Biological Conservation 236 (2019) 315–323

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Orthoptera community shifts in response to land-use and climate change – Lessons from a long-term study across different grassland habitats

Franz Löffler[a,*], Dominik Poniatowski[a], Thomas Fartmann[a,b]

[a] Department of Biodiversity and Landscape Ecology, Osnabrück University, Barbarastraße 11, 49076 Osnabrück, Germany
[b] Institute of Biodiversity and Landscape Ecology (IBL), An der Kleimannbrücke 98, 48157 Münster, Germany

ARTICLE INFO

Keywords:
Agricultural abandonment
Biodiversity conservation
Climate change
Community Temperature Index
Land-use change
Range shift

ABSTRACT

Semi-natural grasslands are among the most species-rich ecosystems worldwide. However, the maintenance of grassland biodiversity is seriously threatened by land-use change. Additionally, climate change is increasingly affecting biotic communities in grasslands. In this study, we examine Orthoptera community shifts in response to land-use and climate change in three different grassland habitats in a Central European low mountain landscape.

Orthoptera strongly responded to environmental changes between 1994 and 2015. Both annual and summer temperatures increased during the study period. Apart from climatic changes, the studied habitats were unequally affected by land-use change. Due to the continuity of habitat management, habitat quality has not substantially changed in calcareous and mesic grasslands. However, abandonment has frequently contributed to habitat deterioration in wet grasslands. Orthoptera species richness in the well-managed grassland types increased, while it did not change in wet grasslands. The increase in species richness was mainly caused by an expansion of habitat generalists and mobile species in response to global warming. In comparison, the number of habitat specialists and species with limited dispersal ability did not change in any of the grassland types. Species-turnover rates were higher in mesic and wet grasslands. Accordingly, we detected an increase of the Community Temperature Index (CTI) in these habitats.

The results of our study imply that the response of Orthoptera communities to global warming depend on the quality and availability of suitable habitats. Hence, sustaining traditional land use in semi-natural grasslands and the establishment of dense habitat networks is essential to promote Orthoptera diversity.

1. Introduction

Since the extinction rate of species is currently up to 1000 times higher than during pre-human periods, counteracting biodiversity loss has become one of the greatest challenges of our time (Pimm et al., 2014). Land-use change has been identified as the most decisive driver for the rapid decline of plant and animal life in terrestrial ecosystems (Sala et al., 2000; Tilman et al., 2001). But more recently, human-induced climate change is also affecting biological systems at a fast pace (e.g. Chen et al., 2011; Thomas et al., 2004; Warren et al., 2001). Apart from the obviously detrimental consequences of climate change, various studies have detected rapid range expansions of organisms across several taxa, which may additionally alter community structure and biotic interactions in certain ecosystems (e.g. Hickling et al., 2006; Parmesan et al., 1999; Parmesan and Yohe, 2003).

Promoted by traditional land use, grasslands now cover > 20% of the EU-28 land surface and are among the most species-rich ecosystems in Europe (EC, 2018; Feurdean et al., 2018). However, due to the transition from pre-industrial to modern agricultural land use, the extent of species-rich, semi-natural grasslands has dramatically decreased, mainly driven by agricultural intensification and abandonment (WallisDeVries et al., 2002). As a result, grassland specialists of several taxa have undergone a substantial population decline with consequent adverse effects on ecosystem functioning (e.g. Hautier et al., 2015; Kuussaari et al., 2007; Schuch et al., 2011).

The ecological response to climate change varies considerably between species (e.g. Chen et al., 2011; Guo et al., 2009; Parmesan, 2006; Warren et al., 2001). Thermophilic organisms may benefit from climate change, whereas species adapted to cool temperatures or sensitive to drought will become increasingly threatened (Hickling et al., 2006; Parmesan, 2006; Streitberger et al., 2016; Tayleur et al., 2016). Thus, it is generally assumed that the effects of global warming on grassland biodiversity in Europe become most obvious in areas with cool climates (e.g. mountain ranges) (Nieto-Sanchez et al., 2015; Thuiller, 2017). In

* Corresponding author.
E-mail address: franz.loeffler@uos.de (F. Löffler).

https://doi.org/10.1016/j.biocon.2019.05.058
Received 28 February 2019; Received in revised form 24 May 2019; Accepted 31 May 2019

addition, the effects of climate change may vary across habitats in Central Europe, mainly depending on their sensitivity to drought and the degree of habitat fragmentation (Streitberger et al., 2016). It is predicted that the increasing risk of summer drought will cause species in wet grasslands to become more severely threatened, while biodiversity in dry grasslands may be encouraged (Streitberger et al., 2016). Moreover, former studies indicate that habitat specialists are less able to keep up with climate change, while range expansions of mobile species and habitat generalists have frequently been observed (e.g. Beckmann et al., 2015; Hickling et al., 2006; Warren et al., 2001). However, it is likely that the limited availability of suitable habitats and dispersal corridors in fragmented landscapes will hamper grassland specialists' ability to contend with global warming (Hill et al., 2001). Understanding the interactions between processes underlying biodiversity shifts is essential in establishing novel management strategies that may enable species to cope with altered environmental conditions (Mantyka-Pringle et al., 2015). Nevertheless, former investigations have often failed to quantify the impact of climate change among other drivers such as land-use change. In this light, the Species and Community Temperature Indices (STI and CTI) can improve the traceability of climate change among other factors altering biodiversity (Devictor et al., 2008). This approach has been established as a robust tool for quantifying the impact of climate change on recent insect-community shifts (e.g. butterflies: Devictor et al., 2012; beetles and moths: Thomsen et al., 2016), but has not yet been applied to other climate-sensitive taxa, such as Orthoptera.

Due to their significant role as both herbivores and prey, Orthoptera are of great functional importance to grassland ecosystems (Samways, 2005). The distribution of Orthoptera in Europe is predominantly determined by climate and land use (Ingrisch and Köhler, 1998; Hochkirch et al., 2016). As most species depend on high ambient temperatures for successful development (Willott and Hassall, 1998), Orthoptera diversity decreases towards northern latitudes that are characterised by less favourable climatic conditions (Fischer et al., 2016). Land use affects Orthoptera distribution mainly due to its impact on habitat quality and availability, which have been identified as the key factors determining the persistence of grassland specialists in human-modified landscapes such as Central Europe (Löffler and Fartmann, 2017; Poniatowski and Fartmann 2010; Poniatowski et al., 2018a). Due to their sensitivity to both land-use and climate change, Orthoptera are generally well-suited organisms to investigate the effects of recent environmental changes in grasslands (e.g. Bazelet and Samways, 2011; Fartmann et al., 2012). For instance, about a half of the Orthoptera species in Germany have suffered long-term declines as a consequence of habitat loss due to land-use intensification and abandonment (Maas et al., 2011). Although land-use change is still a major threat to Orthoptera, recent large-scale assessments in Central and North-western Europe have revealed that an increasing number of thermophilic species are currently expanding their ranges northwards (e.g. Bakker et al., 2015; Beckmann et al., 2015; Poniatowski et al., 2018b). The study by Steck et al. (2007) assumes that global warming may have a positive impact on local Orthoptera species richness, but only if habitat availability is sufficient. However, very little is known as to what extent recent range shifts have affected the community structure of grassland Orthoptera and how climate interacts with other environmental stressors such as land-use change.

This paper deals with the effects of recent environmental alterations on Orthoptera communities across three different grassland habitats in a Central European low mountain landscape. We investigated Orthoptera community shifts in 67 grassland patches in consideration of changes in species richness (overall as well as classified by habitat specificity and dispersal ability) and thermal composition reflected by the Community Temperature Index (CTI, cf. Devictor et al., 2008) between 1994 and 2015. We analysed long-term changes in temperature and precipitation in the study area, as well as habitat-quality shifts in the studied grassland patches. We hypothesise that recent range expansions have led to Orthoptera community shifts towards more thermophilic species. As there are currently no clear signs of negative effects of climate change on Orthoptera in the study area, these expansions may also have contributed to an increase in local species richness, particularly in well-managed grasslands. We also assume that the positive impact of climate change can be overridden by the lack of suitable habitats or limited dispersal ability, which may necessitate novel management practices to counteract future biodiversity loss (cf. Oliver et al., 2016).

2. Material and methods

2.1. Study area

The study area is situated in the Eifel low mountain range, about 40 km southwest of the City of Bonn (North Rhine-Westphalia, Germany; 50°20′ N/6°37′ E and 50°28′ N/6°46′ E). It covers an area of 125 km^2 of the Upper Ahr Valley that ranges from an elevation of 330 to 580 m above sea level (a.s.l). The climate of the study area is suboceanic with a mean annual temperature of 8.0 °C and an average annual precipitation of 857 mm (Weather station: Kall-Sistig at 505 m a.s.l.; reference period 1981–2010; DWD, 2018). According to its altitudinal gradient, precipitation increases with altitude from < 700 to 950 mm/a, whilst mean annual temperature decreases from approximately 9 to 7 °C (DWD, 2018).

The Upper Ahr Valley is part of the 'Limestone and Volcanic Eifel' German biodiversity hotspot (Ackermann and Sachteleben, 2012). It is an ancient cultural landscape that is characterised by a high diversity of habitats of conservation concern and outstanding species richness (Council of Euskirchen, 2008). Due to the large-scale maintenance of traditional land-use practices (e.g. low-intensity mowing without fertiliser application, shepherding, rough cattle grazing), the study area still holds a dense network of well-managed nutrient-poor grasslands that are of major importance for biodiversity conservation in Europe (Veen et al., 2009).

2.2. Study design

To detect possible Orthoptera community shifts in montane grasslands, we compared presence-absence data provided by Weber and Weidner (1995) with those from our own field surveys in 2015. In summer 2015, all patches studied in 1994 were re-visited and Orthoptera occurrence, as well as several environmental parameters, were surveyed using the same methods that had been applied in the former study (cf. Sections 2.2.2 and 2.2.3). In addition to the analysis of overall species richness, we classified Orthoptera by their habitat specificity and dispersal ability (cf. Section 2.2.4). Data on temperature and precipitation were used to identify annual and seasonal (summer: April–September) effects of climate change in the study area. As climate assessments should generally refer to a period of at least three decades (WMO, 2017), climatic trends were calculated for a 30-year reference period prior to the second survey year (data period: 1985–2014; weather station: Kall-Sistig; DWD, 2018). Furthermore, we calculated the Community Temperature Index (CTI) as a community weighted mean of species temperature preferences reflected by the Species Temperature Index (STI) (cf. Devictor et al., 2008, for details see Section 2.2.5).

2.2.1. Study sites

In total, we studied 67 patches belonging to three grassland types: (i) calcareous grasslands (CAL = order: *Brometalia erecti*, alliance: *Bromion erecti*, $N = 21$), (ii) mesic grasslands (MES = order: *Arrhenatheretalia*, alliances: *Arrhenatherion elatioris* and *Cynosurion cristati*, $N = 23$) and (iii) wet grasslands (WET = order: *Molinietalia caeruleae*, alliances: *Calthion* and *Filipendulion ulmariae*, $N = 23$). The phytosociological nomenclature of the grassland types follows

Rennwald (2000).

In 2015, > 70% of the studied calcareous grasslands were well-managed as conservation measures were steadily intensified since the late 1980s (Council of Euskirchen, 2008). They were usually managed as rough pastures for sheep (57%); only a small number of the patches were mown once a year in late July to August (14%). More than two thirds (70%) of the studied mesic grasslands were under management in 2015. They were mostly mown twice a year in June and August (40%) or used as cattle pastures with low stocking densities (30%). The wet grasslands in the study area were usually situated along small stream valleys. In former times, these grasslands were mown once to twice a year or grazed by cattle in a low intensity. However, at least 70% of the studied wet grasslands have not been managed for > 30 years. As a result of long-term abandonment, these patches have now become partly overgrown by tall-forb communities.

2.2.2. Habitat quality

Habitat quality was assessed in July by determining habitat management and vegetation structure according to the categories of Weber and Weidner (1995). In detail, management was defined by three land-use categories (1–3): (1) abandoned, (2) mown and (3) grazed. Additionally, we classified land-use frequency of the patches using five categories (1–5): (1) no land-use/abandoned, (2) periodical land use (every 2–5 years), (3) once a year, (4) twice a year, (5) three or more times a year. Furthermore, the cover of the field layer was recorded applying four categories (1–4) representing the cover of the field layer at different heights above ground level: (1) < 50% cover at the ground, (2) < 50% cover at a height of 0.5 m, (3) < 50% cover at a height of 1 m and (4): > 50% cover at a height of 1 m. Shrub and tree layer cover were estimated in four categories (1–4): (1) no cover, (2) < 10% cover, (3) < 50% and (4) > 50%.

2.2.3. Orthoptera sampling

In 2015, Orthoptera were sampled twice between the middle of July and the end of August with at least three weeks between each visit following the methods of Weber and Weidner (1995). Accordingly, in each patch all available habitat structures were surveyed for the occurrence of Orthoptera species under favourable 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 to survey grassland Orthoptera (Fischer et al., 2016; Ingrisch and Köhler, 1998; Samways et al., 2010). Shrub-dwelling and tree-dwelling species, which occasionally occur in grasslands, were excluded from the analyses as our sampling techniques do not produce reliable data for these species. Species identification was performed in the field by sound and morphological characteristics using Bellmann (2006). To detect quiet or high-frequency stridulating species, such as *Conocephalus fuscus* and *Metrioptera brachyptera*, a bat detector was used (Fischer et al., 2016). The scientific nomenclature follows Fischer et al. (2016).

2.2.4. Orthoptera classification

We classified Orthoptera by their habitat specificity. Habitat specialists represent steno- and oligotopic species which are predominantly restricted to a few similar habitats, while habitat generalists frequently occur in a broad range of different habitats. The classification in our study is derived from habitat information of all Orthoptera records surveyed in a recent Orthoptera recording scheme in Bavaria (Schlumprecht and Waeber, 2003). According to these data, species that were predominantly restricted to not more than two out of eleven main habitat types (i.e. > 50% of all records are restricted to one or two habitat types) were classified as habitat specialists (Table 3) (cf. Schlumprecht and Waeber, 2003). All other species were considered as habitat generalists. The results of our approach largely fit with classifications of former studies (e.g. Fartmann et al., 2012; Reinhardt et al., 2005) and clearly correspond with descriptive autecological information on the species (cf. Schlumprecht and Waeber, 2003).

Additionally, we classified Orthoptera by their dispersal ability according to Poniatowski et al. (2018b) and Reinhardt et al. (2005) (Table 3). All long-winged species which are known to have a high flight capability were classified as mobile species. Moreover, we classified the wing-dimorphic species *Chrysochraon dispar* and *Roeseliana roeselii* as species with high dispersal ability. Although both species are predominantly short-winged, rapid range expansions have recently occurred in large parts of Central and North-western Europe (*C. dispar*: Bakker et al., 2015; *R. roeselii*: e.g. Beckmann et al., 2015; Poniatowski et al., 2012). In contrast, *Metrioptera brachyptera* and *Pseudochorthippus parallelus* were considered as less-mobile species as there are currently no indications for expansions and long-winged individuals are very rare in both species (Poniatowski and Fartmann, 2011; Weyer et al., 2012).

2.2.5. Species and Community Temperature Index

We calculated the Species Temperature Index (STI) for each of the detected Orthoptera species (Table 3) (Devictor et al., 2008). The STI was obtained from German distribution data underlying the maps provided in Fischer et al. (2016) and grid maps of long-term mean temperatures during the summer season (April–September) in Germany (1 km × 1 km grid maps; long-term means [April–September]: 1981–2010; DWD, 2018). The STI values were computed by intersecting distribution and temperature maps using the 'Zonal Statistics' tool in ArcGIS 10.2 (for more details see Appendix in Tayleur et al., 2016). Afterwards, the Community Temperature Index (CTI) of each study site was calculated by averaging the STI of all species occurring in the particular patch (cf. Devictor et al., 2008, 2012).

2.3. Statistical analysis

Differences in habitat quality between 1994 and 2015 were tested using pairwise comparisons (Wilcoxon Signed Rank test for ordinal-scaled variables or McNemar test in the case of nominal variables, respectively). To assess the effects of recent climate change, i.e. changes in temperature and precipitation (annual and summer) in the study area, we applied Generalised Linear Models (GLM, Gaussian error distribution) on the long-term climate data (package lme4, Bates et al., 2018). Furthermore, we compared the CTI between the two study years by applying Wilcoxon Signed Rank tests for each grassland type separately. Shifts in the number of species between the two study years were tested by a Wilcoxon Signed Rank test, considering overall species richness along with the number of species classified by their habitat specificity and dispersal ability, respectively. Furthermore, the McNemar test was used to detect changes in the frequencies of the occurrence of single Orthoptera species between the two study periods. Species turnover between 1994 and 2015 was calculated using Whittaker's beta diversity index (β_w) (Whittaker, 1960), which is among the most frequently used metrics to detect dissimilarities in biotic communities (Koleff et al., 2003):

$$\beta w = \frac{a + b + c}{(2a + b + c)/2} - 1$$

where a is the number of species detected in both study years (1994 and 2015), b the number of species detected only in 1994 and c the number of species detected only in 2015.

Differences in species-turnover rates between the grassland types were tested using Kruskal-Wallis H ANOVA with Dunn's test as a post hoc test.

All statistical analyses were performed using R 3.4.0 statistical package (R Development Core Team, 2017).

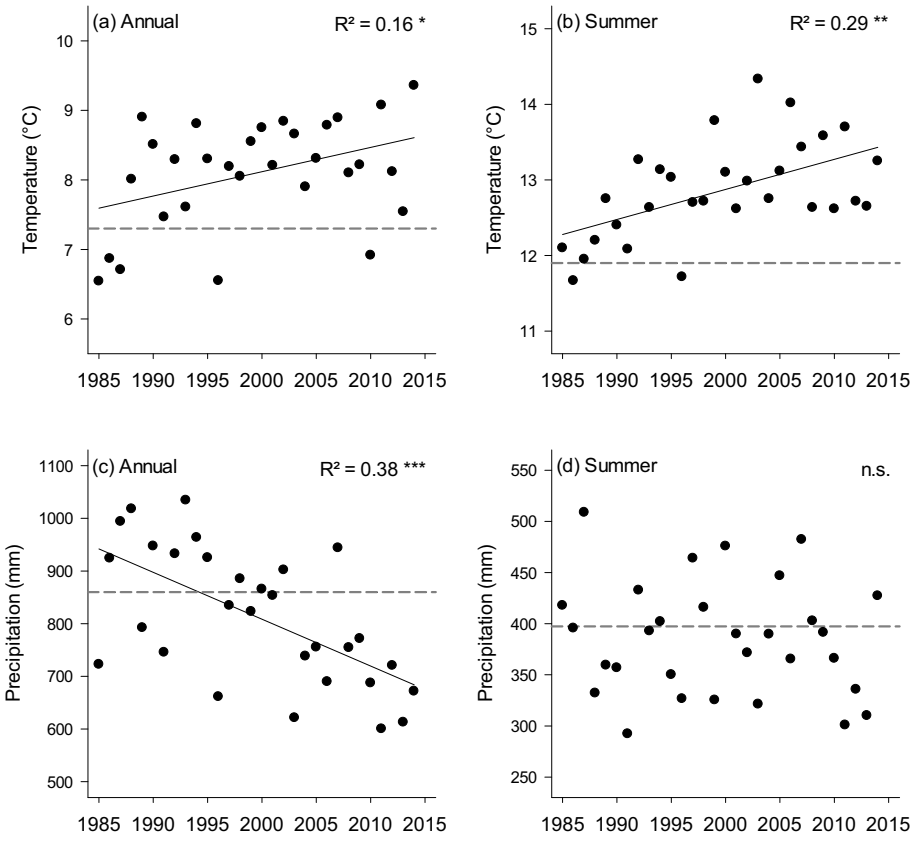

Fig. 1. Changes in annual/summer (April–September) temperature and precipitation in the study area (data period: 1985–2014; weather station: Kall-Sistig; DWD, 2018). Dashed lines represent the long-term mean (most recent international standard reference 1961–1990; DWD, 2018). Changes were tested by Generalised Linear Models with a Gaussian error distribution. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. $p > 0.05$. (a) $y = 0.0349 \times x + 7.559$; (b) $y = 0.0398 \times x + 12.237$; (c) $y = -8.896 \times x + 950.882$.

3. Results

3.1. Environmental shifts

Both, annual and summer temperatures significantly increased from 1985 to 2014 (Fig. 1a and b). In contrast, annual precipitation significantly decreased during that period, whereas summer precipitation did not change (Fig. 1c and d).

Although we did not detect changes in habitat management or land-use intensity in any of the three studied grassland types (Tables 1 and 2), the cover of shrubs in calcareous and wet grasslands significantly increased between 1994 and 2015. In addition, the cover of the field layer in wet grasslands was significantly higher in 2015 compared to 1994 (Table 2).

3.2. Orthoptera community shifts

In total, 19 grassland Orthoptera species were observed in the patches during the two study periods (Table 3). In each of the study periods, 18 species were found. *Stenobothrus stigmaticus* was only observed in 1994 and *Roeseliana roeselii* was detected in 2015 for the first time.

In both study years, overall Orthoptera species richness in calcareous grasslands was almost twice as high as in the two other grassland types (Fig. 2). In calcareous and mesic grasslands, the number of species significantly increased between 1994 and 2015. In contrast, species richness did not change in wet grasslands. However, turnover rates in mesic and wet grasslands were significantly higher compared to the more species-rich calcareous grasslands (Fig. 3). The number of habitat generalists and mobile species significantly increased in calcareous and mesic grasslands (Fig. 2). Although there was no change of overall species richness in wet grasslands, the number of mobile species also increased. In contrast, species richness in habitat specialists and low mobile species did not change in any of the grassland types.

In 1994, *Pseudochorthippus parallelus* was the most frequent species in all studied grassland types (CAL: 100%, MES: 96%, WET: 87%) (Table 3). In calcareous grasslands, it was followed by *Chorthippus biguttulus* (96%), *Bicolorana bicolor* and *Omocestus viridulus* (both 81%). With a frequency of 83% and 48%, respectively, *O. viridulus* and *C. biguttulus* were among the three most frequent species in mesic grasslands. In wet grasslands, *P. parallelus* (87%), *O. viridulus* (83%),

Table 1
Differences in land use between the two surveys in 1994 and 2015. CAL = calcareous grasslands, $N = 21$; MES = mesic grasslands, $N = 23$; WET = wet grasslands, $N = 23$. Absolute and relative frequencies are given as follows: N (%). Differences were tested using McNemar test (categorical parameter: land-use type – [i] abandoned, [ii] mown, [iii] grazed). n.s. $p > 0.05$.

Parameter	CAL			MES			WET		
	1994	2015	P	1994	2015	P	1994	2015	P
Land-use type									
(i) abandoned	10 (48)	6 (29)	n.s.	7 (30)	7 (30)	n.s.	16 (70)	19 (82)	n.s.
(ii) mown	3 (14)	3 (14)		9 (40)	9 (40)		3 (13)	2 (9)	
(ii) grazed	8 (38)	12 (57)		7 (30)	7 (30)		4 (17)	2 (9)	

Table 2
Differences in environmental parameters between the two surveys in 1994 and 2015. CAL = calcareous grasslands, $N = 21$; MES = mesic grasslands, $N = 23$; WET = wet grasslands, $N = 23$. Mean ± SE are given. Differences were tested using Wilcoxon Signed Rank text (ordinal parameters: land-use intensity – [i] abandoned, [ii] periodical land use, [iii] 1 ×/year, [iv] 2 ×/year, [v] ≥ 3 ×/year); field-layer cover – [i] < 50% at ground, [ii] < 50% at 0.5 m, [iii] < 50% at 1 m and [iv] > 50% at 1 m; shrub and tree layer – [i] no cover, [ii] < 10%, [iii] < 50% and [iv] > 50%, respectively (cf. Section 2.2.2). ** $p < 0.01$, * $p < 0.05$, n.s. $p > 0.05$.

Parameter	CAL			MES			WET		
	1994	2015	P	1994	2015	P	1994	2015	P
Land-use intensity	1.0 ± 0.2	1.3 ± 0.2	n.s.	1.5 ± 0.2	1.4 ± 0.2	n.s.	0.8 ± 0.2	0.5 ± 0.2	n.s.
Cover field layer	1.1 ± 0.1	1.4 ± 0.1	n.s.	2.1 ± 0.1	2.0 ± 0.2	n.s.	2.4 ± 0.1	2.7 ± 0.1	*
Cover shrub layer	1.1 ± 0.1	1.4 ± 0.1	**	0.5 ± 0.1	0.7 ± 0.2	n.s.	0.7 ± 0.1	1.0 ± 0.2	*
Cover tree layer	0.9 ± 0.2	1.0 ± 0.1	n.s.	0.3 ± 0.1	0.4 ± 0.1	n.s.	0.4 ± 0.1	0.6 ± 0.2	n.s.

Pholidoptera griseoaptera (56%) were among the most common species.

From 1994 to 2015, we detected a significant increase of the habitat generalists *C. dispar*, *P. griseoaptera* and *R. roeselii* across all grassland types. Furthermore, *Tettigonia viridissima* became significantly more frequent in calcareous and wet grasslands. In addition, the habitat specialists *Stenobothrus lineatus* and *Tetrix tenuicornis* significantly increased in calcareous grasslands. In contrast, *Chorthippus brunneus*, *O. viridulus*, and *P. parallelus* significantly decreased in wet grasslands.

Whereas *P. parallelus* was still the most widespread species in calcareous (95%) and mesic grasslands (96%) in 2015, the dominant Orthoptera species in wet grasslands was now *P. griseoaptera* (96%). Additionally, *C. dispar* and *R. roeselii* were now among the most frequent species in all studied grassland types (*C. dispar* – CAL: 86%, MES: 70%, WET: 74%; *R. roeselii* – CAL: 90%, MES: 91%, WET: 61%).

3.2.1. Species and Community Temperature Index (STI and CTI)

The STI values of the detected species ranged from 12.6 to 13.4 °C. *Conocephalus fuscus*, *Bicolorana bicolor*, and *Nemobius sylvestris* were identified as the three species with the highest macroclimatic temperature demands, whereas *Metrioptera brachyptera*, *Decticus verrucivorus*, and *Omocestus viridulus* had the lowest STI values in this study (Table 3). In accordance with higher turnover rates, we found a significant increase of the CTI in both mesic and wet grasslands between 1994 and 2015. In contrast, the CTI did not change in calcareous grasslands (Fig. 2).

4. Discussion

In this study, Orthoptera strongly responded to altered environmental conditions in semi-natural grasslands between 1994 and 2015. Both annual and summer temperatures increased in the study area. Due to the continuity of habitat management, habitat quality remained stable in calcareous and mesic grasslands, but particularly decreased in predominantly abandoned wet grasslands. As a result of global warming, Orthoptera species richness in the well-managed grassland types (i.e. calcareous and mesic grasslands) increased. In contrast,

Table 3
Frequency (%) of recorded Orthoptera species in the study area classified by habitat specificity (HS; S = specialist; G = generalist) as well as dispersal ability (DA; H = high mobility; L = low mobility) and Species Temperature Index (STI; cf. Devictor et al., 2008). CAL = calcareous grasslands, $N = 21$; MES = mesic grasslands, $N = 23$; WET = wet grasslands, $N = 23$. Differences were tested using McNemar test. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. $p > 0.05$.

Species	HS	DA	STI	CAL			MES			WET		
				1994	2015	P	1994	2015	P	1994	2015	P
Bicolorana bicolor	S	H	13.12	81	81	n.s.	26	4	n.s.	4	.	n.s.
Chorthippus biguttulus	G	H	12.97	96	86	n.s.	48	61	n.s.	30	13	n.s.
Chorthippus brunneus	G	H	12.98	76	52	n.s.	39	26	n.s.	30	4	*
Chrysochraon dispar	G	H	13.10	10	86	***	17	70	**	43	74	*
Conocephalus fuscus	S	H	13.35	5	.	n.s.	.	.	n.s.	9	17	n.s.
Decticus verrucivorus	S	L	12.59	14	10	n.s.	.	.	n.s.	.	.	n.s.
Metrioptera brachyptera	S	L	12.57	71	86	n.s.	13	4	n.s.	4	4	n.s.
Myrmeleotettix maculatus	S	L	12.99	38	19	n.s.	.	.	n.s.	.	.	n.s.
Nemobius sylvestris	S	L	13.11	10	5	n.s.	4	.	n.s.	4	.	n.s.
Omocestus viridulus	G	L	12.74	81	81	n.s.	83	61	n.s.	83	52	*
Pholidoptera griseoaptera	G	L	12.97	29	76	**	26	52	*	52	96	**
Pseudochorth. parallelus	G	L	12.96	100	95	n.s.	96	96	n.s.	87	52	*
Roeseliana roeselii	G	H	12.95	.	90	***	.	91	***	.	61	***
Stenobothrus lineatus	S	H	12.89	52	81	*	.	9	n.s.	.	.	n.s.
Stenobothrus stigmaticus	S	L	12.78	5	.	n.s.	.	.	n.s.	.	.	n.s.
Stethophyma grossum	S	H	12.96	.	.	n.s.	.	.	n.s.	9	9	n.s.
Tetrix tenuicornis	S	L	13.00	29	62	**	4	.	n.s.	.	.	n.s.
Tetrix undulata	G	L	12.99	19	19	n.s.	22	26	n.s.	17	9	n.s.
Tettigonia viridissima	G	H	13.06	43	76	*	13	35	n.s.	22	57	*

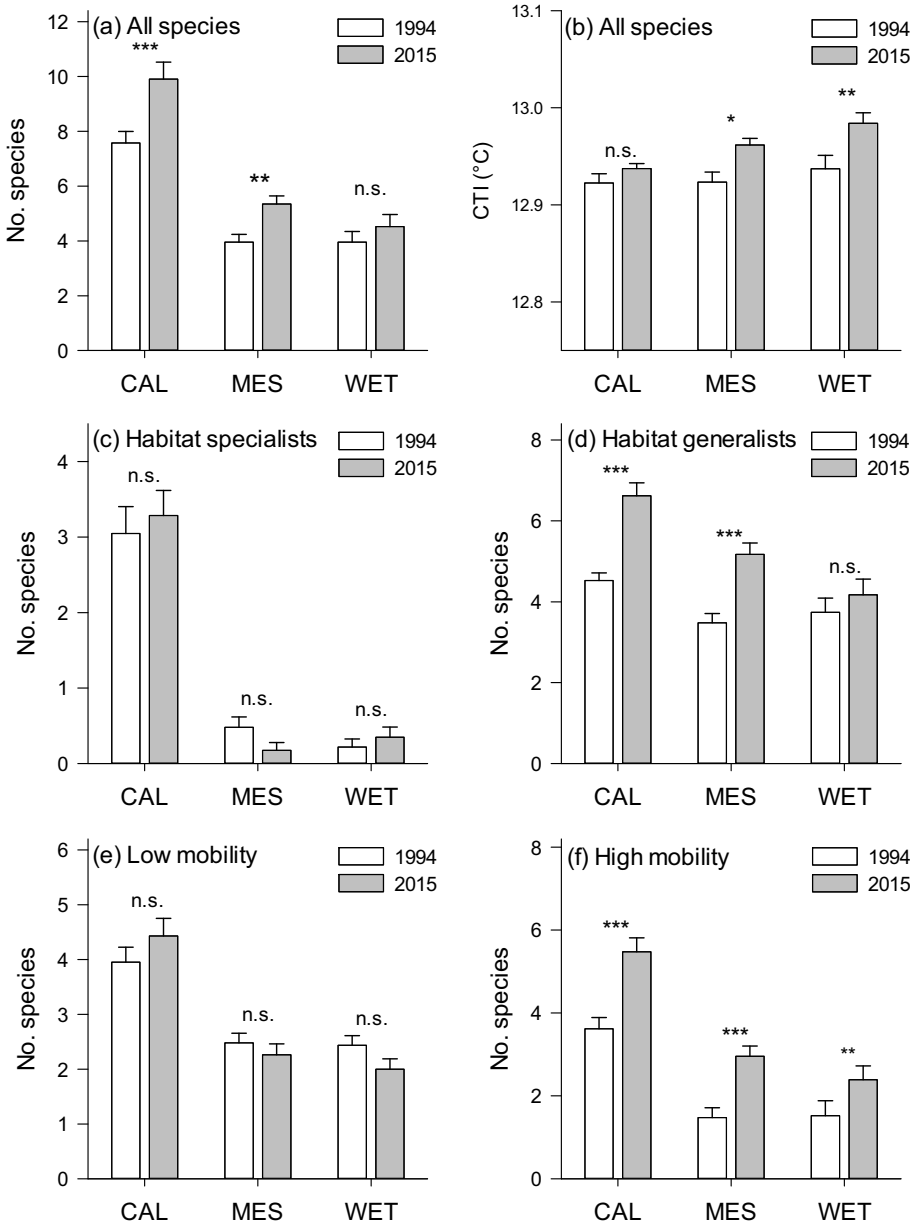

Fig. 2. Differences in a) overall species richness, b) Community Temperature Index (cf. Devictor et al., 2008), c) number of habitat specialists, d) number of habitat generalists, e) species with low and f) high mobility (cf. Table 3) between 1994 and 2015. CAL = calcareous grasslands, $N = 21$; MES = mesic grasslands, $N = 23$; WET = wet grasslands, $N = 23$. Differences were tested using Wilcoxon Signed Rank test. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. $p > 0.05$.

overall species richness in wet grasslands did not change, even though many of the grasslands have been subject to the negative effects of long-term abandonment. The increase in species richness was mainly due to an expansion of habitat generalists and mobile species, but the number of habitat specialists and species with limited dispersal ability did not increase in any of the grassland types. We also detected an increase of the CTI in mesic and wet grasslands.

Orthoptera are known to be very sensitive to both land-use and climate change (e.g. Beckmann et al., 2015; Hickling et al., 2006; Thomas et al., 2001). There is a broad consensus that habitat loss caused by land-use change is the most severe threat to Orthoptera (Fartmann et al., 2012; Hochkirch et al., 2016; Maas et al., 2011; Marini et al., 2009). Conversely, as most Orthoptera species depend on high ambient temperatures (Willott and Hassall, 1998), it has been documented that global warming is the driving force behind recent range expansions of Orthoptera across temperate Europe (e.g. Beckmann et al., 2015; Poniatowski et al., 2012, 2018b; Thomas et al., 2001). However, former studies often failed to disentangle the effects of land-use and climate change on Orthoptera community shifts. A possible way to objectify the climate-driven rate of community shifts is the calculation of the CTI, which reflects the relative composition of thermophilic versus cold-adapted species (cf. Devictor et al., 2008). To our knowledge, this study is the first to quantify the impact of climate change on recent Orthoptera community shifts by applying the approach of Devictor et al. (2008). As there was an increase in the CTI between 1994 and 2015, we found clear evidence that Orthoptera communities were more frequently composed of species adapted to warmer macroclimates, which was in particular true for the relatively species-poor mesic and wet grasslands. There was also an increase of species richness in calcareous grasslands, but the CTI did not change in this grassland type. This result can be explained by the generally higher Orthoptera species richness in calcareous grasslands and, hence, lower turnover rates compared to the two other grassland types. Additionally, it should be considered that the STI values only provide information on the

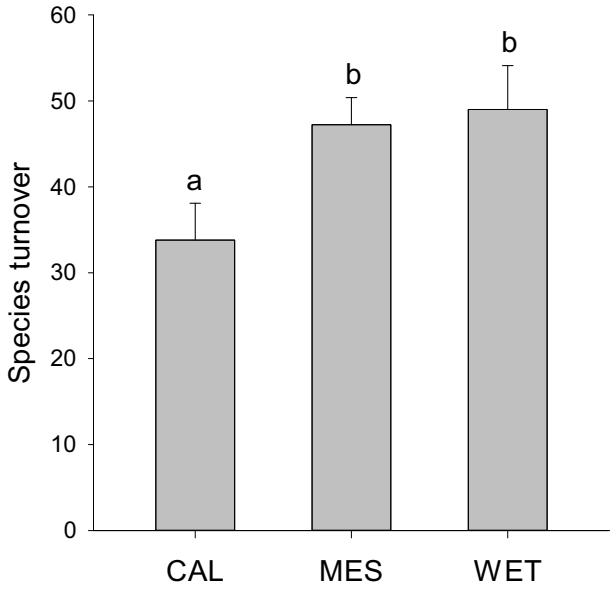

Fig. 3. Species turnover (Whittaker's beta diversity index [Whittaker, 1960]) between 1994 and 2015. CAL = calcareous grasslands, $N = 21$; MES = mesic grasslands, $N = 23$; WET = wet grasslands, $N = 23$. Differences were tested using Kruskal-Wallis H ANOVA ($H = 9.88$; $df = 2$; $p < 0.01$) with Dunn's test as post hoc test. Different letters indicate significant differences among the grassland types ($p < 0.05$).

macroclimate across the range of a species and does not take into account the microclimate of the colonised habitats. As microclimate is one of the key factors determining Orthoptera patch occupancy, especially the occurrence of habitat specialists (Fartmann et al., 2012; Wünsch et al., 2012; Helbing et al., 2014), it may override the impact of macroclimate on species distribution in some cases.

Several studies indicate that global warming may primarily foster mobile habitat generalists, whereas the majority of habitat specialists or species with low dispersal ability are assumed to be less able to adapt to climate change (e.g. Beckmann et al., 2015; Hickling et al., 2006; Warren et al., 2001; Poniatowski et al., 2012). In accordance with these findings, the increase in Orthoptera species richness in calcareous and mesic grasslands in the study area was mainly driven by the strong expansion of mobile habitat generalists. For two of these species, *C. dispar* and *R. roeselii*, recent range expansions across Central and Northwestern Europe are well-documented (e.g. Bakker et al., 2015; Beckmann et al., 2015; Poniatowski et al., 2012, 2018b; Thomas et al., 2001). Both species are characterised by low habitat specificity, high dispersal capability, and require a warm macroclimate (Ingrisch and Köhler, 1998; Poniatowski et al., 2018b). Prior studies revealed that the interaction of such traits determines whether species are able to persist or even thrive under recent environmental change (Beckmann et al., 2015; Nadeau and Fuller, 2016; Reinhardt et al., 2005).

Until the 1980s, the distribution of *C. dispar* and *R. roeselii* in the Eifel was restricted to the most climatically favourable valleys, even though structurally suitable habitats were largely available in the landscape (Ingrisch, 1984; Weber and Weidner, 1995). However, annual as well as summer temperatures increased over the last decades by almost 1 °C. As a consequence, both species have rapidly expanded their ranges to higher altitudes. Whereas *C. dispar* was rare and *R. roeselii* even absent from the study area in 1994 (Weber and Weidner, 1995), both species were among the most dominant species in all studied grassland types in 2015. *P. griseoaptera* and *T. viridissima* were two further habitat generalists that rarely colonised the higher altitudes of the Eifel in the past (Ingrisch, 1984), but have now increased in patch occupancy across all studied grassland types. Whereas *T. viridissima* is also a highly mobile species, *P. griseoaptera* is flightless and so generally has limited dispersal ability. However, Diekötter et al. (2007) showed that dispersal success of *P. griseoaptera* clearly increases in heterogeneous landscapes. Consequently, we explain the strong expansion of this species in the study area by the high availability of movement corridors such as forest edges, hedgerows, and verges (Council of Euskirchen, 2008).

Habitat quality is another key factor determining Orthoptera occurrence and diversity in fragmented landscapes (Löffler and Fartmann, 2017; Poniatowski and Fartmann, 2010, 2018a). It comprises a multifactorial complex of environmental factors, such as land use, vegetation structure and microclimate (Poniatowski et al., 2018a). For Orthoptera, it has been shown that a good habitat quality (i.e. conditions which promote overall Orthoptera species richness) strongly depends on land use (e.g. Fartmann et al., 2012; Löffler and Fartmann, 2017; Marini et al., 2009). Consequently, Orthoptera diversity is negatively affected by abandonment, mainly due to its adverse effects on microclimate (Fartmann et al., 2012; Helbing et al., 2014; Marini et al., 2009). The calcareous and mesic grassland in the study area are mostly protected by the EU Habitats Directive and, thus, were generally well-managed (cf. Section 2.2.1) (EC, 1992). Consequently, there were only minor changes of habitat quality in these habitats (i.e. slight increase in shrub cover in calcareous grasslands). In contrast, wet grasslands that are not protected by the Habitats Directive have more frequently suffered from long-term abandonment leading to forms of habitat deterioration such as an increase in field-layer and shrub cover. As a result, decreases in patch occupancy were observed in wet grasslands for three species, *Chorthippus brunneus*, *Omocestus viridulus*, and *Pseudochorthippus parallelus*. All three species are common and did not decline in the two other well-managed (warmer and drier) grassland types. Since these species usually colonise early to mid-successional stages of grassland succession (Poniatowski and Fartmann, 2008; Fartmann et al., 2012; Schlumprecht and Waeber, 2003) it is very likely that habitat degradation due to succession is the reason for their decline.

Discrepancies between our study and findings from previous long-term research can be partly explained by differences in macroclimate, geographic isolation, and habitat connectivity. Schuch et al. (2011) found little evidence for climate-driven community shifts in protected dry grasslands in the East German agricultural landscape. Due to farmland consolidation during the socialism period (1945–1990), the landscape is dominated by large-scale fields that are about 10 times the size of the parcels in the study area (EC, 2018). As the availability of dispersal corridors is strongly limited in such homogeneous landscapes (cf. Diekötter et al., 2007), it is very likely that the low landscape connectivity may have restricted species dispersal in that study (cf. Beckmann et al., 2015; Pryke and Samways, 2012). Moreover, the study area was characterised by warm summers and low precipitation and so was already rich in thermophilic species at the beginning of their study (cf. Schuch et al., 2011). In contrast, large-scale range expansions of Orthoptera in Great Britain were mainly restricted to only two species (*Conocephalus fuscus* and *R. roeselii*), even though habitat connectivity was relatively high (Beckmann et al., 2015). Due to rather unfavourable climatic conditions and geographic isolation, Great Britain is characterised by a generally low Orthoptera diversity and, in particular, only a few thermophilic species that may respond to climate warming.

5. Conclusion

Despite the short time period between the two surveys (1994 vs. 2015), we found clear evidence that global warming has resulted in range shifts of mobile habitat generalists during recent decades and, consequently, has promoted Orthoptera species richness in semi-natural grasslands in the low mountain range of the study area. In contrast, the number of habitat specialists and less mobile species has not changed in the studied grasslands. Even though we found a positive response of Orthoptera communities to recent global warming, the findings should be interpreted cautiously as progressing climate change may also have

negative effects on Orthoptera. This also includes a risk of biotic homogenisation in insect communities (cf. Streitberger et al., 2016). Although we could not yet detect a decline of hygrophilous Orthoptera species, some of them may suffer from increasing drought in the study area in the long run. In line with this assumption, previous studies have already shown that some hygrophilous or alpine Orthoptera species have become increasingly threatened due to climate change (cf. Guo et al., 2009; Hochkirch et al., 2016; Poniatowski et al., 2018b; Wessely et al., 2017). Moreover, the results of our study imply that the effects of global warming on Orthoptera communities also depend on the availability and connectivity of suitable habitats (cf. Hill et al., 2001). We therefore emphasise that abandonment and land-use intensification are serious threats to Orthoptera in Central European grasslands, even though an array of thermophilic Orthoptera species are benefiting from rising temperatures (cf. Poniatowski et al., 2018b). Hence, monitoring of Orthoptera should also receive great attention in future work. Those studies should ideally comprise a broad range of habitats within different climate and landscape contexts. It is now the challenge to establish evidence-based conservation practices that can help maintain species richness in times of global change. In this light, the maintenance or reintroduction of traditional land use is essential to sustain a good habitat quality and promote Orthoptera diversity in semi-natural grasslands (WallisDeVries et al., 2002; Fartmann et al., 2012). These conservation measures should especially facilitate low-intensity mowing (1–2 times per year without fertiliser application) in meadows and low-intensity grazing in pastures. Furthermore, management should be targeted on establishing dense habitat networks within a heterogeneous landscape matrix which may increase the resilience of grassland ecosystems to global warming (Pryke and Samways, 2012; Streitberger et al., 2016).

Acknowledgements

We are particularly grateful to the team of the 'Biological Station of the Council Euskirchen', especially to Julia Zehlius who gave helpful comments at the initial stage of the study. For their hospitality and providing an accommodation during the period of field work we would like to thank Heike Günther, Werner Poensgen and Simone Wolf. Harald Groß (Conservation authority of the Council Euskirchen) gave the permission to survey Orthoptera in protected areas of the study area. Furthermore, we thank three anonymous reviewers for their suggestions and helpful comments on a former version of the manuscript.

Funding

This study was funded by a PhD scholarship of the German Environmental Foundation (DBU).

References

Ackermann, W., Sachteleben, J., 2012. Identifizierung der Hotspots der Biologischen Vielfalt in Deutschland. BfN-Skripten 315, 1–133.
Bakker, W.H., Bouwman, J.H., Brekelmans, F., Colijn, E.C., Felix, R., Grutters, M.A.J., Kerkhof, W., Kleukers, R.M.J.C., 2015. De Nederlandse sprinkhanen en krekels (Orthoptera). EIS, Leiden.
Bates, D., Maechler, M., Bolker, B., Walker, S., 2018. lme4: linear mixed-effects models using 'Eigen' and S4. R package version 1.1-19. http://CRAN.R-project.org/web/packages/lme4, Accessed date: 26 February 2019.
Bazelet, C.S., Samways, M.J., 2011. Identifying grasshopper bioindicators for habitat quality assessment of ecological networks. Ecol. Indic. 11, 1259–1269.
Beckmann, B.C., Purse, B.V., Roy, D.B., Roy, H.E., Sutton, G.P., Thomas, C.D., 2015. Two species with an unusual combination of traits dominate responses of British grasshoppers and to environmental change. PLoS One 10, e0130488.
Bellmann, H., 2006. Der Kosmos Heuschreckenführer: Die Arten Mitteleuropas sicher bestimmen. Kosmos, Stuttgart.
Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333, 1024–1026.
Council of Euskirchen, 2008. Naturschutzgroßprojekt Ahr 2000 – 1993–2005 - Endbericht. Final Report of the Ahr 2000 Project, Euskirchen.
Devictor, V., Juliirad, R., Denis, C., Jiguet, F., 2008. Birds are tracking climate warming, but not fast enough. Proc. R. Soc. B 275, 2743–2748.
Devictor, V., van Swaay, C., Bereton, T., Brotons, L., Chamberlain, D., Heliöla, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Å., Reif, J., Roy, D.B., Schweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., Wallis DeVries, M., Wynhoff, I., Jiguet, F., 2012. Differences in the climatic debts of birds and butterflies at a continental scale. Nat. Clim. Chang. 2, 121–124.
Diekötter, T., Speelmans, M., Dusoulier, F., van, Wingerden.W.K.R.E., Maelfait, J.-P., Crist, T.O., Edwards, P.J., Dietz, H., 2007. Effects of landscape and habitat structure on movement patterns of the flightless bush cricket *Pholidoptera griseoaptera*. Environ. Entomol. 36, 90–98.
DWD (German Meteorological Service), 2018. Climate Data Center. https://www.dwd.de/DE/leistungen/cdcftp/cdcftp.html, Accessed date: 5 October 2018.
EC (European Commission), 1992. The Habitats Directive. Council Directive 92/43/EEC of 21 May 1992 on the Conservation of Natural Habitats and of Wild Fauna and Flora.
EC (European Commission), 2018. Eurostat – Land Cover/Use Statistics (LUCAS). https://ec.europa.eu/eurostat/web/lucas/links, Accessed date: 22 November 2018.
Fartmann, T., Krämer, B., Stelzner, F., Poniatowski, D., 2012. Orthoptera as ecological indicators for succession in steppe grassland. Ecol. Indic. 20, 337–344.
Feurdean, A., Ruprecht, E., Molnár, Z., Hutchinson, S.M., Hickler, T., 2018. Biodiversity-rich European grasslands: ancient forgotten ecosystems. Biol. Conserv. 228, 224–232.
Fischer, J., Steinlechner, D., Zehm, A., Poniatowski, D., Fartmann, T., Beckmann, A., Stettmer, C., 2016. Die Heuschrecken Deutschlands und Nordtirols. Bestimmen–Beobachten–Schützen. Quelle & Meyer, Wiebelsheim.
Guo, K., Hao, S.-G., Sun, O.J., Kang, L., 2009. Differential responses to warming and increased precipitation among three contrasting grasshopper species. Glob. Chang. Biol. 15, 2539–2548.
Hautier, Y., Tilman, D., Isbell, F., Seabloom, E.W., Borer, E.T., Reich, B.P., 2015. Anthropogenic environmental changes affect ecosystem stability via biodiversity. Science 348, 336–340.
Helbing, F., Blaeser, T.P., Löffler, F., Fartmann, T., 2014. Response of Orthoptera communities to succession in alluvial pine woodlands. J. Insect Conserv. 18, 215–224.
Hickling, R., Roy, D.B., Hill, J.K., Fox, R., Thomas, C.D., 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Glob. Chang. Biol. 12, 450–455.
Hill, J.K., Collingham, Y.C., Thomas, C.D., Blakeley, D.S., Fox, R., Moss, D., Huntley, B., 2001. Impacts of landscape structure on butterfly range expansion. Ecol. Lett. 4, 313–321.
Hochkirch, A., Nieto, A., García Criado, M., Cálix, M., Braud, Y., Buzzetti, F.M., Chobanov, D., Odé, B., Presa Asensio, J.J., Willemse, L., Zuna-Kratky, T., Barranco Vega, P., Bushell, M., Clemente, M.E., Correas, J.R., Dusoulier, F., Ferreira, S., Fontana, P., García, M.D., Heller, K.-G., Iorgu, I.S., Ivkovic, S., Kati, V., Kleukers, R., Krištín, A., Lemonnier-Darcemont, M., Lemos, P., Massa, B., Monnerat, C., Papapavlou, K.P., Prunier, F., Pushkar, T., Roesti, C., Rutschmann, F., Sirin, D., Skejo, J., Szövényi, G., Tzirkalli, E., Vedenina, V., Barat Domenech, J., Barros, F., Cordero Tapia, P.J., Defaut, B., Fartmann, T., Gomboc, S., Gutiérrez-Rodríguez, J., Holuša, J., Illich, I., Karjalainen, S., Kočárek, P., Korsunovskaya, O., Liana, A., López, H., Morin, D., Olmo-Vidal, J.M., Puskás, G., Savitsky, V., Stalling, T., Tumbrinck, J., 2016. European Red List of Grasshoppers, Crickets and Bush-crickets. Publications Office of the European Union, Luxembourg.
Ingrisch, S., 1984. Zur Verbreitung und Vergesellschaftung der Orthopteren in der Nordeifel. Decheniana 137, 79–104.
Ingrisch, S., Köhler, G., 1998. Die Heuschrecken Mitteleuropas. Westarp Wissenschaften, Magdeburg.
Koleff, P., Gaston, K.J., Lennon, J.J., 2003. Measuring beta diversity for presence-absence data. J. Anim. Ecol. 72, 367–382.
Kuussaari, M., Heliola, J., Pöyry, J., Saarinen, K., 2007. Contrasting response of butterfly species preferring semi-natural grasslands, field margins and forest edges in northern Europe. J. Insect Conserv. 11, 351–366.
Löffler, F., Fartmann, T., 2017. Effects of landscape and habitat quality on Orthoptera assemblages of pre-alpine calcareous grasslands. Agric. Ecosyst. Environ. 248, 71–81.
Maas, S., Detzel, P., Staudt, A., 2011. Rote Liste und Gesamtartenliste der Heuschrecken (Saltatoria) Deutschlands. Naturschutz und Biologische Vielfalt 70, 577–606.
Mantyka-Pringle, C.S., Visconti, P., Di Marco, M., Martin, T.G., Rondini, C., Rhodes, J.R., 2015. Climate change modifies risk of global biodiversity loss due to land-cover change. Biol. Conserv. 187, 103–111.
Marini, L., Fontana, P., Battisti, A., Gaston, K.J., 2009. Response of orthopteran diversity to abandonment of semi-natural meadows. Agric. Ecosyst. Environ. 132, 232–236.
Nadeau, C.P., Fuller, A.K., 2016. Combining landscape variables and species traits can improve the utility of climate change vulnerability assessments. Biol. Conserv. 202, 30–38.
Nieto-Sanchez, S., Gutierrez, D., Wilson, R.J., 2015. Long-term change and spatial variation in butterfly communities over an elevational gradient: driven by climate, buffered by habitat. Divers. Distrib. 21, 950–961.
Oliver, T.H., Smithers, R.J., Beale, C.M., Watts, K., 2016. Are existing biodiversity conservation strategies appropriate in a changing climate? Biol. Conserv. 193, 17–26.
Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37, 637–669.
Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.
Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A., Warren, M., 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399, 579–583.
Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science 344, 987–997.

Poniatowski, D., Fartmann, T., 2008. The classification of insect communities: lessons from Orthoptera assemblages of semi-dry calcareous grasslands in central Germany. Eur. J. Entomol. 105, 659–671.
Poniatowski, D., Fartmann, T., 2010. What determines the distribution of a flightless bush-cricket (*Metrioptera brachyptera*) in a fragmented landscape? J. Insect Conserv. 14, 637–645.
Poniatowski, D., Fartmann, T., 2011. Dispersal capability in a habitat specialist bush cricket: the role of population density and habitat moisture. Ecol. Entomol. 36, 717–723.
Poniatowski, D., Heinze, S., Fartmann, T., 2012. The role of macropters during range expansion of a wing-dimorphic insect species. Evol. Ecol. 26, 759–770.
Poniatowski, D., Stuhldreher, G., Löffler, F., Fartmann, T., 2018a. Patch occupancy of grassland specialists: habitat quality matters more than habitat connectivity. Biol. Conserv. 225, 237–244.
Poniatowski, D., Münsch, T., Helbing, F., Fartmann, T., 2018b. Arealveränderungen mitteleuropäischer Heuschrecken als Folge des Klimawandels. Natur und Landschaft 93, 553–561.
Pryke, J.S., Samways, M.J., 2012. Ecological networks act as extensions of protected areas for arthropod biodiversity conservation. J. Appl. Ecol. 49, 591–600.
R Development Core Team, 2017. R: A Language and Environment for Statistical Computing. https://www.R-project.org/, Accessed date: 24 May 2019.
Reinhardt, K., Köhler, G., Maas, S., Detzel, P., 2005. Low dispersal ability and habitat specificity promote extinctions in rare but not in widespread species: the Orthoptera of Germany. Ecography 28, 593–602.
Rennwald, E., 2000. Verzeichnis und Rote Liste der Pflanzengesellschaften Deutschlands. Schriftenreihe für Vegetationskunde 35 Landwirtschaftsverlag Münster, Bonn.
Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Biodiversity – global biodiversity scenarios for the year 2100. Science 287, 1770–1774.
Samways, M.J., 2005. Insect Diversity Conservation. Cambridge University Press, Cambridge.
Samways, M.J., McGeoch, M.A., New, T.R., 2010. Insect Conservation. Oxford University Press, New York.
Schlumprecht, H., Waeber, G., 2003. Heuschrecken in Bayern. Ulmer, Stuttgart.
Schuch, S., Bock, J., Leuschner, C., Schaefer, M., Wesche, K., 2011. Minor changes in orthopteran assemblages of Central European protected dry grasslands during the last 40 years. J. Insect Conserv. 15, 811–822.
Steck, C.E., Bürgi, M., Bolliger, J., Kienast, F., Lehmann, A., Gonseth, Y., 2007. Conservation of grasshopper diversity in a changing environment. Biol. Conserv. 138, 360–370.
Streitberger, M., Jedicke, E., Fartmann, T., 2016. Auswirkungen des rezenten Klimawandels auf die Biodiversität in Mittelgebirgen – eine Literaturstudie zu Arten und Lebensräumen. Naturschutz und Landschaftsplanung 48, 37–45.
Tayleur, C.M., Devictor, V., Gäuzere, P., Jonzén, N., Smith, H.G., Lindström, Å., 2016. Regional variation in climate change winners and losers highlights the rapid loss of cold-dwelling species. Divers. Distrib. 22, 468–480.
Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M., Conradt, L., 2001. Ecological and evolutionary processes at expanding range margins. Nature 411, 577–581.
Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. Nature 427, 145–148.
Thomsen, P.F., Jørgensen, P.S., Bruun, H.H., Pedersen, J., Ris-Nielsen, T., Jonko, K., Slowinska, I., Rahbek, C., Karsholt, O., 2016. Resource specialists lead local insect community turnover associated with temperature-analysis of an 18-year full-seasonal record of moths and beetles. J. Anim. Ecol. 85, 251–261.
Thuiller, W., 2017. Biodiversity: climate change and the ecologist. Nature 448, 550–552.
Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberhoff, D., Swackhamer, D., 2001. Forecasting agriculturally driven global environmental change. Science 292, 281–284.
Veen, P., Jefferson, R., de Smidt, J., van der Straaten, J., 2009. Grasslands in Europe of High Nature Value. KNNV Publishing, Zeist.
WallisDeVries, M.F., Poschlod, P., Willems, J.H., 2002. Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. Biol. Conserv. 104, 265–273.
Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffocate, S., Harding, P., Willis, S.G., Greatorex-Davies, J.N., Moss, D., Thomas, C.D., 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414, 65–69.
Weber, T., Weidner, A., 1995. Gewässersystem Obere Ahr und Nebenbäche– Ökologische und faunistische Untersuchungen der Heuschrecken–Beitrag zum Pflege- und Entwicklungsplan Ahr 2000. Environmental assessment on behalf of the Council of Euskirchen, Bonn.
Wessely, J., Hülber, K., Gattringer, A., Kuttner, M., Moser, D., Rabitsch, W., Schindler, S., Dullinger, S., Essl, F., 2017. Habitat-based conservation strategies cannot compensate for climate-change-induced range loss. Nat. Clim. Chang. 7, 823–827.
Weyer, J., Weinberger, J., Hockirch, A., 2012. Mobility and microhabitat utilization in a flightless wetland grasshopper, *Chorthippus montanus* (Charpentier, 1825). J. Insect Conserv. 16, 379–390.
Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30, 279–338.
Willott, S.J., Hassall, M., 1998. Life-history responses of British grasshoppers (Orthoptera: Acrididae) to temperature change. Funct. Ecol. 12, 232–241.
WMO (World Meteorological Organization), 2017. WMO Guidelines on the Calculation of Climate Normals. WMO No. 1203, Geneva.
Wünsch, Y., Schirmel, J., Fartmann, T., 2012. Conservation management of coastal dunes for Orthoptera has to consider oviposition and nymphal preferences. J. Insect Conserv. 16, 501–510.