# Grasshoppers facing land-use and climate change: range shifts, community dynamics and implications for conservation

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**Zusammenfassung:** Der Landnutzungswandel gilt als die Hauptursache des gravierenden Insektenrückgangs in Mitteleuropa. Dabei hat sowohl die landwirtschaftliche Intensivierung als auch die Nutzungsaufgabe seit den 1950er-Jahren zu einem großflächigen Lebensraumverlust und einer Abnahme der Habitatqualität für Insekten geführt. Darüber hinaus unterliegen die Insektengemeinschaften in den verbliebenen Habitatfragmenten zunehmend dem Einfluss der anthropogenen Klimaerwärmung. Während thermophile Arten oft in der Lage sind, ihre mitteleuropäischen Areale zu erweitern, werden für Arten, die an kühle oder feuchte Klimabedingungen angepasst sind, zumeist negative Auswirkungen des Klimawandels prognostiziert. Da Heuschrecken äußerst sensibel auf Veränderungen der Landnutzung und des Klimas reagieren, gelten sie als gute Indikatoren rezenter Umweltveränderungen in Offenland-Ökosystemen. Die Ergebnisse unserer aktuellen Studien belegen, dass sich das Verbreitungsgebiet vieler mitteleuropäischer Heuschreckenarten in der zweiten Hälfte des 20. Jahrhunderts infolge des Landnutzungswandels dramatisch verkleinert hat. Starke Rückgänge ließen sich vor allem für Habitatspezialisten mit einer geringen Mobilität feststellen, die stark an das Vorhandensein landwirtschaftlich extensiv genutzter Habitate (= High-Nature-Value-Farmland) gebunden sind. Im Gegensatz dazu haben sich in den letzten 30 Jahren wärmeliebende, mobile Heuschreckenarten in Mitteleuropa stark ausgebreitet. In einer Wiederholungsuntersuchung haben wir zudem klare Belege gefunden, dass sich die Zusammensetzung der Heuschreckengemeinschaften im Grünland der Eifel in den vergangenen Jahrzehnten deutlich verändert hat. Während die Ausbreitung mobiler Habitatgeneralisten in extensiv genutzten Grünlandhabitaten der Eifel zu einer Erhöhung der Artenvielfalt geführt hat, könnte diese Entwicklung in intensiv genutzten und brachliegenden Lebensräumen langfristig zu einer biotischen Homogenisierung der Heuschreckengemeinschaften führen. Die Ergebnisse der behandelten Arbeiten verdeutlichen die Herausforderungen für den Naturschutz in Zeiten des globalen Wandels. Zukünftige Schutzmaßnahmen sollten darauf abzielen, die Anpassungsmöglichkeiten an klimatische Veränderungen für möglichst viele Arten zu erhöhen. Dies kann zum einen durch die Erhöhung der Habitatheterogenität und zum anderen durch die Verbesserung des Biotopverbunds zwischen den Habitaten gefördert werden. Darüber hinaus kann durch die Etablierung standardisierter Monitoringprogramme, die Entwicklung der Heuschreckenbestände zukünftig besser nachvollzogen und Populationsrückgängen frühzeitig entgegengewirkt werden.

**Key words:** distribution change, global warming, habitat loss, insect decline, Orthoptera

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## Introduction

During recent decades, many insects have undergone severe population declines throughout Central Europe. This development is mainly a result of large-scale habitat loss and degradation due to land-use intensification and abandonment (Löffler & al., 2020; Fartmann & al., 2022a). As a consequence, the availability of suitable habitats is limited for many insect species. More recently, climate change has contributed to severe shifts in insect distribution and community composition (e.g. Löffler & al., 2019; Poniatowski & al., 2020). However, there is much variation in the response of species to global

warming across taxa and functional groups (Streitberger & al., 2016; Engelhardt & al., 2022). Especially habitat specialists with low mobility have to struggle with a lack of suitable habitats in Central Europe's fragmented landscapes and thus they are often not able to keep up with recent global warming in (Platts & al., 2019; Löffler, 2021).

Since they respond rapidly to both land-use and climate change, Orthoptera (hereinafter grasshoppers) are well-suited indicators to study the effects of recent environmental changes in grassland ecosystems (Fartmann & al., 2012). Here, we synthesize the content of three of our recent studies investigating changes in grasshopper distribution and community composition: (i) Poniatowski & al. (2020); (ii) Löffler & al. (2019) and (iii) Fartmann & al. (2022b). In the first study (Poniatowski & al., 2020), we investigated historical and recent range shifts of Central European grasshoppers in response to land-use and climate change. Since we expected that climate-driven range shifts also caused changes in grasshoppers community composition, we additionally conducted a re-survey of grasshopper assemblages in calcareous, mesic and wet grasslands in the Eifel uplands (W Germany, Löffler & al., 2019). Apart from temperature increase, climate change led to an increase in the frequency of summer drought, which likely causes detrimental effects on phytophagous insects, such as most grasshoppers (Lenhart & al., 2015; Streitberger & al., 2016). To shed light on this, we finally studied grasshoppers in semi-natural grasslands along an elevation gradient in the Diemel Valley (NW Germany, Fartmann & al., 2022b). Overall, we hypothesized that both land-use and climate change cause distinct changes in grasshopper distribution and community composition in Central Europe. While we assumed that the former is detrimental to grasshoppers across the board, the latter may foster thermophilic habitat generalists, which are able to expand their distribution ranges under recent global warming. The results of our studies demonstrate the key challenges for grasshopper conservation in times of global change. To account for the interacting effects of land-use and climate change on the grasshopper fauna of Central Europe, we outline implications for conservation, which may help species to cope with recent environmental changes.

**Methods**

The methods underlying the studies synthesized here are briefly described below. More detailed information about the methodology can be found in the original papers.

(i) Grasshopper range shifts in Central Europe (Poniatowski & al., 2020): In the first study, we modelled the distribution trends of 58 grasshopper species in Germany. Distribution modelling was done using Spatial Point Pattern Analysis based on > 100,000 aggregated observational records. Using Generalized Linear Models (GLM), historical (pre-1990 vs. 1990 – 2000) and recent (1990 – 2000 vs. 2000 – 2017) range shifts were compared among four functional groups: habitat specialists and generalists with low and high mobility, respectively. Furthermore, the observed distribution trends were analyzed against the Species Temperature Index (STI) and Species Farmland Index (cf. Löffler & al., 2019; Fumy & al., 2020).

(ii) Grasshopper community dynamics in semi-natural grasslands (Löffler & al., 2019): In the second study, we examined grasshopper community shifts in three different grassland habitats – (a) calcareous grassland, (b) mesic grassland, (c) wet grassland – in the Eifel uplands. In total, 67 patches studied in 1994 were re-surveyed in 2015 using the same sampling methods. Based on these data, we analyzed differences in overall species richness, the number of habitat specialists/generalists, the number of mobile/less mobile grasshopper species as well as the Community Temperature Index (CTI, cf. Devictor & al., 2012) using pairwise statistical comparisons.

(iii) Effects of summer drought on grasshopper abundance in semi-natural grasslands (Fartmann & al., 2022b): In the third study, we studied grasshopper abundance in semi-natural grasslands with low-intensity land use. The plots included calcareous and mesic grasslands (each 27 plots), which were randomly distributed along an elevation gradient in the Diemel Valley (100 – 600 m a.s.l.). In these plots, grasshoppers were sampled in 2020 using a box quadrat, which accounts for the most accurate methods to ascertain species richness and abundance of grasshoppers (Fischer & al., 2020). To unravel the impact of summer drought on grasshopper assemblages, we applied Generalized Linear Mixed-effect Models (GLMM) including both habitat and climate parameters.

**Results and discussion**

Our studies revealed a strong response of grasshoppers to both land use and climate change. While many grasshopper species historically experienced strong declines, an increasing number of species recently expanded their Central European distribution ranges in response to global warming. However, at the same time, we found that drought may cause negative effects on grasshopper abundance in semi-natural grasslands exposed to warm summer temperatures.

(i) In the range shift study, we found that many grasshopper species historically suffered from large-scale habitat loss prior to the 1990s (Poniatowski & al., 2020). This was especially true for habitat specialists, which are associated with low-intensity land use and are highly sensitive to environmental changes in their habitats (e.g. Fartmann & al., 2012). For instance, the loss of nutrient-poor habitats historically caused a severed decline in the Central European distribution of many habitat specialists. Accordingly, historical range retractions were strongly related to species with high SFI values (= species requiring a high extent of High Nature Value farmland). A typical example is the Lesser mottled grasshopper (*Stenobothrus stigmaticus*), which strongly depends on the occurrence of nutrient-poor grasslands and heathlands (Fischer & al., 2020). Since the extent of these habitats severely declined during the 20th century, this species now has to struggle with limited habitat availability (Fig. 1). By contrast, an increasing number of grasshopper species recently expanded their distribution range. Range expansions occurred mostly among species with high STI values (= species requiring a warm macroclimate) with high mobility. This has been exemplarily shown for Roesel's bush-cricket (*Roeseliana roeselii*), which is able to occur in a wide range of habitats and can become highly mobile under favourable climatic conditions (Fig. 1; Poniatowski & al., 2012; Fischer & al., 2020). In particular, warm springs promote high densities of larvae of *R. roeselii*. This finally leads to an increased development of long-winged individuals of this species, which have strongly been associated with its rapid expansion during the last decades (Poniatowski & al., 2012). The findings of our study broadly correspond to previous research on other insect taxa providing evidence that mainly thermophilic species, which are able to overcome the distances between remaining habitat fragments, can keep pace with recent global warming (e.g. Devictor & al., 2012; Platts & al., 2019; Termaat & al., 2019).

(ii) According to the results of the range-shift study (Poniatowski & al., 2020), we also found distinct changes in the composition of grasshopper assemblages across different grassland habitats in the Eifel uplands between 1994 and 2015 (Löffler & al., 2019). While the overall species richness increased in well-managed calcareous and mesic grasslands in the study area, grasshopper species richness did not change in wet grasslands, which were often lacking management and thus exhibited a decline in habitat quality (Scherer & al., 2021). Furthermore, in this study, only the number of habitat generalists and mobile species increased but not the number of habitat specialists and species with low dispersal ability. This largely corroborates the results of the first study showing that habitat generalists historically were less strongly affected by land-use change and recent range shifts mainly occurred among mobile species (Poniatowski & al., 2020). At the same time, we found an increase in the Community Temperature Index (CTI) in mesic and wet grasslands of the study area, which was caused by high turnover rates towards more thermophilic species. In line with Fumy & al. (2020), our study revealed that climate-driven range shifts of thermophilic species can increase grasshopper species richness in well-managed habitats in the rather cool climate of Central Europe. By contrast, there was an increasing risk of biotic homogenization in abandoned wet grasslands with a low habitat quality for most grasshopper species (cf. Fumy & al., 2020).

(iii) During recent years, summer drought increasingly affected Central European grassland ecosystems. Though the majority of grasshoppers is thermophilic, the results of the third study revealed that grasshopper abundance decreased with increasing summer temperature in semi-natural grasslands (Fartmann & al., 2022b). The study was done in the Diemel Valley in summer 2020, which was extraordinarily dry and warm. As a result, the vegetation in plots with higher summer temperatures started to wither early in the summer season. This can lead to food shortage among phytophagous insects such as grasshoppers and thus likely causes negative effects on grasshopper abundance

(Lenhart & al., 2015; Fartmann & al., 2022a). Whereas grasshopper abundance was still high at higher elevations in the study area, it usually was low in lower situated grassland areas, which were characterized by high summer temperatures and low levels of precipitation. Apart from its detrimental effects on grasshopper food supply, drought can also result in a limited development of larvae, especially among hygrophilous grasshopper species (Ingrisch & Köhler, 1998).

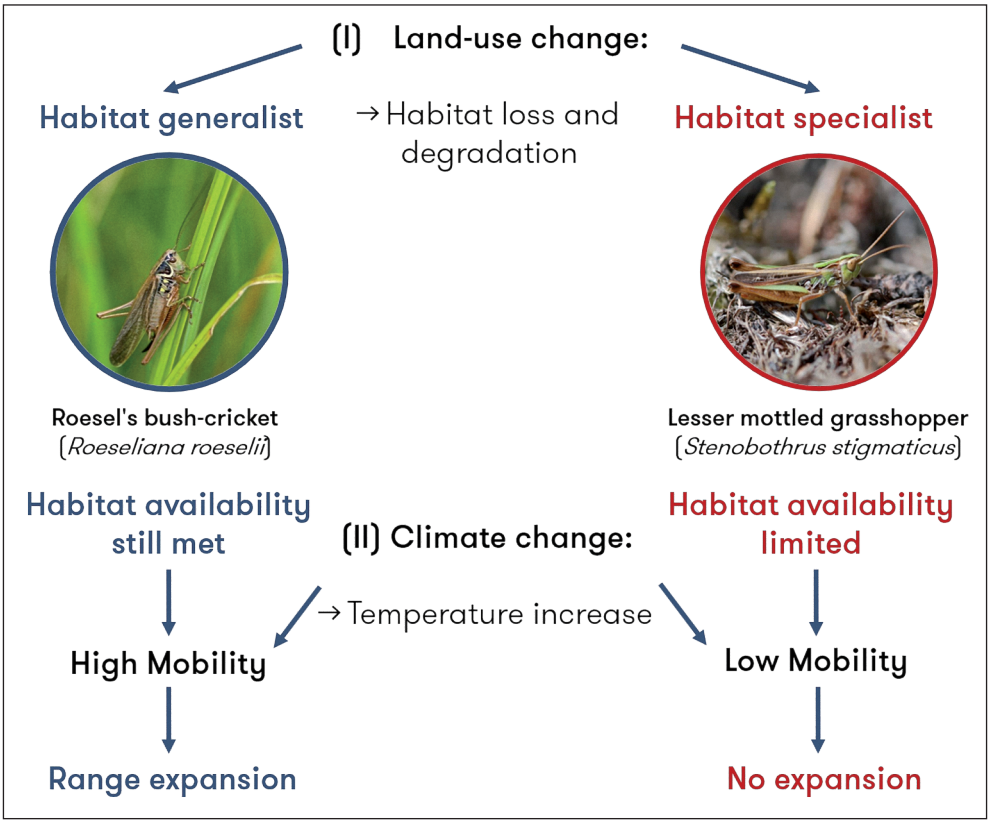


**Fig. 1:** Schematic illustration of the effects of land-use and climate change based on the examples of Roesel's bush-cricket (*Roeseliana roeselii*) as a mobile habitat generalists and Lesser mottled grasshopper (*Stenobothrus stigmaticus*) as a habitat specialist with low mobility. Illustration according to the results of Poniatowski & al. (2020) (Photos: *R. roeselii* by F. Löffler, *S. stigmaticus* by T. Fartmann).

**Conclusions**

Our studies have shown that both land-use and climate change had severe effects on grasshoppers in Central Europe. While the distribution of many grasshopper species historically experienced strong declines due to the large-scale loss of High Nature Value Farmland, thermophilic species with high dispersal ability recently expanded their ranges in response to climate change (Poniatowski & al., 2020). At the same time, less mobile habitat specialists were not able to keep up with global warming due to the lack of their habitats in Central Europe's fragmented landscapes. The changes in grasshopper distribution also caused severe changes in grasshopper communities in temperate grassland ecosystems (Löffler & al., 2019; Fumy & al., 2020). While we found evidence that the expansion of thermophilic species throughout Central Europe can even lead to an increase in overall species richness in well-managed grasslands, there is an increasing risk of biotic homogenization in habitats with low habitat

quality (Löffler & al., 2019). Therefore, future conservation actions need to increase the availability of suitable habitats and build dispersal corridors between existing habitat fragments. This may foster the dispersal of species facing global warming and allow them to keep pace with recent global warming. Furthermore, conservation management should additionally aim to increase habitat heterogeneity within existing habitats, which may increase the capability of species to evade from detrimental environmental conditions such as drought (Streitberger & al., 2016). Finally, there is a vital need for standardized monitoring schemes. Monitoring data could especially help to assess the population status of grasshoppers, to identify potential threats at an early stage and to increase knowledge on the response of grasshoppers to global change in the long run.

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