Global warming meets habitat fragmentation

Challenges for biodiversity conservation in semi-natural grasslands

UNIVERSITÄT OSNABRÜCK

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Date of disputation:	______________________________
Date of doctoral graduation:	______________________________

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A thesis submitted for the degree of

Doctor rerum naturalium

Osnabrück University
Faculty of Biology/Chemistry
Department of Biodiversity and Landscape Ecology

submitted by

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Osnabrück | 2021

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Funding
This PhD thesis was funded by the Scholarship Programme of the German Environmental Foundation
(Deutsche Bundesstiftung Umwelt – DBU, funding period: 01/2016–12/2018).

Front & back cover
Front: Large-scale calcareous grassland in the Natura 2000-area 'Upper Ahr Valley' (Ahrhütte / Germany).
with characteristic species (from left to right) German gentian (*Gentianella germanica*), Dark green fritillary (*Argynnis aglaja*), Stripe-winged grasshopper (*Stenobothrus lineatus*).
Back: Montane calcareous grassland with flowering Round-headed rampion (*Phyteuma orbiculare*) (Blankenheim / Germany).

The author declares that he has authored this thesis independently, has not used other than the referenced sources, and has marked all material which has been quoted either literally or by content from the used sources.

Osnabrück University, 2021

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Chapter I

General introduction

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The importance of biodiversity

Biodiversity reflects the number and variability among living organisms on our planet, including their taxonomic, genetic and functional diversity. Its maintenance is of crucial importance to ecosystem functionality and human welfare all over the globe (Cardinale et al., 2012; Cardoso et al., 2020; CBD, 1992). On the one hand, a healthy biodiversity leads to a higher resistance and resilience of ecosystems against several environmental changes (e.g., Chapin et al., 2000; Hooper et al., 2005). On the other hand, biodiversity benefits humanity through the provision of a variety of essential ecosystem services, such as pollination, biological pest control, prevention of infectious diseases, climate regulation and nutrient cycling, which are significant from an ecological but also an economic point of view (Bengtsson et al., 2019; Cardoso et al., 2020; Samways, 2020). For instance, the value of insect pollination amounts to approximately 3.8 billion dollars per year in Germany alone (Lippert et al., 2021). Therefore, recent calculations suggest that the socio-economic damages of biodiversity loss in human-modified landscapes are usually far higher than the costs of large-scale conservation measures which are widely lacking so far (e.g., Lippert et al., 2021; Yao et al., 2019). But biodiversity also offers a variety of non-monetary values that can directly be linked to our well-being, for instance due to its attraction for recreational activities and tourism (MEA, 2005; Samways, 2020).

Since the beginning of the industrial era, man-made habitat alterations have caused a substantial loss of wild biota across several taxonomic groups and ecosystems (Cardinale et al., 2012; Sanchez-Bayo & Wyckhuys, 2019; Thomas et al., 2004). Consequently, scientists recently warned that we are heading towards a sixth mass extinction e (Chapin et al., 2000). Therefore, halting the global decline in biodiversity has recently become one of the greatest challenges facing humanity today (Cardoso et al., 2020; Pimm et al., 2014). During the last decades, there has been growing scientific interest to identify the driving forces behind species extinctions in order to establish effective conservation measures (Mulder et al., 2015). Although policy makers have started to increase their efforts in biodiversity conservation since the adoption of the Convention on Biological Diversity in 1992 (Kleijn & Sutherland, 2003), biodiversity loss has recently reached a level up to 1,000 times higher than during pre-human periods (Pimm et al., 2014). As a consequence, conservationists are currently facing unprecedented challenges, which require effective evidence-based strategies that may help to counteract the future biodiversity loss and sustain ecosystem functioning in the long run (Hooper et al., 2005; Samways et al., 2020).

Key drivers of biodiversity loss

The global biodiversity loss is a complex response to several human-induced alterations of the environmental conditions within ecosystems, including habitat changes due to altered land use, climate change, the spread of non-native species, overexploitation and increased input of agrochemicals, such as synthetic fertilizer and pesticides (Butchart et al., 2010; Foley et al., 2005; Sala et al., 2000; MEA, 2005). Among these factors, habitat loss and degradation caused by land-use change has been identified as the most important driver behind the severe decline of plant and animal life in terrestrial ecosystems (Sala et al., 2000). In Europe, this process has especially been accelerated by severe agricultural changes during the second half of the 20th century which caused a sharp decline in habitat diversity within agricultural landscapes (Henle et al., 2008; Robinson & Sutherland, 2002). Especially traditionally managed habitats, such as heathlands, wood pastures and semi-natural grasslands, have suffered large-scale area losses (e.g., Fartmann, 2006; Stoate et al., 2009; Wallis de Vries et al., 2002). As a result, species associated with low-intensity land use frequently suffered strong population declines (e.g., Diekmann et al., 2019; Robinson & Sutherland, 2002; Salz & Fartmann, 2009). Although habitat loss has recently been slowed down by intensified conservation measures under the EU Habitats Directive (cf. Carvalheiro et al., 2013), the remaining habitats are still frequently facing a decline in habitat quality (e.g., Fartmann et al., 2012). This is primarily due to the frequent lack of proper habitat management along with other drivers, for instance, increased nitrogen input and climate-driven habitat changes (e.g., Butchart et al., 2010; Diekmann et al., 2019; Fartmann et al., 2012).

In the more recent past, anthropogenic climate change has become another important driver of biodiversity change in our ecosystems (Bellard et al., 2011; Sala et al., 2000). The average European annual temperature during the last decade was already 1.7 °C above the pre-industrial level and current projections expect that the temperature will continue to rise between 1.0 to 4.5 °C by the end of the century (EEA, 2020). An increasing number of studies found evidence that global warming is already affecting biological systems at a fast pace (e.g., Chen et al., 2011; Hickling et al., 2006; Parmesan, 2006; Warren et al., 2001). Climate change especially causes shifts in species phenologies and distributions, which also affect trophic interactions between organisms within biotic communities (e.g., Bellard et al., 2012; Parmesan, 2006; Parmesan & Yohe, 2003). However, it has been demonstrated that there is much variation in the response to climate change across taxa and habitats (e.g., Chen et al., 2011; Guo et al., 2009; Parmesan, 2006; Warren et al., 2001). Whereas species adapted to cool temperatures or sensitive to drought will generally suffer from the effects of climate change, thermophilic organisms are predominantly expected to benefit from global warming at least in temperate ecosystems (e.g., Chen et al., 2011; Hickling et al., 2006; Parmesan, 2006; Streitberger et al., 2016). According to these assumptions, biodiversity scientists predicted that the biodiversity of Europe's mountain areas is particularly vulnerable to climate change (Streitberger et al., 2016; Thuiller et al., 2005). In addition, scientists hypothesized that the biodiversity of wet habitats will become endangered by the increasing risk of desiccation, whereas species associated with dry and warm habitat conditions could possibly become less vulnerable (Gibson & Newman, 2019; Streitberger et al., 2016). Even though the thermal tolerance of warm-adapted organisms could enable them to cope with current global warming, their response to climate change vitally depends on the availability of suitable habitats (e.g., Hill et al., 2001; Platts et al., 2019). Since climate change is expected to cause even more severe effects on biodiversity in the future, current conservation strategies should include immediate and long-term actions aiming to mitigate biodiversity loss due to current and future global warming (Harvey et al., 2019; Streitberger et al., 2016).

Global change in European grassland ecosystems

Human land use has promoted Europe's biodiversity for many centuries (Poschlod & Wallis de Vries, 2002; Veen et al., 2009). Until today, large parts of the European landscape are shaped by agriculture (Henle et al., 2008). Hence, agricultural habitats, such as semi-natural grasslands, play a vital role for biodiversity conservation (Henle et al., 2008; Veen et al., 2009).

Covering more than 20% of the EU-27 land surface, grasslands are among the most dominant ecosystems in Europe. The majority of these grasslands evolved through traditional land-use practices, such as low-intensity mowing and rough grazing (Poschlod & Wallis de Vries, 2002; Veen et al., 2009). Until today, these semi-natural grasslands rank among the most species-rich ecosystems in Europe (Feurdean et al., 2018, Poschlod & Wallis de Vries, 2002; Wilson et al., 2012). Especially nutrient-poor grasslands are characterized by a unique biodiversity which gives them a high conservation priority (Veen et al., 2009). Owing to their outstanding species richness, the majority of these grasslands are now protected under the EU Habitats Directive (EC, 1992). However, their extent dramatically decreased, mainly due to the transition from traditional land use to modern agriculture (Poschlod & Wallis de Vries, 2002, Stoate et al., 2001).

The severe decline of semi-natural grasslands was driven by two contrasting processes: (i) the intensification of agricultural land use on productive soils and (ii) the abandonment of marginal land as consequence of the cessation of traditional land-use practices (Henle et al., 2008, Stoate et al., 2001). Agricultural intensification was reflected in the conversion of semi-natural grasslands into arable land or improved grasslands, which frequently caused rapid biodiversity declines (Stoate et al., 2001). The cessation of traditional land use usually resulted in gradual habitat deterioration towards later successional stages, which are also known to have a negative impact on the species richness within semi-natural grasslands in the long term (Fartmann et al., 2012; Uchida & Ushimaru, 2014; Veen et al., 2009).

Apart from these agriculturally driven changes, climate change has increasingly altered the habitat conditions within semi-natural grasslands during recent years (Gibson & Newman, 2019; Streitberger et al., 2016). However, there is still little empirical evaluation on the effects of climate change on grassland biodiversity. In temperate Europe, especially mountain grasslands are considered vulnerable to climate change as they are important refuges for many cold-adapted species which are hardly able to keep up with global warming (Streitberger et al., 2016; Stuhldreher & Fartmann, 2018). Furthermore, it is expected that the increasing frequency of summer drought could mitigate grassland taxa associated with moist habitat conditions (Diekmann et al., 2019; Streitberger et al., 2016). In contrast, climate change could have a positive impact on the biodiversity of semi-dry grasslands, where thermophilic species could possibly benefit from warmer and drier habitat conditions (Chen et al., 2011; Diekmann et al., 2019; Streitberger et al., 2016). According to current knowledge, climate-induced changes within plant and animal assemblages will likely pose an important challenge for future biodiversity conservation and management in semi-natural grasslands (Hopkins & Del Prado, 2007; Streitberger et al., 2016).

Persistence in fragmented landscapes

As a consequence of large-scale habitat loss and fragmentation, species-rich grasslands in Europe are today mostly restricted to a few isolated remnants which are often embedded within a hostile landscape matrix (Brückmann et al., 2010; Fartmann, 2017; Veen et al., 2009). The fundamental metapopulation research of Hanski (1999) revealed that the long-term survival of species in fragmented habitat networks depends on a shifting balance of extinctions and recolonizations. There is broad consensus that the persistence of species in fragmented landscapes is mainly driven by three factors operating at different spatial scales: (i) habitat quality within the patches, (ii) patch area and (iii) the isolation of the habitat patches (e.g., Anthes et al., 2003; Fahrig, 2003; Thomas et al., 2001). However, the relative importance of these metapopulation factors is still under debate (Thomas et al., 2001). It can generally be assumed that the role of the factors on the persistence of species differs depending on various traits, such as habitat specificity, dispersal ability and the population structure of the organisms under investigation (e.g., Fartmann, 2017; Pöyry et al., 2009; Warren et al., 2001). Moreover, there are indications that their impact varies between landscapes, dependent on the degree of habitat fragmentation (cf. Brückmann et al., 2010; Krämer et al., 2012).

Recent studies suggest that habitat quality is of prior importance for the long-term survival of species in habitat fragments (e.g., Münsch et al., 2019; Poniatowski & Fartmann, 2010; Stuhldreher & Fartmann, 2014). This is especially true for species with a low mobility which often build closed populations (Fartmann, 2017). Those species are usually able to persist in highly fragmented habitats for several decades, provided that the remaining habitat islands are still large enough and offer an adequate habitat quality (cf. Kuussaari et al., 2009). In particular, plants and grasshoppers include many characteristic examples (e.g., Helm et al., 2006, Poniatowski & Fartmann, 2010). For instance, the study of Poniatowski & Fartmann (2010) revealed that the flightless Bog bush cricket *Metrioptera brachyptera*, showed a weak response to habitat fragmentation, but strongly depended on the maintenance of habitat quality provided by low-intensity land use in calcareous grasslands. Nevertheless, species living in closed populations may also require working habitat networks for their dispersal under global warming (Fartmann, 2017; Hill et al., 2001; Streitberger et al., 2016). In this light, it should be noted that many species could become forced to shift their current distribution to evade detrimental environmental conditions. Therefore, connectivity between suitable habitats will become increasingly important for the survival of species; especially for those with a limited dispersal ability (Streitberger et al., 2016; Wessely et al., 2017).

Species underlying metapopulation dynamics depend even more vitally on habitat area and connectivity. This has especially become evident for butterflies which usually have a higher mobility than many other invertebrate groups (Anthes et al., 2003; Hanski, 1999; Thomas et al., 2001). Therefore, it is not surprising that butterfly species depending on large-scale and well-connected semi-natural grasslands have undergone the most severe population declines during the last decades (e.g., Anthes et al., 2003; Salz & Fartmann, 2009; van Strien et al., 2011). Previous studies highlighted the negative impact of reduced habitat area and connectivity on butterfly species richness in fragmented semi-natural grasslands (e.g., Brückmann et al., 2010; Krämer et al., 2012). Although it is very likely that the landscape composition between habitat fragments may also have a crucial impact on their biodiversity (e.g., Fahrig et al., 2011; Krämer et al., 2012), the role of the landscape matrix on the persistence of species has been less investigated and thus requires more attention in future metapopulation research (Adriaensen et al., 2003; Öckinger et al., 2012).

The majority of fragmentation studies investigated the effects of present landscape characteristics on the occurrence of species (e.g., Brückmann et al., 2010; Münsch et al., 2019; Poniatowski & Fartmann, 2010). However, biodiversity scientists recently noted that the time-delayed response of species to past habitat fragmentation additionally contributes to current biodiversity loss and thus could lead to misleading assessments of their current conservation status (e.g., Helm et al., 2006; Hylander & Ehrlén, 2013; Kuussaari et al., 2009). The results of recent studies demonstrated that it often can take 50 up to 100 years until a species may become extinct after the onset of habitat fragmentation (Lindborg & Eriksson, 2004; van Strien et al., 2011). Despite there is still uncertainty how such time-delayed extinctions of species (i.e., the existence of an extinction debt) contribute to a future decline of biodiversity in fragmented habitats, it has been highlighted as an important challenge to consider in biodiversity conservation (Kuussaari et al., 2009).

Interactions between land-use and climate change

It is widely known that both land-use and climate change have a crucial impact on the biodiversity of semi-natural habitats (e.g., Oliver et al., 2016; Sala et al., 2000). However, there are only few studies which have investigated the simultaneous and interacting effects of these factors on biotic communities (e.g., Mantyka-Pringle et al., 2015; Oliver et al., 2016). Despite species across several taxa expanded their ranges in the last decades, it has become evident that the limited availability of suitable habitats and dispersal corridors will hamper many species to keep up with global warming in human-modified landscapes (Hill et al., 2001; Platts et al., 2019; Warren et al., 2001). Previous research indicates that especially habitat specialists and sedentary species suffer from climate change, while thermophilic generalists with a higher mobility were frequently able to expand their distribution ranges (e.g., Beckmann et al., 2015; Parmesan et al., 1999; Warren et al., 2001). For instance, it has been shown that the Speckled Wood Butterfly (*Pararge aegeria*) - a highly mobile woodland habitat generalist – strongly expanded its British range during the second half of the last century (Parmesan et al., 1999). Given that the species occupies several woodland habitats which were largely available during the whole study period, it has become certain that the northward expansion of the species was induced by global warming (Parmesan et al., 1999). In contrast, the range of the Silver-studded Blue (*Plebejus argus*) has declined by almost 30% since the 1970s, although large parts of Southern Britain have also become climatically suitable for this thermophilic species due to global warming (Hill et al., 2001). However, this species vitally depends on nutrient-poor habitats, such as calcareous grasslands, which occur only scattered throughout the study area. Owing to the low dispersal ability of *P. argus* along with the limited habitat availability in the study area, it clearly lags behind global warming. These examples demonstrate that the contrasting response of species to global warming could increasingly alter the community structure within fragmented grassland ecosystems (cf. Pöyry et al., 2009). Hence, there might be an increasing risk of biotic homogenization within plant and animal communities which may also affect ecosystem functioning (Clavel et al., 2011; Mantyka-Pringle et al., 2015).

Indicators of grassland biodiversity

Due to the differential response of species to environmental changes, the effects of land-use and climate change should be ideally assessed using various indicator groups. In this thesis, we focused on plants and various insect groups as indicators of grassland biodiversity. Given their sensitivity to land use and climate change, both plants and insects, such as butterflies and grasshoppers, are known to be good bioindicators and are considered as suitable surrogates for overall grassland biodiversity (e.g., Ellenberg & Leuschner, 2010; Fartmann et al., 2012; van Swaay et al., 2010).

Plants are among the most diverse species group within grassland ecosystems (Wallis de Vries et al., 2002; Wilson et al., 2012). Their specific habitat requirements, makes them well-suited organisms to study the response of biodiversity to altered environmental conditions (Ellenberg & Leuschner, 2010). Furthermore, they play a key role for ecosystem functioning, especially due to their role as primary producers and their crucial impact on the habitat structure and the composition of insect assemblages in semi-natural grasslands. Recent studies revealed declines in plant species richness across different grassland habitats (e.g., Diekmann et al., 2019; Wesche et al., 2012). However, it has been found that plants often show a rather slow response to environmental changes due to their generally longer life cycles (Helm et al., 2006). In contrast, the majority of insect species are short-lived and thus they usually respond more rapidly to habitat alterations (Kuussaari et al., 2009).

Grasshoppers play an important role as herbivores and provide an essential food resource for many vertebrate species, such as insectivorous birds (Benton et al., 2002; Hochkirch et al., 2016). They are sensitive to both land-use and climate change (Fartmann et al., 2012; Hochkirch et al., 2016; Poniatowski et al., 2018). The occurrence of grasshoppers in semi-natural grasslands is predominantly determined by an appropriate habitat quality (Fartmann et al., 2012; Helbing et al., 2014; Poniatowski & Fartmann, 2010). Whereas many specialized grasshopper species historically suffered from large-scale habitat loss and deterioration across temperate Europe (e.g., Fartmann et al., 2012; Marini et al., 2009), there is increasing evidence that thermophilic grasshopper species recently expanded their distribution ranges (e.g., Beckmann et all., 2015; Poniatowski et al., 2018). As grasshoppers generally require high ambient temperatures (Willott & Hassall, 1998), it seems reasonable that global warming is the driving force behind these distributional shifts (Beckmann et al., 2015, Poniatowski et al., 2012). However, there are no studies to date which have investigated how and to what extent these expansions have altered grasshopper assemblages within semi-natural grasslands.

Butterflies are also important indicators of grassland biodiversity and play a vital role for ecosystem functioning, mainly due to their importance as pollinating insects (van Swaay et al., 2010). The decline of butterflies in Europe exceeds those of many other plant and animal taxa associated with semi-natural grasslands (e.g., Thomas et al., 2004). This is likely due to their complex life cycles and specific food and habitat requirements at different spatial scales (Thomas et al., 2004; van Swaay et al., 2010). Since many butterflies depend on metapopulation dynamics, they are highly vulnerable to landscape-scale changes, such as reduced connectivity and habitat area (e.g., Brückmann et al., 2010; Hanski, 1999). In addition, the majority of butterfly species have specific habitat requirements, especially with regard to their host plants and larval habitats (García-Barros & Fartmann, 2009). Therefore, they are also highly sensitive to habitat alterations at the habitat and microhabitat scale (e.g., Löffler et al., 2013; Stuhldreher & Fartmann, 2014; Eichel & Fartmann, 2008; Krämer et al., 2012). Recent studies provide evidence for climate-driven changes in butterfly assemblages (Devictor et al., 2012; Pöyry et al., 2009). Given that Europe's butterfly fauna includes several cold-adapted butterfly species with boreo-montane distribution patterns, these species are thought to be especially sensitive to global warming (Habel et al., 2011; Stuhldreher & Fartmann, 2018).

Aims and outline of the thesis

As a result of the large-scale habitat loss in the second half of the 20th century (Henle et al., 2008; Stoate et al., 2009), many species associated with semi-natural grasslands have become particularly vulnerable throughout Europe (Veen, 2009). More recently, climate change has altered the environmental conditions within the remaining habitats and thus has become another important driver of biodiversity change in grassland ecosystems (Pöyry et al., 2009; Sala et al., 2000).

Addressing these issues urgently requires evidence-based conservation strategies, which should increasingly take into account the effects of climate change (cf. Thomas et al., 2011). To meet these challenges, this thesis seeks to gain profound insights into the effects of habitat fragmentation and global warming on the persistence of species and biodiversity patterns within semi-natural grasslands. It comprises two main chapters: (a) Effects of habitat fragmentation and deterioration on grassland biodiversity (*Chapter II*) and (b) Interactions between land-use and climate change on grassland biodiversity (*Chapter III*). Overall, the present thesis includes eight studies covering different areas of global change ecology, including discussions about the practical applications of our main research findings. It is mainly aimed at biodiversity scientists and conservationists, with a particular focus on strengthening the maintenance of biodiversity in semi-natural grasslands in times of global change.

Chapter II deals with the role of habitat quality, patch area and connectivity, which are known to be the main drivers of grassland biodiversity in fragmented landscape (Hanski, 1999; Thomas et al., 2001). This chapter mainly aimed to test for the impact of these factors on specialized grassland insects (*Paper 1* and *2*) and grasshopper assemblages (*Paper 3*) in calcareous grasslands. A particular goal of *Paper 1* was to determine the relative importance of habitat and landscape-scale factors for the patch occupancy of semi-natural grassland specialists across different taxonomic groups. Furthermore, least-cost modelling techniques were applied in order to investigate the role of the landscape matrix (i.e., functional connectivity) on the persistence of grassland specialists (*Paper 2;* cf. Adriaensen et al., 2003). Since it has been shown for plants and butterflies that the abovementioned factors have a crucial impact on grassland biodiversity (e.g., Brückmann et al., 2010; Krämer et al., 2012), the impact of habitat quality and landscape-scale factors was now related to the species richness in grasshoppers (*Paper 3*), which only have received little attention in previous metapopulation research. In addition, *Chapter II*, investigates the role of extinction debt due to time-delayed responses of species to habitat fragmentation (*Paper 4*).

In *Chapter III*, the response of biodiversity to the opposing effects of land-use and climate change in Central Europe was investigated. In order to assess the impact of habitat fragmentation and deterioration, especially in the light of climate change, we conducted a case study on the Violet Copper butterfly (*Lycaena helle*) – a post-glacial relict species – which is known to be highly sensitive to global warming and thus ranks among the most threatened butterfly species in Europe (*Paper 5*) (Habel et al., 2011). Whereas shifts in butterfly distribution and assemblages were several times related to global change in previous studies (e.g., Devictor et al., 2012; Pöyry et al., 2009), equivalent knowledge is still lacking for less popular insect groups, such as grasshoppers. Hence, a particular goal of *Chapter III* was to assess the long-term effects of land-use and climate change on grasshopper distribution and their effects at the assemblage level, which has only marginally been studied so far. *Paper 6* represents the first large-scale study investigating range shifts among several common grasshoppers in Central Europe. In this study, grasshopper range shifts were related to species' functional traits and two global change indices. The latter were derived from the well-established concept of the Species Temperature Index (STI) provided by Devictor et al. (2012), which has now been supplemented by the Species Farmland Index (SFI). The application of these tools can help to get a better understanding of the compounding effects of land-use and climate change on grassland biodiversity. Moreover, *Chapter III* includes two long-term studies dealing with grasshopper assemblage shifts across different grassland habitats with varying land-use history (*Paper 7* and *8*). These studies especially address the question how grasshopper range shifts may have altered the species richness and composition of grasshopper assemblages within semi-natural grasslands in Central Europe. They furthermore aim to unravel the main reasons for the contrasting response of grasshopper assemblages to land-use and climate change across the studied grassland types. Based on the findings, recommendations for future grassland management including climate-adaption measures are given (e.g., *Chapter IV*).

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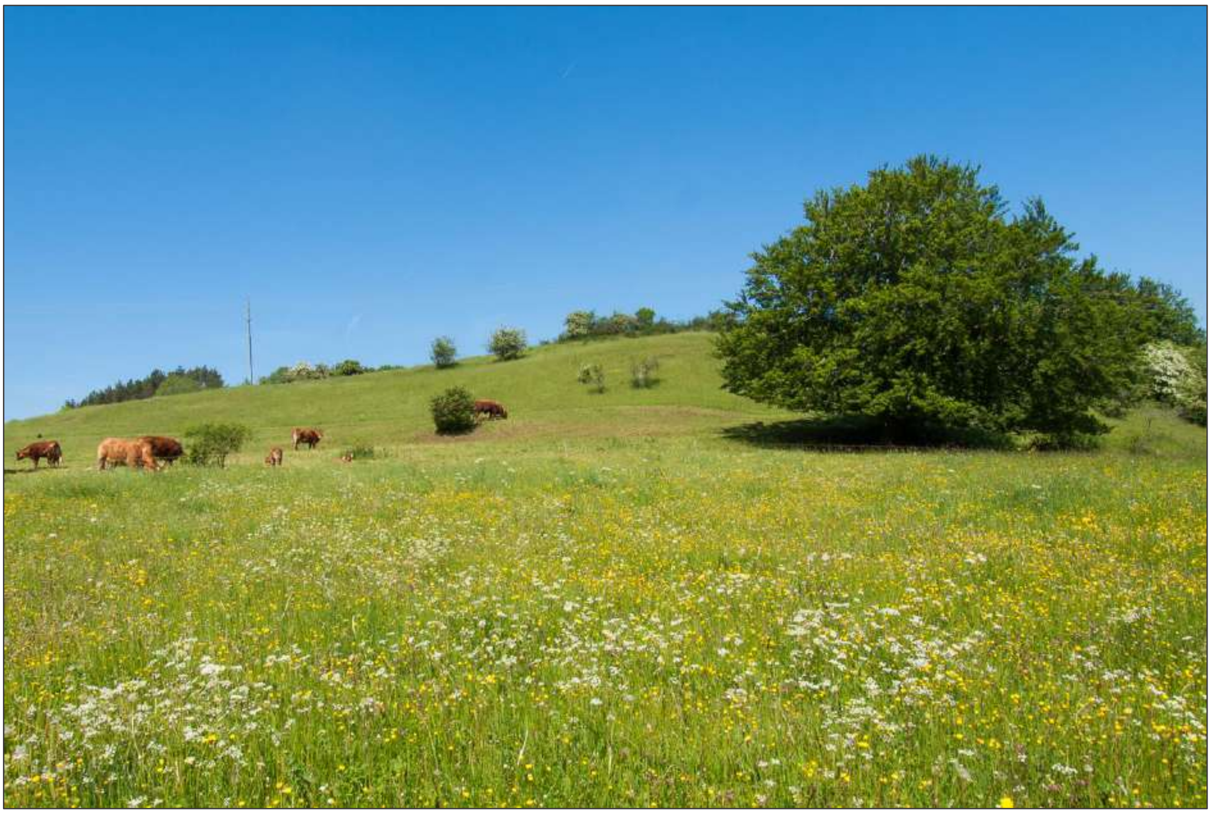

Owing to their high species richness, the majority of semi-natural grasslands are protected under the EU Habitats Directive. The maintenance of grassland biodiversity vitally depends on traditional land use, like rough cattle grazing on a mesic pasture within the NATURA 2000-area 'Upper Ahr Valley' (Eifel) shown in the picture (Alendorf / Germany).

The extent of nutrient-poor grassland ecosystems strongly decreased throughout Europe, mainly due to agricultural intensification and the abandonment of traditional land use. As a consequence, those grasslands are now mostly restricted to a few isolated remnants which are often embedded within a hostile landscape matrix. The picture shows calcareous grassland fragments with *Juniperus communis*, interrupted by improved grassland within the NATURA 2000-area 'Upper Ahr Valley' (Eifel) (Alendorf / Germany).

Chapter II

Effects of habitat fragmentation and deterioration on species persistence in semi-natural grasslands

(1) Patch occupancy of grassland specialists: habitat quality matters more than habitat connectivity

DOMINIK PONIATOWSKI, GREGOR STUHLDREHER, FRANZ LÖFFLER & THOMAS FARTMANN (2018)
Biological Conservation 225: 237–244. doi.org/10.1015/j.biocon.2018.07.018

ABSTRACT

Land-use change has caused degradation, loss and fragmentation of semi-natural habitats, especially in grassland ecosystems. Today, the remaining habitats are often situated in a matrix of intensively used agricultural land and are therefore more or less isolated from each other. Connectivity, area and quality of habitat patches have been identified as the most important drivers for the persistence of grassland specialists living in metapopulations. However, the relative importance of these factors is still under debate. We used a large-scale, multi-taxon approach to obtain a general pattern which would facilitate conservationists to promote many, instead of one, species. We studied the patch occupancy of 13 grassland specialists belonging to three different insect orders within a Central European landscape with 89 fragments of calcareous grasslands. To disentangle the relative importance of the three metapopulation parameters, generalized linear models (GLM) and variation-partitioning techniques were used. Our study revealed that habitat quality was the most important factor determining the occurrence of specialized species, followed by habitat area. In comparison to habitat connectivity, the variance explained by habitat quality was significantly higher across the studied species. Nevertheless, the persistence of at least six model organisms depended on the degree of habitat connectivity. We conclude that maintaining a high habitat quality on large patches should be the first choice for the conservation of habitat specialist insects in fragmented landscapes. As a secondary measure, conservationists should concentrate on the restoration of relict sites. This increases not only the habitat area, but also contributes to better habitat connectivity.

KEYWORDS

Calcareous grassland; Fragmented landscape; Functional connectivity; Habitat specialist, Multi-taxon approach; Variation partitioning

Calcareous grasslands are important refuges for specialized plant and ainmal species. The Diemel Valley holds the largest network of this habitat type in the nothern half of Germany. The persistence of habitat specialists in calcareous grasslands especially depends on large-scale patches with a high habitat quality, conditions which can for example be found at the 'Sommerberg' (Lower Diemel Valley) shown in the picture (Photo: Thomas Fartmann) (Sielen / Germany).

The Dark green fritillary (*Argynnis aglaja*) mainly occurs in large calcareous grassland patches providing open habitat conditions and a high abundance of its host plant *Viola hirta*. Owing to its high mobility, the species appears to be less sensitive to habitat isolation, at least in areas with a relatively low degree of habitat fragmentation, such as the Diemel Valley.

(2) Functional connectivity as an indicator for patch occupancy in grassland specialists

DOMINIK PONIATOWSKI, FRANZ LÖFFLER, GREGOR STUHLDREHER, FABIAN BORCHARD, BENJAMIN KRÄMER & THOMAS FARTMANN (2016)
Ecological Indicators 67: 735–742. dx.doi.org/10.1016/j.ecolind.2016.03.047

ABSTRACT

Habitat specialists living in metapopulations are sensitive to habitat fragmentation. In most studies, the effects of fragmentation on such species are analyzed based on Euclidean inter-patch distances. This approach, however, ignores the role of the landscape matrix. Recently, therefore, functional distances that account for the composition of the landscape surrounding the habitat patches have been used more frequently as indicators for patch occupancy. However, the performance of functional and non-functional connectivity measures in predicting patch occupancy of such species has never been compared in a multi-species approach. Here we evaluate the effect of habitat connectivity on the patch occupancy of 13 habitat specialists from three different insect orders (Auchenorrhyncha, Lepidoptera, Orthoptera) in fragmented calcareous grasslands. In order to calculate functional distances, we used four different sets of resistance values and rankings. We then modelled species' occurrence using both Euclidean and functional (based on least-cost modelling) inter-patch distances as predictors. We found that functional connectivity measures provided better results than the non-functional approach. However, a functional connectivity measure that was based on very coarse land-cover data performed even better than connectivity measures that were based on much more detailed land-use data. In order to take into account possible effects of the landscape matrix on patch occupancy by habitat specialists, future metapopulation studies should use functional rather than Euclidean distances whenever possible. For practical applications, we recommend a 'simple approach' which requires only coarse land-cover data and in our study performed better than all other functional connectivity measures, even more complex ones.

KEYWORDS

Calcareous grassland, Dispersal, Habitat fragmentation, Invertebrate, Landscape matrix, Least-cost modelling

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(3) Effects of landscape and habitat quality on Orthoptera assemblages of pre-alpine calcareous grasslands

Franz Löffler & Thomas Fartmann (2017)

Agriculture, Ecosystems & Environment 248: 71–81. dx.doi.org/10.1016/j.agee.2017.07.029

ABSTRACT

Due to the transition from traditional land use to modern agriculture throughout Europe, semi-natural grasslands are subject to severe environmental changes. Both agricultural intensification and abandonment have caused degradation, loss and fragmentation of semi-natural grasslands with adverse effects on biodiversity. We analysed the effects of landscape and habitat quality on Orthoptera in pre-alpine calcareous grasslands of the Northern Limestone Alps. At the landscape level, we focused on the effects of functional connectivity, patch size and habitat heterogeneity on Orthoptera species richness of 13 randomly selected grassland patches. At the habitat level, we studied the effects of land use on vegetation structure and microclimate as well as on Orthoptera species richness and abundance on 50 randomly chosen plots within these patches. At the landscape level, the number of Orthoptera species in well-connected pre-alpine calcareous grasslands increased with habitat heterogeneity, which was inter-related with patch size. Functional connectivity, however, had no effect on species richness. At the habitat level, species richness and abundance of Orthoptera were driven by land use together with vegetation structure and microclimate. In general, the explanatory power of our abundance models was at least twice as high as those of the species richness models. Based on the results of our study, conservation management of grassland Orthoptera should primarily focus on improving habitat heterogeneity and habitat quality within patches.

KEYWORDS

Conservation management; Functional connectivity; Habitat fragmentation, Habitat heterogeneity; Land-use change, Species richness

The Northern Limestone Alps still hold large areas of pre-alpine calcareous grasslands (also known as 'hummocky meadows') shown in the center of the picture. Due to their unique microrelief and small-scale land-use diversity, these nutrient-poor grasslands are characterized by heterogeneous habitat conditions. The high habitat heterogeneity within the meadows favors the coexistence of species with contrasting habitat demands and has been identified as a key factor for their outstanding biodiversity (Photo: Thomas Fartmann) (Mittenwald / Germany).

In Central Europe, the Wart-biter (*Decticus verrucivorus*) is an endangered grasshopper species. *D. verrucivorus* requires small-scale mosaics of different microhabitats. It especially depends on bare ground for oviposition, sparsely vegetated microhabitats for the development of its thermophilic nymphs and taller vegetation providing the adults song posts and shelter from predators.

(4) Extinction debt across three taxa in well-connected calcareous grasslands

FRANZ LÖFFLER, DOMINIK PONIATOWSKI & THOMAS FARTMANN (2020)
Biological Conservation 246: 108588. doi.org/10.1016/j.biocon.2020.108588.

ABSTRACT

The biodiversity in calcareous grasslands suffered from severe habitat loss due to land-use intensification and abandonment across Europe. Although these grasslands are now protected under the EU Habitats Directive, many species in the remaining habitat patches are still declining. Recent studies suggest that species across different taxa may become extinct with a substantial time delay, even without further habitat loss. Consequently, there might be an extinction debt, which poses a major challenge for conservation. Here, we analysed the response of plant, grasshopper and butterfly species richness in calcareous grasslands to habitat fragmentation over the last five decades. In this study, habitat area and connectivity have undergone a marked decline between 1970 and 1990 but have only slightly declined during the last three decades. Despite this, the current richness of specialist and generalist species among plants and butterflies was equally or better explained by past than present landscape conditions. This finding indicates the existence of an extinction debt in both taxa in the still well-connected grasslands of the study area. We conclude that increased conservation measures since the 1990s have favoured species persistence, despite severe habitat loss in the more distant past. By contrast, grasshopper diversity weakly responded to habitat area and connectivity; rather it is likely to depend mainly on habitat quality. To inhibit future extinctions, it is crucial to maintain large-scale patches by traditional land-use practices (i.e. rough grazing or mowing once a year), as well as restore former habitat to facilitate species dispersal in fragmented landscapes.

KEYWORDS

Biodiversity conservation; Habitat fragmentation, Land-use history, Metapopulation dynamic, Semi-natural grassland, Species loss

Despite severe habitat loss in the second half of the 20th century, the calcareous grasslands in the Natura 2000-area 'Upper Ahr Valley" (Eifel) are still an important biodiversity hotspot. This is mainly a result of increased conservation measures since the late 1980s, which have likely contributed to the persistence of several habitat specialists. However, their current species richness is rather a relict of past landscape conditions and thus it is expected that several species could still face delayed extinctions (i.e., they contribute to extinction debt) (Alendorf / Germany).

The Mountain everlasting (*Antennaria dioica*) is a perennial species, whose present ccurrence is largely restricted to historically large nutrient-poor grasslands. Owing to its ability for clonal growth, the species is able to survive for many years, even if germination is hampered by altered environmental conditions in the remaining grassland fragments (Photo: Thomas Fartmann).

Chapter III

Interactions between land-use and climate change on grassland biodiversity

(5) Abandonment of traditional land use and climate change threaten the survival of an endangered relict butterfly species

GWYDION SCHERER, FRANZ LÖFFLER & THOMAS FARTMANN (2021)
Insect Conservation & Diversity (online first). doi.org/10.11111/icad.12485

ABSTRACT

1. The decline of butterflies exceeds those of many other animal taxa due to their high sensitivity to habitat alterations driven by land-use change. Moreover, cold-adapted species frequently suffer severe range retractions due to rising temperatures at their trailing-edge range margins.

2. In this study, we aim to identify drivers of occupancy of the post-glacial relict species *Lycaena helle* at three spatial scales – (i) landscape, (ii) habitat, and (iii) microhabitat – in one of its last refuges in central Europe.

3. In our study in the Eifel low mountain range (western Germany), the occurrence of *L. helle* was mainly driven by the (i) isolation, (ii) size, and (iii) quality of habitat patches. *Lycaena helle* formed metapopulations that were dependent on networks of interconnected but often small habitat patches.

4. Habitat quality within the semi-natural grasslands was determined by (i) macro- and mesoclimate, (ii) host-plant abundance, and (iii) vegetation structure, which was interrelated with microclimate. *Lycaena helle* preferred moist, nutrient-poor grasslands in deep, narrow valleys at the highest elevations of the study area, which were characterised by (i) cold winters, (ii) high abundance of the host plant, and (iii) short and sparse swards providing a warm microclimate in summer.

5. According to these findings, abandonment of traditional land use and climate change are considered the most severe threats for long-term survival of the species. Hence, conservation measures should aim at maintaining and restoring networks of large and well-connected habitat patches of high quality, preferably in cold-air depressions within mountain systems.

KEYWORDS

Global warming, Habitat fragmentation, Host-Plant abundance, Land-use change, *Lycaena helle*, Microclimate

The Violet copper (*Lycaena helle*) is a post-glacial relict species with a boreo-montane distribution in the Palearctic. The European populations of this species recently suffered strong decreases due to the cessation of traditional land use and global warming. Therefore, *L. helle* now ranks among the most threatened butterfly species in Europe. The picture shows an adult male basking in wet grassland in the Eifel low-mountain range, which represents one of the last strongholds of *L. helle* in Central Europe.

The Violet copper (*Lycaena helle*) mainly occurs in periodically managed or abandoned wet grasslands with a dense litter lay and a high cover of its host plant – the Common bistort (*Bistorta officinalis*). Occupied habitat patches are usually restricted to cold-air depressions, like the wet grasslands in the deep valley of the 'Nonnenbach' within the NATURA 2000-area 'Upper Ahr Valley' (Eifel) shown in the picture (Nonnenbach / Germany).

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

DOMINIK PONIATOWSKI, CHRISTIAN BECKMANN, FRANZ LÖFFLER, THORSTEN MÜNSCH, FELIX HELBING, MICHAEL J. SAMWAYS & THOMAS FARTMANN (2020)

Global Ecology & Biogeography 29, 2190–2202. doi.org/10.1111/geb.13188

ABSTRACT

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

Location: Central Europe.

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

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

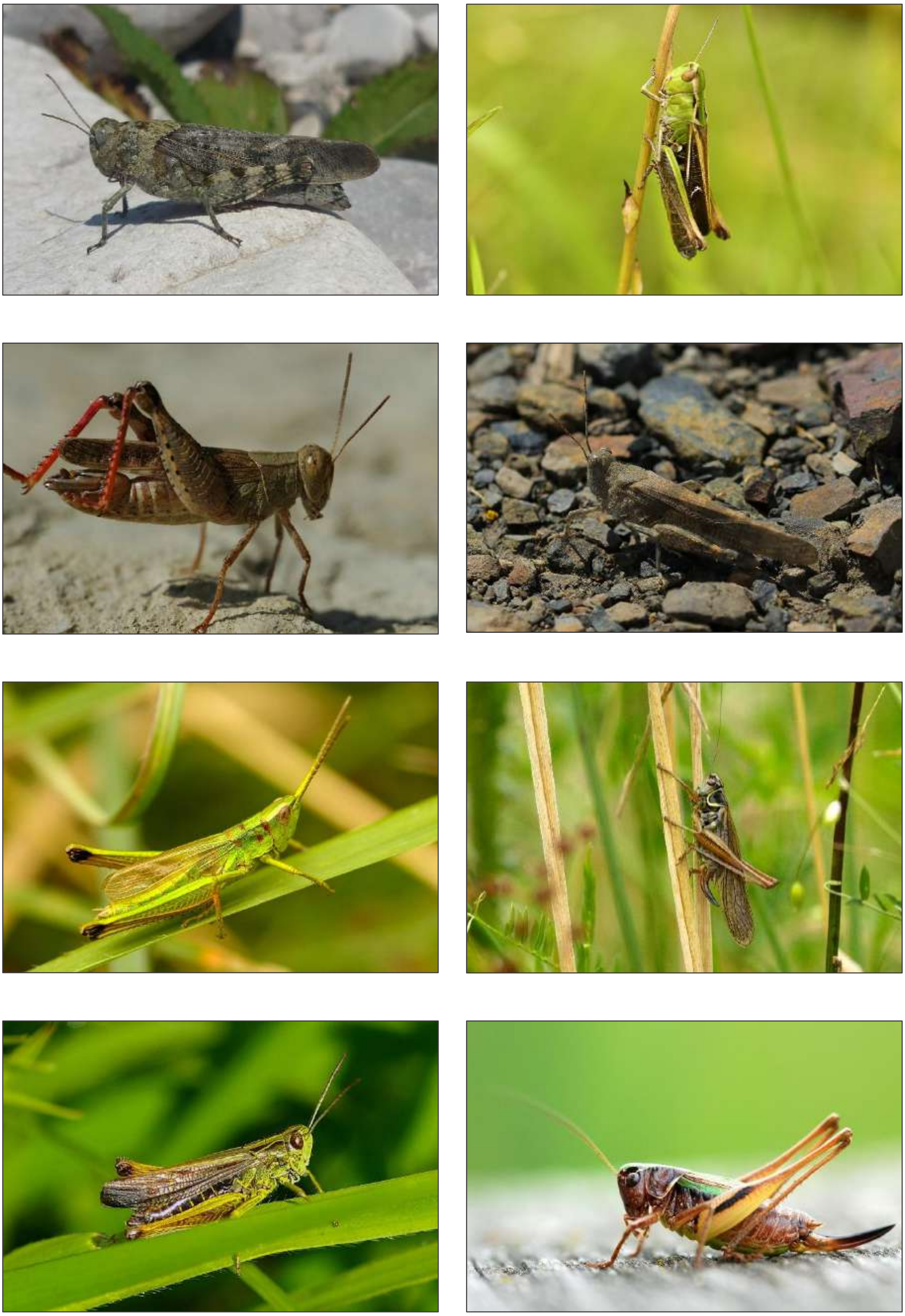
Methods: We used an advanced modelling approach within the framework of spatial point pattern analysis (SPPA) to calculate distributional changes of 58 grasshopper species based on more > 100,000 aggregated observational records. Historical and recent range shifts were compared among four functional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

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

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

KEYWORDS

Biodiversity loss, Dispersal ability, Distribution modelling, Functional trait, Global warming, Habitat specificity, Insect conservation, Orthoptera, Species Farmland Index, Species Temperature Index



In Central Europe, many grasshopper specialists experienced severe range losses, for instance (in rows from left to right): 1st row – *Bryodemella tuberculata*, *Stenobothrus lineatus* and 2nd row – *Calliptamus italicus*, *Sphingonotus caerulans*. However, as they require a warm macroclimate, the latter two recently expanded their ranges in response to global warming. Range expansions also occurred among many mobile generalists (e.g., 3rd row – *Chrysochraon dispar, Roeseliana roeselii*). By contrast, future climate change could pose a serious threat to hygrophilous grasshopper species (e.g., 4th row – *Omocestus viridulus, Metrioptera brachyptera*) (Photos of *C. italicus* and *M. brachyptera* by Thomas Fartmann).

(7) Orthoptera community shifts in response to land-use and climate change – Lessons from a long-term study across different grassland habitats

FRANZ LÖFFLER, DOMINIK PONIATOWSKI & THOMAS FARTMANN (2019)
Biological Conservation 236, 315–323. doi.org/10.1016/j.biocon.2019.05.058

ABSTRACT
Semi-natural grasslands are among the most species-rich ecosystems worldwide. However, the maintenance of grassland biodiversity is seriously threatened by land-use change. Additionally, climate change is increasingly affecting biotic communities in grasslands. In this study we examine Orthoptera community shifts in response to land-use and climate change in three different grassland habitats in a Central European low mountain landscape. Orthoptera strongly responded to environmental changes between 1994 and 2015. Both annual and summer temperatures increased during the study period. Apart from climatic changes, the studied habitats were unequally affected by land-use change. Due to the continuity of habitat management, habitat quality has not substantially changed in calcareous and mesic grasslands. However, abandonment has frequently contributed to habitat deterioration in wet grasslands. As a result of global warming, Orthoptera species richness in the well-managed grassland types increased, while it did not change in wet grasslands. The increase in species richness was mainly caused by an expansion of habitat generalists and mobile species. In comparison, the number of habitat specialists and species with limited dispersal ability did not change in any of the grassland types. Species-turnover rates were higher in mesic and wet grasslands. Accordingly, we detected an increase of the Community Temperature Index (CTI) in these habitats. The results of our study imply that the response of Orthoptera communities to global warming depend on the quality and availability of suitable habitats. Hence, sustaining traditional land use in semi-natural grasslands and the establishment of dense habitat networks is essential to promote Orthoptera diversity.

KEYWORDS
Agricultural abandonment, Biodiversity conservation, Climate change, Community Temperature Index, Land-use change, Range shift

The calcareous grasslands in the Natura 2000-area 'Upper Ahr Valley' (Eifel) are protected under the EU Habitats Directive and are generally well-managed. They are usually used as rough pastures and thus are characterized by heterogeneous and open habitat conditions providing a warm microclimate which is beneficial to the majority of specialized grasshopper species. Their grasshopper diversity recently increased, due to the expansions of mobile habitat generalists (Alendorf / Germany).

In former times, the wet grasslands in the Natura 2000-area 'Upper Ahr Valley' (Eifel) were grazed by cattle or mown in a low intensity. However, at least 70% of the wet grasslands in the study region have not been managed for at least 30 years. As a result, many patches have now become overgrown by tall-forb communities which is detrimental to the majority of grasshopper species (Blankenheim / Germany).

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

FLORIAN FUMY, FRANZ LÖFFLER, MICHAEL J. SAMWAYS & THOMAS FARTMANN (2020)
Journal of Environmental Management 256, 109919. doi.org/10.1016/j.envman.2019.109919

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 analyze 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 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 homogenization 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

Chapter IV

Synopsis

Synopsis

The role of metapopulation factors

It has become evident that the fragmentation of semi-natural grasslands and the deterioration of the remaining habitat patches are among the most severe threats to biodiversity in human-modified landscapes (e.g., Fahrig, et al., 2011; Fartmann, 2017; Haddad et al., 2015). Several papers included in *Chapter II* revealed that the persistence of habitat specialists in semi-natural grasslands is crucially determined by factors operating at (i) the landscape scale and (ii) the habitat scale. At the landscape scale, both patch size and connectivity affected the occurrence of several grassland specialists in the Diemel Valley (NW Germany) – one of the most important strongholds of calcareous grasslands in Central Europe (*Paper 1*). At the habitat scale, the quality within the studied patches also played a vital role for the patch occupancy in the studied species. Although the impact of these metapopulation factors varied among the study organisms, the overall variance explained by habitat quality and patch size performed better compared to connectivity. Therefore, it can generally be suggested that the maintenance of large-scale habitat patches with a high habitat quality is of prior importance for biodiversity conservation in semi-natural grasslands (cf. Thomas et al., 2011; Zulka et al., 2014). Nevertheless, the importance of habitat connectivity on grassland biodiversity should not be underestimated, as it usually becomes more important in highly fragmented landscapes (e.g., Maes & Bonte, 2006; Brückmann et al., 2010; Tscharntke et al., 2002). Moreover, recent studies highlighted that a dense and heterogeneous habitat network will especially become vital for species dispersal under recent global warming (e.g., Platts et al., 2019; Pöyry et al., 2009; Stuhldreher & Fartmann, 2018).

To further assess the impact of the landscape matrix, we tested the impact of functional connectivity on the patch occupancy of habitat specialists in calcareous grasslands in the Diemel Valley (*Paper 2*). We applied least-cost modelling with different resistance values of the matrix elements. This approach allows to investigate the effects of the matrix structure on habitat connectivity and thus could yield novel insights for the conservation of habitat specialists in fragmented landscapes (cf. Adriaensen et al., 2003). Corresponding the findings of previous fragmentation studies (e.g., Chardon et al., 2003; Verbeylen et al., 2003), we found that functional connectivity was a more powerful predictor of patch occupancy in habitat specialists than non-functional connectivity. Therefore, we suggest that the role of the landscape matrix should generally be given greater consideration in applied metapopulation research and conservation. As least-cost modeling is usually based on non-empirical assumptions on the resistance of landscape elements, it is, however, often subject to some uncertainty (Rayfield et al., 2010). Therefore, there is still a need for further research to evaluate the practical benefits of this approach in building habitat networks.

Increasing habitat connectivity may additionally provide a successful way to facilitate species to keep pace with global warming. The key role of working habitat networks under the impact of global warming is underlined by the findings of *Paper 5*. This study highlighted that the effects of habitat fragmentation, long-term abandonment and climate change pose serious threats to the Violet copper (*Lycaena helle*) in the Eifel low-mountain range (W Germany). *L. helle* is among the most vulnerable butterfly species in Europe (Maes et al., 2019). In temperate Europe, this cold-dwelling species is largely restricted to a few relict populations, mainly situated within low-mountain systems (Kudrna et al., 2011). The Eifel represents one of its last strongholds in Central Europe. Here, we found evidence that *L. helle* suffers from increased winter temperatures. As the present occurrence of the species in the study area was limited to habitats close to the regional upper elevational limit, regional uphill-shifts are strongly limited by the lack of refuge habitats at higher elevations. Consequently, the conservation of *L. helle* requires the restoration of heterogeneous habitat networks which could enable the species to evade from detrimental environmental conditions (cf. Goffart et al., 2014).

Effects of landscape-scale and habitat factors on grasshopper assemblages

Given that both landscape-scale and habitat factors are crucial for the survival of several grassland specialists, they are also thought to affect the overall species richness in semi-natural grasslands (e.g., Fahrig, 2003; Krämer et al., 2012; Krauss et al., 2010; Wettstein & Schmid, 1999). Whereas previous metapopulation studies revealed a negative response of butterfly species richness to both habitat fragmentation and deterioration in the remaining habitats (e.g., Brückmann et al., 2010; Krämer et al., 2012), there are indications that grasshopper diversity is mainly dependent on the habitat quality of grasslands (Eckert et al., 2017; Fartmann, 2017; Poniatowski & Fartmann, 2010). To date many studies investigated the role of traditional land use for grasshoppers in semi-natural grasslands (Fartmann et al., 2012; Marini et al., 2009; Uchida & Ushimaru, 2014). These studies consistently found that land use has a crucial impact on vegetation structure and microclimate. It especially promotes early and intermediate successional stages which are essential to maintain grasshopper species richness in semi-natural grasslands (Fartmann et al., 2012). *Paper 3* confirmed the outstanding importance of low-intensity land-use for the maintenance of a high habitat quality in pre-alpine calcareous grasslands in the Northern Limestone Alps (S Germany). The findings of this work are in line with previous studies showing that both agricultural intensification and abandonment cause habitat deterioration with detrimental effects on grasshopper species richness and abundance (e.g., Fartmann et al., 2012, Kruess & Tscharntke, 2002; Marini et al., 2009; Uchida & Ushimaru, 2014). We also found a positive impact of habitat heterogeneity (interrelated with patch size), on the overall species richness and the occurrence of threatened species in the studied grasslands. Habitat heterogeneity in large grassland patches usually favors the coexistence of grasshopper species with contrasting habitat preferences (cf. Schouten et al., 2007). Furthermore, it usually promotes mosaics of various microhabitats which are essential for different life-cycle stages in specialized grasshopper species, such as the Wart-biter (*Decticus verrucivorus*) (cf. Schirmel et al., 2010). Even though there is evidence that grasshopper diversity decreases with reduced connectivity in highly fragmented habitats (Eckert et al., 2017), there was no effect of isolation in the pre-alpine study area, which still holds a dense network of semi-natural grasslands (cf. Krämer et al., 2012). Therefore, it can be concluded that habitat connectivity seems to be of subordinate importance in still well-connected landscapes.

Extinction debt: a challenge for biodiversity conservation

Although short-lived organisms, such as most insects, are expected to show a faster response to habitat loss than long-lived taxa like plants (Helm et al., 2006; Krauss et al., 2010; Kuussaari et al., 2009), we found a similar response of vascular plant and butterfly species richness to habitat fragmentation in well-connected calcareous grasslands in the Eifel low-mountain range (W Germany) (*Paper 4*). Despite habitat area and connectivity strongly declined between 1970 and 1990, the present richness of specialist and generalist species among plants and butterflies was more strongly related to past landscape conditions. This indicates an extinction debt in both taxa (cf. Kuussaari et al., 2009). The existence of extinction debt may obscure the fact that the existing populations of several species are not viable in the long term, even without further environmental changes (cf. Kuussaari et al., 2009). Therefore, we recommend that the occurrence of such time-delayed extinctions should be given more attention in future conservation practice to avoid misleading conclusions for the management of semi-natural grasslands.

Large-scale grasshopper range shifts in response to land-use and climate change

While many species associated with semi-natural grasslands suffered a severe decline due to habitat loss in the second half of the 20th century, thermophilic species across various insect taxa frequently expanded their distribution ranges during the last decades (e.g., Hickling et al., 2006; Pöyry et al., 2009). However, the majority of studies focused on charismatic insect taxa, such as butterflies (e.g., Devictor et al., 2012; Parmesan, 1999; Pöyry et al., 2009), whereas the knowledge on range shifts among other important indicator groups has been poor to date (but see Beckmann et al., 2015).

Paper 6 represents the first large-scale study that quantifies both historical and recent range shifts of several common grasshopper species in Central Europe. The results of this study suggest that historical range losses, especially among habitat specialists, were caused by the severe loss of semi-natural habitats through agricultural changes pre-1990 (cf. Carvalheiro et al., 2013). Large-scale range retractions were mainly related to species associated with 'High Nature Value Farmland' (cf. Veen et al., 2009) (i.e., those with a higher Species Farmland Index – SFI). In contrast, recent global warming has led to rapid range expansions of several thermophilic grasshopper species (i.e., those with a higher Species Temperature Index – STI) during the last two decades. Especially, highly mobile species were able to expand their ranges. In contrast, we could hardly detect distributional changes among less mobile grasshopper species.

These findings demonstrate that the limited availability of semi-natural habitats in the agricultural landscape of Central Europe restricted many species to keep pace with recent climate change, which especially applies to habitat specialists with a low dispersal capacity (cf. Hill et al., 2001; Pöyry et al., 2009). In the long run, this development may also change trophic interactions, which increases the risk of biotic homogenization within plant and animal assemblages of semi-natural grasslands (cf. Mantyka-Pringle et al., 2015).

Grasshopper assemblage shifts across different grassland habitats

Recent studies revealed that climate-driven range shifts have altered the composition of biotic communities towards more thermophilic species (e.g., Devictor et al., 2012; Tayleur et al., 2016). In *Paper 7* and *8*, we intended to unravel the role of the compounding effects of land-use and climate change on grasshopper assemblages across different grassland habitats in two central European low-mountain ranges. In both studies, grasshopper assemblages clearly responded to altered environmental conditions. We found a strong increase of annual and summer temperatures in both study regions. However, the response of grasshopper assemblages to global warming varied between the studied grassland types. In the first long-term study, habitat quality remained stable in traditionally managed calcareous and mesic grasslands in the Eifel low-mountain range (W Germany) (*Paper 7*), whereas wet grasslands frequently suffered from abandonment in this region. Although thermophilic habitat generalists and mobile species have increased across all grassland types, their expansions only contributed to an increase of species richness in the well-managed habitats. These results underpin that the quality of habitats has a crucial impact on how species assemblages change due to global warming (cf. Hill et al., 2001). Therefore, the maintenance of traditional land-use practices appears crucial to enable species to cope with the effects of global warming.

In a second-long term study, we found an increase in grasshopper species richness associated with climate-driven range expansions in low-intensity common pastures in the southern Black Forest (SW Germany) (*Paper 8*). But neither the Community Farmland Index (CFI) nor the Community Temperature Index (CTI) changed in these traditionally managed grazing systems. However, the CFI decreased and the CTI clearly increased in wet and mesic grasslands in the study area. Both grassland habitats were frequently affected by land-use change during the last decades. Whereas wet grasslands suffered from habitat deterioration due to the cessation of traditional land use, mesic grasslands were often subject to land-use intensification. Therefore, both have undergone marked habitat-quality declines. As our study indicates that habitat specialists could be replaced by more widespread species under recent global warming, it can be assumed that the lower habitat quality in mesic and wet grasslands likely increase the risk of biotic homogenization. In contrast, the grasshopper assemblages within common pastures appear to be more resilient against the effects of climate change. This is likely due to the long-standing continuity of traditional grazing which sustained heterogeneous habitat conditions.

General implications for biodiversity conservation in times of global change

Since the introduction of the EU Habitats Directive, strengthening biodiversity conservation has become an important issue among European policy makers (EC, 1992). Given that they rank among the most species-rich ecosystems, particular attention must be paid to the conservation of semi-natural grasslands (Veen et al., 2009; Wallis de Vries et al., 2002). Due to the differential response of species to environmental changes, habitat management should be ideally oriented towards target species across various indicator groups. (cf. Oliver et al., 2016). Measures aiming to improve the habitat conditions for these taxa usually also promote the overall biodiversity within grassland ecosystems (Fartmann, 2017). To ensure the long-term survival of species in semi-natural grasslands (i) a high habitat quality, (ii) a sufficient patch area and (iii) a high connectivity should be maintained (e.g., Anthes et al., 2003; Fahrig, 2003; Thomas et al., 2011).

According to the key findings of this thesis, a favorable habitat quality within semi-natural grasslands is mandatory for several grassland specialists. It must be noted that the majority of species require early to intermediate successional stages (Fartmann et al., 2012), which depend on either natural dynamics or human land use (Fartmann, 2006; Helbing et al., 2014). Therefore, especially traditional land-use practices should be more strongly promoted by the common agricultural policies of the EU. In semi-natural grasslands, this mainly applies to low-intensity mowing (1–2 times per year without fertilizer application) and rough grazing (e.g., Fartmann et al., 2012; Krämer ete al., 2012; Veen et al., 2009).

It is furthermore important to maintain large-scale habitats or enlarge existing habitat fragments, which especially allows species with high demands on the minimum habitat area to maintain viable populations in the long run (e.g., Anthes et al., 2003; Hanski 1999; Salz & Fartmann, 2009). Larger patches are usually characterized by a higher heterogeneity, which increases species richness in semi-natural grasslands (e.g., Öster et al., 2007). Moreover, heterogeneous habitat conditions could help many species to persist within the remaining habitats under recent global warming (Fartmann, 2017; Streitberger et al., 2018).

Habitat connectivity is another key factor for the survival of species in fragmented landscapes, especially for those depending on metapopulation dynamics (Anthes et al., 2003; Hanski, 1999; Thomas et al., 2011). The findings of this thesis underpin the assumption, that working habitat networks will become increasingly crucial for habitat specialists. This is in line with recent studies which have shown that the availability of refuge habitats is mandatory for species to keep pace with climate change (e.g., Platts et al., 2019; Pöyry et al., 2009; Streitberger et al., 2016). Therefore, current conservation measures adapted to climate change need to promote heterogenous landscapes providing potential dispersal corridors between suitable habitats.

As there is still much uncertainty how species will respond to the interacting effects of land-use and climate change (Streitberger et al. 2016; Thuiller et al., 2019), future studies should seek to evaluate the effectiveness of conservation actions and climate-adaption measures in semi-natural grasslands. In this light, long-term monitoring appears to be crucial to document biodiversity shifts and to counteract emerging threats at an early stage (Samways et al., 2020). But it should also be noted that time-delayed extinctions could still contribute to future biodiversity loss in the remaining habitat fragments, even if appropriate conservation measures are established now. Therefore, the restoration of former habitats will likely become an increasingly important tool for conservationists to increase habitat availability and prevent future species loss in semi-natural grasslands (e.g., Poniatowski et al., 2020; Helbing et al., 2015; Helbing et al., 2021).

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Semi-natural grasslands rank among the most species-rich ecosystems in Europe and are of prior importance for the conservation of threatened plant and insect species, for instance (in rows from left to right): 1st row- Black-veined white (*Aporia crataegi*), Burnt tip orchid (*Orchis ustulata*), 2nd row – Large marsh grasshopper (*Stethophyma grossum*) (Photo of *S. grossum* by Thomas Fartmann)., Scarlet tiger moth (*Callimorpha dominula*), 3rd row – German gentian (*Gentianella germanica*), Purple-edged copper (*Lycaena hippothoe*), 4th row – Slender Scotch burnet (*Zygaena loti*), Devil's bit (*Succisa pratensis*).

Acknowledgements

Throughout the writing of this thesis, I received a great deal of support and assistance. I would first like to thank my supervisor, apl. Prof. Dr. Thomas Fartmann, who guided my way as a biodiversity scientist from the very beginnings of my studies. I am deeply grateful that I had the opportunity to benefit from his outstanding ecological knowledge and his broad scientific experience. I especially appreciate his patient willingness to talk about my studies which pushed my research to a higher level.

Furthermore, I am grateful to Prof. Dr. Christoph Leuschner, who kindly agreed to be the second supervisor of my thesis.

This thesis was generously funded by a scholarship of the German Environmental Foundation (DBU). I am filled with gratitude for the financial support and mentorship throughout the years of my PhD.

I also would like to express my thanks and appreciation to my colleagues from the Department of Biodiversity and Landscape Ecology at Osnabrück University. Sincere thanks especially go to Florian Fumy, Felix Helbing, Steffen Kämpfer, Thorsten Münsch, Dr. Dominik Poniatowski, Gwydion Scherer and Dr. Gregor Stuhldreher, who co-authored papers, provided me with statistical advices and have given significant amount of feedback on my studies.

I would like to extend my appreciations to Prof. Michael J. Samways who has supported my work with valuable and encouraging comments from the initial stage of my PhD.

The conservation authorities of the following administrative bodies gave permissions to conduct field work in protected areas: Districts of Freiburg, Euskirchen and Garmisch-Partenkirchen, Regional Council of Kassel.

Finally, I would like to thank my dear family and friends who accompanied and supported my life during and beyond my research activities in many ways.

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Awards and scholarships

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2016	*Best Oral Presentation Award* at the *12th International Congress of Orthopterology* in Ilhéus (Brazil). Löffler, F., Poniatowski, D., Fartmann, T., 2016. Survival in a changing environment – Effects of land-use and climate change on Orthoptera in montane grasslands.
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2010	*Master studies Scholarship of the Federal State of North Rhine*-Westphalia (10/2010–09/2012).

Publications and conference contributions

International publications (peer-reviewed)

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Conference contributions

Löffler, F., Freienstein, F. M., Dorner, S., Fartmann, T.: Artenschutz und Teichwirtschaft – Die Bedeutung von Karpfenteichen für Amphibien und Libellen in der sächsischen Kulturlandschaft. *Fachtag Aquakultur und Fischerei,* Landesamt für Umwelt, Landwirtschaft und Geologie Sachsen (LfULG), Königswartha (Germany) (03/2020) (invited talk).

Löffler, F., Dorner, S., Fartmann, T.: Fischereiwirtschaft und Artenschutz im Einklang – Die Bedeutung von Karpfenteichen für die Amphibiendiversität in der sächsischen Kulturlandschaft, V*ortragsreihe des Arbeitskreises Isis Budissina (NfGOL)*, Bautzen (Germany) (04/2019) (invited talk).

Löffler, F., Poniatowski, D., Fartmann, T.: Extinction debt of grassland specialists in a Central European biodiversity hotspot. *13th International Congress of Orthopterology*, Agadir (Morocco) (03/2019)

Poniatowski, D., Stuhldreher, G., **Löffler, F.**, Fartmann, T.: Patch occupancy of specialised grassland insects: Habitat quality matters more than connectivity. *25. Mitteleuropäische Zikadentagung*. Arnhem (Netherlands) (09/2018).

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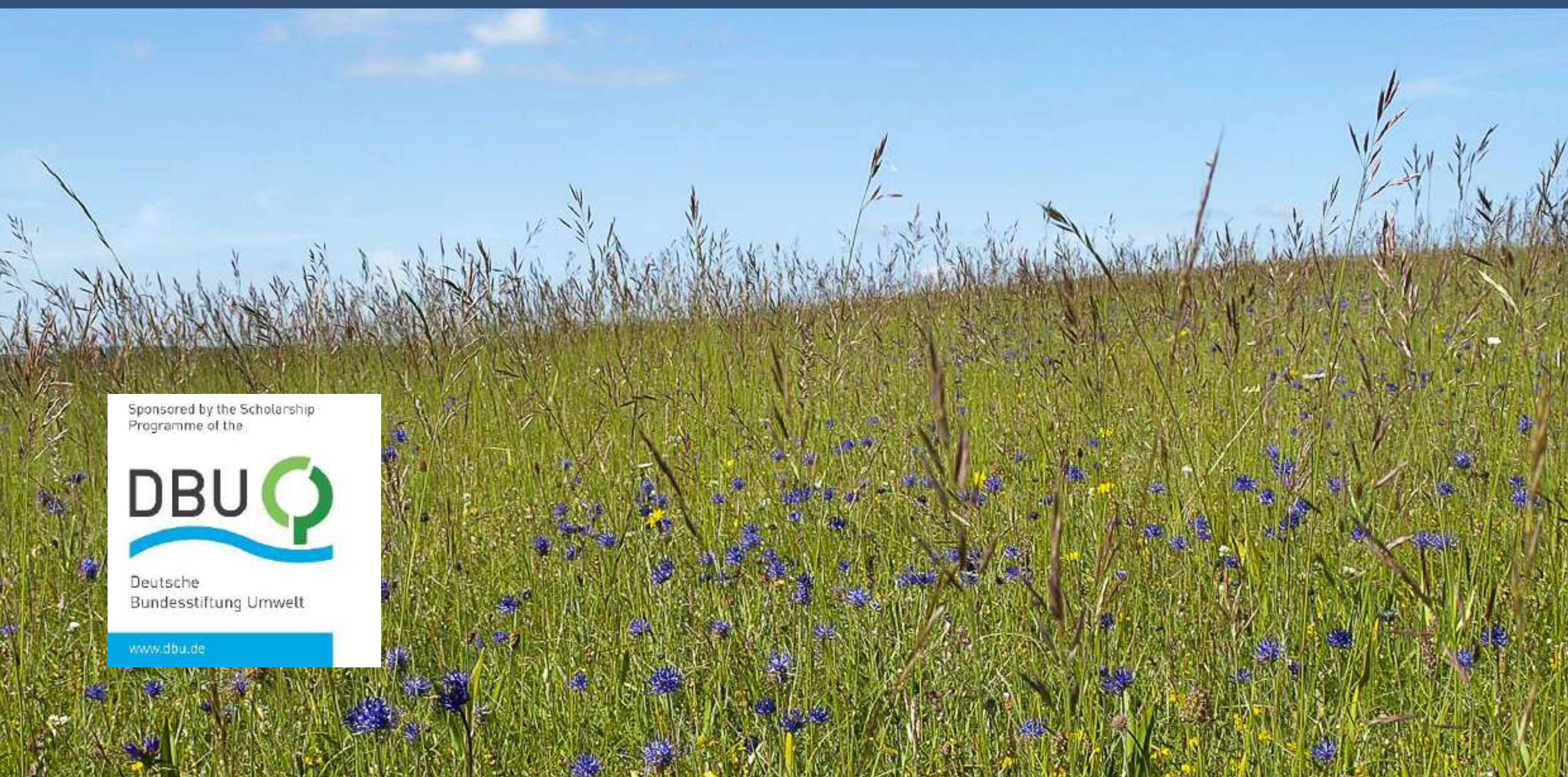

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