of the dominant OTUs across grasslands or due to the fact that DNA detection is not restricted to active or living organisms.

In contrast, insect larval abundance distributions showed high dominance of a few families and were more similar to the abundance structures of aboveground groups. Additionally, insect larvae were the only belowground group (with one exception in arbuscular mycorrhizal fungi), which often responded to land-use modes in similar ways as the aboveground groups. This is not surprising, as the adult stages of most insect larvae live aboveground. We might hence propose that there is a fundamental difference between the abundance structures of exclusively belowground groups as opposed to groups living partly or exclusively aboveground. Whether this difference holds also in other ecosystems, will require further exploration.

Among the aboveground groups, average abundance structures showed a lower variability, but the changes with increasing land-use intensity differed remarkably. In such

cases, it becomes clear how changes in dominance and rarity can explain the mechanisms behind an overall change in abundance structure. Plants showed an increase in the steepness of their abundance distributions and a decrease in the proportion of rare species with increasing land-use intensity. These changes are inherently related to management as more intense grassland management aims at increasing productivity, thereby fostering fast-growing and highly competitive plants (Gaujour *et al.*, 2012). This in turn suppresses the growth of less-competitive species, mostly of dicot herbs which comprise the majority of rare species (Socher *et al.*, 2013). While the proportion of rare plant species decreased with increasing land-use intensity, the dominance of the commonest species did not change. This indicates that increased nutrient availability does not promote a single species at a time, but several of the more abundant species.

The group with the closest link to plants –herbivorous arthropods– also showed steeper abundance-distributions under more intensive land use. In contrast to plants, this change was not driven by a decrease in the proportion of rare species but by an increase in dominance. Hence we can conclude that changes in abundance structure of one group cannot be expected to be indicative of changes in other groups, even for groups with close trophic links. This conclusion is also strengthened by the finding that pollinators did not show any changes in community structure.

Across the different groups, effects of the land-use modes on the abundance decay rate tended to be more often accompanied by an effect on dominance than by an effect on rarity. This indicates that the change in abundance decay rate was more often caused by an increase in the relative abundance of the most abundant taxon (species or equivalent). The close link between abundance decay rate and dominance encourages the use of a simple index such as the Berger-Parker dominance, which requires only the reliable recognition of the commonest species for rapid or initial community structure assessments.

Our study demonstrates that characteristics of species-abundance distributions are easily comparable and a useful tool to compare changes in communities across a range of taxonomic groups. Such a comparison is only possible if the communities are sampled in the same locations, i.e. under the same abiotic and land-use conditions. However, using the same sampling locations and size does not take into account the scales on which the different taxa react to their environment. In fact, the present study spans a large range of possibly effective scales, from square centimeters for soil prokaryotes to square kilometers for birds and bats. The study design ensured that soil conditions were homogenous within the sampled grasslands, but it does not control for landscape heterogeneity. While effects of landscape diversity are outside the scope of this study, we know that land-use intensity of the single grasslands is not correlated with the surrounding landscape diversity, i.e. more intensively managed grasslands are not more likely part of simplified landscapes (Gamez-Virues *et al.*, 2015). Hence, we can assume that the reactions of highly mobile species to land-use intensity are not a reflection of their reaction to the surrounding landscape. Nevertheless, landscape diversity might influence the attractiveness of individual grasslands for mobile species which was e.g. shown for feeding activity in bats (Treitler *et al.*, 2016).

This scale-dependency makes it clear that single groups have limited effectiveness as biodiversity indicators for other taxa, especially if these react on largely different scales. For example, soil prokaryotes will not be suitable indicators for taxa which are not restricted to the grassland sites (e.g. mobile arthropods or vertebrates) and birds or bats will not be suitable indicators for less mobile taxa (e.g. insect larvae). Several other authors (Lawton *et al.*, 1998; Billeter *et al.*, 2007; Dormann *et al.*, 2007; Gossner *et al.*, 2013) have already cautioned against the use of single indicator taxa for management or conservation strategies and our findings strengthen their arguments.

4.2 Differences between land-use modes

The intensity of grassland management reflects the desired level of plant biomass production with very productive sites being intensively managed. An increase in fertilizer application therefore often goes along with an increase in grazing or mowing intensity. One might hence expect similar effects on abundance structures for the different land-use modes. If effects are similar for the individual land-use modes, we also expect an even stronger effect for the combined LUI index. Contrary to this expectation, we did not find stronger effects of LUI compared to single land-use modes across groups and, in fact, detected some divergent effects among the single land-use modes.

Mowing and fertilization intensity increased the steepness of insect larvae abundance distributions, but grazing intensity had the opposite effect. One important effect of mowing for belowground organisms is that the shorter vegetation leads to an increase in soil temperature after mowing, leading to more opportunities for oviposition and faster larval development with higher soil temperature. Larval abundance has indeed been found to increase with the percentage cover of bare soil in the same plots (I. Sonnemann, *pers. comm.*). While higher soil temperatures should benefit all larvae, positive effects are expected to be most pronounced in dominant families, which may exhibit a more r-strategic life history (high fecundity and shorter life spans) and for which season and other environmental factors are also optimal at time of sampling. The dominant families were Bibionidae, Cecidomyiidae (both Diptera, flies) and Staphylinidae (Coleoptera, beetles), comprising between 80% and 96% of all individuals on plots with high mowing frequency. While mowing increases soil temperature evenly across a grassland, grazing creates patches of dry-warm and of cold-moist soil. This increase in small-scale habitat diversity may accommodate species with distinct tolerances and physiological optima, and can reduce the steepness of the abundance distribution in insect larvae under this particular land-use mode.

For the sampled vertebrate groups – bats and birds – a higher level of grazing intensity entailed a higher proportion of rare species; conversely, this proportion decreased with increasing mowing and fertilization intensity. Possible reasons for the negative effect of mowing and fertilization could be a more homogeneous vegetation structure which is not attractive for ground-breeding birds such as the Eurasian skylark (*Alauda arvensis*), which has been found to be very sensitive to agricultural activities in grasslands (Donald *et al.*, 2002). A homogenous canopy structure also lacks taller plants (e.g. thistles) which are used by different birds as stalking perches. By contrast, grazing produces a patchy vegetation cover including spots of bare soil (important as dust baths for some birds) or water holes. The feces of grazing animals may also increase the abundance of dung beetles, flies, and other insects. Those can hide less well in the short vegetation and are hence easily captured by birds and bats. Additionally, the dominance of herbivorous arthropods increased with increasing grazing, suggesting that resource availability for carnivorous birds also increases. All those factors should lead to a decreased competition for resources among predaceous vertebrates on grazed sites, which allows more species to persist ('More Individuals Hypothesis'; Srivastava and Lawton, 1998).

Our results show that each land-use mode has distinct effects on different groups and needs to be considered separately when studying land-use effects on ecological communities. Again, using dominance and rarity as additional parameters to the overall shape of abundance structures shed light on the potential mechanisms behind the different effects of individual land-use modes.

5. Conclusions

Species-abundance distributions (SADs), together with species richness and species composition, represent the primary properties of ecological communities (Vellend, 2016) and, as such, offer a number of insights into the structure of ecological communities. Granted that one cannot demonstrate causal mechanisms from pattern analysis alone (but see Shipley, 1999), candidate processes are suggested by distinct patterns and indicate avenues for further research (e.g. Magurran, 2005). By using simple descriptors of SADs we bypass the a priori choice of a particular theoretical model, which commits one to its assumptions and particular parameters, and also avoid the shotgun fit of data to an array of different models without regard to their conceptual basis or implications.

Our analysis showed that within communities, effects of land-use intensity can be stronger on community structure than on species richness. Therefore, we recommend the inclusion of species-abundance distributions in the standard toolkit of biodiversity studies in terrestrial habitats. They are easy to use, comparable across groups and disentangle effects on common and rare species. We also showed that the intensification of different land-use modes has divergent effects on community abundance structures and that effects are not consistent between different groups. Hence, studies on land-use effects on biodiversity should consider the different modes on land use as well as multiple taxonomic or functional groups.

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Figure legends

Figure 1: Conceptual figure of the three SAD descriptors (left graph) and examples of species-abundance distributions from our data set (right graphs). The abundance decay rate indicates the steepness of the distribution (indicated by the grey solid line). Berger-Parker's dominance is a descriptor of the dominance of the most common taxonomic unit (species, family or OUT) and calculated as the relative abundance of this commonest taxonomic unit in relation to the overall abundance (indicated by the grey arrow). Fisher's alpha is a descriptor of the proportion of rare species (indicated by the grey points). The upper right graph shows data from pollinators which were sampled on an unfertilized, grazed grassland in the region Hainich-Dün and was selected as it shows the highest abundance decay rate in a community with more than 20 species. The lower right graph shows data from plants (i.e. vascular plants, bryophytes and lichens) which were sampled on an unfertilized, grazed grassland in the region Schwäbische Alb and was selected as it shows the lowest abundance decay rate among the communities with a similar number of species as the other examples.

Figure 2: Effects of combined land-use intensity (A-C) and fertilization intensity (D-F) on the three descriptors of the species-abundance distributions of seven groups (different colors). Lines show the predicted values from linear mixed effect models with the shaded area indicating the standard deviation of the slope and intercept between regions within groups. For abundance decay rate and dominance, mixed effect models were calculated for residuals taken from linear models between taxonomic richness and abundance decay rate and dominance, respectively, to estimate the effect of land-use intensity independent of the effects on taxonomic richness. Solid lines indicate significant ($p < 0.05$) interactions between the respective group and the slope from t- tests conducted on the linear mixed effect models.

Figure 3: Effects of mowing (A-C) and grazing (D-F) intensity on the three descriptors of the species-abundance distributions of seven groups (different colors). Lines show the predicted values from linear mixed effect models with the shaded area indicating the standard deviation of the slope and intercept between regions within groups. For abundance decay rate and dominance, mixed effect models were calculated for residuals taken from linear models between taxonomic richness and abundance decay rate and dominance, respectively, to estimate the effect of land-use intensity independent of the effects on taxonomic richness. Solid lines indicate significant ($p < 0.05$) interactions between the respective group and the slope from t- tests conducted on the linear mixed effect models.

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826

827 **Data Accessibility**

828 Species-abundance data are already published for the following taxa:

- 829 • Herbivorous arthropods: Simons, N. K., M. M. Gossner, T. M. Lewinsohn, S. Boch, M.
830 Lange, J. Müller, E. Pašalić, S. A. Socher, M. Türke, M. Fischer, and W. W. Weisser.
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- 833 • Plants: Simons, N. K., M. M. Gossner, T. M. Lewinsohn, S. Boch, M. Lange, J. Müller,
834 E. Pašalić, S. A. Socher, M. Türke, M. Fischer, and W. W. Weisser. 2014. Resource-
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- 837 • Pollinators (anonymized, species names available upon request): Weiner, C. N., M.
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- 841 • Birds (2008): Renner, S. C., M. M. Gossner, T. Kahl, E. K. Kalko, W. W. Weisser, M.
842 Fischer, and E. Allan. 2014. Temporal changes in randomness of bird communities
843 across Central Europe. Plos One 9:e112347.

844 The following species-abundance matrices are made publicly available after an embargo period
845 within the Biodiversity Exploratories Information System at <https://www.bexis.uni-jena.de>

- 846 • Insect larvae: 16746 (Data Identifier)
- 847 • Bats & Birds: 13146 & 15187
- 848 • Bryophytes & Lichens: 4140 & 5522
- 849 • Arbuscular mycorrhizal fungi: 19786
- 850 • Soil prokaryotes: 18086

851 **Supporting Information**

852 The following Supporting Information for this article is available online:

853 Appendix A: Detailed methods for the sampling of arbuscular mycorrhizal fungi.

854 Appendix B: Effects of the combined land-use intensity and the land-use modes on taxonomic
855 richness.

856 Appendix C: Example for the difference in p-values depending on the selected control group
857 within the mixed effect models.

858 Appendix D: Full statistic tables of linear mixed effect models on species richness and SAD
859 descriptors for combined land-use intensity and the three land-use modes.

860 Appendix E: Full statistic tables of linear mixed effect models on species richness and SAD
861 descriptors including grazing intensity without the highest grazing intensity.

Figure 1

Figure 2

Figure 3