Biodiversity and global change: Lessons from a low-mountain range

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PhD Thesis

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2021

Title page: View from the Belchen, Southern Black Forest (Wieden 2017/02/12)

UNIVERSITÄT
OSNABRÜCK

Biodiversity and global change: Lessons from a low-mountain range

Inauguraldissertation

zur Erlangung des Doktorgrades der Naturwissenschaften
im Fachbereich Biologie/Chemie
der Universität Osnabrück

AG Biodiversität und Landschaftsökologie

vorgelegt von Florian Fumy
2021

Gefördert durch das
Stipendienprogramm der
DBU
Deutsche
Bundesstiftung Umwelt
www.dbu.de

Erstgutachter: Apl. Prof. Dr. Thomas Fartmann

Zweitgutachter: Prof. Dr. Gert Rosenthal

Tag der mündlichen Prüfung: 08.04.2022

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Bei der Auswahl und der Auswertung des folgenden Materials haben mir die nachstehend aufgeführten Personen in der jeweils beschriebenen Weise geholfen.

Artikel 1

Fumy, F. and Fartmann, T. 2021. Climate and land-use change drive habitat loss in a mountain bird species. – Ibis 117: 135.

Thomas Fartmann: Redigieren des Artikels. Anteil: 10 %

Zusätzlich haben *Claudia Frank* und *Markus Frenzel* jeweils ca. 1/3 der analysierten Ringdrosselvorkommen im Jahr 2017 erfasst.

Artikel 2

Fumy, F., Kämpfer, S. and Fartmann, T. 2021. Land-use intensity determines grassland Orthoptera assemblage composition across a moisture gradient. – Agr Ecosyst Environ 315.

Steffen Kämpfer: Unterstützung bei der Datenanalyse, Redigieren des Artikels. Anteil: 10 %

Thomas Fartmann: Redigieren des Artikels. Anteil: 10 %

Artikel 3

Fumy, F., Löffler, F., Samways, M. J. and Fartmann, T. 2020. Response of Orthoptera assemblages to environmental change in a low-mountain range differs among grassland types. – Journal of Environmental Management 256: 109919.

Franz Löffler: Berechnung der STI und SFI Werte, Redigieren des Artikels. Anteil 40 %

Michael Samways: Redigieren des Artikels. Anteil: 10 %

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Artikel 4

Fumy, F and Fartmann, T. Low-intensity land use fosters species richness of threatened butterflies and grasshoppers in mires and grasslands.

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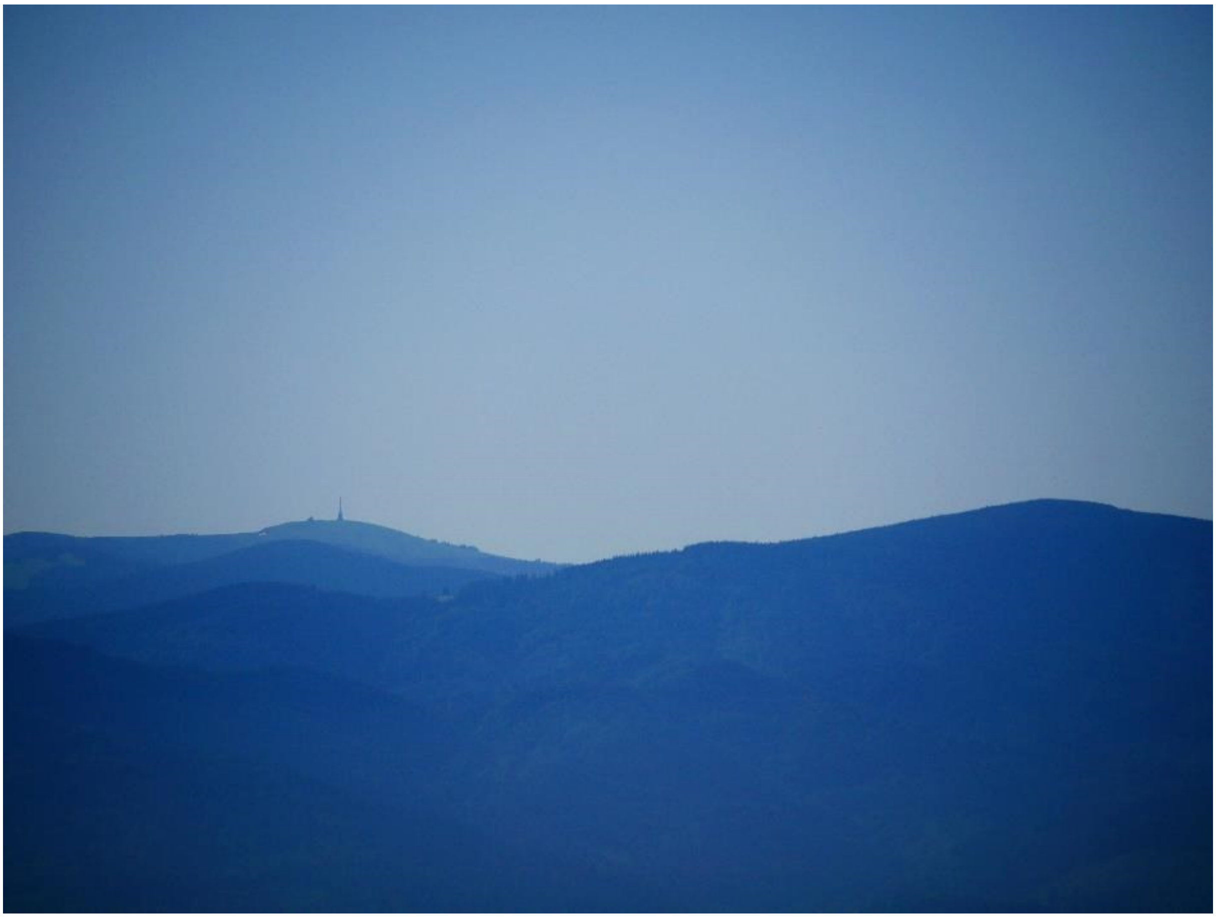
Thank you.

Contents



Back page: The beautiful southern Black Forest with its highest peak, the Feldberg [1493 m a.s.l.] (Kaiserstuhl 2018/04/12)

Chapter I

Motivation: Biodiversity, global change and conservation

Common pasture with *Arnica montana* and *Genista sagittalis* (Kohlhütte, Ibach 2018/06/19)

PREAMBLE

The existence of life is arguably the most striking characteristic of planet Earth. Throughout billions of years of evolution, the tree of life has ramified into unimaginable diversity. Millions of species have evolved, and many of them have disappeared over the course of time. Whole ecosystems have arisen and perished. Despite several events of mass extinction, biological diversity has generally become ever more complex. Nowadays, there is overwhelming genetic and functional diversity within and across the ecosystems of the planet.

We—the humans—are one of the youngest species on Earth. However, the impact of our species on the functioning of the planet is certainly outstanding. In what is just a blip in the history of life, humanity has evolved into the most influential keystone species on Earth. The pace and magnitude of how we change the planet is fascinating and menacing at the same time. The whole planet has become an all-encompassing anthroposphere—even the most remote areas are not untainted by the human footprint.

With our ability to change the foundations of life on earth comes the responsibility to evaluate our action. However, it is remarkable how little we understand about the impact of our activities on the planet's biological diversity. Although it is evident a.) that the current decline of life on Earth is related to human activities, b.) that the alteration and devastation of habitats and ecosystems has negative consequences for biodiversity and c.) that other human-induced global processes such as climate change, chemical, light, acoustic and plastic pollution or the introduction of alien species each have the potential to further push biodiversity beyond safe limits, it remains unclear how these drivers affect species, populations, habitats and ecosystems and how these drivers interact. Furthermore, we know very little about tipping points, functional redundancies and ecosystem functioning in general. Our lack of knowledge means that we do not have the power to halt biodiversity loss.

Losing large proportions of the global biological diversity is a silent catastrophe. While the impact and potential danger of climate change, for example, are perceived much more by society, the consequences of biodiversity loss seem to be widely ignored. This is noteworthy especially since one main issue concerning climate change is its potential to perturb ecosystems and ecosystem functioning. It can only be speculated why biodiversity loss is a blind spot—perhaps the causes lie in the fact that the value and benefits of biodiversity are somewhat diffuse and in the indirect nature of the consequences of biodiversity loss.

I am convinced that life is the most valuable good in the world. In this light, I decided to dedicate my research to biodiversity. I hope to contribute to a scientific debate about the past, present and future of human-environment interaction and biodiversity conservation.

THE DIVERSITY OF LIFE ON EARTH

Biological diversity

'Biological diversity' or 'biodiversity' is the variability among living organisms including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species, between species and of ecosystems (COP 1992). The current diversity of life on Earth is a snapshot of the ever-ongoing process of evolution and as such is subject to permanent change as species arise and become extinct and as the ranges of species, habitats and ecosystems shift, expand and contract. The total number of species inhabiting the planet remains subject to high uncertainty. However, evidence suggests that the ~ 1.3 million species known to humanity only represent a small fraction of the total number (Caley et al. 2014, Stork 2018).

Biodiversity patterns

The diversity of life on Earth is distributed unequally across the globe. Patterns of diversity result from evolutionary processes, namely speciation, persistence and extinction, which in turn are mainly driven by climate, topography and their interactions as well as species' dispersal distance, evolutionary rate, time for speciation and intensity of competition (Badgley et al. 2017, Rangel et al. 2018, Muellner-Riehl et al. 2019). Patterns of diversity can thus be found along climatic and topographic gradients. The most species-rich ecosystems are located in the tropics and in mountain environments–the Amazonian-Andean rainforest is arguably the most species-rich region in the world (Hoorn et al. 2010). An estimated one-third of terrestrial species diversity as well as large proportions of endemic species are supported by mountain ranges (Körner et al. 2017, Noroozi et al. 2018). The outstanding species richness of mountain areas is due to their topographic complexity which sets the stage for speciation, especially under climatic cycles, and also facilitates accumulation of species with different life history traits along strong environmental gradients (Badgley et al. 2017, Flantua and Hooghiemstra 2018, Perrigo et al. 2020). Additionally, mountain ranges feature larger climatic niche space than flatlands and thus support more species under variable climates–both in the past and at present (Muellner-Riehl et al. 2019).

The globe hosts a large variety of ecosystems, each with specific biogeochemistry and evolutionary history. Accordingly, ecosystems differ largely in species richness and organisational complexity. There is a general correlation of ecosystem age and species richness (Wiens 2011). Moreover, specific combinations of climatic variables—most prominently precipitation and temperature—are important drivers of species richness within ecosystems (Hawkins et al. 2003). Untouched forests, such as parts of the Amazonian rainforest, but also ecosystems with long land-use history, such as the Mediterranean range, are among the most species-rich terrestrial ecosystems. In temperate regions, such as Central Europe, grasslands, most of them dominated by land use, are among the most species-rich ecosystems (Veen et al. 2009, Feurdean et al. 2018).

The value of biodiversity

What is the value of biodiversity? It is nearly impossible to find a comprehensive answer to this question. Of course, difficulties arise when putting value on something that is only known by approximately 10%. Besides, biodiversity comprises an extremely high level of complexity with intricate and understudied interdependences which makes it difficult to produce an overall picture that can be put into context (Fosci and West 2016, Bartkowski 2017).

There are two seemingly competing concepts of the value that can be attributed to biodiversity: instrumental and intrinsic value. The instrumental value can be described as the worth biodiversity has as an utility for humanity, whereas the intrinsic value of biodiversity rather is an objective value that exists independently from a human viewer (Fosci and West 2016). One attempt to quantify the instrumental value of biodiversity is the concept of ecosystem services, which focuses on the contributions of ecosystem structure and function to human well-being (Burkhard and Maes 2017). It assumes that mankind is strongly dependent on well-functioning ecosystems. The ecosystem services concept provides the basis for the quantification of the value of biodiversity in economic terms (e.g. Costanza et al. 2014, Bartkowski 2017, Augeraud-Véron et al. 2019, Hanley and Perrings 2019). Such approaches seem appealing perhaps because humans are used to expressing value in monetary equivalents (Arias-Arévalo et al. 2017). However, other parameters such as biophysical and socio-cultural values are no less important and should be evaluated equally (Martín-López et al. 2014, Arias-Arévalo et al. 2017).

In contrast to the instrumental value, the intrinsic value completely evades measurement and comparison—from a human perspective, the intrinsic value of biodiversity is subject to moral consideration (Fosci and West 2016). Nevertheless, both instrumental and intrinsic value do cohabit in the human mind and serve as guidelines for biodiversity appreciation and protection (Fosci and West 2016, Arias-Arévalo et al. 2017).

GLOBAL BIODIVERSITY CRISIS

Biodiversity loss

Biodiversity is declining on a global scale and at an unprecedented rate (IPBES 2019). The world-wide loss of habitats, species and genetic variability ranges are among the most appalling crises humanity has ever faced (Sala et al. 2000, Mittermeier et al. 2011, Johnson et al. 2017). By analogy with the other large processes of global change, human activity by far is the most important driver of this development (Díaz et al. 2006, Johnson et al. 2017). Although it is difficult to predict the impact on ecosystem functioning, there is overwhelming evidence that biodiversity loss negatively affects a large number of ecosystem services with the magnitude of consequences for society rivaling the impacts of other global drivers of environmental change (Foley et al. 2005, Cardinale et al. 2012, Hautier et al. 2015). It has been widely accepted that impeding the ever-accelerating decrease of biodiversity is fundamental to preserving the basis of life on Earth, at the latest since the 1992 Earth Summit in Rio de Janeiro (Díaz et al. 2006, Cardinale et al. 2012, Pimm et al. 2014, Cardoso et al. 2020). However, global goals to reduce the rate of biodiversity loss have mostly not been achieved (Johnson et al. 2017). The reasons for this disconcerting fact are manifold and can be described as a sinister embrace of lacking action and lacking knowledge (Mehring et al. 2017). This implies that decision makers have to put biodiversity and the risks linked with its decline much more into focus, but also that further research on drivers of biodiversity is needed.

Biodiversity and land use change

The history of humankind is also a history of land use and land-use change. Since the beginnings of agriculture in the early Holocene, humans have systematically changed their environment (Rottenberg 2017). Ever since, land use has been an important driver of material cycles, climate and biodiversity (Kaplan et al. 2017). Land use has always been subject to change. However, the magnitude of change has increased dramatically since the beginning of the industrial era (Donald et al. 2006, Johnson et al. 2017). While land use had often contributed to high regional biodiversity in 'traditional' agricultural regimes, the recent industrialisation and homogenisation of agriculture has reduced biosphere intactness below safe limits in most terrestrial ecosystems (Newbold et al. 2016, Fuller et al. 2017). Across all terrestrial biomes, land-use change is often referred to as the most important driver of biodiversity loss (Sala et al. 2000, Foley et al. 2005, Pimm et al. 2014, Newbold et al. 2016, Fuller et al. 2017, Johnson et al. 2017, Poschlod 2017, Samways 2019).

Land-use change has a multitude of manifestations. Grasslands, for example, either suffer from intensification or abandonment (Veen et al. 2009). Although much research has been carried out on general and fine scale patterns of land-use-biodiversity relationships, detailed knowledge about the impact of land use and land-use change on the distribution of species is often lacking (see e.g. Horrocks et al. 2016). This is especially true for areas still featuring considerable species numbers, probably due to a general notion of ‘least concern” for these areas and the complexity of the respective species communities. However, land-use change does not leave these areas unaffected: on the one hand, land-use changes in the surrounding matrix most likely have considerable impacts on species-rich habitats (Häkkilä et al. 2017, Löffler and Fartmann 2017, but also Poniatowski et al. 2018b). On the other, nowadays even most of the remaining species-rich agricultural landscapes are directly affected by either abandonment or land-use intensification (Poschlod 2017, Löffler et al. 2019, Fumy et al. 2020). The impact of land-use change on biodiversity in species-rich areas thus remains a matter of further research.

Biodiversity and climate change

Climate determines the spatial distribution of ecosystems, habitat types and species on the globe. Changes in climate thus induce changes in these distributions. However, evidence suggests that distribution changes occur dissimilarly across species with different traits and across differently structured landscapes which leads to nearly unpredictable alterations in coenosis-composition and ecosystem functioning (La Sorte and Jetz 2010, Engler et al. 2011, Jenouvrier 2013, Pecl et al. 2017). Climate change comprises changes in a large array of environmental parameters, including temperature and precipitation. These parameters do not change synchronously, which results in new combinations of climatic variables. Moreover, the magnitude of change is distributed highly disparate in space (IPCC 2013). Mountain areas for example are expected–and also have been observed–to experience much greater changes than neighboring lowlands (Brunetti et al. 2009, Engler et al. 2011). All in all, the impact of climate change on biodiversity is thus rather difficult to assess. However, there is broad consensus that climate change is the second most important driver of the recent global decline of life on Earth. It is even predicted to outcompete the impacts of land-use change in several ecosystems and taxonomic groups in the future (Sala et al. 2000, Warren et al. 2001, Chen et al. 2011, Cardinale et al. 2012, Jenouvrier 2013).

Interactions between climate and species’ distribution as well as diversity are complex. Due to the relative novelty of observable climate change, the scientific community has only recently had the opportunity to carry out research in this area. Moreover, there are manifold interdependences of climate change, land-use change, biodiversity loss and other drivers of global change, most of which are only poorly understood (Prestele et al. 2017, Doelman et al. 2018). In this light, it is hardly surprising that we are only just starting to understand climate-diversity interactions in the different biomes of the planet.

Conserving biodiversity

Biodiversity is decreasing at an unprecedented rate, with potentially catastrophic consequences for life on Earth in general, but also for human life on the planet in particular. All attempts to stop biodiversity loss on the globe have failed so far—however, there are promising approaches and many examples of successful biodiversity conservation on smaller scales (compare e.g. Tucker et al. 2019). It seems evident that, in order to halt biodiversity loss, it is crucial that limited available resources be guided to those regions featuring particularly high species numbers and large proportions of endemic species (Mittermeier et al. 2011). Accordingly, biodiversity hotspots have been identified on a global scale, for biogeographic regions like the Palearctic, and on national scales, e.g. for the extent of Germany (Mittermeier et al. 2011, Sluys et al.

2011, Ackermann and Sachteleben 2012). Pooling conservation efforts and directing them to these hotspots on all spatial scales is a promising strategy to protect a substantial fraction of local, regional and global biodiversity (Kareiva and Kareiva 2016).

Conservation comprises completely different approaches in different ecosystems, ranging from refraining from any human activity (e.g. wilderness conservation) to decidedly controlling land-use management (e.g. agri-environmental schemes in cultural landscapes) (Mittermeier et al. 2003, Brooks et al. 2006, Mittermeier et al. 2011, Johnson et al. 2017).

BIODIVERSITY IN CENTRAL EUROPE

The vast majority of the Central European landscapes have a long history of agriculture. Humans in Central Europe have developed a wide range of differing management systems, especially for hay meadows and pastures, taking into account specific local environmental conditions such as climate or soil properties as well as specific local social realities such as land ownership or food supply chains (Poschlod 2017, Burton and Riley 2018). Socio-agricultural systems prominently included common lands, often used as pastures. These common pastures were usually large in size and unfenced. Due to the shared use of the land, management of common pastures comprised only a minimum of investment into land improvement combined with rather high grazing pressure (Moor et al. 2016). As a result, common pastures featured high habitat heterogeneity and high species richness (Poschlod 2017, Schwarz et al. 2018). Altogether, traditional land-use practices have for centuries contributed to the development of semi-natural ecosystems, especially grassland systems with high structural diversity, great habitat variety and outstanding species richness (Plieninger et al. 2006, Veen et al. 2009, Poschlod 2017).

However, since the beginning of the industrial era, land use has changed severely throughout Central Europe. This includes, among other things, intensive application of artificial fertilizers, use of large agricultural machines, substantial reduction of crop cultivar and livestock breed variety, livestock fencing, increased field sizes, abandonment of less suited sites, reallocation of land and land improvement measures. These processes together result in increasing landscape uniformity and have led to a substantial loss of wild biota (Donald et al. 2006, Johnson et al. 2017). Grasslands and peatlands, which are among the most species-rich ecosystems in Central Europe, suffer particularly from the industrialisation of agriculture. Consequently, the extent of semi-natural grasslands and natural or at least intact peatlands of high conservation value has greatly decreased (Wallis de Vries et al. 2002, Veen et al. 2009, Dengler et al. 2014, Newbold et al. 2016, Joosten et al. 2017, Feurdean et al. 2018). As a result, Central Europe (among other regions of the world) is on the brink of losing high proportions of its biodiversity (Donald et al. 2006, Plieninger et al. 2006)

Although nowadays land use is very much dominated by industrial practices, some remnants of traditional land use can still be found. Due to their remoteness and topographic complexity, most of these remnants are located in mountain areas which, consequently, host a large proportion of the remaining species-rich habitats in Central Europe (Plieninger et al. 2006).

ASSESSING BIODIVERSITY

Ecological indicators

Due to its complexity, the assessment of biodiversity as a whole is impossible (Westgate et al. 2017). Thus, research focuses on different indicators of biodiversity. Among others, these indicators comprise species numbers of selected taxonomic groups, habitat type diversity and environmental DNA metabarcode diversity (e.g. Fartmann et al. 2012, Herzog et al. 2017, Fartmann et al. 2018, Bakker et al. 2019, Löffler et al. 2019, Fumy et al. 2020). In community ecology, certainly by far the most common approach is to focus on selected indicator groups with the assumption of relatively good representativeness for the respective communities (Chiarucci et al. 2011). Provided that the selected taxa are ecologically associated to a large number of co-existing species, such umbrella taxa can indeed be good representatives of overall biodiversity of a target community or landscape (Fartmann et al. 2012, Borchard et al. 2014, Fartmann et al. 2018, Stuhldreher and Fartmann 2018). Birds, butterflies and Orthoptera are among the best suited taxa to be considered 'biological indicators'.

Birds

On a global scale, birds are among the most intensively studied groups of organisms. Birds and bird assemblages have been shown to react very sensitively to changes in their environment and are considered very good indicators of overall habitat and in particular farmland biodiversity, on both the habitat and landscape level (Donald et al. 2001, Gregory et al. 2003, Gregory and van Strien 2010, Fartmann et al. 2018, Schwarz et al. 2018, Fumy and Fartmann 2021). Science has provided evidence for changes in birds' phenology, population development, species ranges and ecological differentiation due to climate change (Wormworth and Sekercioglu 2011, Jenouvrier 2013, Dunn and Møller 2019, Fumy and Fartmann 2021). The strongest impacts have been shown for species with small populations, small geographic ranges and high degrees of specialisation (Jenouvrier 2013).

In Central Europe, however, the severe decline of bird populations and farmland birds in particular is (still) mainly due to habitat degradation and destruction, especially as a consequence of land-use intensification (Wahl et al. 2015, Newton 2017). Land-use intensification affects birds mainly through reductions in food and breeding site availability, increasing numbers of generalist predators and direct effects of pesticides on the survival rate of nestlings as well as adult birds (Donald et al. 2001, Donald et al. 2006, Fuller 2012, Newton 2017, Kämpfer and Fartmann 2019). The red list of breeding birds of Germany yields an alarming example of the decline of the avifauna in Central Europe: 248 bird species are considered native to Germany. Out of these, 13 are classified as extinct and 105 as threated with extinction, endangered or extremely scarce; additionally, 18 species are listed on the early warning list–only 45% of the bird species native to Germany do not fall into one of these categories. Considering only farmland birds, the numbers are even more concerning: only 13% of the native farmland bird species in Germany are of least conservation concern (Grüneberg et al. 2016).

Butterflies

Insects are by far the most species-rich group of multicellular organisms, with more than one million species known to humanity and several million expected unknown species. Their compositional, structural and functional diversity outcompete those of vertebrates on the planet by several magnitudes (Samways 2019). Lepidoptera are one of the most speciose orders and comprise about ten percent of all described species (Powell 2009). Among these, butterflies are by far the most intensively studied group.

Most butterfly species have narrow ecological niches (García-Barros and Fartmann 2009), and many species form metapopulations that depend on a network of suitable habitat patches (Eichel and Fartmann 2008). The larvae of most species have specific requirements with respect to microclimate and host-plant species as well as configuration (Wallis de Vries and van Swaay 2006, García-Barros and Fartmann 2009, Stuhldreher and Fartmann 2018). Consequently, butterflies react sensitively to environmental change and function as sensitive ecological indicators (Thomas et al. 2004, Nieto-Sánchez et al. 2015, van Halder et al. 2017, Stuhldreher and Fartmann 2018).

In the most recent red list for Germany, which dates back to 2011, half of the 189 German butterfly species are considered extinct or threatened or are listed on the early warning list (Binot-Hafke et al. 2011). Presumably, the conservation status of most species has been further aggravated in the time since. The severe decline of butterflies (not only) in Central Europe is mainly due to habitat loss and deterioration caused by recent land-use change and chemical pollution (Warren et al. 2021). Besides, climate change alters the habitat quality for most species, which has adverse effects on different species at different locations (Stuhldreher and Fartmann 2018, Warren et al. 2021).

Orthoptera

Orthoptera constitute a prominent and well-studied group of insects, and their taxonomy and distribution patterns are well-known (Bazelet and Samways 2012, Fartmann et al. 2012, Gardiner 2018). Habitat selection in Orthoptera is mainly based on the often intercorrelated parameters vegetation structure and microclimate. Orthoptera react sensitively to alterations of these environmental parameters (Fartmann et al. 2012, Löffler and Fartmann 2017, Gardiner 2018, Löffler et al. 2019, Schirmel et al. 2019, Fumy et al. 2020). Many species are highly specialized and strictly bound to specific habitat types (e.g. Münsch et al. 2013, Löffler et al. 2016). An impressive example of Orthopterans' response to climate warming, for example, is the rapid northward range expansions of several thermophilic Orthoptera species during recent decades in Central Europe (e.g. Bakker et al. 2015, Beckmann et al. 2015, Poniatowski et al. 2018a, Löffler et al. 2019). Orthoptera play an important functional role in grassland ecosystems due to their often high biomass, which makes them important vegetation consumers and one of the main food resources of different vertebrate taxa such as birds or reptiles (Belovsky and Slade 1993).

Despite the advanced level of knowledge on Orthoptera ecology, half of the species occurring in Germany are considered extinct or threatened or are listed on the early warning list in the most recent red list, which dates back to 2011 (Maas et al. 2011). The main reasons for the decline of Orthoptera are habitat loss and deterioration due to land-use change (Fartmann et al. 2012, Gardiner 2018). Additionally, it is highly evident that climate change has the potential to drastically alter Orthoptera assemblages (compare e.g. Löffler et al. 2019, Fumy et al. 2020).

THE THESIS

Aim

The main goal of this thesis is to use an endangered mountain bird, the ring ouzel (*Turdus torquatus alpestris*), and grassland butterfly and Orthoptera assemblages as model organisms to investigate how land-use change and climate change affect biodiversity in a Central European biodiversity hotspot.

The alpine ring ouzel (*Turdus torquatus alpestris*) is a passerine bird, occurring in the Alps, Pyrenees, Balkans, Greece and Asia Minor (Glutz von Blotzheim and Bauer 1988). Smaller, potentially genetically-differentiated populations occur in the low mountain ranges north of the Alps (Bacht et al. 2013). The birds' wintering grounds are located in NW Africa, especially the High Atlas (Glutz von Blotzheim and Bauer 1988). The species breeds in the upper elevations of mountain ranges, in the submontane–alpine zone (Bacht et al. 2013). Characteristic breeding habitats of the ring ouzel are mosaics of sparse montane conifer forests, semi-open and open landscapes with a cool and humid microclimate (Schirutschke 2005, Bauer et al. 2013, Ciach and Mrowiec 2013). The nests are usually built in the branch forks of evergreen conifers, mainly spruce (*Picea abies*) and fir (*Abies alba*) (Glutz von Blotzheim and Bauer 1988). Foraging takes place on the ground, and earthworms are the staple food of the nestlings (Glutz von Blotzheim and Bauer 1988).

In Germany, the largest population outside the Alps is located in the southern Black Forest, Baden-Württemberg, where the ring ouzel breeds at elevations above 900 m (Knoch 1970, Mann 1990). The population size in the Black Forest is estimated to range from 300–500 (Bauer et al. 2013) to 370–950 (Gedeon et al. 2014) breeding pairs. In Baden-Württemberg, the species, which was not formerly classified as threatened, is now considered to be threatened with extinction (Bauer et al. 2013).

The ring ouzel is a mobile vertebrate that is restricted to montane environments. Being a mountain specialist and a species of mosaic-like landscapes, it is probably highly sensitive to both climate and land-use change and thus is a good indicator of mountain biodiversity in heterogeneous landscapes. The species represents a high trophic level and is possibly affected by changes at lower trophic levels. Also, birds have complex behavioural traits and can possibly adapt to changing environments by changes in their behaviour, either by phenotypic plasticity or by selection of different genotypes.

The southern Black Forest hosts remarkable butterfly and Orthoptera diversity, including highly specialized species such as the butterflies *Argynnis niobe*, *Boloria aquilonaris*, *Colias palaeno*, *Hesperia comma*, *Lycaena hippothoe*, *Lycaena alciphron* and *Pseudophilotes baton* and the Orthoptera *Decticus verrucivorus*, *Miramella alpina*, *Omocestus rufipes*, *Psophus stridulus*, *Stauroderus scalaris*, *Stenobothrus stigmaticus* and *Stethophyma grossum*. These highly specialized species are particularly dependent on habitat structure, ambient temperature and humidity, which renders them optimal indicators for biodiversity reactions to global change. Additionally, butterfly and Orthoptera species determination is possible in the field for most species—thus, both are practical study groups in field ecology.

Birds, butterflies and Orthoptera represent three different levels of mobility, with birds being the most and Orthoptera the least mobile groups. Similarly, the minimum area that can hold a viable population of a certain species typically is large for birds and relatively small for Orthoptera—even some highly specialized species such as *Stenobothrus stigmaticus* have been shown to survive in small landscape fragments (Fischer et al. 2016). Many butterfly species form metapopulations that require a network of suitable habitats (Thomas and Hanski 1997). In contrast to many bird species that feed on other animals, butterflies and Orthoptera are primary consumers. Analysing such different study groups in the light of land-use and climate change allows for a relatively comprehensive perspective on the impact that global change has on biodiversity as a whole.

In the context of this thesis, I conducted several field studies on the ring ouzel and on butterfly and Orthoptera communities in the southern Black Forest. Additionally, I used data on the occurrence of the ring ouzel and on Orthoptera assemblages dating back 30 and 20 years, respectively, which allowed me to compare the recent and historic population size, species' distribution and assemblage composition of these groups.

Study area

The study area comprises the submontane, montane and subalpine zones of the southern Black Forest in the federal state of Baden-Württemberg (SW Germany, 900–1493 m a.s.l.). Compared to the average climatic conditions of Central Europe, the climate is cool and wet with a mean annual temperature of 3.8–5.5 °C and a mean annual precipitation of 1650–2200 mm (CDC 2018). Due to the harsh climate, the nutrient-poor soils on acidic bedrock and the complex topography, the study area features a heterogeneous landscape with extensive semi-natural pastures, montane conifer forests, bogs and a huge variety of microclimatic conditions (Geis et al. 2013, MLR-BW 2016).

There is evidence of land use in the Neolithic in terms of summer highland pastures (Kienlin and Valde-Nowak 2004). Although there already had been a few early settlements in the Early Middle Ages (research suggests that), only in the High Middle Ages did considerable seizure of territories and consequent land use take place (Mutton 1938, Reinbolz 2004, Knopf et al. 2015). After a period of deforestation in favor of semi-natural grasslands, the past decades were characterized by a converse process with considerable loss of open land in favour of forests (Konold et al. 2014, Peppler-Lisbach 2014). At the same time, land-use change has led to agricultural intensification as well as abandonment tendencies in the remaining grasslands– intensification mainly at more productive sites used as hay meadows, abandonment at unfavourable sites, namely the bogs but also considerable proportions of little productive pastures (Hermle and Deil 2002, Konold et al. 2014). However, large parts of the cultural landscape in the study area are still dominated by semi-natural, species-rich grasslands. Consequently, it is part of the German biodiversity hotspot ‘Hochschwarzwald mit Alb-Wutach-Gebiet’ (Ackermann and Sachteleben 2012). Exceptional for Central Europe, several of the pastures in the study area are still managed as common pastures (Regional Office for Environment 2004, Regional Council Freiburg 2011). Due to their outstanding habitat and biodiversity, these heterogeneous pastures are of high conservation value and, additionally, make a unique contribution to the German cultural heritage (Lederbogen et al. 2004, Schwarz et al. 2018, Fumy et al. 2020).

Outline

This thesis contains four scientific papers, organized in chapters two and three. In chapter two, I focus on the comparison of species’ historic and recent distribution in relation to environmental change. In the first paper, I use the ring ouzel *Turdus torquatus alpestris* as a model organism for montane biodiversity and explore past and recent habitat occupancy across a time span of 30 years. The second paper focuses on past and recent Orthoptera assemblage composition across a time span of 20 years. Both studies use climatic parameters and habitat structure as explanatory variables. Through the use of historic data, both papers disentangle the effects of climate and land-use change, which opens space for a precise discussion on adequate responses to the two main drivers of biodiversity loss.

In chapter three, I explore the effects of land-use intensity on habitat properties and consequences for butterfly and Orthoptera assemblages. The first paper considers Orthoptera assemblages in three different grassland types and the forth paper focuses on threatened butterfly and Orthoptera species across five habitat types. In both studies, I relate species assemblage composition to habitat structure and land-use intensity.

Chapter four comprises a synthesis of the results and indicates strategies for biodiversity conservation.

Pastures in the Southern Black Forest: as a result of partial abandonment, many of these species-rich habitats have lost key properties such as sparse vegetation and bare soil (top) in favour of dense grass and dwarf shrub mats (bottom). Nevertheless, the large pastures in the Black Forest are still of high conservation value. (Seebuck 2018/11/17 and Blasiwald 2018/05/17)

Low-intensity land use: traditional hay meadow (top) and pasture (bottom) management is labour intensive and produces little revenue. On the other hand, low-intensity land use is the key for biodiversity conservation in Central Europe. (Lindau [Hotzenwald] 2018/06/19 and Ibach 2018/08/25)

Chapter II

Biodiversity responses to changing environments

Ring Ouzel foraging at sunrise (Belchen 2017/06/09)

CHAPTER II

Chapter II focuses on the comparison of species' historic and recent distribution in relation to environmental change. It consists of two papers, both of which use data on historic and recent occurrence patterns of different model organisms for biodiversity in the Southern Black Forest. Paper I explores past and recent habitat occupancy of the ring ouzel *Turdus torquatus alpestris* across a time span of 30 years. Paper II focuses on past and recent Orthoptera assemblage composition across a time span of 20 years.

Paper I

Climate and land-use change drive habitat loss in a mountain bird species

Paper II

Response of Orthoptera assemblages to environmental change in a low-mountain range differs among grassland types

Climate and land-use change drive habitat loss in a mountain bird species

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ABSTRACT

Mountain areas still feature remnants of traditional land use and consequently comprise a large proportion of the remaining species-rich habitats in Central Europe. However, their biodiversity is increasingly threatened by changes in climate and land use. The Alpine Ring Ouzel Turdus torquatus alpestris is a typical mountain bird that has recently declined in most of its breeding range. In this study we compared the historic (1986–1987) and recent (2017) distribution of breeding Ring Ouzels in 62 randomly selected 750 × 750 m plots and analysed local colonisation and extinction patterns in 558 subunits (= ‘grid cells’) in the southern Black Forest (south-western Germany). Our study revealed that habitat occupancy decreased by about one third, mainly at lower elevations and in depressed landforms, during the past three decades. Local colonisation amounted to 25 % and extinction to 66 % of the previously vacant or occupied grid cells, respectively. Habitat occupancy and local colonisation and extinction were driven by climate and habitat parameters. The Ring Ouzel preferred convex landscape formations such as mountain peaks and ridges with long snow-cover duration for breeding. Sites with high proportions of deciduous forest and abandoned pasture were avoided. Local colonisation was higher at convex landscape formations and by high coniferous forest coverage and forest-edge length. Local extinction on the other hand was lower at convex landscape formations and high-elevation sites. Our results suggest that shorter persistence of snow fields caused by climate change and degradation of feeding grounds through land-use abandonment might severely deteriorate food availability for the species, which is likely to have contributed to the observed decline. For conservation of the Alpine Ring Ouzel, we recommend adopting measures to mitigate the negative effects of climate warming and improve habitat quality. The creation of small-scale mosaics of sparse conifer forests and regularly grazed pastures, especially on north- and east-facing slopes on the lee sides of hills, mountain peaks or ridges, should be supported.

KEYWORDS

Abandonment, Alpine Ring Ouzel, Turdus torquatus alpestris, Black Forest, Conservation management, Global warming, Grazing.

IBIS Journal of Avian Science 117 (2021). https://doi.org/10.1016/j.nedt.2008.07.004

INTRODUCTION

The recent loss of biodiversity is among the most severe threats to life on Earth (Johnson et al. 2017). Current species extinction rates exceed the natural background rate by about a thousand times, and the trend is rising (Pimm et al. 1995, Vos et al. 2014). There is overwhelming evidence that the ongoing biodiversity crisis is mainly driven by human-induced global change, in particular changes in climate and land use (Foley et al. 2005, IPCC 2013).

The magnitude of climate change is particularly large in mountain areas, with the rate of warming being twice that of the global average (Brunetti et al. 2009). Additionally, mountain ranges harbour many cold-adapted species, which are likely to be extremely vulnerable to climate change (La Sorte and Jetz 2010, Streitberger et al. 2016b). Altitudinal range shifts and habitat loss have been shown for a variety of species in montane environments in response to climate warming (e.g. Lehikoinen et al. 2014, MacLean and Beissinger 2017, Löffler et al. 2019, Fumy et al. 2020).

In Central Europe, traditional land-use practices have for centuries contributed to the development of semi-natural ecosystems harbouring outstanding species richness (Plieninger et al. 2006, Poschlod 2017). However, since the beginning of the industrial era, land-use change has led to a substantial loss of wild biota (Donald et al. 2006, Johnson et al. 2017). Remnants of traditional land use are mainly found in mountain areas which, consequently, host a large proportion of the remaining species-rich habitats in Central Europe (Plieninger et al. 2006).

Birds are excellent indicators of biodiversity in general (Gregory et al. 2008, Gregory and van Strien 2010, see also Sander and Chamberlain 2020). They respond sensitively to climate change (Crick 2004, Jenouvrier 2013, Lehikoinen et al. 2014) and habitat alteration (Fuller 2012), which is especially true for alpine species (e.g. Oswald et al. 2020). Due to their complex habitat requirements, they are also frequently used as umbrella species whose conservation is expected to secure the protection of a large number of naturally co-occurring species (Roberge and Angelstam 2004).

The Alpine Ring Ouzel *Turdus torquatus alpestris* (Brehm, CL, 1831) is a typical mountain bird, occurring in the Alps, Pyrenees, Balkans, Greece and Asia Minor (Glutz von Blotzheim and Bauer 1988). Smaller, potentially genetically differentiated populations occur in the low mountain ranges north of the Alps (Bacht et al. 2013). In Germany, the largest population outside the Alps is located in the southern Black Forest, Baden-Württemberg. It has recently been debated whether the current decline of the species in the Alps is driven by climate change or habitat alteration (dem Bussche et al. 2008, Knaus et al. 2018, Barras et al. 2019) and there is evidence that the population declines and range contractions of the subspecies *T. t. torquatus* (Linnaeus, 1758) are linked to climate change (Beale et al. 2006). In the northern Black Forest, Anger et al. (2020) observed a strong decline of the species and local extinctions at lower elevations. Similar range retractions have been assumed for the southern Black Forest (Bauer et al. 2013). However, population dynamics, distribution change and underlying mechanisms have not been studied so far in this region.

In this study, we compare the historic (1986–1987) and recent (2017) distribution of breeding Ring Ouzels in the southern Black Forest. In order to identify the drivers of habitat loss, we relate Ring Ouzel breeding territory occupancy as well as local colonisation and extinction with climate and habitat parameters. Based on the results, we give recommendations for the conservation of the Ring Ouzel in times of global change.

METHODS

Study area

The study area comprises the submontane, montane and subalpine zones of the southern Black Forest in the federal state of Baden-Württemberg (SW Germany, 900–1493 m a.s.l.; Fig. 1). Compared to the average conditions of Central Europe, the climate is cool and wet with a mean annual temperature of 3.8–5.5 °C and a mean annual precipitation of 1650–2200 mm (30 year period 1981–2010; CDC 2018). Due to the harsh climate, the nutrient-poor soils on acidic bedrock and the pronounced relief, the study area features a heterogeneous landscape with extensively managed semi-natural pastures, montane conifer forests, bogs and a huge variety of microclimatic conditions (Geis et al. 2013, MLR-BW 2016). Exceptionally for Central Europe, several of the pastures in the study area are common pastures, which have been under low-intensity grazing management by the local communities for centuries (Regional Office for Environment 2004), and which are of high nature conservation value (Schwarz et al. 2018, Fumy et al. 2020). The conifer forests comprise a large gradient from dense and dark stands with closed canopy to sparse woodlands with a high degree of shrub cover, mainly

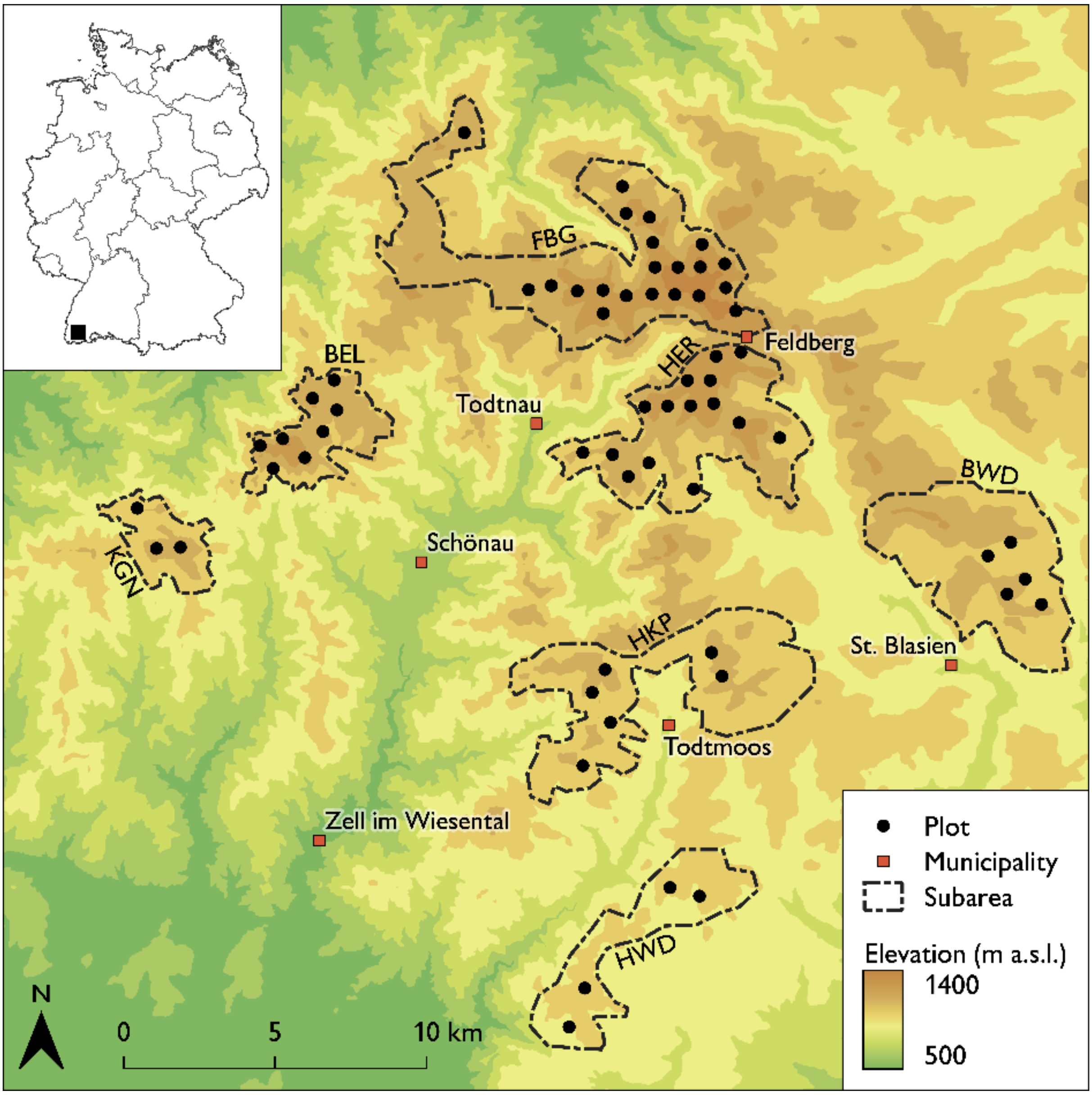

Figure 1. Location of the study area and plots in the southern Black Forest (SW Germany)

Vaccinium myrtillus (Ludemann 2012, Wippel et al. 2016). The landscape heterogeneity results in a high species richness. Consequently, the study area is part of the German biodiversity hotspot 'Hochschwarzwald mit Alb-Wutach-Gebiet' (Ackermann and Sachteleben 2012). Some of the mountain peaks are major tourist attractions, such as the Feldberg and Belchen (Regional Office for Environment 2004, Geis et al. 2013). Most of the more remote areas, in contrast, are rarely visited by tourists.

Study species

The Ring Ouzel *Turdus torquatus* is a passerine bird, with the subspecies *T. t. alpestris* being a typical inhabitant of the Central European mountain ranges. Its breeding range extends from the northern Iberian Peninsula and Central Europe to the Carpathians. Breeding is restricted to the sub-montane–alpine zone and the birds' wintering grounds are located in NW Africa, especially the High Atlas (Glutz von Blotzheim and Bauer 1988, Bacht et al. 2013).

Characteristic breeding habitats of the Ring Ouzel are mosaics of sparse montane conifer forests, semi-open and open landscapes with a cool and humid microclimate (Schirutschke 2005, Bauer et al. 2013). The nests are usually built in the branch forks of evergreen conifers, mainly Norway Spruce *Picea abies* and European Silver Fir *Abies alba*. In contrast to leafless deciduous trees, evergreen conifers provide hidden places for nest building at the beginning of the breeding season (Glutz von Blotzheim and Bauer 1988, Gatter and Mattes 2018). The Ring Ouzel forages on the ground (Glutz von Blotzheim and Bauer 1988). The staple food of the nestlings are earthworms (Glutz von Blotzheim and Bauer 1988). In the Black Forest, the species breeds at elevations above 900 m a.s.l. (Knoch 1970, Mann 1990).

Germany hosts 2600–5000 breeding pairs of the Ring Ouzel, but numbers are decreasing (Gedeon et al. 2014). The largest populations in Germany occur in the Alps and the southern Black Forest. The population size in the Black Forest is estimated to range from 300–500 (Bauer et al. 2013) to 370–950 (Gedeon et al. 2014) breeding pairs. In Baden-Württemberg the species is now considered to be threatened with extinction (Bauer et al. 2013).

Sampling design

Bird surveys

In this study, we compared the historic (1986–1987; hereafter referred to as 1987) and recent (2017) distribution of breeding Ring Ouzels in the southern Black Forest. Data for the historic distribution were derived from Mann (1990), who conducted an area-covering survey of Ring Ouzel territories in the southern Black Forest. In 2017 we mapped territories (Bibby et al. 2000, Andretzke et al. 2005) at 62 plots of 750 × 750 m in seven subareas of the study area (Fig. 1). Random plot selection was based on a spatial grid that was superimposed on the area surveyed by Mann (1990) and stratified across the respective elevation gradient. Contiguous mountain ridges were defined as subareas which represent the entire elevation gradient occupied by the Ring Ouzel in the Black Forest. Survey methods were identical to those described by Mann (1990). Mapping of Ring Ouzel breeding territories took place from April to June 2017. Each plot was visited three times in good weather conditions with an interval of at least ten days between each visit (Fischer et al. 2005). Mapping was conducted between one hour before and 90 minutes after sunrise. All observations of territorial behaviour, such as singing, were recorded according to Bibby et al. (2000) on a map (scale 1:1500) by following a non-linear transect covering the entire plot. Based on the guidelines provided by Andretzke et al. (2005), establishment of a territory was assumed if a bird showed territorial behaviour at least twice within a span of ten days between each survey and at least one of these observations was from mid-May onwards.

In contrast to our study, clustered breeding was not differentiated into single breeding

Table 1. Mean (± standard error) of environmental parameters in the study plots. Climate parameters are averaged over five-year periods (1983–87 and 2013–2017). Parameters included as coefficients in multivariate models (1987, 2017: occupancy ratio models; Col, Ext: colonisation and extinction models) are indicated with letters c (climate models), h (habitat type models) and s (synthesis models). Parameters included in the calculation of the habitat diversity index are indicated in column *H'*.

Parameter	Mean ± se		Multivariable model				*H'*
	1987	2017	1987	2017	Col	Ext	
Topography							
Elevation (m a.s.l.)	1190 ± 15		·	·	c	cs	·
TPI (m)[1]	48.4 ± 5.4		c	cs	cs	cs	·
Climate							
Spring temperature (°C)	7.18 ± 0.1	8.46 ± 0.08	·	·	·	·	·
Spring precipitation (mm)	499 ± 3.8	471 ± 5.6	c	·	·	·	·
Snow-cover duration (days/yr.)	151 ± 1.8	114 ± 1.9	c	cs	·	·	·
Habitat characteristics							
Habitat type (%)							
Forest	·	66.6 ± 3.0	·	·	·	·	·
Coniferous forest	·	42.7 ± 2.9	·	·	hs	h	✓
Deciduous forest	·	20.6 ± 2.5	·	h	h	·	✓
Glade	·	3.31 ± 0.37	·	h	h	h	✓
Open land	·	32.6 ± 2.9	·	·	·	·	·
Nutrient-poor pasture	·	19.8 ± 2.3	·	h	·	·	✓
Abandoned pasture	·	8.74 ± 1.4	·	hs	h	·	✓
Improved grassland	·	2.82 ± 0.81	·	h	h	·	✓
Copse	·	1.29 ± 0.28	·	·	h	h	✓
Other habitats[2]	·	0.78 ± 0.18	·	·	h	h	·
Habitat diversity (*H'*)	·	0.6 ± 0.01	·	h	·	·	·
Forest-edge length (km)	·	2.16 ± 0.17	·	·	hs	hs	·
Highly-frequented area (%)[3]	·	7.26 ± 1.2	·	hs	h	h	·

[1] Topographic position index (TPI) values ranged from –53 m to 143 m. Negative values indicate study plots that are situated lower than the surrounding landscape (e.g. valleys or depressions), positive values indicate hills, mountain peaks or ridges surmounting the adjacent landscape.

[2] Built-up areas, roads and water bodies.

[3] Buffer of 150 m around managed and 15 m around private mountain huts.

territories by Mann (1990). Accordingly, his study does not provide information on population densities within the plots, but instead it presents fine-scaled data on the spatial distribution of clustered or single breeding territories. To compare these data with those of our study, we divided each plot into nine grid cells of 250 × 250 m and used the percentage of occupied grid cells per plot (= 'occupancy ratio') as a response variable in further analyses. Grid cells were considered 'occupied' when at least one territory centre was located inside the respective unit.

Habitat quality

To determine habitat quality, we gathered data on climate, elevation, topography and habitat composition in each plot. As the Ring Ouzel is a relatively long-lived passerine species with high breeding-site fidelity (Knoch 1970), and to account for possible inter-annual variation, we averaged climate data over a period of five years with the survey year as the last year of each period (1983–1987 and 2013–2017, respectively). We considered spring (April–June) mean temperature and precipitation sum as well as snow-cover duration (days per year), which were provided by the German Meteorological Service (resolution: 1 × 1 km; CDC 2018).

Elevation data were provided by the U.S. Geological Survey and had a resolution of 75 × 75 m (EROS 2018). These data were also used to calculate the topographic position index (TPI) according to Weiss (2001), with a search radius of 975 m around the centre of each grid cell, using the 'spatialEco' package (Evans 2019). TPI values ranged from –48 to +148 m. Negative values indicate grid cells with an elevation lower than the surrounding landscape (e.g. valleys or depressions), positive values indicate hills, mountain peaks or ridges surmounting the adjacent landscape. For further analysis, elevation and TPI data were averaged per plot. In each plot we mapped the cover of the habitat types listed in Table 1 in the field according to Riecken (2014). The Shannon index of habitat types served as a measure of habitat diversity *H'* (Fartmann et al. 2018, Schwarz et al. 2018):

$$H' = -\sum_i p_i \cdot \ln p_i \text{ with } p_i = \frac{n_i}{N}$$

where N is the number of habitat types per plot and n_i is the area of each habitat type in the plot. We mapped managed and private mountain huts with a buffer of 150 m and 15 m, respectively, as areas highly frequented by tourists. Additionally, we manually measured the forest-edge length from aerial imagery using straight line segments of 20 m length to represent the treeline. For spatial analysis we used the open source software R (R Core Team 2020) and QGIS (QGIS Development Team 2018).

Statistical analysis

Differences between historic and recent period

Differences in plot occupancy, occupancy ratio (= proportion of occupied grid cells per study plot) and climatic conditions between the historic and recent period were tested using the McNemar test (plot occupancy) and the Wilcoxon test (all other variables).

Habitat occupancy and environmental parameters

In order to determine the relationship between Ring Ouzel habitat occupancy and environmental parameters, we computed generalized linear mixed-effects models (GLMMs) with a proportional binomial error structure and random intercepts. Separate models were calculated for the historic (only topography and climate; data on historic habitat characteristics were not available) and recent period, using the respective occupancy ratio as a dependent variable ('lme4' package; Bates et al. 2015). Possible spatial autocorrelation was taken into account by adding subarea as a random effect. At first, we conducted a GLMM for each environmental parameter separately (Appendix A1 and A2). *P* values were obtained from likelihood ratio tests comparing model fits for each parameter to the intercept-only model. In the next step, we calculated multivariable models evaluating the following categories: climate in the historic period and climate, habitat and synthesis in the recent period. The synthesis model was calculated using the significant predictor variables from the respective climate and habitat models.

In order to increase model robustness and identify the most important environmental parameters in the models, we conducted model averaging based on an information-theoretic approach (Burnham and Anderson 2010, Grueber et al. 2011). Proceeding from an all-coefficients full model, we evaluated all possible fixed-effect combinations for each category. From these, we subsequently calculated average models including the top-ranked models within $\Delta AIC_C < 3$ (Grueber et al. 2011). Only significant variables of the climate and habitat model were integrated into the synthesis model. These analyses were carried out using the 'MuMIn' package (Bartoń 2017). For all models, we computed Nakagawa's conditional and marginal pseudo-R^2 (Nakagawa et al. 2017).

Prior to these multivariable analyses, Spearman rank correlations (r_s) of all numerical variables listed in Table 1 were conducted to identify those with strong inter-correlations ($|r_s| \geq 0.5$; see Appendix A3 for the historic and Appendix A4 for the recent period) (Dormann et al. 2013). Intercorrelated variables were not allowed together in one model. For each category (climate, habitat and synthesis), we calculated preliminary models with all permissible maximum variable combinations. Final variable selection for the full models used in the actual analyses was based on the AIC of these preliminary models. Table 1 lists the full-model variable combinations of all categories.

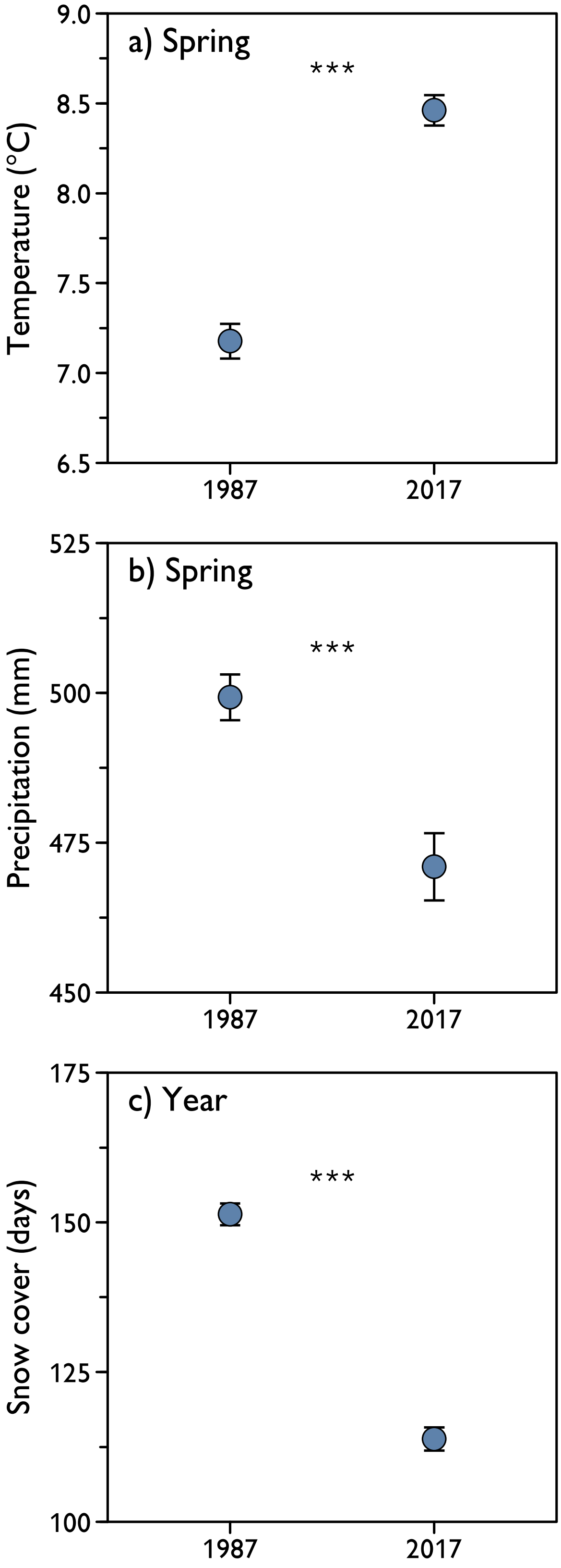

Figure 2. Mean (± standard error) of climate parameters: spring temperature (a), spring precipitation (b) and annual snow cover (in days) (c). $n_{\text{plots}} = 62$. Differences between historic and recent climatic conditions were tested using the paired Wilcoxon test: a) $V = 1812$, $^{***}P < 0.001$; b) $V = 1745$, $^{***}P < 0.001$; c) $V = 1953$, $^{***}P < 0.001$.

Fine scale changes in habitat occupancy

We examined changes in habitat occupancy between the two study periods. Therefore, we analysed 'local colonisation' and 'local extinction' based on historic and recent grid-cell occupancy. Our data were split in two datasets according to their occupancy status in the historic period. Of all grid cells not occupied in the historic period (= dataset one), we defined those occupied in the recent period as 'local colonisation' events. Conversely, of all grid cells occupied in the historic period (= dataset two), those not occupied in the recent period were considered 'local extinction' events.

'The analyses followed a similar path to the habitat occupancy analyses: we conducted univariable and subsequently multivariable binomial GLMMs on local colonisation and extinction using study plot nested in subarea as random factors and only environmental variables from the recent period as fixed effects in the models. The climate parameters were excluded from this analyses because they were at too course a scale relative to the other variables. Variable combination selection and model averaging followed the same procedures as described in *Habitat occupancy and environmental parameters*. See Appendix A4 for variable intercorrelations and Table 1 for final variable selection for the multivariable analyses.

Preliminary models showed that across all modelling approaches, there were no quadratic effects of the considered environmental parameters on the target variables used. Hence, we did not consider quadratic terms in our models. We also included all possible combinations of interaction effects of non-intercorrelated variables in explorative models at all stages of multivariable analyses. Since none of these improved our models, we decided not to include interaction terms in our final analyses.

We used R 3.6.1 for all statistical analyses (R Core Team 2020).

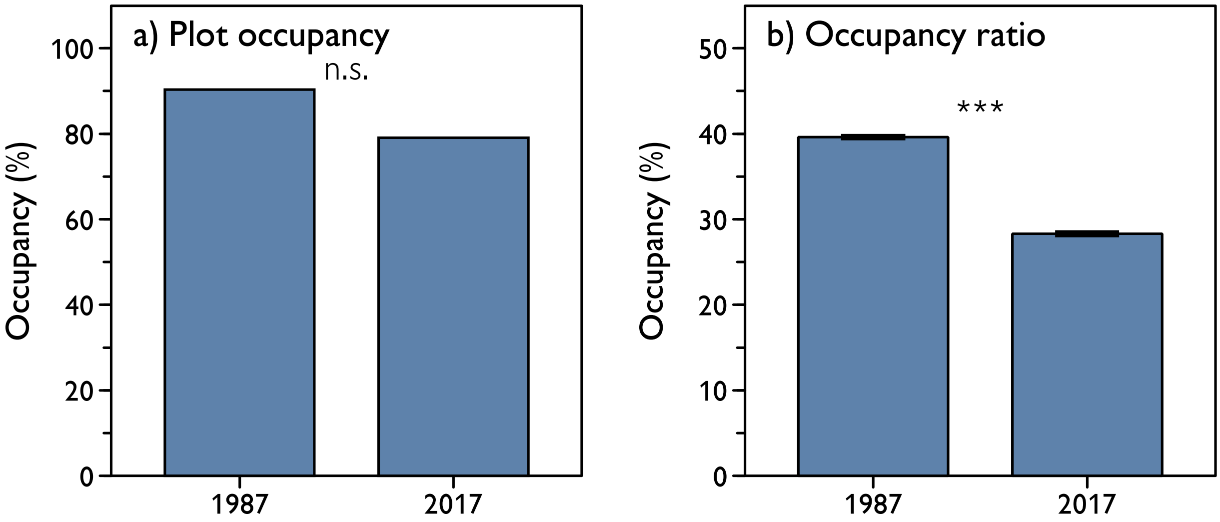

Figure 3. Habitat occupancy. a) Plot occupancy and b) Occupancy ratio ± se of breeding Ring Ouzels in 1987 and 2017. $n_{\text{plots}} = 62$. Differences in plot occupancy and occupancy ratio were tested by McNemar test and paired Wilcoxon test, respectively: a) McNemar's chi-squared = 2.77, $df = 1$, n.s. (not significant) $P > 0.05$; b) $V = 988$, ***$P < 0.001$.

Table 2. Results of model-averaged GLMMs: Relationship of climate parameters with historic (1987) recent (2017) occupancy ratio of the 62 study plots, local colonisation ($n_{grid\ cells} = 337$) and local extinction ($n_{grid\ cells} = 221$). Model-averaged coefficients (full average) derived from the top-ranked models ($\Delta AIC_C < 3$). Occupancy ratio was analysed via a GLMM with proportional binomial error structure, with number of occupied grid cells per plot as response variable and subarea ($N = 7$) as a random factor; colonisation and extinction models were analysed via a GLMM with binomial error structure, occupancy status of grid cells as response variable and plot ($N = 62$) nested in subarea ($N = 7$) as random factors. All fixed effects were standardized prior to the analyses. For each average model, Nakagawa's conditional (R^2_c) and marginal (R^2_m) pseudo-R^2 of the respective best single model is presented. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Parameter	1987		2017		Colonisation		Extinction	
	Est. ± se	***P***	**Est. ± se**	***P***	**Est. ± se**	***P***	**Est. ± se**	***P***
a) Climate model	$R^2_c=0.19$, $R^2_m=0.17$		$R^2_c=0.21$, $R^2_m=0.18$		$R^2_c=0.48$, $R^2_m=0.23$		$R^2_c=0.15$, $R^2_m=0.12$	
Intercept	–0.40 ± 0.16	*	–0.88 ± 0.18	***	–1.43 ± 0.25	***	0.97 ± 0.21	***
TPI	0.41 ± 0.11	***	0.32 ± 0.13	**	1.04 ± 0.23	***	–0.5 ± 0.2	*
Elevation	·	·	·	·	·	·	–0.42 ± 0.18	*
Snow cover	·	·	0.47 ± 0.16	**	·	·	·	·
b) Habitat model	·	·	$R^2_c=0.23$, $R^2_m=0.15$		$R^2_c=0.4$, $R^2_m=0.11$		$R^2_c=0.08$, $R^2_m=0.07$	
Intercept	·	·	–0.98 ± 0.24	***	–1.41 ± 0.38	***	0.79 ± 0.19	***
Conif. forest	·	·	·	·	0.63 ± 0.19	**	·	·
Decid.forest	·	·	–0.33 ± 0.14	*	·	·	·	·
Aband. Past.	·	·	–0.34 ± 0.15	*	·	·	·	·
Forest edge	·	·	·	·	0.37 ± 0.18	*	–0.47 ± 0.18	**
Freq. area	·	·	–0.37 ± 0.16	*	·	·	·	·
c) Synthesis model	·	·	$R^2_c=0.27$, $R^2_m=0.21$		$R^2_c=0.36$, $R^2_m=0.31$		$R^2_c=0.16$, $R^2_m=0.13$	
Intercept	·	·	–0.94 ± 0.2	***	–1.4 ± 0.24	***	0.93 ± 0.21	***
TPI	·	·	·	·	1.01 ± 0.22	***	–0.43 ± 0.22	*
Elevation	·	·	·	·	·	·	–0.5 ± 0.19	*
Snow cover	·	·	0.66 ± 0.19	***	·	·	·	·
Conif. forest	·	·	·	·	0.53 ± 0.19	**	·	·
Aband.past.	·	·	–0.42 ± 0.16	**	·	·	·	·
Forest edge	·	·	·	·	0.39 ± 0.18	*	·	·

RESULTS

Environmental conditions

The mean elevation of the plots ranged from 928 to 1402 m a.s.l.; on average (± se) the plots were situated at an elevation of 1194 ± 15 m (Table 1). A mean TPI of 48.4 ± 5.5 m indicates that most plots were clearly above the surrounding landscape. In 1987, the average values of spring precipitation, spring temperature and snow cover were 499.0 ± 3.8 mm, 7.2 ± 1.0 °C and 151 ± 1.8 days, respectively. From 1987 to 2017 climatic conditions in the plots had changed (Fig. 2). Mean spring temperatures increased by 1.28 ± 0.03 °C, mean spring precipitation decreased by 28.3 ± 4.4 mm and mean annual snow cover declined by 37.0 ± 0.5 days.

Forests covered two thirds of the plots in 2017; the remaining third was occupied by open land. Two thirds of the forests were coniferous and one third was deciduous forest. Open land was composed of two thirds nutrient-poor pasture and one third abandoned pasture. Other habitat types covered only very small proportions of the plots. The mean habitat diversity was 0.49 ± 0.01 and forest edges had an average length of 3.2 ± 0.2 km per plot. Areas that were highly frequented by tourists had a mean share of 7.3 ± 1.2% within the plots (Table 1).

Habitat occupancy

In 1987, 56 (90%) of the 62 studied plots were inhabited by at least one breeding pair of Ring Ouzels. In 2017, we detected 219 territories on only 49 occupied plots (79%). However, this decrease in plot occupancy was not significant (Fig. 3). The occupancy ratio, on the other hand, declined significantly between the historic and recent study period: in 1987, 40 ± 0.3 % of the grid cells were occupied per plot, whereas in 2017 this was only true for 28 ± 0.3 % (Fig. 3). Of 221 grid cells occupied in the historic period, 146 went extinct, and of 337 historically vacant grid cells, 83 were colonised in the recent period.

Model results

The occupancy ratio was related to climate and habitat parameters. In the univariable models, historic and recent occupancy ratio increased with spring precipitation, snow-cover duration, elevation and TPI, and decreased with spring temperature (Appendix A1). Habitat parameters were only analysed for the recent

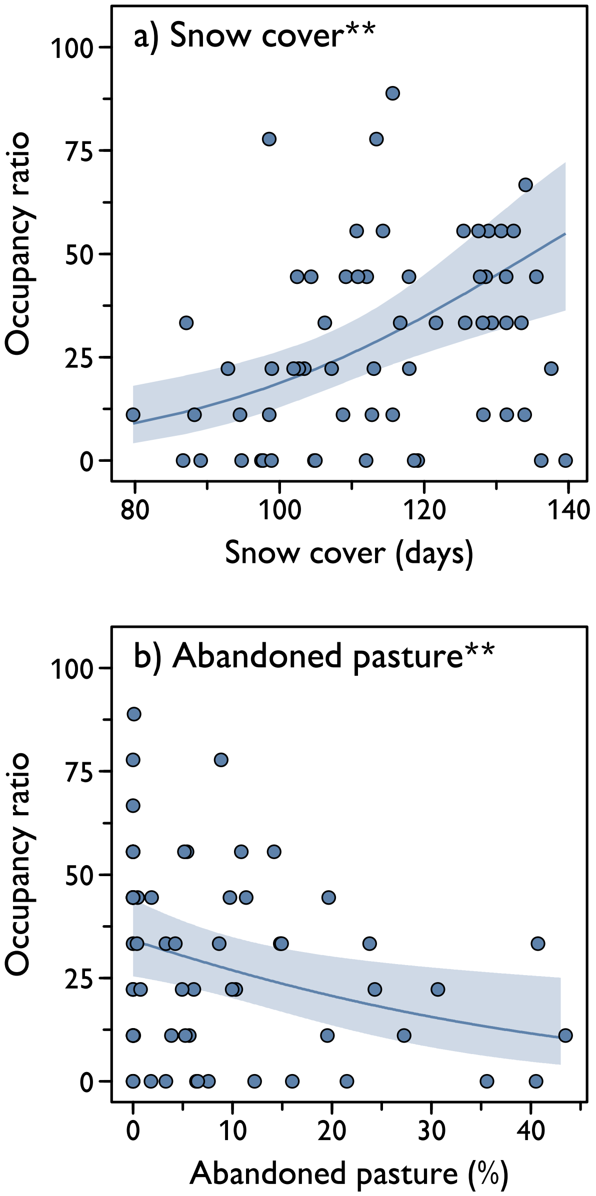

Figure 4. Relationship between occupancy ratio and the significant parameters of the averaged synthesis model. $n_{\text{plots}} = 62$. The regression slopes were fitted using multivariable predictor GLMMs with proportional binomial error structure (see Table 2). ** $P < 0.01$

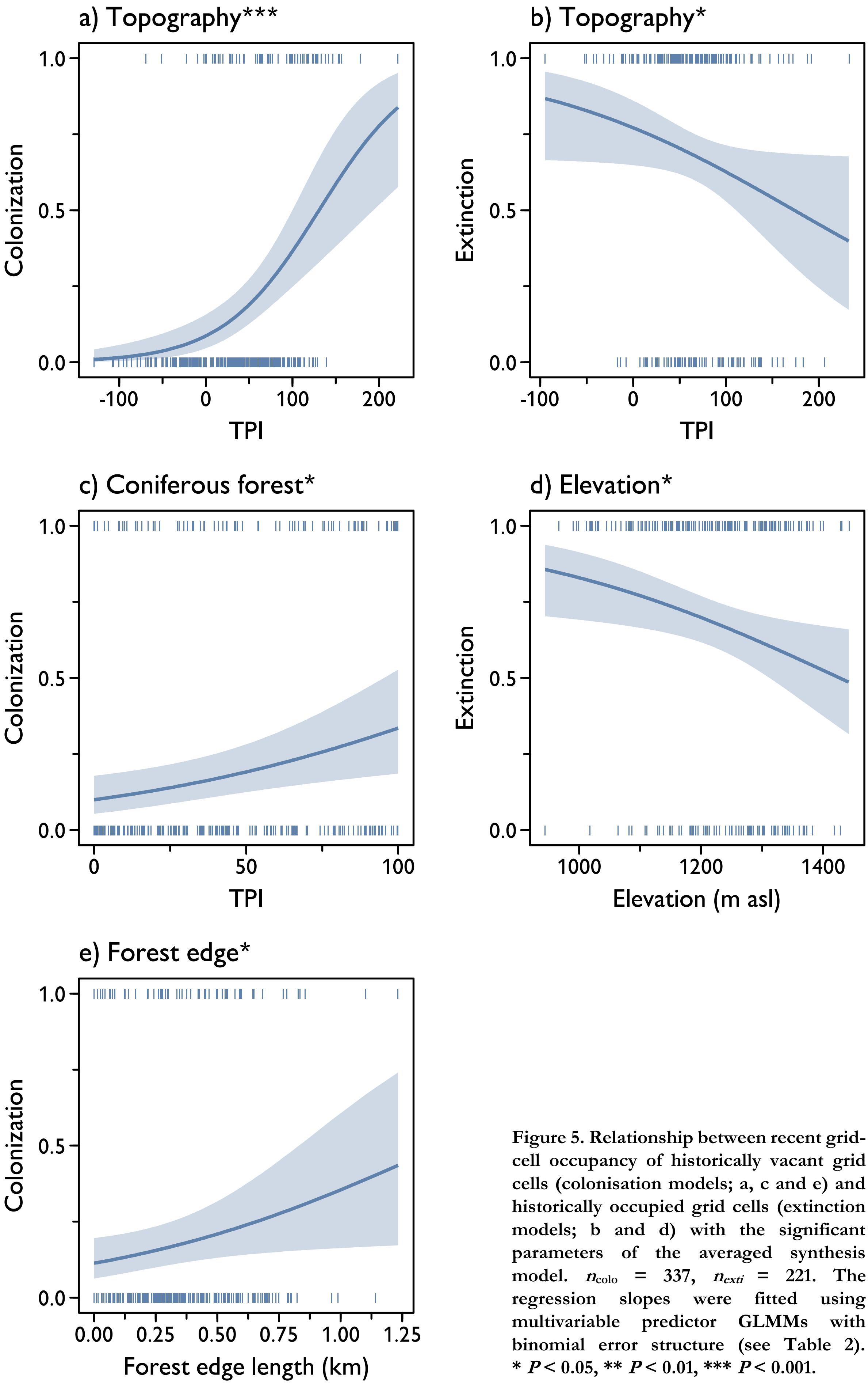

Figure 5. Relationship between recent grid-cell occupancy of historically vacant grid cells (colonisation models; a, c and e) and historically occupied grid cells (extinction models; b and d) with the significant parameters of the averaged synthesis model. n_{colo} = 337, n_{exti} = 221. The regression slopes were fitted using multivariable predictor GLMMs with binomial error structure (see Table 2). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

period. The occupancy ratio increased with the cover of conifer forests and glades, but decreased with deciduous forest, open-land, abandoned-pasture and highly-frequented-area coverage (Appendix A2).

In the multivariable climate models for both study periods, the TPI had a positive effect on the occupancy ratio (Table 2). In the recent period, occupancy also increased with snow-cover duration. In the multivariable habitat model for the recent period, a negative effect of deciduous forests, abandoned pastures and highly frequented areas on occupancy was observed. The multivariable synthesis model identified positive effects of snow-cover duration and negative effects of proportion of abandoned-pasture on recent Ring Ouzel occurrence (Table 2, Fig. 4). Marginal pseudo-R^2 for the multivariable models of occupancy ratio ranged between 0.15 and 0.21, and conditional pseudo-R^2 ranged between 0.19 and 0.27 (Table 2). In the univariable models, local colonisation was related positively to elevation, TPI, coniferous forest cover and forest-edge length, but negatively to deciduous forest cover and highly-frequented area proportion (Appendix A1 and A2). Local extinction was related negatively to elevation, TPI and forest-edge length. In the multivariable models, local colonisation was positively related to the TPI (climate and synthesis model), coniferous forest cover and forest-edge length (habitat and synthesis model; Table 2, Fig. 5). Local extinction was related negatively to the TPI and elevation (climate and synthesis model) as well as forest-edge length (habitat model). Marginal pseudo-R^2 ranged from 0.11 to 0.31 and from 0.07 to 0.13, conditional pseudo-R^2 from 0.36 to 0.48 and from 0.08 to 0.16, for the colonisation and extinction models respectively.

DISCUSSION

Our study revealed that over the past three decades, habitat occupancy by the Ring Ouzel has decreased by about one third in the southern Black Forest, mainly at lower elevations and in depressed landforms. Local habitat occupancy changes were relatively frequent: 66% of the historically occupied grid cells were not occupied in the recent survey, whereas local colonisation occurred in 25% of the historically vacant grid cells. Both the occupancy ratio and local changes in habitat occupancy were driven by climate and habitat parameters: The Ring Ouzel preferred convex landscape formations (high TPI values), such as mountain peaks and ridges, that were characterized by long periods of snow cover for breeding. In contrast, sites with high cover of deciduous forests and abandoned pastures were avoided as breeding habitats in the recent period. Local colonisation was more likely at convex landscape formations with long snow-cover duration as well as at sites with high coniferous forest cover and long forest-edge length. Local extinction, on the other hand, was more likely at depressed sites (low TPI values) with short snow-cover duration and at sites with short forest-edge length.

As a result of climate change, spring temperatures had increased from 1987 to 2017 in the study plots whereas spring precipitation and snow-cover duration had decreased. All three parameters were a function of elevation (except precipitation in the historic period). Disentangling the effects of the different climate parameters on Ring Ouzel habitat use was therefore not straightforward. However, models with the variable ‘snow cover duration’ performed slightly better than those with the other climate parameters.

Persistence of snow fields was reflected by three variables, ‘snow-cover duration’ and the intercorrelated ‘elevation’ as well as 'topographic position index' (TPI). High TPI values indicated long persistence of snow fields at a finer spatial scale than the relatively coarse-grained data of days with snow cover (resolution 1 × 1 km, cf. *Habitat quality*). In most high-elevation mountain ranges, snow accumulation is mainly driven by avalanches leading to long-lasting snow beds in small valley bottoms. The study area, however, is characterized by a smoother relief so that the lee-sides of convex landscape formations such as hills, mountain peaks or ridges (= high TPI values) were usually characterized by thick snow cornices in spring (pers. obs.; Geiger et al. 1995). All three parameters, especially TPI, were among the most important environmental variables in all multivariable models of our study and indicated a positive effect of long-persisting snow on the Ring Ouzel.

The Ring Ouzel is a cold-adapted species restricted to mountain ranges. Like other mountain species, it is potentially highly vulnerable to climate warming, which might have caused the observed range retraction through uphill shifts at the lower distribution boundary (e.g. Stuhldreher and Fartmann 2018, Ewing et al. 2020). The mechanisms driving such range shifts and retractions can differ strongly across different taxa. Whereas poikilothermic species, such as invertebrates, might be affected by climate change immediately, e.g. through accelerated metabolism (e.g. Stuhldreher et al. 2014, Stuhldreher and Fartmann 2018), homoiothermic species should rather be affected by changes in the complex ecological networks of which they are part.

In spring we often observed Ring Ouzels feeding in moist microhabitats with short vegetation that had only recently become free of snow. Especially during the breeding season, Ring Ouzels mainly feed on earthworms and other belowground invertebrates (Glutz von Blotzheim & Bauer 1988). For hunting Ring Ouzels, a key property of soils is thus their penetrability, which largely depends on their moisture content (Barras et al. 2019). Slowly melting snowfields imbue subjacent and surrounding soils at a fairly constant rate, rendering them suitable hunting grounds. Due to the fast runoff and the mostly shallow soils, the continuous water supply is of special interest in mountainous areas: the soil penetrability is probably driven to a much greater extent by the snowpack than by precipitation. Additionally, it has been shown that invertebrate activity and density is particularly high shortly after thaw (Harry et al. 2019). A strong dependence of foraging Ring Ouzels on patches with short swards and moist soils, which appear in the vicinity of snow beds after snow melt, has also been reported for the Swiss Alps (Barras et al. 2019). In the face of climate change, snow fields with their important foraging habitats disappear earlier in spring. Additionally, reduced precipitation rates generally lead to drier, less penetrable soils. These developments have great potential to negatively affect the breeding success of the species. We conclude that the ever-earlier thaw of snow fields is probably one of the main reasons for the observed decline of the species at lower elevations and in depressed landforms.

Snow is an important, yet perhaps underestimated environmental factor (but compare e.g. Stuhldreher et al. 2014). Among the species adapted to cold environments, the Ring Ouzel is thus probably not an exception with respect to its dependency on long snow-cover duration. In the study area, other endangered cold-adapted species such as the Moorland Clouded Yellow *Colias palaeno* or the Citril Finch *Carduelis citronella* might also depend on long periods of snow cover. Further examples of possible snow cover–areal relationships include the Eurasian Dotterel *Charadrius morinellus* (Ewing et al. 2020) or the Woodland Ringlet *Erebia medusa* (Stuhldreher et al. 2014, Stuhldreher and

Fartmann 2018). Future research should thus focus more on the impact of advanced thawing.

The Ring Ouzel is known to be a characteristic breeding bird of mosaics of sparse montane conifer forests with semi-open and open habitats (Schirutschke 2005, Bauer et al. 2013). In accord with this, the occupancy ratio was positively related to conifer forests and glades, whereas deciduous forests and abandoned pastures were avoided. Among these four predictors, the cover of abandoned pastures was the only significant variable in the synthesis model. The fine-scale models on local colonisation and extinction indicated that the forest-edge length is another decisive habitat factor for territory establishment, underpinning the specialisation of the species on ecotones.

Alpine Ring Ouzels build their nests in coniferous trees. Feeding, however, mainly takes place in open habitats (Glutz von Blotzheim and Bauer 1988, Ciach and Mrowiec 2013, Barras et al. 2019). We frequently observed hunting Ring Ouzels in grasslands with short-growing, sparse vegetation, whereas high-growing grasslands were avoided. These observations are in line with the findings from the Carpathians (Ciach and Mrowiec 2013) and Alps (Barras et al. 2019). Similar feeding behaviour has also been reported for the subspecies *T. t. torquatus* in Scotland (Burfield 2002). Low-growing, sparsely-vegetated grasslands are characteristic of traditional grassland management, which has increasingly been abandoned in European mountain areas (Caraveli 2000, MacDonald et al. 2000), including the Black Forest (Regional Office for Environment 2004, Geis et al. 2013, MLR-BW 2016). The abandoned pastures, and also those which are grazed only sporadically, in the study area were characterized by dense and tall swards and partly encroached by shrubs (pers. obs.). These grasslands thus probably are of low importance for feeding Ring Ouzels. The abandonment of traditional grazing similarly threatens several other bird species which also require short-growing, sparsely-vegetated feeding grounds such as the Common Wheatear *Oenanthe oenanthe*, the Meadow Pipit *Anthus pratensis*, the Rock Bunting *Emberiza cia*, the Tree Pipit *Anthus trivialis*, the Water Pipit *Anthus spinoletta* and the Woodlark *Lullula arborea* (Ebenhöh 2003, Regional Office for Environment 2004, Bauer et al. 2013). In contrast, land-use intensification played a minor role in our study area and seems to mainly impact lower-elevated sites in the Black Forest (Fumy et al. 2020).

Close vicinity of feeding grounds (short-growing grasslands) with coniferous trees which serve as song posts and nest-sites probably facilitates successful breeding. This assumption is supported by the importance of forest-edge length in our analyses for local habitat colonisation and extinction. Long forest-edge length (up to 1.2 km in a plot of 250 × 250 m) indicates a strong interconnection of forest and open land. As a consequence of landscape homogenisation in the course of land-use change, the extent of such ecotones has been greatly reduced in Central Europe (Poschlod 2017). Not so much is known about the effects of ecotone loss on biodiversity in general. However, it seems obvious that the numerous species specialised on these complex habitats – such as the Ring Ouzel – could be affected negatively.

Besides the effects of climate change and habitat alteration by land-use abandonment, disturbance by humans can also affect bird species (Monz et al. 2013, Coppes et al. 2017). We observed a negative relationship between occupancy ratio and areas that were highly frequented by tourists. Hence, the ever-increasing touristic activity (e.g. e-mountainbiking, 'premium mountain huts', etc.) indeed may be an additional driver of the species' decline. This assumption is supported by Anger et al. (2020) who linked the abandonment of the most important, traditional breeding sites of Ring Ouzels in the northern Black Forest to the installation of touristic attractions.

To sum up, we have strong indications that both climate and land-use change were responsible for the habitat loss of the Ring Ouzel in the study area. We consider long-persisting snow fields as key requisites for foraging during spring and early summer, and hence for the breeding success of the species. Due to climate change, snow-cover duration decreased substantially between 1987 and 2017. As a consequence, the species retreated into higher elevations and to the most exposed sites with plentiful snow. At the same time, the abandonment of grazing reduced the extent of short-growing, sparsely vegetated grasslands, which are the main feeding grounds of the species. The presence of touristic infrastructure further limited the availability of breeding habitats.

IMPLICATIONS FOR CONSERVATION

For the conservation of the Ring Ouzel, we recommend measures to (i) mitigate the negative effects of climate change and (ii) improve the quality of the habitats. In the Black Forest and many other low mountain ranges, the Ring Ouzel already occupies the highest elevations (Knoch 1970, Mann 1990, Knaus et al. 2018) and further uphill shifts in response to climate change are impossible. Accordingly, the creation or maintenance of suitable habitat should be supported, especially on north and east facing slopes on the lee sides of hills, mountain peaks or ridges (Streitberger et al. 2016b, Stuhldreher and Fartmann 2018). In general, we recommend the maintenance and creation of small-scale mosaics of conifer forests and pastures. Within the forests, sparse stands should be established. Grassland management must include the re-introduction of regular livestock grazing without the application of fertilizers, preferably with traditional local breeds (e.g. "*Hinterwälder*"). Areas with appropriate habitat configuration and long-lasting snow-cover should be protected from excessive visitor numbers in spring and early summer. Such measures should foster the Ring Ouzel, but also a large set of other mountain taxa (Braunisch et al. 2014, Knaus et al. 2018, Barras et al. 2019, Fumy et al. 2020).

ACKNOWLEDGEMENTS

For their hospitality and providing accommodation during the period of field work, we would like to thank Dr. Gerhard Geis-Tyroller and Notburga Tyroller as well as Sigrid and Andreas Wiessler. We are grateful to Claudia Frank and Markus Frenzel for help during field work. The Department of Nature and Landscape Conservation of the Regierungspräsidium Freiburg (Regional Nature Conservation Authority) gave permission to survey the Ring Ouzel in protected areas of the study area. Darin McNeil made helpful comments on a statistical issue. Additionally, we would like to thank two anonymous reviewers for valuable comments on an earlier version of the manuscript.

FUNDING

This study was funded by a PhD scholarship from the German Environmental Foundation (DBU) allocated to Florian Fumy.

DATA AVAILABILITY STATEMENT

The data collected in this study are available on request from the authors.

APPENDIX

A1. Climate and occupancy patterns. Significant relationships of climate parameters with historic (1987) and recent (2017) occupancy ratio of the 62 study plots, local colonisation ($n_{grid\ cells}$ = 337) and local extinction ($n_{grid\ cells}$ = 221). Occupancy ratio was analysed via univariate GLMMs with proportional binomial error structure, number of occupied grid cells per plot as response variable and subarea ($N = 7$) as a random factor; colonisation and extinction models were analysed via univariate GLMMs with binomial error structure, occupancy status of grid cells as response variable and plot ($N = 62$) nested in subarea ($N = 7$) as random factors. All fixed effects were standardized prior to the analyses. P values were obtained from likelihood ratio tests comparing model fits for each parameter to the intercepts-only model via ANOVA. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Nakagawa's conditional (R^2_c) and marginal (R^2_m) pseudo-R^2 are presented.

Parameter	**1987**				**2017**			
	Est. ± se	P	R^2_c	R^2_m	**Est. ± se**	P	R^2_c	R^2_m
Spring temperature	–0.31 ± 0.15	*	0.09	0.03	–0.57 ± 0.15	***	0.14	0.09
Spring precipitation	0.38 ± 0.12	**	0.06	0.04	0.63 ± 0.12	***	0.13	0.12
Snow-cover duration	0.36 ± 0.14	*	0.12	0.08	0.59 ± 0.18	***	0.19	0.12
Elevation	0.5 ± 0.16	**	0.12	0.07	0.62 ± 0.17	***	0.17	0.13
TPI[1]	0.43 ± 0.11	***	0.11	0.05	0.36 ± 0.12	**	0.1	0.03
	Colonisation				**Extinction**			
Elevation	1.16 ± 0.31	***	0.3	0.16	–0.56 ± 0.21	**	0.06	0.05
TPI[1]	1.11 ± 0.23	***	0.26	0.15	–0.52 ± 0.2	**	0.06	0.04

[1] Topographic position index (TPI) values ranged from –48 m to 148 m. Negative values indicate grid-cells that are situated lower than the surrounding landscape (e.g. valleys or depressions), positive values indicate hills, mountain peaks or ridges surmounting the adjacent landscape.

A2. Habitat characteristics and occupancy patterns. Relationship of habitat parameters with recent occupancy ratio (n_{plots} = 62), local colonisation ($n_{grid\ cells}$ = 337) and local extinction ($n_{grid\ cells}$ = 221), respectively. Occupancy ratio was analysed via univariate GLMMs with proportional binomial error structure, number of occupied grid cells per plot as response variable and subarea (N = 7) as a random factor; colonisation and extinction models were analysed via univariate GLMMs with binomial error structure, occupancy status of grid cells as response variable and plot (N = 62) nested in subarea (N = 7) as random factors. All fixed effects were standardized prior to the analyses. P values were obtained from likelihood ratio tests comparing model fits for each parameter to the intercepts-only model via ANOVA. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Nakagawa's conditional (R^2_c) and marginal (R^2_m) pseudo-R^2 are presented.

Parameter	Occupancy ratio				Colonisation				Extinction			
	Est. ± se	P	R^2_c	R^2_m	Est. ± se	P	R^2_c	R^2_m	Est. ± se	P	R^2_c	R^2_m
Habitat type												
Forest	0.22 ± 0.13	0.09	0.16	0.01	0.3 ± 0.14	0.09	0.28	0.03	0.15 ± 0.18	0.41	0.01	0
Coniferous forest	0.37 ± 0.11	***	0.2	0.04	0.55 ± 0.17	***	0.31	0.14	–0.14 ± 0.16	0.38	0.01	0
Deciduous forest	–0.38 ± 0.14	**	0.22	0.04	–0.39 ± 0.17	*	0.32	0.09	0.29 ± 0.16	0.06	0.04	0.03
Glade	0.3 ± 0.1	**	0.16	0.03	0.07 ± 0.21	0.73	0.27	0	–0.05 ± 0.11	0.64	0.01	0
Open land	–0.28 ± 0.13	*	0.17	0.02	–0.3 ± 0.14	0.08	0.29	0.03	–0.14 ± 0.18	0.44	0.01	0
Nutrient-poor pasture	–0.09 ± 0.13	0.49	0.16	0	–0.28 ± 0.14	0.11	0.29	0.02	–0.24 ± 0.19	0.2	0.02	0.01
Abandoned pasture	–0.34 ± 0.14	*	0.15	0.07	–0.05 ± 0.13	0.79	0.27	0.01	0.11 ± 0.21	0.61	0.02	0
Improved grassland	–0.22 ± 0.16	0.14	0.15	0.01	–0.1 ± 0.14	0.57	0.27	0	0.03 ± 0.6	0.96	0.01	0
Copse	0.13 ± 0.11	0.24	0.16	0	0.1 ± 0.15	0.5	0.28	0	0.06 ± 0.17	0.71	0.01	0
Other habitats[1]	–0.18 ± 0.16	0.23	0.16	0.05	–0.22 ± 0.18	0.24	0.29	0.02	0.46 ± 0.5	0.31	0.02	0.01
Habitat diversity (H')	0.08 ± 0.11	0.51	0.16	0	–0.11 ± 0.13	0.77	0.28	0	0.01 ± 0.16	0.95	0.01	0
Forest-edge length	–0.14 ± 0.12	0.23	0.17	0	0.23 ± 0.13	*	0.27	0.08	–0.29 ± 0.15	*	0.1	0.09
Highly-frequented area[2]	–0.39 ± 0.13	**	0.13	0.04	–0.44 ± 0.21	*	0.29	0.08	0.23 ± 0.21	0.25	0.02	0.01

[1] Built-up area, roads and water bodies.

[2] Buffer of 150 m around managed and 15 m around private mountain huts.

A3. Results of Spearman rank correlations (r_s) among climate parameters in the historic period. Variables with strong inter-correlations ($|r_s| \geq 0.5$) are in bold type. For further information, see *Statistical analysis*. TPI = Topographic position index. n.s. (not significant) $P > 0.05$; *** $P < 0.001$.

Variable	TPI	Precipitation	Temperature	Snow cover
Elevation	$0.38^{n.s.}$	$0.24^{n.s.}$	$\mathbf{-0.90}^{***}$	$\mathbf{0.89}^{***}$
TPI	/	$0.16^{n.s.}$	$-0.13^{n.s.}$	$0.20^{n.s.}$
Precipitation	.	/	$-0.36^{n.s.}$	$-0.42^{n.s.}$
Temperature	.	.	/	$\mathbf{-0.96}^{***}$

A4. Results of Spearman rank correlations (r_s) among environmental parameters in the recent period. Variables with strong inter-correlations ($|r_s| \geq 0.5$) are in bold type. For further information, see *Statistical Analyses*. TPI = Topographic position index. n.s. (not significant) $P > 0.05$; *** $P < 0.001$.

Parameter	TPI	Preci	Temp	Snow	Forest	ConFo	DecFo	Glade	OpenL	NpPas	APas	IGras	Copse	OHab	H'	FoLeng	HfArea
i) Study Plots																	
Elevation	0.38$^{\text{n.s.}}$	**0.69*****	**–0.91*****	**0.92*****	–0.14$^{\text{n.s.}}$	0.21$^{\text{n.s.}}$	–0.48$^{\text{n.s.}}$	0.14$^{\text{n.s.}}$	0.17$^{\text{n.s.}}$	0.22$^{\text{n.s.}}$	0.35$^{\text{n.s.}}$	**–0.53*****	0.03$^{\text{n.s.}}$	–0.10$^{\text{n.s.}}$	0.11$^{\text{n.s.}}$	0.13$^{\text{n.s.}}$	–0.07$^{\text{n.s.}}$
TPI	/	0.27$^{\text{n.s.}}$	–0.20$^{\text{n.s.}}$	0.19$^{\text{n.s.}}$	0.27$^{\text{n.s.}}$	0.29$^{\text{n.s.}}$	–0.14$^{\text{n.s.}}$	0.07$^{\text{n.s.}}$	–0.25$^{\text{n.s.}}$	–0.17$^{\text{n.s.}}$	–0.07$^{\text{n.s.}}$	–0.36$^{\text{n.s.}}$	–0.17$^{\text{n.s.}}$	–0.30$^{\text{n.s.}}$	0.06$^{\text{n.s.}}$	–0.25$^{\text{n.s.}}$	–0.31$^{\text{n.s.}}$
Precipitation	.	/	**–0.75*****	**0.71*****	–0.04$^{\text{n.s.}}$	0.15$^{\text{n.s.}}$	–0.30$^{\text{n.s.}}$	0.32$^{\text{n.s.}}$	0.07$^{\text{n.s.}}$	0.20$^{\text{n.s.}}$	0.16$^{\text{n.s.}}$	–0.45$^{\text{n.s.}}$	0.00$^{\text{n.s.}}$	–0.28$^{\text{n.s.}}$	0.17$^{\text{n.s.}}$	0.13$^{\text{n.s.}}$	–0.16$^{\text{n.s.}}$
Temperature	.	.	/	**–0.97*****	0.21$^{\text{n.s.}}$	–0.15$^{\text{n.s.}}$	0.45$^{\text{n.s.}}$	–0.18$^{\text{n.s.}}$	–0.24$^{\text{n.s.}}$	–0.29$^{\text{n.s.}}$	–0.38$^{\text{n.s.}}$	0.43$^{\text{n.s.}}$	–0.07$^{\text{n.s.}}$	0.09$^{\text{n.s.}}$	–0.11$^{\text{n.s.}}$	–0.17$^{\text{n.s.}}$	0.03$^{\text{n.s.}}$
Snow–cover duration	.	.	.	/	–0.27$^{\text{n.s.}}$	0.12$^{\text{n.s.}}$	**–0.50*****	0.14$^{\text{n.s.}}$	0.29$^{\text{n.s.}}$	0.37$^{\text{n.s.}}$	0.33$^{\text{n.s.}}$	–0.47$^{\text{n.s.}}$	0.16$^{\text{n.s.}}$	–0.09$^{\text{n.s.}}$	0.14$^{\text{n.s.}}$	0.21$^{\text{n.s.}}$	–0.01$^{\text{n.s.}}$
Forest	.	.	.	.	/	**0.63*****	0.34$^{\text{n.s.}}$	0.39$^{\text{n.s.}}$	**–0.99*****	**–0.85*****	**–0.54*****	0.31$^{\text{n.s.}}$	**–0.53*****	–0.28$^{\text{n.s.}}$	–0.16$^{\text{n.s.}}$	**–0.69*****	**–0.52*****
Coniferous forest	.	.	.	.	.	/	–0.44$^{\text{n.s.}}$	0.41$^{\text{n.s.}}$	**–0.64*****	**–0.55*****	–0.29$^{\text{n.s.}}$	–0.29$^{\text{n.s.}}$	–0.30$^{\text{n.s.}}$	–0.19$^{\text{n.s.}}$	–0.25$^{\text{n.s.}}$	–0.46$^{\text{n.s.}}$	–0.36$^{\text{n.s.}}$
Deciduous forest	.	.	.	.	.	.	/	–0.14$^{\text{n.s.}}$	–0.35$^{\text{n.s.}}$	–0.29$^{\text{n.s.}}$	–0.27$^{\text{n.s..}}$	0.09$^{\text{n.s}}$	–0.23$^{\text{n.s.}}$	0.02$^{\text{n.s..}}$	0.17$^{\text{n.s}}$	–0.16$^{\text{n.s.}}$	–0.11$^{\text{n.s.}}$
Glade	.	.	.	.	.	.	.	/	–0.38$^{\text{n.s.}}$	–0.27$^{\text{n.s.}}$	–0.16$^{\text{n.s.}}$	–0.32$^{\text{n.s.}}$	–0.25$^{\text{n.s.}}$	–0.30$^{\text{n.s.}}$	0.09$^{\text{n.s.}}$	–0.21$^{\text{n.s.}}$	–0.23$^{\text{n.s.}}$
Open land	.	.	.	.	.	.	.	.	/	**0.87*****	**0.53*****	0.29$^{\text{n.s.}}$	**0.53*****	0.22$^{\text{n.s.}}$	0.16$^{\text{n.s.}}$	**0.68*****	0.48$^{\text{n.s.}}$
Nutrient–poor pasture	.	.	.	.	.	.	.	.	.	/	0.22$^{\text{n.s.}}$	0.09$^{\text{n.s.}}$	**0.58*****	0.02$^{\text{n.s.}}$	0.29$^{\text{n.s.}}$	**0.64*****	0.32$^{\text{n.s.}}$
Abandoned pasture	.	.	.	.	.	.	.	.	.	.	/	0.05$^{\text{n.s.}}$	0.07$^{\text{n.s.}}$	0.25$^{\text{n.s.}}$	0.20$^{\text{n.s.}}$	0.39$^{\text{n.s.}}$	0.37$^{\text{n.s.}}$
Improved grassland	.	.	.	.	.	.	.	.	.	.	.	/	0.14$^{\text{n.s.}}$	0.26$^{\text{n.s.}}$	–0.21$^{\text{n.s.}}$	0.23$^{\text{n.s.}}$	0.28$^{\text{n.s.}}$
Copse	.	.	.	.	.	.	.	.	.	.	.	.	/	0.14$^{\text{n.s.}}$	0.34$^{\text{n.s.}}$	**0.52*****	0.34$^{\text{n.s.}}$
Other habitats	.	.	.	.	.	.	.	.	.	.	.	.	.	/	–0.12$^{\text{n.s.}}$	0.20$^{\text{n.s.}}$	**0.65*****
Habitat diversity (H')	.	.	.	.	.	.	.	.	.	.	.	.	.	.	/	0.43$^{\text{n.s}}$	0.08$^{\text{n.s}}$
Forest-edge length	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	/	0.42$^{\text{n.s}}$

Parameter	TPI	Preci	Temp	Snow	Forest	ConFo	DecFo	Glade	OpenL	NpPas	APas	IGras	Copse	OHab	H'	FoLeng	HfArea
ii) Grid cells: colonisation																	
Elevation	0.46***	.	.	.	-0.11*	0.11*	-0.36***	-0.01$^{n.s.}$	0.14*	0.11*	0.26***	-0.41***	-0.03$^{n.s.}$	-0.1$^{n.s.}$	-0.31***	0.03$^{n.s.}$	-0.13*
TPI	/	.	.	.	0.16**	0.21***	-0.14*	0$^{n.s.}$	-0.12*	-0.15**	0.05$^{n.s.}$	-0.28***	-0.12*	-0.2***	-0.31***	-0.14**	-0.24***
Forest	.	.	.	.	/	**0.63*****	0.47***	0.33***	**–0.96*****	**–0.77*****	–0.48***	–0.31***	–0.41***	–0.28***	–0.26***	–0.43***	–0.4***
Coniferous forest	.	.	.	.	.	/	–0.25***	0.37***	**–0.63*****	**–0.54*****	–0.21***	–0.18***	–0.22***	–0.17**	–0.24***	–0.16**	–0.23***
Deciduous forest	.	.	.	.	.	.	/	0.13*	–0.45***	–0.32***	–0.32***	–0.07$^{n.s.}$	–0.26***	–0.09$^{n.s.}$	0.3***	–0.12*	–0.18**
Glade	.	.	.	.	.	.	.	/	–0.47***	–0.38***	–0.19***	–0.15**	–0.17**	–0.16**	0.15**	–0.11*	–0.22***
Open land	.	.	.	.	.	.	.	.	/	**0.81*****	**0.5*****	0.31***	0.34***	0.23***	0.21***	0.47***	0.37***
Nutrient–poor pasture	.	.	.	.	.	.	.	.	.	/	0.11*	0.06$^{n.s.}$	0.34***	0.12*	0.23***	0.42***	0.26***
Abandoned pasture	.	.	.	.	.	.	.	.	.	.	/	0.11*	0.11*	0.19***	0.14**	0.37***	0.22***
Improved grassland	.	.	.	.	.	.	.	.	.	.	.	/	0.07$^{n.s.}$	0.33***	0.44***	0.17**	0.37***
Copse	.	.	.	.	.	.	.	.	.	.	.	.	/	0.11*	0.27***	0. 39***	0.08$^{n.s.}$
Other habitats	.	.	.	.	.	.	.	.	.	.	.	.	.	/	0.16**	0.13*	**0.64*****
Habitat diversity (H')	.	.	.	.	.	.	.	.	.	.	.	.	.	.	/	**0.54*****	0.15**
Forest-edge length	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	/	0.18***
iii) Grid cells: extinction																	
Elevation	0.21**	.	.	.	-0.4***	0.05$^{n.s.}$	-0.46***	0.03$^{n.s.}$	0.39***	0.31***	0.43***	-0.25***	0.09$^{n.s.}$	0.08$^{n.s.}$	-0.06$^{n.s.}$	0.36***	0.17*
TPI	/	.	.	.	-0.11$^{n.s.}$	-0.04$^{n.s.}$	-0.03$^{n.s.}$	0.07$^{n.s.}$	0.05$^{n.s.}$	0.04$^{n.s.}$	0.05$^{n.s.}$	-0.18**	0.03$^{n.s.}$	-0.1$^{n.s.}$	0.04$^{n.s.}$	0$^{n.s.}$	-0.13$^{n.s.}$
Forest	.	.	.	.	/	**0.53*****	0.29***	–0.04$^{n.s.}$	**–0.81*****	**–0.73*****	**–0.54*****	–0.1/	–0.34***	–0.24***	–0.49***	**–0.67*****	–0.25***
Coniferous forest	.	.	.	.	.	/	**–0.53*****	0.16*	–0.46***	–0.45***	–0.29***	–0.07$^{n.s.}$	–0.24***	–0.12$^{n.s.}$	**–0.66*****	–0.33***	–0.17*
Deciduous forest	.	.	.	.	.	.	/	–0.06$^{n.s.}$	–0.25***	–0.2**	–0.24***	0.02$^{n.s.}$	–0.09$^{n.s.}$	–0.08$^{n.s.}$	0.48***	–0.15*	–0.06$^{n.s.}$
Glade	.	.	.	.	.	.	.	/	–0.4***	–0.36***	–0.23***	–0.17**	–0.03$^{n.s.}$	–0./	0.12$^{n.s.}$	–0.34***	–0.06$^{n.s.}$
Open land	.	.	.	.	.	.	.	.	/	**0.89*****	**0.65*****	0.2**	0.25***	0.22**	0.33***	**0.87*****	0.2**
Nutrient–poor pasture	.	.	.	.	.	.	.	.	.	/	0.35***	0.15*	0.27***	0.21**	0.36**	**0.75*****	0.16*
Abandoned pasture	.	.	.	.	.	.	.	.	.	.	/	0$^{n.s.}$	0.15*	0.17**	0.17*	**0.57*****	0.26***
Improved grassland	.	.	.	.	.	.	.	.	.	.	.	/	–0.0/	0.0/	0.16*	0.21**	–0.02$^{n.s.}$
Copse	.	.	.	.	.	.	.	.	.	.	.	.	/	0.3***	0.31***	0.26***	0.21**
Other habitats	.	.	.	.	.	.	.	.	.	.	.	.	.	/	0.19**	0.26***	**0.62*****
Habitat diversity (H')	.	.	.	.	.	.	.	.	.	.	.	.	.	.	/	0.38***	0.17*
Forest-edge length	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	/	0.24***

Response of Orthoptera assemblages to environmental change in a low-mountain range differs among grassland types

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ABSTRACT

Grasslands are among the most species-rich ecosystems in Europe. However, their biodiversity has become increasingly threatened by land-use and climate change. Here, we analyse Orthoptera assemblage shifts between 1996 and 2017 across three grassland types in the Black Forest (SW Germany) ($N = 63$): (i) formerly managed wet grasslands which have been frequently abandoned in recent decades (WET) ($N = 15$); (ii) common pastures which are still traditionally managed by rough grazing (COMMON) ($N = 29$), and (iii) mesic grasslands which have recently suffered from land-use intensification (MESIC) ($N = 19$).

Both annual and summer temperatures increased during the study period. Orthoptera assemblages strongly responded to the altered environmental conditions in the grasslands. However, effects differed clearly among grassland types. Despite a strong increase in overall species richness in common pastures, neither the Community Farmland Index (CFI) nor the Community Temperature Index (CTI) had changed. In contrast, in the two other grassland types, the CFI decreased and the CTI increased.

The CFI–established here for Orthoptera–helped to disentangle the effects of climate and land-use change on Orthoptera assemblage composition. Based on our study, climate warming has led to biotic homogenisation of the Orthoptera assemblages of wet grasslands affected by abandonment, and mesic grasslands affected by land-use intensification towards a dominance of more widespread species. In contrast, common pastures characterized by a high heterogeneity and low-intensity management were more resilient to the effects of climate warming.

KEYWORDS

Agricultural abandonment, climate change, Community Farmland Index, Community Temperature Index, land-use change, range shift

Journal of Environmental Management 256 (2020). https://doi.org/10.1016/j.jenvman.2019.109919

INTRODUCTION

Grasslands are among the most species-rich ecosystems in Europe and cover >20% of the EU-28 land surface (Wilson et al. 2012, Feurdean et al. 2018, EC 2019). Most of the European grasslands have been shaped by human agricultural practices (Veen et al. 2009, Feurdean et al. 2018). However, due to the transition from pre-industrial land use to industrial agriculture, the extent of semi-natural grasslands of high conservation value has greatly decreased, mainly driven by agricultural intensification and land-use abandonment (Wallis de Vries et al. 2002). As a result, biodiversity of European grassland ecosystems has become increasingly threatened.

Human-induced climate change has caused further habitat changes in grasslands (Streitberger et al. 2016a, Gibson and Newman 2019). However, the ecological response to climate change varies considerably across taxa (Warren et al. 2001, Parmesan 2006, Chen et al. 2011). Whereas in temperate Europe several thermophilic organisms have benefited from global warming, species adapted to cool climates or sensitive to drought have been adversely affected by climate change (Hickling et al. 2006, Parmesan 2006, Streitberger et al. 2016b, Tayleur et al. 2016). In particular, mountain grasslands are among the ecosystems most severely threatened by climate change (Engler et al. 2011). However, range expansions of warm-adapted species towards higher elevations can also contribute to assemblage shifts, and may even temporarily increase species richness in some taxonomic groups (Steck et al. 2007, Roth et al. 2014, Löffler et al. 2019).

Mobile generalists in particular have expanded their geographical ranges in response to increasing temperatures, whereas specialists with low mobility are often more vulnerable to global warming (Hill et al. 2001, Warren et al. 2001, Hickling et al. 2006, Beckmann et al. 2015, Löffler et al. 2019). Hence, there is growing evidence that the availability of suitable habitats determines whether a species can maintain its overall population level in the face of global warming (Mantyka-Pringle et al. 2015). In a Central European low-mountain range, Löffler et al. (2019) detected an increase of Orthoptera species richness due to global warming in well-managed grasslands, whereas the number of species did not change in abandoned grasslands. These results demonstrate that sustaining traditional land use in semi-natural grasslands might be of great importance for maintaining ecosystem resilience under climate change, which may also reduce the risk of biotic homogenisation (cf. Mantyka-Pringle et al. 2015).

Orthoptera play a significant role as both herbivores and prey and, thus, are of great functional importance in grassland ecosystems (Samways 2005). Furthermore, they are among the most suitable indicator groups to investigate the effects of land-use and climate change (e.g. Bazelet and Samways 2012, Fartmann et al. 2012). As most species require high ambient temperatures (Willott and Hassall 1998), Orthoptera diversity in Europe generally decreases towards northern latitudes due to less-favourable climatic conditions in these areas (Hochkirch et al. 2016). However, distribution of Orthoptera species may be overridden by a lack of suitable habitats in fragmented landscapes. While it is evident that land-use change (i.e. habitat loss and deterioration) is a major threat to Orthoptera in Europe (Maas et al. 2011), it has remained difficult to identify the effects of climate change due to possible interactions with other environmental stressors. Although it has been shown that thermophilic species are rapidly expanding their ranges northwards during recent decades (e.g. Bakker et al. 2015, Beckmann et al. 2015, Poniatowski et al. 2018a, Löffler et al. 2019), it is still poorly understood how Orthoptera assemblages respond to climate change across habitats which have been affected unequally by land-use change.

Here, we analyse Orthoptera assemblage shifts across three grassland types with contrasting land-use history in the Black Forest (SW Germany) (*N* = 63): (i) formerly managed wet grasslands which have frequently become abandoned in recent decades (WET) (*N* = 15); (ii) common pastures which are still traditionally managed by rough grazing (COMMON) (*N* = 29), and (iii) mesic grasslands which have recently suffered from land-use intensification (MESIC) (*N* = 19). To this end, we analysed changes in Orthoptera species richness (i.e. all, as well as species with high and low mobility) between 1996 and 2017. In addition, we applied two indices to provide evidence whether Orthoptera assemblage shifts were driven by land-use or by climate change: (i) the Community Farmland Index (CFI) as a community mean of species' sensitivity to 'High Nature Value Farmland (HNV') and (ii) the Community Temperature Index (CTI) as a community mean of species' temperature preferences (c.f. Devictor et al. 2008). The CTI has recently been established as a useful tool to analyse processes underlying biodiversity shifts in insect communities (e.g. Devictor et al. 2012, Löffler et al. 2019, Termaat et al. 2019) In contrast, the CFI is a new measure which may help to deepen our understanding of the drivers of community shifts. In particular, we address the following research questions:

(i) How did species richness, CFI and CTI of Orthoptera assemblages shift between 1996 and 2017 due to land use and climate change?

(ii) Does the response of Orthoptera assemblages differ among the main grassland types?

(iii) What are the implications of the observed Orthoptera assemblage shifts for conservation management in Central Europe in times of rapid global change?

MATERIAL AND METHODS

Study area

The study area, the 'Hotzenwald' in the southern Black Forest (Baden-Württemberg, Germany; 47°7' N/8°1' E), has an area of about 100 km², ranging from 700 to 1 100 m a.s.l. Compared to the average climatic conditions in Central Europe, the climate is cool and wet, with a mean annual temperature of 6.3 °C, and an average annual precipitation of 1 700 mm (reference period 1981–2010; CDC 2018). However, the study area is well connected to the nearby 'High Rhine Valley', which is characterized by a warmer and drier climate, through north-south oriented river valleys. In accordance with the elevation gradient in the study area, precipitation increases with elevation from about 1 600 to 1 900 mm/a, while mean annual temperature decreases from 6.8 to 5.7 °C (CDC 2018).

The Hotzenwald is part of the German biodiversity hotspot 'Hochschwarzwald mit Alb-Wutach-Gebiet' (Ackermann and Sachteleben 2012). Large parts of the cultural landscape in the study area are dominated by semi-natural grasslands which are of major importance for biodiversity conservation in Europe (Veen et al. 2009, Feurdean et al. 2018). As a relic of traditional farming practices in Central Europe, many of them have been managed as commons for centuries (Eggers 1957, Hermle and Deil 2002). Despite severe agricultural changes in most parts of Central Europe, these common pastures are still grazed by cattle with low stocking rates. Due to their outstanding biodiversity, these heterogeneous pastures are of high conservation value and, additionally, make a unique contribution to the German cultural heritage (Lederbogen et al. 2004). Besides the common pastures in the study area, mesic grasslands are frequently used as hay meadows (Regional Council Freiburg 2011). In addition, the study area holds a network of various wet grasslands, often in close proximity to small bogs (Geis et al. 2013).

Study design

To detect possible Orthoptera assemblage shifts in the focal grasslands, we compared Orthoptera presence/absence data in 1996 with those from our own field surveys in 2017. The historical data represent the first detailed assessment of Orthoptera occurrence in the study area (Detzel 1997). In summer 2017, all patches studied in 1996 were re-visited and Orthoptera occurrence was surveyed using the same methods that had been applied in the former study (cf. *Orthoptera sampling*). We analysed changes in species richness and in patch occupancy of single species. Apart from considering overall Orthoptera species richness, we additionally classified Orthoptera by their dispersal ability (cf. *Orthoptera classifications and indices*). Furthermore, we applied two indices to understand whether Orthoptera assemblage shifts are driven by land-use or by climate change: (i) the Community Farmland Index (CFI) as a community mean of species' habitat preferences concerning 'High Nature Value Farmland' (HNV) reflected by the Species Farmland Index (SFI) (for more details see *Orthoptera classifications and indices*) and (ii) the Community Temperature Index (CTI) as a community mean of species' temperature preferences reflected by the Species Temperature Index (STI) (Devictor et al. 2008).

To analyse annual and seasonal (summer: May–September) changes in temperature during the study period, we used grid data of these proxies (temporal resolution: monthly, spatial resolution 1 × 1 km) provided by the German Meteorological Service (CDC 2018). Prior to the analyses, the temperature grid data were averaged for the whole study area in R statistical environment (R Core Team 2020) using the *spatialEco* package (Evans 2019). Afterwards, we used linear models with autocorrelation (AR1) structure to evaluate long-term temperature trends (thirty-year period ending in 2016, the year before to the second survey was conducted).

Study patches

In total, we studied 63 patches belonging to three grassland types: (i) wet grasslands (WET, $N = 15$), (ii) common pastures (COMMON, $N = 29$), and (iii) mesic grasslands (MESIC, $N = 19$). Patches were regarded as discrete when they were isolated from the nearest neighbouring patch by > 50 m of non-habitat, such as forest or improved grassland (cf. Fartmann et al. 2012, Poniatowski et al. 2018b). The size of the patches varied between 1 ha and 29 ha (mean ± SE: 6.3 ha ± 0.7). In all studied patches the grassland type did not change between 1996 and 2017.

Due to differences in land-use history over the last few decades, the three studied grassland types represent a gradient of land-use intensity. Many of the studied wet grasslands were traditionally mown once to twice a year, or grazed by cattle at low stocking rates (Geis et al. 2013). However, as a consequence of abandonment of management or irregular management for more than 20 years, many of these wet grassland patches have now become partly overgrown by tall-forb communities, or are dominated by a few grass species such as *Molinia caerulea*.

In contrast, most of the common pastures were still under traditional management by rough grazing with a local cattle breed (called 'Hinterwälder') (Regional Office for Environment 2004, Regional Council Freiburg 2011). Additionally, a small area of the common pastures was mown once a year in late summer. Due to a mosaic of various nutrient-poor grassland habitats, such as wet mesic or dry acidic grasslands, the common pastures are usually characterized by a very high habitat heterogeneity.

Most of the studied mesic grasslands were used as hay meadows, mown at least twice a year (May and September). However, due to regular application of fertilizer and an increasing mowing frequency, these grasslands have recently suffered from land-use intensification. Furthermore, some of the surveyed mesic grasslands were currently used as cattle pastures with intermediate stocking densities.

Orthoptera sampling

Orthoptera were sampled twice between mid-July and the end of August, with at least three weeks between each visit. In each patch, all available habitat structures were surveyed for the occurrence of Orthoptera species under favourable weather conditions (temperature > 15 °C, cloud cover < 50%) using acoustic and visual detection as well as sweep netting which are among the most frequently used methods for surveying grassland Orthoptera (Fischer et al. 2016, Samways 2019). Arbusticolous and arboricolous species that rarely occur in grasslands were excluded from all analyses, as our sampling techniques do not produce reliable data for these species. Species identification was performed in the field by song and morphological characteristics using Fischer et al. (2016). To improve the detection of quiet or high-frequency stridulating species, such as *Conocephalus fuscus* and *Metrioptera brachyptera*, a bat detector was used. The scientific nomenclature follows Fischer et al. (2016).

Orthoptera classifications and indices

We classified Orthoptera by their dispersal ability according to Poniatowski et al. (2018a) and Reinhardt et al. (2005). All long-winged species which are known to have a high flight capability as well as the wing-dimorphic species *Chrysochraon dispar* and *Roeseliana roeselii*, which are known to have a high dispersal ability, were classified as mobile species (Table 1) (cf. Poniatowski and Fartmann 2011, Löffler et al. 2019).

We calculated the Species Temperature Index (STI) for all Orthoptera species included in our analyses according to Devictor et al. (2008, 2012). This Index has recently been applied to detect climate-driven shifts in Orthoptera assemblages (Löffler et al. 2019).

Applying the same procedure, we introduced the Species Farmland Index (SFI) which indicates the relationship between the

Table 1: List of Orthoptera species recorded in the study area classified by their dispersal ability (DA; H = high mobility; L = low mobility), Species Farmland Index (SFI) and Species Temperature Index (STI).

Species	DA	SFI	STI
Bicolorana bicolor	H	19.37	13.12
Calliptamus italicus	H	19.18	13.68
Chorthippus biguttulus	H	16.04	12.97
Chorthippus brunneus	H	16.34	12.98
Chrysochraon dispar	H	18.23	13.10
Conocephalus fuscus	H	15.90	13.35
Decticus verrucivorus	L	25.90	12.59
Euthystira brachyptera	L	24.62	12.57
Gomphocerippus rufus	L	20.18	12.94
Gryllus campestris	L	20.52	13.07
Mecostethus parapleurus	H	28.47	13.22
Metrioptera brachyptera	L	20.24	12.58
Miramella alpina	L	42.28	10.49
Myrmeleotettix maculatus	L	17.04	12.99
Nemobius sylvestris	L	18.52	13.11
Omocestus rufipes	L	27.60	12.75
Omocestus viridulus	L	18.68	12.74
Pholidoptera griseoaptera	L	16.12	12.97
Platycleis albopunctata	H	15.90	13.34
Pseudochorthippus montanus	L	19.28	12.82
Pseudochorthippus parallelus	L	16.03	12.96
Psophus stridulus	L	32.72	11.81
Roeseliana roeselii	H	16.41	12.95
Stauroderus scalaris	H	54.24	11.37
Stenobothrus lineatus	H	18.73	12.89
Stenobothrus stigmaticus	L	18.29	12.78
Stethophyma grossum	H	17.68	12.96
Tetrix bipunctata	L	22.09	12.37
Tetrix subulata	H	15.82	13.07
Tetrix tenuicornis	L	16.28	13.00
Tetrix undulata	L	16.18	12.99
Tettigonia cantans	L	18.45	12.59

distribution of a species and the availability of high-nature-value farmland in its range. Both STI and SFI were obtained from German Orthoptera distribution data (cf. graphical maps in Fischer et al. 2016), based on a grid-map system with a spatial resolution of 10 km × 11 km (in Germany 3,004 grid cells i.e. 'Messtischblätter'; cf. Reinhardt et al. 2005). The majority of the data were originally compiled for the preparation of the assessment of German Orthoptera (Maas et al. 2002). More recent data (until 2017) were provided by several local Orthoptera societies and federal state authorities (for more details see Fischer et al. 2016). Overall, the dataset included 211,954 single records from 1990–2017. For the calculation of STI and SFI, the distribution data of each species were layered with maps of long-term mean summer temperatures of the most recent 30-year reference period (1 km × 1 km grid–timescale: 1981–2010; CDC 2018; compare also to WMO 2017) and the share of high-nature-value farmland in the open landscape (the most recent and updated version of a European HNV map; 100 m × 100 m grid; EEA 2018), respectively. For each species, all occupied grid cells were considered for the calculation of the indices. Grid cells were classified as occupied if one or more observations existed between 1990 and 2017. The computing was done using the zonal statistics tool in ArcGIS 10.3 (i.e. the mean temperature value and the mean value of the ratio of high-nature value farmland were calculated for all occupied grid cells, respectively). Finally, STI and SFI values were calculated as the mean of the computed zonal-statistic values across the whole species' range in Germany. Due to the spatial limitation to the extent of Germany and to the relatively large time span of data collection, both indices do not necessarily reflect the species' optima. They should be viewed as relative measurements of habitat demands.

RESULTS

Climate change

Both annual and summer temperatures increased from 1987 to 2016 (fig. 1a and b)

Orthoptera assemblage change

In total, 32 species of grassland Orthoptera were recorded in the 63 patches during the two study years (Table 1). Five species were only recorded in 2017: *Calliptamus italicus*,

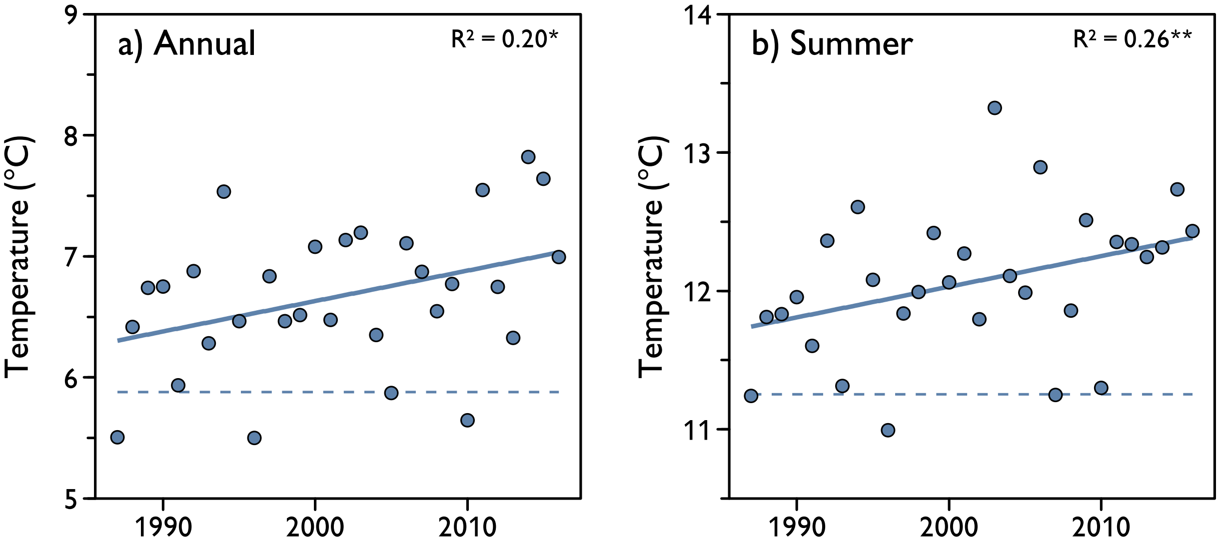

Figure 1: Changes in annual (a) and summer temperature (May-October) (b) in the study area (data period 1987–2016; DWD 2019). The dashed lines represent the long-term mean (most recent international standard reference 1961–1990; DWD 2019). Linear relationships were tested using linear models with autocorrelation (AR1) structure (* $P < 0.05$, ** $P < 0.01$). (a) $y = 0.025 \times x - 43.6$; (b) $y = 0.022 \times x - 32.26$. Pseudo $R^2_{(\text{Nagelkerke})}$ values are given.

Conocephalus fuscus, *Mecostethus parapleurus*, *Platycleis albopunctata* and *Tetrix undulata*. For 12 species, patch occupancy increased from 1996 to 2017: *Chorthippus biguttulus*, *Chorthippus brunneus*, *Chrysochraon dispar*, *C. fuscus*, *Gomphocerippus rufus*, *Gryllus campestris*, *M. parapleurus*, *Nemobius sylvestris*, *P. albopunctata*, *Stenobothrus lineatus*, *Tetrix bipunctata* and *T. undulata* (fig. 2). In contrast, no species became locally extinct or decreased in patch occupancy.

Overall species richness increased in common pastures and mesic grasslands between 1996 and 2017, whereas it did not change in wet grasslands (fig. 3a). In particular, species with high mobility were responsible for this increase in species richness, and their richness increased in all three grassland types (fig. 3b). In contrast, the number of species with low mobility only increased in common pastures (fig. 3c).

The SFI largely differed among species detected in our study (Table 1), with values ranging from 15.82% to 54.24%. *Stauroderus scalaris* (SFI = 54.24%), *Miramella alpina* (42.28%) and *Psophus stridulus* (32.72%) were the three species detected which most strongly dependent on high nature value farmland at the national German spatial scale.

By contrast, *Tetrix subulata* (SFI = 15.82%), *C. fuscus* (SFI = 15.90%) and *P. albopunctata* (SFI = 15.90%) had the lowest SFI values.

The STI of the detected species ranged from 10.49 to 13.68 °C (Table 1). *Calliptamus italicus* (STI = 13.68 °C), *C. fuscus* (13.35 °C) and *P. albopunctata* (13.34 °C) were the three species with the highest macroclimatic demands (Table 1). All three species were detected in the study area in 2017 for the first time (see above). *Miramella alpina* (10.49 °C), *S. scalaris* (11.37 °C) and *P. stridulus* (11.81 °C) were the species with the lowest STI values.

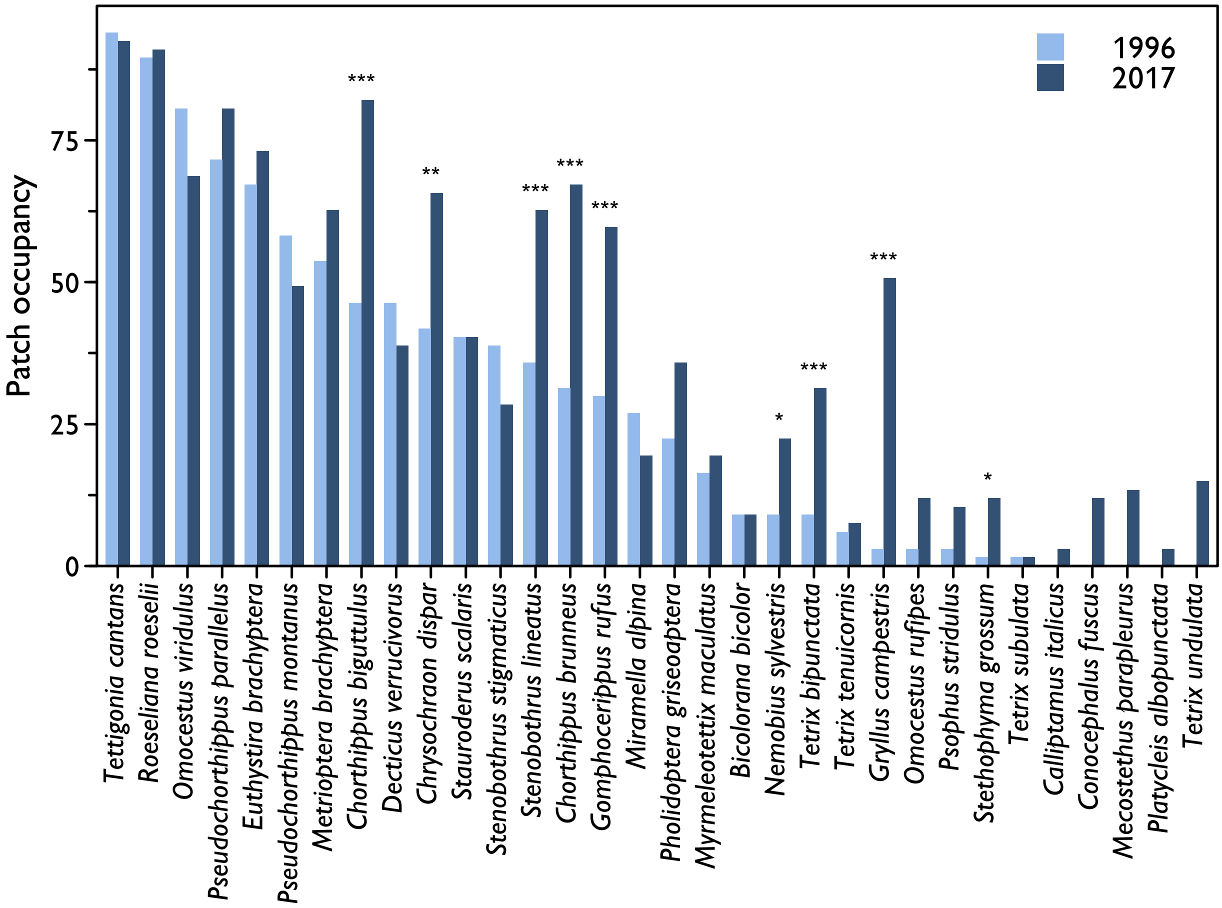

Figure 2: Patch occupancy of Orthoptera species in 1996 and 2017. Differences were tested using McNemar test. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

The CFI decreased in both wet and mesic grasslands between 1996 and 2017 (fig. 4a), whereas the CTI increased in both grassland types (fig. 4b). On the contrary, both indices remained stable in common pastures (fig. 4a and b).

DISCUSSION

Both annual and summer temperatures increased in the study area during the study period. Orthoptera assemblages strongly responded to these changed environmental conditions in the grasslands. However, the effects differed greatly among the grassland types, in particular between common pastures and the two other grassland types. Despite a strong increase in overall species richness in common pastures, neither the CFI nor the CTI changed. In contrast, in the two other grassland types, the CFI decreased and the CTI increased.

Most Orthoptera species depend on high ambient temperatures (Willott and Hassall 1998). Consequently, global warming is considered the main driver behind recent range expansions of Orthoptera across temperate Europe (Thomas et al. 2001, Poniatowski et al. 2012, Beckmann et al. 2015, Poniatowski et al. 2018a).

Five species, *C. italicus*, *C. fuscus*, *M. parapleurus*, *P. albopunctata* and *T. undulata*, were new to the study area. The first four had the highest STI values (> 13.2 °C) of all detected species. Besides *C. fuscus*, *M. parapleurus* and *T. undulata*, another eight species, *C. biguttulus*, *C. brunneus*, *C. dispar*, *G. rufus*, *G. campestris*, *N. sylvestris*, *S. lineatus* and *T. bipunctata* increased in patch occupancy. Except *T. bipunctata*, all these species had higher STI values than the average STI (± SE) of 12.79 ± 0.11. Accordingly, we explain the new colonisation of the study area by thermophilic species and the increase in patch occupancy of thermophilic species as a response to the observed climate warming. The increase in the CTI in wet and mesic grassland

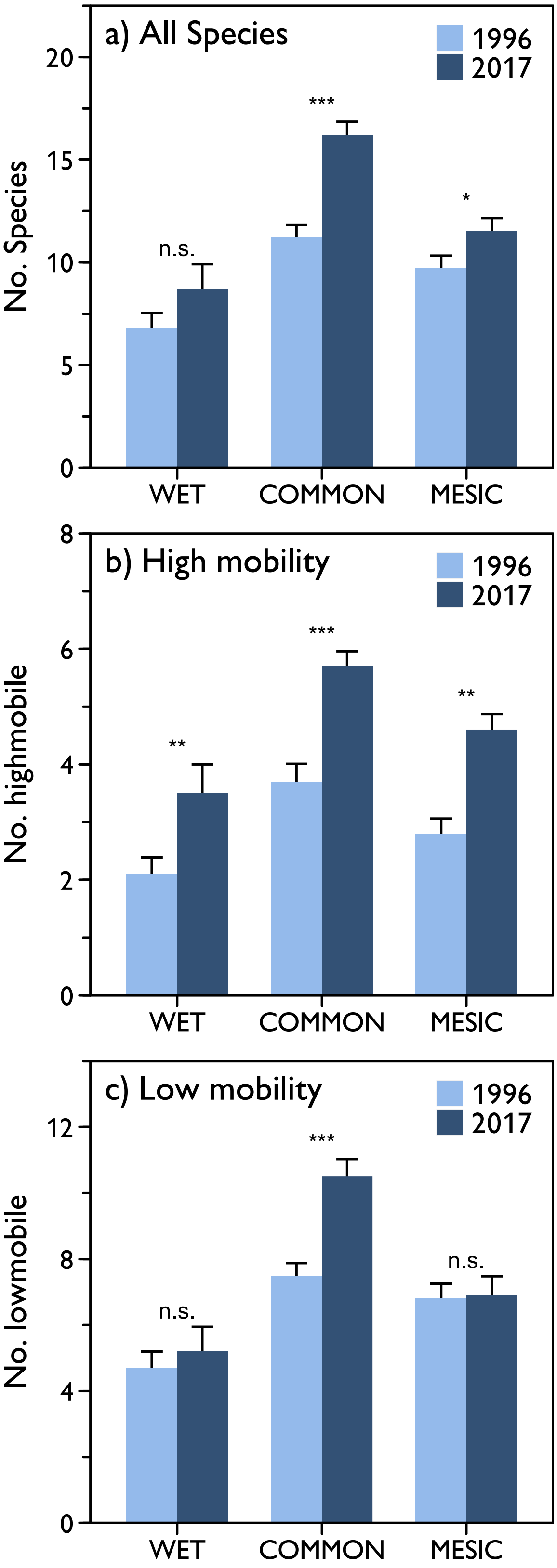

Figure 3: Changes in the number of all species (a), species with high (b) and species with low mobility (c) between 1996 and 2017 in the three grassland types. Mean values ± SE are shown. WET = wet grassland, $N = 15$; COMMON = common pasture, $N = 29$; MESIC = mesic grassland, $N = 19$. Differences were tested using Wilcoxon Signed Rank test (* $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, n.s. $P > 0.05$).**

underpins this assumption.

By contrast, the increase in patch occupancy in the two cryptic groundhopper species *T. bipunctata* and *T. undulata* might also be the result of a more intensive survey for the species in their preferred bare ground-rich microhabitats (cf. Detzel 1997, Schlumprecht and Waeber 2003). For *T. bipunctata* in particular, this seems to be very likely as the species has a relatively low STI (12.37 °C) (cf. Table 1) and within Central Europe, it also occurs regularly in areas with cool summers (Maas et al. 2011, Fischer et al. 2016).

In our study, species richness of mobile species increased in all three grassland types. These results corroborate findings of previous studies indicating that global warming primarily fosters mobile species, whereas most species with low dispersal ability are unable to track climate change (Poniatowski et al. 2012, Beckmann et al. 2015, Löffler et al. 2019).

Orthoptera are very sensitive not only to changes in climate, but also in land use (Thomas et al. 2001, Hickling et al. 2006, Beckmann et al. 2015). There is broad consensus that habitat loss and deterioration caused by land-use change are the most severe threats to Orthoptera in Central Europe (Marini et al. 2009b, Schirmel et al. 2011, Fartmann et al. 2012). The newly introduced CFI for Orthoptera in this study provides the opportunity to disentangle the effects of climate and land-use change on Orthoptera assemblage composition more precisely. In both wet and mesic grasslands, the CFI decreased. Hence, the current Orthoptera assemblages were composed of species less dependent on high nature value farmland, i.e. more habitat generalist or widespread species, than in 1996. In wet grasslands, overall species richness did not change, and species with a high SFI were substituted by more widespread species. We attribute the decrease in high nature value farmland species to the abandonment of most of the wet grasslands (see *Study patches*). Succession is known to have negative effects on habitat specialist Orthoptera in open habitats of the temperate zone, in particular through changes in microclimate (Marini et al. 2009b, Schirmel et al. 2011, Fartmann et al. 2012, Helbing et al. 2014, Löffler et al. 2019). Abandonment of grassland management leads to tall vegetation with litter accumulation (Ellenberg and Leuschner 2010) and a cool microclimate, even in times of macroclimatic warming

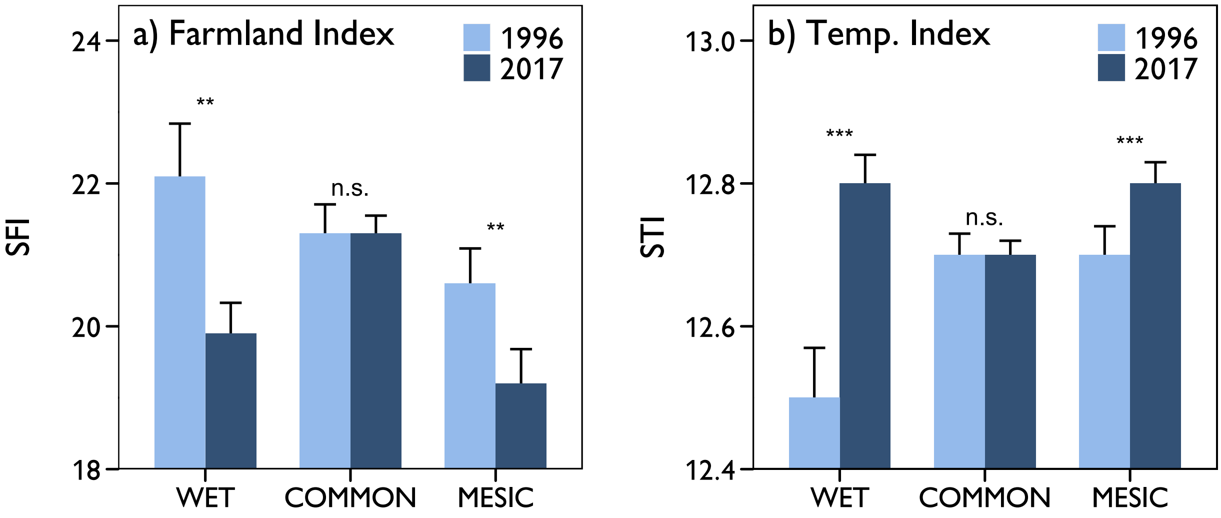

Figure 4: Changes in the Community Farmland Index (CFI) (a) and the Community Temperature Index (CTI) (b) between 1996 and 2017 in the three grassland types. Mean values ± SE are shown. WET = wet grassland, $N = 15$; COMMON = common pasture, $N = 29$; MESIC = mesic grassland, $N = 19$. Differences were tested using Wilcoxon Signed Rank test (* $P < 0.001$, ** $P < 0.01$, n.s. $P > 0.05$).**

(cf. Wallis de Vries and van Swaay 2006). In contrast, in mesic grasslands, which suffered from land-use intensification in the study area (see *Study patches*), overall species richness increased. However, this increase was attributed only to widespread species, as the decreasing CFI indicates. In summary, climate and land-use change in both wet and mesic grasslands led to a biotic homogenisation of the respective Orthoptera assemblages with more widespread species replacing habitat specialists.

In common pastures, both the CFI and the CTI did not change, despite an increase in overall species richness. Common pastures were also the only grassland type where the number of species with low mobility increased and where these poor dispersers were able to track climate change. The common pastures were characterized by mosaics of various nutrient-poor grassland habitats, ranging from wet to dry grasslands and had by far the highest habitat heterogeneity of the three studied grassland types (see *Study patches*). As a consequence, we conclude that heterogeneous grasslands with long environmental gradients and low-intensity management, such as the common pastures in our study, are more resilient to the effects of climate warming (cf. Mantyka-Pringle et al. 2015, Streitberger et al. 2016b). Under such conditions, Orthoptera species with both low and high mobility are able to track rising temperatures in landscapes with well-connected grasslands.

CONCLUSIONS

Löffler et al. (2019) showed that approaches based on the CTI are powerful tools for detecting the effects of climate change on Orthoptera assemblage shifts. Additionally, the CFI–developed here–helped to disentangle the effects of climate and land-use change on Orthoptera assemblage composition. In sum, we found that climate warming has led to biotic homogenisation of the Orthoptera assemblages of wet grasslands affected by abandonment, and mesic grasslands affected by land-use intensification. In contrast, common pastures, characterized by a high heterogeneity with long environmental gradients and low-intensity management, were more resilient to the effects of climate warming. In these grasslands not only widespread species with high mobility were able to track rising temperatures but also more specialized species with low mobility.

Based on the results here, we recommend the maintenance or reintroduction of traditional land use in grasslands to promote Orthoptera assemblages–and presumably also other insect assemblages–with high species richness and many specialized species (Wallis de Vries et al. 2002, Fartmann et al. 2012, Torma et al. 2014, 2019). Such conservation measures are low-intensity mowing (1–2 times per year without fertilizer application) in meadows, and low-intensity grazing in pastures (cf. Löffler et al. 2019). Additionally, management should also aim at establishing dense habitat networks within a heterogeneous landscape which increases the resilience of grassland ecosystems to global warming (Pryke and Samways 2012, Streitberger et al. 2016a).

ACKNOWLEDGEMENTS

We are grateful to Dr. P. Detzel for providing historical Orthoptera data from the study area. For their hospitality and providing an accommodation during the period of field work we would like to thank Dr. G. Geis-Tyroller and N. Tyroller. The conservation authority of the administrative district of Freiburg gave permission for us to survey Orthoptera in protected areas. Additionally, we would like to thank two anonymous reviewers for valuable comments on an earlier version of the manuscript.

FUNDING

This study was funded by two PhD scholarships of the German Environmental Foundation (DBU) allocated to Florian Fumy and Franz Löffler.

Chapter III

Land-use intensity, habitat heterogeneity and biodiversity

Decticus verrucivorus **(Lindau [Hotzenwald] 2018/07/25)**

CHAPTER III

Chapter III explores the effects of land-use intensity on habitat properties and consequences for butterfly and Orthoptera assemblages. Paper III considers Orthoptera assemblages in three different grassland types. Paper IV focuses on threatened butterfly and Orthoptera species across five habitat types. Both studies cover a large hydrologic gradient and relate recent species assemblage composition to habitat structure and land-use intensity.

Paper III

Land-use intensity determines grassland Orthoptera assemblage composition across a moisture gradient

Paper IV

Low-intensity land use fosters species richness of threatened butterflies and grasshoppers in mires and grasslands

Land-use intensity determines grassland Orthoptera assemblage composition across a moisture gradient

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ABSTRACT

Two of the main principles of global and national conservation strategies consist in focusing on the most species-rich and most vulnerable ecosystems. In this study, we investigated the Orthoptera species assemblages of species-rich grasslands in the southern Black Forest, one of 30 German biodiversity hotspots. Across a moisture gradient, we considered the three dominant grassland types within the study area: (i) dry, (ii) mesic and (iii) wet grasslands. In order to analyse the drivers of biodiversity in a landscape of high conservation value, we related (i) differences in Orthoptera assemblage composition between the three grassland types and (ii) the relationship of Orthoptera assemblage composition within each grassland type to environmental conditions.

In our study, we detected considerable variation in land-use intensity which dropped from high in mesic to low in dry and again to near-zero in wet grasslands. Land-use intensity was the only predictor of Orthoptera species richness in the multivariable Generalized Linear Mixed-effects Models. The mean number of both all and threatened species was highest in the grassland type with low land-use intensity, dry grasslands, differing from those of mesic (high land-use intensity) and wet (mostly abandoned) grasslands. Additionally, dry grasslands had the highest number of all, threatened and exclusive indicator species. Both (i) intensive land use in mesic grasslands and (ii) abandonment of land use in wet grasslands led to a homogenisation of the habitat structures and the species assemblages. In contrast, dry grasslands with low land-use intensity and high habitat heterogeneity were hotspots of Orthoptera species richness.

KEYWORDS

Biodiversity conservation, Environmental change, Grazing management, Hay meadow, Insect diversity, Pasture

Agriculture, Ecosystems & Environment 315 (2021). https://doi.org/10.1016/j.agee.2021.107424

INTRODUCTION

The loss of biodiversity ranks among the most appalling natural crises in human history (IPBES 2019, Cardoso et al. 2020). The conservation of biodiversity from the local to the global scale is, thus, one of the most urgent challenges for humankind (Dirzo and Raven 2003, Mittermeier et al. 2011, Samways et al. 2020). In order to protect biodiversity, conservation efforts should be guided systematically. Two of the main principles of global and national conservation strategies consist in focusing on the most species-rich and most vulnerable ecosystems (Brooks et al. 2006). Accordingly, biodiversity hotspots have been designated on global (see for example Mittermeier et al. 2011) and national scales. These hotspots harbour outstandingly species-rich ecosystems and high shares of endangered species. In Germany, one fundamental aspect of the national strategy for biodiversity conservation is the realisation of conservation measures in national biodiversity hotspots (Ackermann and Sachteleben 2012).

Many of the European biodiversity hotspots exhibit high shares of grasslands, which are among the most species-rich ecosystems in Europe and cover >20% of the EU-28 land surface (Wilson et al. 2012, Feurdean et al. 2018, EC 2019). Most of the European grasslands have been shaped by human agricultural practice (Veen et al. 2009, Feurdean et al. 2018). However, due to the transition from pre-industrial land use to industrial agriculture, the extent of semi-natural grasslands of high conservation value has dramatically decreased, mainly driven by agricultural intensification, but also by land-use abandonment (MacDonald et al. 2000, Wallis de Vries et al. 2002, Dengler et al. 2014). As a result, the biodiversity of European grassland ecosystems has become increasingly threatened.

Because of the significant role Orthoptera play both as herbivores and prey, they are of great functional importance in grassland ecosystems (Samways 2005). Furthermore, they are among the most suitable indicator groups to investigate the effects of land-use change (e.g. Bazelet and Samways 2012, Fartmann et al. 2012, Löffler et al. 2019). The habitat requirements of Orthoptera are complex. Particularly, the often interrelated parameters of vegetation structure (Poniatowski and Fartmann 2008, Fartmann et al. 2012) and microclimate (Gardiner and Dover 2008) define habitat quality.

In this study, we investigated the Orthoptera species assemblages of semi-natural grasslands in the southern Black Forest (SW Germany). Due to the high share of species-rich grasslands, the study area is part of one of 30 German biodiversity hotspots (Ackermann and Sachteleben 2012). Species richness of Orthoptera has been shown to be very high in the study area and includes a large number of specialized and threatened species (Detzel 1997, Fumy et al. 2020). Across a moisture gradient, we considered the three dominant grassland types within the study area: (i) dry, (ii) mesic and (iii) wet grasslands. In order to analyse the drivers of biodiversity in a landscape of high conservation value, we related (i) differences in Orthoptera assemblage compositions between the three grassland types and (ii) the relationship of Orthoptera assemblage compositions within each grassland type to environmental conditions. Based on the results, we give recommendations for effective strategies for biodiversity conservation in temperate grassland ecosystems, which are expected to foster Orthoptera but also a wide range of other taxa.

MATERIAL AND METHODS

Study area

The study area, the 'Hotzenwald' in the southern Black Forest (federal state of Baden-Württemberg, SW Germany; 47°7' N/8°1' E), occupies about 100 km², ranging from 700 to 1,100 m a.s.l. For Central Europe, the climate is rather cool and wet, with a mean annual temperature of 6.3 °C and an average annual precipitation of 1,700 mm (reference period 1981–2010; German Meteorological Service 2021). Along the elevation gradient, precipitation increases from about 1,600 to 1,900 mm/a and mean annual temperature decreases from 6.8 to 5.7 °C (German Meteorological Service 2021).

The Hotzenwald is part of the German biodiversity hotspot 'Hochschwarzwald mit Alb-Wutach-Gebiet' (Ackermann and Sachteleben 2012). Large parts of the cultural landscape in the study area are dominated by semi-natural grasslands which are of major importance for biodiversity conservation in Europe (Veen et al. 2009, Feurdean et al. 2018). In accordance with their soil moisture, these grasslands can be classified into three types: (i) dry, (ii) mesic and (iii) wet grasslands.

Most of the dry grasslands have been managed as commons for centuries (Eggers 1957, Hermle and Deil 2002). Although a relatively large share of the grasslands is still in communal property, the management of the common pastures has undergone substantial changes since the 1930s through administrative interventions and technical innovation, such as the introduction of electric fences (MEBW 2016). However, traditional rough grazing, in many cases with a local cattle breed called 'Hinterwälder', is still widespread (Konold et al. 2014). Due to their high habitat diversity and species richness, these heterogeneous pasture ecosystems have an outstanding conservation value and, additionally, make a unique contribution to German cultural heritage (Lederbogen et al. 2004, Regional Council Freiburg 2011).

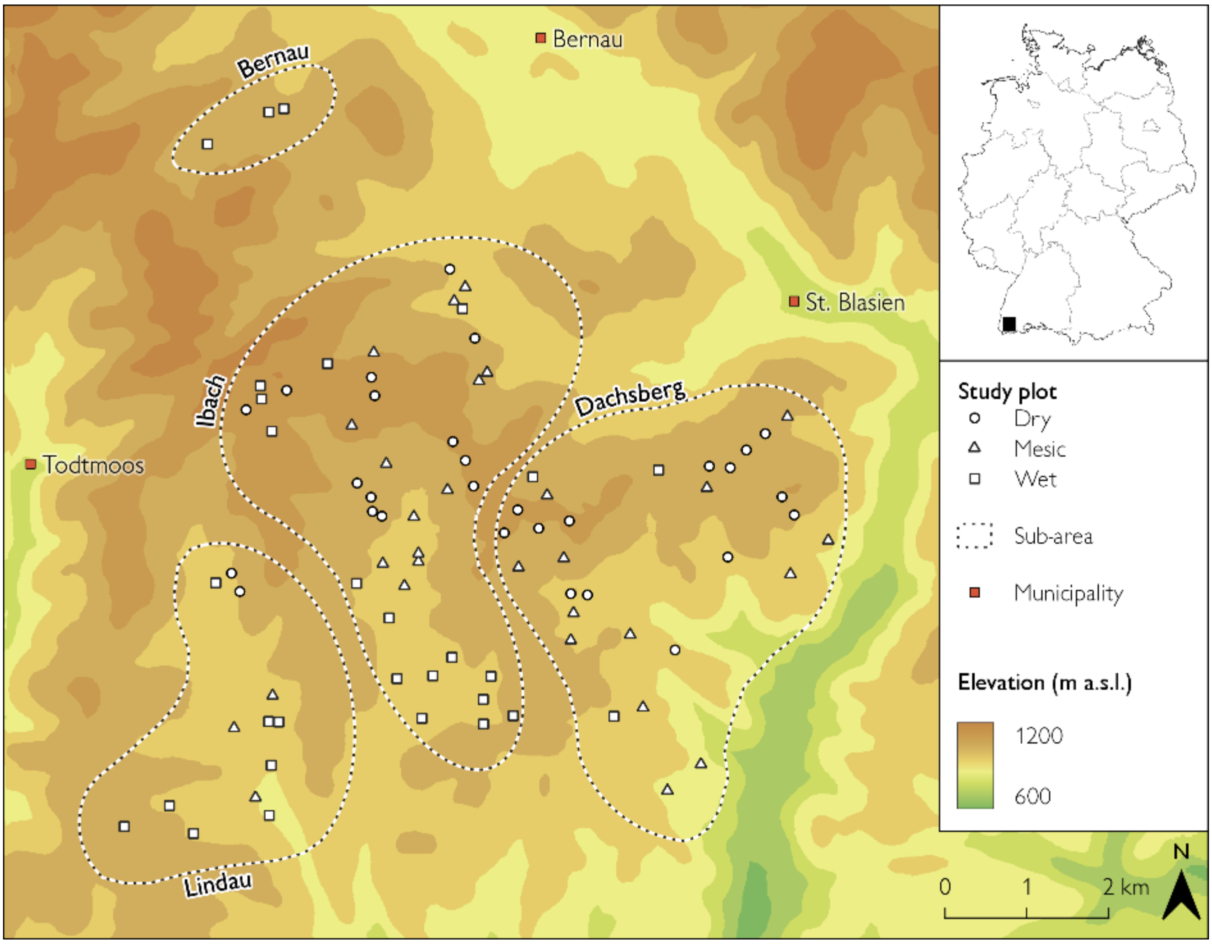

Figure 1: Location of the study area and plots in the southern Black Forest (SW Germany).

Historically, the mesic grasslands were predominantly mown once or twice per year (Regional Office for Environment 2004) and managed as irrigation meadows (Borcherdt 1985, Schellberg 2005, Leibundgut and Vonderstrass 2016). However, many of these grasslands have recently suffered from land-use intensification, reflected by a regular application of fertilizer and an increasing mowing frequency (Nowak and Schulz 2002, Konold et al. 2014). Ditch irrigation systems for the former irrigation meadows have been abandoned completely (Schellberg 2005). Despite these general changes in land use, some of the mesic grasslands are still characterized by low land-use intensity and species-rich insect assemblages (Fumy et al. 2020).

The wet grasslands in the study area were traditionally mown once or twice a year, or grazed by cattle at low stocking rates (Regional Council Freiburg 2011, Geis et al. 2013). However, as a consequence of irregular management or complete abandonment for over 20 years, many of these formerly species-rich wet grasslands are now homogeneous, high-growing, rich in litter and dominated by tall forbs (e.g. *Filipendula ulmaria*) or grasses (e.g. *Molinia caerulea*) (own observation). Although some sites suffered from drainage, the study area still features an extensive network of hydrologically intact wet grasslands.

Study design

Study plots

We compared Orthoptera species assemblages of the three dominant grassland types in the study area: (i) dry, (ii) mesic and (iii) wet grasslands. Prior to the plot selection, we mapped habitat types in the field according to Finck et al. (2017) and classified the grasslands according to the EUNIS (European Nature Information System; EEA 2017) habitat classification (E1 = dry, E2 = mesic, D2 = wet grasslands). Characteristic plant communities were the Polygalo-Nardetum and Festuco-Genistelletum in dry, Cynosurion and Polygono-Trisetion communities in mesic and Calthion communities as well as the Caricion fuscae and Juncetum squarrosi in wet grasslands (Dierschke 1997, Peppler-Lisbach and Petersen 2001, Burkart et al. 2004, Köppler 2004).

Orthoptera occurrence was surveyed in 87 plots, each having a size of 100 m × 100 m. Per grassland type, we randomly selected 29 plots with homogeneous vegetation structure (stratified random sampling). The minimum distance between plots was set to 50 m. To avoid edge effects from adjacent habitat types (Schirmel et al. 2010), each plot had to be surrounded by a buffer of at least 20 m of the focal grassland type (dry, mesic or wet). In order to account for possible spatial autocorrelation, the study area was divided into four sub-areas according to aggregations of the study plots (Fig. 1).

Sampling design

Environmental conditions

For each plot, we calculated the mean elevation based on an elevation grid (provided by Sonny 2020) with a spatial resolution of “1”, which corresponds to a resolution of approx. 20 m × 30 m in the study area.

Using the same elevation data, we calculated i.) the heatload index (HLI) according to McCune and Keon (2002) as a measure of radiation influx and ii.) the topographic position index (TPI)—with a search radius of two elevation grid cells—according to Weiss (2001) as a measure of topographic variety. Both the HLI and the TPI were calculated using the ‘spatialEco’ package by Evans (2019). For both variables, we used the range per plot as an explanatory variable in our models. The HLI and TPI ranges reflect the difference between the elevation grid cells with the highest and lowest radiation or prominence values—within each plot—respectively. Both indicate topographic diversity of the study plots.

We ascertained land-use intensity on an ordinal scale. Within each plot, we mapped the land-use types in the field. Each land-use type in the plots was assigned a land-use intensity value ranging from 0 to 5 (Table 1). The land-use intensity was then calculated for each plot as the weighted mean of the land-use values of all land-use types relative to their coverage within the respective plot.

Orthoptera assemblages

Orthoptera species were sampled at three times between June and August 2018 with at least three weeks between each visit. In each plot, all available habitat structures were surveyed for the occurrence of Orthoptera species under favourable weather conditions (temperature > 15 °C, cloud cover < 50%) using acoustic and visual detection as well as sweep netting (Fischer et al. 2016, Samways 2019). Arbusticolous and arboricolous species that rarely occur in grasslands were excluded from all analyses, as our sampling techniques do not produce reliable data for these species. Species identification was performed in the field using song and morphological characteristics in line with Fischer et al. (2016). To improve the detection of quiet or high-frequency stridulating species, such as *Conocephalus fuscus* and *Metrioptera brachyptera*, a bat detector was used. The scientific nomenclature follows Fischer et al. (2016).

Statistical analysis

All statistical analyses were performed using R 3.6.3 statistical environment (R Core Team 2020). Differences in environmental parameters between the three studied grassland types were tested using Kruskal–Wallis' *H* test and Dunn's test as a post-hoc test using the 'dunn.test' package (Dinno 2017). We chose this nonparametric approach because mixed-

Table 1: Land-use types in the study plots and their assigned land-use intensity values. Land-use intensity ranges from 0 (no land use) to 5 (very high land-use intensity). For each plot, land-use intensity was calculated as the weighted mean intensity of the land-use types present in the respective plot.

Land-use intensity	Value	Description
No land use	0	Abandoned semi-natural grassland
Very low	0.5	Semi-natural grassland: sporadically grazed, at most two to four weeks per year
Low	1	Semi-natural grassland: meadows mown once or pastures with low stocking rates
Moderate	2	Improved grassland: meadows mown twice or pastures with intermediate stocking rates
Moderate/high	3	Improved grassland: meadows mown thrice or pastures with strip grazing and a rotation cycle of two to four weeks
High	4	Improved grassland with liquid-manure fertilisation: meadows mown thrice or highly intensive strip grazing with a rotation cycle of two to five days
Very high	5	Improved grassland with liquid-manure fertilisation: meadows mown four times

effects models could not be applied due to overdispersion. Differences in numbers of (i) all and (ii) threatened species between the three studied grassland types were tested using Generalized Linear Mixed-effects Models (GLMM) with Poisson error structure, *grassland type* as a categorical predictor and *sub-area* as a random factor. 'Threatened species' considered all species identified as nearly threatened or threatened in the current red list of Orthoptera species for the federal state of Baden-Württemberg (Detzel et al. 2021; see also Tab. A1). Pairwise comparisons between the grassland types were made using the 'glht' function in the 'multcomp' package by Hothorn et al. (2008), using Tukey's test as a post hoc test (homogeneity of variance and equal group sizes were given).

To assess the effects of the environmental parameters on species richness of (i) all and (ii) threatened species, we conducted GLMMs with Poisson error structure for each grassland type separately. Multicollinearity was low for all predictors in all models ($|r_s| < 0.5$, VIF < 2)

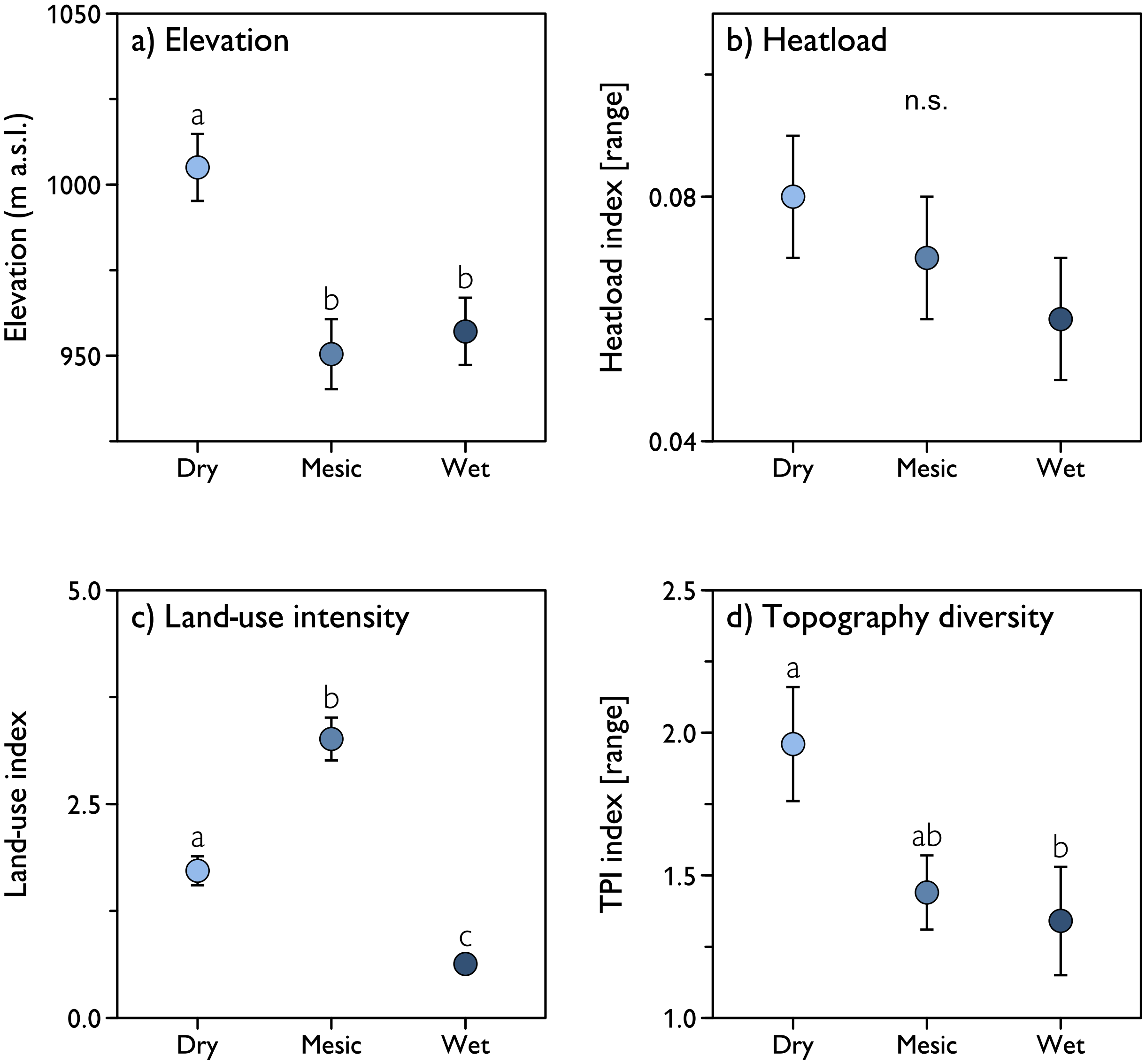

Figure 2: Mean (± SE) elevation (a), heatload (b, range), land-use intensity (c) and topography (d, range) in the three studied grassland types (*N* for each type = 29). Differences were tested using Kruskal–Wallis' *H* test and Dunn's post-hoc test. Different letters indicate significant differences between grassland types. $Chi^2_{\mathrm{Elevatio}N=}$14.47; $Chi^2_{\mathrm{Heatload}}$ =2.5; $Chi^2_{\mathrm{Land\text{-}use\ intensity}}$ = 50.08; $Chi^2_{\mathrm{Topography\ diversity}}$ = 7.89.

(see Graham 2003, Zuur et al. 2010). Possible spatial autocorrelation was taken into account by adding *sub-area* as a random factor. In order to increase the robustness of models with multiple predictors and identify the most important environmental parameters, we conducted model averaging based on an information-theoretic approach including the top-ranked models within $\Delta AIC_C < 3$ (Burnham and Anderson 2010, Grueber et al. 2011). We used the 'lme4' package of Bates et al. (2015) for all GLMM analyses and the 'dredge' and the 'model.avg' functions in the R package 'MuMIn' by Bartoń (2017) for model averaging.

We conducted an indicator species analysis for the three studied grassland types using the 'multipatt' function in the R package 'indicspecies' by Cáceres and Legendre (2009). We considered indicator relationships of single species with single and combined grassland types and used the 'IndVal.g' association index according to Cáceres et al. (2010). The statistical significance of this indicator value was tested using a permutation test; the number of permutations was set to 999 (for further details see Cáceres and Legendre 2009).

RESULTS

Environmental conditions

Land-use intensity was the only environmental parameter that differed between all three grassland types; it varied from high intensity in mesic grasslands to low intensity in dry grasslands to near-zero intensity in wet grasslands. Dry grasslands were situated at the highest elevations, differing from both mesic and wet grasslands. The topographic diversity was highest in dry grasslands, differing from wet grasslands; mesic grasslands had an intermediate position. Contrastingly, the HLI range did not differ between the three grassland types (Fig. 2).

Orthoptera assemblages and their response to environmental conditions

In total, we recorded 32 Orthoptera species in the 87 plots (Table A1). Species richness per plot ranged from 1 to 21 species, with a mean (± SE) of 9.1 ± 0.4 species. The number of threatened species varied from 0 to 13 with a mean of 4.8 ± 0.3 species. The most widespread species were *Roeseliana roeselii*,

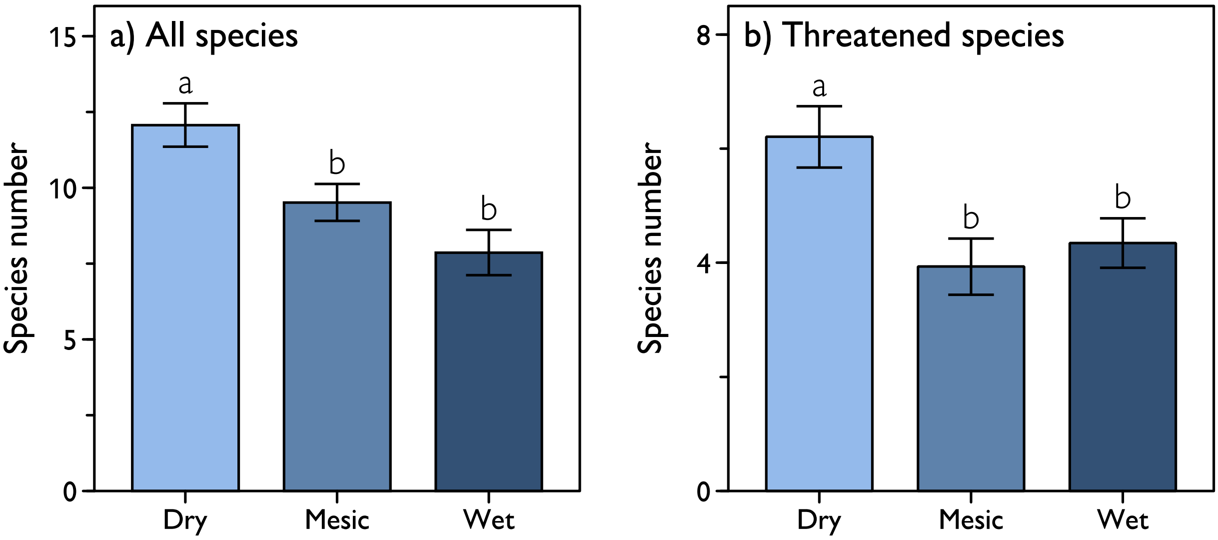

Figure 3: Mean species richness (± SE) of all (a) and threatened (b) Orthoptera species in the three studied grassland types (*N* for each type = 29). Differences between the grassland types were tested using mixed-effects models (GLMM) with *sub-area* (*N* = 4) as a random factor. Different letters indicate significant differences between grassland types (P < .05).

Chorthippus biguttulus and *Pseudochorthippus parallelus*, which were present in 80%, 76% and 65% of the plots, respectively (Table A1). The mean numbers of (i) all species and (ii) threatened species were highest in the dry grasslands, differing from mesic and wet grasslands (Fig. 3).

The dry grasslands had the highest number of indicator species: ten species, among them six threatened species (Table 2). Mesic grasslands followed with seven characteristic species (one threatened species) and wet grasslands with five species (two threatened species). Additionally, dry grasslands had the highest number of exclusive indicator species with five species mainly occurring in this grassland type. Wet grasslands followed with three exclusive indicator species. In contrast, none of the indicator species of mesic grasslands were solely restricted to this grassland type. Land-use intensity was the only predictor of species richness of (i) all and (ii) threatened Orthoptera species in the multivariable GLMMs (Table 3, Fig. 4). With increasing land-use intensity, the number of all and threatened species increased in the wet grasslands and decreased in the mesic grasslands. In the dry grasslands, only threatened species decreased with an increase in land-use intensity.

Table 2: Indicator species for the three studied grassland types. Threatened species (cf. Table A1) are indicated in bold type. Specificity indicates the degree of grassland-type restriction of the species (0 = species occurred exclusively in other grassland types; 1 = species occurred in no other grassland type). Sensitivity indicates the fidelity of the species to the considered grassland type (0 = species did not occur in any study plot of the focal grassland type; 1 = species occurred in all study plots of the focal grassland type). The indicator value (IV) indicates the association of the species with the respective grassland type, considering both, Specificity and sensitivity (0 = species not associated with the focal grassland type; 1 = species perfectly associated with the focal grassland type). Significances are indicated as follows: $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Indicator species	**Grassland type**			**Specificity**	**Sensitivity**	**IV**	***P***
	Dry	**Mesic**	**Wet**				
Decticus verrucivorus	✓	.	.	0.65	0.76	0.70	***
Stenobothrus stigmaticus	✓	.	.	0.68	0.72	0.70	***
Bicolorana bicolor	✓	.	.	1.00	0.28	0.53	***
Myrmeleotettix maculatus	✓	.	.	0.82	0.31	0.50	**
Psophus stridulus	✓	.	.	1.00	0.14	0.37	*
Pseudochorthippus parallelus	✓	✓	.	0.90	0.95	0.93	***
Chorthippus biguttulus	✓	✓	.	0.82	1.00	0.90	***
Stenobothrus lineatus	✓	✓	.	0.88	0.78	0.83	***
Gomphocerippus rufus	✓	✓	.	0.89	0.72	0.80	***
Gryllus campestris	✓	✓	.	0.97	0.64	0.79	***
Chrysochraon dispar	.	✓	✓	0.82	0.71	0.76	***
Conocephalus fuscus	.	✓	✓	1.00	0.22	0.47	*
Pseudochorthippus montanus	.	.	✓	0.71	0.86	0.79	***
Metrioptera brachyptera	.	.	✓	0.66	0.86	0.75	***
Stethophyma grossum	.	.	✓	0.77	0.34	0.52	**

Table 3: Results of multivariable GLMM (Poisson error structure): Relationship of Orthoptera species richness of all (a) and threatened (b) species with environmental parameters in the three studied grassland types (*N* for each type = 29). *Sub-area* (*N* = 4) was set up as a random factor. Presented are the averaged models (full average) from the top-ranked models ($\Delta AIC_C < 3$). Both conditional and marginal R^2 [delta] are given: R^2_c = variance explained by both fixed and random effects, R^2_m = variance explained by fixed effects only (Nakagawa et al. 2017). Significances are indicated as follows: n.s. (not significant), $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Parameter	All species			Threatened species		
	Estimate ± SE	z	*P*	Estimate ± SE	z	*P*
i) Dry	R^2_c 0.21–0.32; R^2_m 0.21–0.31			R^2_c 0.36–0.41; R^2_m 0.35–0.41		
Intercept	2.19 ± 1.05	2.06	*	1.32 ± 1.75	0.74	n.s.
Land-use intensity	–0.14 ± 0.08	1.67	n.s.	–0.28 ± 0.13	2.09	*
TPI [range] [1]	0.07 ± 0.06	1.05	n.s.	0.08 ± 0.09	0.97	n.s.
Heatload [range]	0.10 ± 0.49	0.20	n.s.	0.2 ± 0.78	0.32	n.s.
Elevation	0 ± 0	0.38	n.s.	0 ± 0	0.46	n.s.
ii) Mesic	R^2_c 0.39–0.4; R^2_m 0.39–0.39			R^2_c 0.53–0.53; R^2_m 0.53–0.53		
Intercept	2.86 ± 0.73	3.75	***	2.5 ± 1.12	2.13	*
Land-use intensity	–0.19 ± 0.04	4.12	***	–0.38 ± 0.07	5.31	***
TPI [range] [1]	0 ± 0.03	0.02	n.s.	–0 ± 0.05	0.01	n.s.
Heatload [range]	0.09 ± 0.5	0.16	n.s.	0.11 ± 0.8	0.13	n.s.
Elevation	0 ± 0	0.03	n.s.	–0 ± 0	0.02	n.s.
iii) Wet	R^2_c 0.41–0.47; R^2_m 0.4–0.46			R^2_c 0.28–0.29; R^2_m 0.28–0.29		
Intercept	1.45 ± 0.9	1.55	n.s.	0.83 ± 1.24	0.64	n.s.
Land-use intensity	0.54 ± 0.17	3.13	**	0.58 ± 0.17	3.12	**
TPI [range] [1]	0.02 ± 0.05	0.42	n.s.	0.01 ± 0.04	0.19	n.s.
Heatload [range]	–0.41 ± 1.38	0.29	n.s.	–0.1 ± 1	0.1	n.s.
Elevation	0 ± 0	0.12	n.s.	0 ± 0	0.17	n.s.

[1] The topographic position index (TPI) range reflects the difference between the least and the most prominent elevation grid cell within the respective plot. It thus indicates the topographic diversity of the plots.

DISCUSSION

In our study, we detected considerable variation in land-use intensity across three grassland types in a German biodiversity hotspot. Average land-use intensity dropped from high in mesic to low in dry and again to near-zero in wet grasslands. The mean number of both all and threatened species was highest in the grassland type with low land-use intensity, the dry grasslands, differing from those in mesic (high land-use intensity) and wet (mostly abandoned) grasslands. Additionally, the dry grasslands had the highest numbers of all and threatened as well as overall and exclusive indicator species. For all grassland types, land-use intensity was the only predictor of Orthoptera species richness in the multivariable GLMMs.

Generally, the main parameters determining habitat quality for Orthoptera are (i) a favourable (warm) microclimate, (ii) sufficient food, (iii) adequate oviposition sites and (iv) shelter against predators or extreme weather (Willott and Hassall 1998, Gardiner and Dover 2008, Wünsch et al. 2012). Such complex requirements are often best fulfilled in heterogeneous habitats (Kruess and Tscharntke 2002, Schirmel et al. 2010, Fartmann et al. 2012, Helbing et al. 2014, Löffler and Fartmann 2017). Habitat heterogeneity is associated with high availability of microsites and, hence, is generally known to foster species richness (Tews et al. 2004, Steinmann et al. 2011). Due to a mostly low land-use intensity, the dry grasslands had the most heterogeneous swards (own observation) and were the hotspots of Orthoptera diversity in our study. Most dry grasslands were used as cattle pastures with low to at most intermediate stocking rates (own observation, Bogenrieder 2012). Such pastures are known for their spatial heterogeneity, consisting of patches with bare ground, latrines, short grazing laws and spots with taller vegetation (Ellenberg and Leuschner 2010, Bogenrieder 2012, Török et al. 2014, Gardiner 2018).Mesic and wet grasslands represented the two extremes across the land-use-intensity gradient. Mesic grasslands had the highest land-use intensity with adverse effects on Orthoptera species richness. Intensive grassland management results in homogeneous

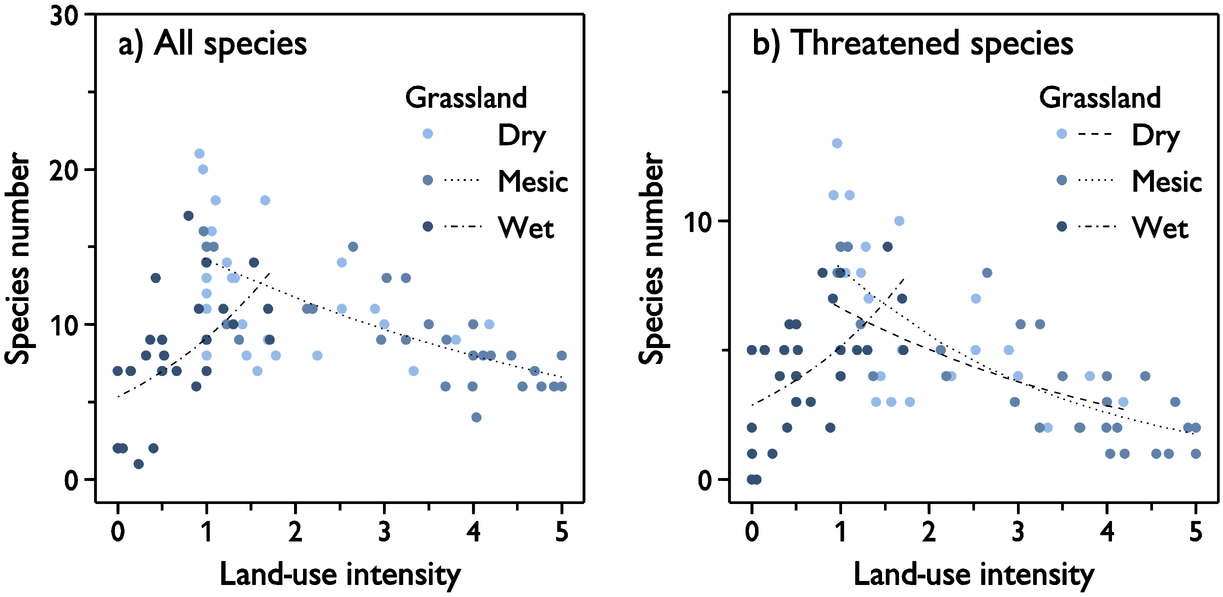

Figure 4: Relationship of Orthoptera species richness of all (a) and threatened (b) species with land-use intensity in the three studied grassland types (*N* for each type = 29). The curves (dashed: dry grasslands, dotted: mesic grasslands; dot-dashed: wet grasslands) depict the averaged models with significant coefficients from Table 3 (see there for details on the models).

and dense swards (Ellenberg and Leuschner 2010) which lack in key microhabitats for Orthoptera. For instance, such swards lack in suitable oviposition sites, such as bare ground or patches of taller vegetation which remain during winter (see above) (Gardiner 2018). Additionally, each mowing event and each period of intensive grazing cause direct mortality of Orthoptera and increase the risk of predation through insectivorous vertebrates (e.g. birds) (Humbert et al. 2012, Wünsch et al. 2012, Buri et al. 2013).

By contrast, in wet grasslands Orthoptera species had suffered from abandonment or irregular land use. Abandonment of management in the wet, formerly species-rich grasslands had mostly resulted in homogeneous and high-growing stands, rich in litter and dominated by tall forbs (e.g. *Filipendula ulmaria*) or grasses (e.g. *Molinia caerulea*) (cf. *Study area*). In such stands, patches of bare ground for soil-breeding species are largely missing (own observation) and the microclimate is rather cool (Stoutjesdijk and Barkman 1992), hampering the establishment of species-rich Orthoptera assemblages (Bieringer 2003, Marini et al. 2009b, Helbing et al. 2014).

The only group of Orthoptera species that was not affected by land use was that of all species in dry grasslands. We explain the lack of relationship by (i) the generally low land-use intensity in dry grasslands and (ii) the lower sensitivity of non-threatened species compared to that of threatened species to more intensive land use. It is well-known that at least some non-threatened, generalist Orthoptera species are able to cope with much higher land-use intensity compared to most threatened, specialist species (Detzel 1998, Schlumprecht and Waeber 2003).

All three grassland types were characterized by certain indicator species. However, only the two grassland types with low land-use intensity, dry and wet grasslands, had exclusive indicator species. Concerning the soil moisture, mesic grasslands mediate between dry and wet grasslands. Hence, some similarities in indicator species of mesic grasslands and one of the other grassland types are plausible. Additionally, we explain the absence of unique indicator species in the mesic grasslands by a homogenisation of the Orthoptera assemblages due to the high land-use intensity. The high numbers of indicator species, especially of exclusive indicator species, indicate that the studied grassland types feature rather specific and definable Orthoptera assemblages. Hence, Orthoptera diversity on the landscape level relies on all three grassland types, especially the dry and wet grasslands.

In summary, land-use intensity was the key driver of Orthoptera species richness in the studied grasslands. Both (i) intensive land use—mostly in the mesic grasslands—and (ii) abandonment—mostly in the wet grasslands—led to a homogenisation of the habitat structures and the species assemblages. By contrast, grasslands with low land-use intensity and high habitat heterogeneity, which applied to most of the dry, but also to some of the mesic and wet grasslands, were hotspots of Orthoptera species richness.

IMPLICATIONS FOR CONSERVATION

Throughout Europe, grasslands with low land-use intensity and high biodiversity have endured especially at higher elevations of mountain areas, as these are generally characterized by an adverse climate or soil conditions that hamper more intensive land use (MacDonald et al. 2000). This was also true for the study area in a German biodiversity hotspot: the species-rich, mostly dry grasslands were generally located at the highest elevations and had the highest topographic diversity. By contrast, at lower elevated sites with lower topographic diversity, land use has been strongly intensified in the productive mesic grasslands and completely abandoned in the unproductive wet grasslands (cf. *Study area*).

Our study has shown that grasslands with low land-use intensity are of prime importance for the conservation of species-rich Orthoptera assemblages. Besides their outstanding conservation value, which has also been acknowledged for other taxa (e.g. birds; Fumy and Fartmann 2021), these heterogeneous habitats are more resilient against the negative effects of climate warming (Fumy et al. 2020).

Due to their topographic diversity, land-use intensification is unlikely for most of the dry grasslands. However, in the future, abandonment may become a threat. Accordingly, we recommend a conservation policy that secures the maintenance of low-intensity land use, in particular grazing in the dry grasslands. In mesic grasslands, management should aim at a reduction of land-use intensity and creation of more heterogeneous swards. Suitable measures are: omitting the application of liquid manure and chemical fertilizers, reducing pasture stocking rates, not exceeding more than two cuts per year on meadows and leaving annually about 10 % of the meadow area uncut in a rotational manner (Humbert et al. 2012, Buri et al. 2013). For wet grasslands and their specific Orthoptera assemblages, we recommend the reintroduction of at least irregular low-intensity management. Both grazing and mowing are possible management alternatives. Additionally, special attention has to be payed to an intact hydrology in the wet grasslands.

ACKNOWLEDGEMENTS

For their hospitality and accommodation during the field-work period we would like to thank Dr. G. Geis-Tyroller and N. Tyroller. The conservation authority of the administrative district of Freiburg gave us permission to survey Orthoptera in protected areas. We are grateful for valuable comments of three anonymous reviewers and the editor.

FUNDING

This study was funded by two PhD scholarships of the German Environmental Foundation (DBU) allocated to Florian Fumy and Steffen Kämpfer.

Low-intensity land use fosters species richness of threatened butterflies and grasshoppers in mires and grasslands

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ABSTRACT

Insects are by far the most species-rich branch of the tree of life and fundamental parts of extensive networks of biotic interactions. However, insect populations are declining dramatically and many species are facing extinction in the course of global change. In this study, we investigate assemblages of threatened butterfly and grasshopper species in mires and grasslands in a low-mountain range in SW Germany: the southern Black Forest. Altogether, 84 randomly selected plots (100 m × 100 m) were surveyed. Across a hydrological gradient, each plot belonged to one of the five following habitat types: raised bog n = 17, fen n = 20, mesic grassland n = 15, semi-dry grassland n = 18 and dry grassland n = 14. Our study revealed strong differences in environmental conditions and in assemblage composition of threatened butterfly and grasshopper species in mire and grassland habitats. Species richness and the number of indicator species of both groups peaked in fens and dry grasslands, and to a lesser extent in semi-dry grasslands. All three habitat types were characterized by low to intermediate levels of land use. In line with this, land-use intensity was the key driver of habitat heterogeneity and, hence, of species richness of threatened butterflies and grasshoppers. We recommend a conservation policy that secures the maintenance or re-establishment of low-intensity land use. In particular, we suggest low-intensity cattle grazing, which has been shown to best promote high habitat heterogeneity.

KEYWORDS

Biodiversity conservation, environmental change, grazing management, habitat heterogeneity, hay meadow, hydrologic gradient, pasture

INTRODUCTION

Large ungulate herbivores have shaped entire biomes for thousands of years, and, accordingly, biodiversity has co-evolved with them (Konvička et al. 2021). However, during the late Pleistocene and early Holocene, humans extirpated or at least strongly reduced these megaherbivores on most continents. Subsequently, preindustrial farmers and pastoralists took on the role of the wild ungulates in creating species-rich habitats (Hejcman et al. 2013, Konvička et al. 2021). Since the beginning of the industrial era, severe and ever accelerating changes in land use have led to the modern-day agriculture that dominates farmland nowadays and has caused severe biodiversity declines (Stoate et al. 2009, Hejcman et al. 2013, Fartmann et al. 2021). At the same time, traditional land use such as large-scale low-intensity cattle grazing has ceased almost completely. However, remnants of traditional land use have persisted in mountainous landscapes where intensive agriculture is impeded by the pronounced relief and shallow soils (MacDonald et al. 2000, Plieninger et al. 2006).

Insects are by far the most species-rich branch of the tree of life and fundamental parts of extensive networks of biotic interactions (Cardoso et al. 2020). However, insect populations are declining dramatically and many species are facing extinction in the course of global change. Two of the most suitable indicator groups to investigate the effects of environmental change in open habitats are butterflies and Orthoptera (hereinafter termed 'grasshoppers') (Thomas 2005, Bazelet and Samways 2012, Fartmann et al. 2013, Poniatowski et al. 2020). This is especially true for threatened species since most of them are habitat specialists and have recently undergone the most severe declines (Purvis et al. 2000, Poniatowski et al. 2016). The habitat requirements of both butterflies and grasshoppers are highly complex. Particularly, vegetation composition and microclimate, which are often interrelated, define habitat quality (Gardiner and Dover 2008, García-Barros and Fartmann 2009, Marini et al. 2009a, Fartmann et al. 2012, Poniatowski et al. 2018b, Stuhldreher and Fartmann 2018).

Our study area comprises a low-mountain range in SW Germany: the southern Black Forest. Due to its high share of species-rich mires and grasslands, it is part of one of 30 German biodiversity hotspots (Ackermann and Sachteleben 2012). In a previous study in the dominant grassland types of the same area, Fumy et al. (2021) identified land-use intensity as the main predictor of grasshopper species richness, especially of threatened species.

In this study, we investigate assemblages of threatened butterfly and grasshopper species in mires and grasslands. Altogether, 84 randomly selected plots belonging to one of the five following habitat types across a hydrological gradient were surveyed: raised bog n = 17, fen n = 20, mesic grassland n = 15, semi-dry grassland n = 18 and dry grassland n = 14. In order to analyse the drivers of biodiversity in a landscape of high conservation value, we related (i) differences in species assemblage composition between the five habitat types and (ii) the relationship of species assemblage composition across all habitat types to environmental conditions. Based on the results, we give recommendations for effective strategies for biodiversity conservation in mire and grassland ecosystems, which are expected to foster not only threatened butterflies and grasshoppers but also a wide range of other taxa.

MATERIAL AND METHODS

Study area

The study area, the 'Hotzenwald' in the southern Black Forest (federal state of Baden-Württemberg, SW Germany; 47°7' N/8°1' E), has an area of about 100 km² and covers an elevation gradient of 700 to 1,100 m a.s.l. For

Central European conditions, the climate is rather cool and wet, with a mean annual temperature of 6.6 °C and an average annual precipitation of 1,650 mm (reference period 1991–2020; German Meteorological Service, 2021). Along the elevation gradient, precipitation increases from about 1,470 to 1,840 mm/a and mean annual temperature decreases from 7.3 to 5.6 °C. The Hotzenwald is part of the German biodiversity hotspot 'Hochschwarzwald mit Alb-Wutach-Gebiet' (Ackermann & Sachteleben, 2012). The cultural landscape of the study area is rich in open mire ecosystems and semi-natural grasslands (Fumy and Fartmann 2021). Most of the mires and grasslands have been managed as commons for centuries (Hermle and Deil 2002, Regional Office for Environment 2004). Although a relatively large share of them is still in communal property, management has undergone substantial changes since the 1930s through administrative interventions and technical innovation (Regional Council Freiburg 2011). However, traditional rough grazing, in many cases with a local cattle breed called 'Hinterwälder', is still widespread in mires and semi-natural grasslands. (Konold et al. 2014). Due to their high habitat heterogeneity and species richness, these pastures have an outstanding conservation value and, additionally, make a unique contribution to the German cultural heritage (Lederbogen et al. 2004, Fumy et al. 2021, Fumy and Fartmann 2021). On some of the least productive soils however, irregular management or complete abandonment for over 20 years has resulted in the replacement of formerly species-rich mires and semi-natural grasslands by homogeneous, high-growing vegetation rich in litter and dominated by tall forbs (e.g. *Filipendula ulmaria*), dwarf shrubs (e.g. *Vaccinium myrtillus*, *V. uliginosum*) or grasses

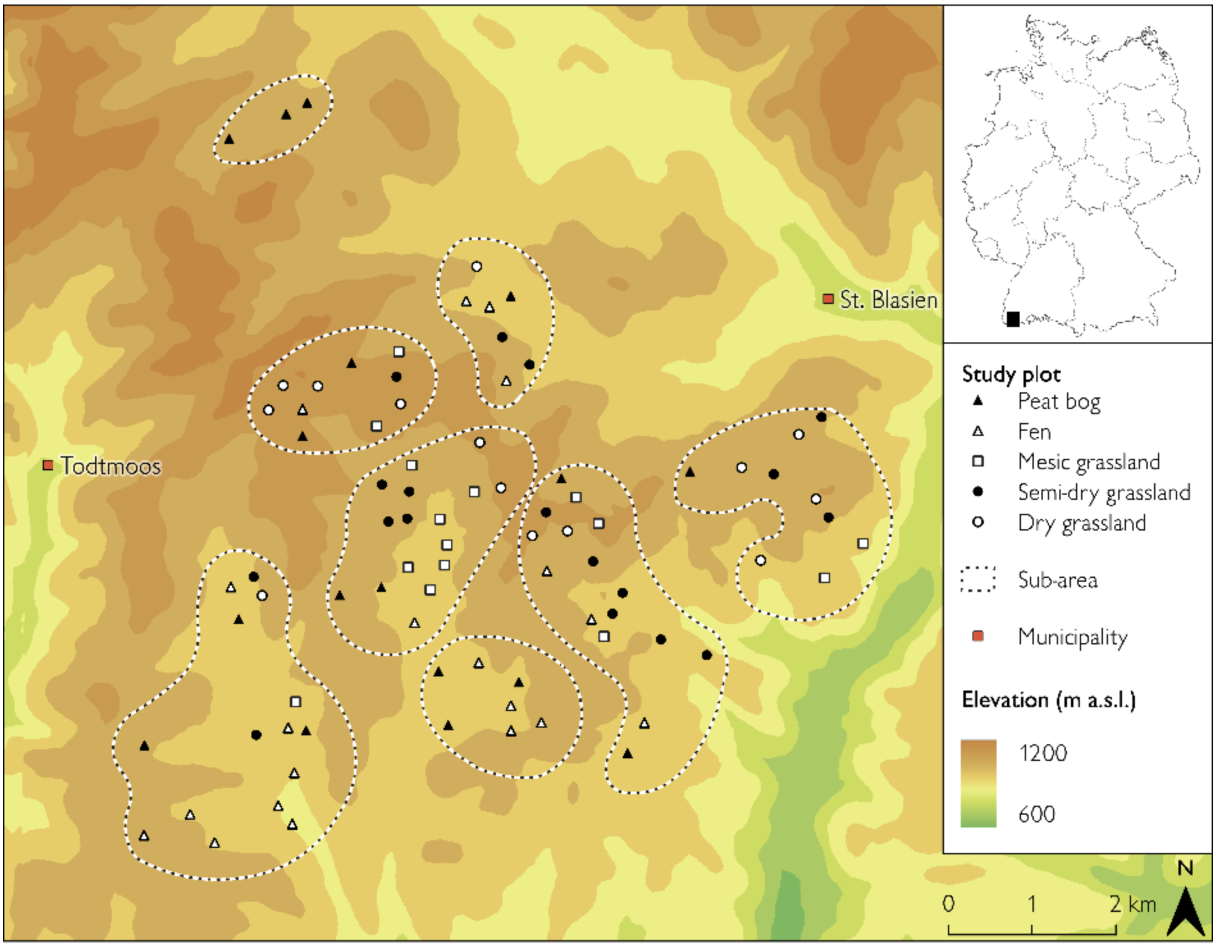

Figure 1: Location of the study area and plots in the southern Black Forest (SW Germany).

(e.g. *Molinia caerulea*, *Nardus stricta*) (Geis et al. 2013; own observation, Fumy et al. 2021).

In contrast to the pastures on nutrient-poor soils, the grasslands on more productive soils historically were predominantly mown once or twice per year (Regional Office for Environment 2004) and managed as irrigation meadows (Leibundgut and Vonderstrass 2016). However, many of them have recently suffered from land-use intensification, reflected by a regular application of fertilizer and an increasing mowing frequency (Konold et al. 2014). Despite these general changes in land use, some of the meadows in the study area are still characterized by low-intensity land use and species-rich insect assemblages (Fumy et al. 2020, Fumy et al. 2021).

Study design

Study plots

Within the study area, we mapped mire and grassland habitats in the field according to Finck et al. (2017). Altogether, 84 randomly selected plots (100 m × 100 m) were surveyed. Across a hydrological gradient, each plot belonged to one of the five following habitat types: raised bog *n* = 17, fen *n* = 20, mesic grassland *n* = 15, semi-dry grassland *n* = 18 and dry grassland *n* = 14. Characteristic plant communities of raised bogs were the *Sphagnetum magellanici* and at higher elevations also the *Eriophoro-Trichophoretum cespitosi*, the *Pino mugo-Sphagnetum* and *Vaccinium-uliginosum* shrubberies. The *Juncetum squarrosi* and communities of the *Scheuchzerio-Caricetea* such as the *Caricion fuscae*, *Caricetum limosae* and *Caricetum rostratae* were typical of fens. *Cynosurion* and *Polygono-Trisetion* communities were characteristic of mesic, the *Polygalo-Nardetum* of semi-dry and the *Festuco-Genistelletum* of dry grasslands (Dierschke 1997, Peppler-Lisbach and Petersen 2001, Burkart et al. 2004, Regional Office for Environment 2004). The minimum distance between two plots was set to 100 m. Moreover, to avoid edge effects from adjacent habitats (Schirmel et al. 2010), each plot had to be surrounded by a buffer of at least 20 m of the focal habitat type. In order to account for possible spatial autocorrelation, the study area was divided into eight sub-areas according to the landscape configuration (Fig. 1).

Table 1: Mean (± SE) of environmental parameters at the habitat and landscape level and relationship to butterfly and grasshopper species richness. Low-int. = low-intensity. Species richness was analysed via GLMM with Poisson error structure. *Sub-area* (*N* = 8) and *habitat type* (*N* = 5) were set up as random factors. All fixed effects were standardized prior to the analyses. *P* values were obtained from comparison of the respective model with the intercept-only model via an ANOVA. Significance levels are indicated as follows: n.s. (not significant) *P* > 0.05, * *P* ≤ 0.05, ** *P* ≤ 0.01, * *P* ≤ 0.001.**

Parameter	**Mean ± SE**	**Butterflies**			**Grasshoppers**		
		Estimate ± SE	*P*	AUC	Estimate ± SE	*P*	AUC
Habitat level							
Elevation (m a.s.l.)	972 ± 6	–0.04 ± 0.07	n.s.	.	0.13 ± 0.07	n.s.	.
Heat-load index (HLI)	0.68 ± 0.01	–0.01 ± 0.06	n.s.	.	0.03 ± 0.06	n.s.	.
Land-use intensity	1.71 ± 0.16	–0.13 ± 0.12	n.s.	►0.84	0.11 ± 0.14	n.s.	►0.89
Land-use intensity^2	·	–0.46 ± 0.11	***		–0.42 ± 0.1	***	
Habitat heterogeneity	9.01 ± 0.55	0.19 ± 0.07	**	0.70	0.29 ± 0.05	**	0.85
Landscape level							
Open habitats	49 ± 3	–0.13 ± 0.07	n.s.	.	0.11 ± 0.06	n.s.	.
Low-int. open habitats	20 ± 2	0.19 ± 0.08	*	0.72	0.32 ± 0.05	***	0.84

Sampling design

Environmental conditions

For each plot, we sampled data on several environmental parameters (Table 1 and 2). We calculated the mean elevation based on an elevation grid (provided by Sonny 2020) with a spatial resolution of "1", which corresponds to a resolution of approx. 20 m × 30 m in the study area. Using the same elevation data, we calculated the mean heatload index (HLI) according to McCune and Keon (2002) as a measure of radiation influx using the 'spatialEco' package by Evans (2019).

We ascertained land-use intensity on an ordinal scale based on Fumy et al. (2021). Within each plot, we mapped the land-use types in the field. Each land-use type in the plots was assigned a land-use intensity value ranging from 0 to 5 (Table 2). The land-use intensity was then calculated for each plot as the weighted mean of the land-use values of all land-use types relative to their cover within the respective plot. Additionally, we counted the number of the following habitat layers within each plot in the field: bare ground, stones, litter, dwarf shrubs, shrubs, mosses, dead wood, trees and low (< 5cm), mid (5 – 15 cm) and high (> 15 cm) growing tussock grass, other grass and herbs, respectively. We only considered layers with a minimum cover of 5%. We calculated the sum of the different layers per plot as the habitat-heterogeneity score, which could take values between 1 and 17. Additionally, we mapped the share of open habitats in general and with low-intensity land use (land-use values: 0–2; see Table 2) in a buffer of 100 m around each plot in the field.

Butterfly and grasshopper assemblages

In 2018, we surveyed threatened butterfly and grasshopper species (including near-threatened species) according to the red data books of Baden-Württemberg (butterflies: Ebert et al. 2005, grasshoppers: Detzel et al. 2021). Threatened butterfly species were sampled on each plot at four times between May and August with at least three weeks between each visit. Butterflies were surveyed by walking each plot in a loop-like manner for 30 minutes,

Table 2: Land-use types in the plots and their assigned land-use intensity values. Land-use intensity ranges from 0 (no land use) to 5 (very high land-use intensity).

Land-use intensity	Value	Description
No land use	0	Abandoned open mire and semi-natural grassland
Very low	0.5	Open mire and semi-natural grassland: sporadically grazed, at most two to four weeks per year
Low	1	Open mire and semi-natural grassland: meadows mown once or pastures with low stocking rates
Moderate	2	Improved grassland: meadows mown twice or pastures with intermediate stocking rates
Moderate/high	3	Improved grassland: meadows mown thrice or pastures with strip grazing (rotation cycle of two to four weeks)
High	4	Improved grassland with liquid-manure fertilisation: meadows mown thrice or highly intensive strip grazing (rotation cycle of two to five days)
Very high	5	Improved grassland with liquid-manure fertilisation: meadows mown four times

excluding time taken for species determination. Species were identified visually or using net catches and released after identification. Butterfly sampling was only conducted under favourable weather conditions (Settele et al. 2015, temperature > 13 °C [sunshine] or > 17 °C [cloud cover 40–80%] and low wind speed [maximum: 4 bft.]; BfN 2019). The scientific nomenclature follows Settele et al. (2015).

Threatened grasshopper species were sampled at three times between June and August with at least three weeks between each visit. In each plot, all available habitat structures were surveyed for the occurrence of grasshopper species under favourable weather conditions (temperature > 15 °C, cloud cover < 50%) using acoustic and visual detection as well as sweep netting; all individuals were released after identification (Fischer et al. 2016, Samways 2019). Arbusticolous and arboricolous species that rarely occur in open habitats were excluded from all analyses as our sampling techniques do not produce reliable data for these species. To improve the detection of quiet or high-frequency stridulating species, such as *Conocephalus fuscus* and *Metrioptera brachyptera*, a bat detector was used. The scientific nomenclature follows Fischer et al. (2016).

Statistical analysis

All statistical analyses were performed using R statistical environment (R Core Team 2020). Differences in environmental parameters between the five studied habitat types were analysed using the Kruskal-Wallis *H* test and Dunn's test as a post-hoc test using the 'dunn.test' package (Dinno 2017). We chose this nonparametric approach because Generalized Linear Mixed-effects Models (GLMM) could not be applied due to overdispersion.

Differences in the numbers of threatened butterfly and grasshopper species between the five studied habitat types were analysed using GLMMs with Poisson error structure, *habitat type* as a categorical predictor and *sub-area* as a random factor. Pairwise comparisons between the habitat types were made using the 'glht' function in the 'multcomp' package by Hothorn et al. (2008), with the Tukey test as a post-hoc test (homogeneity of variance was given).

To assess the effect of land-use intensity on habitat heterogeneity, we conducted a GLMM with *habitat heterogeneity* as the response variable and *land-use intensity* (centred and scaled values) as a fixed effect with negative binomial error structure. Graphical inspection of the data suggested a unimodal rather than a linear relationship between the response and predictor variable, so centred, scaled and squared values of the predictor were additionally entered in the model. The variables *sub-area* and *habitat type* served as random factors. The model was compared to the respective intercept-only model via ANOVA.

To identify species indicative for the five studied habitat types, we conducted an indicator species analysis using the 'multipatt' function in the R package 'indicspecies' by Cáceres and Legendre (2009). We considered indicator relationships of single species with single and combined habitat types and used the 'IndVal.g' association index according to Cáceres et al. (2010). The statistical significance of this indicator value was tested using a permutation test; the number of permutations was set to 999 (for further details see Cáceres and Legendre 2009).

To assess the effects of the environmental parameters on species richness of threatened butterflies and grasshoppers, we conducted uni- and multivariable GLMMs with Poisson error structure. Multicollinearity was low for all predictors in all models ($|r_s| < 0.5$, VIF < 2) (see Graham 2003, Zuur et al. 2010). Since habitat heterogeneity significantly depended on land-use intensity (unimodal relationship; see

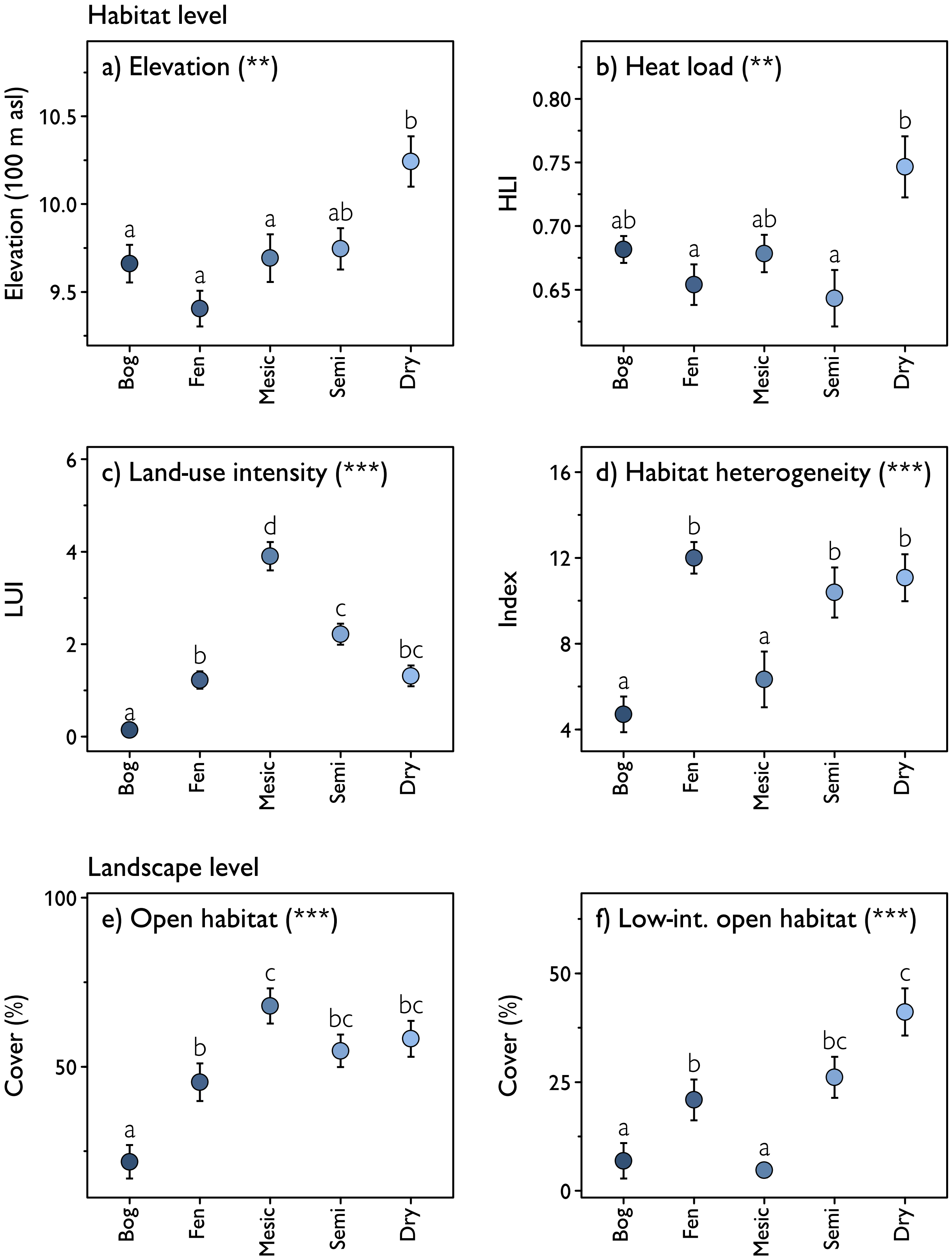

Figure 2: Mean (± SE) elevation (a), heat load (b), land-use intensity (c), habitat heterogeneity (d), open habitat (e) and low-intensity open habitat (f) in the five studied habitat types. Peat bog (*n* = 17), fen (*n* = 20), mesic grassland (*n* = 15), semi-dry grassland (*n* = 18) and dry grassland (*n* = 14). Differences were tested using the Kruskal-Wallis *H* test and Dunn's test as a post-hoc test. Different letters indicate significant differences between grassland types ($P \leq 0.05$).

Environmental conditions), it was not included in the multivariable GLMMs. Possible autocorrelation in space and within the considered habitat types was taken into account by adding *sub-area* and *habitat type* as random factors. All fixed effects were centred and scaled. Graphical inspection suggested a unimodal rather than linear relationship between both response variables and land-use intensity, so we additionally added centred, scaled and squared values of land-use intensity to all models. In order to increase the robustness of models with multiple predictors and identify the most important environmental parameters, we conducted model averaging based on an information-theoretic approach including the top-ranked models within ΔAIC_C <3 (Burnham and Anderson 2010, Grueber et al. 2011). We used the 'lme4' package of Bates et al. (2015) for all GLMM analyses and the 'dredge' and the 'model.avg' functions in the R package 'MuMIn' by Bartoń (2017) for model averaging.

RESULTS

Environmental conditions

Environmental conditions differed strongly between the habitat types (Fig. 2). At the plot level, dry grasslands were situated at the highest elevations and had the highest heat-load-index values, usually differing from most of the four other habitat types. Land-use intensity peaked in mesic grasslands and decreased towards both ends of the studied hydrological gradient. Raised bogs were characterized by the lowest land-use intensity; most of them were even abandoned. Habitat heterogeneity was highest in fens, dry grasslands and semi-dry grasslands differing from mesic grasslands and raised bogs.

At the landscape level, the cover of open habitats was highest in dry and semi-dry grasslands and lowest in raised bogs. Fens had an intermediate position differing from both raised bogs and the three grassland types. The cover of open habitats with low land-use intensity in the surrounding of the plots decreased from dry and semi-dry grasslands to fens to raised bogs and mesic grasslands. Land-use intensity predicted habitat heterogeneity within the plots and was highest at low to intermediate levels of land use and lowest in abandoned and intensively used plots (Fig. 3).

Species assemblages

In total, we recorded 24 threatened butterfly and 19 threatened grasshopper species (see Appendix 1). The most widespread butterfly species were *Argynnis aglaja*, *Melitaea athalia* and *Argynnis adippe*, which were present in 49, 48 and 38% of the plots, respectively. The most common grasshopper species were *Euthystira brachyptera*, *Stenobothrus lineatus* and *Tettigonia cantans*, occurring in 62, 56 and 49% of the plots, respectively. Species richness differed between the five habitat types (Fig. 4). The number of butterfly species was highest in fens followed by dry grasslands and lowest in mesic grasslands; semi-dry grasslands and raised bogs

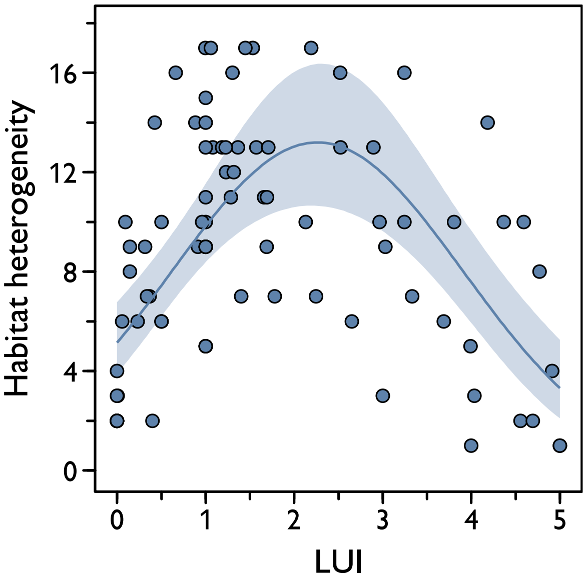

Figure 3: Relationship between land-use intensity and habitat heterogeneity within the plots analysed via GLMM with negative binomial error structure. *Sub-area* (N = 8) and *habitat type* (N = 5) were set up as random factors. All fixed effects were standardized prior to the analyses. P values were obtained from comparison of the respective model with the intercept-only model via an ANOVA. Significance level $P \leq 0.001$.

had an intermediate position. Species richness of grasshoppers was highest in dry grasslands, intermediate in fens, semi-dry and mesic grasslands and lowest in raised bogs.

Altogether, 13 butterfly and 14 grasshopper species were indicative for one or more habitat types (Table 3). The two habitat types with the highest overall species richness, dry grasslands and fens, also had the highest number of indicator species in general (19 and 14 species, respectively) and exclusive indicator species (7 and 3 species, respectively). Semi-dry grasslands (10 species), raised bogs (8 species among them one exclusive species) and mesic grasslands (6 species) had clearly lower numbers of indicative species.

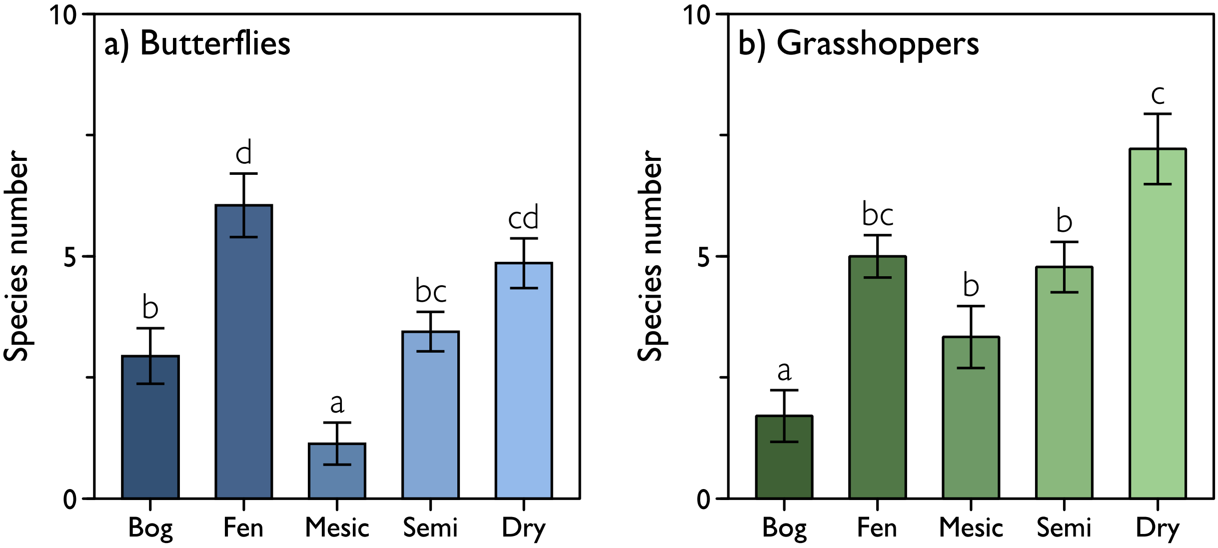

Figure 4: Mean species richness (± SE) of threatened butterfly (a) and grasshopper (b) species in the five studied habitat types. Peat bog (*N* = 17), fen (*N* = 20), mesic grassland (*N* = 15), semi-dry grassland (*N* = 18) and dry grassland (*N* = 14). Differences between the habitat types were tested using Generalized Mixed-effects Models (GLMM) with *sub-area* (*N* = 8) as a random factor. Different letters indicate significant differences between habitat types (*P* ≤ 0.05).

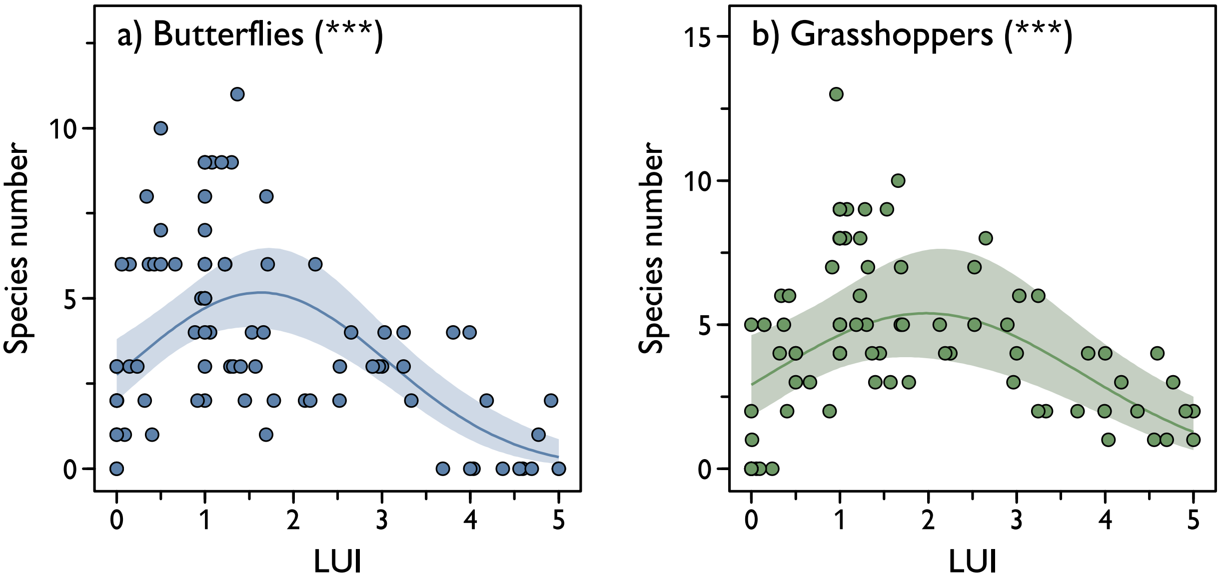

Figure 5: Relationship of threatened butterfly (a) and grasshopper (b) species richness to significant parameters from the multivariable GLMM. For model details see Table 4.

Table 3: Indicator species for the five studied habitat types. Taxon: B = butterfly, G = grasshopper. Specificity (Spec) indicates the degree of habitat-type restriction of the species (0 = species occurred exclusively in other habitat types; 1 = species occurred in no other habitat type). Sensitivity (Sens) indicates the fidelity of the species to the considered habitat type (0 = species did not occur in any plot of the focal habitat type; 1 = species occurred in all plots of the focal habitat type). The indicator value (IV) indicates the association of the species with the respective habitat type, considering both specificity and sensitivity (0 = species not associated with the focal habitat type; 1 = species perfectly associated with the focal habitat type). Significance levels are indicated as follows: n.s. (not significant) $P > 0.05$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

Indicator species	**Taxon**	**Habitat type**					**Spec**	**Sens**	**IV**	***P***
		Bog	Fen	Mesic	Semi	Dry				
Plebejus optilete	B	✓	.	.	.	.	0.88	0.35	0.56	***
Pseudochorthippus montanus	G	✓	✓	.	.	.	0.79	0.73	0.76	***
Colias palaeno	B	✓	✓	.	.	.	1.00	0.46	0.68	***
Boloria aquilonaris	B	✓	✓	.	.	.	0.82	0.46	0.62	**
Melitaea athalia	B	✓	✓	.	✓	✓	0.97	0.57	0.74	***
Argynnis adippe	B	✓	✓	.	✓	✓	0.96	0.45	0.66	**
Metrioptera brachyptera	G	✓	✓	.	.	✓	0.88	0.57	0.71	***
Boloria selene	B	✓	✓	.	.	✓	0.89	0.35	0.56	*
Aporia crataegi	B	.	✓	.	.	.	0.70	0.45	0.56	**
Boloria titania	B	.	✓	.	.	.	0.63	0.50	0.56	***
Miramella alpina	G	.	✓	.	.	.	0.71	0.30	0.46	*
Boloria eunomia	B	.	✓	✓	.	.	1.00	0.26	0.51	***
Euthystira brachyptera	G	.	✓	✓	✓	✓	0.91	0.70	0.80	**
Omocestus viridulus	G	.	✓	✓	✓	✓	0.94	0.46	0.66	*
Argynnis aglaja	B	.	✓	.	✓	✓	0.84	0.67	0.75	***
Stenobothrus lineatus	G	.	.	✓	✓	✓	0.88	0.85	0.87	***
Stenobothrus stigmaticus	G	.	.	✓	✓	✓	0.95	0.57	0.74	***
Stauroderus scalaris	G	.	.	✓	✓	✓	0.87	0.43	0.61	**
Decticus verrucivorus	G	.	.	.	✓	✓	0.74	0.69	0.71	***
Hesperia comma	B	.	.	.	✓	✓	0.79	0.44	0.59	**
Argynnis niobe	B	.	.	.	.	✓	0.62	0.71	0.67	***
Erebia medusa	B	.	.	.	.	✓	0.61	0.71	0.66	***
Psophus stridulus	G	.	.	.	.	✓	1.00	0.29	0.54	**
Tetrix bipunctata	G	.	.	.	.	✓	0.75	0.36	0.52	**
Myrmeleotettix maculatus	G	.	.	.	.	✓	0.68	0.36	0.49	**
Platycleis albopunctata	G	.	.	.	.	✓	1.00	0.21	0.46	**
Bicolorana bicolor	G	.	.	.	.	✓	0.72	0.29	0.45	*
No. species		**8**	**14**	**6**	**10**	**19**				
No. exclusive species		**1**	**3**	**.**	**.**	**7**				

Threatened butterfly and grasshopper species richness were determined by the same drivers. The univariable GLMMs revealed (i) humpback-shaped responses of species richness to land-use intensity, (ii) an increase in species numbers with habitat heterogeneity and (iii) positive relationships of species numbers with the cover of low-intensity open habitats in the surrounding of the plots (Table 1). In the multivariable GLMMs, land-use intensity was the only predictor of species richness (Table 4, Fig. 5). Threatened butterfly and grasshopper species richness both showed a unimodal response to this variable, peaking at low to intermediate land-use intensity. The explanatory power of all models was high with AUC values ranging from 0.70 to 0.89.

DISCUSSION

Our study revealed strong differences in environmental conditions and in assemblage composition of threatened butterfly and grasshopper species in mire and grassland habitats. Species richness and the number of indicator species of both groups peaked in fens and dry grasslands and to a lesser extent in semi-dry grasslands. All three habitat types were characterized by low to intermediate levels of land use. In line with this, land-use intensity was the main predictor of species richness across the five studied habitat types.

Threatened Central European butterfly and grasshopper species are usually habitat specialists that rely on very specific habitat characteristics (Schlumprecht and Waeber 2003, Bräu 2013, Poniatowski et al. 2016). The main parameters determining habitat quality for both groups are (i) a favourable microclimate, which is interrelated with suitable host plants for butterflies), (iii) sufficient food and (iv) shelter against predators or extreme weather (Willott and Hassall 1998, Gardiner and Dover 2008, Erhardt and Mevi-Schütz 2009, García-Barros and Fartmann 2009, Wünsch et al. 2012, Stuhldreher and Fartmann 2018). These complex requirements are often best fulfilled in heterogeneous habitats (Kruess and Tscharntke 2002, Marini et al. 2009a, Schirmel et al. 2010, Fartmann et al. 2012, Helbing et al. 2014, Löffler and Fartmann 2017).

Our GLMM analysis showed that the habitat heterogeneity within the plots depended in a humpback-shaped pattern on land-use intensity. Fens, dry and semi-dry grasslands had the highest habitat heterogeneity. Most of them were managed by large-scale low-intensity cattle grazing (own observation). Such pastures generally feature high habitat heterogeneity with spatial mosaics of patches with bare ground, short grazing lawns

Table 4: Multivariable GLMM (Poisson error structure): Relationship of threatened butterfly and grasshopper species richness with environmental parameters. *Sub-area* (*N* = 8) and *grassland type* (*N* = 5) were set up as random factors. All fixed effects were standardized prior to the analyses. Presented are the averaged models (full average) from the top-ranked models (ΔAIC$_C$ <1). The area under the ROC curve (AUC) is given. Significance levels are indicated as follows: n.s. (not significant) *P* > 0.05, * *P* ≤ 0.05, ** *P* ≤ 0.01, * *P* ≤ 0.001.**

Parameter	**Butterflies (AUC = 0.85)**			**Grasshoppers (AUC = 0.89)**		
	Estimate ± SE	*Z*	*P*	Estimate ± SE	*Z*	*P*
Intercept	1.58 ± 0.14	11.2	***	1.72 ± 0.17	9.94	***
Elevation	–0.08 ± 0.08	0.97	n.s.	.	.	.
Land-use intensity	–0.14 ± 0.11	1.24	n.s.	0.13 ± 0.14	0.92	n.s.
Land-use intensity^2	–0.46 ± 0.11	3.94	***	–0.40 ± 0.10	3.92	***
Low-intensity open habitat	0.04 ± 0.07	0.52	n.s.	0.07 ± 0.08	0.88	n.s.

and taller vegetation (Bogenrieder 2012, Török et al. 2014, Gardiner 2018, Schwarz et al. 2018, Fumy et al. 2021) and thus fulfil most of the aforementioned conditions that are necessary for species-rich assemblages of specialized butterflies and grasshoppers. As a result, all three habitat types were characterized by high levels of insect-species richness.

Mesic grasslands and raised bogs were located at the two ends of the land-use intensity gradient. Mesic grasslands exhibited an intensive management, especially mowing thrice or more and regular liquid manure application, and a species-poor, homogeneous vegetation (Fumy et al., 2021; own observation). In the vast majority of the raised bogs, the land had not been in use for more than two decades (cf. *Study area*). Additionally, all bogs had been affected by historic drainage and, hence, most of them were dominated by a monotonous vegetation with low plant-species richness due to encroachment of grasses (*Molinia caerulea*), dwarf shrubs (*Vaccinium myrtillus*, *V. uliginosum*) or shrubs (Geis et al. 2013; own observation, Fumy et al. 2021). As a consequence, and by contrast with fens, dry and semi-dry grasslands, both mesic grasslands and raised bogs featured very low levels of habitat heterogeneity and insect species richness.

The explanatory power of land-use intensity for species richness was higher than that of habitat heterogeneity in the univariable GLMMs. Accordingly, further parameters that depend upon land-use intensity may add to the observed biodiversity patterns. This seems to be especially true for plots with intensive land use. We assume that additional effects of fertilisation and mowing also contributed to the observed low species richness in these plots. The vast majority of insects, especially of habitat specialists, is dependent on nutrient-poor environments and suffers from excessive nitrogen in their food resources (WallisDeVries 2014). In line with this, it has been observed that fertilisation alters plant quality, with negative effects on butterfly and grasshopper species (Nijssen et al. 2017, Kurze et al. 2018). Moreover, each mowing event causes direct mortality of insects and results in higher predation rates through insectivorous vertebrates (e.g. birds) as a consequence of the removal of all protective vegetation (Wünsch et al. 2012, Buri et al. 2013, van Klink et al. 2019).

Our study highlights the prime importance of high habitat quality for species-rich assemblages of threatened butterflies and grasshoppers, which is driven by land-use intensity and the interrelated habitat heterogeneity. This is in accordance with previous research from other landscapes with high habitat availability and connectivity (Maes and Bonte 2006, Fartmann et al. 2012, Uchida and Ushimaru 2014, Löffler and Fartmann 2017, Münsch et al. 2019, Klein et al. 2020, Poniatowski et al. 2020). However, many of the studied species have high area requirements (Salz and Fartmann 2009) and depend on dense habitat networks for long-term survival since they build metapopulations (Poniatowski et al. 2018b). Therefore, the landscape configuration should have an effect on species richness, even in landscapes of high conservation value such as the study area (Cappellari and Marini 2021). Indeed, the number of threatened butterfly and grasshopper species increased with the cover of open habitats with low land-use intensity in the surroundings of the study plots.

Summing up, our study showed that low to intermediate levels of land use, such as cattle grazing with low stocking rates, promoted habitat heterogeneity and fostered species richness of specialized butterflies and grasshoppers in open mires and grasslands. By contrast, both abandonment and intensive land use resulted in monotonous swards that featured little diversity and hence led to biotic homogenisation.

IMPLICATIONS FOR CONSERVATION

In our study, land-use intensity was the key driver of habitat heterogeneity and, hence, species richness of threatened butterflies and grasshoppers. Accordingly, we recommend a conservation policy that secures the maintenance or re-establishment of low-intensity land use. In particular, we suggest low-intensity cattle grazing, in the study area preferably with the local cattle breed 'Hinterwälder'. It has been shown that such a grazing regime most effectively promotes high habitat heterogeneity and biodiversity in general (Adler et al. 2001, Bucher et al. 2016, Schwarz et al. 2018, Hall and Bunce 2019). Where grazing is not an option, mowing once or twice per year while annually leaving about 10 % of the meadow area uncut in a rotational manner can offer an alternative (Humbert et al. 2012, Buri et al. 2013). The application of liquid manure and chemical fertilizers must cease completely. Solid manure could be an alternative but should be applied with caution and only on grasslands on more nutrient-rich soils. Abandoned mires and grasslands suffer from advanced succession, so that shrubs and trees have to be cleared prior to the re-introduction of regular management (Geis et al. 2013). In drained mires, it is also necessary to block the drainage ditches in order to stabilize the water level.

Our results suggest that the loss of habitat heterogeneity due to the ongoing processes of land-use intensification and abandonment still poses a severe threat to insect diversity in Europe, especially in landscapes of high conservation value rich in remnants of traditional land use. In contrast to low-intensity land use, modern, revenue-oriented farming does not fulfil the role of wild ungulates in creating species-rich habitats, a role that was taken on by preindustrial farmers and pastoralists thousands of years ago (Hejcman et al. 2013, Konvička et al. 2021). Consequently, we are confident that the maintenance and re-introduction of low-intensity large-scale cattle grazing is one of the most effective strategies for the conservation of threatened insect species and biodiversity in general in mire and grassland ecosystems across Europe.

ACKNOWLEDGEMENTS

For their hospitality and accommodation during the field-work period we would like to thank Dr. G. Geis-Tyroller and N. Tyroller. The conservation authority of the administrative district of Freiburg gave us permission to survey butterflies and grasshoppers in protected areas. We acknowledge support by Deutsche Forschungsgemeinschaft (DFG) and Open Access Publishing Fund of Osnabrück University.

FUNDING

This study was funded by a PhD scholarship of the German Environmental Foundation (DBU) allocated to Florian Fumy

APPENDIX

Appendix A1: Plot occupancy of all Butterfly (a) and Grasshopper (b) species recorded in the study.

A1a

Butterfly species	Occupancy
Aporia crataegi	14
Argynnis adippe	38
Argynnis aglaja	49
Argynnis niobe	21
Boloria aquilonaris	24
Boloria dia	6
Boloria eunomia	11
Boloria selene	24
Boloria titania	18
Brenthis ino	12
Colias hyale	2
Colias palaeno	20
Erebia ligea	21
Hesperia comma	21
Lycaena alciphron	2
Lycaena hippothoe	7
Lycaena phlaeas	2
Lycaena tityrus	2
Melitaea athalia	48
Melitaea diamina	24
Phengaris arion	4
Plebejus argus	1
Plebejus optilete	8
Pseudophilotes baton	1

A1b

Grasshopper species	Occupancy
Bicolorana bicolor	7
Calliptamus italicus	1
Decticus verrucivorus	37
Euthystira brachyptera	62
Metrioptera brachyptera	39
Miramella alpina	10
Myrmeleotettix maculatus	10
Omocestus rufipes	4
Omocestus viridulus	39
Platycleis albopunctata	4
Pseudochorthippus montanus	39
Psophus stridulus	5
Stauroderus scalaris	29
Stenobothrus lineatus	56
Stenobothrus stigmaticus	35
Tetrix bipunctata	8
Tetrix tenuicornis	2
Tetrix undulata	6
Tettigonia cantans	49

Chapter IV

Synthesis and perspectives

Lycaena hippothoe **on flowering** ***Arnica montana*** **(Schwarze Säge 2018/07/02)**

CHAPTER IV

In chapter IV, the main findings of the studies presented in chapters II and III are summarized and their implications for conservation in times of global change are discussed.

BIODIVERSITY RESPONSES TO CHANGING ENVIRONMENTS

The studies on the influence of climate and land-use change on the occurrence of the ring ouzel *Turdus torquatus alpestris* and on species assemblage composition of grassland Orthoptera showed that both drivers have considerable effects on population dynamics and distribution patterns of important indicators of biodiversity.

I found that the ring ouzel has lost about one third of its previous habitat in the Black Forest during the past three decades. This loss was mainly due to deteriorated food resources: on the one hand, there was an increasing temporal mismatch of snow-bed melting and breeding season of the ring ouzel. At the snow melting frontier, soils become wet and penetrable and soil organisms, such as earthworms, become active when the soil temperatures suddenly rise. Melting snow beds thus represent optimal foraging grounds for the ring ouzel–however, with ever advanced melting, this important resource is increasingly less available during the critical periods of chick hatching and feeding. On the other hand, very low or absent grazing pressure led to much denser herbaceous vegetation and scrub encroachment in previously short-growing and sparsely vegetated pastures. This process is probably even enhanced by the extending vegetation period due to climate warming. Just like many other specialized grassland birds, the ring ouzel forages on the ground and thus relies on permeable vegetation, so the observed changes reduce food accessibility for the species.

Orthoptera assemblage composition was strongly affected by climate change. Mean species number per patch as well as the total species number in the study area have considerably increased during the past 20 years. This might seem to be ‘good news’ for biodiversity. However, the increased numbers could only be attributed to thermophilous mobile generalist species and were not consistent across the three studied grassland types. Moreover, the community farmland index, which is a measure of assemblages’ habitat specialisation, decreased significantly in wetlands and mesic grasslands, but was stable in common pastures. Thus, it can be argued that despite the increased total numbers, overall biodiversity has rather reduced in wetlands which generally were characterized by land-use abandonment and mesic grasslands

As a consequence of climate change, species that rely on cold and moist habitats such as *Miramella alpina* (top) and *Tettigonia cantans* (bottom) are on retreat. (Silberbrunnenmoos 2018/06/15 and Gunzesried 2021/08/12)

which had been subject to land-use intensification. Common pastures, which still are under low-intensity land use–however with sufficient grazing pressure, as opposed to the generally higher elevated patches in the ring ouzel study–were more resilient to the effects of climate change and served as a refuge for the more specialized, less mobile and also the cold-adapted species. Local species richness in these patches was indeed enhanced by the immigration of thermophilous species from lower elevations.

My results suggest that climate change already has a severe impact on the distribution of species in the study area. Cold-adapted species are on retreat, especially at low-elevated sites. Mobile thermophile species on the other hand were able to track the warmer climatic conditions and colonized higher-elevated sites. In comparison to abandoned and intensively managed sites, local extinctions driven by climate change were much less frequent than at those that were under low-intensity management.

Specialized species such as *Stauroderus scalaris* (top) and *Omocestus viridulus* (bottom) occur mainly in the common pastures, which typically are under low-intensity management. These heterogeneous pastures provide a large variety of microclimatic conditions and consequently offer species the possibility to react locally in response to changing climatic conditions. (Ibach 2018/08/03)

LAND-USE INTENSITY, HABITAT HETEROGENEITY AND BIODIVERSITY

The studies on effects of land-use intensity on habitat properties and consequences for butterfly and Orthoptera assemblages revealed that grassland habitat quality is strongly related to land-use intensity. In both studies, I assessed land-use intensity based on the local management, which proved to be a simple yet promising approach.

In both studies, species assemblage composition was strongly controlled by land-use intensity. It is noteworthy that the direction of the observed relationship varied greatly across the considered hydrologic gradients: dry habitats were generally characterized by low-intensity land use and featured high species numbers and large shares of threatened species. Mesic habitats were mostly under intensive management, whereas many of the wet habitats suffered from land-use abandonment. Both types often featured rather monotonous vegetation and poor species assemblages, mainly consisting of ubiquistic generalists. Species numbers and the share of threatened species across all considered habitat types in both studies were highest under low-intensity management. As a result, land-use intensity was positively related to species diversity in the wet habitat types, especially in the peat bogs, and negatively in the mesic and to a lesser extent in the dry habitat types.

Habitat heterogeneity is an important driver of species richness. I found that the habitat heterogeneity was consistently related to land-use intensity across the wide moisture gradient that was considered in the studies. It was highest at low to intermediate land-use intensity. On both ends of the land-use-intensity gradient, at virtually absent as well as under intensive management, the studied grasslands were characterized by rather monotonous, dense vegetation stands featuring low habitat heterogeneity. My results suggest that the reduction of microhabitat diversity may be the main driver of species richness reduction induced by both intensive and absent land use. Other effects of land use such as direct mortality caused by mowing and food quality deterioration due to fertilisation probably play a minor role, but contribute further to the adverse effects of high land-use intensity on biodiversity.

Many butterfly and Orthoptera species depend on specific resources and have small (micro)climatic niches—especially the eggs and larvae often have very narrow habitat and ambient-temperature as well as humidity requirements. Structurally diverse patches supported more species, probably because they feature a larger set of resources and greater microclimatic variety, so that more specific habitat-requirement combinations can be met. Land use, which is one of the main drivers of habitat configuration and habitat heterogeneity, thus plays a crucial role for species assemblage composition: both the intensively managed and the abandoned grassland patches featured structurally monotonous vegetation and simplified species assemblages.

Generally, wet habitat types tend to suffer from abandonment and mesic habitats from intensive land use in the study area, whereas drier habitat types often were under low-intensity management. Most of these dryer grasslands were managed as large-scale cattle pastures, which featured extraordinary species numbers. However, wet and mesic habitat types were characterized by similarly high species numbers when managed accordingly. Land management should thus be considered one of the most decisive factors controlling habitat heterogeneity and hence insect diversity.

In cultural landscapes, low-intensity management is a key driver of open-habitat heterogeneity. In European grass and peatlands, low-intensity management thus is a prerequisite for the occurrence of many threatened species which often have complex habitat requirements. Examples from the study area include *Argynnis niobe* (top), *Psophus stridulus* (middle) and *Boloria titania* (bottom). (Ibach 2018/06/15)

CONSERVATION OF BIODIVERSITY IN THE FACE OF CLIMATE AND LAND-USE CHANGE

As described in more detail in the introduction, biodiversity is declining in all regions of the Planet. In terrestrial ecosystems, the main drivers of this decline are the recent land-use and climate change. This development has potentially catastrophic consequences for life on Earth in general, but also for human life on the planet in particular. Consequently, humanity is obliged to invest as much as possible in order halt the loss of biological diversity. One of the most promising approaches in biodiversity conservation consists in focusing on the most species-rich regions, the so-called biodiversity hotspots. Such hotspots have been identified on a global scale, for biogeographic regions like the Palearctic, and on national scales.

The studies conducted in the course of this thesis focused on grassland and—to a lesser extent—peatland ecosystems, which both harbour large shares of the European biodiversity and which both suffer particularly from the recent land-use change. The study area, the Southern Black Forest, is located in the Centre of Europe and is part of a German biodiversity hotspot. It is particularly affected by recent climate and land-use change. These properties render the study area a perfect model region for European biodiversity-conservation strategies. Hence, the results of this thesis allow for the development of recommendations for biodiversity conservation in species-rich grassland and peatland ecosystems throughout Europe.

In my research there was strong evidence that the effects of climate and land-use change on biodiversity are interrelated. In a bad-case scenario, the additive effects of both lead to marked further biodiversity loss in the near future. Indeed, cold-adapted habitat specialists are already under threat of extinction in the study area. Considering that the study area is among the regions with highest biodiversity in Germany, this development is an alarming signal for biodiversity conservation in Europe.

Biodiversity hotspots feature extraordinary species diversity, including many threatened species such as *Aporia crataegi* (top), *Colias palaeno* (middle) and *Boloria aquilonaris* (bottom). However, climate and land-use change pose severe threats to these species rich landscapes. Conservation should focus on the maintenance and re-establishment of low-intensity land use and on mitigating the effects of climate warming by focusing north oriented slopes. (Schwarze Säge and Leimenlöcher 2018/06/15)

The results of my research suggest that land-use management is the key tool for biodiversity conservation in open habitats of cultural landscapes. The control of the type and intensity of land use provides the possibility to shape the vegetation structure and foster habitat heterogeneity in general. Conservation policies should focus on the maintenance and re-establishment of low-intensity land use. On the one hand, habitats that are under low-intensity management feature high habitat heterogeneity and thus provide a high micro-habitat diversity suited for a large variety of species, including specialized and threatened species. On the other hand, low-intensity land use leads to high microclimatic diversity which offers species the possibility to adapt to changing climatic conditions on a very local scale. This applies to the studied grasslands and peatlands alike—note that, in contrast to pristine peat bogs, the vast majority of peatlands in Central Europe (and in the study area) is hydrologically degraded. As a result, these peatlands rely on a regular management preventing shrub and tree encroachment.

Generally, the maintenance and re-establishment of low-intensity land use are the most effective strategy to maintain and create landscapes with high habitat and micro-habitat variability including the associated species richness. Additionally, and although local conservation management has no means to halt global climate change, appropriate land use could possibly cushion the adverse effects of global warming on biodiversity in grassland and peatland ecosystems.

Since biodiversity in Europe has evolved in the course of several millennia in which large-scale cattle grazing was the most prevalent form of human land use, this type of management should be favoured whenever possible. This theoretical assumption is supported by the outstanding habitat and species diversity of the large-scale cattle pastures in the study area. Ideally, local cattle breeds should be favoured over conventional breeds since these are often more resilient and frugal and also contribute to the local cultural heritage. On a side note, in that way biodiversity conservation can also contribute to domestic animal diversity through the preservation of local cattle breeds that often are threatened with extinction. Based on the results of the research presented here, the minimum requirements of a biodiversity-friendly management are:

- The application of liquid manure and artificial fertilizers should generally not be considered.
- Management should be carried out on a regular basis, especially in now abandoned grass and peatlands.
- Mowing in hay meadows should be carried out in a mosaic-like manner across the landscape (the sites should not be mown simultaneously), ideally leaving about 10 % of each meadow uncut. Meadows should not be mown more than twice per year.
- Pastures should be large enough to support variable grazing and trampling patterns by self-organized livestock. Grazing pressure must be high enough to keep parts of the vegetation short and sparse.
- In order to support cold-dwelling mountain species, management should focus more on north-oriented slopes and hilltops

Action is urgently needed: such as the study area, many species-rich grassland and peatland ecosystems in Europe have suffered considerable biodiversity loss during the past century, particularly during the past two or three decades (Habel et al. 2013, Joosten et al. 2017). There is an ongoing trend of decline, especially in habitat specialists and cold-adapted mountain taxa. Land use is a considerable threat to biodiversity, but also the key to its conservation. Thus, conservation policies need to create convincing proposals for local farmers to engage in appropriate management.

Whether we assign biodiversity a rather instrumental or intrinsic value, there is no alternative to biodiversity conservation. In that spirit, I hope that my work contributes to effective strategies and good practice in European biodiversity conservation—especially in the Southern Black Forest that I was happy enough to fall in love with during the field work for this thesis.

Species-rich common pastures, such as the pasture in the foreground, have been shaped by cattle grazing in the course of several centuries. The pasture in the back had been converted into a coniferous forest as a result of grazing abandonment. Only recently, a low-intensity cattle grazing regime has been re-established after clearcutting the whole pasture. The close vicinity to a species-rich pasture with long land-use continuity probably fostered the fast recolonization by large parts of the typical common-pasture fauna, including specialized species such as *Hesperia comma*, *Myrmeleotettix maculatus* and *Stenobothrus stigmaticus*. (Ibach 2018/06/14)

The Ring Ouzel *Turdus torquatus alpestris* is a good model organism for montane biodiversity. As such, it is a particularly vulnerable species with respect to climate as well as land-use change. The persistence of the species depends on an appropriate conservation management that encompasses large proportions of the climatically suited area, especially in low-mountain ranges where vertical areal shifts are not possible. Illustration by Hannah Staiger (2017).

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Back page: Field work (Silberbrunnenmoos, 2018/06/15)