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Relative impacts of land-use and climate change on grasshopper range shifts have changed over time

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Abstract

Aim: Stopping the decline of biodiversity is one of today's greatest challenges. To help address this, we require studies that disentangle the effects of the most important drivers behind species range losses and shifts. In this large-scale study, we aim to evaluate the relative impacts of changes in land use and climate on distributional changes in grasshoppers.

Location: Central Europe.

Time period: Historical (pre-1990 vs. 1990–1999); recent (1990–1999 vs. 2000–2017).

Major taxa studied: Orthoptera (hereafter referred to as grasshoppers).

Methods: We used an advanced modelling approach within the framework of spatial point pattern analysis (SPPA) to calculate distributional changes of 58 grasshopper species based on > 100,000 aggregated observational records. Historical and recent range shifts were compared among four functional groups and analysed against: (a) the species temperature index (STI); and (b) the species farmland index (SFI).

Results: During the earlier historical period, most species suffered from large range losses, with habitat specialists declining more than generalists with equal mobility. Range retractions were related to species with high SFI values; that is, species associated with farmland having a high natural value. In contrast, during the recent period the distribution of less mobile species generally remained stable, whereas highly mobile species even expanded their ranges, irrespective of their habitat specificity. Additionally, range expansions occurred mostly among thermophilic species; that is, those with high STI values.

Main conclusions: This is the first large-scale study world-wide that quantifies both historical and recent range shifts of numerous grasshopper species. Our results suggest that historical range losses were mainly caused by severe loss of semi-natural habitats pre-1990. Recently, global warming has led to range expansions of several grasshopper species. The challenge now is to ensure the persistence of species that might not be able to evade future climate change owing to the increasing lack of suitable refuge habitats in intensive agricultural landscapes.

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KEYWORDS
biodiversity loss, dispersal ability, distribution modelling, functional trait, global warming, habitat specificity, insect conservation, Orthoptera, species farmland index, species temperature index

1 | INTRODUCTION

The global decline in biodiversity is one of the greatest challenges facing humanity today (Rockström et al., 2009). Among insects, it is assumed that up to 500,000 species have become extinct since the beginning of the industrial era (Cardoso et al., 2020). As species loss continues, there is an urgent need for large-scale studies disentangling the effects of the most important drivers of recent biodiversity range shifts (Samways et al., 2020; Sirami et al., 2017; Titeux et al., 2017).

Change in land use is a major driver of biodiversity decline worldwide (Maes & Van Dyck, 2001; Sala et al., 2000; van Strien, van Swaay, van Strien-van Liempt, Poot, & WallisDeVries, 2019). In the industrial era, the area of semi-natural habitats sharply decreased across Europe, mainly owing to agricultural intensification and abandonment (Burns et al., 2016; Stoate et al., 2009; WallisDeVries, Poschlod, & Willems 2002). Today, the remaining habitat fragments are often situated in an intensively used matrix (Poniatowski, Stuhldreher, Löffler, & Fartmann, 2018). Although large-scale habitat loss has recently been mitigated, in part, by increased conservation efforts in Central Europe (Carvalheiro et al., 2013; van Strien et al., 2019), the remaining habitats are still often subject to degradation of habitat quality and fragmentation (Fartmann, Krämer, Stelzner, & Poniatowski, 2012; Fischer & Lindenmayer, 2007; Helbing, Fartmann, Löffler, & Poniatowski, 2017).

More recently, climate change has altered environmental conditions in European ecosystems and has become another important driver of biodiversity change (Devictor et al., 2012; Sala et al., 2000). However, the ecological response to climate warming varies considerably among species (Parmesan et al., 1999; Warren et al., 2001). Among various insect taxa, especially thermophilic species, there have been many range expansions (Hickling, Roy, Hill, Fox, & Thomas, 2006; Pöyry, Luoto, Heikkinen, Kuussaari, & Saarinen, 2009; Termaat et al., 2019). In contrast, wetland and cold-adapted species are expected to decline under global warming (Buse & Griebeler, 2011; Freeman, Lee-Yaw, Sunday, & Hargreaves, 2018; Stuhldreher & Fartmann, 2018; Wessely et al., 2017).

Distributional changes of well-known and charismatic insect taxa, such as bumble bees, butterflies and dragonflies, have been well documented (e.g., Devictor et al., 2012; Pöyry et al., 2009; Soroye, Newbold, & Kerr, 2020; Termaat et al., 2019). In contrast, equivalent knowledge is still lacking for less popular insect groups. However, owing to the longstanding history of species recording across Central Europe, extensive occurrence data are available for some of these groups from unsystematically recorded observations. Although these opportunistic distribution data were frequently used for national atlas projects (e.g., Maas, Detzel, & Staudt, 2002), they have rarely been used for scientific evaluations of species range shifts because of concerns about potential bias owing to unstandardized species recording. However, advanced modelling techniques addressing these concerns have recently become available and thus have enabled analyses of such opportunistic data (Carvalheiro et al., 2013; Isaac, van Strien, August, de Zeeuw, & Roy, 2014; van Strien et al., 2019).

Here, we apply spatial point pattern analysis (SPPA) to quantify range shifts based on a data set of > 100,000 aggregated observational records on the distribution of 58 well-sampled Central European Orthoptera species (hereafter referred to as grasshoppers). This method enables modelling of the relative probability of occurrence of a species based on opportunistic distribution data and local sampling intensity. The main advantage of SPPA for the purpose of our study is that it reduces potential biases attributable to differences in sampling effort across space and time (cf. Bivand, Pebesma, & Gomez-Rubio, 2013; van Strien, van Swaay, & Termaat, 2013).

Grasshoppers are excellent indicators of changes in both land use and climate (e.g., Bazelet & Samways, 2011; Fartmann et al., 2012; Löffler, Poniatowski, & Fartmann, 2019). Earlier Central European work on large grasshopper species sets found that it was mainly habitat specialists that had declined historically, owing to change in land use in the past (Maas et al., 2002; Reinhardt, Köhler, Maas, & Detzel, 2005; Schuch, Bock, Leuschner, Schaefer, & Wesche, 2011). Yet these studies found no effects of climate change on species range shifts. However, more recent studies of regional scope provide clear evidence that thermophilic habitat generalists have recently expanded their ranges in response to climate warming (Fumy, Löffler, Samways, & Fartmann, 2020; Löffler et al., 2019; Poniatowski, Heinze, & Fartmann, 2012). Despite these findings, to date there are no large-scale studies that evaluate the relative impact of changes in both land use and climate on distributional changes in a comprehensive set of grasshopper species.

Here, we calculate range shifts for comparison between two time periods: a historical one, with two comparative time intervals embedded within it (pre-1990 vs. 1990–1999), and a recent one, also with two embedded comparative time intervals (1990–1999 vs. 2000–2017). Owing to rapid habitat loss before 1990 (e.g., Carvalheiro et al., 2013), we hypothesize that severe range retractions took place in several Central European grasshopper species in that early period. However, climate change has probably become an increasingly important factor driving grasshopper range shifts in recent years, as has been shown for butterflies (Pöyry et al., 2009). In order to test the relative impacts of changes in land use and climate on both early and recent distributional changes of Central European grasshoppers, observed range shifts were related to: (a)

the species temperature index (STI); and (b) the species farmland index (SFI) (cf. Devictor et al., 2012; Fumy et al., 2020). In addition, we also analysed grasshopper range shifts relative to four functional groups that represent interactions between mobility and habitat specificity: (a) less mobile generalists; (b) highly mobile generalists; (c) less mobile specialists; and (d) highly mobile specialists. According to previous research, the extent of range shifts among insect species depends on both habitat specificity and mobility (cf. Buse & Griebeler, 2011; Hill et al., 2002; Steck et al., 2007). Although we hypothesize that grasshopper specialists have suffered greater range losses than generalists owing to their higher sensitivity to change in land use, we expect that highly mobile grasshopper species might cope better with environmental changes than less mobile grasshopper species owing to their higher dispersal ability.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area consisted of Germany (centre: 51°9′48″ N, 10°26′52″ E), covering more than one-third of Central Europe (Ellenberg & Leuschner, 2010; Figure 1). Germany is divided into seven biogeographical regions: (a) the north-western and (b) north-eastern lowlands (hereafter considered as North German Plain), which pass southwards to (c) the western, (d) the eastern and (e) the south-western low mountain ranges (hereafter considered as Central German Uplands), extending to (f) the foothills of the Alps, which then adjoin (g) the Northern Limestone Alps (hereafter considered as Alps and Alpine Foreland) (cf. Maas et al., 2002). Elevation ranges from slightly below sea level in the

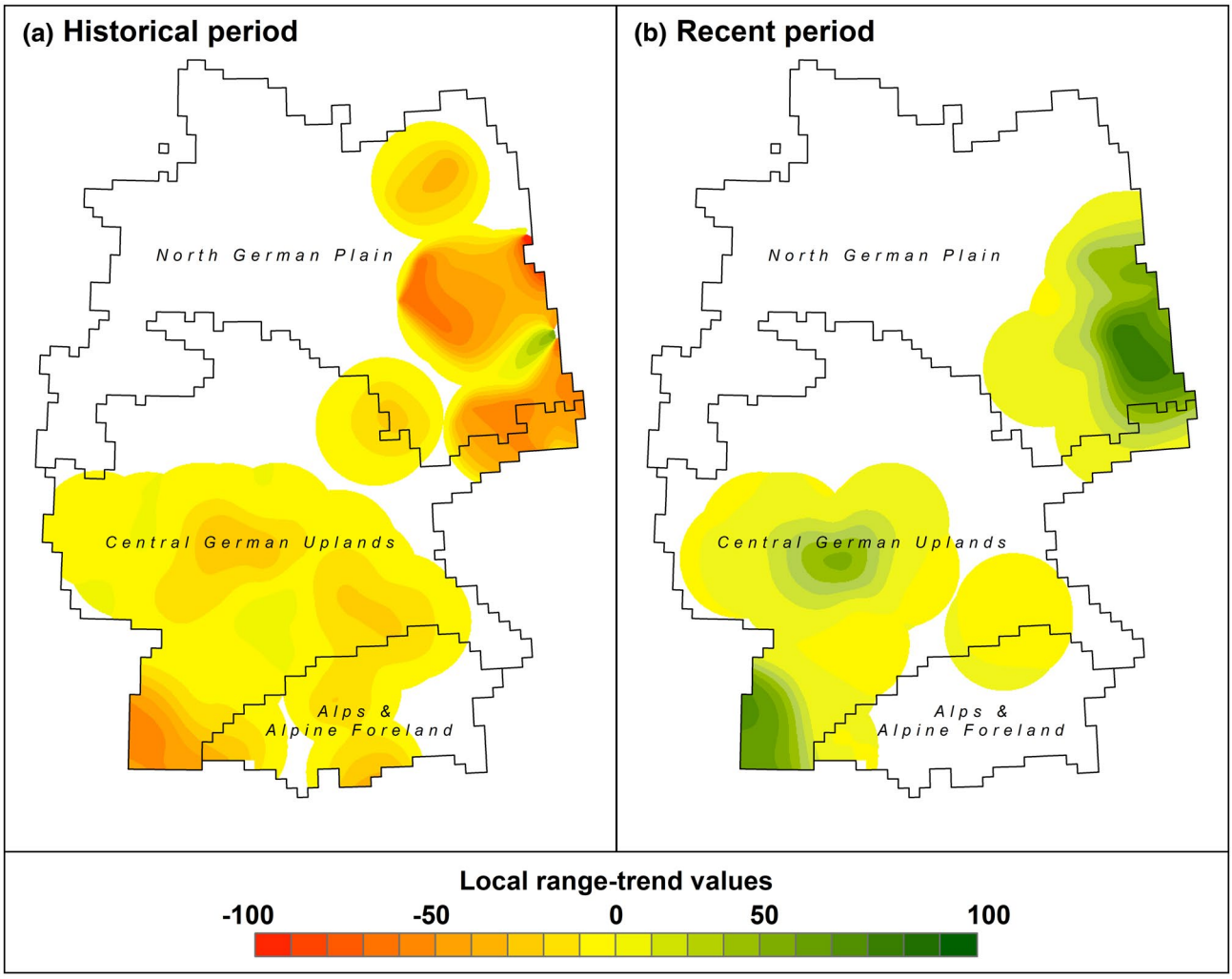

FIGURE 1 The (a) historical range shifts (pre-1990 vs. 1990–1999) and (b) recent range shifts (1990–1999 vs. 2000–2017) of *Calliptamus italicus* in Germany are intended to illustrate the modelling approach, which is based on spatial point pattern analysis (see Section 2.3.4). Local range-trend values of the species were calculated as the differences between the "local relative raster frequencies" of two time intervals that are taken into account within the respective time period (historical or recent) (see Section 2.3.4). To represent the overall distribution trend (range shift) of a species across its German range, the mean of all local range-trend values was calculated. In the case of *C. italicus*, its range changed on average by −15.06 in the historical period (a) and by 11.54 in the recent period (b) (cf. Table 1) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Historical (pre-1990 vs. 1990–1999) and recent (1990–1999 vs. 2000–2017) range shifts among all studied grasshopper species classified by habitat specificity (HS; S = habitat specialist; G = habitat generalist) and mobility (M; H = high mobility; L = low mobility)

	Range shift							
Species	Historical		Recent		HS	M	STI	SFI
Aiolopus thalassinus	−1.71	=	7.51	↑	S	H	14.87	13.08
Bicolorana bicolor	−7.20	↓	3.55	=	S	H	13.12	19.37
Bryodemella tuberculata	−14.24	↓↓	−1.34	=	S	H	8.99	47.19
Calliptamus italicus	−15.06	↓↓↓	11.54	↑↑	S	H	13.68	19.18
Chorthippus albomarginatus	11.68	↑↑	0.81	=	G	H	13.03	14.88
Chorthippus apricarius	3.51	=	−3.15	=	G	L	13.10	14.30
Chorthippus biguttulus	1.96	=	0.68	=	G	H	12.97	16.04
Chorthippus brunneus	3.97	=	−4.30	=	G	H	12.98	16.34
Chorthippus dorsatus	−4.12	=	3.72	=	G	H	13.04	16.98
Chorthippus mollis	−10.68	↓↓	−1.04	=	S	H	13.35	13.67
Chorthippus pullus	−27.16	↓↓↓	3.16	=	S	L	11.25	34.63
Chorthippus vagans	−5.50	↓↓	1.50	=	S	L	13.32	19.44
Chrysochraon dispar	1.88	=	11.75	↑↑	G	H	13.10	18.23
Conocephalus dorsalis	−0.24	=	−0.86	=	S	L	13.20	12.97
Conocephalus fuscus	4.97	=	10.20	↑↑	G	H	13.35	15.90
Decticus verrucivorus	−16.04	↓↓↓	1.21	=	S	L	12.59	25.90
Ephippiger diurnus	−7.77	↓	5.72	↑	S	L	13.55	12.74
Euthystira brachyptera	−4.01	=	−1.61	=	G	L	12.57	24.62
Gampsocleis glabra	−6.19	↓	2.06	=	S	L	13.17	40.17
Gomphocerippus rufus	−8.40	↓	−0.65	=	G	L	12.94	20.18
Gryllus campestris	−10.71	↓↓	7.32	↑	G	L	13.07	20.52
Gryllotalpa gryllotalpa	−21.21	↓↓↓	−2.85	=	S	H	13.17	20.98
Isophya krausii	−6.40	↓	−1.38	=	G	L	12.60	23.03
Leptophyes albovittata	−7.28	↓	3.32	=	S	L	13.33	16.70
Mecostethus parapleurus	−1.78	=	8.64	↑	S	H	13.22	28.47
Metrioptera brachyptera	−16.75	↓↓↓	−4.55	=	S	L	12.58	20.24
Myrmeleotettix maculatus	−10.25	↓↓	−10.28	↓↓	S	L	12.99	17.04
Nemobius sylvestris	−9.46	↓	0.30	=	G	L	13.11	18.52
Oecanthus pellucens	5.55	↑	11.56	↑↑	S	H	13.93	13.57
Oedipoda caerulescens	−15.93	↓↓↓	11.73	↑↑	S	H	13.45	14.44
Oedipoda germanica	−13.71	↓↓	2.79	=	S	L	13.20	14.74
Omocestus haemorrhoidalis	−16.00	↓↓↓	−2.86	=	S	L	13.26	16.99
Omocestus rufipes	−17.88	↓↓↓	−1.78	=	S	L	12.75	27.60
Omocestus viridulus	−7.72	↓	−7.42	↓	G	L	12.74	18.68
Phaneroptera falcata	6.64	↑	30.51	↑↑↑	S	H	13.28	14.41
Phaneroptera nana	.	.	15.47	↑↑↑	G	H	14.79	11.14
Pholidoptera griseoaptera	3.62	=	0.20	=	G	L	12.97	16.12
Platycleis albopunctata	−6.79	↓	7.78	↑	S	H	13.34	15.90
Polysarcus denticauda	−2.46	=	0.95	=	S	L	11.97	42.97
Pseudochorthippus montanus	−6.83	↓	−11.37	↓↓	S	L	12.82	19.28
Pseudochorthippus parallelus	0.36	=	−0.30	=	G	L	12.96	16.03
Psophus stridulus	−24.53	↓↓↓	3.56	=	S	L	11.81	32.72

(Continues)

TABLE 1 (Continued)

Species	Range shift				HS	M	STI	SFI
	Historical		Recent					
Pteronemobius heydenii	−1.02	=	5.91	↑	S	L	13.24	40.16
Roeseliana roeselii	3.47	=	7.36	↑	G	H	12.95	16.41
Ruspolia nitidula	−6.05	↓	18.41	↑↑↑	S	H	13.99	29.85
Sphingonotus caerulans	−5.04	↓	6.52	↑	S	H	13.62	12.95
Stenobothrus lineatus	−12.56	↓↓	1.28	=	S	H	12.89	18.73
Stenobothrus nigromaculatus	−9.78	↓	1.22	=	S	L	12.48	27.30
Stenobothrus stigmaticus	−12.99	↓↓	1.11	=	S	L	12.78	18.29
Stethophyma grossum	−3.10	=	10.88	↑↑	S	H	12.96	17.68
Tetrix bipunctata	−16.69	↓↓↓	−4.62	=	S	L	12.37	22.09
Tetrix subulata	1.04	=	0.41	=	S	H	13.07	15.82
Tetrix tenuicornis	−15.22	↓↓↓	−4.24	=	S	L	13.00	16.28
Tetrix tuerki	−16.25	↓↓↓	1.29	=	S	L	9.56	39.57
Tetrix undulata	1.07	=	−10.21	↓↓	G	L	12.99	16.18
Tettigonia cantans	−10.03	↓↓	1.29	=	G	L	12.59	18.44
Tettigonia caudata	−7.94	↓	0.21	=	G	L	13.83	13.91
Tettigonia viridissima	−1.43	=	−0.27	=	G	H	13.06	15.47

Note: Range shifts were calculated as described in Figure 1 (see also Section 2.3.4). The species temperature index (STI) and species farmland index (SFI) are given (see Section 2.5). Trend symbology: = (0–5); ↑ (5–10); ↑↑ (10–15); ↑↑↑ (> 15); the same symbology was used for negative values, respectively. Dots indicate no observations of the species within the given time period.

northern lowlands to almost 3,000 m above sea level (a.s.l.) in the Alps (Zugspitze, 2,962 m a.s.l.). Most of Germany is characterized by a moderate, oceanic climate, which is primarily influenced by the warm Gulf Stream and prevailing west winds. Summer temperatures seldom exceed 30 °C, and winter temperatures rarely drop below −20 °C (Ellenberg & Leuschner, 2010). With increasing distance from the sea, climate becomes more continental. The driest regions in Germany, with particularly warm summers and an annual precipitation of < 600 mm, are the northern Upper Rhine Valley and the lowlands of eastern Germany. In contrast, the higher elevations of the low mountain ranges and the Alps are often characterized by cool temperatures and precipitation >1,500 mm/year (DWD, 2018).

2.1.1 | Change in land use

For centuries, Central Europe was characterized by low-intensity land use, resulting in open and heterogeneous cultural landscapes (Ellenberg & Leuschner, 2010). However, since the beginning of the industrial era, both intensification of land use and land abandonment have led to a severe loss of semi-natural habitats, habitat fragmentation and homogenization of the landscape (Burns et al., 2016; Stoate et al., 2009; WallisDeVries et al., 2002). These changes were especially severe during the period from 1950 to 1990 (Carvalheiro et al., 2013; Stoate et al., 2009; van Strien et al., 2019). Since then, the rate of landscape change has slowed, and the remaining habitats have been increasingly protected [e.g., by the Habitats Directive (EC, 1992)] and managed to maintain their biodiversity (Carvalheiro et al., 2013; Löffler, Poniatowski, & Fartmann, 2020). Nevertheless, biodiversity in these remnants still suffers frequent degradation of habitat quality and fragmentation (Fartmann et al., 2012; Fischer & Lindenmayer, 2007; Helbing et al., 2017).

2.1.2 | Climate change

Since the end of the 19th century, the mean annual temperature in Germany has increased by 1.3 °C (Brasseur, Jacob, & Schluck-Zöller, 2017). However, global warming became especially evident in the late 1980s and has now reached an unprecedented level (IPCC, 2014). Accordingly, temperature anomalies increased significantly in Germany (across all biogeographical regions). As a result, recent annual temperatures usually exceeded the long-term mean over the last three decades (Supporting Information Figure S1). Given that actions against climate change are still insufficient, it is expected that temperatures will increase by at least a further 2.6 °C, and possibly up to 3.7 °C by the end of the 21st century (Brasseur et al., 2017; IPCC, 2014).

Although annual precipitation has increased slightly, drought periods during summer have become more frequent owing to shifts in precipitation from summer to winter and higher evapotranspiration rates from increased summer temperatures (Brasseur et al., 2017). Depending on the scenario, a 20–30% decline in summer precipitation is predicted (UBA, 2006), especially likely for the continental areas of Germany.

2.2 | Model organisms

Currently, 79 grasshopper species are regarded as indigenous to Germany (Fischer et al., 2020). Of these, 58 species with sufficient availability of distribution data were analysed here (Table 1; Supporting Information Table S1). To ensure statistical reliability, only species with a frequency of > 10 occupied grid cells in at least one time interval per reference time period (see Section 2.3.2) were included in analyses. Synanthropic, data-deficient, non-resident and cryptic species that have been inadequately sampled were not considered (cf. Reinhardt et al., 2005; van Strien et al., 2013). Owing to possible sampling deficits in high mountain areas (cf. Gedeon et al., 2014), we additionally excluded predominantly alpine species within their German range. Taxonomic nomenclature follows Fischer et al. (2020).

2.3 | Range shifts

2.3.1 | Distribution data

Most of the data used were originally compiled for a comprehensive atlas project on German grasshoppers (Maas et al., 2002). Additionally, more recent data (2002–2017) were provided by the federal state authorities and regional grasshopper societies in the German federal states (see Acknowledgments). Grasshopper distribution data were based on a grid-map system with a spatial resolution of 10 km × 11 km covering the whole of Germany (in total, Germany comprises 3,004 of these grid cells, known in German as "Messtischblatt"; cf. Reinhardt et al., 2005). Grid cells were classified as occupied when at least one observation in the considered time interval was available (cf. Termaat et al., 2019; van Strien et al., 2019). Overall, the data set included 109,351 aggregated observational records (redundant information for the respective grid cells were excluded before the analyses; see also Section 2.3.2).

2.3.2 | Reference time periods and intervals

Grasshopper range shifts were analysed for two reference time periods. Within each of the two time periods, we compared "local relative raster frequencies" of a species between the time interval before and after the threshold year of the time periods, respectively (see also Section 2.3.4; Supporting Information Supplementary methods).

1. Historical time period: comparison between the time intervals pre-1990 and 1990–1999.
2. Recent time period: comparison between the time intervals 1990–1999 and 2000–2017.

For each of the time intervals, the amount of available data was high and similar (pre-1990: 28,648 observations; 1990–1999: 46,009 observations; 2000–2017: 34,694 observations).

The two reference time periods show clear differences in the intensity of change in land use and climate. The historical period (pre-1990 vs. 1990–1999) represents an era of severe change in land use, but only weak effects of climate change (see Sections 2.1.1 and 2.1.2). In contrast, the recent period (1990–1999 vs. 2000–2017) was characterized by rapid climatic change, whereas habitat loss and deterioration have slowed (see Sections 2.1.1 and 2.1.2).

2.3.3 | Reference grid cells

As the basis for spatial analyses, we defined well-surveyed reference grid cells (see Section 2.3.4). A grid cell was considered well surveyed if all national and regional grasshopper reference species were recorded during the respective time interval (Supporting Information Table S2). The national reference species represent common species that are assumed to be present throughout Germany. Owing to physiogeographical differences within the study area, we additionally defined regional reference species for each of the seven biogeographical regions of Germany (see Section 2.1; cf. Maas et al., 2002). These regionally common species were expected to occur in each grid cell within a certain biogeographical region. Given that observations of common species clearly tend to be underreported in opportunistic data sets compared with those of rare and threatened species (cf. Smith, Parker, & Schaefer, 2019; Soroye, Ahmed, & Kerr, 2018), it is likely that less common species have also been well surveyed when the reference species have been mapped. Hence, this procedure ensures equal sampling intensity within the studied grid cells and reduces potential effects of sampling bias on the observed patterns. A similar procedure has been used in other studies (e.g., Maes & Van Dyck, 2001).

2.3.4 | Spatial analyses

To detect species range shifts using presence-only distribution data, we chose a modelling approach derived from case–control studies in spatial epidemiology and based on kernel smoothing; a method from spatial point pattern analysis (SPPA). The general idea behind our approach is to model the relative probability of occurrence (i.e., local relative raster frequency) of a species based on sizeable distribution data (i.e., occupied grid cells) and local sampling intensity (i.e., the local density of well-surveyed grid cells around occupied grid cells) (cf. Figure 1). Differences in "local relative raster frequencies" in the time intervals before and after the threshold years were calculated to quantify range shifts during the historical and recent period, respectively (see Section 2.3.2). The main advantage of this method for distribution modelling is that it reduces potential biases attributable to differences in sampling effort across space and time (cf. Bivand et al., 2013; van Strien et al., 2013). A detailed description of the spatial analyses is available in the Supporting Information (Supplementary methods).

2.4 | Functional groups

We classified grasshopper species by their mobility (less mobile versus highly mobile species) and habitat specificity (habitat generalists versus specialists). These traits crucially affect the response of grasshoppers to environmental change (e.g., Fartmann et al., 2012; Löffler et al., 2019; Reinhardt et al., 2005). The classification underlying our analyses was mainly derived from Reinhardt et al. (2005). However, we revised this classification for some species by considering more recent information on habitat selection and species mobility (cf. Löffler et al., 2019; Poniatowski, Münsch, Helbing, & Fartmann, 2018; Table 1). Afterwards, we differentiated four functional groups representing interactions of mobility and habitat specificity: (a) less mobile generalists; (b) highly mobile generalists; (c) less mobile specialists; and (d) highly mobile specialists (Figure 2).

2.5 | Global change indices

We calculated the species temperature index (STI) and the species farmland index (SFI) for all grasshopper species included in our analyses. The STI is defined as the mean temperature within the distribution range of a species (cf. Devictor et al., 2012). It should be noted that the STI is a relative measure usually based on geographically restricted distribution data. Thus, STI values might differ from the "true thermal niche" of a species across its entire range. Despite these minor limitations of the STI, Devictor, Jullirad, Denis and Jiguet (2008) concluded that this index is a robust tool that can be used to prove the relationship between species range shifts and climate change (cf. Ram, Axelsson, Green, Smith, & Lindström, 2017; Scridel et al., 2017). The SFI indicates the average availability of farmland with a high natural value (HNV farmland) across a species range (cf. Fumy et al., 2020). Both indices have recently been used to relate grasshopper assemblage shifts in response to changes in land use and climate (Fumy et al., 2020; Löffler et al., 2019).

The calculation of the indices was based on German grasshopper distribution data (see Section 2.3.1). Only distribution data from the recent time period were considered for the calculation of STI and SFI, because they correspond to the time-scale of available climate and HNV farmland data. For calculation of the STI, all recently occupied grid cells were intersected with raster data representing the most recent long-term mean temperatures during the summer period (April–September) (spatial resolution of raster data: 1 km × 1 km; time-scale: 1981–2010; DWD, 2018). The SFI was computed by intersecting occupied grid cells with raster data covering the most recent distribution of HNV farmland and the overall open landscape in Germany (spatial resolution of raster data: 100 m × 100 m; EEA, 2018), respectively. Accordingly, the SFI was calculated as the percentage of HNV farmland of the overall open landscape.

The statistical computing of the species-specific indices was done using the *Zonal Statistics* tool in ArcGIS v.10.3, calculating a mean temperature (STI) or HNV farmland (SFI) value across all occupied grid cells within Germany.

2.6 | Statistical analyses

In order to detect the most important drivers behind species range shifts at the national scale, we calculated multivariate linear models (LMs), for both the historical and the recent time period (Table 2). Species traits (i.e., mobility and habitat specificity; see also Section 2.4) were used as categorical predictors in these models. Furthermore, they included the STI and SFI as continuous measures of species sensitivity to changes in climate and land use (see also Section 2.5). The STI and SFI were transformed before the analyses [e^x and ln(x), respectively; Figure 3; Table 2]. In order to determine the impact and relative variable importance (RI) of the predictors in the two time periods, we applied model averaging based on an information-theoretic approach (Grueber, Nakagawa, Laws, & Jamieson, 2011). Model averaging was conducted using the "dredge" function (R package *MuMIn*; Bartón, 2020) and included only top-ranked models within $\Delta AIC_C < 3$ (cf. Grueber et al., 2011).

We additionally calculated univariate LMs, in order to illustrate the role of mobility and habitat specificity responsible for grasshopper range shifts in Germany (Figure 2). The relationships between STI/SFI and historical or recent range shifts were additionally proved at a regional scale using univariate LMs (Supporting Information Table S3). Statistical differences in these models were assessed using likelihood ratio tests (type III test).

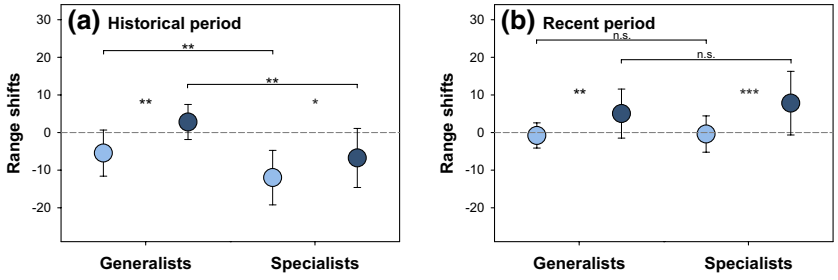

FIGURE 2 (a) Historical range shifts (pre-1990 vs. 1990–1999) and (b) recent range shifts (1990–1999 vs. 2000–2017) (mean ± *SD*) of habitat generalists and habitat specialists with low (light blue) and high (dark blue) mobility. Differences between the groups were tested using univariate linear models (LMs; see Section 2.6). Statistical significances are indicated as follows: n.s. $p > .05$; *$p < .05$; **$p < .01$; ***$p < .001$. Range shifts were calculated as described in Figure 1 (see also Section 2.3.4) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Results of multivariate linear model analyses (model averaging)

Parameter	Estimate	*SE*	*z*	RI	*p*
(a) Historical range shifts (R^2 = 0.25–0.29)					
(Intercept)	1.15	13.91	0.08	–	n.s.
Habitat specificity (generalist)	6.99	2.15	3.19	1.00	**
SFI (ln)	−6.80	3.12	2.13	0.64	*
STI (exp)	5.76×10^{-6}	2.75×10^{-6}	2.05	0.56	*
Mobility (high)	3.79	1.94	1.90	0.55	n.s.
(b) Recent range shifts (R^2 = 0.31–0.33)					
(Intercept)	−6.59	7.75	0.84	–	n.s.
Mobility (high)	6.29	1.68	3.67	1.00	***
STI (exp)	4.46×10^{-6}	1.89×10^{-6}	2.31	1.00	*
SFI (ln)	3.73	2.60	1.40	0.36	n.s.
Habitat specificity (generalist)	−1.76	1.62	1.06	0.23	n.s.

Note: Influence of species temperature index (STI), species farmland index (SFI) (see Section 2.5), mobility and habitat specificity (see Section 2.4) on (a) historical (pre-1990 vs. 1990–1999) and (b) recent (1990–1999 vs. 2000–2017) range shifts of the 58 grasshopper species (Table 1). Model-averaged coefficients (conditional average) were derived from the top-ranked linear model ($\Delta AIC_C < 3$; RI = relative parameter importance; see Section 2.6). The R^2 values represent the range of model accuracies within the top-ranked models. Statistical significances are indicated as follows: n.s. $p \geq .05$; *$p < .05$; **$p < .01$; ***$p < .001$.

We analysed long-term climate trends using LMs with autocorrelation (AR1) structure on temperature data (package *nlme*; Pinheiro & Bates, 2020; Supporting Information Figure S1). All statistical analyses were performed using the statistical package R v.3.4.3 (R Development Core Team, 2019).

3 | RESULTS

3.1 | Historical range shifts

During the historical period (pre-1990 vs. 1990–1999), 77% of species showed distinct range retractions, whereas only 23% of species expanded their ranges (Table 1; Figure 2a). Habitat specificity has been identified as the driver with the highest relative variable importance (RI = 1.00) considering historical range shifts (Table 2a). Except for highly mobile habitat generalists, which extended their ranges, all other functional groups suffered from severe range reductions during the historical period (Figure 2a). Considering highly mobile species, range shifts of habitat generalists were significantly different from those of habitat specialists. Although both less mobile habitat generalists and specialists have undergone range retractions, habitat specialists experienced significantly greater range losses than habitat generalists. In addition, range shifts of highly mobile habitat generalists and specialists differed significantly from those of the less mobile ones.

The SFI exhibited a significantly negative correlation with historical range shifts (RI = 0.64; Figure 3c; Table 2a). This means that species with a higher SFI underwent more severe range losses during the historical period. Furthermore, we found a positive relationship between the STI and historical range shifts (RI = 0.56; Figure 3a; Table 2a), which indicates that thermophilic species experienced smaller range losses or even expanded their ranges. The findings of the national analyses largely correspond to the results at the regional scale. Although we found a negative relationship between historical range shifts and SFI across all biogeographical regions, the positive impact of STI on historical distribution trends was restricted to the North German Plain (Supporting Information Table S3a).

3.2 | Recent range shifts

During the recent period (1990–1999 vs. 2000–2017), 60% of the species expanded their ranges, whereas the remaining 40% of species still experienced range retractions (Table 1). Although recent range shifts were significantly driven by the mobility of the species (RI = 1.00), they were no longer affected by habitat specificity (Table 2b). Recent range expansions were mostly observed in highly mobile species, including both habitat generalists and specialists (Figure 2b). In contrast, ranges of less mobile species on average remained stable in the study area.

Furthermore, recent range shifts exhibited a significantly positive relationship to STI (RI = 1.00; Figure 3b). However, there was no relationship between SFI and recent grasshopper range shifts (Figure 3d). This was confirmed by the regional analyses, which revealed that SFI did not affect recent range shifts accross the biogeographical regions, whereas theVy were significantly driven by STI in the North German Plain and Central German Uplands (Supporting Information Table S3b).

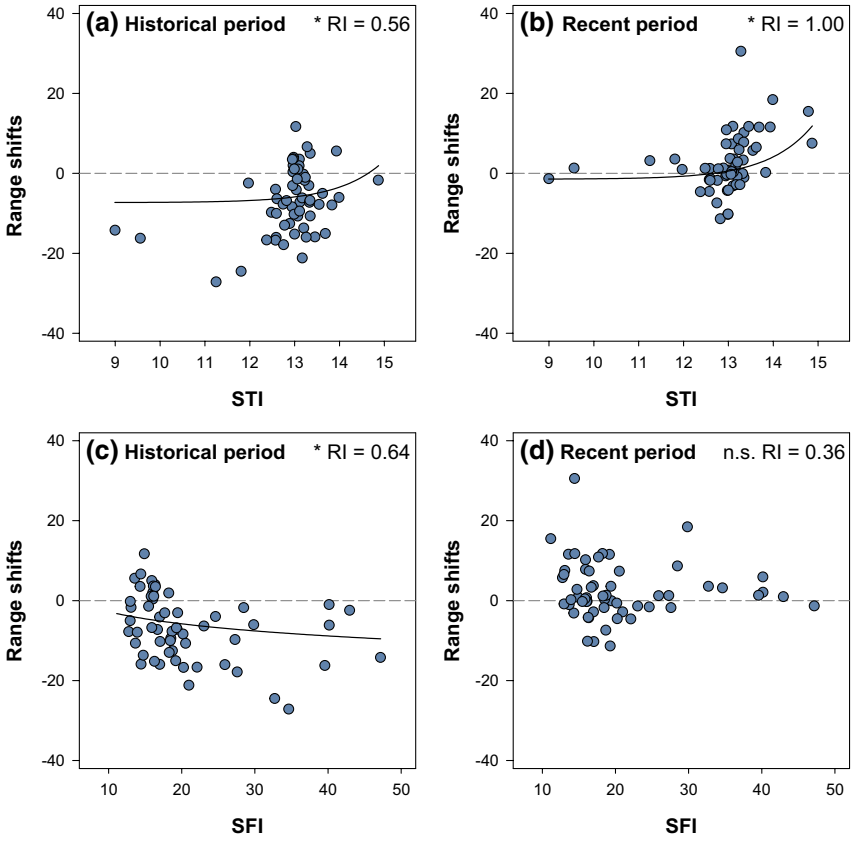

FIGURE 3 Relationship between (a,c) historical range shifts (pre-1990 vs. 1990–1999) or (b,d) recent range shifts (1990–1999 vs. 2000–2017) (58 species) and species temperature index (STI; a,b) or species farmland index (SFI; c,d). Regression slopes and significant differences were fitted based on the results of multivariate linear models (LMs; Table 2; see Section 2.6). RI, relative parameter importance, see Section 2.6. Statistical significances are indicated as follows: n.s. $p \geq .05$; $^{*}p < .05$ [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Most of the grasshopper species examined here have experienced large-scale range shifts over the last few decades. However, the patterns differed clearly between the two reference time periods (historical and recent). During the historical period (pre-1990 vs. 1990–1999), most species experienced severe range losses. Furthermore, habitat specialists declined to a muVch greater extent than generalists with equal mobility. These range retractions were related to species associated with HNV farmland (i.e., species with high SFI values). In contrast, during the recent period (1990–1999 vs. 2000–2017) the distribution of less mobile species generally remained stable, and highly mobile species even expanded their ranges, irrespective of their habitat specificity. Also, range expansions were correlated with thermophilic species, with high STI values.

4.1 | Historical range shifts (pre-1990 vs. 1990–1999)

Change in land use contributed to a severe loss of semi-natural habitats across Europe before 1990 (Carvalheiro et al., 2013; Stoate et al., 2009; van Strien et al., 2019; see Section 2.1.1). For butterflies, habitat loss and deterioration have been the main reasons for the severe decline of these insects in open habitats across Europe during the second half of the 20th century (cf. Maes & Van Dyck, 2001; van Strien et al., 2019; van Swaay, Warren, & Loïs, 2006). Grasshoppers are also highly sensitive to changes in land use (Löffler & Fartmann, 2017; Marini, Fontana, Battisti, & Gaston, 2009; Torma, Gallé, & Boszó, 2014), especially in the case of habitat specialists (Fartmann et al., 2012; Poniatowski & Fartmann, 2010). Our findings are in accordance with these, with range retractions of habitat specialist grasshoppers during the historical study period generally being greater than those of habitat generalists. Irrespective of the spatial scale (i.e., national or regional), the grasshopper species with the highest SFI values generally showed the greatest declines. This species group includes HNV farmland species (e.g., *Decticus verrucivorus*, *Omocestus rufipes* and *Psophus stridulus*), depending on the maintenance of low-intensity land use (Maas et al., 2002), and additionally, species inhabiting dynamic, alpine river systems (e.g., *Bryodemella tuberculata*, *Chorthippus pullus* and *Tetrix tuerki*). In Central Europe, the few remaining habitats of the latter species group are embedded in the traditionally managed alpine landscape (Helbing, Blaeser, Löffler, & Fartmann, 2014; Fischer et al., 2020). Their SFI values are correspondingly high.

Climate change was becoming evident in the late 1980s (IPCC, 2014; see Section 2.1.2). Accordingly, it had not yet been seen as playing any major role in the observed range shifts during the historical period (cf. Pöyry et al., 2009). However, species with high STI values had already experienced small range losses or, alternatively, had already expanded their ranges slightly in the 1990s across Germany. However, regional analyses revealed that this trend was mainly evident in the North German Plain, were temperatures might already have become favourable for some thermophilic grasshoppers during

the historical period (cf. Supporting Information Figure S1b). With the exception of a few highly mobile specialists, such as *Oecanthus pellucens* and *Phaneroptera falcata*, historical range shifts were especially true for highly mobile habitat generalists. These findings are in accordance with previous studies, where only a few highly mobile and predominatly generalist species benefited from increased temperatures during the initial stage of elevated anthropogenic global warming (e.g., Beckmann et al., 2015; Hill et al., 2002; Warren et al., 2001).

4.2 | Recent range shifts (1990–1999 vs. 2000–2017)

Many species that experienced large-scale range losses in earlier years have recently shown a more stable distribution or have even expanded their ranges. This corroborates findings of two previous studies on pollinators, showing that intensified conservation measures from the 1990s (e.g., implementation of the EU Habitats Directive) onwards have contributed significantly to slow further large-scale range retractions of insects across Europe (Carvalheiro et al., 2013; van Strien et al., 2019). However, the designation of protected areas under the EU Habitats Directive only mitigated habitat loss in Central and Northwestern Europe, but did not increase the availability of suitable habitats (cf. Carvalheiro et al., 2013; Löffler et al., 2020). It should also be noted that these protected areas dominated by open, semi-natural habitats make up < 5% of the terrestrial area of Germany (cf. Ellwanger, Raths, Benz, Glaser, & Runge, 2015), and thus habitat availability is currently strongly limited, especially for less mobile habitat specialists, such as *Chorthippus pullus*, *Gampsocleis glabra*, *Psophus stridulus*, *Stenobothrus nigromaculatus* and *Tetrix tuerki*. Today, the populations of these species are highly localized in Central Europe (Holusa, 2012; Maas et al., 2002; Reinhardt et al., 2005).

Especially in the North German Plain and in the Central German Uplands, numerous species were able to colonize new areas. Given that range expansions were most obvious for species with high STI values, it can be assumed that these positive shifts were driven mainly by climate change. This is in accordance with previous studies, which provided evidence that climate warming has led to range expansions of thermophilic insects in general (Devictor et al., 2012; Hickling et al., 2006; Termaat et al., 2019) and grasshoppers in particular (Fumy et al., 2020; Löffler et al., 2019). However, in contrast to previous studies that detected range expansions attributable to climate warming largely restricted to habitat generalists (Beckmann et al., 2015; Hill et al., 2002; Warren et al., 2001), we found that both generalists and specialists were able to track global warming in the recent period, as long as they were of high mobility. For example, dry grassland specialists, such as *Calliptamus italicus*, *Oedipoda caerulescens*, *Platycleis albopunctata* and *Sphingonotus caerulans*, which all experienced severe range losses pre-1990 (Maas et al., 2002; Reinhardt et al., 2005), rapidly expanded their ranges over the last two decades. High summer temperatures are known to increase insect flight activity (Kuussaari, Rytteri, Heikkinen, Heliölä, & von Bagh, 2016) and favour colonization of areas where the climate was previously unsuitable (Hickling et al., 2006; Hill et al., 2002; Parmesan et al., 1999). Although the biodiversity of wet habitats is generally assumed to be threatened by climate change (Streitberger et al., 2016), even highly mobile wet grassland specialists, such as *Mecostethus parapleurus*, *Ruspolia nitidula* and *Stethophyma grossum*, have recently expanded their range, as we show here. These species require sufficient habitat moisture only during winter (i.e., the high-precipitation season; see Section 2.1.2) for successful egg development (Poniatowski, Münsch, et al., 2018). The situation is different for other hygrophilous species, such as *Omocestus viridulus*, *Pseudochorthippus montanus* and *Tetrix undulata*. They are among the few species with range retractions during the recent period, which is probably attributable to their high sensitivity to summer drought (cf. Gardiner, 2010; Poniatowski, Münsch, et al., 2018).

4.3 | Outlook on future range shifts

Although many insects, especially habitat specialists, across different taxa have experienced severe range losses during the second half of the 20th century (Maes & Van Dyck, 2001; Reinhardt et al., 2005; van Swaay et al., 2006; Warren et al., 2001), we found that many grasshopper species have recently expanded their ranges across Central Europe. However, it is uncertain whether these species will continue to benefit from future climate change. Steck et al. (2007) predicted that climate change will foster grasshopper species richness in Central Europe. In contrast, Wessely et al. (2017) suggested that recent conservation strategies might not compensate for climate-induced range losses in the future. Although that study focused mainly on alpine or rare species, further habitat loss and deterioration might be so great that many grasshopper species will be unable to react to further increased global warming by movement (Buse & Griebeler, 2011; Hill et al., 2002; Steck et al., 2007). If that is the case, we expect that future climate change will be particularly threatening to hygrophilous and alpine species unable to make use of suitable refuge habitats in intensive agricultural landscapes.

Many less mobile habitat specialists among grasshoppers have become extinct in large parts of Central Europe as a result of past habitat destruction (Holusa, 2012; Maas et al., 2002; Reinhardt et al., 2005). This development has also affected numerous other groups of insects, such as bees, butterflies and carabid beetles (Brooks et al., 2012; Goulson, Lye, & Darvill, 2008; van Strien et al., 2019; Wagner, 2020). Given that the intensive agricultural landscape in Central Europe is largely unsuitable for most insect species, their remaining populations are currently dependent on a few isolated remnants of semi-natural habitats (Helbing et al., 2017; Maes & Van Dyck, 2001; Öckinger & Smith, 2007). However, habitat quality within these remnants continues to decrease, which is likely to lead to time-delayed local species extinctions (Kuussaari et al., 2009; Löffler et al., 2020). This means that conservation measures should focus on adaptation to future climate changes by building ecosystem resilience and

maintaining large-scale habitat networks within a heterogeneous landscape matrix (Harvey et al., 2020; Samways & Pryke, 2016).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

D.P. and T.F. conceived the idea. C.B., D.P. and F.L. designed the study. T.M., F.H. and D.P. coordinated data collection. C.B., F.L. and D.P. carried out the analyses with inputs from T.F. and M.J.S. D.P., F.L. and T.F. led writing of the manuscript. All co-authors carefully revised the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All data supporting the results are available from Table 1 and Supporting Information Table S1.

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BIOSKETCH

In our recent studies, we focus on the effects of changes in land use and climate on biodiversity patterns (global change ecology). Furthermore, we investigate how species richness of ecosystems is influenced by disruptive events, such as windthrow, fire and floods (disturbance ecology). In the field of restoration ecology, we evaluate habitat management and measures that aim to restore threatened ecosystems. We use a wide range of model organisms. The most important indicator groups are plants, birds, amphibians, spiders, dragonflies and damselflies, Orthoptera, leafhoppers, carabid beetles, butterflies and burnet moths. Please visit http://fartmann.net/

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Supplementary methods: Detailed description of the spatial analyses (Section 2.3.4)

To model the distribution of a species during each of the considered time intervals, we first calculated the local density of occupied grid cells, as well as local density of well-surveyed reference grid cells (see Section 2.3.3) using kernel smoothing (based on grid cell centroids with a kernel bandwith of 50 km and quartic kernel function). This was done for each species. Kernel smoothing is a statistical technique which can be applied to model continuous distribution of a species based on observational, opportunistic data. Kernel smoothing was performed in R 3.4.3 (R Development Core Team, 2019) using the package *splancs* (Bivand, 2017). This procedure resulted in raster datasets, representing the 'local density of occupied grid cells or reference grid cells', respectively (spatial resolution of grid cells: 1 km × 1 km).

Local density of occupied grid cells was then related to the local density of well-surveyed reference grid cells by calculating the ratio between the corresponding cell values. The calculated grid cell values range from zero to one. While cell values close to one indicate that a species occurred in nearly all reference grid cells, a value of zero means that the species was absent within the applied kernel bandwidth. This resulted in a raster dataset including the 'local relative raster frequencies', which represent the probability of occurrence of a species within the focal time interval. The evaluation was done separately for the time interval prior to and after the threshold year of the time periods, respectively. For both the historical and the recent time period, range shifts were then calculated as the difference of the 'local relative raster frequencies' from these two time intervals (see Section 2.3.2). Areas where the species was absent during the whole time period were excluded from the analyses. This resulted in raster datasets representing local range-trend values of a species including grid cell values theoretically ranging from –1 to 1. While negative values indicate local range retractions, positive ones express range expansions, while values close to zero denote no change (Figure 1). To represent overall distribution trend of a species across its German range, we finally calculated the mean of all local range-trend values (Figure 2 and 3; Table 1). For ease of interpretation, it was multiplied by 100.

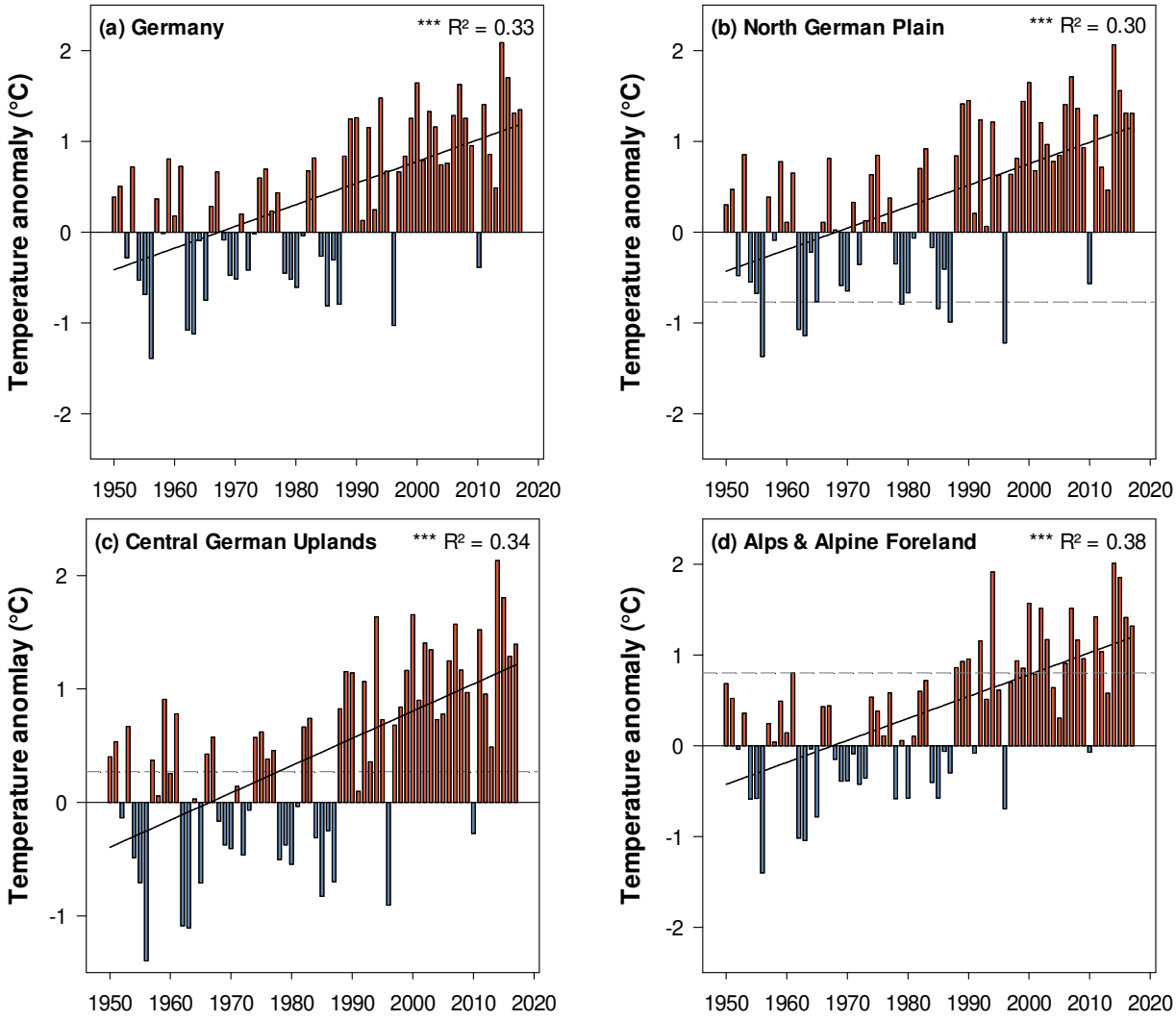

Figure S1 Time series of national (a) and regional (b–d) mean temperature anomalies in Germany (1950–2017). Annual anomalies from long-term mean temperatures (timescale: 1961–1990) were derived from grid maps of annual mean temperatures (DWD, 2018). Dashed lines in (b), (c) and (d) represent the differences between the national long-term mean temperature and regional-long-term mean temperatures. Statistical trends and significances were assessed using linear models with autocorrelation (AR1) structure on temperature data (package *nlme*; Pinheiro & Bates, 2020).

Table S1 Regional historical (pre-1990 vs. 1990–1999) and recent range shifts (1990–1999 vs. 2000–2017) among all studied grasshopper species. Dots indicate a lack or very low raster frequency (< 10 occupied grid cells) of a species within a biogeographic region. For the classification of the biogeographic regions please see Section 2.1. Range shifts were calculated as described in Figure 1 (see also Section 2.3.4).

Species	**Range shifts**					
	North German Plain		**Central German Uplands**		**Alps & Alpine Foreland**	
	Historical	Recent	Historical	Recent	Historical	Recent
Aiolopus thalassinus	·	·	–1.46	7.51	·	·
Bicolorana bicolor	–8.41	7.39	–3.63	0.63	–17.42	3.53
Bryodemella tuberculata	–11.43	·	·	·	–26.69	–1.33
Calliptamus italicus	–24.67	17.52	–11.34	9.02	·	·
Chorthippus albomarginatus	1.56	–1.64	20.83	2.70	16.81	3.44
Chorthippus apricarius	10.18	–1.31	1.28	–4.71	–14.59	–4.54
Chorthippus biguttulus	3.10	2.11	0.89	–0.44	1.60	–0.80
Chorthippus brunneus	0.88	–4.34	6.92	–4.29	4.84	–4.27
Chorthippus dorsatus	–14.28	0.98	5.09	7.80	1.11	–1.38
Chorthippus mollis	–11.03	–3.36	–3.64	0.40	–37.80	3.20
Chorthippus pullus	–31.52	7.08	–20.15	·	–27.12	3.05
Chorthippus vagans	–4.30	0.08	–1.69	–0.09	·	·
Chrysochraon dispar	1.68	7.37	5.10	17.39	–10.51	6.72
Conocephalus dorsalis	–1.00	–2.83	3.18	2.70	–11.12	–7.05
Conocephalus fuscus	6.53	15.85	4.01	8.21	4.33	0.11
Decticus verrucivorus	–20.78	–0.58	–11.17	0.84	–16.51	10.03
Ephippiger diurnus	·	·	–9.11	6.06	·	·
Euthystira brachyptera	–6.41	–2.24	–3.39	–1.39	–1.14	–1.29
Gampsocleis glabra	–7.57	2.05	·	·	·	·
Gomphocerippus rufus	–17.69	11.68	–4.97	–6.61	–1.63	–2.83
Gryllus campestris	–21.16	9.44	–5.16	5.64	7.03	6.54
Gryllotalpa gryllotalpa	–37.93	2.18	–8.30	–4.90	–5.45	–14.18
Isophya krausii	–15.64	·	–2.33	–2.02	·	·
Leptophyes albovittata	–7.92	5.97	–7.60	2.50	–3.89	–1.57
Mecostethus parapleurus	·	·	–1.14	9.67	–3.28	7.35
Metrioptera brachyptera	–29.26	–0.90	–5.98	–8.34	–8.35	–4.30
Myrmeleotettix maculatus	–17.18	–10.29	–1.76	–12.39	–16.11	–1.49
Nemobius sylvestris	–11.92	4.44	–8.20	–2.60	–8.74	0.28
Oecanthus pellucens	3.21	18.03	7.86	10.22	·	·

Table S1 Continued.

Species	Range shifts					
	North German Plain		Central German Uplands		Alps & Alpine Foreland	
	Historical	Recent	Historical	Recent	Historical	Recent
Oedipoda caerulescens	–13.76	7.64	–12.47	16.57	–38.77	8.30
Oedipoda germanica	·	·	–13.13	3.23	·	·
Omocestus haemorrhoidalis	–22.96	–4.91	–7.78	–2.47	–21.57	4.62
Omocestus rufipes	–21.40	–3.53	–12.00	–3.40	–29.32	9.93
Omocestus viridulus	–16.45	–7.77	1.75	–8.64	–9.89	–0.92
Phaneroptera falcata	8.03	41.30	7.51	18.77	–2.17	35.88
Phaneroptera nana	·	·	·	15.47	·	·
Pholidoptera griseoaptera	4.60	1.63	2.74	–1.40	3.06	–2.86
Platycleis albopunctata	–2.65	6.25	–6.46	9.38	–21.53	6.70
Polysarcus denticauda	·	·	–2.54	0.69	·	·
Pseudochorthippus montanus	–16.92	–14.27	0.95	–10.69	3.77	–1.77
Pseudochorthippus parallelus	0.72	–0.63	0.11	–0.06	–0.07	0.05
Psophus stridulus	–26.07	·	–19.12	2.01	–41.04	2.75
Pteronemobius heydenii	·	·	6.02	3.59	–6.25	7.76
Roeseliana roeselii	2.97	10.87	4.73	5.50	0.82	0.00
Ruspolia nitidula	·	·	·	19.06	·	16.78
Sphingonotus caerulans	–9.41	7.88	–1.21	6.20	–4.79	3.01
Stenobothrus lineatus	–11.41	6.04	7.67	15.72	–12.41	11.57
Stenobothrus nigromaculatus	–17.03	6.12	–5.76	–4.16	–22.27	3.90
Stenobothrus stigmaticus	–13.47	2.23	–4.95	0.56	–23.91	2.17
Stethophyma grossum	–16.27	0.30	–7.92	0.34	–21.78	7.25
Tetrix bipunctata	–22.54	2.12	–7.55	–7.40	–32.38	–13.26
Tetrix subulata	–4.79	5.80	7.23	–0.25	0.45	–19.55
Tetrix tenuicornis	–20.21	1.61	–8.01	–6.58	–25.39	–17.18
Tetrix tuerki	·	·	·	·	–19.52	1.59
Tettigonia undulata	–3.64	–6.31	6.66	–12.12	–2.08	–18.66
Tettigonia cantans	–17.37	–3.90	–3.19	–0.93	–7.54	3.55
Tettigonia caudata	–4.83	0.33	·	·	·	·
Tettigonia viridissima	–1.87	0.69	–1.04	0.96	–1.28	–9.31

Table S2 National and regional reference species for the seven biogeographic regions of Germany. For the classification of the biogeographic regions please see Section 2.1. Reference species were used to identify well-surveyed grid cells (see Section 2.3.3).

Reference species	North German Plain		Central German Uplands			Alpine Foreland	Alps
	W	E	W	E	SW		
NATIONAL							
Chorthippus biguttulus	×	×	×	×	×	×	×
Chorthippus brunneus	×	×	×	×	×	×	×
Pseudochorthippus parallelus	×	×	×	×	×	×	×
Tettigonia viridissima/cantans	×	×	×	×	×	×	×
REGIONAL							
Chorthippus albomarginatus	×	.	.	.	.	.	.
Chorthippus dorsatus	.	.	.	.	.	×	×
Chorthippus mollis	.	×	.	.	.	.	.
Conocephalus dorsalis	×	×	.	.	.	.	.
Conocephalus fucus	.	.	.	.	.	×	.
Decticus verrucivorus	.	.	.	.	.	.	×
Euthystira brachyptera	.	.	.	.	.	×	×
Gomphocerippus rufus	.	.	.	.	×	×	×
Gryllus campestris	.	.	.	.	×	×	.
Metrioptera brachyptera	.	.	.	.	.	.	×
Omocestus viridulus	.	.	×	.	.	.	×
Pholidoptera griseoaptera/aptera	.	.	×	.	×	×	×
Roeseliana roeselii	.	×	.	×	×	×	×
Stenobothrus lineatus	.	.	.	.	.	.	×
Tetrix undulata	×	.	.	.	.	.	.

Table S3 Relationship between (a) historical (pre-1990 vs. 1990–1999) or (b) recent (1990–1999 vs. 2000–2017) range shifts and Species Temperature Index (STI)/Species Farmland Index (SFI) differentiated for the three major biogeographic regions within study area (see Section 2.1). The statistical analysis based on the regional range-trend values of the species (Supporting Information Table S2). Significant differences were assessed using Linear Models (LM) (see Section 2.6). Statistical significances are indicated as follows: n.s. $p \geq 0.05$; * $p < 0.05$; *** $p < 0.001$.

a) Historical range shifts

	Biogeographic regions								
	North German Plain			Central German Uplands			Alps & Alpine Foreland		
	t	p	R^2	t	p	R^2	t	p	R^2
STI (exp)	2.5	*	0.10	0.9	n.s.	–	1.9	n.s.	–
SFI (ln)	–3.8	***	0.22	–2.9	*	0.10	–2.2	*	0.08

b) Recent range shifts

	Biogeographic regions								
	North German Plain			Central German Uplands			Alps & Alpine Foreland		
	t	p	R^2	t	p	R^2	t	p	R^2
STI (exp)	2.7	*	0.12	3.5	***	0.18	1.6	n.s.	–
SFI (ln)	–0.8	n.s.	–	–1.0	n.s.	–	1.1	n.s.	–

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