Losers, winners, and opportunists: How grassland land-use intensity affects orthopteran communities

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Abstract. Land use and corresponding habitat loss are major drivers of local species extinctions. Orthoptera as important grassland herbivores showed different responses to land-use intensity in different studies, and the susceptibility of this group remains unclear. We sampled annually for seven years 150 temperate grassland sites across three regions in Germany, for which land-use gradients were quantified as mowing, grazing, and fertilization intensity. We analyzed the effects of land-use intensity on orthopteran diversity and community abundance. To describe species-specific responses to environmental gradients, we employed a new approach termed “niche model,” coupled with a randomization procedure, which is sensitive even for rare species for which trends may otherwise be difficult to detect. Based on abundance-weighted means for each species, we quantified the species’ occurrence along land-use gradients and identified potential losers and winners of intensive land use. Overall, high land-use intensity negatively affected orthopteran diversity across years and regions, corresponding to decreases with high fertilization, mowing, and grazing intensity. Intensive mowing and grazing negatively affected abundance. Diversity and abundance increased with the time after the last cut. The niche model detected 15 of 29 Orthoptera species as losers of land use, showing significantly higher abundance in grasslands with low-intensity land use. Two species were winners of high land-use intensity, whereas the remaining 12 were assigned as opportunists. Most species were losers of high fertilization intensity, followed by frequent mowing. Grazing intensity was least detrimental at the species level. Omnivorous, herbivorous, and graminivorous species did not differ in their response to land-use intensity, whereas bryovorous/lichenivorous Tetrix species showed consistently negative responses to intensive land use. Our highly replicated, long-term and large-scale survey suggests that further land-use intensification threatens many Orthoptera and causes a consistent diversity loss. Low intensity of fertilization, infrequent mowing, and variable grazing will help to maintain a high diversity of orthopterans. The generality of our niche model approach advances studies on species’ susceptibility in various study systems.

Key words: anthropogenic disturbance; Biodiversity Exploratories; effective Shannon diversity; feeding habit; grasshoppers; grassland management; habitat niche; insect herbivory; land use; mowing date; Orthoptera.

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INTRODUCTION

The current loss of species is to a great extent caused by anthropogenic influences (Pimm et al. 1995, Hooper et al. 2005), especially by land-use change and intensification (Tilman et al. 2001) and by the corresponding loss or fragmentation of habitats (Krauss et al. 2010). Intensified land use is often described to decrease biodiversity, such as plant species richness (Haddad et al. 2000, Kleijn et al. 2009) and insect diversity (Haddad et al. 2000, Allan et al. 2014). These negative effects are often related to nitrogen input by fertilization (Van Den Berg et al. 2011, Socher et al. 2012, Simons et al. 2014). Decreased biodiversity translates into decreased ecosystem performance and stability, which can partly be explained by a loss of functional diversity (Tilman et al. 1997, Birkhofer et al. 2015). Reduced plant species richness, for instance, has a negative effect on the temporal stability of net productivity (Tilman et al. 2006) and may decrease the resistance of communities against invasive species (Hooper et al. 2005). Many trophic levels in turn suffers from reduced species richness of plants. Microbial biomass and fungal abundance decline with decreasing plant species richness (Zak et al. 2003) and arthropod species richness declines (Haddad et al. 2001, 2009, Allan et al. 2014, Simons et al. 2014), especially of herbivorous insects (Scherber et al. 2010).

Among arthropods, Orthoptera are important herbivores in grassland ecosystems as they consume a considerable portion of grasses and forbs (Köhler et al. 1987, Blumer and Diemer 1996), regulate plant community structure (Zhang et al. 2011), and are important food organisms for birds (Ingrisch and Köhler 1998), spiders, and lizards (Ingrisch and Köhler 1998). The functional role of Orthoptera in grassland ecosystems is also illustrated by their influence on nutrient cycling by enhancing the conversion of biomass through their easily transformable frass (Samways 1994). Orthoptera are widespread across grasslands and often sensitive to environmental changes (Guido and Gianelle 2001, Gardiner et al. 2002, Jonas and Joern 2007, Bharamal and Koli 2014), which makes them suitable for studying land-use effects on biodiversity.

Responses of Orthoptera communities to land use and other disturbances have been described by different studies across different ecosystems and showed distinct consequences. Studies in temperate grasslands showed that intensive grazing reduced orthopteran species richness and Shannon diversity (Branson and Sword 2010), fertilization led to reduced survival (Ebeling et al. 2013) or decline in orthopteran species richness (Marini et al. 2008), and mowing strongly reduced grasshopper densities (Humbert et al. 2010). In addition to direct management effects such as increased mortality by mowing, indirect effects such as changes in plant community composition can also affect orthopteran communities (Jonas et al. 2002, Schaffers et al. 2008, Unsicker et al. 2010, Hao et al. 2015). However, also positive effects of nitrogen addition on orthopteran densities (Haddad et al. 2000, Ritchie 2000) have been reported. Grazing and mowing showed both positive and negative effects on Orthoptera diversity and abundance (Ingrisch and Köhler 1998), depending on management intensity. Data from extensive long-term studies with consideration of the susceptibility of all local Orthoptera species—abundant species as well as rare species—are needed to better understand the variation in susceptibility of this important group of herbivores.

We studied responses of Orthoptera to grassland land use within a large-scale and long-term project in three regions of Germany (Fischer et al. 2010). These grasslands are managed by fertilization, mowing, and grazing with different intensities (Blüthgen et al. 2012). By covering a broad range of land-use intensities, this research platform provides unique opportunities to study determinants of orthopteran community structure in an authentic scenario, which is an alternative to laboratory and artificial field studies.

Here, we examined the effects of land-use intensity on orthopteran abundance, diversity, and community composition, particularly the influence of the different management types: fertilization, mowing, and grazing. To infer causal effects of the three management types on orthopteran communities, we compared Orthoptera diversity and abundance with their incidence. In extension to other studies on Orthoptera responses to land use, we investigated these responses on a species-specific level and analyzed the niche breadth of single species with a niche model combined with a randomization approach. For each Orthoptera
species, we defined a “habitat niche” based on the occurrence and abundance across 150 grassland sites of variable land-use intensities during seven years, allowing us to distinguish losers, winners, and opportunists of intensified land use. In contrast to aggregate diversity measures such as the common Shannon diversity, species richness or other multispecies indices (Vačkář et al. 2012), this methodology considers rare species and gives an opportunity to evaluate each species’ response along environmental gradients. Our simple approach can also be used to describe the species’ responses to other environmental gradients, for example, temperature, pH, or moisture.

Based on findings from other studies (Hohl et al. 2005, Marini et al. 2008, Branson and Sword 2010, Humbert et al. 2010), we expected intensive land use to decrease orthopteran abundance and diversity, leading to more species being losers than winners within the community, that is, more species predominantly occur at low-intensity grasslands.

Materials and Methods

Study site

The study was conducted within the framework of the Biodiversity Exploratories, which covers three different regions across Germany (Fischer et al. 2010), the biosphere reserve Schorfheide-Chorin (SCH; 53°02′ N, 13°83′ E, 2–139 m a.s.l., area about 1300 km², annual mean precipitation 500–600 mm, mean annual temperature 8–8.5°C) in the northeast, the national park of Hainich-Dün and its surrounding areas (HAI; 51°20′ N, 10°41′ E, 285–550 m a.s.l., 1300 km², 500–800 mm, 6.5–8°C) in the center, and the biosphere reserve Schwäbische Alb (ALB; 48°43′ N, 9°37′ E, 460–860 m a.s.l., 420 km², 700–1000 mm, 6–7°C) in the southwest of Germany. Every area contains 50 grassland sites (each 50 m × 50 m), which represent agriculturally used meadows or pastures along a land-use intensity gradient and are managed by local farmers. Type and intensity of management is assessed yearly since 2006 by standardized interviews with the farmers and landowners. The three components that shape land-use intensity of grasslands—fertilization (kg N·ha⁻¹·yr⁻¹), mowing (cuts/yr), and grazing (livestock units·grazing days·ha⁻¹·yr⁻¹)—are combined in an index of land-use intensity (LUI; Blüthgen et al. 2012). The LUI was calculated as the sum of the globally standardized land-use components (intensities per site were divided by the global mean of all sites in all regions) of each site and then square-root-transformed for a more even distribution.

Sampling design

The study was conducted from 2008 to 2014, assessing orthopterans in 150 grassland sites of the three regions. In 36 of 1050 sampling occasions, sites could not be sampled in a given year because entering was not permitted at the survey time. Sampling from 2008 to 2013 was conducted twice per year in June and August, where each site was sampled by standardized sweep-netting during a long-term arthropod survey (Simons et al. 2015). On each grassland site, 60 double sweeps were conducted along the borders of the site, which are 200 m in length. For the analyses, we only included sites which were sampled twice per year. In 2014, we conducted a more specific sampling campaign for orthopterans with a biocenometer (1 m × 1 m area, height 0.6 m), which is an aluminum frame covered with gauze and is quickly placed on an area to prevent insects from fleeing from the area before capture. This method provides an assessment of standardized densities of both active and inactive individuals and a more complete sampling by covering the herb as well as the ground layer. In August 2014, each region was sampled within 14 d, by randomly sampling ten units of 1 m² on each site along the same transect as above. All Orthoptera were collected and determined to species level (determination 2014: M. N. Chisté; 2008–2013: G. Köhler). Our analyses are based on a total of 3752 adult individuals (2099 in 2014 with the biocenometer; 1653 by sweep-netting in 2008–2013) we found from 2008 to 2014.

Data analysis

Combined land-use intensity (LUI) effects on diversity and abundance.—Orthopteran diversity was analyzed as a response to gradually increasing land-use intensity. To quantify diversity, Shannon’s diversity index $H'$ was calculated for each site and year, which considers both species richness and the abundance distribution. For analysis and graphics, the more tangible effective Shannon diversity $eH'$ (Jost 2006) was used, which can be interpreted as “effective” number of
of the three management types, that is, fertilized/ 
were then compared with the incidence of each 
for the effects of LUI. Our response variables 
were related to these factors as described above 
mowing, and grazing, our response variables 
of the individual management types, fertilization, 
diversity and abundance. —To assess the influence 
therefore not included in our model. This factor is 
way as the respective site, and found no effect of 
this factor on all response variables. This factor is 
50 × 50 m sites, which is managed in the same 
size of the whole grassland, containing our 
random effects.

Effects of fertilization, mowing, and grazing on diversity and abundance. — To assess the influence of the individual management types, fertilization, mowing, and grazing, our response variables were related to these factors as described above for the effects of LUI. Our response variables were then compared with the incidence of each of the three management types, that is, fertilized/ unfertilized, mown/unmown, and grazed/ ungrazed. In addition to the effects on all sites, we analyzed the effects of mowing, grazing, and fertilization intensity with exclusion of unmown, ungrazed, and unfertilized sites. Modeling occurred as described above. For the temporal effects of mowing, our response variables were related, exemplarily for 2014, to the number of days between the last cut and the sampling date by linear modeling for the sites, where this information was available.

Abundance-weighted means and niche model. — To define the ecological niches of orthopterans on a species level, abundance-weighted means (AWMs) of land-use intensity for each species were calculated. AWMs of the LUI, fertilization, mowing, and grazing intensity were calculated. AWMi of a species i was calculated as

$$AWM_i = \sum_{s=1}^{150} \sum_{y=2008}^{2014} p_{i,s,y} \cdot L_{s,y}$$

where $$p_{i,s,y}$$ is the proportion of individuals of species i found in site s in year y in relation to its total abundance across all sites and all years ($$\sum_s \sum_y p_{i,s,y} = 1$$) and $$L_{s,y}$$ is the land-use intensity on site s in year y. $$L_{s,y}$$ was calculated for each year using respective land-use intensities of the sampling year. We also checked the analyses with previous years’ LUI and found that AWMs of previous years strongly correlated with AWMs of respective years. As a proxy for the niche breadth of a species, we also calculated the abundance-weighted SD (AWSD), weighted by the proportion of abundance.

For statistical analysis of the AWMs, we have chosen a randomization approach, based on the null model that an Orthoptera species can occur on every site with the same likelihood and describes the most probable site conditions for that species. The null model chooses LUI, mowing, grazing, or fertilization intensities of random sites for each species, considering the number of sites, where this species occurs, and calculates after 10,000 iterations an expected value of the site conditions for each species. To avoid repeated consideration of sites, intensities were averaged across the years 2008–2014 for the null model. The null model was restricted to the one, two, or three regions in which the species was recorded (Appendix S1: Table S2); for example, when a
species only occurred in region ALB, the null model picked a given number of sites from the pool of 50 sites in ALB only. The objective of this restriction was to consider distribution boundaries of single species across Germany. As in any randomization model, the proportion of AWMs from 10,000 null models with greater or smaller AWMs respectively than the observed value provides the $P$-value for the significance of the deviation between observed and expected values. Species with significantly smaller observed than expected AWMs were declared as “losers,” and species with significantly higher AWMs than expected were declared as “winners.” For species which could be classified neither as “losers” nor as “winners,” we tested whether they could be specialized on intermediate land-use levels, that is, whether they have an intermediate AWM with a narrower niche than expected. Therefore, we compared the observed and expected weighted coefficient of variation (CV = AWSD/AWM) to account for the increase in SD with increasing mean. This comparison allows us to distinguish “opportunists” (observed CV ≥ expected CV) from species that are “specialized” on intermediate land-use intensities (observed CV < expected CV and species not only occurred on one site, i.e., CV ≠ 0); the latter apply only to those species that are not significant winners or losers.

The different feeding habits of each species (Ingrisch and Köhler 1998) were classified, which are herbivorous (H) feeding on different plants, graminivorous (G) feeding on grass only, omnivorous (O) feeding on animals and plants, and bryovorous–herbivorous (BH) species feeding on moss, algae, lichens, and plants, and tested if AWMs responded differently to the feeding habits based on an ANOVA.

Leptophyes punctatissima (Bosc, 1792), Meconema thalassinum (De Geer, 1773), and Tettigonia viridissima (Linnaeus, 1758) were excluded from the niche analysis, because these species are shrub or tree-dwelling and occur only coincidently in grasslands (Ingrisch and Köhler 1998).

**RESULTS**

**Combined land-use intensity (LUI) effects on diversity and abundance**

A total of 32 Orthoptera species out of eight subfamilies were recorded in 150 sites, thereof 19 in ALB, 19 in SCH, and 14 in HAI. The mean ($±$SE) orhtopteran effective Shannon diversity $e_{H}$ of 2008–2014 (Fig. 1a) was highest in region SCH (1.51 ± 0.05), followed by HAI (0.87 ± 0.05) and ALB (0.82 ± 0.06). Mean abundance per site (Fig. 1c) was highest in region SCH (5.72 ± 0.66), followed by ALB (2.90 ± 0.31) and HAI (2.88 ± 0.34). Both diversity and abundance differed significantly across regions in 2014, but not based on the earlier data set (Appendix S1: Table S3).

Orthopteran diversity, but not abundance, declined significantly with increasing land-use intensity, consistently across all regions and years, both in 2008–2013 ($F_{1,424.4} = 10.42, P < 0.01$) and in 2014 ($F_{1,134} = 13.21, P < 0.001$; further information in Appendix S1: Table S3).

When analyzing years separately, in four of seven years increasing LUI significantly reduced orthopteran diversity (Fig. 1b); in the remaining three years, no significant effects despite a consistent trend (Appendix S1: Table S4) were found. LUI significantly decreased Orthoptera abundance in 2013, but not in the remaining years (Fig. 1d; Appendix S1: Table S4). Predominant negative slopes also confirmed negative effects on orthopteran diversity and abundance, even in years or regions, where effects were not significant (Appendix S1: Table S4). Results for species richness were consistent with results for $e_{H}$ (Appendix S1: Table S3).

**Effects of fertilization, mowing, and grazing on diversity and abundance**

Fertilization intensity had a significant negative effect on $e_{H}$ in 2008–2013 in all regions, but not in 2014 (Table 1). Abundance in all years and all regions was not significantly affected by fertilization intensity. Mowing frequency had a significant negative effect on Orthoptera abundance in 2008–2013, but not in 2014 (Table 1). Diversity $e_{H}$ significantly decreased with mowing frequency in 2014, but not in 2008–2013. For 2014, we found a significant interaction between region and mowing intensity for diversity. Mowing-intensity effects on $e_{H}$ were negative in region ALB ($F_{1,46} = 13.37, P < 0.01$) and HAI ($F_{1,48} = 0.001, P = 0.982$) and positive but not significant in region SCH ($F_{1,40} = 0.07, P = 0.796$). Grazing intensity significantly reduced $e_{H}$ and orthopteran abundance in 2014, while in the
remaining years grazing had no significant effects. Orthoptera abundance and \( e^{HF} \) differed significantly across regions for the three different management types (Table 1). Results for species richness were consistent with results for \( e^{HF} \), except that mowing intensity in 2014 had a significant effect on species richness in all three regions (Appendix S1: Table S5).

Analyzing the incidence of land use (Fig. 1e–p; Appendix S1: Tables S6 and S7), we found that
fertilized sites were significantly less diverse than unfertilized sites across the first six sampling years (Fig. 1e; \( F_{\text{NumDF}} = 1 \), \( F_{\text{DenDF}} = 368.35 \), \( F_{\text{P}} = 5.518 \), \( p = 0.019 \)). Within fertilized sites, orthopteran diversity significantly decreased with increasing nitrogen amounts applied in 2008–2013 (\( F_{1,307.04} = 5.637 \), \( p = 0.018 \)), but not in 2014 (Fig. 1f; \( F_{1,140} = 0.912 \), \( p = 0.345 \)). Mown sites had a smaller diversity (Fig. 1i; \( F_{1,140} = 6.941 \), \( p = 0.009 \)) and species richness than unmown sites in 2014 and showed lower abundances of orthopterans in 2008–2013 (Table S6 and S7; \( F_{1,266.59} = 4.323 \), \( p = 0.039 \)). Grazed and ungrazed sites did not differ in diversity (Fig. 1m; 2014: \( F_{1,140} = 0.865 \), \( p = 0.174 \); 2008–2013: \( F_{1,348.07} = 0.771 \), \( p = 0.380 \)) or abundance (Fig. 1o; 2014: \( F_{1,140} = 1.358 \), \( p = 0.246 \); 2008–2013: \( F_{1,334.57} = 1.288 \), \( p = 0.257 \)) in all sampling years. In 2014, cattle-grazed sites were significantly less diverse (Fig. 1n; \( F_{1,95} = 9.704 \), \( p = 0.002 \)) and species-rich (Appendix S1: Table S7) than sheep-grazed sites, and within sheep-grazed sites, diversity of Orthoptera also declined significantly with the intensity of grazing (\( F_{1,38} = 4.49 \), \( p = 0.041 \)). Abundance did not differ between sheep-grazed and cattle-grazed sites (Fig. 1p; 2014: \( F_{1,95} = 0.031 \), \( p = 0.862 \); 2008–2013: \( F_{1,107.55} = 0.078 \), \( p = 0.748 \)).

Concerning the timing of mowing in 2014, diversity (\( F_{1,60} = 4.50 \), \( p = 0.031 \)) and abundance (\( F_{1,60} = 4.25 \), \( p = 0.047 \)) of Orthoptera significantly increased with the time span since the last cut (Fig. 2a, b).

**Notes:** We distinguish between effects of intensity (Int) of fertilization (kg N·ha\(^{-1}\)·yr\(^{-1}\)), mowing (cuts/yr), and grazing (livestock units·grazing days·ha\(^{-1}\)·yr\(^{-1}\)), of the sampling region, and of the interaction between region and intensity on orthopteran effective Shannon diversity \( eH_{\text{uni}} \) and abundance in all three regions during the two sampling periods. Significant effects of management intensity are shown in bold. This analysis includes all 150 sampling sites, and also unfertilized, unmown, or ungrazed sites.

### Table 1. Management effects on Orthoptera diversity and abundance.

| Response | 2008–2013 | 2014 |
|----------|-----------|------|
|          | Int Region | Int × region | Int Region | Int × region |
| **Fertilization** | | | | |
| Diversity | Slope | -0.002 | -0.006 |
|           | \( F \) | 8.619 | 19.472 |
|           | \( P \) | 0.003 | <0.0001 |
| Abundance | Slope | -0.004 | -0.039 |
|           | \( F \) | 0.428 | 7.447 |
|           | \( P \) | 0.513 | 0.001 |
| **Mowing** | | | | |
| Diversity | Slope | -0.075 | -0.282 |
|           | \( F \) | 1.578 | 8.362 |
|           | \( P \) | 0.210 | <0.001 |
| Abundance | Slope | -0.398 | -0.780 |
|           | \( F \) | 4.694 | 6.183 |
|           | \( P \) | 0.031 | 0.002 |
| **Grazing** | | | | |
| Diversity | Slope | <0.0001 | -0.001 |
|           | \( F \) | 0.564 | 18.368 |
|           | \( P \) | 0.453 | <0.0001 |
| Abundance | Slope | 0.001 | -0.011 |
|           | \( F \) | 0.023 | 6.101 |
|           | \( P \) | 0.880 | 0.003 |

**Notes:** We distinguish between effects of intensity (Int) of fertilization (kg N·ha\(^{-1}\)·yr\(^{-1}\)), mowing (cuts/yr), and grazing (livestock units·grazing days·ha\(^{-1}\)·yr\(^{-1}\)), of the sampling region, and of the interaction between region and intensity on orthopteran effective Shannon diversity \( eH_{\text{uni}} \) and abundance in all three regions during the two sampling periods. Significant effects of management intensity are shown in bold. This analysis includes all 150 sampling sites, and also unfertilized, unmown, or ungrazed sites.

Most species were found on sites with land-use intensities lower than the mean intensities over all years across all regions. This is illustrated by their AWM on the left side of the dashed line in Fig. 3. Only few species were winners of high land-use intensity or of high intensities in the three management types (Fig. 3, Table 2; more detailed in Appendix S1: Table S8).
The vast majority of Orthoptera species occurred at higher abundance on sites with low land-use intensity; that is, their observed abundance-weighted mean (AWM) of LUI was lower than the expected mean LUI based on a random selection of sites (Fig. 3a, Table 2). One half of our Orthoptera species showed a significant deviation from the null model (losers), and about 40% of species showed no higher abundances on specific LUI (opportunists). More than 90% had an AWM of fertilization less than expected by the null model, thereof almost a third of the sampled species occurred only on unfertilized sites. Almost a third of our sampled species significantly occurred on less intensively fertilized sites (losers); the rest of the species were opportunists. There was no winner of fertilization intensity (Fig. 3b, Table 2). Most orthopterans occurred on rarely mown sites, more than a quarter had significantly smaller observed than expected AWMs of mowing (losers), and more than 60% were opportunistic concerning mowing intensity (Fig. 3c, Table 2). Most orthopteran AWMs for grazing intensity were smaller than the expected mean value (Fig. 3d, Table 2) with almost the same number of species significantly occurring either on strongly grazed sites or on weakly grazed sites, which means that the number of winners and losers of grazing intensity was similar. More than 70% of opportunistic orthopterans concerning grazing intensity were found.

Omnivores, herbivores, and graminivores did not differ in their sensitivity to compound LUI (Fig. 3) and were found throughout the different land-use intensities. Bryovorous species (Tetrix spec.), however, were found predominantly on low-intensity sites (Fig. 2) and differed significantly from herbivorous species concerning their AWM for the compound LUI (Tukey test, \( P < 0.01 \)). Herbivorous Orthoptera differed significantly from bryovorous (\( P < 0.01 \)), graminivorous (Tukey test, \( P < 0.01 \)), and omnivorous species (\( P < 0.001 \)) concerning their AWM for grazing intensity.

**DISCUSSION**

Orthoptera diversity generally decreased with increasing grassland land-use intensity. Among the three management types, fertilization had the strongest negative effect, followed by mowing and grazing. Total Orthoptera abundance did not show a consistent decline, but revealed strong effects at the species level: Most orthopterans had higher abundances at low-intensity grasslands, particularly at unfertilized and infrequently mown sites. This species-level pattern, revealed by a newly developed method that describes the species’ tolerance by combining weighted means with a null model approach, corresponds to diversity decline, but also allows for a more informative and powerful analysis than the analysis of diversity decline alone. Orthopterans seem to be more affected by combined land-use intensity, as we found higher proportions of opportunists within the single management types.
Fig. 3. Land-use niches of each orthopteran species, reflecting those grasslands in which they occur most frequently: (a) abundance-weighted mean of the compound land-use intensity (LUI) of their sites, (b) the fertilization intensity (kg N·ha⁻¹·yr⁻¹), (c) mowing intensity (cuts/yr), and (d) grazing intensity (livestock units·grazing days·ha⁻¹·yr⁻¹) from 2008 to 2014, along with weighted SDs (corresponding to niche breadth). Open dots in the top represent the mean and SD of land-use levels across all 150 sites from 2008 to 2014; abundance is shown in parentheses behind species names. Feeding habits of the different species are herbivorous (H), omnivorous (O), graminivorous (G), and bryovorous–herbivorous (BH).
General effects of land use (LUI)

Grasslands with increasing combined land-use intensity (LUI) hosted less diverse orthopteran communities and were often also less frequented by Orthoptera. Also at the species level, we found that most of the species were losers of high LUI, some were opportunists, and only three species were winners of combined LUI. The combination of the three management types adds up to a stronger disadvantage to grasshoppers than each of them alone. Diversity declines of different insect taxa through intensified land use are known from previous studies (Haddad et al. 2000, Allan et al. 2014, Simons et al. 2014), where frequent disturbance and habitat loss may be the major reasons for declining diversity. Orthoptera may be susceptible to fluctuations in the appearance of their habitats in intensively managed grasslands, like changes in vegetation height (Gardiner et al. 2002), which alter the microhabitats they need. Different management types will result in different microhabitats and changes, which are discussed below.

The regional differences in orthopteran diversity and abundance are mainly based on the geographical and thus climatic and ecological differences of the three regions and did not occur unexpectedly. Communities differ regionally and species have different altitudinal and habitat distribution boundaries across Germany (Ingrisch and Köhler 1998).

Fertilization

Fertilization was the most influential land-use type in grasslands, showing the strongest negative effects on diversity and single species occurrences with many species not tolerating fertilization at all. Although fertilization increases plant productivity (Ritchie 2000), it often reduces plant species diversity (Bakelaar and Odum 1978, Haddad et al. 2000). Insect species diversity (Haddad et al. 2000), especially of herbivorous insects including orthopterans (Scherber et al. 2010), is positively related to plant species richness in experimental grassland systems, and naturally assembled grasslands (Simons et al. 2014). Plant species richness may also have positive effects on the fitness of grasshoppers (Unsicker et al. 2010). Indeed, in the sampled grasslands researchers also found a strong decrease in plant diversity with increasing land-use intensity (Socher et al. 2013, Simons et al. 2014), corresponding to the decline in Orthoptera species diversity. Simons and colleagues (2014) also concluded that herbivore diversity (including Orthoptera) is more strongly affected by changes in plant diversity than by changes in plant biomass. Fertilization had the most consistent negative effect on plant diversity and positive effect on plant biomass across two years and the three regions (Simons et al. 2014). The increase in plant biomass did however not increase herbivore biomass which could have in turn increased herbivore diversity. Diversity of plants seems thus to play a key role in the context of diversity loss of Orthoptera.

Both plants and herbivores usually benefit physiologically from higher nutrient availability and thus fertilization (Ritchie 2000), but species may suffer from an increased interspecific

| Intensity | Losers | Winners | Opportunists |
|-----------|--------|---------|--------------|
| LUI       | obs = 0 | obs < exp (P < 0.05) | obs > exp (P < 0.05) | obs < exp | obs > exp |
| Fertilization | 9 (31.0%) | 9 (31.0%) | 18 (62.1%) | 2 (6.9%) | 18 (62.1%) | 3 (10.3%) |
| Mowing | 5 (17.2%) | 8 (27.6%) | 3 (10.3%) | 0 | 15 (51.7%) | 3 (10.3%) |
| Grazing | 1 (3.4%) | 4 (13.8%) | 3 (10.3%) | 18 (62.1%) | 4 (13.8%) | 4 (13.8%) |

Notes: Number and percentage of the 29 Orthoptera species that occurred with significantly higher abundances on lower land-use intensity than expected (obs < exp) are shown in bold and declared as “losers.” Species with “obs = 0” were only found on sites with intensities of zero (none of the sites had a LUI of zero) and are included in species percentages with bold “obs < exp.” Species that occurred with significantly higher abundances on higher land-use intensities than expected (obs > exp) are shown in bold and declared as “winners.” “Opportunists” are species with no significantly higher abundance on specific land-use intensities; directions of their occurrences are shown as “obs < exp” or “obs > exp.” We show losers, winners and opportunists of the compound land-use intensity index (LUI), fertilization intensity (kg N·ha⁻¹·yr⁻¹), mowing (cuts/yr) and grazing (livestock units·grazing days·ha⁻¹·yr⁻¹).
competition—one important reason why diversity declines whereas abundance remains unchanged or even increases. In fact, higher fertilization intensity led to steeper abundance decay of the whole insect community, including Orthoptera, in the same grasslands through an increased dominance of the most abundant species (Simons et al. 2015). Hence, the fertilization-tolerant and most abundant species *Chorthippus parallelus* (Zetterstedt, 1821) may either outcompete fertilization-intolerant species or at least compensate for their absence and thereby stabilizes orthopteran abundance levels. Higher nutrient levels in plant tissues can be beneficial to plant-feeding Orthoptera (Haddad et al. 2000) and can increase performance and reproductive success of the grasshopper *C. parallelus* (Ebeling et al. 2013), consistent with our finding that this species predominantly occurred on intensively used and fertilized areas. *C. parallelus* seems to be an appropriate indicator for intensive management.

*Tetrix kraussi* (Saulcy, 1888) was one of the most susceptible species of this study and is known to prefer calcareous habitats with a dry microclimate, listed as threatened in the Red List for Germany. Also the remaining Tettigidae (*Tetrix* spec.) preferably colonize less intensively managed habitats and thus turn out to be probably useful indicators for extensive grassland management. With fertilization enhancing the productivity of grasslands, open soil spaces disappear (Hochkirch et al. 1999), which are important habitat parameters for Tettigidae.

An essential reason for the negative effect of fertilization may be a higher vegetation structure and density of grassland plants, because many grasshopper species prefer open grasslands with exposed soil, probably due to climatic conditions and microhabitat preferences for egg-laying (Ingrisch and Köhler 1998).

**Mowing**

Negative effects of mowing on Orthoptera, as in this study, have often been described, with the killing of individuals through the physical intervention (Humbert et al. 2010), destruction of vital food resources, increased predation pressure (Cizek et al. 2012), and disturbance of a suitable microclimate (Ingrisch and Köhler 1998, Gardiner and Hassall 2009), listed as major reasons. Migration of disturbed populations to intact habitats can also play a role for population decline of several species (Guido and Gianelle 2001). Mowing can reduce orthopteran densities by 65–85%, depending on the properties of the mower such as cutting height (Humbert et al. 2010). The significant reduction of abundance of several Orthoptera species on frequently mown meadows in our study is consistent with current knowledge and corroborates findings of other studies (Humbert et al. 2009). We have looked into the dynamics of diversity changes following mowing: Orthopteran diversity and total abundance increased with the time span between sampling and last cut, which may probably be due to more time for migration from neighboring habitats, repopulation, and egg hatching.

Species such as *Euthystira brachyptera* (Ocskay, 1826), *Phaneroptera falcata* (Poda, 1761), *Platycleis albopunctata* (Goeze, 1778), or *Leptophyes punctatissima* (Bosc, 1792) lay their eggs in plants and not into soil and were particularly threatened by mowing, which was also encouraged by Ingrisch and Köhler (1998), who stated reduced ecological resistance to environmental changes for orthopterans with plant-derived egg-laying substrates.

**Grazing**

Grazing intensity resulted in decreases in orthopteran diversity and abundance, but appeared to be the least disturbing management type, as the proportion of species that were significantly reduced on heavily grazed sites was lower than for fertilization and mowing. Studies have already shown that grazing affects grasshopper community composition (Jonas and Joern 2007) and decreases their abundance (Simons et al. 2015). Reported effects of grazing on diversity were ambiguous, ranging from positive (Joern 2005) to negative (Branson and Sword 2010) when contrasting grazed and ungrazed sites. In fact, we found that as many species benefited as suffered from grazing. We found no differences between grazed and ungrazed sites, but between sheep-grazed and cattle-grazed sites. Grazing intensity and species identity of grazing animals, their selectivity, and body size are major factors that may influence the direction of grazing effects (Rook et al. 2004). Grazing represents a more patchy and gentle way of mowing, because grazing animals are slower and
more selective and occur relatively patchy on a pasture, which is likely to facilitate avoidance by mobile grasshoppers. Grazing is also linked to nutrient recycling and high nitrogen availability through animal feces (Bilotta et al. 2007), which may have parallels to the impact of fertilization on insect communities although it is often spatially more heterogeneous. Grazing or mowing has another positive effect, as it prevents the grasshoppers’ habitat from unfavorably high and dense vegetation or even disappearance by long-term scrub encroachment in otherwise untreated grasslands. The advantages of grazing are probable reasons that species, which lay their eggs into plant parts, are less disturbed by grazing than by mowing. The date of mowing or grazing plays an important role, as an early date might erase a majority of present less mobile nymphs, whereas a midsummer date may potentially disturb reproducing adults.

**Feeding habits**

The consideration of the feeding habits in this study did not show a disadvantage of higher trophic levels with increasing land-use intensity, as it is predicted in other studies (Haddad et al. 2011, Herbst et al. 2013). Specialized grass feeders as much as polyphagous Orthoptera occurred on differently managed sites. The only pattern we could find was that species that feed on moss, algae, and plants (Tetrigidae) were more often found on low-intensity sites. Bryophytes are known to decrease with strong fertilization, frequent mowing (Müller et al. 2012), and high plant productivity in grasslands (Müller et al. 2014), which increases with land-use intensity (Haddad et al. 2000). Bryophyte species richness is highest on sites with bare ground (Müller et al. 2012), which is also favorably frequented by Tetrigidae.

We found that herbivorous Orthoptera (not graminivorous) differed in their weighted means from all the other feeding guilds, which must be treated with caution, because we only found three individuals out of two species of this feeding guild.

**Management implications**

The diversity of grassland arthropods like Orthoptera can be supported by a patchy application of mowing (Cizek et al. 2012), or by leaving uncut patches on meadows as refuges (Humbert et al. 2009, 2010), which has the same effect. The selection of equipment together with the mowing date also strongly influences the number of depleted grassland fauna (Humbert et al. 2009, 2010). Later mowing dates in autumn are better than in the phenological peak of orthopterans. There is no perfect mowing time for all grassland organisms, however, and it seems likely that a yearly rotating mowing date would be best for biodiversity, corresponding to a positive effect of interannual variability in land use found for multidiversity (Allan et al. 2014). Annual variation in land-use intensity on the sites may enable the reproduction of species with different phenologies and thus increases diversity. As grazing had the least effects of the examined management types, the proportion of grazed sites should be promoted as it can increase diversity compared with mown sites. However, a moderate intensity and duration of grazing is crucial to preserve biodiversity. Land use as such supports grassland biocoenoses in Central Europe and prevents grasslands from scrub encroachment adding to landscape diversity in addition to forests.

**Conclusion**

Our well-founded data showed that the majority of Orthoptera species were “losers”; that is, they were more common in low-intensity grasslands, which may ultimately add to their vulnerability and local extinction risk. Such negative impacts may be particularly well detectable in an analysis of individual species’ land-use responses like the niche model, rather than in aggregate analyses at the community level. Note that abundance-weighted diversity indices such as Shannon have an inherent bias for abundant species and are not sensitive for rare species, for which the probability of detection is lower than for common ones. In contrast, our new species-level niche model is very sensitive to depict quantitative responses to environmental gradients such as land use, even for rare species, and revealed that a high proportion of species declines with land-use intensity. A species’ sensitivity often corresponds to its rarity, either as a cause or as a consequence. It is thus crucial to disentangle responses for each species with an unbiased approach, which is applicable for different organisms and environmental parameters. Our study
enhances our knowledge of the susceptibility of orthopteran diversity and abundance to different types of land use in grasslands. Sustainable management, low intensity of fertilization, infrequent mowing, and variable grazing would help to maintain a high diversity of orthopterans and surely other grassland organisms.

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Literature Cited

Allan, E., et al. 2014. Interannual variation in land-use intensity enhances grassland multidiversity. Proceedings of the National Academy of Sciences USA 111:308–313.

Bakelaar, R. G., and E. P. Odum. 1978. Community and population level responses to fertilization in an old-field ecosystem. Ecology 59:660–665.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: linear mixed-effects models using eigen and S4. R package version 1.1-7. http://CRAN.R-project.org/package=lme4

Bharamal, D. L., and Y. J. Koli. 2014. Grasshoppers as multidisciplinary model organism in changing environment. International Journal of Current Microbiology and Applied Science 3:372–380.

Bilotta, G. S., R. E. Brazier, and P. M. Haygarth. 2007. The impacts of grazing animals on the quality of soils, vegetation, and surface waters in intensively managed grasslands. Advances in Agronomy 94:237–280.

Birkhofer, K., H. G. Smith, W. W. Weisser, V. Wolters, and M. M. Gossner. 2015. Land-use effects on the functional distinctness of arthropod communities. Ecography 38:889–900.

Blüthgen, N., et al. 2012. A quantitative index of land-use intensity in grasslands: integrating mowing, grazing and fertilization. Basic and Applied Ecology 13:207–220.

Braun, D. H., and G. A. Sword. 2010. An experimental analysis of grasshopper community responses to fire and livestock grazing in a northern mixed-grass prairie. Environmental Entomology 39: 1441–1446.

Cizek, O., J. Zameck, R. Tropek, P. Kocarek, and M. Konvicka. 2012. Diversification of mowing regime increases arthropods diversity in species-poor cultural hay meadows. Journal of Insect Conservation 16:215–226.

Ebeling, A., E. Allan, J. Heimann, G. Köhler, M. Scherer-Lorenzen, A. Vogel, A. Weigelt, and W. W. Weisser. 2013. The impact of plant diversity and fertilization on fitness of a generalist grasshopper. Basic and Applied Ecology 14:246–254.

Fischer, M., et al. 2010. Implementing large-scale and long-term functional biodiversity research: the Biodiversity Exploratories. Basic and Applied Ecology 11:473–485.

Gardiner, T., and M. Hassall. 2009. Does microclimate affect grasshopper populations after cutting of hay in improved grassland? Journal of Insect Conservation 13:97–102.

Gardiner, T., M. Pye, R. Field, and J. Hill. 2002. The influence of sward height and vegetation composition in determining the habitat preferences of three *Chorthippus* species (Orthoptera: Acrididae) in Chelmsford, Essex, UK. Journal of Orthoptera Research 11:207–213.

Guido, M., and D. Gianelle. 2001. Distribution patterns of four Orthoptera species in relation to microhabitat heterogeneity in an ecotonal area. Acta Oecologica 22:175–185.

Haddad, N. M., G. M. Crutsinger, K. Gross, J. Haarstad, J. M. Knops, and D. Tilman. 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. Ecology Letters 12:1029–1039.

Haddad, N. M., G. M. Crutsinger, K. Gross, J. Haarstad, and D. Tilman. 2011. Plant diversity and the stability of foodwebs. Ecology Letters 14:42–46.
Hooper, D. U., et al. 2005. Effects of biodiversity on grassland insect communities. Oecologia 124:73–84.

Haddad, N. M., D. Tilman, J. Haarstad, M. Ritchie, and J. M. H. Knops. 2001. Contrasting effects of plant richness and composition on insect communities: a field experiment. American Naturalist 158:17–35.

Hao, S., S. Wang, A. Cease, and L. Kang. 2015. Land harvesting techniques and their impacts on farmland biodiversity and land-use intensity in Europe. Proceedings of the Royal Society of London B: Biological Sciences 276:903–909.

Köhler, G., H.-P. Brodhun, and G. Schaller. 1987. Ecological energetics of Central European grasshoppers (Orthoptera: Acrididae). Oecologia 74:112–121.

Krauss, J., et al. 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecology Letters 13:597–605.

Marini, L., P. Fontana, M. Scotton, and S. Klimek. 2008. Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps. Journal of Applied Ecology 45:361–370.

Müller, J., J. Heinze, J. Joshi, S. Boch, V. H. Klaus, M. Fischer, and D. Prati. 2014. Influence of experimental soil disturbances on the diversity of plants in agricultural grasslands. Journal of Plant Ecology 7:509–517.

Müller, J., V. H. Klaus, T. Kleinebecker, D. Prati, N. Hövelz, and M. Fischer. 2012. Impact of land-use intensity and productivity on bryophyte diversity in agricultural grasslands. PLoS ONE 7:e51520.

Pimm, S. L., G. J. Russell, J. L. Gittleman, and T. M. Brooks. 1995. The future of biodiversity. Science 269:347–349.

Pinheiro, J., D. Bates, S. DebRoy, S. Sarkar, and R Core Team. 2014. nlme: linear and nonlinear mixed effects models. R package version 3.1-118. http://CRAN.R-project.org/package=nlme

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Ritchie, M. E. 2000. Nitrogen limitation and trophic vs. abiotic influences on insect herbivores in a temperate grassland. Ecology 81:1601–1612.

Rook, A. J., B. Dumont, J. Isselstein, K. Osoro, M. F. WallisDeVries, G. Parente, and J. Mills. 2004. Matching type of livestock to desired biodiversity outcomes in pastures—a review. Biological Conservation 119:137–150.

Samways, M. J. 1994. Insect conservation biology. Chapman & Hall, London, UK.

Schaffers, A. P., I. P. Raemakers, K. V. Sýkora, and C. J. ter Braak. 2008. Arthropod assemblages are best predicted by plant species composition. Ecology 89:782–794.

Scherber, C., et al. 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468:553–556.
Simons, N. K., et al. 2014. Resource-mediated indirect effects of grassland management on arthropod diversity. PLoS ONE 9:e107033.
Simons, N. K., M. M. Gossner, T. M. Lewinsohn, M. Lange, M. Türke, and W. W. Weisser. 2015. Effects of land-use intensity on arthropod species abundance distributions in grasslands. Journal of Animal Ecology 84:143–154.
Socher, S. A., et al. 2013. Interacting effects of fertilization, mowing and grazing on plant species diversity of 1500 grasslands in Germany differ between regions. Basic and Applied Ecology 14:126–136.
Socher, S. A., D. Prati, S. Boch, J. Müller, V. H. Klaus, N. Hölzel, and M. Fischer. 2012. Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. Journal of Ecology 100:1391–1399.
Tilman, D., J. Fargione, B. Wolff, C. D’Antonio, A. Dobson, R. Howarth, D. Schindler, W. H. Schlesinger, D. Simberloff, and D. Swackhamer. 2001. Forecasting agriculturally driven global environmental change. Science 292:281–284.
Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. Science 277:1300–1302.
Tilman, D., P. B. Reich, and J. M. H. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441:629–632.
Unsicker, S. B., A. Franzke, J. Specht, G. Köhler, J. Linz, C. Renker, C. Stein, and W. W. Weisser. 2010. Plant species richness in montane grasslands affects the fitness of a generalist grasshopper species. Ecology 91:1083–1091.
Vačkář, D., B. ten Brink, J. Loh, J. E. M. Baillie, and B. Reyers. 2012. Review of multispecies indices for monitoring human impacts on biodiversity. Ecological Indicators 17:58–67.
Van Den Berg, L. J. L., P. Vergeer, T. C. G. Rich, S. M. Smart, D. Guest, and M. R. Ashmore. 2011. Direct and indirect effects of nitrogen deposition on species composition change in calcareous grasslands. Global Change Biology 17:1871–1883.
Zak, D. R., W. E. Holmes, D. C. White, A. D. Peacock, and D. Tilman. 2003. Plant diversity, soil microbial communities, and ecosystem function: Are there any links? Ecology 84:2042–2050.
Zhang, G., X. Han, and J. J. Elser. 2011. Rapid top–down regulation of plant C: N: P stoichiometry by grasshoppers in an Inner Mongolia grassland ecosystem. Oecologia 166:253–264.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1545/full