Thomas Fartmann | Dominik Poniatowski

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DISTRIBUTION ATLAS OF GRASSHOPPERS AND PRAYING MANTISES IN GERMANY

BfN
Bundesamt für Naturschutz

Thomas Fartmann | Dominik Poniatowski
(Ed.)

Distribution Atlas of Grasshoppers and Praying Mantises in Germany

201 Pictures
83 Distribution Maps

Contents

Species Profiles of Grasshoppers and Praying Mantises in Germany

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Preface

We associate the song of grasshoppers with a summerly walk. It can be heard from field margins, grasslands, shrubberies or along Alpine rivers. What we hear is the buzzing, chirping or creaking that the animals create by means of their wings or legs. These sounds, together with their morphological characteristics, are the basis for the determination of the grasshopper species in their different habitats.

The threat status of each of the grasshopper species in Germany has been documented since 1977 through national red lists by the Federal Agency for Nature Conservation. The recent red-data book from 2024 includes 82 grasshopper and one praying mantis species. Altogether, 31,7 % of the species are considered threatened and four have even become extinct.

More than 20 years after the publication of the first atlas of German grasshopper species, this book gives a summary of the current distribution of all native species. It served as the basis for the threat analysis within the national red list in 2024. It was intensively prepared for many years, and extensive voluntary surveys preceded it. The authors gathered large data sets and, therefore, also used observation portals such as OrthopteraWeb. OrthopteraWeb was developed within the project 'Tools for the Collection of Biological Observation Data in Germany' (Werkzeuge zur Erfassung biologischer Beobachtungsdaten in Deutschland (WerBeo)) within the Federal Programme Biological Diversity, which was funded by the Federal Agency for Nature Conservation. It is now maintained by Osnabrück University with the help of the University of Rostock and is available under the URL https://www.heuschrecken-monitoring.de.

Overall, 35 experts have intensively contributed to this atlas and have successfully worked together with voluntary researchers, natural history associations, non-governmental and governmental nature conservation organisations as well as scientific institutions. At this point, I would like to thank them – especially all the voluntary researchers – for all their tireless work!

The atlas brings together an extensive set of available grasshopper and praying mantis data. It shows the current distribution patterns of all species native to Germany. To document possible range shifts in the future, the distribution maps in the book are linked by a QR code with the online maps of https://www.heuschrecken-monitoring.de.

Besides information on the distribution of each species, the present book includes a detailed description of their preferred habitats and main threats. Moreover, it deals with the biogeography, habitat selection and monitoring of grasshoppers. Ecological indices are also presented. Thus, for nature conservationists, it is an important basis for the planning and conduction of conservation measures. I hope that this atlas will contribute significantly to the continued commitment to grasshopper conservation.

Grasshoppers have become increasingly important due to their response to land-use and climate change and within the Insect Conservation Action Programme of the federal government. They are key organisms in grassland ecosystems since they are essential primary consumers and a crucial food source for species of higher trophic levels. Accordingly, they are an integral part of the German Insect Monitoring Scheme, which started in 2020/21 with the pilot phase.

The book at hand is a reference work that sums up our current knowledge on many interesting topics. Both the text and the illustrations are vivid. The information on the distribution of the species invites us to continue recording regularly together and, thus, to contribute to the conservation of biological diversity in the future.

Dr. Sandra Balzer
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THOMAS FARTMANN & DOMINIK PONIATOWSKI

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However, due to the decentralised recording possibilities, it was a great challenge to bring together the available data. The project 'Tools for recording biological observation data in Germany' (WerBeo), which was developed in cooperation with the University of Rostock and the 'Institute for Enduring and Environmentally Friendly Development of Natural Spaces' (DUENE e. V.) in Greifswald and funded by the Federal Agency for Nature Conservation (BfN) with funds from the Federal Ministry for the Environment, Nature Conservation, Nuclear Safety and Consumer Protection (BMUV) as part of the Federal Biological Diversity Programme (Grant no.: 3517685C08), helped in this matter.

The data from the WerBeo project formed the basis for the revision of the new red list of the grasshoppers and praying mantises in Germany, which was recently published (Poniatowski et al. 2024a). In this context, we would like to thank the team of the German Red List Centre (RLZ) for the always very pleasant and constructive cooperation. The new red list was funded by the German Aerospace Center (DLR) on behalf of the Federal Agency for Nature Conservation (BfN) with funds from the Federal Ministry for the Environment, Nature Conservation, Nuclear Safety and Consumer Protection (BMUV) (Grant no.: D/396/67279024).

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Introduction

THOMAS FARTMANN & DOMINIK PONIATOWSKI

Scientific studies on grasshoppers have a long tradition in Germany. Here and hereinafter, the term grasshoppers is usually used as a pars pro toto for bush-crickets, crickets, grasshoppers, groundhoppers, locusts and praying mantises. Regional species lists have been published since the end of the 18th century (Poniatowski & Fartmann 2023). However, until the mid-20th century, only a few naturalists and scientists dealt with grasshoppers. The first identification key was published by Kurt Harz (Harz 1957), the initiator of the German Orthopterists' Society. However, his epochal, nearly 500-page-long book was very scientific and hence unsuitable for a wide audience. The situation changed with the field guide of Heiko Bellmann, an instructively illustrated and compact book (Bellmann 1985). For the first time, it enabled the identification of all German grasshoppers in the field. It triggered a wave of surveys and scientific studies on grasshoppers across large parts of Germany. As a result of the rapidly increasing knowledge, Sigfrid Ingrisch and Günter Köhler published a comprehensive textbook on the biology and ecology of Central European grasshoppers (Ingrisch & Köhler 1998). At roughly the same time, the first extensive distribution atlases for some federal states were released. Among them, those for Baden-Württemberg (Detzel 1998) and Bavaria (Schlumprecht & Waeber 2003) should be particularly emphasised since they included in addition to very extensive species profiles an analysis of most of the relevant Central European literature. The first complete German distribution atlas of grasshoppers was published in the early 2000s (Maas et al. 2002). Since then, the populations and distribution patterns of grasshoppers have been highly dynamic. Progressing land-use change and increasing climatic alterations have contributed to this in particular (e. g. Poniatowski et al. 2018a, 2020; see also chapter Land-use and climate change). In recent times, for example, many thermophilic species have expanded their range. Simultaneously, a lot of populations have become extinct, mainly those of habitat specialists; however, some relatively widespread species have also declined. Moreover, recording of grasshopper occurrence has strongly increased owing to the establishment of some online platforms such as OrthopteraWeb or Observation (Poniatowski & Fartmann 2023). The strong changes in distribution and significant increase in data during the past 20 years as well as many new scientific findings called for a recent overview of the distribution of grasshoppers in Germany.

The main component of the distribution atlas are the species profiles, which concisely present current knowledge concerning distribution, habitat, and population trend and threats. The text on the distribution of the species is supplemented by visually appealing grid maps. The different topics of the species profiles are also part of the introductory chapters. However, their focus is on the explanation of general distribution patterns (see chapters Distribution, Habitats as well as Land-use and climate change). In the chapter 'Monitoring', grasshopper monitoring as part of the German Insect Monitoring Scheme is introduced and the importance of re-surveys for detecting changes in grasshopper assemblages is mentioned. The chapter 'Ecological indices' presents several categorical and metric parameters of ecological preferences and functional traits of species, which are highly relevant for the analysis of grasshopper data. For example, the Species Temperature Index (STI) and the Species Farmland Index (SFI) have distinctly proven their value (Löffler et al. 2019, Fumy et al. 2020, Poniatowski et al. 2020, Riggi & Berggren 2020, Fartmann et al. 2021b, 2022b, Thorn et al. 2022; see chapter Land-use and climate change). For the first time, for all grasshopper species of open habitats, specific temperature and moisture indicator values are introduced. The indicator values are inspired by those known for plants by Ellenberg et al. (2001) and can be used to characterise the ecological conditions of a habitat. The following chapter on the data basis mentions all data sources that were used to create the grid maps. The chapter 'Range of species, nomenclature and taxonomy' explains which species were considered and why this was the case. The last of the introductory chapters deals with the structure of the species profiles. It outlines the structure and content of the text. Moreover, it provides information for the interpretation of the distribution maps.

Distribution

DOMINIK PONIATOWSKI, FELIX HELBING & THOMAS FARTMANN

The distribution range of a species is determined by various environmental factors. The macroclimate is of overriding importance. As ectothermic organisms whose development and survival depend on ambient temperatures, many species generally require high temperatures. This connection can be seen in Europe. The diversity hotspots are in southern Europe (Fig. 1). For example, over 300 species occur on the Iberian Peninsula (Heller et al. 1998) (Fig. 2). Greece and Italy have the greatest diversity with 378 and 382 species, respectively (Willemse et al. 2018, Iorio et al. 2019). As the geographical latitude increases, the number of species decreases significantly. The Central European fauna only contains around 160 species (Fischer et al. 2020). Of these, 82 species are considered native in Germany (Poniatowski et al. 2024a). In Northern Europe, the grasshopper fauna is even more impoverished. There, fewer than 40 species can cope with the low temperatures (Karjalainen 2009, Hansen & Olsen 2010, Kindvall 2018).

At the regional level, however, other factors influence species richness. Within areas with a uniform macroclimate, species richness is determined in particular by their habitat diversity. The diversity of habitats is in turn an expression of land use. Heavily cleared landscapes with large arable fields and few grassland-like habitats (Fig. 3) are significantly poorer in species than historical cul-

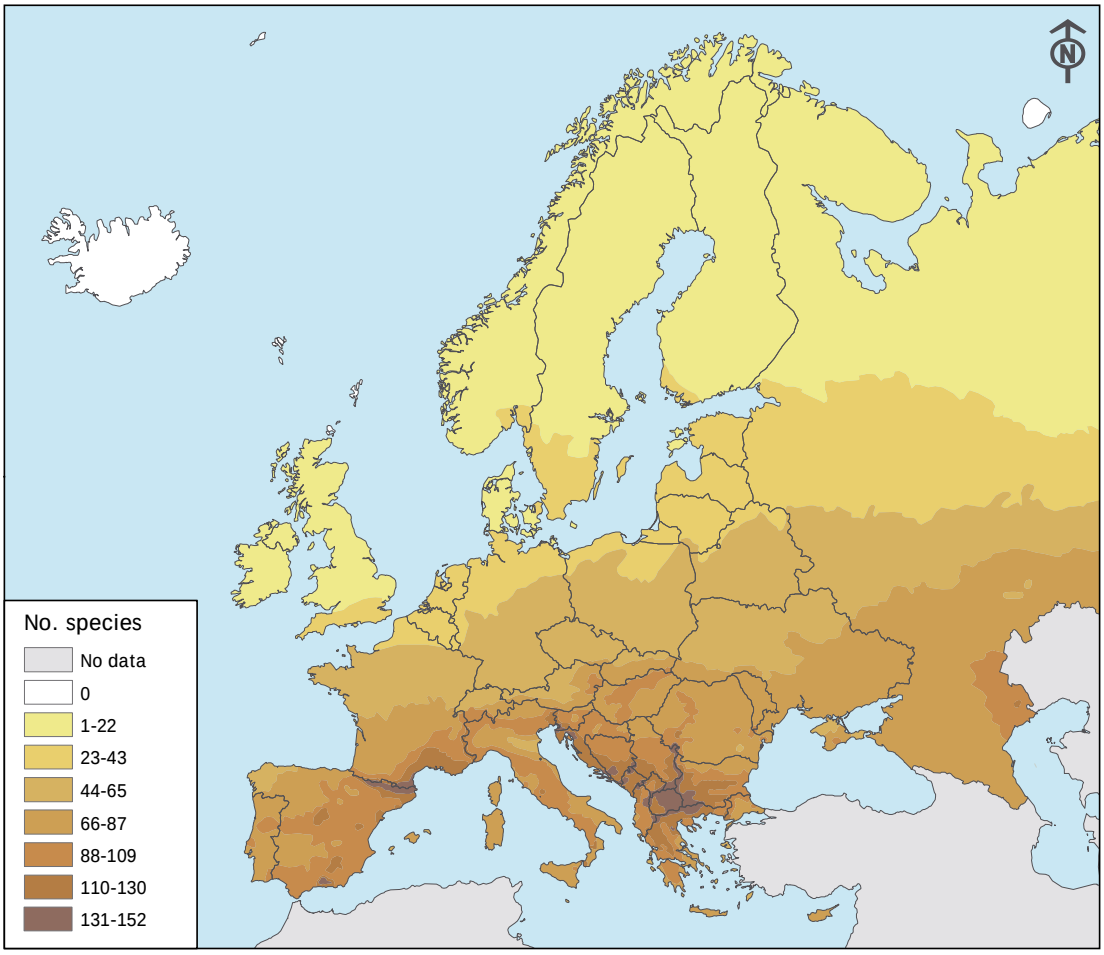


Fig. 1: Generalised illustration of grasshopper diversity in Europe. (Source: Hochkirch et al. 2016, modified)

Fig. 2: *Eumigus cucullatus* is endemic to the Iberian Peninsula. As in the whole of southern Europe, a particularly large number of grasshopper species can be found there. (Photo credit: Dominik Poniatowski)

tivated landscapes, which are characterised by a high number of small fields and numerous structural elements such as copses, fringes and hedges (Fig. 4). In addition to habitat type diversity, topography can also have a strong influence on species richness. Uplands often have higher species numbers than areas in the lowlands (Pauler et al. 2019, Löffler et al. 2023). This is due to the strong elevational and thus climatic gradient, which provides suitable living conditions for numerous species. In addition, the intensity of land use decreases with elevation in many mountainous regions (MacDonald et al. 2000, Hülber et al. 2020). The uneven relief, a harsh climate and the fact that some of the locations are difficult to access mean that intensive land use is often not possible here. Therefore, in the montane elevational zone, threatened biotope types such as heathlands, nutrient-poor grasslands and wet meadows still exist in many places; these biotopes serve as habitats for

Fig. 3: Intensively used agricultural landscape north of Warburg (North Rhine-Westphalia). (Photo credit: Felix Helbing)

Fig. 4: Heterogeneous cultural landscape in the Lower Diemel Valley (Hesse). (Photo credit: Dominik Poniatowski)

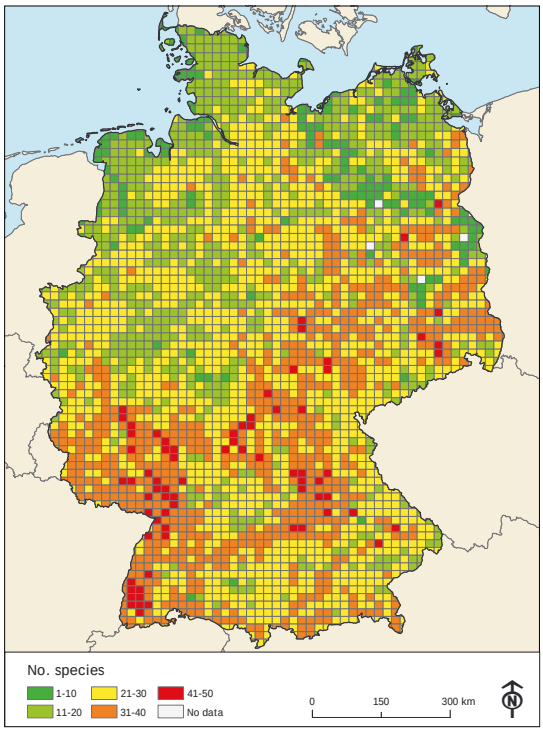


Fig. 5: Number of grasshopper species in Germany per 10 × 6 geographic minute grid cells (period: 1990 to 2023). (Source: author's own diagram)

numerous grasshopper species (Fischer et al. 2020, Fartmann et al. 2021a).

The diversity factors that apply at the European level, such as climate, landscape structure and topography, can also be witnessed in Germany. The warm summer regions of southern and eastern Germany, for example, are characterised by a particularly high species richness (Fig. 5). Among the centres of species diversity are the regional heat islands – in particular Kaiserstuhl, the Upper Rhine Valley, the Middle Rhine Valley, Main-Franconia, the Franconian Basin, Grabfeld and Kyffhäuser (Fig. 6). However, some heterogeneous low mountain ranges in southern Germany also have high species numbers. The southern part of the Black Forest as well as Swabian and Franconian Jura are particularly noteworthy. These areas are characterised by a high proportion of grassland of high nature conservation value (HNV farmland) (Fig. 7), from which numerous grasshopper species benefit.

The diversity of grasshopper species in Germany must also be seen in the context of the last ice age more than 10,000 years ago. At that time, the Fennoscandian ice sheet extended as far as the North German Lowlands. To the south of this was large-scale permafrost – i. e. permanently frozen ground. Its boundary ran roughly through southern France, along the Alps and from there eastwards through the Pannonian Basin to the northern edge of the Pontic region on the Black Sea (French 2018). The current distribution of species in Germany is therefore the result of immigration processes from various glacial refugial areas such as Anatolia and the Balkans as well as the coastal and southern areas of the Iberian and Italian peninsulas (Ingrisch & Köhler 1998, Hewitt 1999). In the course of recolonisation in Germany, various geographical barriers such as the Vosges in the west, the Alps in the south and the Bavarian and Bohemian Forests in the east had to be crossed, depending on the species. Detzel (1995) names five post-glacial immigration routes (Fig. 8):

1. Lorraine, the Moselle, Nahe and Main valleys,
2. the Burgundian Gate and the Rhine Valley,
3. the North German and Polish Plain,
4. the Moravian Gate and
5. the Danube Valley.

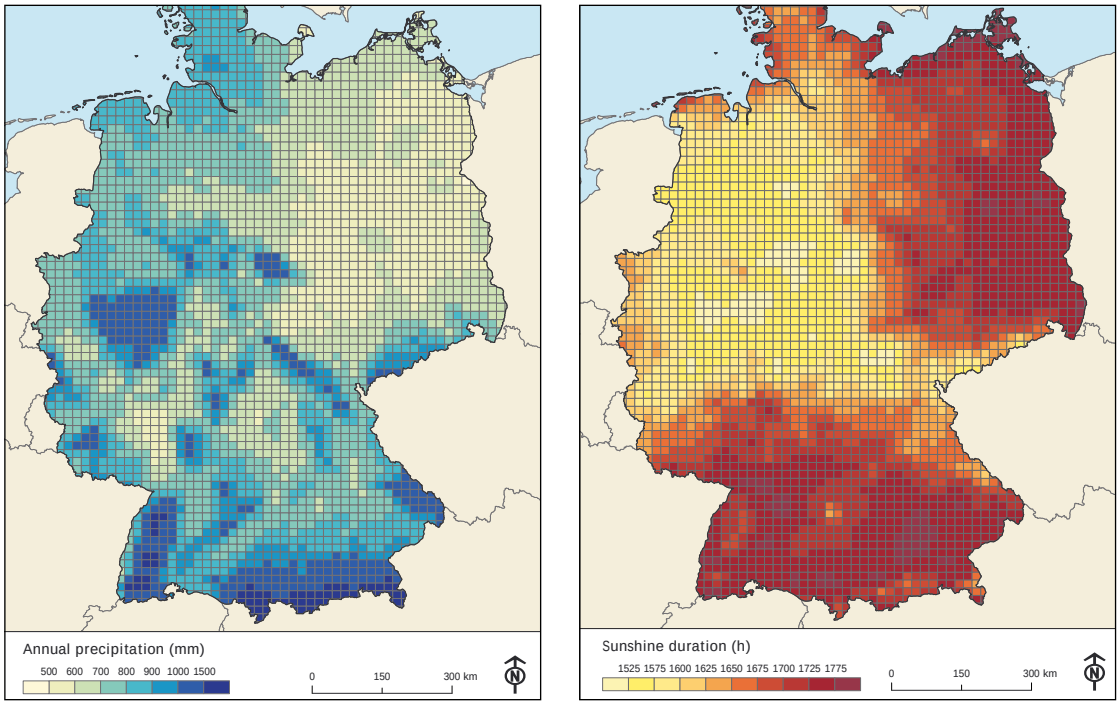
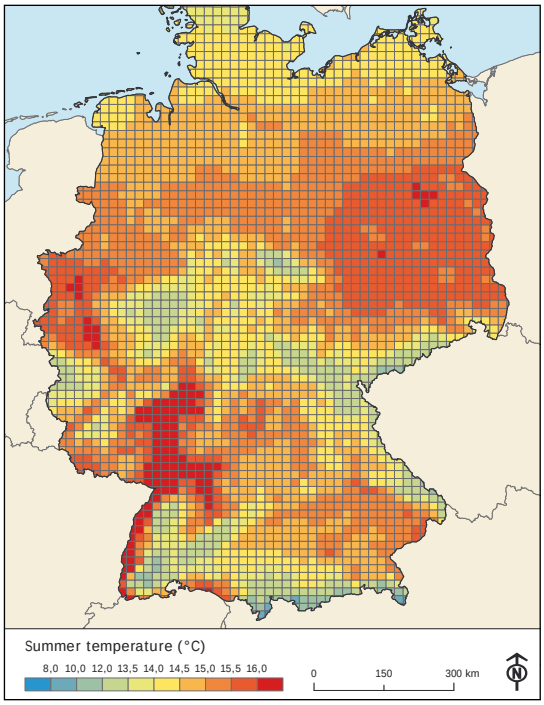


Fig. 6: Mean annual precipitation (left), hours of sunshine per year (right) and summer temperatures (April to September, top of page 17) in Germany (period: 1991 to 2020). (Data source: DWD 2024)

The natural landscape after the last ice age probably consisted of heterogeneous and sometimes very light woodlands, which were interspersed in large parts with open habitats of varying sizes (Feurdean et al. 2018). Various factors such as drought, fire, snowfall, windthrow and large wild ungulates such as Aurochs (*Bos primigenius*) and Wisent (*Bison bonasus*) probably contributed to keeping the landscape open (e. g. Svenning 2002). Locally, Beavers (*Castor fiber*) may also have been influential, regularly creating new open habitats through their activities in floodplains (Harthun 1999, Wells et al. 2000). In addition, various special sites such as bogs, coastal dunes, gravel banks, rocky knolls and screes were also free of wood (Ellenberg & Leuschner 2010). Some grasshopper species were able to recolonise Central Europe comparatively quickly. Hewitt (1990) assumes that the Meadow Grasshopper (*Pseudochorthippus parallelus*) reached Germany and subsequently the British Isles more than 8,000 years ago, i. e. at a time when there was still a land connection with mainland Europe (see also Hewitt 1999).

With the beginning of agriculture and livestock farming in Central Europe, the so-called Neolithic Revolution, around 6,000 to 5,000 years BC, the natural landscape was gradually transformed into a cultivated landscape (Poschlod 2017). This process promoted the dispersal of numerous species as it created new grasshopper habitats. Another important factor was migrating herds of domestic animals (Fischer et al. 1995, Bugla & Poschlod 2006), which already existed in the Neolithic (Poschlod 2017). The study by Fischer et al. (1996) shows that not only the diaspores of plants but also grasshopper individuals can be spread by sheep.

In the 14th and 15th centuries, transhumance experienced a strong upswing as large areas of fallow fields were available for grazing due to the late medieval deserted period. Sheep farming reached its peak towards the mid-19th century. At this time, there were over 25 million sheep in Germany (Poschlod 2017). The herds sometimes covered large distances on their migrations (Dolek & Geyer 2002). Transhumance can therefore be regarded as the most effective mobile biotope network in our cultural landscape (Fischer et al. 1995, Poschlod et



al. 1996). However, cheap wool from overseas led to a trend reversal in sheep farming towards the end of the 19th century, which caused the population to decrease to less than 10 million animals towards the beginning of the 20th century (Poschlod 2017). Around 1.5 million sheep are currently kept in Germany (Federal Statistical Office 2023).

The decline in sheep populations has not only led to a deterioration in habitat connectivity, but also to the loss of large areas of typical grasshopper habitats such as heathlands and nutrient-poor grasslands as a result of afforestation or succession (Poschlod 2017, Fartmann et al. 2021a). On nutrient-rich sites, on the other hand, land use has been heavily intensified – especially since the mid-20th century (Dierschke & Briemle 2002, Sturm et al. 2018). Both developments have led to the loss of many local grasshopper populations (Poniatowski et al. 2024a). Low-mobility habitat specialists in particular, whose populations are restricted to landscapes with a high proportion of grassland of high conservation value (high species-specific SFI, see also chapter Ecological indices, p. 33), have suffered severe population losses (Poniatowski et al. 2020). This applies, for example, to the Woodland Grasshopper (*Omocestus rufipes*), the Rattle Grasshopper (*Psophus stridulus*) and the Black-spotted Toothed Grasshopper (*Stenobothrus nigromaculatus*). All three species can now only be found scattered in Germany (pp. 154, 180 and 186).

Despite the deterioration in habitat availability, numerous grasshopper species have expanded their range northwards in Germany over the last 20 to 30 years – in line with the sharp rise in mean annual temperatures (IPCC 2023). Conspicuous new colonisations have been documented in particular for formerly summer-cool regions such as the Northwest German Lowland and the higher elevations of some low mountain ranges (e. g. Brose & Peschel 1998, Grein 2007, Löffler et al. 2019, Fartmann et al. 2021b). However, the extent of range expansion varies greatly from species to species and depends on various factors such as habitat specificity and species-specific mobility. In any case, it is significant that the expanding species generally have a high or even a very high STI (p. 33) and therefore prefer a warm macroclimate.

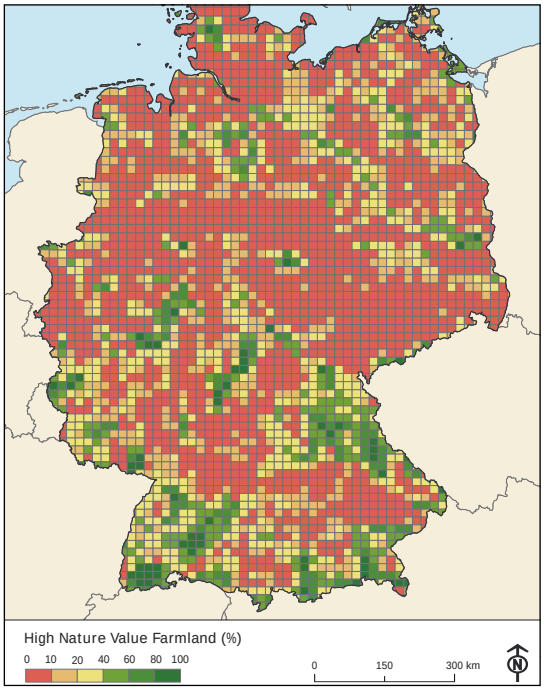


Fig. 7: Current proportion of High Nature Value farmland (HNV farmland = grassland of high nature conservation value in a broader sense) in the open landscapes of Germany. (Data source: EEA 2024)

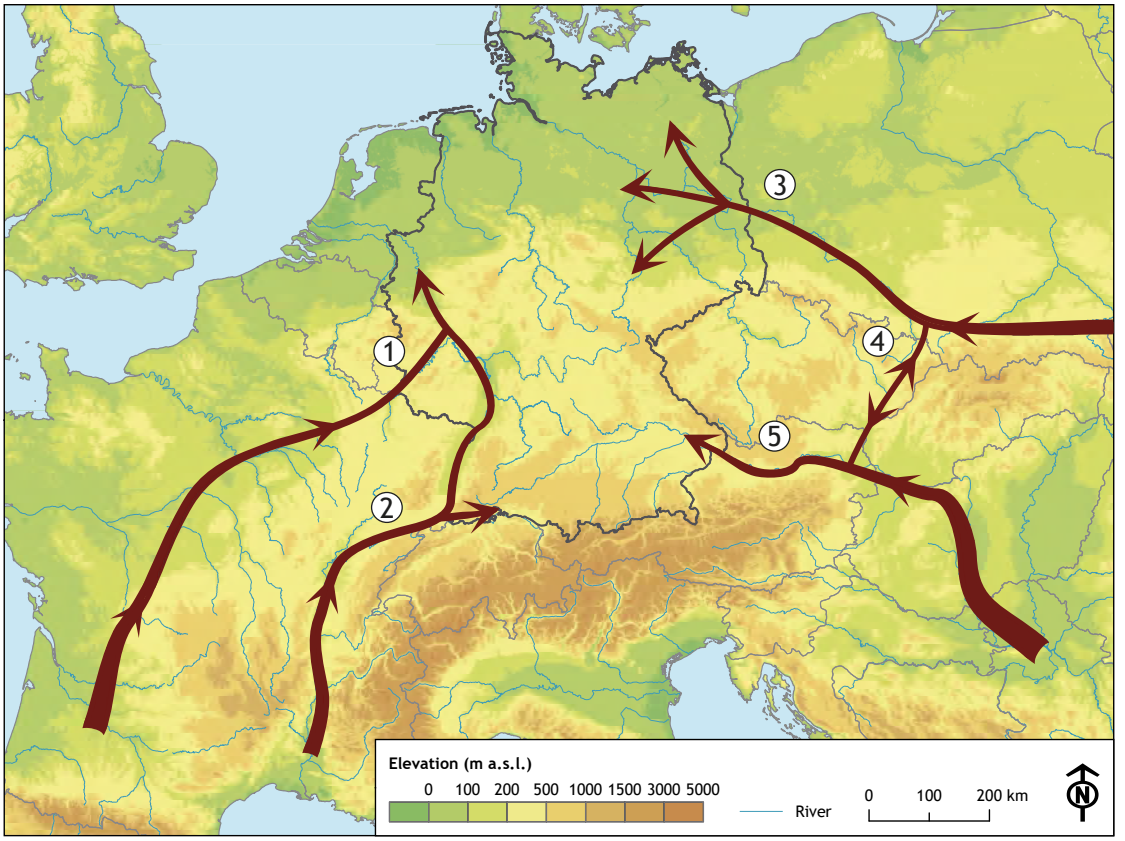


Fig. 8: Potential post-glacial migration routes of grasshopper species currently occurring in Germany (author's own diagram, based on Detzel [1995] and Hewitt [1999]): 1 – Moselle Valley, 2 – Burgundian Gate, 3 – North German and Polish Plain, 4 – Moravian Gate, 5 – Danube Valley.

Climate change is therefore largely responsible for this development (e. g. Trautner & Hermann 2008, Pfeifer 2012, Kettermann & Fartmann 2018). According to Poniatowski et al. (2018a), over 30 % of the native species currently benefit from climate change. Many of these are habitat generalists such as the Large Gold Grasshopper (*Chrysochraon dispar*), the Long-winged Conehead (*Conocephalus fuscus*) and Roesel's Bush-cricket (*Roeseliana roeselii*), which do comparatively well in intensively used cultivated landscapes (cf. Poniatowski et al. 2024a). Compared to earlier studies, however, it is now clear that both generalists and specialists have been able to disperse in recent years, provided they have a high degree of mobility (Poniatowski et al. 2018a, 2020). For example, the Blue-winged Sand Grasshopper (*Sphingonotus caerulans*), the Italian Locust (*Calliptamus italicus*) and the Large Marsh Grasshopper (*Stethophyma grossum*) are among the dispersing habitat specialists.

In some cases, passive dispersal of eggs, nymphs or adults has also contributed to the spread. Transportation by vehicles is well documented, for example, for the Southern Oak Bush-cricket (*Meconema meridionale*) (e. g. Köhler et al. 2022b, c). Other species are regularly transported with plants or potting soil – as is assumed, for example, for the Praying Mantis (*Mantis religiosa*) and the Southern Sickle Bush-cricket (*Phaneroptera nana*) (Aßmann & Ritt 2021, Beckerbauer et al. 2024, Hochkirch et al. 2023). There are also indications of anthropogenically induced occurrences for the Italian Cricket (*Oecanthus pellucens*) and the two species of Bush-crickets *Leptophyes albovittata* and *Leptophyes punctatissima* (Samu & Wischhof 2000, Sczepanski 2005, Pfeifer 2012, p. 118). In

addition, species such as the Blue-winged Grasshopper (*Oedipoda caerulescens*), the Blue-winged Sand Grasshopper (*Sphingonotus caerulans*) or the Bordeaux Cricket (*Eumodicogryllus bordigalensis*) can occasionally be dispersed by gravel or sand transportation (Köhler et al. 2001, Pfeuffer 2018, Brauner & Ristow 2022). Hydrochory – i. e. the drifting of plant material with corresponding developmental stages of grasshoppers along rivers or even the seashore – has been documented for the Striped Bush-cricket (*Leptophyes albovittata*), the Short-winged Conehead (*Conocephalus dorsalis*) and the Long-winged Conehead (*Conocephalus fuscus*), among others, and is also suspected for the Italian Cricket (Fartmann 2004, Wallaschek et al. 2004, Lehmann & Haacks 2006, Pfeifer et al. 2012).

Although many species are currently expanding their range, it should not be forgotten that the ongoing intensification of land use in open areas is leading to the loss of further grasshopper habitats (Finck et al. 2017). If habitat loss continues, at some point even the mobile species will no longer be able to cover the large distances between the remaining habitat islands (Hill et al. 1999, Buse & Griebeler 2011).

Population declines in the course of climate change are difficult to detect as they are less obvious than conspicuous new colonisations in well-studied areas at the edge of the range (Trautner & Hermann 2008, Pfeifer 2012). Nevertheless, regressive population and range developments are likely for some species. Poniatowski et al. (2018a) list six species whose populations may be negatively affected by climate change. One of these is the Green Mountain Grasshopper (*Miramella alpina*) – a glacial relict. Population losses of this species have been documented for the Black Forest and the neighbouring Vosges Mountains, among other sites (e. g. Hafner & Zimmermann 2019, Fumy et al. 2020, d'Agostino & Vacher 2021, p. 148). It is currently unclear whether other species belong to the group of 'climate change losers.' In general, however, it can be stated that climate change poses a particular threat to grasshopper species in humid-wet or boreal-montane habitats (Rabitsch et al. 2011, Streitberger et al. 2016a, b, Poniatowski et al. 2018a).

Habitats

DOMINIK PONIATOWSKI & THOMAS FARTMANN

Grasshoppers occur in almost all terrestrial habitats (Fischer et al. 2020). By far the most important habitat type for grasshoppers are nutrient-poor dry grasslands (Dolek 1994, Zehm 1997, Löffler et al. 2019, Köhler et al. 2023a). Across Germany, they provide a habitat for almost 70 % of all native grasshopper species (Fig. 9). Dry grasslands include, among others, calcareous, sandy and acidic grasslands as well as steppe grasslands (Fig. 10–14). They are located on marginal sites – i. e. areas that are very unproductive due to their steep slopes and/or nutrient-poor soils, for example, and are therefore only used with low intensity. Such habitats are often characterised by a mosaic of low and tall-growing vegetation as well as patches of bare ground, stones and shrubs (Fig. 15). Occasionally, rocks are also part of the habitat. This high structural diversity results in a high number of species (Zehm 1997, Hemp & Hemp 2000, Löffler & Fartmann 2017). Other important habitats are mesic and wet grasslands as well as heathlands and tall herbaceous fringes (Fig. 16).

To a certain extent, this also applies to moorlands (Fig. 9). Grazed fens and transition mires in particu-

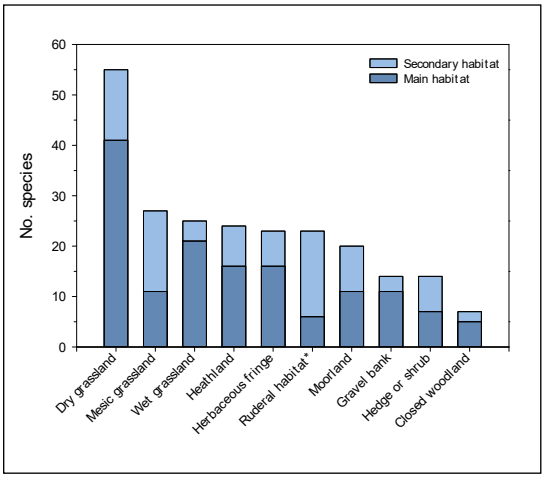


Fig. 9: Total species numbers for the most important grasshopper habitats in Germany. (Data source: Fischer et al. 2020). Secondary habitat = species occurs occasionally in this habitat type; however, it does not have its main focus here; main habitat = species occurs mainly in this habitat type; *collective term for extraction sites, industrial wasteland, post-mining landscapes, railway tracks and spoil heaps.

Fig. 10: Dry grassland on gypsum rock in the Schloßberg-Solwiesen Nature Reserve (Thuringia: Kyffhäuser; 180 m a. s. l.). Occurring species: e. g. *Mantis religiosa*, *Oecanthus pellucens*, *Stenobothrus crassipes* and *S. nigromaculatus*. (Photo credit: Dominik Poniatowski)

Fig. 11: Subcontinental sandy dry grassland in the Müllerberge Nature Reserve (Brandenburg: Uckermark; 60 m a. s. l.). Occurring species: e. g. *Bicolorana bicolor*, *Chorthippus apricarius*, *C. mollis*, *Myrmeleotettix maculatus*, *Oedipoda caerulescens* and *Omocestus haemorrhoidalis*. (Photo credit: Thomas Fartmann)

Fig. 12: Calcareous grasslands on the Stiegelesfelsen (Baden-Württemberg: Upper Danube Valley; 640 m a. s. l.). Occurring species: e. g. *Euthystira brachyptera*, *Gomphocerippus rufus*, *Platycleis albopunctata* and *Tetrix bipunctata*. (Photo credit: Dominik Poniatowski)

Fig. 13: Acidic grassland with Common Broom (*Cytisus scoparius*) near Medelon (North Rhine-Westphalia: Medebach Bay; 420 m a. s. l.). Occurring species: e. g. *Chorthippus biguttulus*, *Omocestus viridulus*, *Pseudochorthippus parallelus* and *Stenobothrus stigmaticus*. (Photo credit: Dominik Poniatowski)

Fig. 14: Heterogeneous pasture with Winged Broom (*Genista sagittalis*) in the Upper Hotzenwald (Baden-Württemberg: Black Forest; 875 m a. s. l.). Occurring species: e. g. *Decticus verrucivorus*, *Omocestus rufipes*, *Psophus stridulus* and *Stauroderus scalaris*. (Photo credit: Thomas Fartmann)

Fig. 15: Heterogeneous sandy dry grassland in the Tennenloher Forst Nature Reserve (Bavaria: Franconian Basin; 314 m a. s. l.). The area is grazed by Przewalski's horses and provides a habitat for numerous grasshopper species. (Photo credit: Dominik Poniatowski)

lar can harbour species-rich grasshopper assemblages (Dolek et al. 1999, Bamann 2018, Schwarz & Fartmann 2022) (Fig. 17). Gravel banks are also considered valuable grasshopper habitats (Lemke et al. 2010, Pfeuffer 2015, 2020) (Fig. 18). Although species numbers are low in these sparsely vegetated sites, some highly specialised and therefore highly endangered species such as the Speckled Buzzing Grasshopper (*Bryodemella tuberculata*), the Gravel Grasshopper (*Chorthippus pullus*) and the Alpine Groundhopper (*Tetrix tuerki*) occur there (Poniatowski et al. 2024a). Scrubs and closed forests, on the other hand, are less important for grasshoppers as they only serve as the main habitat for a few species. The situation is different with light woodlands such as coppice woodland and wood pastures, which have a lush herb layer or are characterised by numerous grassland-like clearings. Many typical species of open habitats can also occur in such forests (Helbing et al. 2014a, Rösch et al. 2019, Liebelt 2021) (Fig. 19 and 20). Ruderalised or heavily anthropogenically modified habitats such as extraction sites, industrial wasteland, post-mining landscapes, railway tracks and spoil heaps have a special status (Fig. 21). They can be valuable secondary habitats, especially in urban areas or in regions used intensively for agriculture (Hamann & Weber 2012, Eckert et al. 2017, Kettermann & Fartmann 2018, Pfeuffer 2018).

Fig. 16: Mesic to moist mountain grassland in the Long Rhön (Bavaria: Rhön Mountains; 750 m a. s. l.). Occurring species: e. g. *Chorthippus biguttulus*, *Omocestus viridulus*, *Pseudochorthippus parallelus* and *Tettigonia cantans*.
(Photo credit: Thomas Fartmann)

Fig. 17: Litter meadow with Siberian Iris (*Iris sibirica*) in the Murnauer Moos (Bavaria: Pre-Alpine Hills and Moorland; 650 m a. s. l.). Occurring species: e. g. *Metrioptera brachyptera*, *Pseudochorthippus montanus*, *Pteronemobius heydenii* and *Stethophyma grossum*.
(Photo credit: Thomas Fartmann)

Fig. 18: Dolomite alluvial fan of the Friedergries (Bavaria: Ammergau Alps; 920 m a. s. l.). Occurring species: e. g. *Bryodemella tuberculata*, *Chorthippus pullus* and *Psophus stridulus*.
(Photo credit: Thomas Fartmann)

Fig. 19: Historic cattle pasture with flowing transitions between open woodland, sandy dry grassland and heathland in the Borkener Paradies Nature Reserve (Lower Saxony: Emsland; 10 m a. s. l.). Occurring species: e. g. *Chorthippus biguttulus* and *Stenobothrus stigmaticus*. (Photo credit: Thomas Fartmann)

Fig. 20: Coppice with standards with a lush herb layer near Bad Kissingen (Bavaria: Main-Franconia; 350 m a. s. l.). Occurring species: e. g. *Gomphocerippus rufus*, *Leptophyes punctatissima*, *Meconema thalassinum*, *Nemobius sylvestris* and *Pholidoptera griseoaptera*. (Photo credit: Dominik Poniatowski)

Fig. 21: Spoil heap of Mottbruch in Gladbeck-Brauck (North Rhine-Westphalia: Ruhr Area; 115 m a. s. l.). Occurring species: e. g. *Chorthippus brunneus*, *Oedipoda caerulescens*, *Sphingonotus caerulans* and *Tettigonia viridissima*.
(Photo credit: Felix Helbing)

Grasshoppers reach high population densities (abundances) especially in grassland-like habitats (Fartmann et al. 2024). At the top of the list is wet grassland with an average of 25.8 individuals per 10 m^2 (Fig. 22). However, other grassland types such as acidic, calcareous and mesic grassland have similarly high abundances (Ø 20.3 to 22.3 individuals per 10 m^2). Tussock grasslands occupy an intermediary position with 12.1 individuals per 10 m^2. In other habitat types, the population densities are significantly lower. Heathlands, moorland and light woodland can be listed here in decreasing order.

Habitat requirements can vary greatly from species to species. Two types can be roughly distinguished: habitat generalists (eurytopic species) and habitat specialists (stenotopic species) (see also chapter Ecological indices). While the generalists are relatively undemanding in their choice of habitat, the specialists are restricted to a few habitats. Whether a species can develop and reproduce in a habitat is determined by several environmental factors. A distinction can be made between two spatial levels, which, taken together, determine a species' choice of habitat:

Landscape level: grasshoppers are cold-blooded organisms. Their occurrence at the landscape level is therefore strongly determined by the macroclimate (see also chapter Distribution). In addition to the macroclimate, the habitat size and connectivity of the habitat can also influence the occurrence of a species (Appelt & Poethke 1997, Carlsson & Kindvall 2001). Habitat specialists are particularly affected by this, as their habitats are often very isolated in a landscape that is otherwise unsuitable for them. The Speckled Buzzing Grasshopper (*Bryodemella tuberculata*), for example, depends on a well-connected network of these so-called habitat islands as it can only exist in the long term through a regular exchange of individuals with neighbouring populations (Stelter et al. 1997, Reich 2006, p. 160). By contrast, there are a number of less mobile species such as the Heath Grasshopper (*Chorthippus vagans*) or the Bog Bush-cricket (*Metrioptera brachyptera*) that can survive for long periods in highly isolated habitats without exchange. However, this is only possible if the requirements at the habitat level are continuously fulfilled and the habitat sizes are large enough to provide sufficient space for stable populations in the long term.

Habitat level: habitat specificity at the habitat level depends on a complex of factors that is dominated by the influence of the microclimate (Gardiner & Dover 2008, König et al. 2024). For successful development and reproduction, the temperature and moisture requirements of all developmental stages (eggs, nymphs and adults) must be achieved (Ingrisch 1978a, b, 1979a, 1983a, b, 1988). The egg is of particular importance here as it is the most sensitive stage. In contrast to the nymphs and adults, it cannot react to changing environmental conditions by changing location. The females therefore lay their eggs in places that meet the climatic requirements of the eggs – even under fluctuating environmental conditions (Ingrisch & Boekholt 1983). The degree of specialisation depends primarily on the drought resistance and/or the temperature requirements of the eggs (Ingrisch 1979a, 1983a, 1988). For example, the eggs of the Marsh Grasshopper (*Pseudochorthippus montanus*) are very sensitive to desiccation (Ingrisch 1983a). The species can

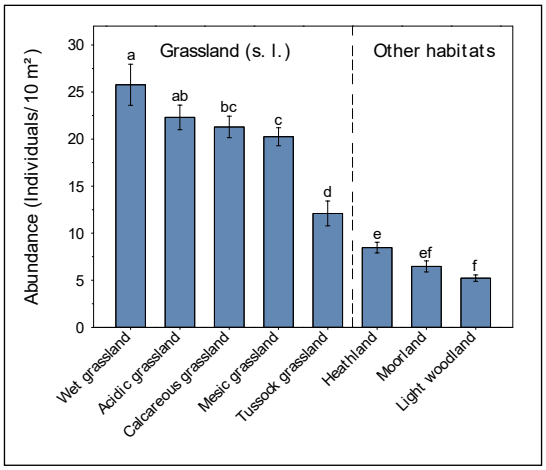


Fig. 22: Mean population density (± SE) of all grasshopper species in July/August differentiated in eight intensively sampled habitat types in Germany (*N* = 2,419 sample plots) (Fartmann et al. 2024, modified). Tussock grassland = initial psammophitic communities (*Koelerion glaucae* and *Spergulo-Corynephoretum*), moorland = transition mires and raised bogs. Different letters indicate significant differences between the habitat types ($P < 0.05$).

therefore only occur in moist and wet grasslands with an intact water balance (p. 220).

The vegetation structure is also of great importance for the occurrence or absence of species (Hemp & Hemp 2000, Jerrentrup et al. 2014, Kenyeres et al. 2024). In addition to its influence on the microclimate, it represents the structured space to which the species must be adapted in terms of shape, coloration and behaviour (Sänger 1977, Fartmann 1997a, Zehm 1997) (Fig. 23). According to Ingrisch & Köhler (1998), two types of behaviour can be roughly distinguished: the ground-dwelling species generally colonise open, sparsely vegetated habitats. Accordingly, they are mostly grey-brown in colour. Examples of this group would be the Blue-winged Grasshopper (*Oedipoda caerulescens*) (Fig. 24), the Mottled Grasshopper (*Myrmeleotettix maculatus*) or the Long-horned Groundhopper (*Tetrix tenuicornis*). The species living in the vegetation, on the other hand, often have a green or green-brown base colour. Three subtypes can be distinguished in this group. While the horizontally oriented species such as the Common Dark Bush-cricket (*Pholidoptera griseoaptera*) (Fig. 25) like to stay on broad leaves, the so-called long grass dwellers such as the Long-winged Conehead (*Conocephalus fuscus*) (Fig. 26) are vertically oriented species. There is also an intermediate behavioural type – i. e. species that live both on leaves and on stems. This group includes the Green Mountain Grasshopper (*Miramella alpina*) (Fig. 27) and the Rufous Grasshopper (*Gomphocerippus rufus*).

The microclimatic and structural requirements of the species are mostly linked to the influence of the habitat management (Fartmann & Mattes 1997). For example, land use has an effect on the vegetation structure and thus indirectly on the microclimate. In long-term fallows, for example, numerous species fail because the dense vegetation and litter accumulation only allow the topsoil to warm up slowly. Most species are therefore dependent on at least sporadic mowing or grazing of their habitats (Fumy & Fartmann 2023). However, if the land-use intensity is too high, the negative effects predominate (Poniatowski et al. 2024a, b). Meadows that

Fig. 23: Species-rich salt marsh (left) on the island Usedom (Mecklenburg-Western Pomerania) as an example of a dense and tall-growing habitat and tussock grassland (right) in a sand pit near Bremen (Lower Saxony) as an example of a sparsely vegetated habitat. (Photo credits: Dominik Poniatowski)

Fig. 24: The Blue-winged Grasshopper (*Oedipoda caerulescens*) is a geophilic species whose coloration is perfectly adapted to the nature of stony or sandy habitats.
(Photo credit: Dominik Poniatowski)

Fig. 25: The Common Dark Bush-cricket (*Pholidoptera griseoaptera*) – here a reddish coloured male – likes to stay on large leaves in fringes, hedges and shrubs.
(Photo credit: Dominik Poniatowski)

Fig. 26: The Long-winged Conehead (*Conocephalus fuscus*) is considered a vertically oriented species. It can therefore mainly be found in tall-growing habitats such as stands of rushes (*Juncus* spp.), sedges (*Carex* spp.) and Wood Small-reed (*Calamagrostis epigejos*). (Photo credit: Thomas Fartmann)

Fig. 27: The Green Mountain Grasshopper (*Miramella alpina*) is a phytophilous species. It requires a heterogeneous herb layer.
(Photo credit: Dominik Poniatowski)

are mowed early and often as well as heavily grazed areas lack tall-growing structures that are essential for some species – for example as a shelter, stridulation platform or oviposition substrate (Kruess & Tscharntke 2002, Fumy et al. 2023). In addition, intensive meadow use causes very high losses due to mowing and the discharge of eggs from plant-laying species (Schwarz et al. 2023, Schoof et al. 2024). On pastures with high stocking densities, the consumption of egg clutches and cattle trampling – especially under cold and wet weather – can lead to high losses (Fartmann & Mattes 1997). In combination with the influences on the vegetation structure, intensively used meadows and pastures are therefore not a suitable habitat for the majority of species living in open land (Poniatowski et al. 2024a). There are also a number of other factors that can influence the occurrence or absence of species. For example, the food supply can become a limiting factor in open, sparsely vegetated habitats.

Land-use and climate change

THOMAS FARTMANN, FELIX HELBING, FRANZ LÖFFLER & DOMINIK PONIATOWSKI

In this chapter, we introduce the general drivers of biodiversity changes. Subsequently, we explain how land-use and climate change affect the grasshopper fauna in Germany. In detail, we do this by presenting case studies.

Drivers of biodiversity change

The recent biodiversity crisis is among the most serious problems of our age (Rockström et al. 2009, Butchart et al. 2010, Naeem et al. 2012). Current species extinction rates are 10 to 100 times higher than the average of the last ten million years (Díaz et al. 2019). For terrestrial habitats, land-use change is considered the main driver of species decline (Newbold et al. 2015, Díaz et al. 2019, Cardoso et al. 2020). For a long time, natural dynamics and traditional land use have created and maintained species-rich grasshopper habitats (Bonari et al. 2017, Feurdean et al. 2018, Fartmann 2024; see also chapter Habitats). However, with increasing industrialisation of land use since the beginning of the 19th century and particularly after World War II, the area of grasshopper habitats has dramatically decreased and hence the remaining patches are today often highly fragmented (Poniatowski et al. 2024a). Mainly two large-scale processes have been responsible for this, namely: (i) intensification of land use on the one hand and (ii) abandonment and afforestation on the other hand (Squires et al. 2018, Prangel et al. 2023, Fartmann 2024). Land-use intensification has mainly occurred in the lowlands (Löffler et al. 2023), but is now also becoming increasingly relevant in the uplands (Fumy et al. 2021). By contrast, marginal soils have strongly been affected by abandonment and afforestation (MacDonald et al. 2000, Fumy et al. 2021, Prangel et al. 2023). This has especially been true for wet soils that can hardly be drained or mountain ranges with a varied relief that do not allow for intensive agriculture. Today, the remaining habitat patches are mostly embedded in a hostile matrix, which often consists of intensively used agricultural land (e. g. arable fields or improved grassland) (Öckinger et al. 2012, Poniatowski et al. 2018a). Additionally, many habitat remnants only exhibit a low habitat quality due to inappropriate land-use, eutrophication as a result of airborne nitrogen deposition or climate change (Marini et al. 2009, Fumy et al. 2021, Harvey et al. 2023, Vogels et al. 2023).

Key drivers of survival in fragmented landscapes

Habitat quality, size and connectivity are considered the main drivers of patch occupancy of insects in general and grasshoppers in particular in fragmented landscapes (Fartmann 2024; Fig. 28). Usually, habitat quality is the most decisive one among these predictors. However, species traits (e. g. habitat specificity or mobility) and landscape configuration (i. e. the spatial distribution, size and abundance of habitat patches) affect the relative importance of each of the three key drivers (Öckinger et al. 2010, Löffler & Fartmann 2017, Poniatowski et al. 2018a, Fartmann 2024). The majority of the native grasshopper species has a low mobility (see chapter Ecological indices) and builds closed populations (Poniatowski & Fartmann 2010, Poniatowski et al. 2018a). These species are able to survive in isolated habitat patches, as long as the habitat quality is permanently sufficient and the patch is large enough to harbour a long-term viable population of the species (Fartmann 2024). For an expansion in response to climate change and the colonisation of vacant or newly created habitat patches, however, these species also depend on a high habitat connectivity. By contrast, there are also some mobile grasshopper species that form metapopulations (see chapter Habitats) and necessarily require a network of high-quality habitats of sufficient size in spatial proximity.

Among the parameters that define habitat quality, the heterogeneity of a habitat has the strongest impact on species richness of grasshoppers (Löffler & Fartmann 2017). A high habitat heterogeneity fosters species richness in three different ways (Fartmann 2024):

For many grasshopper species, structurally diverse habitats are mandatory since they undergo microhabitat shifts during their ontogenetic development. A typical example is the Common Wart-biter (*Decticus verrucivorus*) (Fig. 29) (Cherrill & Brown 1992, Schuhmacher & Fartmann 2003a, p. 90): the species requires bare soil for

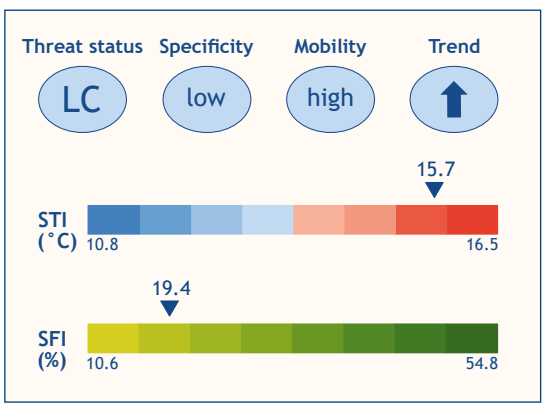
Species Profiles of Grasshoppers and Praying Mantises in Germany

A mosaic of open and scrubby dry grasslands ranks among the typical habitats of Praying Mantis (*Mantis religiosa*) at the southern Upper Rhine Valley (Baden-Württemberg: Kaiserstuhl).
(Photo credit: Dominik Poniatowski)

Female Praying Mantis (*Mantis religiosa*).
(Photo credit: Dominik Poniatowski)

Praying Mantis – *Mantis religiosa* (Linnaeus, 1758)

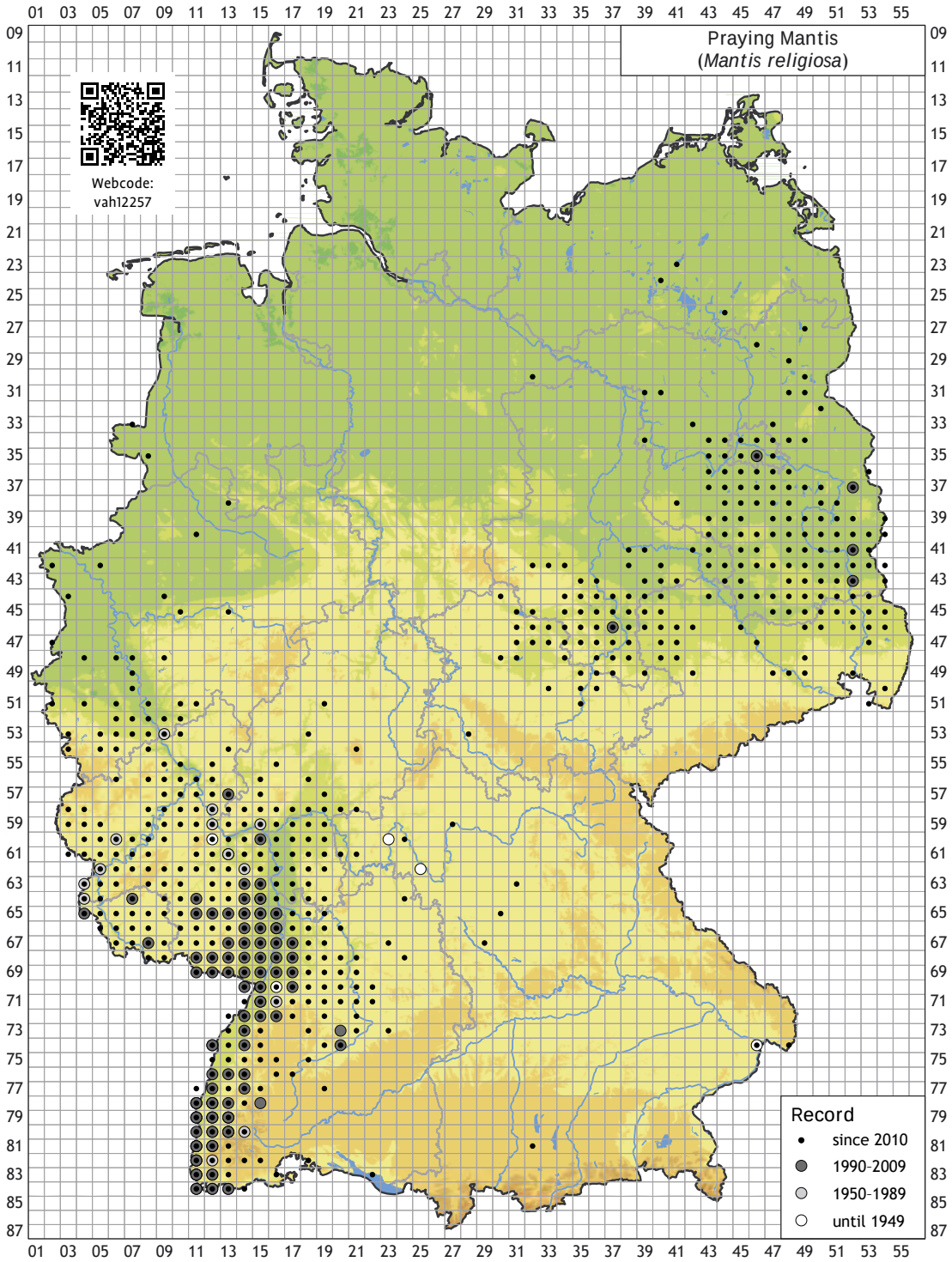
Distribution In Germany, the Praying Mantis was originally almost completely restricted to the southern Upper Rhine Valley, which is characterised by extraordinarily warm summers. Additionally, there were historic records from adjacent regions: the northern Upper Rhine Valley, the Middle Rhine and Moselle Valley, Main-Franconia as well as the Danube Valley near Passau. Originating from the southern Upper Rhine Valley, the species has, particularly since the 2003 heat wave, expanded its range northwards and to warm zones of the Southwestern and Western Uplands. Moreover, a second stronghold has been established, stretching from the Thuringian Basin to the southern part of the Northeast German Lowland, which is also characterised by warm summers. Besides active dispersal, passive dispersal and release of individuals have contributed to the range expansion. The strong dependence of the Praying Mantis on warm summers is reflected by an STI of 15.7 °C.



Habitat In former times, at the southern Upper Rhine Valley, the Praying Mantis inhabited calcareous and sandy grasslands, dry ruderal habitats as well as vineyard fallows and slopes. However, due to climate change, the species has broadened the range of colonised habitats to now include gardens, orchards and former mining areas or quarries. In the course of the development from egg to adult, the species undergoes a microhabitat shift: the oothecae are deposited in short, sparsely vegetated sunny swards; young nymphs also live there. By contrast, older, larger nymphs and particularly adults mainly colonise tall, dense structures.

Population trend and threats Climate change has resulted in a positive population trend and a strong range expansion of the Praying Mantis in Germany. Accordingly, the species is considered of least concern.

STEFAN STÜBING

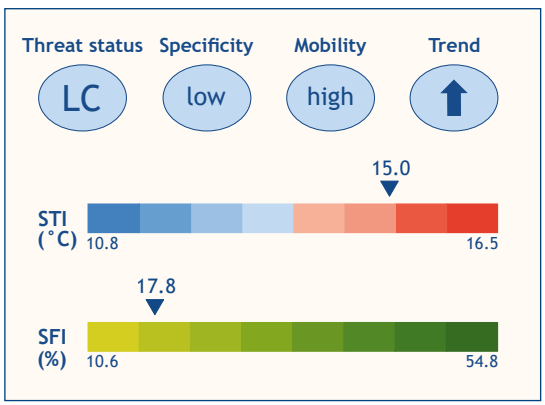

Praying Mantis
(Mantis religiosa)
Webcode:
vah12257
Record
since 2010
1990-2009
1950-1989
until 1949

Abandoned semi-dry grasslands are typical habitats of the Common Sickle Bush-cricket (*Phaneroptera falcata*) (Baden-Württemberg: Upper Danube Valley).
(Photo credit: Dominik Poniatowski)

Female Common Sickle Bush-cricket (*Phaneroptera falcata*).
(Photo credit: Thomas Fartmann)

Common Sickle Bush-cricket – *Phaneroptera falcata* (Poda, 1761)

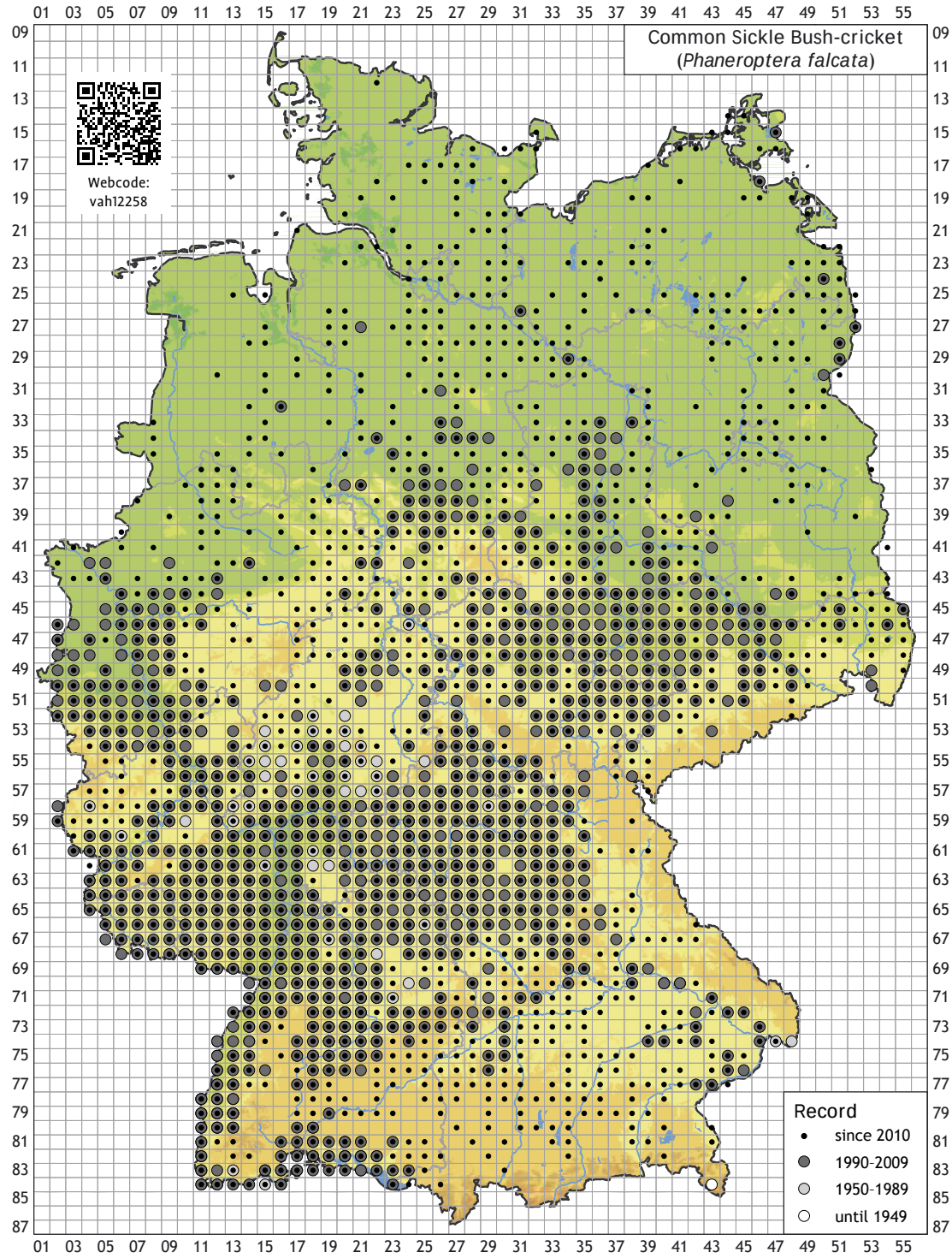
Distribution The Common Sickle Bush-cricket ranks among the more thermophilic grasshopper species in Germany; its STI is 15.0°C. For a long time, it was restricted to those regions that are characterised by the warmest summers: strongholds were the lower elevations of the Southwestern and Western Uplands as well as the Cologne Bay, Lake Constance region, Thuringian Basin and parts of the Leipzig Bay. However, since the 1990s, the species has strongly expanded its range due to climate change. The Common Sickle Bush-cricket is still absent solely in the coolest regions, particularly the most oceanic northwest of Germany, and the higher elevations of the low mountain ranges and Alps.



Habitat The Common Sickle Bush-cricket prefers open and semi-open habitats characterised by no land use or a low land-use intensity. Consequently, fringes, abandoned grasslands or shrubby semi-dry grasslands rank among the typical habitats. Within settlements, the species also occurs in urban brownfields. Moreover, in warm regions, wetlands are colonised by the Common Sickle Bush-cricket. Characteristic components of the strongly vertically structured habitats are usually stands of tall forbs and grasses with some admixed shrubs.

Population trend and threats The Common Sickle Bush-cricket is considered of least concern in Germany. Due to its long wings, it is capable of flight and highly mobile. Consequently, the species is regularly be found far away from known populations. As a profiteer of climate change, the Common Sickle Bush-cricket will further expand its range. By contrast, local population losses as a result of reintroduction of management or habitat destruction have so far not affected the overall positive population trend.

ANDREAS KRONSHAGE


Common Sickle Bush-cricket
(Phaneroptera falcata)
Webcode:
vah12258
Record
since 2010
1990-2009
1950-1989
until 1949

Woody plants in settlements are currently the main habitat of the Southern Sickle Bush-cricket (Rhineland-Palatinate: northern Upper Rhine Valley).
(Photo credit: Manfred Alban Pfeifer)

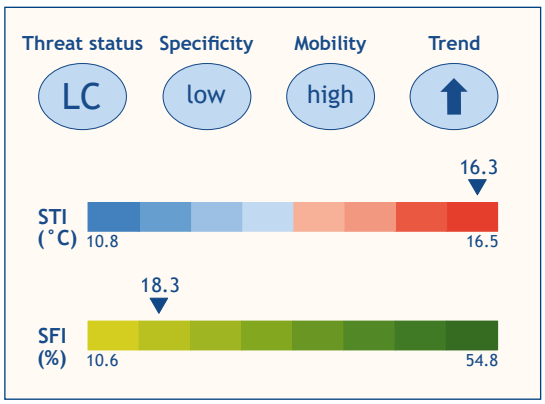
Female Southern Sickle Bush-cricket (*Phaneroptera nana*).
(Photo credit: Jürgen Fischer)

Southern Sickle Bush-cricket – *Phaneroptera nana*

Fieber, 1853

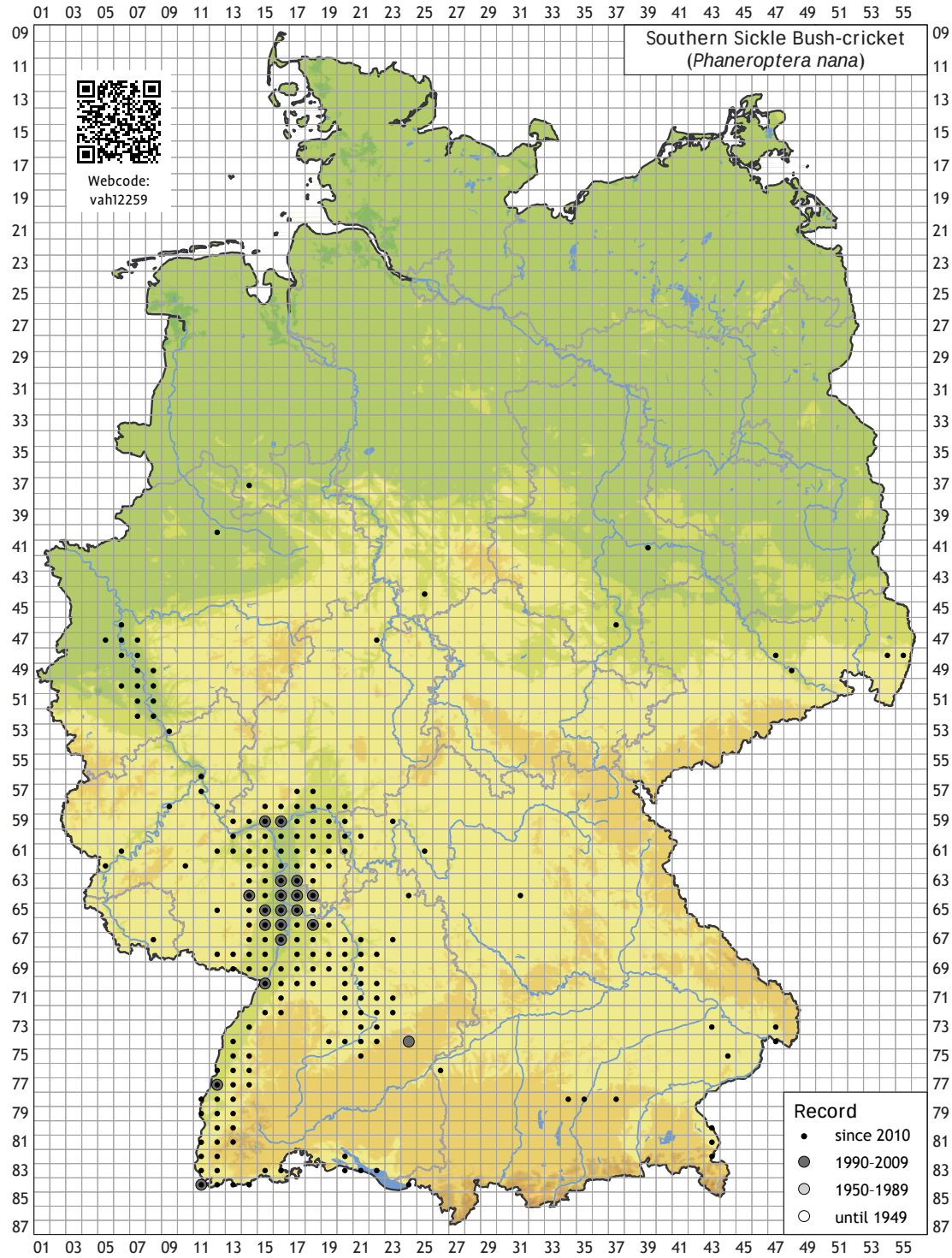
Distribution The Pontic-Mediterranean and very thermophilic (STI: 16.3 °C) Southern Sickle Bush-cricket was first recorded in Germany in 2003 in the Upper Rhine Valley north of Basel. Since then, the species has expanded its range northwards. This has especially been the case along the very warm Rhine Valley up to the Cologne Bay. The Southern Sickle Bush-cricket recently arrived in Bavaria from the southeast and is now spreading to the north. Additionally, the species has been observed far away from these two dispersal corridors, partly also further north.

Habitat The Southern Sickle Bush-cricket exhibits a strong dependence on woody plants, whether evergreen or deciduous. Since urban areas are heat islands and woody plants are common there, such areas have been the strongholds of the species within the already very warm Rhine Valley. However, an expansion is currently taking place from the settlements to the wider countryside, for example, to the southern Palatinate Forest. Characteristic habitats of the Southern Sickle Bush-cricket in urban areas and their suburbs are gardens, hedges, industrial brownfields, market gardens, parks and tree nurseries. In the surrounding landscape, the species occurs in orchards as well as in shrubby dry grasslands and vineyards.



Population trend and threats The Southern Sickle Bush-cricket is highly capable of flight. Hence, due to climate-change driven temperature increases, it is actively expanding its range in Germany northwards and also to higher elevations. Moreover, passive dispersal through plant material from market gardens and tree nurseries is very likely also contributing to the colonisation of new areas.

MANFRED ALBAN PFEIFER

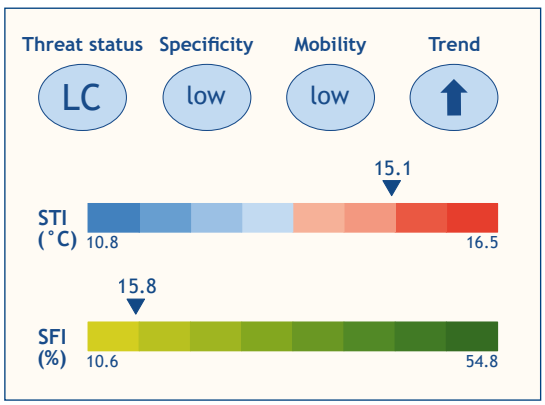

Southern Sickle Bush-cricket
(Phaneroptera nana)
Webcode:
vah12259
Record
since 2010
1990-2009
1950-1989
until 1949

Sunny hedges and adjacent fringes in semi-dry calcareous grasslands are typical habitats of the Speckled Bush-cricket (Baden-Württemberg: Kaiserstuhl). (Photo credit: Marcel Kettermann)

Male Speckled Bush-cricket (*Leptophyes punctatissima*). (Photo credit: Jürgen Fischer)

Speckled Bush-cricket – *Leptophyes punctatissima* (Bosc, 1792)

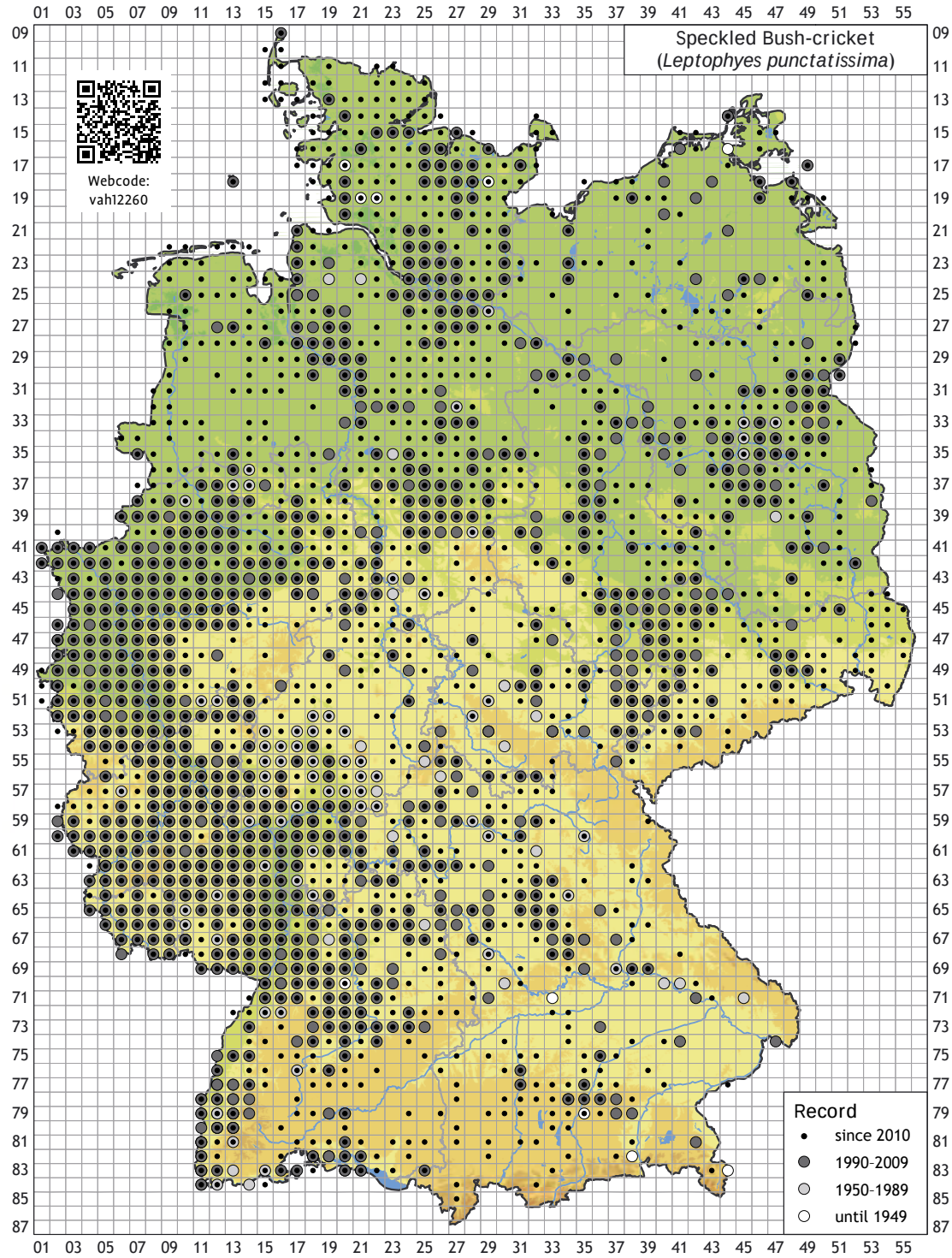
Distribution The strongholds of the Speckled Bush-cricket in Germany have always been the warm lowlands and urban agglomerations, which exhibit a warmer climate than the surrounding landscapes. The species' dependence on a warm climate is reflected by an above average STI of 15.1 °C. Since the 1990s, the Speckled Bush-cricket has strongly expanded its range and now also increasingly colonises the coastal regions, higher elevations of the low mountain ranges and even the Alps. The expansion of the flightless species has mainly been the result of passive dispersal of eggs, nymphs or adults (e. g. by woody plants from garden centres) by humans. Due to climate change, these individuals have been able to build viable populations at the new, formerly climatically unsuitable locations.



Habitat Due to the pronounced small-scale habitat shift, the Speckled Bush-cricket is characteristic of ecotones. For oviposition, woody plants with soft or cracked bark are used. By contrast, nymphs develop in the adjacent herbaceous vegetation close to the ground. The adults can later again be found in the woody plants. Accordingly, typical habitats of the Speckled Bush-cricket are sunny clear-cuts, dry grasslands, ruderal habitats and stands of tall forbs with some woody plants or forest edges and orchards. Urban areas, cemeteries, gardens and parks are also among the typical habitats.

Population trend and threats Both the long- and short-term population trends of the Speckled Bush-cricket in Germany are positive. Currently, the species is unthreatened. Since 15 % of the global populations and 10 % of the core range are located in Germany, the country has a high responsibility for the long-term survival of the species.

THORSTEN MÜNSCH


Speckled Bush-cricket
(Leptophyes punctatissima)
Webcode:
vah12260
Record
since 2010
1990-2009
1950-1989
until 1949

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