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Habitat availability and climate warming drive changes in the distribution of grassland grasshoppers

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ABSTRACT

Land use and climate change are considered the major drivers of current insect declines. However, in intensively used agricultural landscapes the impacts of both on Orthoptera (hereinafter termed 'grasshoppers') are still poorly understood. We analysed grasshopper assemblages in two grassland types (patches, $N = 63$ and verges, $N = 118$) by comparing two surveys – one in 1995 and one in 2012 – in an agricultural landscape of the NW-German Lowland. Despite the short time period between the two surveys, we detected strong changes in environmental conditions and grasshopper assemblages. In contrast to grassland verges, grassland patches suffered from severe habitat loss. More than a quarter of all grassland patches were converted to other biotope types, in particular, arable fields cropped with maize. Additionally, summer temperatures rose by 1.1 °C. Species richness and the Community Temperature Index also increased in grassland patches and verges. By contrast, the Community Farmland Index decreased. The ongoing cultivation of maize as a bioenergy crop was responsible for a severe loss of grassland patches leading to a homogenization at the landscape level. However, due to the high connectivity of grasslands, thermophilous and generalistic grasshopper species with both low and high dispersal ability were able to track global warming. Based on our study, (i) the availability of suitable habitats and (ii) climate warming were the major drivers of grasshopper assemblage shifts. With the ongoing loss of grassland patches, grassland verges become increasingly important not only as dispersal corridors, but also as refuges for biodiversity.

1. Introduction

Insects are the most species-rich taxonomic group across the globe (Stork, 2018). Due to their outstanding value for ecosystem functioning, insects are of crucial importance for human well-being on earth (Powney et al., 2019; Samways et al., 2020). However, during the past 200 years, humankind has altered the environmental conditions globally at an unparalleled rate (Rockström et al., 2009), causing a dramatic loss of insect species (Sánchez-Bayo and Wyckhuys, 2019; Cardoso et al., 2020). Since the beginning of the industrial era, at least 250,000 species are estimated to have become extinct (Cardoso et al., 2020) and another 500,000 species are assumed to face extinction (IPBES, 2019). For terrestrial biomes, land-use change is considered the major driver of current insect declines (Cardoso et al., 2020; Wagner, 2020). However, climate change is increasingly becoming a further, serious threat (IPBES, 2019).

The main impacts of land-use change on biodiversity include habitat loss, habitat fragmentation and the decrease in habitat quality of the remaining habitat patches (Poniatowski et al., 2018b; Cardoso et al., 2020). These alterations have predominantly been caused by agricultural intensification (Stoate et al., 2009; Burns et al., 2016) and urban development (McKinney, 2006; Grimm et al., 2008; Nitsch et al., 2012). Grasslands are among the most species-rich ecosystems throughout Europe (Wilson et al., 2012; Feurdean et al., 2018). However, as a result of industrial agriculture and urbanization the extent of species-rich grasslands has greatly decreased and the remaining grassland fragments are often embedded in an intensively used matrix of arable land (Helbing et al., 2017; Poniatowski et al., 2018b). During the last two

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decades, the increasing cultivation of bioenergy crops, in particular maize, has resulted in a further severe loss of grassland habitats due to the conversion to arable fields (Stoate et al., 2009; Nitsch et al., 2012; Lüker-Jans et al., 2017; Jerrentrup et al., 2017; Fartmann et al., 2021).

The effects of climate warming on insects vary considerably between taxonomic groups and species (Warren et al., 2001; Chen et al., 2011; Platts et al., 2019). Especially thermophilous species rank among the winners of climate change and often expand their ranges (Pöyry et al., 2009; Termaat et al., 2019; Poniatowski et al., 2020). By contrast, hygrophilous species are assumed to suffer from global warming (Buse and Griebeler, 2011; Streitberger et al., 2016). Besides climate sensitivity, dispersal ability, occurrence of dispersal corridors, habitat availability and the degree of habitat specialisation are further important predictors of the variation in species' response to climate change (Angert et al., 2011; MacLean and Beissinger, 2017).

Orthoptera (hereinafter termed 'grasshoppers') are of great functional importance in grassland ecosystems due to their key role as herbivores and prey (Samways, 2005). Furthermore, they are highly sensitive to changes in land use (Marini et al., 2008; Fartmann et al., 2012; Bazelet and Samways, 2012; Uchida and Ushimaru, 2014) and climate (Löffler et al., 2019; Fumy et al., 2020; Poniatowski et al., 2020). Consequently, they are widely used as bioindicators to study the effects of global change in grassland ecosystems (Samways, 2005). Recently, several studies from western and central Europe showed that especially thermophilous grasshopper species with low habitat specificity and high dispersal ability expanded their ranges in response to global warming (Poniatowski et al., 2012, 2020; Beckmann et al., 2015; Löffler et al., 2019; Fumy et al., 2020). However, research analysing shifts in the composition of complete grasshopper assemblages due to recent environmental change has focused so far on nature reserves or mountain areas with a generally low land-use intensity (Schuch et al., 2011; Löffler et al., 2019; Fumy et al., 2020). By contrast, in intensively used and highly dynamic agricultural landscapes the impacts of recent land use and climate change on grasshopper assemblages in grasslands are still poorly understood.

Here, we study the effects of land use and climate change on grasshopper-assemblage shifts in a landscape with intensive agriculture in the NW-German Lowland by considering two grassland types: (i) grassland patches ($N = 63$) and (ii) grassland verges (linear grassland habitats, $N = 118$). Therefore, we analysed changes in environmental conditions (habitat loss, climate change) and grasshopper species richness (i.e., all species, species with low and species with high dispersal ability) between 1995 and 2012. Moreover, we used (i) the Community Farmland Index (CFI) as a community mean of species' dependence on 'High Nature Value Farmland' (HNV) (Fumy et al., 2020; Poniatowski et al., 2020) and (ii) the Community Temperature Index (CTI) as a community mean of species' temperature preferences (Devictor et al., 2008) to unravel whether grasshopper-assemblage shifts were driven by land use or by climate change. Both indices have recently been established as valuable tools to identify the causes underlying biodiversity shifts in insect communities (Devictor et al., 2012; Löffler et al., 2019; Termaat et al., 2019; Fumy et al., 2020; Poniatowski et al., 2020). In particular, we address the following research questions:

(i) How did species richness, CFI and CTI of grasshopper assemblages vary between 1995 and 2012 due to land use and climate change?
(ii) What are the main drivers of the variation in grasshopper distribution in a rapidly changing environment?

2. Material and methods

2.1. Study area

The study area has a size of 31,400 ha (Bergmann, 1996) and is located in the NW-German Lowland (district of Steinfurt; 52°09′N, 7°46′E) at the border of the federal states of North Rhine-Westphalia and Lower Saxony. The elevation ranges from 40 to 200 m a.s.l., and the climate is suboceanic with mild winters, moderately warm summers, 1528 h of sunshine per year, a mean annual temperature of 9.4 °C and 760 mm of precipitation per year (1961–1990, Münster/Osnabrück Airport; German Meteorological Service, 2018). The study area is dominated by intensive agriculture, such as improved grassland and arable fields. However, despite the high land-use intensity, the size of the fields and grasslands is relatively small, ranging from 1 to 3.5 ha (Schäuble, 2007). Consequently, the area and number of linear structures, such as field margins, hedgerows, tree lines, alleys or ditches, is high. Due to this small-scale mosaic of different land-use types and the heterogeneous landscape structure, the study area is designated as a 'park landscape'.

2.2. Study design

To assess changes in grasshopper assemblages, we compared the presence/absence data of the survey conducted by Bergmann (1996) in 1995 with those from our field study in 2012. Bergmann (1996) provided complete grasshopper-species lists for 181 grassland plots randomly selected across the study area. The plots consisted of 63 grassland patches (pastures and meadows) and 118 grassland verges (linear grassland habitats without agricultural land use, mostly along agricultural roads). The grassland patches (mean ± SE: 19,134 m^2 ± 3, 395 m^2) were much larger than the linear grassland verges (921 m^2 ± 60 m^2) (Mann-Whitney U test, $U = 290$, $P < 0.001$; data derived from aerial photographs). However, the connectivity of the plots was high for both grassland types. Nature-conservation activities (extent of nature reserves or areas with agri-environmental schemes) did not change substantially between 1995 and 2012 in the study area (P. Schwartze pers. comm, 10/2020; Biological Station Steinfurt district).

2.2.1. Environmental conditions

In summer 2012, all 181 plots studied by Bergmann (1996) were revisited. If a grassland plot had been converted into another biotope type, the new type was noted according to Finck et al. (2017). To assess the effects of climate change we analysed trends in annual and summer (April to September) data of temperature and precipitation between the two studies (1996–2011; weather station Münster/Osnabrück Airport, situated within the study area; German Meteorological Service, 2018).

2.2.2. Grasshopper sampling

In summer 2012, all 181 plots were re-surveyed using the same methods that Bergmann (1996) had applied previously. Grassland grasshoppers were sampled twice between the end of June and the beginning of September with at least three weeks between each visit. Each plot and all habitat structures within a plot were surveyed under favourable weather conditions (temperature > 15 °C, cloud cover < 50%) using acoustic and optical search as well as sweep-netting. These methods are known to produce sound data on grasshopper occurrence in grassland ecosystems (Samways et al., 2010; Löffler et al., 2019; Fumy et al., 2020). Shrub- and tree-dwelling species, which occasionally occur in grasslands, were not noted as our sampling techniques do not generate reliable data for these species. Species identification was done in the field, by sound and morphological characteristics using Bellmann (2006). The occurrence of quiet or high-frequency stridulating species, such as *Conocephalus dorsalis*, *Conocephalus fuscus* or *Metrioptera brachyptera*, was assessed using a bat detector (Fischer et al., 2020). A calliper gauge (0.5 mm accuracy) was used to distinguish between the closely related species *Chorthippus biguttulus*, *Chorthippus brunneus* and *Chorthippus mollis*, because wing length and width are species-specific characteristics. The scientific nomenclature follows Fischer et al. (2020).

2.2.3. Grasshopper classifications and global-change indices

We classified grasshopper species by their dispersal ability (low vs. high), the Species Farmland Index (SFI) and the Species Temperature Index (STI) according to Poniatowski et al. (2020). Dispersal ability is well-known to crucially affect the response of grasshopper species to environmental change (e.g., Reinhardt et al., 2005; Löffler et al., 2019; Fumy et al., 2020). The SFI and STI have recently been introduced to detect grasshopper assemblage shifts due to land-use and climate change (Löffler et al., 2019, Fumy er al, 2020). The calculation of each index was based on recent German grasshopper distribution data (Poniatowski et al., 2020). The SFI was calculated as the percentage of HNV farmland of the overall open landscape within the distribution range of a species (Fumy et al., 2020; Poniatowski et al., 2020). HNV farmland comprises farmland (i) with a high proportion of semi-natural vegetation, (ii) with a mosaic of low intensity agriculture and natural and structural elements (e.g., patches of woodland or field margins, hedgerows, stone walls etc.) and (iii) supporting rare species or a high proportion of European or world populations of a species (Paracchini et al., 2008). The STI is defined as the mean temperature within the distribution range of a species (cf. Devictor et al., 2012). For grasshopper species, mean summer temperatures (April–September) were the reference for the calculation of the STI (Löffler et al., 2019; Fumy et al., 2020; Poniatowski et al., 2020). Finally, the Community Farmland Index (CFI) and the Community Temperature Index (CTI) of each plot were calculated by averaging the SFI and STI, respectively, of all species occurring in the particular plot (cf. Devictor et al., 2008, 2012). Both indices have recently been used successfully to relate grasshopper assemblage shifts to land use and climate change (Löffler et al., 2019; Fumy et al., 2020; Poniatowski et al., 2020).

2.3. Statistical analysis

To assess the effects of recent climate change, i.e., changes in temperature and precipitation in the study area, we applied linear models with an autocorrelation (AR1) structure using the gls function (package nlme; Pinheiro et al., 2018). The McNemar Chi-squared test was used to detect the loss of grassland plots and changes in plot occupancy of each grasshopper species between the two survey periods. Because Chi-squared tests do not allow empty categories, we conservatively set frequencies of 0–1 (Eichel and Fartmann, 2008). Changes in the number of species, the CFI and the CTI in each grassland type between the two surveys were tested using the paired *t* test. All statistical analyses were performed using R statistical environment (R Core Team, 2019).

3. Results

3.1. Environmental change

From the 63 grassland patches studied in 1995 only 46 were still used as grasslands in 2012, which corresponds to a loss of 17 plots (27%) (Fig. 1). The main driver of habitat destruction was the conversion of grassland to arable land. This was true for 15 plots (88%); almost 90% of these arable fields were cropped with maize. The two other destroyed plots were used for the construction of houses (12%). By contrast, nearly all of the 118 grassland verges studied in 1995 still existed in 2012. Solely three plots (3%) were covered by a maize field, a building and an afforested grassland, respectively.

From 1996–2011, summer temperatures increased by 1.1 °C (Fig. 2). By contrast, there was no trend in precipitation (annual and summer) and annual temperature.

3.2. Grasshopper-assemblage change

In total, 23 grasshopper species were recorded in the plots during the two surveys (Table 1). Three very rare species detected in 1995, *Metrioptera brachyptera* (occurrence in one plot), *Myrmeleotettix maculatus* (two plots) and *Tettigonia cantans* (one plot), were not found in 2012. In two cases, one plot formerly occupied by *M. maculatus* and one by *T. cantans*, the local extinctions were attributed to habitat loss. By contrast, in 2012, four species, *Conocephalus fuscus*, *Phaneroptera falcata*, *Roeseliana roeselii* and *Tetrix subulata*, were observed in the remaining plots for the first time.

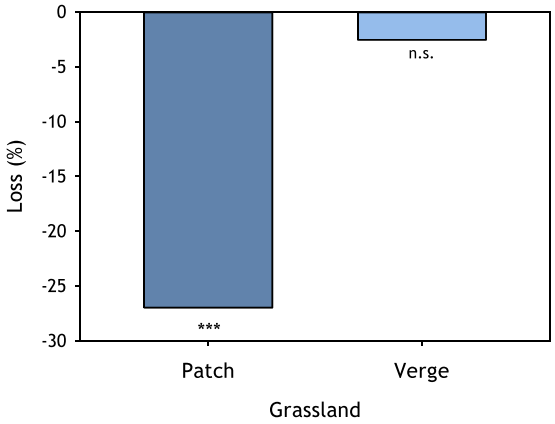

Fig. 1. Loss (%, plots) of grassland patches and verges from 1995 to 2012. Baseline 1995: patches, $N = 63$; verges, $N = 118$. Differences were tested using the McNemar Chi-squared test. n.s. not significant, *** $P < 0.001$.

In 1995, the most widespread species were *Pseudochorthippus parallelus* (occupancy: patches = 85% vs. verges = 74%), *Chorthippus biguttulus* (63% vs. 75%) and *Omocestus viridulus* (65% vs. 63%) (Fig. 3). By contrast, in 2012, the rank order varied, and the most frequent species were *C. biguttulus* (98% vs. 80%), *P. parallelus* (85% vs. 81%) and *Chorthippus brunneus* (72% vs. 67%). Between 1995 and 2012 the frequency of 13 species changed in at least one grassland type. Twelve species were more widespread in 2012. Four of these species, *C. biguttulus*, *C. brunneus*, *Pholidoptera griseoaptera* and *R. roeselii*, even had a higher frequency in both grassland patches and verges. By contrast, only one species, *O. viridulus*, decreased in frequency in both grassland types.

From 1995–2012, species richness (all species, species with low and species with high dispersal ability) and the CTI increased in grassland patches and verges (Fig. 4, Fig. 5). By contrast, the CFI decreased in both grassland types from the first to the second survey (Fig. 5).

4. Discussion

Although the 16-year time period between the two surveys (1995 vs. 2012) was relatively short, we detected strong changes in environmental conditions and grasshopper assemblages in well-connected lowland grasslands. In contrast to grassland verges, grassland patches suffered from severe habitat loss. More than a quarter of all grassland patches were converted to other biotope types, in particular, arable fields cropped with maize. Additionally, summer temperatures rose by 1.1 °C. Species richness and the CTI also increased in grassland patches and verges. By contrast, the CFI decreased in both grassland types.

During the last two decades, the increasing cultivation of bioenergy crops, in particular maize, has been identified as the most important driver of conversion of grasslands to arable fields throughout Europe (Stoate et al., 2009; Fartmann et al., 2021). This is also true for large parts of the German lowlands (Nitsch et al., 2012; Lüker-Jans et al., 2017; Jerrentrup et al., 2017). So far, the negative effects of this development on farmland biodiversity have mostly been evaluated for birds (Teillard et al., 2014; Jerrentrup et al., 2017; Fartmann et al., 2021). Our study now highlights that grassland destruction as a result of the ever-increasing expansion of bioenergy crops poses a serious threat to grasshopper populations, too. Modern-day agriculture on arable fields usually does not allow for the successful development of grasshopper species (Schlumprecht and Waeber, 2003). Consequently, the

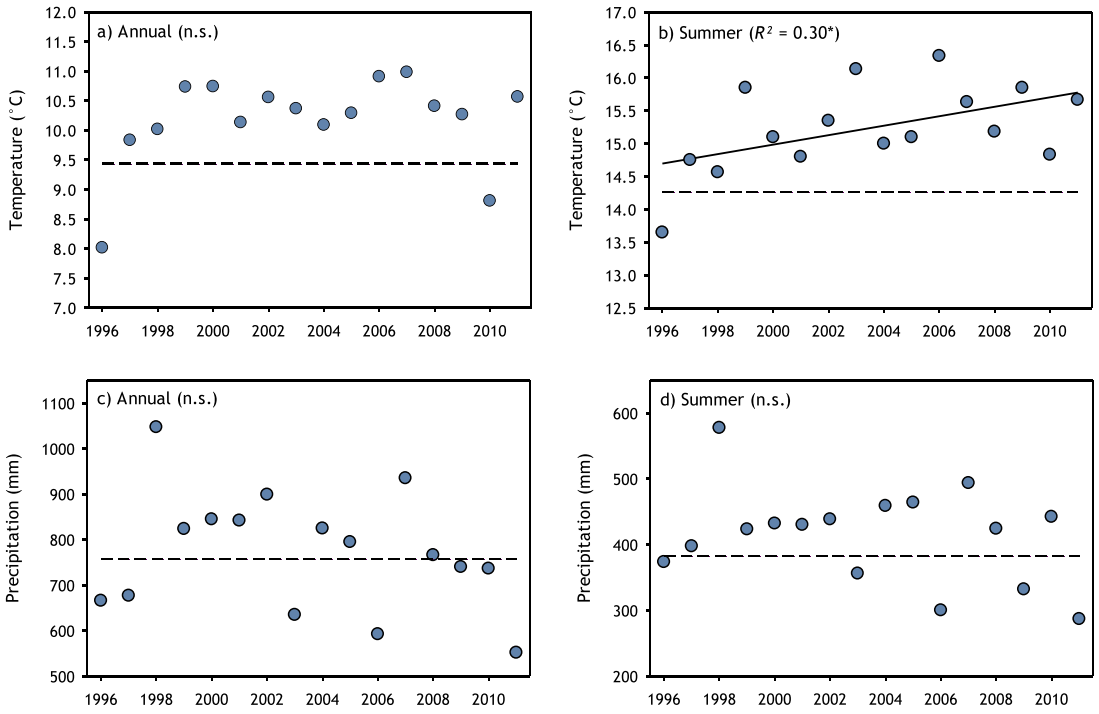

Fig. 2. Changes in temperature (a, b) and precipitation (c, d) from 1996 to 2011 in the study area. Summer: April–September. Dashed lines represent the long-term mean (most recent international standard reference 1961–1990). Relationships were tested using linear models with an autocorrelation (AR1) structure. Pseudo R^2 (Nagelkerke) values are given. n.s. not significant; b) $y = 0.073 \times x - 130.671$, * $P < 0.05$.
Data source: German Meteorological Service (2018).

Table 1
List of grasshopper species recorded in the study area in 1995 and 2012 classified by their dispersal ability (H = high, L = low), Species Temperature Index (STI) and Species Farmland Index (SFI).

Species	Occurrence		DA	STI	SFI
	1995	2012			
Chorthippus albomarginatus	x	x	H	13.03	14.88
Chorthippus apricarius	x	x	L	13.10	14.30
Chorthippus biguttulus	x	x	H	12.97	16.04
Chorthippus brunneus	x	x	H	12.98	16.34
Chorthippus dorsatus	x	x	H	13.04	16.98
Chorthippus mollis	x	x	H	13.35	13.67
Conocephalus dorsalis	x	x	L	13.20	12.97
Conocephalus fuscus	.	x	H	13.35	15.90
Decticus verrucivorus	x	x	L	12.59	25.90
Metrioptera brachyptera	x	.	L	12.58	20.24
Myrmeleotettix maculatus	x	.	L	12.99	17.04
Omocestus viridulus	x	x	L	12.74	18.68
Phaneroptera falcata	.	x	H	13.28	14.41
Pholidoptera griseoaptera	x	x	L	12.97	16.12
Pseudochorthippus montanus	x	x	L	12.82	19.28
Pseudochorthippus parallelus	x	x	L	12.96	16.03
Roeseliana roeselii	.	x	H	12.95	16.41
Stenobothrus lineatus	x	x	H	12.89	18.73
Stethophyma grossum	x	x	H	12.96	17.68
Tetrix subulata	.	x	H	13.07	15.82
Tetrix undulata	x	x	L	12.99	16.18
Tettigonia cantans	x	.	L	12.59	18.44
Tettigonia viridissima	x	x	H	13.06	15.47

Classifications: see Poniatowski et al. (2020).

conversion of grasslands to arable fields leads to a complete loss of the grasshopper assemblage of a certain patch.

The expansion of settlements was the second most prevalent cause of habitat loss in our study. However, its importance was much lower; only three plots were destroyed by housing (2% of the 181 initial plots). Urban areas are the most rapidly growing land-use type worldwide (United Nations, 2019; Fartmann et al., 2021). As is the case in most parts of the more densely populated areas of Central Europe, the study area is under intense pressure from urban development. From 1995–2012, the farmland area (including grasslands) decreased by 3.7%, whereas the extent of settlements and roads increased by 2.8% (LDSNW, 1995; WFST, 2013). Urbanisation is generally known to be a major cause of the decline in biodiversity (McKinney, 2006; Grimm et al., 2008; Cardoso et al., 2020).

Grasshoppers are cold-blooded organisms, and most species depend on high ambient temperatures (Willott and Hassall, 1998). In line with this, the temperature rise from the first to the second survey resulted in a higher CTI of the grasshopper assemblages in grassland patches and verges. Additionally, all four species that were observed for the first time on the plots in 2012 (*C. fuscus*, *P. falcata*, *R. roeselii*, *T. subulata*) and all twelve species that increased in frequency (*C. apricarius*, *C. biguttulus*, *C. brunneus*, *C. dorsatus*, *C. mollis*, *C. dorsalis*, *C. fuscus*, *P. griseoaptera*, *R. roeselii*, *T. subulata*, *T. undulata*, *T. viridissima*) had higher STI values than the mean CTI during the first survey (patches = 12.94, verges = 12.95) (Table 1, Fig. 5). Recently, several other investigations also detected a strong expansion of thermophilous grasshopper species in response to global warming (Poniatowski et al., 2012, 2020; Beckmann et al., 2015; Löffler et al., 2019; Fumy et al., 2020). However, in these studies usually only species with high dispersal ability were able to track climate change. By contrast, in our study both the number of species with high and low dispersal ability increased in the studied plots. We explain the consistent expansion of thermophilous species, irrespective of their mobility, by the high connectivity of the small-scale landscape, rich in linear grassland structures (Section 2.1) (cf. Pryke and Samways, 2012). Among the species with low dispersal ability, *P. griseoaptera* was the one with the strongest increase in frequency in both grassland types. Diekötter et al. (2007) showed that dispersal success in this flightless species increases with landscape heterogeneity. In line with this, Löffler et al. (2019) explained the expansion of *P. griseoaptera* in their study area by a high availability of movement corridors such as forest edges, hedgerows and verges.

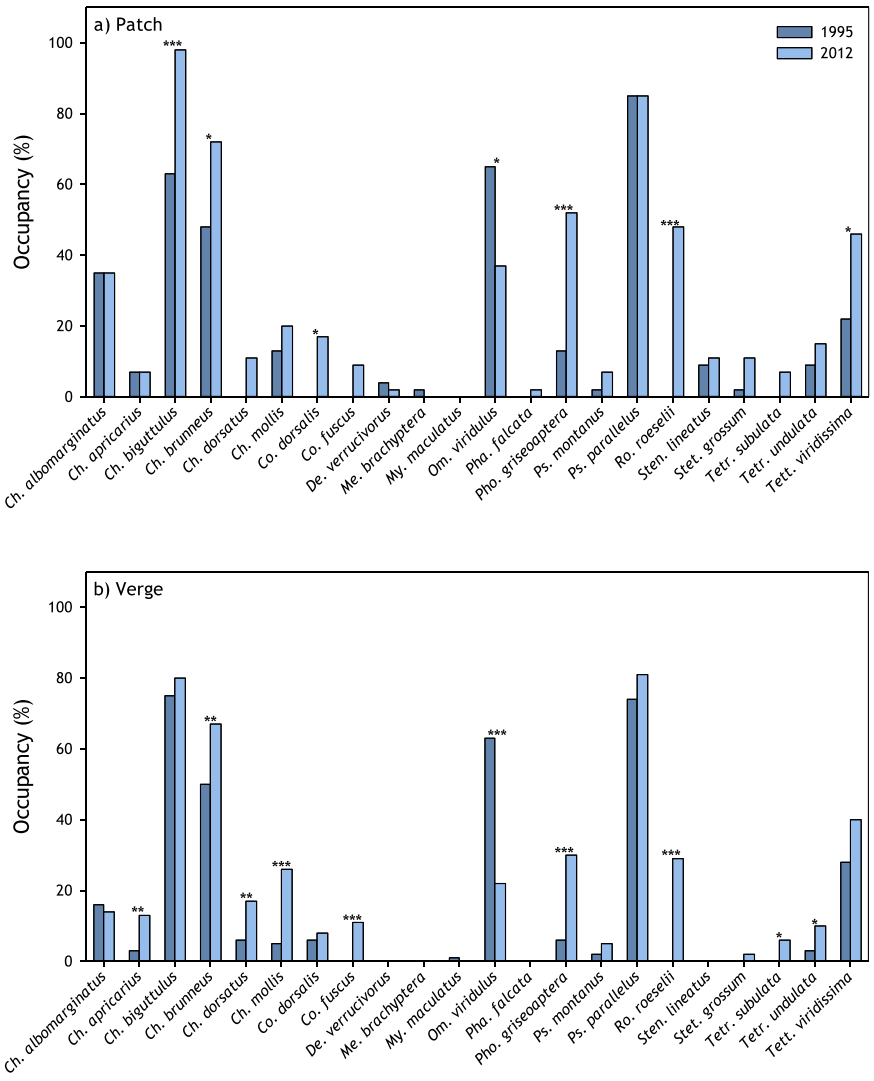

Fig. 3. Plot occupancy of grasshopper species in 1995 and 2012 in grassland patches (a) and grassland verges (b). Differences were tested using the McNemar Chi-squared test. *Ch.* = *Chorthippus*, *Co.* = *Conocephalus*, *De.* = *Decticus*, *Me.* = *Metrioptera*, *My.* = *Myrmeleotettix*, *Om.* = *Omocestus*, *Pha.* = *Phaneroptera*, *Pho.* = *Pholidoptera*, *Ps.* = *Pseudochorthippus*, *Ro.* = *Roeseliana*, *Sten.* = *Stenobothrus*, *Stet.* = *Stethophyma*, *Tetr.* = *Tetrix*, *Tett.* = *Tettigonia*, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Although mean species richness has risen and increasing species (twelve) clearly dominated over decreasing ones (one), the CFI declined in both grassland types. All expanding species, except *C. dorsatus*, had lower, often even clearly lower SFI values than the mean CFI during the first survey (patches = 16.54, verges = 16.39) (Table 1, Fig. 5). Hence, the decrease in the CFI is rather the result of an expansion of more generalistic species (low SFI values) than of a decline in more specialized species depending on HNV farmland (high SFI values). Additionally, these results illustrate that habitat specialists were largely unable to follow global warming. This corroborates previous findings, showing that the limited availability of suitable habitats hinders many habitat specialists to track climate change in our fragmented landscapes (Poniatowski and Fartmann, 2011; Löffler et al., 2019; Fumy et al., 2020).

The only species with a dramatic decline in this study was *O. viridulus*. Although precipitation did not change from 1996 to 2011, evaporation increased due to higher summer temperatures, thus resulting in drier conditions. Summer drought is considered a severe threat to *O. viridulus* (Gardiner, 2010; Poniatowski et al., 2018a, 2020). In accordance with this, the species did not decline in regions with high precipitation such as mountain ranges in western Germany or the Alps and Alpine Foreland (Löffler et al., 2019; Fumy et al., 2020; Poniatowski et al., 2020). Simultaneously, *O. viridulus* reacts sensitively to decreasing habitat quality due to more intensive land use (Gardiner, 2010; Poniatowski et al., 2018a). Although we do not have hard data on land-use intensity in the grassland plots (see above), it seems likely that, at least in some plots, gradual land-use intensification may have additionally contributed to the decrease of the species.

5. Conclusions

Land use and climate changed considerably in the study area from 1995 to 2012. The increasing cultivation of maize as a bioenergy crop was responsible for a severe loss of grassland patches leading to a homogenization at the landscape level. However, due to the high connectivity of grasslands in the still small-scale landscape, thermophilous and generalistic grasshopper species with both low and high dispersal ability were able to track global warming. Through 2012, the negative effects of climate change on grasshopper species were weak in the study area. Only one species, *O. viridulus*, strongly suffered from rising temperatures. However, with ongoing global warming, further species – especially hygrophilous species, such as *P. montanus* or *T. undulata* – might become threatened (cf. Poniatowski et al., 2018a, 2020). Taking this into account, (i) the availability of suitable habitats and (ii) climate

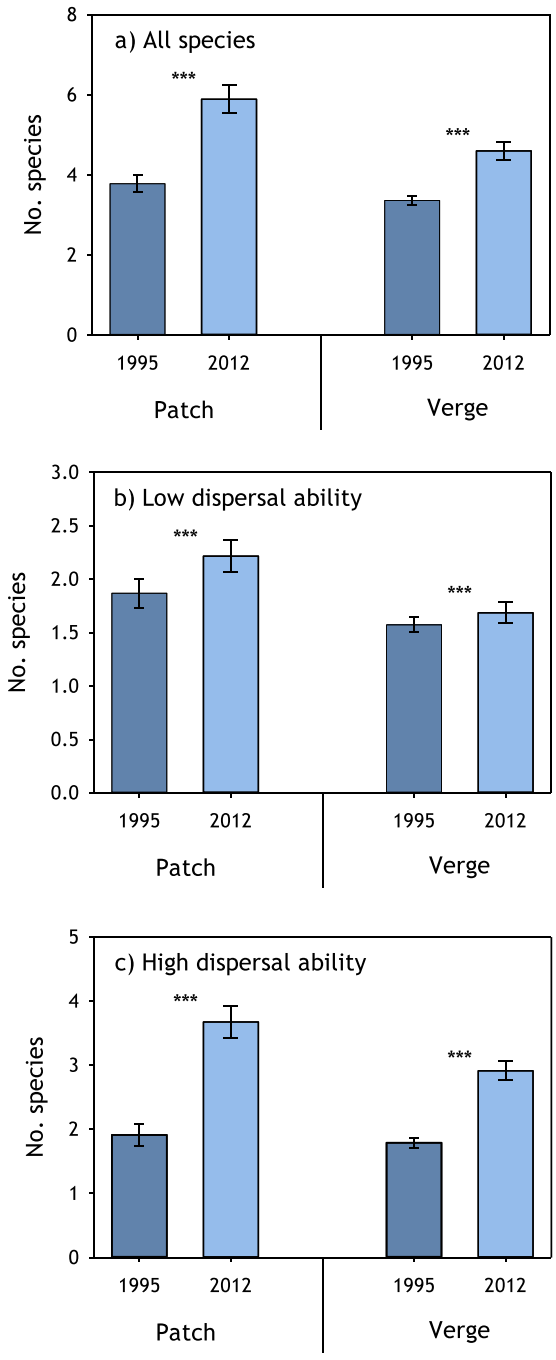

Fig. 4. Changes in the number of all species (a), species with high (b) and species with low dispersal ability (c) between 1995 and 2012 in the two grassland types. Mean values ± SE are shown. Patches, $N = 46$; verges, $N = 115$. Differences were tested using the paired t test. *** $P < 0.001$.

warming were the major drivers of shifts in grasshopper assemblages in our study.

Except for the extent of habitat loss, the observed changes were comparable for grassland patches and verges. Even the species richness was similarly high, although grassland patches were more than 20 times larger than grassland verges (Section 2.2). As our study showed, with the ongoing loss of grassland patches, grassland verges become increasingly important – not only as dispersal corridors (Berggren et al., 2002; Chen et al., 2011; Poniatowski et al., 2012) but also as vital refuges for the biodiversity in our intensively used and fragmented agricultural landscapes (see also Pryke and Samways, 2012; Ouédraogo et al., 2020; Phillips et al., 2020).

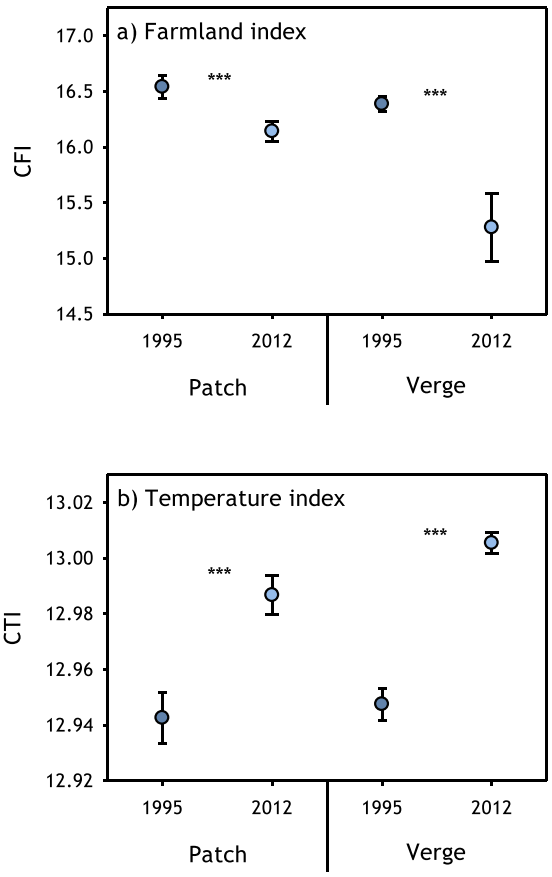

Fig. 5. Changes in the Community Farmland Index (CFI) (a) and the Community Temperature Index (CTI) (b) between 1995 and 2012 in the two grassland types. Mean values ± SE are shown. Patches, $N = 46$; verges, $N = 115$. Differences were tested using the paired t test. *** $P < 0.001$.

CRediT authorship contribution statement

Thomas Fartmann: Conceptualization, Methodology, Formal analysis, Visualization, Writing – original draft. **Lisa Holtmann**: Conceptualization, Investigation, Methodology, Formal analysis, Writing – review & editing. **Dominik Poniatowski**: Conceptualization, Methodology, Writing – review & editing.

Declaration of Competing Interest

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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