GfÖ Ecological Society of Germany, Austria and Switzerland
Basic and Applied Ecology 63 (2022) 83−92
Basic and Applied Ecology
www.elsevier.com/locate/baae

Effects of land-use and climate change on grasshopper assemblages differ between protected and unprotected grasslands

Thomas Fartmann[a,*], Dominik Poniatowski[a], Lisa Holtmann[a]

[a]Department of Biodiversity and Landscape Ecology, University of Osnabrück, Barbarastraße 11, 49076 Osnabrück, Germany

Received 23 August 2021; accepted 12 June 2022
Available online 15 June 2022

Abstract

Land-use and climate change are considered the major drivers of recent insect loss. Orthoptera (hereinafter termed 'grasshoppers') are the main arthropod consumers in grasslands and, hence, are important elements for supporting ecosystem services. However, for intensively-used agricultural landscapes, it is largely unknown to what extent both factors have affected grasshopper assemblages in protected (nature reserves) and unprotected grasslands.

Here, we analysed species richness of grasshopper assemblages in protected (n = 14) and unprotected grasslands (n = 49) by comparing two surveys—one in 1995 and one in 2012—of a landscape with intensive agriculture in the NW-German Lowland. The observed changes were associated with the Community Farmland Index (CFI) and the Community Temperature Index (CTI) in order to disentangle possible effects of land-use and climate change on assemblage shifts.

Between the two surveys, environmental conditions substantially changed. Summer temperatures increased by 1.1°C, and grasslands suffered from a severe loss of patches. However, the latter only occurred in unprotected grasslands. Here, 35% of the patches were converted to other biotope types, in particular maize fields as a result of the expansion of bioenergy-crop cultivation. In the grasslands still existing in 2012, irrespective of its protection status, species richness usually increased, except for species with low dispersal ability in unprotected grasslands. By contrast, the development of the CFI and CTI clearly varied between the two grassland types. In protected grasslands, neither the CFI nor the CTI changed. However, in unprotected grasslands, the CFI decreased but the CTI increased.

Land-use change has led to a biotic homogenisation at the landscape level and within unprotected grassland patches. Additionally, our study highlights that the legal designation of grasslands as a nature reserve successfully prevents the conversion of grasslands. Overall, well-managed grasslands in nature reserves play a vital role for the conservation of grasshopper biodiversity.

Keywords: Biodiversity conservation; Bioenergy-crop cultivation; Community farmland index; Community temperature index; Dispersal ability; Habitat connectivity; Land-use change; Nature reserve; Range shift; Thermophilous species

*Corresponding author.
E-mail address: t.fartmann@uos.de (T. Fartmann).

https://doi.org/10.1016/j.baae.2022.06.005
1439-1791/

Introduction

Globally, biodiversity is in steep decline. Thus, scientists expect that we are heading for a sixth mass extinction (Barnosky et al., 2011; Dirzo et al., 2014). The loss of biodiversity threatens ecosystem functioning and human well-being on earth (Cardoso et al., 2020; Dirzo et al., 2014; IPBES, 2019; Ripple et al., 2017). Hence, halting the biodiversity crisis is one of the major challenges for mankind.

Insects are the most diverse taxonomic group on earth (Stork, 2018). However, they decline more rapidly than most other organisms, such as plants or vertebrates (Cardoso et al., 2020; Sánchez-Bayo & Wyckhuys, 2019; Thomas et al., 2004; Wagner, 2020). The loss of insects has cascading effects on many other species within ecosystems (Cardoso et al., 2020; Wagner, 2020). A decrease in insects, for example, has direct impacts on the populations of insectivorous species that feed on them (e.g. many bird species) (Fartmann, Jedicke, Stuhldreher, & Streitberger, 2021).

Land-use change is considered to be the main driver of both decreasing biodiversity in general and insect decline (Cardoso et al., 2020; IPBES, 2019; Wagner, 2020). In particular, agricultural intensification (Burns et al., 2016; Stoate et al., 2009) and urban development (Grimm et al., 2008; McKinney, 2006; Nitsch, Osterburg, Roggendorf, & Laggner, 2012) have caused severe modifications of our landscapes. Both result in habitat loss, habitat fragmentation and deterioration of habitat quality of the remaining habitat patches with negative impacts on insects (Cardoso et al., 2020).

Grasslands belong to the most species-rich habitats across Europe (Chytrý et al., 2015; Dengler, Janisová, Török, & Wellstein, 2014; Feurdean et al., 2018). However, due to the transition from pre-industrial land use to modern-day agriculture, grasslands have greatly decreased and the remaining patches have often suffered from habitat deterioration (Fartmann, Jedicke, Stuhldreher, & Streitberger, 2021; Poschlod, 2017; Wallis de Vries, Poschlod, & Willems, 2002). Today, the grassland remnants are often surrounded by an intensively used matrix (Helbing, Fartmann, Löffler, & Poniatowski, 2017; Poniatowski, Stuhldreher, Löffler, & Fartmann, 2018). Recently, the increasing cultivation of bioenergy crops and conversion of grasslands to arable fields have further accelerated the loss of grasslands (Jerrentrup et al., 2017; Lüker-Jans, Simmering, & Otte 2017; Nitsch, Osterburg, Roggendorf, & Laggner, 2012; Stoate et al., 2009).

Climate change is another threat for insects and is becoming increasingly important (Cardoso et al., 2020; IPBES, 2019). In particular, thermophilous species benefit from increasing temperatures and, as a result, often exhibit range expansions (Poniatowski et al., 2020; Pöyry et al., 2009; Termaat et al., 2019). Hygrophilous species, however, are assumed to suffer from global warming (Buse & Griebeler, 2011; Streitberger et al., 2016). Furthermore, dispersal ability, the degree of habitat specialisation and the occurrence of dispersal corridors drive the response of the species to global warming (Angert et al., 2011; MacLean & Beissinger, 2017).

Orthoptera (hereinafter termed 'grasshoppers') have a high functional significance since they are the main arthropod consumers in grasslands and, hence, are important elements for supporting ecosystem services (Samways, 2005). Moreover, they rapidly respond to alterations in land use (Bazelet & Samways, 2012; Marini, Fontana, Scotton, & Klimek, 2008; Uchida & Ushimaru, 2014) and climate (Fumy, Löffler, Samways, & Fartmann, 2020; Löffler, Poniatowski, & Fartmann, 2019; Poniatowski et al., 2020). As a result, they are well-established bioindicators for environmental change in grassland ecosystems (Fartmann, Krämer, Stelzner, & Poniatowski, 2012; Sergeev, 2021).

Recently, Rada et al. (2019) showed that protected areas were insufficient to mitigate the negative trend of insect populations since the decline in species richness of butterflies did not differ inside and outside European Natura 2000 sites across Germany. In our study area in NW Germany, grassland patches, in contrast to grassland verges, have strongly suffered since the mid-1990s from habitat loss due to the expansion of bioenergy-crop cultivation (Fartmann, Poniatowski, & Holtmann 2021). In the remaining patches and verges of the well-connected agricultural landscape, however, thermophilous and generalistic grasshopper species with both low and high dispersal ability increased in occupancy in response to climate warming.

Here, we used a data subset of the study to compare the effects of land-use and climate change on grasshopper-assemblage shifts in protected (n = 14, nature reserves) and unprotected grassland (n = 49) patches between 1995 and 2012. The study area in the NW-German Lowland is characterised by intensive agriculture and an increase in summer temperatures of 1.1°C from the first to the second survey (Fartmann, Poniatowski, & Holtmann, 2021). We analysed habitat loss and changes in grasshopper species richness (i.e. all species, species with low and species with high dispersal ability), the Community Farmland Index (CFI) as a community mean of species' dependence on 'High Nature Value Farmland' (HNV) (Poniatowski et al., 2020) and the Community Temperature Index (CTI) as a community mean of species' temperature preferences (Devictor, Jullirad, Dennis, & Jiguet, 2008). We performed these analyses for both grassland types and compared the first survey in 1995 to the second survey in 2012. In particular, we addressed 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 in protected and unprotected grasslands?
(ii) What are the main drivers of the variation in grasshopper distribution between the two grassland types in a rapidly changing landscape?

Materials and methods

Study area

The study area (size: 31,400 ha) is located in the NW of the federal state of North Rhine-Westphalia and part of the NW-German Lowland (40 to 200 m a.s.l.; district of Steinfurt; 52° 09'N, 7°46'E) (Fartmann, Poniatowski, & Holtmann, 2021). It is characterised by a suboceanic climate with mild winters, moderately warm summers, 1,528 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). Within the study area, intensive agriculture dominates and accordingly, improved grasslands and arable fields are the main land-use types. Despite the high land-use intensity, small fields and grasslands prevail (range of size: 1 to 3.5 ha) (Schäuble, 2007). As a result, linear structures, such as field margins, hedgerows, tree lines, alleys or ditches, are widespread. Due to the mosaic of tiny fields and grasslands as well as the richness of linear landscape structures, the study area is designated as a 'park landscape' (Fartmann, Poniatowski, & Holtmann, 2021).

From 1996 to 2011, summer temperatures significantly increased by 1.1 °C in the study area (Fartmann, Poniatowski, & Holtmann, 2021). By contrast, precipitation (annual and summer) and annual temperature did not change. However, since evaporation increased due to higher temperatures, overall conditions have become drier in summer.

Study design

To detect shifts in grasshopper species assemblages, we compared presence/absence data of Orthoptera across grassland patches of the survey conducted by Bergmann (1996) in 1995 with those from our field study in 2012. Through the study of Bergmann (1996), complete lists of grasshopper species for 14 protected and 49 unprotected grassland patches (N = 63) randomly selected across the study area were available. The size of the protected grassland patches (mean ± SE: 22,827 m^2 ± 5,289 m^2) did not differ from unprotected ones (17,520 m^2 ± 4,319 m^2) (Mann-Whitney U test, U = 175, P = 0.25; data derived from aerial photographs for the remaining patches in 2012). However, the connectivity of the patches was high due to the richness of grassy verges (Fartmann, Poniatowski, & Holtmann, 2021). Nature-conservation efforts (extent of nature reserves or areas covered by agri-environmental schemes) did not vary substantially between 1995 and 2012 in the study area (Fartmann, Poniatowski, & Holtmann, 2021).

Sampling of environmental conditions and grasshoppers

In summer 2012, all 14 protected and 49 unprotected grassland patches studied by Bergmann (1996) were resurveyed using the same methods that Bergmann (1996) had applied previously. If a grassland patch had been converted into another biotope type, the new type was noted according to Finck et al. (2017). Grasshoppers were sampled twice between the end of June and the beginning of September with at least three weeks between visits (Fartmann, Poniatowski, & Holtmann, 2021). Within each plot, all habitat structures were surveyed under favourable weather conditions (temperature > 15 °C, cloud cover < 50%) using acoustic and visual search as well as sweep-netting. These methods are known to produce reliable data on grasshopper occurrence in grasslands (Fumy, Löffler, Samways, & Fartmann, 2020; Löffler, Poniatowski, & Fartmann, 2019; Samways, McGeoch, & New, 2010). Shrub- and tree-dwelling species, occasionally occurring in grasslands, were not sampled. Species were identified in the field using Bellmann (2006). Additionally, a bat detector was used in order to detect *Conocephalus dorsalis, Conocephalus fuscus* and *Metrioptera brachyptera* (Fischer et al., 2020). Since wing length and width are species-specific characteristics in the closely related *Chorthippus* species (*C. biguttulus, C. brunneus* and *C. mollis*), a calliper gauge (0.5-mm accuracy) was applied to differentiate between them. Scientific nomenclature is based on Fischer et al. (2020).

Classifications and global-change indices

According to Poniatowski et al. (2020), we classified grasshopper species by their dispersal ability (low vs. high), Species Farmland Index (SFI) and Species Temperature Index (STI). The response of grasshopper species to environmental alterations is often strongly related to their dispersal ability (e.g., Fumy, Löffler, Samways, & Fartmann, 2020; Löffler, Poniatowski, & Fartmann, 2019; Reinhardt, Köhler, Maas, & Detzel, 2005). The SFI and STI have recently been introduced for grasshoppers (Fumy, Löffler, Samways, & Fartmann, 2020; Löffler, Poniatowski, & Fartmann, 2019). Recent distribution data of grasshoppers in Germany provided the basis for the calculation of each of the indices (Poniatowski et al., 2020). The SFI represents the percentage of HNV farmland within the open landscape across the distribution range of a species (Fumy, Löffler, Samways, & Fartmann, 2020; Poniatowski et al., 2020). HNV farmland includes farmland (i) with a high share of semi-natural vegetation, (ii) with mosaics of low-intensity agriculture and natural/structural elements (e.g. patches of woodland or field margins, hedgerows etc.) and (iii) that support rare species or a high proportion of European/world populations of a species (Paracchini et al., 2008). The STI reflects the mean temperature within the distribution range of a species (cf. Devictor et al., 2012). For grasshopper species, the calculation of the STI was based on mean summer temperatures (April−September) (Fumy, Löffler, Samways, & Fartmann, 2020; Löffler, Poniatowski, & Fartmann, 2019;

Poniatowski et al., 2020). By averaging the SFI and STI, respectively, of all species occurring in the particular patch, the Community Farmland Index (CFI) and the Community Temperature Index (CTI) were calculated (cf. Devictor, Jullirad, Dennis, & Jiguet, 2008; Devictor et al., 2012). Both indices have recently been applied successfully to disentangle the effects of land-use and climate change on grasshopper assemblage shifts (Löffler, Poniatowski, & Fartmann, 2019; Fumy, Löffler, Samways, & Fartmann, 2020; Poniatowski et al., 2020).

Statistical analysis

All statistical analyses were performed using R statistical environment (R Core Team, 2021). To detect the loss of grassland patches and changes in patch occupancy of each grasshopper species between the two survey periods, the McNemar Chi-squared test was applied. Since Chi-squared tests do not allow empty categories, we conservatively set frequencies of 0 to 1 (Eichel & Fartmann, 2008). Shifts in the number of species, CFI and CTI for each grassland type between the two survey periods were analysed using the paired *t* test.

Results

Changes in environmental conditions

All of the 14 protected grassland patches studied in 1995 were still used as grasslands in 2012 (McNemar Chi-squared test, not significant). By contrast, only 32 of the 49 unprotected grassland patches during the first survey were still present during the second survey, which corresponds to a patch loss of 35% (McNemar Chi-squared test, $P < 0.001$). This decrease was caused most significantly by the conversion of grasslands to arable fields. This was the case for 15 patches (88%); nearly all of these arable fields were cropped with maize (13 patches, 77%). The two other converted patches were housing lots in 2012 (12%).

Changes in grasshopper assemblages

Overall, during the two surveys, we recorded 21 grasshopper species in the grassland patches (Table 1). One originally very rare species, *Metrioptera brachyptera* (occurrence in one patch in 1995), had disappeared in 2012, although the originally occupied patch was still used as a grassland. By contrast, during the second survey, six species, *Chorthippus dorsatus, Conocephalus dorsalis, Conocephalus fuscus, Phaneroptera falcata, Roeseliana roeselii* and *Tetrix subulata*, were observed in the remaining patches for the first time.

Table 1. List of grasshopper species recorded in the study area in 1995 and 2012. Dispersal ability (DA): high (H), low (L); Species Temperature Index (STI); Species Farmland Index (SFI). Classifications: see Poniatowski et al. (2020).

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	H	13.04	16.98
Chorthippus mollis	x	x	H	13.35	13.67
Conocephalus dorsalis	.	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
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 viridissima	x	x	H	13.06	15.47

During the first survey, the most widespread species were *Pseudochorthippus parallelus* (patch occupancy: protected grassland = 71% vs. unprotected grasslands = 91%), *Chorthippus biguttulus* (71% vs. 59%) and *Omocestus viridulus* (50% vs. 43%) (Fig. 1). By contrast, during the second survey, the ranking had shifted; the most frequent species were *C. biguttulus* (100% vs. 97%), *P. parallelus* (71% vs. 91%) and *C. brunneus* (64% vs. 75%). Between the two study periods, the frequency of five species changed in at least one grassland type. Four species, *C. biguttulus, Pholidoptera griseoaptera, R. roeselii* and *Tettigonia viridissima* were more widespread during the survey in 2012. For *P. griseoaptera* and *R. roeselii,* this was true for both grassland types. By contrast, patch occupancy of *C. biguttulus*, and *T. viridissima* only increased in unprotected grasslands. The only declining species was *Omocestus viridulus*; its patch occupancy decreased in unprotected grasslands.

From the first to the second survey, species richness (all species, species with low and species with high dispersal ability) increased in protected and unprotected grasslands (Fig. 2). The only exception was the number of species with low dispersal ability in unprotected grasslands, which did not change. By contrast, the development of the CFI and CTI clearly differed between protected and unprotected grasslands (Fig. 3). In protected grasslands, neither the CFI nor the CTI changed. In unprotected grasslands, however, the CFI decreased but the CTI increased.

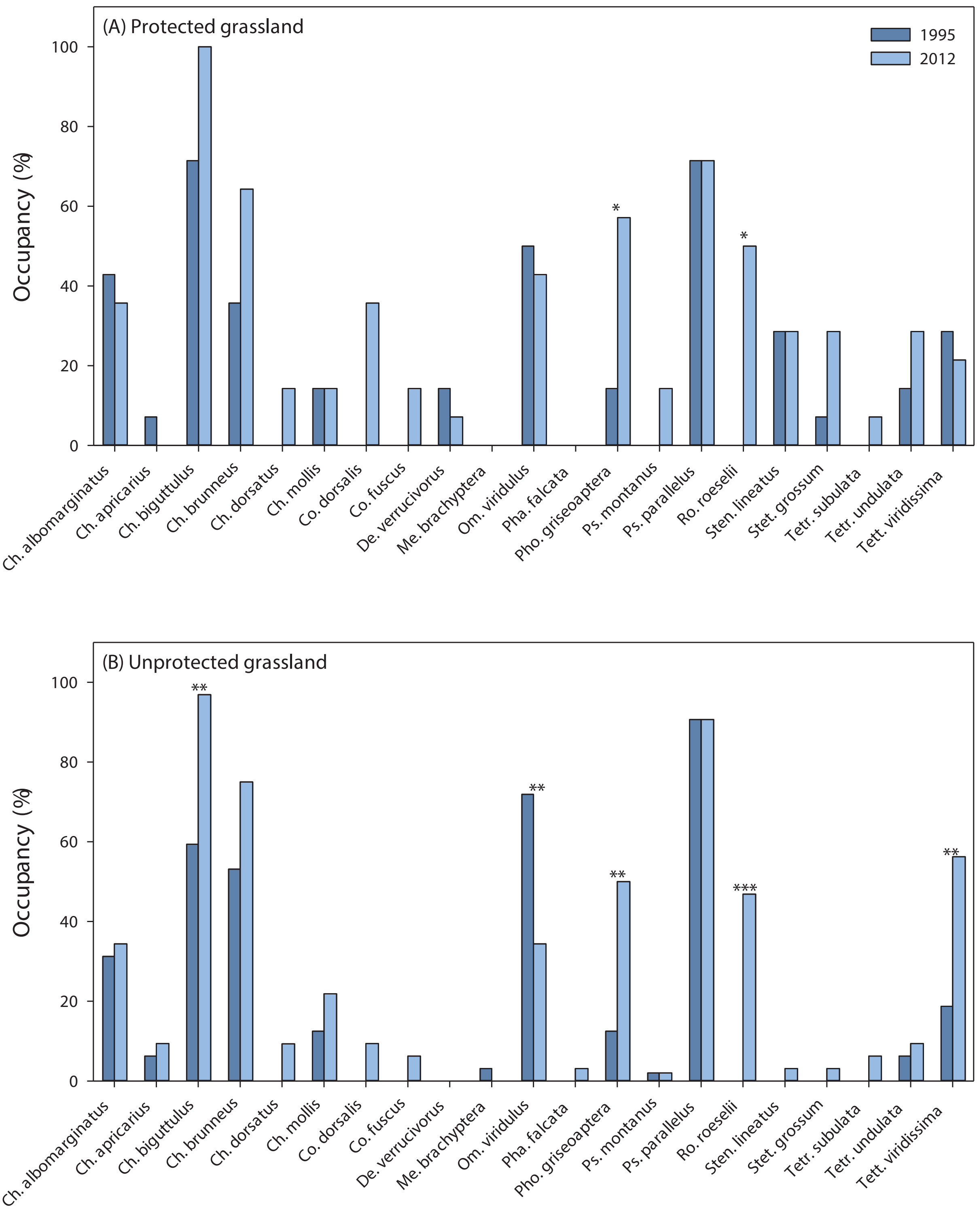

Fig. 1. Plot occupancy of grasshopper species in 1995 and 2012 in protected (A) and unprotected (B) grasslands. Protected grasslands, n = 14; unprotected grasslands, n = 32. Differences were tested using the McNemar Chi-squared test. *Ch.* = *Chorthippus, Co.* = *Conocephalus, De.* = *Decticus, Me.* = *Metrioptera, Om.* = *Omocestus, Pha.* = *Phaneroptera, Pho.* = *Pholidoptera, Ps.* = *Pseudochorthippus, Ro.* = *Roeseliana, Sten.* = *Stenobothrus, Stet.* = *Stethophyma, Tetr.* = *Tetrix, Tett.* = *Tettigonia*, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

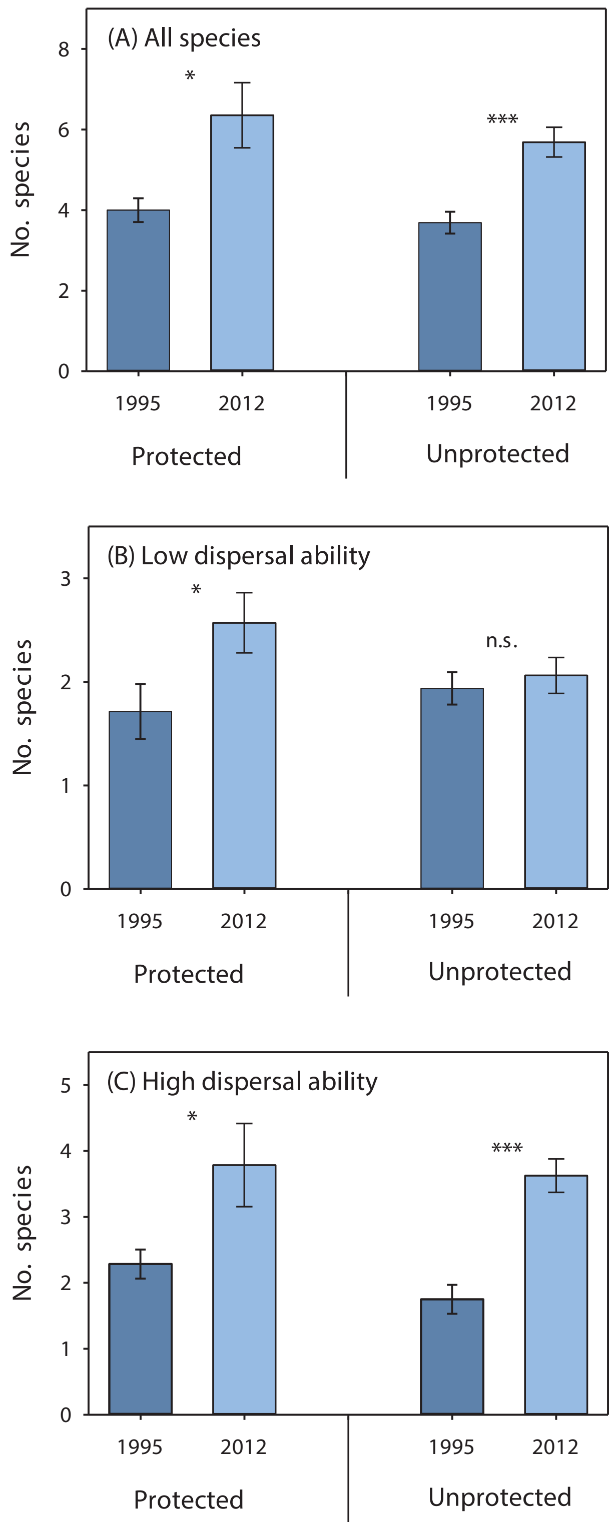

Fig. 2. Changes in the number of all species (A), species with low (B) and species with high dispersal ability (C) between 1995 and 2012 in protected and unprotected grasslands. Mean values ± SE are shown. Protected grasslands, $n = 14$; unprotected grasslands, $n = 32$. Differences were tested using the paired t test. n.s. not significant, * $P < 0.05$, *** $P < 0.001$.

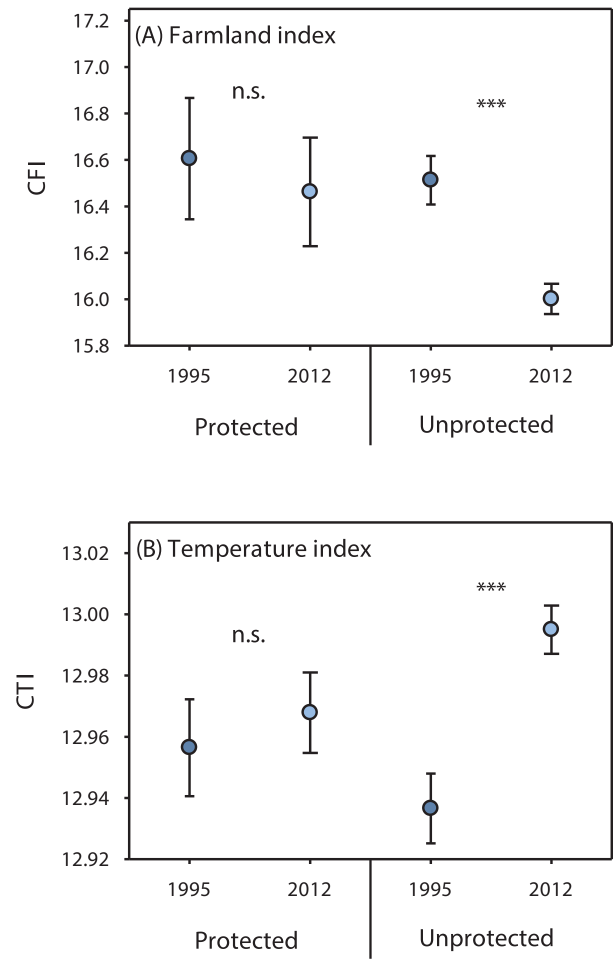

Fig. 3. Changes in the Community Farmland Index (CFI) (A) and the Community Temperature Index (CTI) (B) between 1995 and 2012 in protected and unprotected grasslands. Mean values ± SE are shown. Protected grasslands, $n = 14$; unprotected grasslands, $n = 32$. Differences were tested using the paired t test. n.s. not significant, *** $P < 0.001$.

Discussion

Between the two surveys in 1995 and 2012, environmental conditions substantially changed within the study area in the NW-German Lowland. Summer temperatures increased by 1.1 °C (Fartmann, Poniatowski, & Holtmann, 2021), and grasslands suffered from a severe loss of patches. However, the latter only occurred in unprotected grasslands; here, 35% of the patches were converted to other biotope types, in particular maize fields. In the grassland patches still existing in 2012, irrespective of protection status, species richness usually increased, except for species with low dispersal ability in unprotected grasslands. By contrast, the development of the CFI and CTI clearly varied between the two grassland types. In protected grasslands neither the CFI nor the CTI changed. However, in unprotected grasslands, the CFI decreased but the CTI increased.

Habitat loss is among the most important drivers of the current biodiversity crisis (Cardoso et al., 2020; IPBES, 2019; Wagner, 2020). Across European agricultural landscapes, the expansion of bioenergy-crop cultivation, in particular maize, has been detected as the major cause of grassland loss (Lüker-Jans, Simmering, & Otte 2017; Nitsch, Osterburg, Roggendorf, & Laggner, 2012; Stoate et al., 2009). Globally, urbanisation is known to be another relevant factor for habitat depletion (Cardoso et al., 2020; Grimm et al., 2008; McKinney, 2006). Recently, Fartmann, Poniatowski and Holtmann (2021) observed that the conversion to arable fields for bioenergy production as well as to settlements was responsible for the severe destruction of grasslands in the study area. Our study now highlights that the legal designation of grasslands as a nature reserve, in contrast to unprotected grasslands, successfully prevents the conversion of grasslands and, hence, loss of habitats for grasshoppers and many other organisms.

As cold-blooded organisms, grasshoppers usually depend on high ambient temperatures (Willott & Hassall, 1998). Thus, many species have recently expanded their range due to climate warming (Beckmann et al., 2015; Poniatowski et al., 2020). This is especially true for thermophilous habitat generalists with a high mobility. However, Fartmann, Poniatowski and Holtmann (2021) showed that grasshopper species with a low dispersal ability were also able to track global warming in the study area. They explained this pattern by the high connectivity of the small-scaled landscape, rich in linear grassland verges. By contrast, in our study, the number of species with low dispersal ability only increased in protected grasslands. Both protected and unprotected grasslands were characterised by one expanding species with low dispersal ability, *Pholidoptera griseoaptera*, and one to three spreading species with high dispersal ability (*Chorthippus biguttulus, Roeseliana roeselii, Tettigonia viridissima*). On the contrary, a decrease in frequency was observed for one species with low dispersal ability, *Omocestus viridulus*, but only in unprotected grasslands. Consequently, we attribute the lack of change in the number of species with low dispersal ability in unprotected grasslands especially to the strong decline in *O. viridulus*.

The species is sensitive to habitat deterioration due to land-use intensification or abandonment and summer drought (Gardiner, 2010; Poniatowski, Münsch, Helbing, & Fartmann, 2018; Poniatowski et al., 2020). Since *O. viridulus* only decreased in unprotected grasslands but not in protected ones, we explain the decrease in frequency mainly by the former. Protected grasslands were usually covered by agri-environmental schemes (i.e. continuous low-intensity grazing or mowing; P. Schwartze pers. comm, 07/2021; Biological Station Steinfurt). By contrast, in unprotected grasslands, it is likely that gradual land-use intensification (Fartmann, Poniatowski, & Holtmann, 2021) and also abandonment on marginal soils (own observation) may have contributed to the decline of the species.

Additionally, we attribute the different developments of the CFI and CTI in protected and unprotected grasslands, respectively, also to the decrease of *O. viridulus* in unprotected grasslands. *Omocestes viridulus* was among the species with the lowest STI (12.74) and highest SFI (18.68) of all detected species. Accordingly, the strong decline of *O. viridulus* in unprotected grasslands resulted in a lower CFI and higher CTI in this grassland type. By contrast, in protected grasslands with a stable patch occupancy of *O. viridulus,* both indices did not change. Until now, the negative effects of climate warming (i.e. especially drier summers; cf. Section Study area) on grasshoppers were at least weak in this study area, since no species declined in protected grasslands. Nevertheless, with ongoing climate warming, hygrophilous species in particular will very likely become threatened (Poniatowski, Münsch, Helbing, & Fartmann, 2018; Poniatowski et al., 2020).

Conclusions

Nature reserves successfully protected grasslands against habitat loss and habitat deterioration. As a result, both grasshopper species with low and high dispersal ability were able to track climate warming in the well-connected landscape of the study area. By contrast, unprotected grasslands suffered strongly from habitat loss through the expansion of bioenergy-crop cultivation, in particular maize, but also settlements. Additionally, habitat deterioration due to land-use intensification and abandonment led to a strong decline of *O. viridulus* in the remaining unprotected grassland patches. As a result, less specialised (indicated by a lower CFI value) and more thermophilous species (indicated by a higher CTI value) dominated in the unprotected grassland patches in 2012.

Land-use change has led to a biotic homogenisation at the landscape level and within unprotected grassland patches. Fartmann, Poniatowski and Holtmann (2021) underlined that due to the strong loss of grassland patches, grassland verges have become increasingly important as dispersal corridors (cf. Berggren, Birath, & Kindvall, 2002; Chen et al., 2011; Poniatowski et al., 2012) but also as crucial refuges for biodiversity in the fragmented landscape of the study area (cf. Pryke & Samways, 2012; Ouédraogo et al., 2020; Phillips, Bullock, Osborne, & Gaston, 2020). Our study now highlights that well-managed grasslands in nature reserves also play a vital role for the conservation of grasshopper biodiversity in intensively-used agricultural landscapes.

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.

Acknowledgements

We are grateful to two anonymous reviewers for valuable comments on a previous version of the manuscript.

References

Angert, A. L., Crozier, L. G., Rissler, L. J., Gilman, S. E., Tewksbury, J. J., & Chunco, A. J. (2011). Do species' traits predict recent shifts at expanding range edges? *Ecology Letters*, *14*, 677–689. doi:10.1111/j.1461-0248.2011.01620.x.

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B., & Ferrer, E. A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, *471*, 51–57. doi:10.1038/nature09678.

Bazelet, C. S., & Samways, M. J. (2012). Grasshopper and butterfly local congruency in grassland remnants. *Journal of Insect Conservation*, *16*, 71–85. doi:10.1007/s10841-011-9394-7.

Beckmann, B. C., Purse, B. V., Roy, D. B., Roy, H. E., Sutton, P. G., & Thomas, C. D. (2015). Two species with an unusual combination of traits dominate responses of British grasshoppers and crickets to environmental change. *PloS One*, *10*, e0130488. doi:10.1371/journal.pone.0130488.

Bellmann, H. (2006). *Der Kosmos Heuschreckenführer: Die Arten Mitteleuropas sicher bestimmen*. Kosmos, Stuttgart.

Berggren, Å, Birath, B., & Kindvall, O. (2002). Effect of corridors and habitat edges on dispersal behavior, movement rates, and movement angles in Roesel's bush-cricket (*Metrioptera roeseli*). *Conservation Biology*, *16*, 1562–1569. doi:10.1046/j.1523-1739.2002.01203.x.

Bergmann, S. (1996). *Ökologische Untersuchung der Heuschreckenfauna im Raum Lengerich. Diploma thesis*. Germany: Westfälische Wilhelms-Universität Münster.

Burns, F., Eaton, M. A., Barlow, K. E., Beckmann, B. C., Brereton, T., Brooks, D. R., Brown, P. M. J., Al Fulaij, N., Gent, T., Henderson, I., Noble, D. G., Parsons, M., Powney, G. D., Roy, H. E., Stroh, P., Walker, K., Wilkinson, J. W., Wotton, S. R., & Gregory, R. D (2016). Agricultural management and climatic change are the major drivers of biodiversity change in the UK. *PloS One*, *11*, e0151595. doi:10.1371/journal.pone.0151595.

Buse, J., & Griebeler, E. A. (2011). Incorporating classified dispersal assumptions in predictive distribution models − A case study with grasshoppers and bush-crickets. *Ecological Modelling*, *222*, 2130–2141. doi:10.1016/j.ecolm odel.2011.04.010.

Cardoso, P., Barton, P. S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C. S., Gaigher, R., Habel, J., Hallmann, C. A., Hill, M., Hochkirch, A., Kwak, M. L., Mammola, S., Noriega, J. A., Orfinger, A. B., Pedraza, F., Pryke, J. S., Roque, F. O., Settele, J., Simaika, J. P., Stork, N. E., Suhling, F., Vorster, C., & Samways, M. J. (2020). Scientists' warning to humanity on insect extinctions. *Biological Conservation*, *242*, 108426. doi:10.1016/j.biocon.2020.108426.

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. doi:10.1126/science.1206432.

Chytrý, M., Dražil, T., Hájek, M., Kalníková, V., Preislerová, Z., Šibík, J., Ujházy, K., Axmanová, I., Bernátová, D., Blanár, D., Dančák, M., Dřevojan, P., Fajmon, K., Galvánek, D., Hájková, P., Herben, T., Hrivnák, R., Janeček, S., Janišová, M., Jiráská, Š, Kliment, J., Kochjarová, J., Lepš, J., Leskovjanská, A., Merunková, K., Mládek, J., Slezák, M., Šeffer, J., Šefferová, V., Škodová, I., Uhlířová, J., Ujházyová, M., & Vymazalová, M. (2015). The most species-rich plant communities in the Czech Republic and Slovakia (with new world records). *Preslia*, *87*, 217–278.

Dengler, J., Janisová, M., Török, P., & Wellstein, C (2014). Biodiversity of Palaearctic grasslands: a synthesis. *Agriculture, Ecosystems and Environment*, *182*, 1–14. doi:10.1016/j.agee.2013.12.015.

Devictor, V., Jullirad, R., Denis, C., & Jiguet, F. (2008). Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society B: Biological Sciences*, *275*, 2743–2748. doi:10.1098/rspb.2008.0878.

Devictor, V., van Swaay, C. A., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Å, Reif, J., Roy, D. B., Schweiger, O., Settele, J., Stefanescu, C., van Strien, A. J., van Turnhout, C., Vermouzek, Z., WallisdeVries, M. F., Wynhoff, I., & Jiguet, F. (2012). Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change*, *2*, 121–124. doi:10.1038/nclim ate1347.

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B, & Collen, B (2014). Defaunation in the Anthropocene. *Science*, *345*, 401–406. doi:10.1126/science.1251817.

Eichel, S., & Fartmann, T. (2008). Management of calcareous grasslands for Nickerl's fritillary (*Melitaea aurelia*) has to consider habitat requirements of the immature stages, isolation, and patch area. *Journal of Insect Conservation*, *12*, 677–688. doi:10.1007/s10841-007-9110-9.

Fartmann, T., Jedicke, E., Stuhldreher, G., & Streitberger, M. (2021). *Insektensterben in Mitteleuropa − Ursachen und Gegenmaßnahmen*. Stuttgart: Eugen Ulmer.

Fartmann, T., Krämer, B., Stelzner, F., & Poniatowski, D. (2012). Orthoptera as ecological indicators for succession in steppe grassland. *Ecological Indicators*, *20*, 337–344. doi:10.1016/j.ecolind.2012.03.002.

Fartmann, T., Poniatowski, D., & Holtmann, L. (2021). Habitat availability and climate warming drive changes in the distribution of grassland grasshoppers. *Agriculture, Ecosystems and Environment*, *320*, 107565. doi:10.1016/j.agee.2021.107565.

Feurdean, A., Ruprecht, E., Molnár, Z., Hutchinson, S. M., & Hickler, T. (2018). Biodiversity-rich European grasslands: ancient, forgotten ecosystems. *Biological Conservation*, *228*, 224–232. doi:10.1016/j.biocon.2018.09.022.

Finck, P., Heinze, S., Raths, U., Riecken, U., & Ssymank, A. (2017). Rote Liste der gefährdeten Biotoptypen Deutschlands. *Naturschutz und Biologische Vielfalt*, *156*, 1–642.

Fischer, J., Steinlechner, D., Poniatowski, D., Fartmann, T., Beckmann, A., Stettmer, C., & Zehm, A. (2020). *Die Heuschrecken Deutschlands und Nordtirols. Bestimmen − Beobachten − Schützen* (2nd ed.). Wiebelsheim: Quelle & Meyer.

Fumy, F., Löffler, F., Samways, M. J., & Fartmann, T. (2020). Response of Orthoptera assemblages to environmental change in a low-mountain range differs among grassland types. *Journal* *of Environmental Management*, *256*, 109919. doi:10.1016/j.jenvman.2019.109919.

Gardiner, T. (2010). Precipitation and habitat degradation influence the occurrence of the common green grasshopper *Omocestus viridulus* in southeastern England. *Journal of Orthoptera Research*, *19*, 315–326. doi:10.1665/034.019.0219.

German Meteorological Service. (2018). *Climate Data Center*. . URL https://www.dwd.de/DE/leistungen/cdcftp/cdcftp.html accessed 5 October 2018.

Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., & Briggs, J. (2008). Global change and the ecology of cities. *Science*, *319*, 756–760. doi:10.1126/science.1150195.

Helbing, F., Fartmann, T., Löffler, F., & Poniatowski, D. (2017). Effects of local climate, landscape structure and habitat quality on leafhopper assemblages of acidic grasslands. *Agriculture, Ecosystems and Environment*, *246*, 94–101. doi:10.1016/j.agee.2017.05.024.

IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Service). (2019). *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. Bonn.

Jerrentrup, S., Dauber, J., Strohbach, M. W., Mecke, S., Mitschke, A., Ludwig, J. A., & Klimek, S. (2017). Impact of recent changes in agricultural land use on farmland bird trends. *Agriculture, Ecosystems and Environment*, *239*, 334–341. doi:10.1016/j.agee.2017.01.041.

Löffler, F., Poniatowski, D., & Fartmann, T. (2019). Orthoptera community shifts in response to land-use and climate change − Lessons from a long-term study across different grassland habitats. *Biological Conservation*, *236*, 315–323. doi:10.1016/j.biocon.2019.05.058.

Lüker-Jans, N., Simmering, D., & Otte, A. (2017). The impact of biogas plants on regional dynamics of permanent grassland and maize area − The example of Hesse, Germany (2005−2010). *Agriculture, Ecosystems and Environment*, *241*, 24–38. doi:10.1016/j.agee.2017.02.023.

MacLean, S. A., & Beissinger, S. R. (2017). Species' traits as predictors of range shifts under contemporary climate change: A review and meta-analysis. *Global Change Biology*, *23*, 4094–4105. doi:10.1111/gcb.13736.

Marini, L., Fontana, P., Scotton, M., & Klimek, S. (2008). Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps. *Journal of Applied Ecology*, *45*, 361–370. doi:10.1111/j.1365-2664.2007.01402.x.

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, *127*, 247–260. doi:10.1016/j.biocon.2005.09.005.

Nitsch, H., Osterburg, B., Roggendorf, W., & Laggner, B. (2012). Cross compliance and the protection of grassland − illustrative analyses of land use transitions between permanent grassland and arable land in German regions. *Land Use Policy*, *29*, 440–448. doi:10.1016/j.landusepol.2011.09.001.

Ouédraogo, D.-Y., Villemey, A., Vanpeene, S., Coulon, A., Azambourg, V., Hulard, M., Guinard, E., Bertheau, Y., Flamerie De Lachapelle, F., Rauel, V., Le Mitouard, E., Jeusset, A., Vargac, M., Witté, I., Jactel, H., Touroult, J., Reyjol, Y., & Sordello, R. (2020). Can linear transportation infrastructure verges constitute a habitat and/or a corridor for vertebrates in temperate ecosystems? A systematic review. *Environmental Evidence*, *9*, 13. doi:10.1186/s13750-020-00196-7.

Paracchini, M. L., Petersen, J., Hoogeveen, Y., Bamps, C., Burfield, I., Swaay, C. Van., 2008. High Nature Value Farmland in Europe − An Estimate of the Distribution Patterns on the Basis of Land Cover and Biodiversity Data. Institute for Environment and Sustainability Office for Official Publications of the European Communities Luxembourg. doi: 10.2788/8891

Phillips, B. B., Bullock, J. M., Osborne, J. L., & Gaston, K. J. (2020). Ecosystem service provision by road verges. *Journal of Applied Ecology*, *57*, 488–501. doi:10.1111/1365-2664.13556.

Poniatowski, D., Beckmann, C., Löffler, F., Münsch, T., Helbing, F., Samways, M. J., & Fartmann, T. (2020). Relative impacts of land-use and climate change on grasshopper range shifts have changed over time. *Global Ecology and Biogeography*, *29*, 2190–2202. doi:10.1111/geb.13188.

Poniatowski, D., Heinze, S., & Fartmann, T. (2012). The role of macropters during range expansion of a wing-dimorphic insect species. *Evolutionary Ecology*, *26*, 759–770. doi:10.1007/s10682-011-9534-2.

Poniatowski, D., Münsch, T., Helbing, F., & Fartmann, T. (2018). Range shifts of Central European Orthoptera in response to climate change. *Natur und Landschaft*, *93*, 553–561. doi:10.17433/12.2018.50153645.553-561.

Poniatowski, D., Stuhldreher, G., Löffler, F., & Fartmann, T. (2018). Patch occupancy of grassland specialists: Habitat quality matters more than habitat connectivity. *Biological Conservation*, *225*, 237–244. doi:10.1016/j.biocon.2018.07.018.

Poschlod, P. (2017). *Geschichte der Kulturlandschaft* (2. Ed.). Stuttgart: Eugen Ulmer.

Pöyry, J., Luoto, M., Heikkinen, R. K., Kuussaari, M., & Saarinen, K. (2009). Species traits explain recent range shifts of Finnish butterflies. *Global Change Biology*, *15*, 732–743. doi:10.1111/j.1365-2486.2008.01789.x.

Pryke, J. S., & Samways, M. J. (2012). Ecological networks act as extensions of protected areas for arthropod biodiversity conservation. *Journal of Applied Ecology*, *49*, 591–600. doi:10.1111/j.1365-2664.2012.02142.x.

R Core Team (2021). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rada, S., Schweiger, O., Harpke, A., Kühn, E., Kuras, T., Settele, J., & Musche, M. (2019). Protected areas do not mitigate biodiversity declines: a case study on butterflies. *Diversity and Distributions*, *25*(2), 217–224. doi:10.1111/ddi.12854.

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.

Ripple, W. J., Wolf, C., Newsome, T. M., Galetti, M., Alamgir, M., Crist, E., Mahmoud, M. I., & Laurance, W. F. (2017). World scientists' warning to humanity: a second notice. *BioScience*, *67*(12), 1026–1028. doi:10.1093/biosci/bix125.

Samways, M. J. (2005). *Insect Diversity Conservation*. Cambridge: Cambridge University Press.

Samways, M. J., McGeoch, M. A., & New, T. R. (2010). *Insect Conservation: A Handbook of Approaches and Methods*. Oxford: Oxford University Press.

Sánchez-Bayo, F., & Wyckhuys, K. A. G. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation*, *232*, 8–27. doi:10.1016/j.biocon.2019.01.020.

Schäuble, D. (2007). *PhD Thesis*. Germany: Universität der Bundeswehr München.

Sergeev, M. G. (2021). Distribution patterns of grasshoppers and their kin over the Eurasian steppes. *Insects*, *12*(1), 77. doi:10.3390/insects12010077.

Stoate, C., Báldi, A., Beja, P., Boatman, N. D., Herzon, I., van Doorn, A., de Snoo, G. R., Rakosy, L., & Ramwell, C. (2009). Ecological impacts of early 21st century agricultural change in Europe − a review. *Journal of Environmental Management*, *91*, 22–46. doi:10.1016/j.jenvman.2009.07.005.

Stork, N. E. (2018). How many species of insects and other terrestrial arthropods are there on Earth? *Annual Review of Entomology*, *63*, 31–45. doi:10.1146/annurev-ento-020117-043348.

Streitberger, M., Ackermann, W., Fartmann, T., Kriegel, G., Ruff, A., Balzer, S., & Nehring, S. (2016). *Artenschutz unter Klimawandel: Perspektiven für ein zukunftsfähiges Handlungskonzept: 147* (pp. 1−367). Naturschutz und Biologische Vielfalt.

Termaat, T., van Strien, A. J., van Grunsven, R. H. A., Knijf, G.de, Bjelke, U., Burbach, K., Conze, K.-J., Goffart, P., Hepper, D., Kalkman, V. J., Motte, G., Prins, M. D., Prunier, F., Sparrow, D., van den Top, G. G., Vanappelghem, C., Winterholler, M., & WallisDeVries, M. F. (2019). Distribution trends of European dragonflies under climate change. *Diversity and Distributions*, *25*, 936–950. doi:10.1111/ddi.12913.

Thomas, J. A., Telfer, M. G., Roy, D. B., Preston, C. D., Greenwood, J. J. D, Asher, J., Fox, R., Clarke, R. T., & Lawton, J. H (2004). Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science*, *303*, 1879–1881. doi:10.1126/science.1095046.

Uchida, K., & Ushimaru, A. (2014). Biodiversity declines due to abandonment and intensification of agricultural lands: patterns and mechanisms. *Ecological Monographs*, *84*(4), 637–658. doi:10.1890/13-2170.1.

Wagner, D. L. (2020). Insect declines in the Anthropocene. *Annual Review of Entomology*, *65*, 457–480. doi:10.1146/annurevento-011019-025151.

Wallis de Vries, 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. *Biological Conservation*, *104*(3), 265–273. doi:10.1016/S0006-3207(01)00191-4.

Willott, S. J., & Hassall, M. (1998). Life-history responses of British grasshoppers (Orthoptera: Acrididae) to temperature change. *Functional Ecology*, *12*, 232–241.