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Research article

Response of Orthoptera assemblages to environmental change in a low-mountain range differs among grassland types

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ABSTRACT

Grasslands are among the most species-rich ecosystems in Europe. However, their biodiversity has become increasingly threatened by land-use and climate change. Here, we analyze Orthoptera assemblage shifts between 1996 and 2017 across three grassland types in the Black Forest (SW Germany) (N = 63): (i) formerly managed wet grasslands which have been frequently abandoned in recent decades (WET) (N = 15); (ii) common pastures which are still traditionally managed by rough grazing (COMMON) (N = 29), and (iii) mesic grasslands which have recently suffered from land-use intensification (MESIC) (N = 19).

Both annual and summer temperatures increased during the study period. Orthoptera assemblages strongly responded to the altered environmental conditions in the grasslands. However, effects differed clearly among grassland types. Despite a strong increase in overall species richness in common pastures, neither the Community Farmland Index (CFI) nor the Community Temperature Index (CTI) had changed. In the two other grassland types, the CFI decreased and the CTI increased.

The CFI – established here for Orthoptera – helped to disentangle the effects of climate and land-use change on Orthoptera assemblage composition. Based on our study, climate warming has led to biotic homogenization of the Orthoptera assemblages of wet grasslands affected by abandonment, and mesic grasslands affected by land-use intensification towards a dominance of more widespread species. In contrast, common pastures characterized by a high heterogeneity and low-intensity management were more resilient to the effects of climate warming.

1. Introduction

Grasslands are among the most species-rich ecosystems in Europe and cover >20% of the EU-28 land surface (EC 2019; Feurdean et al., 2018; Wilson et al., 2012). Most of the European grasslands have been shaped by human agricultural practices (Feurdean et al., 2018; Veen et al., 2009). However, due to the transition from pre-industrial land use to industrial agriculture, the extent of semi-natural grasslands of high conservation value has greatly decreased, mainly driven by agricultural intensification and land-use abandonment (Wallis de Vries et al., 2002). As a result, biodiversity of European grassland ecosystems has become increasingly threatened.

Human-induced climate change has caused further habitat changes in grasslands (Gibson and Newman, 2019; Streitberger et al., 2016b). However, the ecological response to climate change varies considerably across taxa (Chen et al., 2011; Parmesan, 2006; Warren et al., 2001). Whereas in temperate Europe several thermophilic organisms have benefited from global warming, species adapted to cool climates or sensitive to drought have been adversely affected by climate change (Hickling et al., 2006; Parmesan, 2006; Streitberger et al., 2016a; Tayleur et al., 2016). In particular, mountain grasslands are among the ecosystems most severely threatened by climate change (Engler et al., 2011). However, range expansions of warm-adapted species towards higher elevations can also contribute to assemblage shifts, and may even increase species richness in some taxonomic groups temporarily (Löffler et al., 2019; Roth et al., 2014; Steck et al., 2007).

Mobile generalists in particular have expanded their geographical ranges in response to increasing temperatures, whereas specialists with low mobility are often more vulnerable to global warming (Beckmann et al., 2015; Hickling et al., 2006; Hill et al., 2001; Löffler et al., 2019; Warren et al., 2001). Hence, there is growing evidence that the availability of suitable habitats determines whether a species can maintain its

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overall population level in the face of global warming (Mantyka-Pringle et al., 2015). In a Central European low-mountain range, Löffler et al. (2019) detected an increase of Orthoptera species richness due to global warming in well-managed grasslands, whereas the number of species did not change in abandoned grasslands. These results demonstrate that sustaining traditional land use in semi-natural grasslands might be of great importance for maintaining ecosystem resilience under climate change, which may also reduce the risk of biotic homogenization (cf. Mantyka-Pringle et al., 2015).

Orthoptera play a significant role as both herbivores and prey and, thus, are of great functional importance in grassland ecosystems (Samways, 2005). Furthermore, they are among the most suitable indicator groups to investigate the effects of land-use and climate change (e.g. Bazelet and Samways, 2012; Fartmann et al., 2012). As most species require high ambient temperatures (Willott and Hassall, 1998), Orthoptera diversity in Europe generally decreases towards northern latitudes due to less-favorable climatic conditions in these areas (Hochkirch et al., 2016). However, distribution of Orthoptera species may be overridden by a lack of suitable habitats in fragmented landscapes. While it is evident that land-use change (i.e. habitat loss and deterioration) is a major threat to Orthoptera in Europe (Maas et al., 2012), it has remained difficult to identify the effects of climate change due to possible interactions with other environmental stressors. Although it has been shown that thermophilic species are rapidly expanding their ranges northwards during recent decades (e.g. Bakker et al., 2015; Beckmann et al., 2015; Löffler et al., 2019; Poniatowski et al., 2018a), it is still poorly understood how Orthoptera assemblages respond to climate change across habitats which have been affected unequally by land-use change.

Here, we analyze Orthoptera assemblage shifts across three grassland types with contrasting land-use history in the Black Forest (SW Germany) (N = 63): (i) formerly managed wet grasslands which have frequently become abandoned in recent decades (WET) (N = 15); (ii) common pastures which are still traditionally managed by rough grazing (COMMON) (N = 29), and (iii) mesic grasslands which have recently suffered from land-use intensification (MESIC) (N = 19). To this end, we analyzed changes in Orthoptera species richness (i.e. all, as well as species with high and low mobility) between 1996 and 2017. In addition, we applied two indices to provide evidence whether Orthoptera assemblage shifts were driven by land-use or by climate change: (i) the Community Farmland Index (CFI) as a community mean of species' sensitivity to 'High Nature Value Farmland (HNV') and (ii) the Community Temperature Index (CTI) as a community mean of species' temperature preferences (c.f. Devictor et al., 2008). The CTI has recently been established as a useful tool to analyze processes underlying biodiversity shifts in insect communities (e.g. Devictor et al., 2012; Löffler et al., 2019; Termaat et al., 2019). In contrast, the CFI is a new measure which may help to deepen our understanding of the drivers of community shifts. In particular, we address the following research questions:

(i) How did species richness, CFI and CTI of Orthoptera assemblages shift between 1996 and 2017 due to land use and climate change?
(ii) Does the response of Orthoptera assemblages differ among the main grassland types?
(iii) What are the implications of the observed Orthoptera assemblage shifts for conservation management in Central Europe in times of rapid global change?

2. Material and methods

2.1. Study area

The study area, the 'Hotzenwald' in the southern Black Forest (Baden-Württemberg, Germany; 47°7′ N/8°1′ E), has an area of about 100 km^2, ranging from 700 to 1100 m a.s.l. Compared to the average climatic conditions in Central Europe, the climate is cool and wet, with a mean annual temperature of 6.3 °C, and an average annual precipitation of 1700 mm (reference period 1981–2010; (DWD German Meteorological Service, 2018). However, the study area is well-connected to the nearby 'High Rhine Valley', which is characterized by a warmer and drier climate, through north-south oriented river valleys. In accordance with the elevation gradient in the study area, precipitation increases with elevation from about 1600 to 1900 mm/a, while mean annual temperature decreases from 6.8 to 5.7 °C (DWD German Meteorological Service, 2018).

The Hotzenwald is part of the German biodiversity hotspot 'Hochschwarzwald mit Alb-Wutach-Gebiet' (Ackermann and Sachteleben, 2012). Large parts of the cultural landscape in the study area are dominated by semi-natural grasslands which are of major importance for biodiversity conservation in Europe (Feurdean et al., 2018; Veen et al., 2009). As a relic of traditional farming practices in central Europe, many of them have been managed as commons for centuries (Eggers, 1957; Hermle and Deil, 2002). Despite severe agricultural changes in most parts of central Europe, these common pastures are still grazed by cattle with low stocking rates. Due to their outstanding biodiversity, these heterogeneous pastures are of high conservation value and, additionally, make a unique contribution to the German cultural heritage (Lederbogen et al., 2004). Besides the common pastures in the study area, mesic grasslands are frequently used as hay meadows (RPF Regierungspräsidium Freiburg, 2011). In addition, the study area holds a network of various wet grasslands, often in close proximity to small bogs (Geis et al., 2013).

2.2. Study design

To detect possible Orthoptera assemblage shifts in the focal grasslands, we compared Orthoptera presence/absence data in 1996 with those from our own field surveys in 2017. The historical data represent the first detailed assessment of Orthoptera occurrence in the study area (Detzel, 1997). In summer 2017, all patches studied in 1996 were re-visited and Orthoptera occurrence was surveyed using the same methods that had been applied in the former study (cf. Section 2.2.2). We analyzed changes in species richness and in patch occupancy of single species. Apart from considering overall Orthoptera species richness, we additionally classified Orthoptera by their dispersal ability (cf. Section 2.2.3). Furthermore, we applied two indices to understand whether Orthoptera assemblage shifts are driven by land-use or by climate change: (i) the Community Farmland Index (CFI) as a community mean of species' habitat preferences concerning 'High Nature Value Farmland' (HNV) reflected by the Species Farmland Index (SFI) (for more details see Section 2.2.3) and (ii) the Community Temperature Index (CTI) as a community mean of species' temperature preferences reflected by the Species Temperature Index (STI) (Devictor et al., 2008).

To analyze annual and seasonal (summer: May–October) changes in temperature during the study period, we used spatial temperature grid data covering the whole study area (data period: 1987–2016, temporal resolution: monthly, spatial resolution 1 km × 1 km) provided by the German Meteorological Service (DWD German Meteorological Service, 2018). Prior to the analyses, the temperature grid data were averaged for the study area in R statistical environment (R Core Team, 2018) using the *spatialEco* package (Evans, 2019). Afterwards, we used linear models with autocorrelation (AR1) structure to evaluate long-term temperature trends (thirty year period ending in 2016, the year before to the second survey was conducted).

2.2.1. Study patches

In total, we studied 63 patches belonging to three grassland types: (i) wet grasslands (WET, N = 15), (ii) common pastures (COMMON, N = 29), and (iii) mesic grasslands (MESIC, N = 19). Patches were regarded as discrete when they were isolated from the nearest neighboring patch by > 50 m of non-habitat, such as forest or improved grassland (cf.

Table 1
List of Orthoptera species recorded in the study area classified by their dispersal ability (DA; H = high mobility; L = low mobility), Species Farmland Index (SFI) and Species Temperature Index (STI).

Species	DA	SFI	STI
Bicolorana bicolor	H	19.37	13.12
Calliptamus italicus	H	19.18	13.68
Chorthippus biguttulus	H	16.04	12.97
Chorthippus brunneus	H	16.34	12.98
Chrysochraon dispar	H	18.23	13.10
Conocephalus fuscus	H	15.90	13.35
Decticus verrucivorus	L	25.90	12.59
Euthystira brachyptera	L	24.62	12.57
Gomphocerippus rufus	L	20.18	12.94
Gryllus campestris	L	20.52	13.07
Mecostethus parapleurus	H	28.47	13.22
Metrioptera brachyptera	L	20.24	12.58
Miramella alpina	L	42.28	10.49
Myrmeleotettix maculatus	L	17.04	12.99
Nemobius sylvestris	L	18.52	13.11
Omocestus rufipes	L	27.60	12.75
Omocestus viridulus	L	18.68	12.74
Pholidoptera griseoaptera	L	16.12	12.97
Platycleis albopunctata	H	15.90	13.34
Pseudochorthippus montanus	L	19.28	12.82
Pseudochorthippus parallelus	L	16.03	12.96
Psophus stridulus	L	32.72	11.81
Roeseliana roeselii	H	16.41	12.95
Stauroderus scalaris	H	54.24	11.37
Stenobothrus lineatus	H	18.73	12.89
Stenobothrus stigmaticus	L	18.29	12.78
Stethophyma grossum	H	17.68	12.96
Tetrix bipunctata	L	22.09	12.37
Tetrix subulata	H	15.82	13.07
Tetrix tenuicornis	L	16.28	13.00
Tetrix undulata	L	16.18	12.99
Tettigonia cantans	L	18.45	12.59

Poniatowski et al., 2018b; Krämer et al., 2012). The size of the patches varied between 1 ha and 29 ha (mean ± SE: 6.3 ha ± 0.7). In all studied patches the grassland type did not change between 1996 and 2017.

Due to differences in land-use history over the last few decades, the three studied grassland types represent a gradient of land-use intensity. Many of the studied wet grasslands were traditionally mown once to twice a year, or grazed by cattle at low stocking rates (Geis et al., 2013). However, as a consequence of abandonment of management or irregular management for more than 20 years, many of these wet grassland patches have now become partly overgrown by tall-forb communities, or are dominated by a few grass species such as *Molinia caerulea*.

In contrast, most of the common pastures were still under traditional management by rough grazing with a local cattle breed (called 'Hinterwälder') (RPF Regierungspräsidium Freiburg, 2011; LUBW 2004). Additionally, a small area of the common pastures was mown once a year in late summer. Due to a mosaic of various nutrient-poor grassland habitats, such as wet mesic or dry acidic grasslands, the common pastures are usually characterized by a very high habitat heterogeneity.

Most of the studied mesic grasslands were used as hay meadows, mown at least twice a year (May and September). However, due to regular application of fertilizer and an increasing mowing frequency, these grasslands have recently suffered from land-use intensification. Furthermore, some of the surveyed mesic grasslands were currently used as cattle pastures with intermediate stocking densities.

2.2.2. Orthoptera sampling

Orthoptera were sampled twice between mid-July and the end of August, with at least three weeks between each visit. In each patch, all available habitat structures were surveyed for the occurrence of Orthoptera species under favorable weather conditions (temperature > 15 °C, cloud cover < 50%) using acoustic and visual detection as well as sweep netting which are among the most frequently used methods for surveying grassland Orthoptera (Fischer et al., 2016; Samways et al., 2010). Arbusticolous and arboricolous species that rarely occur in grasslands were excluded from all analyses, as our sampling techniques do not produce reliable data for these species. Species identification was performed in the field by song and morphological characteristics using Fischer et al. (2016). To improve the detection of quiet or high-frequency stridulating species, such as *Conocephalus fuscus* and *Metrioptera brachyptera*, a bat detector was used. The scientific nomenclature follows Fischer et al. (2016).

2.2.3. Orthoptera classifications and indices

We classified Orthoptera by their dispersal ability according to Poniatowski et al., 2018a and Reinhardt et al. (2005). All long-winged species which are known to have a high flight capability as well as the wing-dimorphic species *Chrysochraon dispar* and *Roeseliana roeselii*, which are known to have a high dispersal ability, were classified as mobile species (Table 1) (cf. Löffler et al., 2019; Poniatowski and Fartmann, 2011).

We calculated the Species Temperature Index (STI) for all Orthoptera species included in our analyses according to Devictor et al. (2008, 2012). This Index has recently been applied to detect climate-driven shifts in Orthoptera assemblages (Löffler et al., 2019). Applying the same procedure, we introduced the Species Farmland Index (SFI) which indicates the relationship between the distribution of a species and the availability of high-nature-value farmland in its range. Both STI and SFI were obtained from German Orthoptera distribution data (cf. graphical maps in Fischer et al., 2016), based on a grid-map system with a spatial resolution of 10 km × 11 km (in Germany 3004 grid cells i.e. 'Messtischblätter'; cf. Reinhardt et al., 2005). The majority of the data were originally compiled for the preparation of the assessment of German Orthoptera (Maas et al., 2002). More recent data (until 2017) were provided by several local Orthoptera societies and federal state authorities (for more details see Fischer et al., 2016). Overall, the dataset included 211,954 single records from 1990 to 2017. For the calculation of STI and SFI, the distribution data of each species were layered with maps of long-term mean summer temperatures of the most recent 30-year reference period (1 km × 1 km grid – timescale: 1981–2010; DWD German Meteorological Service, 2018; compare also to WMO 2017) and the share of high-nature-value farmland in the open landscape (the most recent and updated version of a European HNV map; 100 m × 100 m grid; EEA 2018), respectively. For each species, all occupied grid cells were considered for the calculation of the indices. Grid cells were classified as occupied if one or more observations existed between 1990 and 2017. The computing was done using the zonal statistics tool in ArcGIS 10.3 (i.e. the mean temperature value and the mean value of the ratio of high-nature value farmland were calculated for all occupied grid cells, respectively). Finally, STI and SFI values were calculated as the mean of the computed zonal-statistic values across the whole species' range in Germany. Due to the spatial limitation to the extent of Germany and to the relatively large time span of data collection, both indices do not necessarily reflect the species' optima. Hence, they should be viewed as relative measurements of their habitat demands.

2.3. Statistical analysis

To assess the effects of recent climate change, i.e. changes in temperature in the study area, we applied linear models with autocorrelation (AR1) structure on temperature data using the *gls* function from the *nlme* package (Pinheiro et al., 2018). The McNemar test was used to detect changes in patch occupancy of each Orthoptera species between the two sampling periods. Because chi-square tests do not allow empty categories, we conservatively set frequencies of 0 to 1 (Eichel and Fartmann, 2008). Changes in the number of species (all species as well as species with high and low mobility) as well as in the CFI and CTI in each grassland type between the two study years were tested by a Wilcoxon

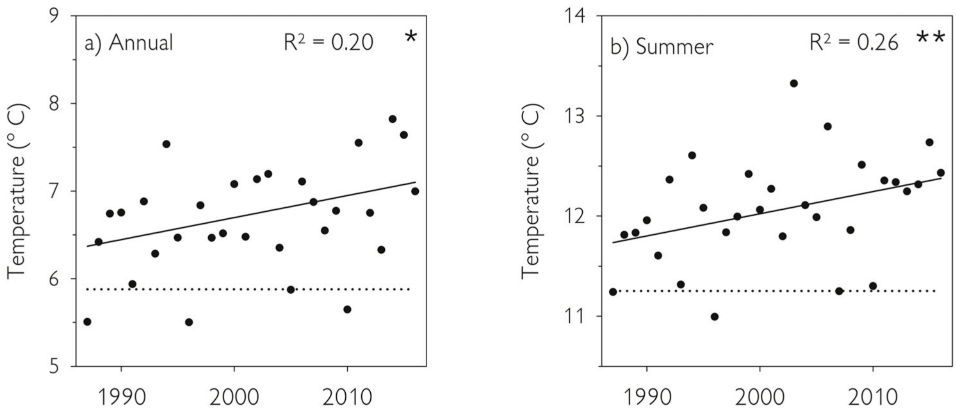

Fig. 1. Changes in annual (a) and summer temperature (May–October) (b) in the study area (data period 1987–2016; DWD German Meteorological Service, 2018). The dotted lines represent the long-term mean (most recent international standard reference 1961–1990; DWD German Meteorological Service, 2018). Linear relationships were tested using linear models with autocorrelation (AR1) structure (*p < 0.05, **p < 0.01). (a) $y = 0.025 \times x - 43.6$; (b) $y = 0.022 \times x - 32.26$. Pseudo $R^2_{(Nagelkerke)}$ values are given.

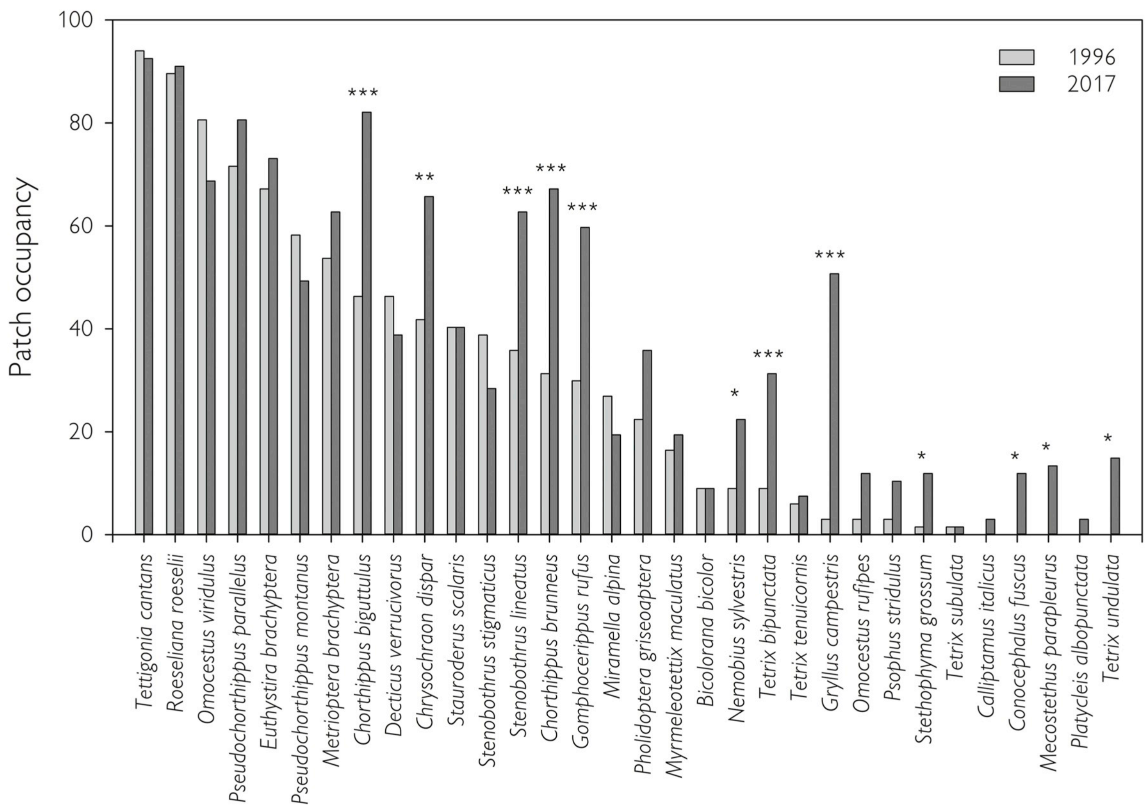

Fig. 2. Patch occupancy of Orthoptera species in 1996 and 2017. Differences were tested using McNemar test. ***p < 0.001, **p < 0.01, *p < 0.05.

Signed Rank test. All statistical analyses were performed using R statistical environment (R Core Team, 2018).

3. Results

3.1. Climate change

Both annual and summer temperatures increased from 1987 to 2016 (Fig. 1a and b).

3.2. Orthoptera assemblage change

In total, 32 species of grassland Orthoptera were recorded in the 63 patches during the two study years (Table 1). Five species were only recorded in 2017: *Calliptamus italicus*, *Conocephalus fuscus*, *Mecostethus parapleurus*, *Platycleis albopunctata* and *Tetrix undulata*. For 12 species, patch occupancy increased from 1996 to 2017: *Chorthippus biguttulus*, *Chorthippus brunneus*, *Chrysochraon dispar*, *C. fuscus*, *Gomphocerippus rufus*, *Gryllus campestris*, *M. parapleurus*, *Nemobius sylvestris*, *P. albopunctata*, *Stenobothrus lineatus*, *Tetrix bipunctata* and *T. undulata* (Fig. 2). In contrast, no species became locally extinct or decreased in patch occupancy.

Overall species richness increased in common pastures and mesic grasslands between 1996 and 2017, whereas it did not change in wet grasslands (Fig. 3a). In particular, species with high mobility were responsible for this increase in species richness, and their richness increased in all three grassland types (Fig. 3b). In contrast, the number of species with low mobility only increased in common pastures (Fig. 3c).

The SFI largely differed among species detected in our study (Table 1), with values ranging from 15.82% to 54.24%. *Stauroderus scalaris* (SFI = 54.24%), *Miramella alpina* (SFI = 42.28%) and *Psophus stridulus* (SFI = 32.72%) were the three species which most strongly depend on high nature value farmland. By contrast, *Tetrix subulata* (SFI

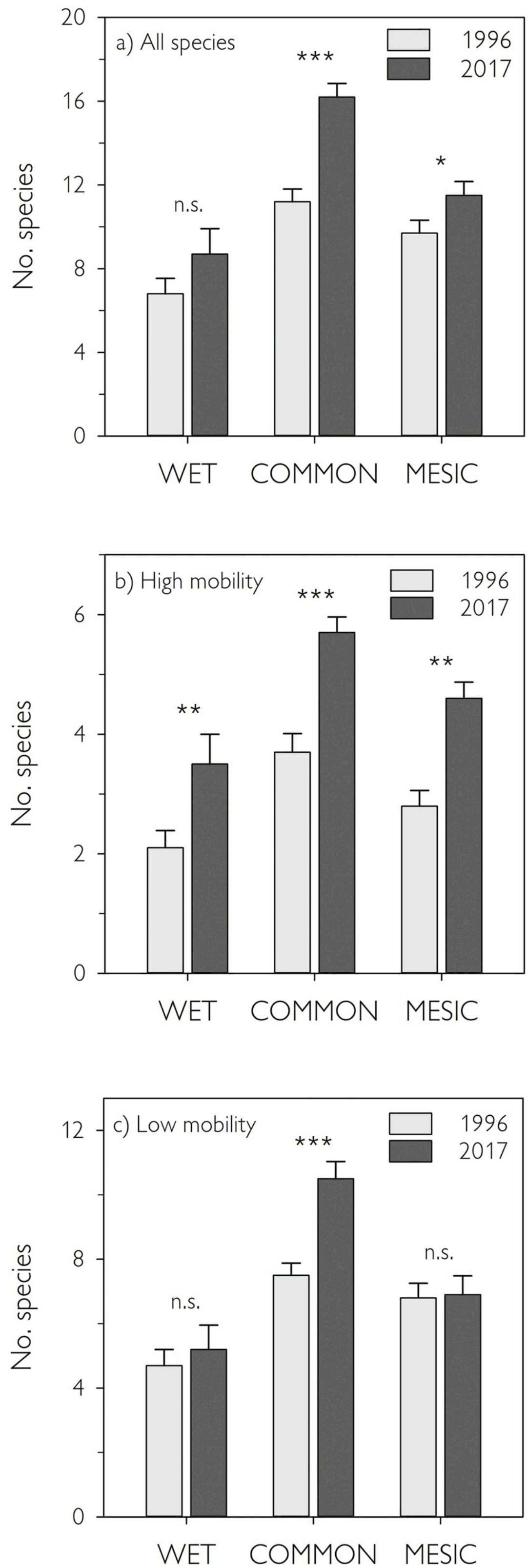

Fig. 3. Changes in the number of all species (a), species with high (b) and species with low mobility (c) between 1996 and 2017 in the three grassland types . Mean values ± SE are shown. WET = wet grassland, N = 15; COMMON = common pasture, N = 29; MESIC = mesic grassland, N = 19. Differences were tested using Wilcoxon Signed Rank test (***p < 0.001, **p < 0.01, *p < 0.05, n.s. p > 0.05).

= 15.82%), *C. fuscus* (SFI = 15.90%) and *P. albopunctata* (SFI = 15.90%) had the lowest SFI values.

The STI of the detected species ranged from 10.49 to 13.68 °C (Table 1). *Calliptamus italicus* (STI = 13.68 °C), *C. fuscus* (STI = 13.35 °C) and *P. albopunctata* (STI =13.34 °C) were the three species with the highest macroclimatic demands (Table 1). All three species were detected in the study area in 2017 for the first time (see above). *Miramella alpina* (STI = 10.49 °C), *S. scalaris* (STI = 11.37 °C) and *P. stridulus* (STI = 11.81 °C) were the species with the lowest STI values.

The CFI decreased in both wet and mesic grasslands between 1996 and 2017 (Fig. 4a), whereas the CTI increased in both grassland types (Fig. 4b). On the contrary, both indices remained stable in common pastures (Fig. 4a and b).

4. Discussion

Both annual and summer temperatures increased in the study area during the study period. Orthoptera assemblages strongly responded to these changed environmental conditions in the grasslands. However, the effects differed greatly among the grassland types, in particular between common pastures and the two other grassland types. Despite a strong increase in overall species richness in common pastures, neither the CFI nor the CTI changed. Contrastingly, the CFI decreased and the CTI increased in the two other grassland types.

Most Orthoptera species depend on high ambient temperatures (Willott and Hassall, 1998). Consequently, global warming is considered the main driver behind recent range expansions of Orthoptera across temperate Europe (Beckmann et al., 2015; Poniatowski et al. 2012, Poniatowski et al., 2018a; Thomas et al., 2001). Five species, *C. italicus*, *C. fuscus*, *M. parapleurus*, *P. albopunctata* and *T. undulata*, were new to the study area. The first four out of them had the highest STI values (STI > 13.2 °C) of all detected species. Besides *C. fuscus*, *M. parapleurus* and *T. undulata*, another eight species, *C. biguttulus*, *C. brunneus*, *C. dispar*, *G. rufus*, *G. campestris*, *N. sylvestris*, *S. lineatus* and *T. bipunctata* increased in patch occupancy. Except *T. bipunctata*, all these species had higher STI values than the average STI (±SE) of 12.79 ± 0.11. Accordingly, we explain the new colonization of the study area by thermophilic species and the increase in patch occupancy of thermophilic species as a response to the observed climate warming. The increase in the CTI in wet and mesic grassland underpins this assumption.

In contrast, the increase in patch occupancy in the two cryptic groundhopper species *T. bipunctata* and *T. undulata* might also be the result of a more intensive survey for the species in their preferred bare ground-rich microhabitats (cf. Detzel, 1997; Schlumprecht and Waeber, 2003). For *T. bipunctata* in particular, this seems to be very likely as the species has a relatively low STI (12.37 °C) (cf. Table 1) and within central Europe, it also occurs regularly in areas with cool summers (Fischer et al., 2016; Maas et al., 2012).

In our study, species richness of mobile species increased in all three grassland types. These results corroborate findings of previous studies indicating that global warming primarily fosters mobile species, whereas most species with low dispersal ability are unable to track climate change (Beckmann et al., 2015; Löffler et al., 2019; Poniatowski et al., 2012).

Orthoptera are very sensitive not only to changes in climate, but also in land use (Beckmann et al., 2015; Hickling et al., 2006; Thomas et al., 2001). There is broad consensus that habitat loss and deterioration caused by land-use change are the most severe threats to Orthoptera in central Europe (Fartmann et al., 2012; Marini et al., 2009; Schirmel et al., 2011). The newly introduced CFI for Orthoptera in this study provides the opportunity to disentangle the effects of climate and land-use change on Orthoptera assemblage composition more precisely. In both wet and mesic grasslands, the CFI decreased. Hence, the current Orthoptera assemblages were composed of species less dependent on high nature value farmland, i.e. more habitat generalist or widespread species, than in 1996. In wet grasslands, overall species richness did not

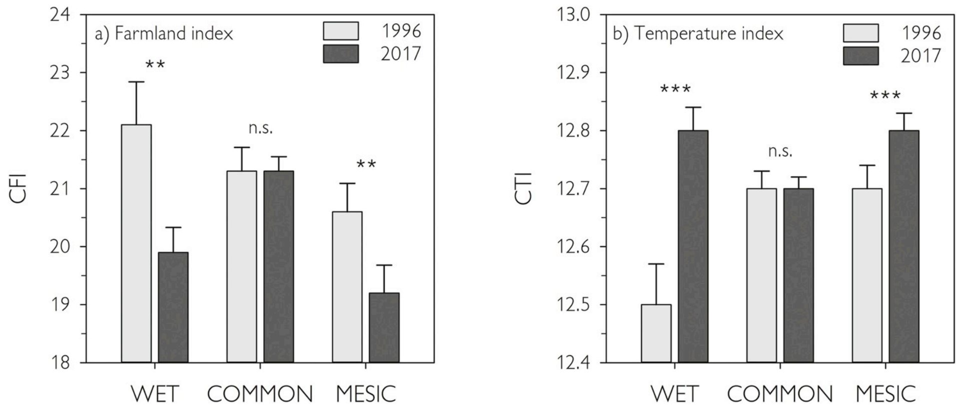

Fig. 4. Changes in the Community Farmland Index (CFI) (a) and the Community Temperature Index (CTI) (b) between 1996 and 2017 in the three grassland types. Mean values ± SE are shown. WET = wet grassland, N = 15; COMMON = common pasture, N = 29; MESIC = mesic grassland, N = 19. Differences were tested using Wilcoxon Signed Rank test (***$p < 0.001$, **$p < 0.01$, n.s. $p > 0.05$).

change, and species with a high SFI were substituted by more widespread species. We attribute the decrease in high nature value farmland species to the abandonment of most of the wet grasslands (see Section 2.2.1). Succession is known to have negative effects on habitat specialist Orthoptera in open habitats of the temperate zone, in particular through changes in microclimate (Fartmann et al., 2012; Helbing et al., 2014; Löffler et al., 2019; Marini et al., 2009; Schirmel et al., 2011). Abandonment of grassland management leads to tall vegetation with litter accumulation (Ellenberg and Leuschner, 2010) and a cool microclimate, even in times of macroclimatic warming (cf. Wallis de Vries and van Swaay, 2006). In contrast, in mesic grasslands, which suffered from land-use intensification in the study area (see Section 2.2.1), overall species richness increased. However, this increase was attributed only to widespread species, as the decreasing CFI indicates. In summary, climate and land-use change in both wet and mesic grasslands led to a biotic homogenization of the respective Orthoptera assemblages with more widespread species replacing habitat specialists.

In common pastures, both the CFI and the CTI did not change, despite an increase in overall species richness. Common pastures were also the only grassland type where the number of species with low mobility increased and where these poor dispersers were able to track climate change. The common pastures were characterized by mosaics of various nutrient-poor grassland habitats, ranging from wet to dry grasslands and had by far the highest habitat heterogeneity of the three studied grassland types (see Section 2.2.1). As a consequence, we conclude that heterogeneous grasslands with long environmental gradients and low-intensity management, such as the common pastures in our study, are more resilient to the effects of climate warming (cf. Mantyka-Pringle et al., 2015; Streitberger et al., 2016b). Under such conditions, Orthoptera species with both low and high mobility are able to track rising temperatures in landscapes with well-connected grasslands.

5. Conclusions

Löffler et al. (2019) showed that approaches based on the CTI are a powerful tool for detecting the effects of climate change on Orthoptera assemblage shifts. Additionally, the CFI – developed here – helped to disentangle the effects of climate and land-use change on Orthoptera assemblage composition. In sum, we found that climate warming has led to biotic homogenization of the Orthoptera assemblages of wet grasslands affected by abandonment, and mesic grasslands affected by land-use intensification. In contrast, common pastures, characterized by a high heterogeneity with long environmental gradients and low-intensity management, were more resilient to the effects of climate warming. In these grasslands not only widespread species with high mobility were able to track rising temperatures but also more specialized species with low mobility.

Based on the results here, we recommend the maintenance or reintroduction of traditional land use in grasslands to promote Orthoptera assemblages – and presumably also other insect assemblages – with high species richness and many specialized species (Torma et al., 2014, 2019; Fartmann et al., 2012; Wallis de Vries et al., 2002). Such conservation measures are low-intensity mowing (1–2 times per year without fertilizer application) in meadows, and low-intensity grazing in pastures (cf. Löffler et al., 2019). Additionally, management should also aim at establishing dense habitat networks within a heterogeneous landscape which increases the resilience of grassland ecosystems to global warming (Pryke and Samways, 2012; Streitberger et al., 2016a).

Author contribution section

Florian Fumy: Conceptualization, Methodology, Formal analysis, Investigation, Writing - Original Draft, Visualization, Funding acquisition, Franz Löffler: Formal analysis, Writing - Review & Editing, Funding acquisition, Michael Samways: Writing - Review & Editing, Thomas Fartmann: Methodology, Writing - Review & Editing, Supervision.

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Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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