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CONSERVATION OF GRASSHOPPER SPECIES RICHNESS  
IN A CHANGING LANDSCAPE

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## SUMMARY

Grasshoppers are considered to be suitable indicator species for biodiversity as well as for habitat disturbances. Because of their sensitiveness to habitat deterioration, many grasshopper species are affected by human-induced landscape changes. In Switzerland, more than half of the grasshopper species are endangered.

In this study, I investigated the spatial pattern of grasshopper species richness with a focus on the impact of environmental change. In the first two parts of the study, I analysed data on grasshopper distribution all over Switzerland. Then, I focussed on North-Western Switzerland using data on selected grasshopper species.

Conservation planning mainly focuses on endangered species. But often, it is not the rare but the common species that are most responsible for richness patterns. As a consequence, the conservation of hotspots, which is an obvious conservation strategy, does not necessarily capture a high percentage of the overall species richness. In the first part of my study, I compared the representativeness of common and of endangered grasshopper species for overall grasshopper species richness. Additionally, I assessed the efficiency of the hotspot approach for grasshopper conservation. Numbers of common, as well as the number of endangered grasshopper species were good predictors for overall grasshopper species richness. Richness hotspots (sites with highest numbers of grasshopper species all over Switzerland) captured more endangered species than rarity hotspots (hotspots of endangered species); they even featured more common grasshopper species than hotspots of common species.

Then I investigated the impact of potential future environmental change on species richness by applying scenarios of environmental change. The effects of the scenarios were assessed for whole Switzerland and in the hotspots identified in the first part of this study. At the national level, the average number of grasshopper species per site decreased markedly under the land-use scenario 'liberalisation' and increased most under the climate change scenario. Species richness in small-scale hotspots was more negatively (or less positively) affected by environmental changes than an average ha plot under most scenarios. Because the response of species richness to the scenarios did not differ significantly between rarity hotspots and hotspots of common species and because of the relatively strong impact of the climate-change scenario, common species as well as the combined effects of land-use and climate change have to be additionally considered in nature conservation.

Species' extinctions frequently follow landscape change with a time lag. Because this aspect was not incorporated in the investigations described above, I studied the key factors for species richness of selected grasshopper species in north-western Switzerland. The selected species are xerophilic and most of them are endangered. I compared the influence of present with historic habitat availability at multiple scales, and with abiotic factors. Historic habitat availability explained more of the current richness pattern than more recent and more detailed habitat data. The results show that even short-lived species like grasshoppers may respond time-delayed to landscape change. This has important implications for the use of indicator species and for conservation planning.



## ZUSAMMENFASSUNG

Heuschrecken gelten als geeignete Biodiversitäts-Indikatoren sowie als Indikatoren für Umweltveränderungen. Auf Grund ihrer Sensibilität gegenüber Lebensraum-Veränderungen sind die meisten Heuschrecken-Arten in der Schweiz gefährdet. In der vorliegenden Studie untersuchte ich die räumliche Verteilung der Heuschrecken-Artenvielfalt unter Berücksichtigung des Landschaftswandels. In den ersten beiden Teilen dieser Untersuchung analysierte ich Heuschrecken-Verbreitungsdaten aus der gesamten Schweiz. Im dritten Teil beschränkte ich die Untersuchung auf ausgewählte Heuschrecken-Arten in der Nordwest-Schweiz.

Die Naturschutzpraxis konzentriert sich in der Regel auf gefährdete Arten. Zentrale Rolle für das räumliche Muster der Artenvielfalt spielen aber häufig die sogenannten „kommunen“ Arten. Folglich beinhalten Biodiversitäts-Hotspots, welche z.B. basierend auf der Anzahl gefährdeter Arten ausgewählt wurden, nicht unbedingt einen hohen Anteil der Gesamtartenzahl. Im ersten Teil meiner Studie verglich ich deshalb die Repräsentativität von kommunen und gefährdeten Heuschrecken-Arten für die gesamte Heuschrecken-Artenvielfalt. Zusätzlich untersuchte ich, wie viele Arten in schweizerischen Hotspots der Heuschrecken-Artenvielfalt vorhanden sind. Es zeigte sich, dass sowohl die kommunen als auch die gefährdeten Heuschreckenarten gute Indikatoren für die gesamte Heuschrecken-Artenvielfalt sind. In „richness hotspots“ (die Flächen mit den gesamtschweizerisch höchsten Artenzahlen) finden sich mehr gefährdete Arten als in „rarity hotspots“ (Flächen mit den höchsten Zahlen gefährdeter Arten), und auch mehr kommune Arten als in „hotspots of common species“.

Weiterhin untersuchte ich den Einfluss möglicher zukünftiger Umweltveränderungen auf die schweizerische Heuschrecken-Artenvielfalt. Hierfür wendete ich verschiedene Szenarien an und untersuchte, wie sich diese auf die Artenvielfalt insgesamt sowie auf die Artenzahlen in den im ersten Teil definierten Hotspots auswirken. Die durchschnittliche Anzahl Heuschrecken-Arten pro Flächeneinheit verringerte sich stark unter dem Landnutzungs-Szenario „liberalisation“ und steigerte sich am deutlichsten unter dem verwendeten Klima-Wandel-Szenario. Auf die Artenvielfalt in den Hotspots wirkten sich die meisten Szenarien negativer bzw. weniger positiv aus als auf eine durchschnittliche schweizerische Fläche. Weil die Artenvielfalt in „hotspots of common species“ und in „rarity hotspots“ vergleichbar auf Umweltveränderungen reagierte und weil das Klima einen grossen Einfluss auf die Artenvielfalt hatte, sollten im Naturschutz auch kommune Arten sowie die positiven Aspekte des Klimawandels berücksichtigt werden.

Häufig reagiert die Artenvielfalt mit einer zeitlichen Verzögerung auf Umweltveränderungen. Daher untersuchte ich in der Nordwest-Schweiz die wichtigsten Einflussgrössen auf ausgewählte Heuschrecken-Arten. Alle der in diesem Teil untersuchten Arten sind xerophil und die meisten davon gelten in der Schweiz als gefährdet. Der Vergleich der Bedeutung der aktuellen mit der historischen Habitat-Verfügbarkeit und mit abiotischen Variablen zeigte, dass die historische Habitat-Verfügbarkeit die aktuelle Verteilung der Artenvielfalt besser erklärt als aktuelle Habitat-Daten. Das heisst, dass selbst kurzlebige Organismen wie Heuschrecken zeitverzögert auf Umweltveränderungen reagieren. Dies hat grundlegende Auswirkungen auf die Eignung von Indikator-Arten und auf die Naturschutz-Praxis.





## 1. INTRODUCTION

### 1.1. Anthropogenic landscape change and species richness

Anthropogenic disturbance of ecosystems is an important factor for species richness. Over centuries, human land use increased and conserved local and regional species richness in tropical rainforests as well as in the cultural landscapes of temperate climates (Pimentel et al. 1992, Nietschmann 1993 in Stevens 1997, Jackson and Jackson 2002, Rosenzweig 2003). During the 20<sup>th</sup> century, cultural landscapes have changed markedly all over the world (e.g., Mason et al. 1987, Bätzing 1996, Skanes and Bunce 1997, Tekle and Hedlund 2000, Brown 2003, Ichikawa et al. 2006) and anthropogenic disturbance of ecosystems did primarily pose a threat to biodiversity (Matson et al. 1997, Tilman et al. 2001). Ewald (1978) was one of the first to quantify the dramatic changes in the European landscape during the 20<sup>th</sup> century. Transformations have not only affected natural habitats like river floodplains but have also been observed in managed forests and agricultural land.

Until World War I, the products of forestry and agriculture were primarily used for private subsistence (Beck 1986, Groh 1986). This led to high structural diversity in the cultural landscape. Forests were not mainly used to supply commercial timber products but mostly to supply firewood. In the Swiss lowlands simple coppice and coppice-with-standards were the dominant forest types in the 19<sup>th</sup> century (Bürgi 1999). Additionally, there was a great demand for non-timber products; people collected litter, fruits of all kinds, they used forests as pasture and they grew potatoes and cereals on clearings (Bürgi 1999). Intensive use and management together with an export of nutrients led to reduced tree-growth and consequently to forest stands with open character (Bürgi 1997, Schiess and Schiess-Bühler 1997). After World War II, forest area increased all over Europe and high forest became the dominant forest type (Beck 1986, Schiess and Schiess-Bühler 1997, Rackham 1998, Bürgi 1999). Forests have become richer in nutrients and their canopies became denser. Consequently, the spatial segregation of agricultural used land and forest has become significantly more distinct.

In the agricultural land of Central Europe, pastures and fields were small and accompanied by linear low-input habitats like hedgerows, stone walls, and field margins before the large-scale intensification of land use. Intensification of land use encompasses increased field size, increased nutrient and pesticide input, and increased disturbance level. The disturbance frequency increased due to higher management frequency, and higher amplitudes of disturbance were caused by the use of machines, chemicals, and by increased input of nitrogen. While, in the 19<sup>th</sup> and in the beginning of the 20<sup>th</sup> century, a relatively high proportion of pastures and fields were nutrient poor and were managed at different times during the season, today's agricultural land is in general rich in nutrients and managed more often and synchronously (Vowinkel 1998). Many low-input habitats (e.g., hedgerows, dry grassland) have been lost (e.e., Ewald 1996).

The spatial segregation of land-use intensity (intensively used agricultural land on the one hand and high forests on the other) as well as urbanization are the main trends in recent landscape development (e.g., Leonard and Cobham 1977, Robinson and Sutherland 2002). The spatial

segregation of land-use intensity has been observed especially in mountainous regions: in the easily accessible valley bottoms land use has been intensified, while sites at higher altitudes have generally been abandoned (e.g., Ales et al. 1992, Bätzing 1996, Garcia-Ruiz et al. 1996, Debussche et al. 1999, Brown 2003, Scozzafava and De Sanctis 2006). Both the segregation of land-use intensity and urbanization cause decreasing habitat availability and habitat quality because low-input habitats in agricultural land and highly structured forests represent exceptionally species rich habitats (e.g., Paoletti and Pimentel 1992, McLaughlin and Mineau 1995, Lindblach 1999, Germann and Holland 2001, Dullinger et al. 2003, Haines-Young et al. 2003, Millán de la Peña et al. 2003, Veken et al. 2004). It is evident that these habitat changes have an impact on biodiversity and species richness (e.g., Aebischer 1991, Paoletti and Pimentel 1992, McLaughlin and Mineau 1995, Sotherton 1998, Lindblach 1999, Chamberlain et al. 2000, Donald et al. 2001, Germann and Holland 2001, Benton et al. 2002, Dullinger et al. 2003, Haines-Young et al. 2003, Millán de la Peña et al. 2003, Veken et al. 2004).

Especially nutrient-poor habitats are very important for species richness in the European cultural landscape. These habitats are inhabited by a high plant diversity, which in turn causes spatially diverse microclimatic conditions that foster insect biodiversity (Heydemann and Müller-Karch 1980). Today, in example, most of the Central European Carabid beetle species (Carabidae) preferring nutrient poor habitats are threatened (Trautner 1992). The higher structural diversity of the historic European cultural landscape likely caused a generally higher diversity of species than can be observed in the today's landscape (Duelli et al. 1990, Maelfait and Keer 1990, Ratschker and Roth 1997, Schmitt and Roth 1997). Furthermore, insect biomass in agricultural used land probably decreased with land-use intensification during the 20<sup>th</sup> century (Heydemann and Meyer 1983, Tietze 1985, Zeltner 1989, Steinborn and Heydemann 1990, Blake et al. 1994, Ganzert 1996, Gerstmeier and Lang 1996, Luka 1996). This led to a decrease of available prey for predators and caused local extinctions (e.g., Little Owl, *Athene noctua*; Bezzel 1993) and marked changes in space use (e.g., Greater Mouse-Eared Bat, *Myotis myotis*; Steck and Güttinger 2006)

In the sum, the changes in the European cultural landscape during the 20<sup>th</sup> century had significant impact on species richness and were responsible for local and regional extinctions (e.g., Desender and Turin 1989, Delis et al. 1996, Köhler et al. 2003). Consequently, the conservation and the restoration of species richness play a key role in the sustainable development of cultural landscapes (Rio Convention, European Common Agricultural Policy).

## **1.2. Strategies for the conservation of species richness**

The conservation of species richness is not an easy task; various approaches exist in nature conservation (e.g., Armsworth et al. 2004). The most outstanding and at the same time contrasting strategies are the conservation of biodiversity hotspots and the large-scale conversion of farmland into low-input habitats as implemented in agri-environmental schemes.

The protection of so-called 'diversity hotspots' is a straightforward strategy for the conservation of species richness (Prendergast et al. 1993). Hotspots are generally defined as sites with relatively high numbers of species of interest. It has recently been discussed to apply the hotspot strategy at

different scales. On a landscape scale, the protection of hotspots may serve as a basis for designing reserve networks complying with the Convention on Biological Diversity (ISCBD 1994, Bonn et al. 2002, Kati et al. 2004). On the other hand, global hotspots may be an obvious tool for the conservation of worldwide biodiversity (Myers et al. 2000). However, the hotspot strategy exhibits several drawbacks. The main points of criticism are low representativeness and political concerns.

Several studies have compared the location of diversity hotspots of different taxonomic groups. These hotspots are in general not identical and, consequently, there is obviously a lack of suitable biodiversity-indicators (Prendergast et al. 1993, Ricketts 1999, Bonn et al. 2002). Therefore, targeting endemic and/or threatened species may be more efficient in representing overall biodiversity (Bonn et al. 2002). But Lennon et al. (2004) showed that it is not the rare but the common species that are most responsible for the spatial pattern of species richness. Consequently, not even rarity hotspots (plots with high numbers of endangered species; Gjerde et al. 2004) necessarily capture a high percentage of species richness.

The political difficulty of the hotspot approach is that decision makers could see the protection of a few diversity hotspots as a cure for all. The consequence might be that the remaining habitats deteriorate to 'coldspots' due to a liberalization of land use (Jepson and Canney 2001, Kareiva and Marvier 2003).

The large-scale conversion of farmland into low-input habitats is an alternative strategy to the hotspot approach. This measure is an important instrument in agri-environmental schemes in Europe and North America; nearly 4 billion euros are paid annually to farmers for making environmental improvements (Kleijn and Sutherland 2003, Donald and Evans 2006). These schemes are applied because agriculture is one of the most responsible sectors for the decline of species richness in cultural landscapes. Target of these schemes is to set land aside and to improve its value for nature conservation by, in example, reducing nutrient input and management frequency. Indeed, newly created low-input habitats feature more species than "normal" agricultural land (Field et al. 2005, Herzog et al. 2005, Knop et al. 2006). Furthermore it is suggested that agri-environmental schemes may carry substantial wider benefits: fragmentation of non-agricultural habitats may be reduced, species may more likely adapt to climate change, the spread of alien and invasive species may be slowed, and they could contribute to reserve networks (Donald and Evans 2006). However, even though species richness in set-aside land is generally fostered by agri-environmental schemes, rare species do not necessarily profit (Herzog et al. 2005). But it is the endangered species that are of major concern for nature conservation due to their above average risk of extinction.

Consequently, both the hotspot strategy and the large-scale conversion of farmland into low-input habitats exhibit severe drawbacks. For the effective conservation of species richness, it is necessary to increase knowledge about the spatial pattern of species richness, the underlying processes and the key factors for species richness (Huston 1995).

### **1.3. Considering time-lag effects**

In conservation planning, it is generally species richness that is considered as the key attribute in reserve selection and other measures. However, a well known phenomenon is rarely incorporated into conservation planning: that is the time-delayed response of species to environmental change. As shown above, habitat quality and the spatial distribution of suitable habitats are not static especially in cultural landscapes. Habitats may deteriorate and the connectivity to other suitable habitats may change over time. Several studies have shown that many species do not respond spontaneously to environmental changes (changes in habitat size, changing connectivity, climate change) but exhibit a time-delayed response. It can take centuries until a new equilibrium in species richness is reached (e.g., Brooks et al. 1999, Lindborg and Eriksson 2004, Lunt and Spooner 2005, Báldi and Vörös 2006, Helm et al. 2006, Paltto et al. 2006, Vellend et al. 2006).

In most of the studies mentioned above, the time-lag response of species to landscape change is to be connected with an “extinction debt” (Tilman et al. 1994). That means that the environmental conditions for species become less suitable over time, but species richness does not decline in a synchronic matter. In contrast, species may persist in unsuitable habitats if they are able to maintain populations over periods of decreasing habitat quality and connectivity.

Creating reserves and reserve networks is not per se successful in conserving species richness because of the time delayed response of species to landscape change (Hanski and Ovaskainen 2002, Lindborg and Eriksson 2004, Berglund and Jonsson 2005). Consequently, for effective nature conservation it is not only important to identify the most important environmental factors controlling species richness. Additionally, the role of landscape history has to be investigated for a better understanding of current richness patterns.

## 2. OBJECTIVES AND APPROACH

### 2.1. Research goals

This study investigates the spatial pattern of grasshopper species richness, its key factors, and the resulting implications for nature conservation. Grasshoppers are, on the one hand, said to be good indicators for overall species richness (Sauberer et al. 2004). On the other hand, they are declared as good indicators for changes in habitat quality, especially in non-forest habitats (Detzel 1992, Báldi and Kisbenedek 1997). Non-intensively used non-forest habitats feature exceptionally high numbers of species in the European cultural landscape (Báldi and Vörös 2006), but these are among those habitats that are most threatened both by intensification of land use and by land-use abandonment (Kleijn and Báldi 2005, Öckinger and Smith 2006). Due to their suitability as indicators and due to the high quantity of data on grasshopper distribution in Switzerland, grasshoppers were chosen as the key species group for this study. The aim of this study was to increase knowledge about the key drivers for spatial patterns of species richness and, consequently, to improve the conservation of biodiversity in the European cultural landscape.

In a first step, the spatial patterns of common and rare grasshopper species and the performance of the hotspot strategy on a high resolution were analysed (chapter 3). The aim was to evaluate the limitations of the hotspot strategy as well as the potential vulnerability of rarity hotspots in order to derive recommendations for biodiversity conservation on the landscape scale. The underlying research questions for the first part of this study were:

- Is it the common or the endangered grasshopper species that are most responsible for the spatial pattern of grasshopper species richness?
- What environmental factors differentiate rarity hotspots from hotspots of common species?
- Are fewer grasshopper species captured by rarity hotspots than by hotspots of common species or by richness hotspots?

The conservation of diversity hotspots is not the only strategy discussed in nature conservation. An alternative way to preserve species richness is the large-scale conversion of farmland into low-input habitats as applied in agri-environmental schemes. The second part of this study (chapter 4) therefore addresses the question to what degree the objectives of the large-scale conservation of species richness and the conservation of diversity hotspots are reached in a dynamic environment. The specific research questions were:

- Which are the major drivers for grasshopper species richness under current conditions?
- How may species richness change on the national and on the local (diversity hotspots) scale under different scenarios of land-use and climate change?
- Do small-scale hotspots benefit from large-scale conservation efforts such as agri-environmental schemes?

As described above, several studies have shown that the current distribution of species richness is not exclusively to be explained by current environmental conditions because of the extinction debt (Tilman et al. 1994, Hanski and Ovaskainen 2002, Lindborg and Eriksson 2004, Berglund and Jonsson 2005). Consequently, the historic environmental conditions may explain more of the current richness pattern than today's conditions. Thus, analysing the influence of the historic landscape may markedly improve the understanding of species distributions and conservation measures. In the third part of this study (chapter 5), the research questions regarding landscape history and its impact on current species richness were:

- To what extent does historic habitat area contribute to the current pattern of species richness?
- How important is the habitat availability in the surroundings for species richness in habitats?
- Are habitat area and availability more important than abiotic parameters (e.g., local climate)?

With this set of questions, the general research interest on the dynamic relationship between species richness and environmental change is focussed on the example of grasshoppers in the Swiss cultural landscape.

## **2.2. Main data source**

All data used in this study were provided by the Swiss Biological Records Centre (CSCF Neuchâtel). The great advantage in using these data was the large amount of grasshopper observations available and their high spatial resolution (data on the scale of 1ha). Using these data was a unique possibility to analyse the spatial pattern of species richness on the national scale. Because only species presences are recorded in this database, absolute data on absences were not available, which is a common constraint on analyses of animal distribution.

For evaluating the effectiveness of the hotspot strategy, all data available from grasshopper surveys made during the time period 1998 to 2003 in Switzerland were analysed (number of 1ha plots with grasshopper observations: 13'429). These data go back to surveys for the red-list project of the CSCF, to surveys done by experts for private studies, and to any other grasshopper data delivered to the CSCF (CSCF 2003). Therefore, it may theoretically be that some hotspots have not been included in this sample. Still, this is relatively unlikely because the most grasshopper species rich habitats are the most attractive for grasshopper experts. Such habitats are easily identified and, therefore, their locations are generally known. It was beyond the scope of this study to identify the "real" top most sites concerning species richness, as the analysis of the effectiveness of the hotspot strategy is based on a comparative approach. Our trust in the quality of the grasshopper data used in this study is further strengthened by the shape of the frequency distribution of grasshopper species richness (chapter 3, figure 1). Its shape corresponds well with figures on richness data based on systematic sampling designs (e.g., Cowley et al. 1999).

For these analyses, a different data set was analysed. At the time of beginning the analyses, the surveys for the Red-List project coordinated by the Swiss Centre for Faunal Cartography (CSCF Neuchâtel) were finished. In this project, professional entomologists collected data on grasshopper distribution based on methodological instructions. Within selected quadrants of 1 km<sup>2</sup> they had to

visit the sites with highest quality as grasshopper habitats. Afterwards, they had to look for other species in the remaining area of the quadrant (Gonseth, personal communication). Consequently, those sites with highest numbers of grasshopper species have evidently been sampled. Due to this sampling strategy, only grasshopper data from the most species-rich 1 hectare plots within a 1 km<sup>2</sup> quadrant were analysed in chapter 3 (7'457 plots of 1 ha).

The dataset used in chapter 4 was reduced another time for analysing the spatial distribution of xerophilic grasshopper species in chapter 5 (59 plots analysed). The reason for data reduction was the reduced study area, which was ranging between Geneva in the west along the Jura Mountains to the Randen region in the north-eastern part of Switzerland.

### **2.3. Relevance of this study for biodiversity conservation**

The conservation of species richness is not an easy task. In the European cultural landscapes, the main problems for nature conservation are the ongoing deterioration and fragmentation of habitats. However, the potential effects of these processes can only be evaluated reliably if the factors driving species richness are known.

Focussing on grasshoppers in Switzerland, the results of this study imply the importance of some problems in nature conservation might be overestimated: the severe constraints on the hotspot approach stated by several authors are not per se valid (chapter 3), positive effects of global warming on species richness can not be neglected (chapter 4), and some endangered species might profit from landscape change (chapter 5). On the other hand, the results show that nature conservation has to combine different strategies to preserve species richness most efficiently (chapters 3 and 4). Furthermore, the consequences of species' time-lag response to environmental change complicate the process of solution finding in conservation practice (chapter 5). It was beyond the scope of this study to present specific solutions for applied nature conservation. Still, scientific insights in the dynamic and highly diverse nature of species richness, as presented in this study, bear the potential to improve the tools and measures of biodiversity conservation.





### 3. HOTSPOTS AND RICHNESS PATTERN OF GRASSHOPPER SPECIES IN CULTURAL LANDSCAPES

Paper 1:

Steck, C.E., M. Bürgi, T. Coch, and P. Duelli (2007): Hotspots and richness pattern of grasshopper species in cultural landscapes. *Biodiversity and Conservation* 16 (7): 2075-2086.

#### **Abstract**

The success of the hotspot approach for biodiversity conservation depends on the spatial scale and the indicator species used. In this study, we investigated grasshopper species richness in Switzerland at a 1 ha resolution including a total of 111 species. We compared the representativeness of common and of endangered grasshopper species for the overall grasshopper species richness and we assessed the efficiency of the hotspot approach for grasshopper conservation. The pattern of overall grasshopper species richness was well represented by both the number of common and the number of endangered grasshopper species. For evaluating the efficiency of different hotspot approaches for conservation, we compared hotspots of common species, hotspots of endangered species (rarity hotspots), and hotspots of all grasshopper species (richness hotspots). Among these hotspot types, richness hotspots not only featured most common grasshopper species, but they even contained more endangered species than the rarity hotspots. The combination of rarity hotspots and hotspots of common species featured more species than the other combinations of hotspot types. However, the gain of combining two hotspot types compared to the single-hotspot approach was low (max. 3 species). About 24% of the species were not contained in any of the hotspots. These grasshopper species require species-specific action plans. As rarity hotspots were located in areas that are rather strongly affected by landscape change, species richness in rarity hotspots may decrease in the future. We conclude that, for grasshoppers, the hotspot approach on the 1 ha scale can be an effective way to conserve a high proportion of species richness.

**Keywords:** *Hotspots, grasshoppers, cultural landscape, endangered species, conservation strategy, Switzerland*

## Introduction

The protection of diversity hotspots is an obvious strategy for the effective conservation of biodiversity (Prendergast et al. 1993, Armsworth et al. 2004). The global application of the hotspot-approach (Myers et al. 2000), however, is disputed because decision makers may see it as a cure all, and the world outside the hotspots would remain or become a 'coldspot' (Jepson and Canney 2001, Kareiva and Marvier 2003). On a regional or national scale, the protection of diversity hotspots could provide a basis for designing reserve networks in the sense of the Convention on Biological Diversity (ISCBD 1994, Bonn et al. 2002, Kati et al. 2004), but also on this smaller scale there are constraints on the hotspot concept.

Several studies have shown that the diversity hotspots of different taxonomic groups are not identical and there is a lack of good biodiversity-indicators (Prendergast et al. 1993, Rickets 1999, Bonn et al. 2002). However, on the landscape scale and with a high resolution, e.g. Duelli and Obrist (1997) and Sauberer et al. (2004) have shown that Heteroptera and Orthoptera can capture a high percentage of the overall species richness. Therefore, the hotspot-strategy based on high resolution surveys of popular taxonomic groups could be an efficient way of conserving biodiversity. In practice, conservation strategies are often tailored to endangered species because they are of major concern due to their above average risk of extinction. Selecting sites for a reserve network by targeting endemic and/or threatened species may therefore be a first step in reserve planning (Bonn et al. 2002). However, species-rich areas frequently do not coincide with the hotspots of rare species (Prendergast et al. 1993, Bonn et al. 2002), and, conversely, it is not the rare but the common species that are most responsible for richness patterns (Lennon et al. 2004). In other words, the conservation of rarity hotspots (plots with high numbers of endangered species; Gjerde et al. 2004) does not necessarily capture a high percentage of the overall species richness. In this study we address the question whether this limitation of the hotspot-strategy at low to intermediate resolutions (Prendergast et al. 1993, Bonn et al. 2002, Lennon et al. 2004) is also effective on fine-scale hotspots (resolution = 1 ha; e.g., Gjerde et al. 2004).

The discordance of the spatial patterns of common and rare species is, among other factors, caused by the markedly differing environmental requirements of these two groups (Jetz and Rahbeck 2002, Duelli and Obrist 2003, Magurran and Henderson 2003). The increasing rarity of species and the impoverishment of biodiversity in the European cultural landscape are partially caused by habitat loss due to human-induced landscape change (e.g., Desender and Turin 1989, Köhler et al. 2003). In Switzerland, the habitats of endangered grasshopper species are mainly relicts of natural habitats like natural floodplains or bogs, and relicts of traditional landscape elements such as poor grassland (Thorens and Nadig 1997). Rarity hotspots should therefore mainly be located in such relicts of either natural or traditional cultural landscapes, while the hotspots of common species can also be situated on sites with higher productivity and more intense agriculture. If the rarity hotspots are actually located in either natural or traditional cultural landscapes, they are in danger of being affected by human-induced landscape changes.

Due to the potential limitation of the hotspot strategy and the potential vulnerability of rarity hotspots, we decided to evaluate the fine-scale hotspots (resolution of 1 ha) of Swiss grasshoppers based on the following research questions:

- Is it the common or the endangered grasshopper species that are most responsible for the spatial pattern of grasshopper species richness?
- What environmental factors differentiate rarity hotspots from the hotspots of common species?
- Are fewer grasshopper species captured by rarity hotspots than by hotspots of common species or by richness hotspots?

## Methods

### Study design

The database for this study consists of the grasshopper surveys in Switzerland made during the time period 1998 to 2003 and collected at the Swiss Biological Records Centre (CSCF Neuchâtel). In this time period 13'429 plots of 1 ha were surveyed (total surface of Switzerland: 4'128'400 ha). Within these plots 111 grasshopper species were found, of which 62 are endangered (Thorens and Nadig 1994) and 49 species are common (not endangered).

Hotspots were defined here as the 50 plots with the highest numbers of grasshopper species (Fig 1). We evaluated rarity hotspots (highest numbers of endangered grasshopper species, Thorens and Nadig 1994), hotspots of common species (not endangered grasshopper species), and richness hotspots (all grasshopper species). The plots of the rarity hotspots were occupied by 9 to 18 endangered grasshopper species, hotspots of common species represent plots with 11 to 15 species, and 17 to 29 grasshopper species were reported in the 50 richness hotspots (number of all plots: 13'429).

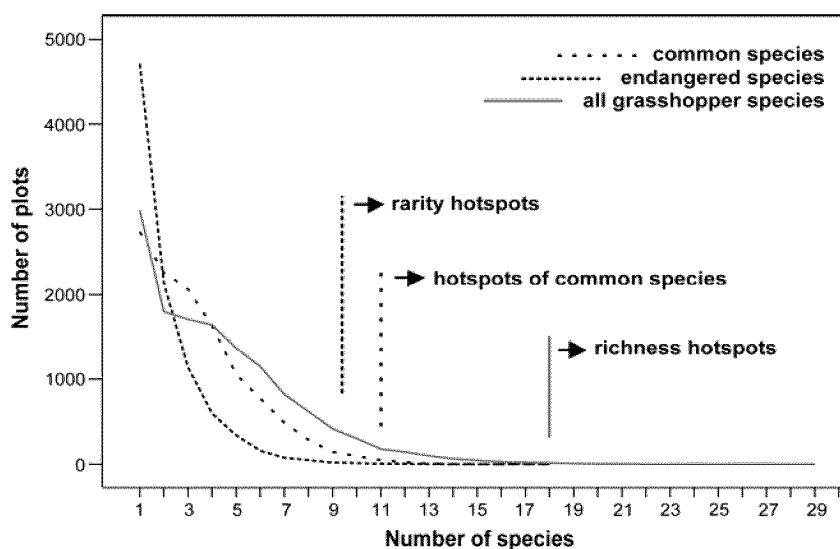


Figure 1: Frequency distribution of grasshopper species richness per 1ha plot (Number of all plots:  $n=13'429$ ). For three groups of grasshopper species, the 50 plots with highest numbers species were defined as hotspots.

### *Representativeness of common and endangered species for the spatial pattern of grasshopper species richness*

A hotspot approach based on endangered species or on rarity hotspots is only valid for the entire taxon, if the endangered species are good indicators of the richness pattern of the whole taxon. To compare the representativeness of endangered grasshopper species and of common grasshopper species, we calculated the bivariate Spearman correlation coefficients between the number of endangered grasshopper species, the number of common grasshopper species, and the number of all grasshopper species. These calculations were done by either including all 13'429 plots with grasshopper surveys or by two subsets, i.e., plots with 1 to 14 species ( $n = 13'298$ ) and plots with 15 to 29 species ( $n = 131$ ).

### *Differences between rarity hotspots and hotspots of common species*

To evaluate the differences in the habitat-characteristics of rarity hotspots (reduced number:  $n = 47$ ) and hotspots of common species ( $n = 50$ ), the plots of these two hotspot types were compared by means of a logistic regression (model:  $\alpha = 0.05$ ; variables:  $\alpha = 0.05$ ; stepwise backwards procedure). In three cases two rarity hotspots touched each other. To minimize autocorrelation one of the two hotspots was removed randomly.

The rarity hotspots were compared with the hotspots of common species according to 8 predictive variables. As a factor for local climate we chose the interaction of the sum of solar radiation in July and the average temperature in July (radiation by temperature; metric factor). Precipitation (sum of rainfall in July; metric) is a measure of either microclimate and of the productivity of the vegetation. The mean slope (metric) is a measure for productivity and for human disturbance, because slope in the study sites was highly correlated with soil depth (Spearman correlation coefficients  $> 0.6$ ) and in steep habitats land use is more difficult. Due to soil depth's high correlation with slope, the factor soil depth was disregarded in the model. Distance to settlements (metric) is an indicator of accessibility. If a plot contains surfaces that are listed in a national inventory of natural floodplains, of bogs, or of poor grassland, it contains a relatively 'old' habitat-type (habitat continuity; boolean factor). Land-use category (categorical factor with 24 classes) is a point survey of the land use in one corner of the studied plots. This survey is based on the interpretation of aerial photographs and was made between 1992 and 1997 (Swiss Federal Statistical Office 2001). Additionally the number of land-use categories (land-use variety, metric factor) in the surroundings (radius = 300m) of the study sites was taken into account in the model. As a measure of landscape change we counted the number of 1ha plots in the surroundings (radius = 300m) of the hotspots, in which the land-use category changed between the surveys of 1979/85 and 1992/97 (Swiss Federal Statistical Office 2001).

### *Representativeness of different hotspot types for grasshopper species richness*

We used two measures to compare the representativeness of rarity hotspots, hotspots of common species, and richness hotspots. First, we counted the number of species occurring in the plots of the different hotspot types and their combinations, and second, we evaluated the number of

occupied plots ('range size' in Lennon et al. 2004) of the grasshopper species in the different hotspot types. The 'range size' of endangered and of common species in the three hotspot types was compared with the Friedman-Test and pair-wise with the Wilcoxon-Test for related samples (Bonferroni adjusted  $\alpha = 0.016$ ).

## Results

### *Representativeness of common and endangered species for the spatial pattern of grasshopper species richness*

Plotting common and endangered species against total numbers of grasshopper species revealed that the representativeness of common and endangered species depends on the number of total grasshopper species per plot (Figure 2). Considering all the plots in Switzerland where grasshopper releves have been made (1 to 29 species,  $n = 13'429$ ) and plots with 14 or less species ( $n = 13'298$ ), common species (Spearman correlation coefficients = 0.88) represent more of the total grasshopper species richness than endangered species (Spearman correlation coefficient = 0.60 and 0.59). In the plots with at least 15 grasshopper species ( $n = 131$ ) the endangered species represent the total grasshopper species richness better (Spearman correlation coefficient = 0.53) than common species (Spearman correlation coefficient = 0.26). In these plots the endangered species and the common species are negatively correlated (Spearman correlation coefficient = -0.61).

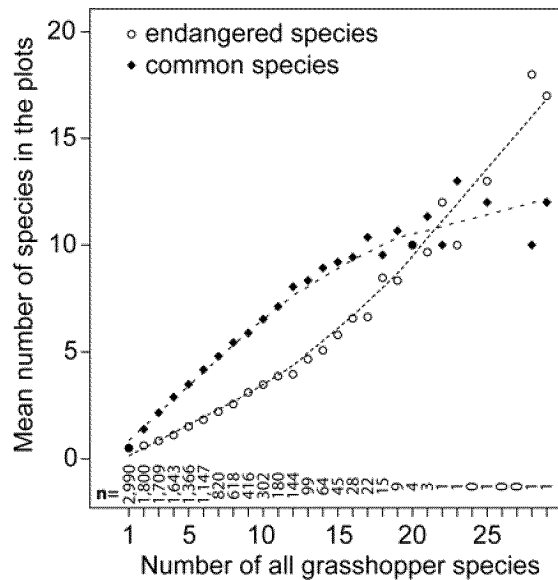


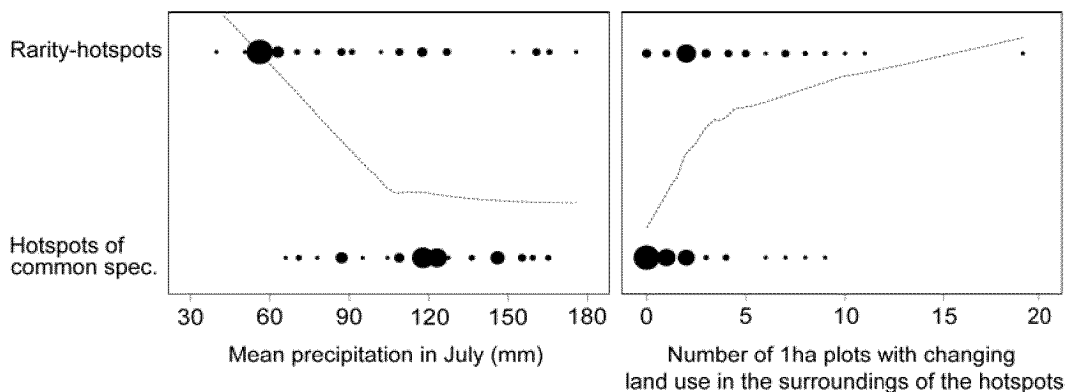
Figure 2: Mean numbers of endangered and common Swiss grasshopper species plotted against the total number of grasshopper species per plot: in the most species rich plots (at least 15 grasshopper species;  $n = 131$ ) the number of endangered species represents the grasshopper richness pattern better than the number of common species does (dotted lines = Loess smoother; standard deviations have been omitted to make the patterns clearer).

### *Differences between rarity hotspots and hotspots of common species*

The model outcome of the logistic regression analysis is highly significant ( $p < 0.001$ ; Table 1). Rarity hotspots and hotspots of common species differed significantly in several variables, namely: habitat-continuity (more rarity hotspots with 'old' habitat-types, Table 1), precipitation (less precipitation in rarity hotspots), and landscape change (more changes in the surroundings of rarity hotspots; Table 1, Figure 3).

*Table 1: Results of the logistic regression to differentiate between rarity hotspots ( $n = 47$ ) and the hotspots of common species ( $n = 50$ ): rarity hotspots and the hotspots of common species differ significantly in the variables precipitation, habitat-continuity and landscape change.*

| Variable                 | B      | S.E.         | $\chi^2$    | df       | p                 |
|--------------------------|--------|--------------|-------------|----------|-------------------|
| Radiation by temperature | -      | -            | -           | -        | -                 |
| Precipitation            | -0.003 | 0.001        | 16.8        | 1        | < 0.001           |
| Slope                    | -      | -            | -           | -        | -                 |
| Distance from settlement | -      | -            | -           | -        | -                 |
| Habitat continuity       | 1.469  | 0.557        | 7.4         | 1        | 0.006             |
| Land-use category        | -      | -            | -           | -        | -                 |
| Land-use variety         | -      | -            | -           | -        | -                 |
| Landscape change         | 0.450  | 0.115        | 23.8        | 1        | < 0.001           |
| <i>Constant</i>          | 1.632  | 0.931        |             |          |                   |
|                          |        | <b>Model</b> | <b>45.4</b> | <b>3</b> | <b>&lt; 0.001</b> |



*Figure 3: Distinguishing between rarity hotspots and hotspots of common species: rarity hotspots ( $n = 47$ ) have a lower precipitation than hotspots of common species ( $n = 50$ ) and their surroundings are more strongly affected by landscape change (dotted line = Loess-smoother).*

*Representativeness of different hotspot types for grasshopper species richness*

Analyzing the spatial distribution of hotspots reveals that richness hotspots, hotspots of common species and rarity hotspots ( $n=50$  each) are distributed differently: whereas richness hotspots and hotspots of common species are located in both northern and southern Switzerland, rarity hotspots are mostly located in southern Switzerland (Figure 4). The 50 richness hotspots consist of 27 rarity hotspots, 17 hotspots of common species, and 10 other plots. Four of the hotspots of common species and rarity hotspots are identical.

The richness hotspots represent 73% of all grasshopper species, and the hotspots of common species and rarity hotspots represent 69% (Table 2). As expected, rarity hotspots represent more endangered and fewer common species than hotspots of common species. By combining different or all hotspot types, a maximum of 3 species are gained (Table 2). In all three hotspot types the endangered species of the Red List category 3 (vulnerable) are better represented than the more threatened species of the Red List categories 1 (critically endangered) and 2 (endangered; Table 3). 14 of the most endangered grasshopper species (Red List categories 1 and 2) are not recorded in the rarity hotspots, and 15 are not represented by hotspots of common species and by richness hotspots (Table 3).

The 'range sizes' (number of occupied plots) of endangered species in the richness hotspots and in the rarity hotspots significantly exceed the range size of endangered species in the hotspots of common species (Friedman-test: chi-square = 31.1;  $p < 0.001$ , Wilcoxon-test:  $Z = -4.7$ ;  $p < 0.001$ ). The range size of common species in the rarity hotspots is significantly lower than in the hotspots of common species (Wilcoxon-test:  $Z = -3.4$ ;  $p = 0.001$ ) and also lower than in the richness hotspots (Wilcoxon-test:  $Z = -4.3$ ;  $p < 0.001$ ). The range size of common species does not differ between the hotspots of common species and the richness hotspots (Wilcoxon-test:  $Z = -1.5$ ;  $p = 0.13$ ).

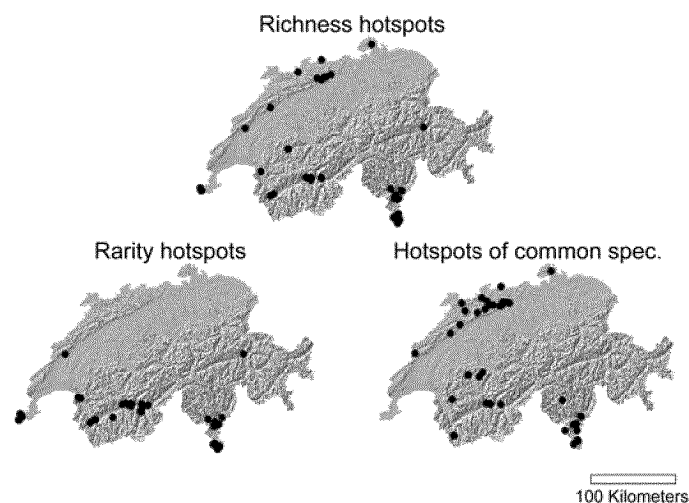


Figure 4: Locations of grasshopper hotspots in Switzerland: rarity hotspots ( $n = 50$ ) are mostly restricted to southern Switzerland, whereas the hotspots of common species ( $n = 50$ ) and richness hotspots ( $n = 50$ ) are also located in northern Switzerland.

*Table 2: Representativeness of the three hotspot types: the richness hotspots feature more species than the rarity hotspots and hotspots of common species.*

|                         | # Species in hotspots |            | # Species not in hotspots |            |
|-------------------------|-----------------------|------------|---------------------------|------------|
|                         | common                | endangered | common                    | endangered |
| 1 Richness hotspots     | 36                    | 45         | 13                        | 17         |
| 2 Rarity hotspots       | 33                    | 44         | 16                        | 18         |
| 3 Hotspots common spec. | 34                    | 43         | 15                        | 19         |
| Hotspot combinations    |                       |            |                           |            |
| 1 + 2                   | 37                    | 46         | 12                        | 16         |
| 1 + 3                   | 37                    | 45         | 12                        | 17         |
| 2 + 3                   | 38                    | 46         | 11                        | 16         |
| 1 + 2 + 3               | 38                    | 46         | 11                        | 16         |

*Table 3: Number of endangered species in hotspots: critically endangered and endangered species (Red List categories 1 and 2) are less well represented by the three hotspot types than the more common, but still endangered, species of Red List category 3 (vulnerable).*

|                       | Critically endangered spec. |      | Endangered spec. |      | Vulnerable spec. |      |
|-----------------------|-----------------------------|------|------------------|------|------------------|------|
|                       | Total                       | in % | Total            | in % | Total            | in % |
| Switzerland           | 14                          |      | 8                |      | 40               |      |
| Richness hotspots     | 4                           | 28.6 | 3                | 37.5 | 38               | 95.0 |
| Rarity hotspots       | 5                           | 35.7 | 3                | 37.5 | 36               | 90.0 |
| Hotspots common spec. | 4                           | 28.6 | 1                | 12.5 | 38               | 95.0 |

## Discussion

### *Representativeness of common and endangered species for the spatial pattern of grasshopper species richness*

Our analyses show that both the number of common grasshopper species and the number of endangered species are good indicators for overall grasshopper species richness. This corresponds with several other studies where rare and/or common species also correlated with the species richness of the whole taxon (e.g., Thomas and Mallorie 1985, Berg and Tjernberg 1996, Gaston and Blackburn 1996, Lehmann et al. 2002, Lennon et al. 2004, Werner and Buszko 2005). In our study, however, it was crucial to differentiate between the species-rich plots and the plots with lower numbers of species as common species contributed more to the richness pattern in areas with lower numbers of grasshopper species. Conversely, the endangered grasshopper species had a higher affinity for the most species rich plots and therefore explained more of the richness pattern in the species-rich areas. Consequently, more than 50% of the richness hotspots coincide with rarity hotspots.



The number of common Swiss grasshopper species per plot rises only to a certain level. With increasing species richness of the whole taxon, the number of common species levels off. Therefore the habitat requirements of common Swiss grasshopper species are likely to be more heterogeneous (i.e. some species prefer dry habitats, some species prefer humid habitats and some species are generalists) than those of the endangered species, which accumulate especially in the most species-rich plots. Many of the endangered species tend to occur only under very specific conditions (e.g., dry and highly structured grassland), where they are more likely to co-exist than common grasshopper species due to their less diverse environmental requirements. Given this and because there is no published evidence that common and endangered grasshopper species differ in their mean mobility, we hypothesize that the frequency and the degree of endangerment of the grasshopper species reflects primarily habitat availability as was suggested generally by Wright et al. (1998). This hypothesis stands in contradiction to the general statements by Tilman (1997) and Hubbell (2001), who suggest that rarity depends mostly on the dispersal ability of a species or on dispersal limitation due to fragmentation.

We conclude that the rarity hotspots of an indicator taxon are likely to capture a high proportion of the overall biodiversity, because endangered grasshopper species are good indicators for grasshopper species richness, and grasshopper species are also good indicators for overall biodiversity (Sauberer et al. 2004). Therefore, the general constraints on the hotspot-strategy proposed by Prendergast et al. (1993), Bonn et al. (2002), and Lennon et al. (2004) are not supported by our results.

#### *Differences between rarity hotspots and hotspots of common species*

The locations of the hotspots of endangered species (rarity hotspots) and the locations of the hotspots of common species differ markedly with regard to several environmental variables: Rarity hotspots are located in areas that are less humid (precipitation), that are more likely to contain old habitat-types, such as natural floodplains, bogs, or poor grassland (habitat-continuity), and that are more strongly affected by landscape change. Due to lower humidity (with the same radiation by temperature), the productivity in rarity hotspots is likely to be lower than in the hotspots of common species. This lower productivity may indicate less land-use intensity. A lower productivity of rarity hotspots would correspond with the generally differing habitat requirements of rare and common species (Jetz and Rahbeck 2002, Magurran and Henderson 2003), and in particular with the higher affinity of endangered Swiss grasshopper species for habitats with low productivity (Thorens and Nadig 1997). These differences in the habitat requirements of endangered and common grasshopper species lead to the different spatial distributions of rarity hotspots and the hotspots of common species in Switzerland, as their habitats are not distributed equally.

We assume that the rarity hotspots of Swiss grasshopper species are relicts of former more common habitats. The relictic character of the areas where rarity hotspots are located is indicated by their relatively low productivity and the high proportion of old habitat types. Low productivity may be a reason for the comparatively high degree of landscape change in the surroundings of the rarity hotspots because land of low productivity is often abandoned leading to the regrowth of scrub and

secondary forests (Bätzing 1996). The process of landscape change is highly relevant for nature conservation as it threatens habitat quality in the hotspots. Furthermore, landscape changes in the surroundings of the hotspots may affect important source populations. If nearby source populations have been lost, landscape changes in the surroundings of the hotspots might lead to a decrease in species richness in the hotspots themselves, even if they are not directly affected by these processes (e.g., Tilman et al. 1994, Hanski and Ovaskainen 2002, Cabeza and Moilanen 2003, Jacquemyn et al. 2003, Lindborg and Eriksson 2004, Roy et al. 2004).

#### *Representativeness of different hotspot types for grasshopper species richness*

In comparison to investigations on other taxa (e.g., Prendergast et al. 1993, Gjerde et al. 2004), each of our three hotspot types feature a relatively high proportion of all Swiss grasshopper species. Interestingly, it is the richness hotspots that capture most common as well as most endangered grasshopper species. Therefore, protecting richness hotspots is more 'efficient' than the other hotspot approaches. The 'range size' of the species (number of occupied hotspots) does not significantly differ from the other two hotspot types. These findings suggest that protecting richness hotspots is most efficient for conservation practice.

Most of the richness hotspots are identical with either rarity hotspots or hotspots of common species. Rarity hotspots and the hotspots of common species differ in their environmental characteristics (Table 2) and spatial distributions (Figure 4). Therefore, we conclude that the richness hotspots encompass a higher diversity of habitat-types than the rarity hotspots or the hotspots of common species. Consequently, richness hotspots are likely to capture a higher proportion of grasshopper species than either the rarity hotspots or the hotspots of common species. But the higher diversity of habitat types is mainly reflected by the 'range size' of the species and only marginally by the set of species featured by the hotspots (see below).

A considerable proportion of Swiss grasshopper species does not occur in any of the three types of hotspots. Especially many critically endangered and endangered species (Red List categories 1 and 2) are not featured by the hotspots. Even combining two or all the three hotspot types does not lead to a remarkable increase in the number of featured grasshopper species. Therefore, very rare species or species that adapted to special habitat types (such as bogs) or special climatic regions (i.e. high altitude) are rarely featured by the hotspots. For these species, especially for the relatively high number of endangered species that do not occur in hotspots, species specific conservation policies are needed, because even a hotspot approach at regional levels would probably fail to protect them adequately.

#### *Conclusions*

In combination with species-specific conservation plans, fine-scale hotspots of species richness (at a resolution of 1 ha) are a valuable tool for biodiversity conservation in cultural landscapes, even with a focus on endangered species. However, there is a trade off between efficiency and conservation needs: while richness hotspots are most efficient in representing grasshopper species

richness, it is the rarity hotspots that are most vulnerable due to landscape changes in their surroundings.

To conserve species richness in the hotspots and increase species richness in their surroundings, it might be appropriate to reintroduce or imitate traditional land-use practices if the hotspots concerned are relicts of traditional cultural landscape elements such as poor grasslands (*sensu* Austad 2000). Converting farmland into low-input habitats is an important instrument in the agri-environmental schemes developed in many European countries (Kleijn and Sutherland 2003). Protecting biodiversity is also a major objective of agri-environmental schemes in Switzerland (Bötsch 1998, Forni et al. 1999). However, endangered species rarely benefit from these schemes (Herzog et al. 2005, Knop et al. 2006). To improve this situation, species richness must be efficiently enhanced by linking the hotspots with other species-rich habitats and by creating new hotspots. This requires having information on the most suitable sites for creating low-input habitats. Here, taxon-specific habitat-suitability models can provide a basis for optimizing the selection of potential hotspots for restoration (e.g., Maes et al. 2003). Although richness hotspots capture more species, our study suggests that focussing conservation efforts on rarity hotspots might be preferred as these sites seem to be currently the most critically threatened by land-use changes.

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#### 4. CONSERVATION OF GRASSHOPPER DIVERSITY IN A CHANGING ENVIRONMENT

Paper 2, in press:

Steck, C.E., M. Bürgi, J. Bolliger, F. Kienast, A. Lehmann, and Y. Gonseth (in press): Conservation of grasshopper diversity in a changing environment. *Biological Conservation*.

##### **Abstract**

Land-use change is a major driver for changes in biodiversity. In this study, we investigated how the objectives of two conservation strategies (large-scale conservation of species richness versus conservation of diversity hotspots) can be achieved for grasshopper diversity under different scenarios of environmental change (land-use and climate change).

Based on surveys of 95 grasshopper species from 2001 to 2004 recorded by the Swiss Centre for Faunal Cartography, we modelled the actual richness pattern as a function of different environmental variables. The impact of potential future environmental change on species richness was evaluated by applying four land-use scenarios ('liberalization', 'business as usual', 'lowered agricultural production', and 'complete conversion of intensive open land') and one climate change scenario. The effects of the scenarios were assessed at the national scale, as well as on small-scale hotspots.

Environmental change has considerable effect on grasshopper species richness. At the national scale, the number of grasshopper species decreased under the 'liberalization' scenario (-0.24 species per 1ha pixel) and increased under a climate change scenario (+0.63 species per 1ha pixel). For most environmental change scenarios, species richness in small-scale hotspots was more negatively affected than on average on the national scale. The response of species richness to the scenarios did not differ significantly between hotspots of endangered and the hotspots of common grasshopper species.

We conclude that conservation efforts at the national scale and small-scale hotspot conservation programs should be combined to conserve species richness most successfully. For the long-term conservation of species richness, common species as well as the combined effects of land-use and climate change have to be considered.

**Keywords:** *species richness, hotspots, land-use change, climate change, scenario, GAM*

## Introduction

Human-induced landscape change can enhance local and regional species richness by increasing the disturbance regime to intermediate levels (Pimentel et al. 1992, Jackson and Jackson 2002, Rosenzweig 2003). Worldwide, however, such landscape changes primarily pose a threat to biodiversity (Matson et al. 1997, Tilman et al. 2001).

During recent decades, the composition and structure of the European cultural landscape have changed dramatically due to urbanisation and segregation of land-use intensities (e.g. Leonard and Cobham 1977, Robinson and Sutherland 2002). The segregation of land-use intensity has been especially widespread in mountainous regions, where land use has intensified in the easily accessible valley bottoms, while sites at higher altitudes, which are more difficult to farm, have generally been abandoned (e.g. Bätzing 1996). Most often, such abandoned land will become covered with forest. The intensification of land use in the more easily accessible land is accompanied by the removal of landscape elements such as hedgerows, stone walls and single trees, and, in general, by habitat deterioration. Similar developments have been recorded in various mountainous areas of the world (e.g. Brown 2003).

Habitat changes brought about by the segregation of land-use intensities have an impact on biodiversity and species richness (e.g. Paoletti and Pimentel 1992, McLaughlin and Mineau 1995, Lindblach 1999, Germann and Holland 2001, Dirnböck et al. 2003, Haines-Young et al. 2003, Millán de la Peña et al. 2003, Veken et al. 2004). Natural afforestation on abandoned land may lead to a short-term increase in species richness, but it will cause decreasing numbers of species in the long term, especially of species depending on open-land habitats (Labaune and Magnin 2002, Dullinger et al. 2003, Bolliger et al. 2007). Intensification of agriculture is likely to be followed by a decrease in species richness primarily caused by increasing disturbance, loss of valuable habitats, use of chemicals, and nitrogen enrichment (Aebischer 1991, Sotherton 1998, Chamberlain et al. 2000, Donald et al. 2001, Benton et al. 2002, Veken et al. 2004).

For a sustainable development of cultural landscapes, the conservation and restoration of species richness is a major objective (Rio Convention, European Common Agricultural Policy). The protection of so-called 'diversity hotspots' (sites with relatively high numbers of species of interest) is a straightforward strategy for the conservation of species richness (Prendergast et al. 1993, Armsworth et al. 2004). On a landscape scale, the protection of such hotspots is seen as a basis for designing reserve networks complying with the Convention on Biological Diversity (ISCBD 1994, Bonn et al. 2002, Kati et al. 2004). However, if conservation efforts confine themselves to a few diversity hotspots, e.g., because decision makers see it as a cure for all, the remaining habitats may deteriorate to 'coldspots' due to a liberalization of land use (Jepson and Canney 2001, Kareiva and Marvier 2003).

An alternative conservation strategy to the hotspot approach is the large-scale conversion of farmland into low-input habitats. This is an important instrument in agri-environmental schemes developed in many European countries (Kleijn and Sutherland 2003). Nevertheless, even though biodiversity in general may benefit from this large-scale conservation approach, rare species are not necessarily supported by agri-environmental schemes (Herzog et al. 2005). Consequently,



hotspots that reveal high numbers of rare and endangered species may not be fostered by large-scale conservation programs such as agri-environmental schemes. Hence, for the development of effective conservation strategies, it is crucial to identify parameters that control species richness at the landscape level (Huston 1995). Combining these parameters with scenarios of environmental change makes it possible to compare the outcomes of different conservation strategies.

In this study, we investigated to what degree the objectives of these conservation strategies (large-scale conservation of species richness, conservation of diversity hotspots) are reached in a dynamic cultural landscape. First, we assessed major drivers for species richness under current conditions on the national scale in Switzerland. Then, we investigated how species richness may change on the national and on the local scale (diversity hotspots) under different scenarios of land-use and climate change. Would a liberalization of land use lead to a large-scale 'coldspot'? How would species richness develop under a 'business as usual' scenario? Will the large-scale conversion of farmland into low-input habitats remarkably foster species richness on the large scale and in small-scale hotspots? At least some small-scale hotspots are suggested to be relict habitats that may not benefit from large-scale conservation efforts such as agri-environmental schemes (Steck et al. in press). Therefore, the impact of certain measures on species richness may be markedly different on a national scale compared to local-scale diversity hotspots.

For all analyses, data on grasshopper species richness have been used. Grasshoppers are considered a good indicator for overall species richness in the European cultural landscape (e.g. Sauberer et al. 2004). Because most of the European grasshoppers are thermophilic, we wanted to additionally evaluate the effect of a climate-change scenario (increasing temperature, decreasing precipitation) on grasshopper species richness. Our aim was to assess whether the effects of climate change surpass the effects of the conversion of farmland into low-input habitats.

## **Methods**

### *Study area*

This study was conducted in Switzerland (surface: 4'128'400 ha), a country with a large proportion of mountainous landscapes, where land-use segregation is generally most obvious (e.g., Bätzing 1996, Brown 2003). Six biogeographic regions are observed for Switzerland: the Jura Mountains (10.4% of the surface), the Plateau (27%) and four different alpine regions (62.6% in total; Bundesamt für Statistik 2001).

### *Biotic input data*

Between 2001 and 2004, professional entomologists collected systematically data on grasshopper distribution for a national Red-List project coordinated by the Swiss Centre for Faunal Cartography (CSCF Neuchâtel) based on the following instructions (Gonseth, personal communication). Within selected quadrants of 1 km<sup>2</sup> they visited the sites with the highest habitat quality for grasshoppers. Afterwards, they looked for other species in the remaining area of the quadrant. In this study, only grasshopper data from the most species-rich 1 hectare plots within a 1 km<sup>2</sup> quadrant were

analysed, as these sites have evidently been very thoroughly sampled. A total of 7'457 plots of 1 ha, containing data on altogether 95 grasshopper species, was included in our analysis. Our measure for grasshopper diversity was the number of grasshopper species.

### *Explanatory variables*

To describe each of the 7'457 plots, we included 9 predictive variables that cover climate variables, topographical characteristics, land use, and the biogeographic regions of Switzerland (Table 1). The 6 biogeographic regions are defined based on vegetation and faunistic data (Gonseth et al. 2001). We used maps of mean temperatures in July, as well as of the mean sum of precipitation in July. These are based on spatial interpolations of meteorological data from the national network of recording stations. A detailed description of how these maps were calculated is outlined in Zimmermann and Kienast (1999). Additionally, we used slope and northness (cosine of the aspect in radians) as predictors of grasshopper species richness.

Nation-wide data on land use is available at a 1ha resolution for two time steps (1985 and 1997) (BFS 1979/85, 1992/97). The original 72 land-use categories were aggregated into 6 categories (Table 1; details, see Bolliger et al. 2007). To take into account neighbourhood effects, we calculated the frequency of selected land-use categories within a radius of 500m). The selected land-use categories included open forest, scrub and non-intensive open land because these categories are exceptionally species rich (e.g. Duelli et al. 1999).

*Table 1: Predictive variables used to model grasshopper species richness.*

| <b>Predictive variable</b>       | <b>Specifications</b>  | <b>Data source</b>                                     |
|----------------------------------|--|--|
| Biogeographic region             | 6 regions (1=Jura Mountains, 2 = Plateau, 3= Northern Alps, 4= Western Alps, 5 = Eastern Alps, 6 = Southern Alps)            | Gonseth et al., 2001                                   |
| Temperature                      | mean temperature in July; in °C  | Zimmermann and Kienast (1999)                          |
| Precipitation                    | mean precipitation in July; in mm  | Zimmermann and Kienast (1999)                          |
| Slope                            | in %   | DHM25 © Bundesamt für Landestopographie                |
| Northness                        | cos (aspect in radians)  | DHM25 © Bundesamt für Landestopographie                |
| Land use                         | 6 categories (1 = closed forest, 2 = open forest, 3 = scrub, 4 = non-intensive open land, 5 = intensive farmland, 0 = other) | Bolliger et al. (2007) based on BFS (1979/85, 1992/97) |
| F. open forest                   | frequency (measured as proportion in percent) of open forest in the surrounding area, (r = 500m)                             | Bolliger et al. (2007) based on BFS (1979/85, 1992/97) |
| F. scrub                         | frequency of scrub in the surrounding area (r = 500m)  | Bolliger et al. (2007) based on BFS (1979/85, 1992/97) |
| F. non-intensively used farmland | frequency of non-intensive open land in the surrounding area (r = 500m)  | Bolliger et al. (2007) based on BFS (1979/85, 1992/97) |

### *Model approach*

We modelled grasshopper species richness to assess its major drivers and predicted its spatial distribution to evaluate the potential impact of environmental changes. As most of the species-environment interactions are likely to be non-linear (Gaston and Williams 1996) we chose a nonparametric model that is able to fit any response curve. We used a generalized additive model (GAM; Hastie and Tibshirani 1986) with a poisson distribution as implemented in the GRASP library (available online from <http://www.cscf.ch/grasp>; Lehmann et al. 2002a) of SPlus (Insightful Corp., Seattle, Washington). The default smoother degree of freedom was set to 4; to test for linear relationships the alternative smoother degree of freedom was set to 1. To optimize the model, we applied a stepwise regression (backward and forward selection). We started with a full model and used the Akaike information criterion (AIC) for analysing the significance of eliminating or adding terms.

To test the model's performance, we validated the selected model with a cross-validation procedure that divided the entire data into 5 subsets of equally numbered and randomly selected data points, as implemented in GRASP.

To predict the spatial distribution of species richness all over Switzerland at the ha-scale, the resulting model was exported as a look-up table. The look-up table can be read in ARCVIEW (ESRI, Redland, California) by an Avenue script (available online from <http://www.cscf.ch/grasp>). This script is written to build spatial predictions (in our case of grasshopper species richness for the whole of Switzerland) by reclassifying the maps of the predictive variables selected by the modelling procedure.

### *Applying scenarios of environmental change*

Five different scenarios were applied to evaluate the changes in species richness due to potential future environmental change. Four land-use scenarios were applied: 'liberalization', 'business as usual', 'lowered agricultural production', and 'complete conversion of intensive open land'. Additionally, a climate-change scenario was used to cross-evaluate the effects of land-use and climate change.

### *Land-use change scenarios*

Conceptual and methodological details on the land-use change scenarios "liberalisation", "business-as-usual", and "lowered agricultural production" are described in detail in Bolliger et al. (2007).

The 'liberalization' scenario assumes that the agricultural market of Switzerland is fully liberalized and that agriculture and biodiversity conservation are not subsidized by the government. This scenario is characterized by a segregation of land-use intensity depending on the terrain. Land use is intensified in the easily accessible lowlands (< 900m asl) and valley bottoms. Here, about 80% of non-intensive open land is converted to intensively used land. In contrast, farms at higher altitudes (> 900m asl) are likely to be abandoned under this scenario. Consequently, 90% of non-intensive and of intensive open land, respectively, is converted to scrub or forest.

The 'business as usual' extrapolates trends observed in land-use change during 15 years (1985-1997) into the future (Bolliger et al. 2007). This scenario was applied to investigate how species richness may develop if the structural changes in agriculture and subsidies for biodiversity conservation continue into the future. This means that the political environment under this scenario remains similar to that of today (Bolliger et al. 2007). Out of each land-use category, 90% or more of the pixels do not change. The scenario 'lowered agricultural production' (Bolliger et al. 2007) assumes a landscape-development strategy where management for conservation purposes is the major goal. Nature conservation is highly subsidized, while food production is subject to market forces. In this scenario non-intensive land use is strongly supported: 80% of the pixels representing intensive open land are transformed to either non-intensively used farmland, to scrub, or to forest (Bolliger et al. 2007). Thus, this scenario is comparable with a widespread and far-reaching agri-environmental scheme.

To explore extremes of land-use scenarios, we developed a scenario called 'complete conversion of intensive open land'. In this scenario, all pixels of the land-use category 'intensive farmland' were converted into 'non-intensive open land'. As the majority of the Swiss grasshopper species prefer open land and depend mostly on non-intensively managed grassland habitats, this scenario should result in the strongest possible promotion of grasshopper species richness within our model.

#### *Climate-change scenario*

Our climate-change scenario is based on a conservative assumption of an increase in the mean temperatures in July of 1<sup>0</sup> C and a decrease in the mean precipitation in July of 15% (Christensen and Christensen 2003, Beniston 2004, OcCC 2007). As this scenario was applied to cross-evaluate the effects of land-use and climate change, it was based on current land-use data.

#### *Implementation of scenarios*

The scenarios were implemented by re-sampling the land-use variables (land-use scenarios) and the climate variables (climate scenario) for all 7'457 plots with grasshopper surveys in the potential future landscapes. Then we built new spatial predictions of grasshopper species richness for each scenario based on each new sample using the formula of the selected model.

#### *Assessing the impact of the scenarios on species richness*

We analyzed the changes in grasshopper species richness by comparing the result of the present-state model with the resulting richness patterns under the five scenarios. This was done on two different scales: (a) for all 1ha pixels of Switzerland, and (b) for hotspots of grasshopper species richness.

We compared the mean number of grasshopper species between the present-state model and each scenario for the whole of Switzerland. Additionally, we assessed the shifts in species richness resulting from the scenarios.

For hotspots of grasshopper species richness, the effects of the scenarios were measured by assessing the shifts in species richness. As relevant hotspots we chose 1ha plots that had been identified as 'richness hotspots', as 'rarity hotspots', or as 'hotspots of common species' by Steck et al. (in press). 'Richness hotspots' encompass 50 1ha plots that feature most grasshopper species (17 to 29 grasshopper species). 'Hotspots of common species' are defined as the 50 1ha plots with the highest numbers of common species (not endangered; 11 to 15 grasshopper species). 'Rarity hotspots' (n=50) contain the highest numbers of endangered grasshopper species (9 to 18 grasshopper species; Thorens and Nadig 1994). To test for significant differences in the changes in species richness between the three hotspot types under the different scenarios, we performed a linear mixed-effect model (Pinheiro and Bates 2000) in SPlus (v.6.1). Hotspot type, scenario and their interaction were fixed effects. The identity/number of the hotspot was the random effect of the scenarios.

## Results

### *Model of the spatial distribution of grasshopper species richness in Switzerland*

The major drivers of grasshopper species richness in Switzerland were identified by modelling the spatial distribution of Swiss grasshopper species richness. The selected model explained more than one third of the total deviance ( $D^2 = 0.383$ ;  $Cor = 0.611$ ; cross validation:  $cvCor = 0.591$ ) in the spatial distribution of grasshopper species richness. All input variables were kept in the final model except the frequency of scrub in the surroundings (f.scrub). The main factor explaining the spatial distribution of grasshopper species richness in Switzerland was temperature, followed by biogeographic region (Figure 1). Precipitation, topography (slope and northness), as well as the land-use variables, explained a relatively small proportion of the spatial variation of grasshopper species richness (Figure 1).

The shapes of the response curves of the individual variables in the model show distinct differences. The relationship between temperature and species richness is not linear, but they correlate positively up to 15°C, levelling off at higher temperatures (Figure 2). The response of species richness to open forest in the surroundings is obvious only in the range of low values, where richness is positively correlated with the frequency of these land-use types in the surroundings. The relationship between grasshopper species richness and the frequency of non-intensive open land in the surroundings is mostly positively correlated. The land-use category 'closed forest' (Figure 2) of the plots themselves has a negative influence on species richness, whereas the more open land-use types scrub and non-intensive open land positively influence grasshopper species richness (Figure 2).

### *Large-scale richness change under different scenarios*

The predicted mean grasshopper species richness in Switzerland was 6.15 species (ranging from 0 to 15 species). It decreased under the scenarios 'liberalization' (-0.24 species per 1ha pixel) and 'business as usual' (-0.04). It increased under the scenarios 'lowered agricultural production'

(+0.19), 'complete conversion of intensive open land' (+0.25) and under the climate-change scenario (+0.63).

The scenarios revealed different magnitudes of change in species richness on the national scale. The shifts in predicted species richness in the individual 1 ha pixels across Switzerland ranged from -4.1 species to +3.3 species (Table 2). Under all scenarios except the climate-change scenario, most pixels revealed changes between -0.5 and +0.5 in predicted species richness per pixel. The scenarios 'liberalization', 'business as usual' and 'lowered agricultural production' led to decreases as well as to increases in species richness. The response of species richness under the scenario 'complete conversion of intensive open land' and under the climate-change scenario was restricted to positive values and to pixels with no response (Table 2).

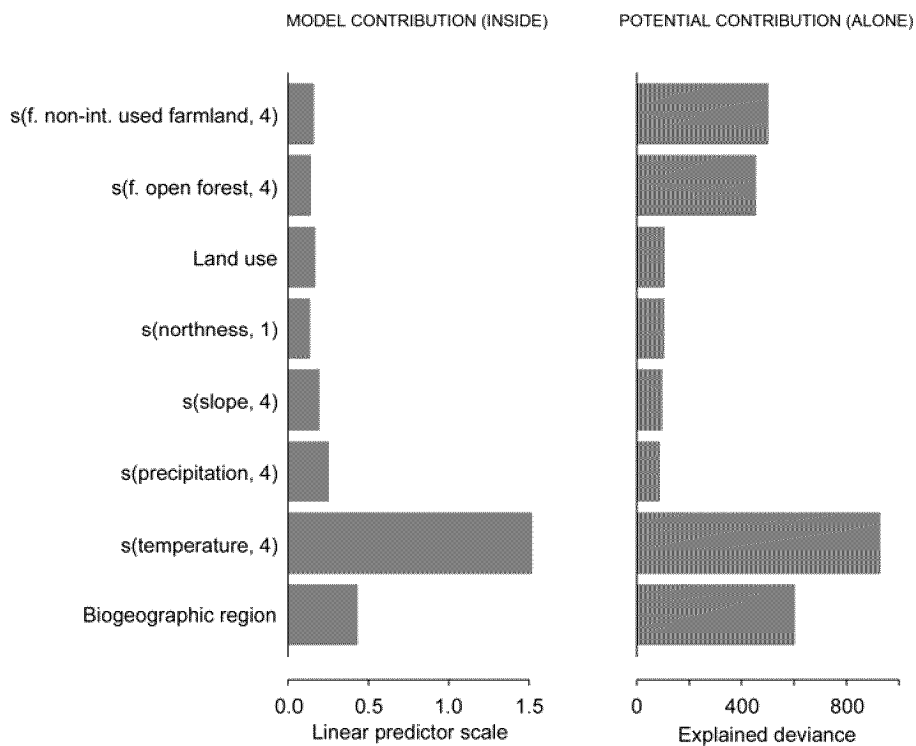


Figure 1: Contributions of environmental variables to the model of grasshopper species richness. Temperature is the most important variable for the spatial distribution of grasshopper species richness in Switzerland. Tested alone, the contribution of the biogeographic region, of the frequency of non-intensively used farmland and of open forest is relatively high. Inside the model, the importance of these variables is less because of correlation with temperature.

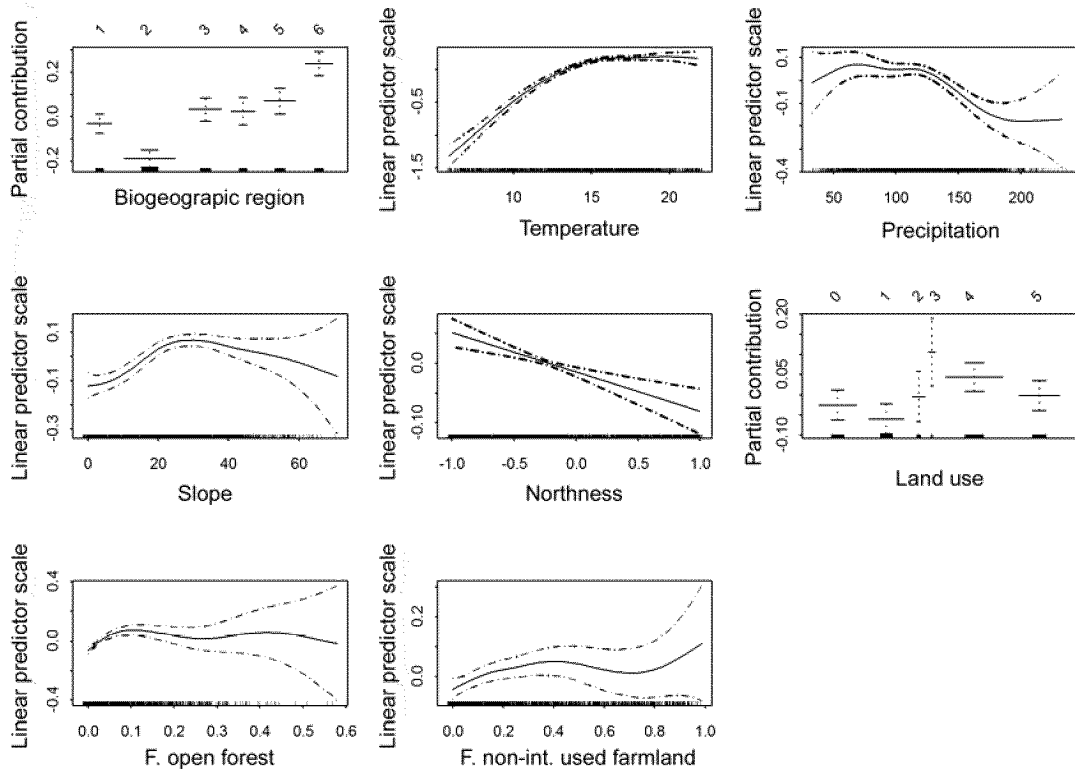


Figure 2: Response curves of the grasshopper species richness model to the environmental variables (for explanation of the variables: see Table 1).

Table 2: Number of 1ha pixels with specific shifts in species richness under different environmental scenarios.

| Scenario                        | Changes in species richness |              |              |              |             |            |            |            |
|---------------------------------|-----------------------------|--------------|--------------|--------------|-------------|------------|------------|------------|
|                                 | -4.5 to -3.5                | -3.5 to -2.5 | -2.5 to -1.5 | -1.5 to -0.5 | -0.5 to 0.5 | 0.5 to 1.5 | 1.5 to 2.5 | 2.5 to 3.5 |
| Liberalization                  | 195                         | 14'565       | 148'027      | 666'731      | 3'154'621   | 136'009    | 4'000      | 15         |
| Business as usual               |                             | 17           | 2'527        | 88'101       | 3'994'562   | 38'283     | 667        | 6          |
| Lowered agricultural production |                             | 63           | 7'587        | 109'006      | 3'103'351   | 845'993    | 57'846     | 317        |
| Complete conversion             |                             |              |              |              | 3'157'682   | 957'582    | 8'899      |            |
| Climate change                  |                             |              |              |              | 1'810'601   | 2'159'322  | 154'240    |            |

### *Changes in species richness in small-scale hotspots*

The number of species in the three hotspot types ('richness hotspots', 'hotspots of common species', 'rarity hotspots') decreased on average under all land-use scenarios except under the scenario 'complete conversion of intensive open land' (Figure 3). Increases are recorded only for hotspots of common species under the scenario 'lowered agricultural production', as well as for all three types of hotspots under the scenario 'complete conversion of intensive open land' and under the climate-change scenario (Figure 3).

Compared to the mean changes in species richness all over Switzerland, species richness in hotspots was more negatively affected under most scenarios (Table 3). In two scenarios which resulted in an overall increase in species richness in Switzerland ('lowered agricultural production', 'climate change'), the numbers for the hotspots also did not increase correspondingly. Only in the case of the scenario 'complete conversion of intensive open land', species richness reacted more positively in small-scale hotspots than in Switzerland as a whole (Figure 3).

The scenarios differed significantly in the response of species richness in all hotspots (factor 'scenario';  $F = 32.60$ ,  $p < 0.0001$ ). The three hotspot types ('richness hotspots', 'rarity hotspots', 'hotspots of common species') did not differ significantly in the mean response of species richness depending on the individual scenarios (interaction of 'scenario' and 'hotspot type';  $F = 1.43$ ,  $p = 0.18$ ). This means that, for each scenario, the response of species richness in the different hotspot types did not differ significantly

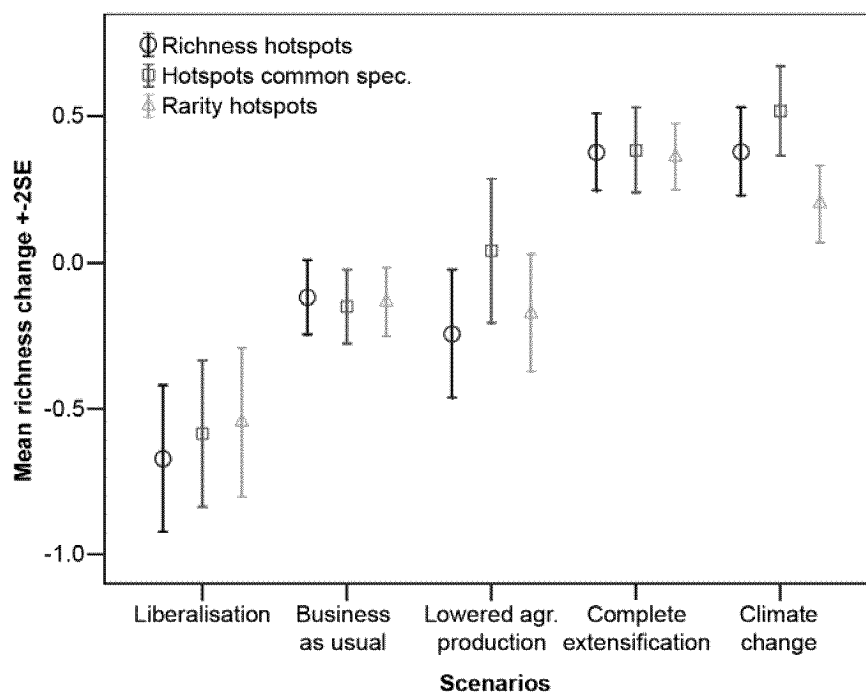


Figure 3: Shifts of species richness in hotspots of common species ( $n=50$ ), rarity hotspots ( $n=50$ ) and in richness hotspots ( $n=50$ ) due to different scenarios of land-use and climate change.



*Table 3: Success of different conservation strategies under different scenarios of future environmental change. ('---' = -0.70 to -0.50 species per plot; '- -' = -0.49 to -0.30; '- ' = -0.29 to -0.10; 'o' = -0.09 to +0.10; '+' = +0.11 to +0.30; '++' = +0.31 to +0.50; '+++' = +0.51 to +0.70)*

| Scenario                           | Large-scale conversion<br>(n=4'128'400<br>1ha plots) | Hotspot-strategy            |   |                           |
|------------------------------------|--|-----------------------------|---|---------------------------|
|                                    |  | Richness hotspots<br>(n=50) | Hotspots of<br>common species<br>(n=50) | Rarity hotspots<br>(n=50) |
| Liberalisation                     | -  | ---                         | ---                                     | ---                       |
| Business as usual                  | o  | -                           | -                                       | -                         |
| Lowered<br>agricultural<br>support | +  | -                           | o                                       | -                         |
| Complete<br>conversion             | +  | ++                          | ++                                      | ++                        |
| Climate change                     | +++  | ++                          | +++                                     | +                         |

## Discussion

### *Methodological considerations*

We modelled and predicted species richness based on land-use, topographical and climatic variables. There are a few limitations to be considered with this widely used approach (Guisan and Zimmermann 2000, Segurado and Araujo 2004, Guisan and Thuiller 2005). For modelling the spatial distribution of grasshoppers, dispersal ability and dispersal limitations are likely to be the most important variables to be combined with niche-related variables. However, these parameters are known only for a few grasshopper species of our study (e.g. Zöller 1995, Schuhmacher and Fartmann 2003); for most of the Swiss grasshopper species these parameters are unknown. Therefore, dispersal-related variables could not be applied in our study.

As species are likely to respond individually to changing environmental conditions, modelling individual species, based on a binary model for each species, may be more appropriate than modelling whole communities (Huntley 1991, Lischke et al. 1998). To predict future distribution, both approaches exhibit similar drawbacks, but several authors have shown that the drawbacks of modelling individual species are less severe (Zimmermann and Kienast 1999, Guisan and Theurillat 2000). Lehmann et al. (2002b), however, showed that both approaches are likely to result in a similar spatial distribution of species richness. For the present study, we also had to take into account that, for a relatively large number of grasshopper species, only limited data are available. When modelling individual species, the minimum number of observations should be at least 10 times the number of predictive variables. Here, this would have resulted in the exclusion of 36 species from the analysis. We therefore decided to model grasshopper species richness on the basis of the whole community rather than the individual species distributions.

*Major drivers of grasshopper species richness*

Climate is the most important factor for the large-scale distribution of grasshopper species richness in Switzerland. This is to be expected as most of the grasshopper species in Switzerland are thermophilic (Thorens and Nadig 1997, Detzel 1998, Schlumprecht and Waeber 2003, Baur et al. 2006). The thermophilic character of the grasshopper community is also reflected in their preference for habitats with a southern aspect (variable 'northness', see Table 1) and with low levels of rainfall (Figure 2).

Additionally, the number of grasshopper species is positively correlated with cultivated land and with the frequency of open land in the surroundings. This coincides with the dependence of most grasshopper species of Central Europe on managed habitats (e.g. meadows). Only a few species live in closed forests (Thorens and Nadig 1997, Detzel 1998, Schlumprecht and Waeber 2003, Baur et al. 2006). The preference for habitats of intermediate slopes may be caused by a lower intensity of land management compared to sites on the plains. However, our model may be improved by adding explanatory variables that yield more information about landscape structure (e.g. With and Crist 1995), habitat quality (e.g. Holland and Fahrig 2000), habitat history (e.g. Hersperger and Forman 2003), as well as about competition, dispersal limitations and population dynamics (Guisan and Thuiller 2005).

*Potential future changes in species richness on the large scale*

Under a laissez-faire policy, which is mimicked by the 'liberalization' scenario, the mean number of grasshopper species per ha decreases considerably. In more than 800'000 ha the number of grasshopper species may decrease in the future because of an increased vulnerability of these sites (that is, on average, -0.24 species per 1ha pixel). This potential future type of land-use change corresponds generally with the land-use changes observed in mountainous landscapes in the decades after WW II (e.g. Leonard and Cobham 1977, Ewald 1978, Bätzing 1996, Robinson and Sutherland 2002, Brown 2003). Hence, species richness is likely to deteriorate if nature conservation concentrates only on a few sites (e.g. small-scale diversity hotspots), which are not relevant on a large scale, or if it is not considered at all in national policy. Only very few habitats might benefit in the short term from this type of land-use change, e.g., if a farm in the alpine region is abandoned and some previously intensively used land will undergo succession and become covered with forest.

The 'business as usual' scenario proposes land-use changes that are similar to those observed in the time period between 1985 and 1997. In our study, these changes led to a relatively slight decrease in the mean number of grasshopper species per hectare. This effect may be realistic as there is no evidence of a decline in grasshopper species richness between 1992 and 2004 (Gonseth, unpublished data). In contrast, grasshopper species richness has benefited from recent conservation programs, namely agri-environmental schemes (Herzog et al. 2005). But these agri-environmental schemes are hardly considered by our 'business as usual' scenario because this scheme has only been applied since the early 1990s (Herzog and Walter 2005). Consequently,

species richness would probably decrease if agri-environmental schemes were not applied. In the long term, this could mean that important species or habitats would be lost.

Kareiva and Marvier (2003) suggest that focussing world-wide nature conservation on a few diversity hotspots might lead to a deterioration of the remaining habitats. On the large scale, however, we conclude that restricting conservation efforts to a few diversity hotspots would not per se degrade all remaining habitats to coldspots because the application of the two scenarios 'liberalization' and 'business as usual' did not lead to a large-scale coldspot. But, these approaches would lead to a drastic long-term decrease in species richness in specific areas. And this could also affect species richness in the small-scale hotspots themselves if the immigration rates of the species concerned were affected by land-use changes in the surrounding areas.

The scenario 'lowered agricultural production' suggests a landscape-development strategy where management for conservation purposes is the major aim. For Swiss grasshoppers, the scenario 'lowered agricultural production' is a strategy that, in general, positively influences species richness. However, in a relatively high proportion of pixels, this type of landscape development could also have negative impact on grasshopper species richness. This effect of the scenario 'lowered agricultural production' is probably due to the increase in open forest, which is likely to foster specialized species but not per se overall grasshopper species richness (Thorens and Nadig 1997, Baur et al. 2006). Under this scenario, the number of species decreases by up to 3 species per ha. Obviously, some habitats may deteriorate under a conservation programme that is thought to maintain and develop species richness (at least as far as grasshoppers are concerned). Therefore, it is essential to have reliable information on the most suitable sites for creating low-input habitats. The selection of habitats for restoration could be optimized by having experts assess habitats or by applying taxon-specific habitat-suitability models (e.g. Maes et al. 2003).

The scenario 'complete conversion of intensive open land' seems the best scenario for enhancing grasshopper species richness in our study. This scenario led to increased species richness for more than 1 million hectares. As most Swiss grasshopper species are open-land species (Thorens and Nadig 1997, Baur et al. 2006),  $\alpha$ -diversity of this indicator group can be enhanced mostly by conversion of land use into low-input habitats. However, open forest and hedgerows are important habitats for other species (e.g. Burel et al. 2004). Therefore, species and communities preferring different habitat types should be considered when developing conservation strategies on a landscape level.

#### *Changing species richness in small-scale hotspots*

In Switzerland, the recently applied agri-environmental scheme enhances species richness by converting farmland into low-input habitats (Herzog et al. 2005, Knop et al. 2006). But rare species are not specifically fostered by this conservation approach (Herzog et al. 2005). Therefore, we investigated the effects of our scenarios on species richness in different types of small-scale hotspots: 'richness hotspots', 'hotspots of common species' and 'rarity hotspots'.

In all hotspot types, the mean number of grasshopper species declined under all land-use scenarios except under the scenario 'complete conversion of intensive open land' and except in

hotspots of common species under the scenario 'lowered agricultural production'. Furthermore, all hotspot types were, on average, more negatively affected by the applied scenarios than an average pixel in Switzerland, except under the scenario 'complete conversion of intensive open land'. That means that the hotspots of grasshopper species richness are in fact special habitats that react differently to large-scale land-use changes than does an average site in Switzerland. This difference might be an effect of the relictic character (habitats that are relics of traditional land-use practices) of at least some of the hotspots (Steck et al. in press).

Species richness in small-scale hotspots is, as in hotspots at the national scale, likely to be threatened by human-induced land-use change (e.g. Witt and Samways 2004, Sodhi et al. 2004). In Switzerland, these small-scale hotspots feature a relatively high amount of the overall grasshopper species richness (Steck et al. in press). Conservation strategies should not restrict all efforts to enhance overall biodiversity, but should pay additional attention to these vulnerable and valuable sites.

Interestingly, the response of species richness in the 'rarity hotspots' did not significantly differ from the response of species richness in the 'hotspots of common species'. Consequently, we cannot completely rule out rarity hotspots being more vulnerable to landscape change than the 'hotspots of common species'. Conservation strategies should not just focus on endangered species alone or on rarity hotspots, but should also consider the more common species as their vulnerability to environmental change might be underestimated (e.g. Leon-Cortes et al. 1999, Cowley et al. 1999).

#### *Impact of climate change on hotspots and remaining habitats*

In our study, the positive effects of climate change exceed the effects of all land-use scenarios except 'complete conversion of intensive open land', as temperature is the outstanding major driver of grasshopper species richness in Switzerland. This high relevance of climate for grasshoppers does not come as a surprise, as most of the Central European grasshopper species are thermophilic (Thorens and Nadig 1997, Detzel 1998, Schlumprecht and Waeber 2003, Baur et al. 2006). The relative contribution of land-use variables could, however, turn out to be greater if better data on habitat structure were available.

Generally, climate change resulting in increasing temperatures and decreasing precipitation favours thermophilic grasshopper species and may also foster species richness in alpine forests (e.g. Dorda 1998, Kienast et al. 1998). But at least in the case of grasshoppers, this general trend could be overdriven by two aspects, i.e., the lack of suitable habitats and secondary effects of climate change. Species may not expand their range size if habitat availability is insufficient. Consequently, species richness will only profit from global warming, if the spatial distribution of these species is mainly limited by climate and not by habitat availability. Therefore, future investigations should focus on the interaction between land-use change and climate change. This was beyond the scope of this study because such investigations require fine-scaled data on habitat quality, which are currently not available for whole Switzerland.

Secondary effects of climate change can diminish insect populations severely. For instance an increase in the frequency of 'weather catastrophes' can cause the extinction of populations (e.g.,

Kindvall 1995). Another limitation of this study is the coarse spatial scale of the climate scenario applied. It is likely that the effects of climate change differ along altitudes (Beniston and Rebetez 1996, Beniston et al. 1997). Therefore, careful interpretation of these results is necessary.

### *Conclusions*

In this study, grasshopper species richness reacted considerably to changes in land-use strategies. Therefore, current and future agricultural policies will have considerable influence on grasshopper diversity. The large-scale conversion of farmland into non-intensively used habitats is likely to be effective in enhancing the species richness of grasshoppers and therefore successfully fits the objectives of a large-scale conservation strategy. However, even if low-input habitats are promoted on large-scale, small-scale hotspots of Swiss grasshopper species may deteriorate in the future. Consequently, combining and coordinating conservation efforts on a large scale and hotspot-specific conservation programs is likely to be the most successful approach in conserving species richness, as stated by Sutherland (2002). But conservation programs should not concentrate on rare species or on rarity hotspots since currently common species are also likely to be negatively affected by future land-use change. With all measures taken to protect biodiversity in the long run, the potential impacts of climate change have to be considered as well.

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## 5. TIME-LAGGED RESPONSE OF GRASSHOPPER SPECIES RICHNESS TO LANDSCAPE CHANGE

Steck, C.E., M. Bürgi, and T. Coch

### **Abstract**

Habitat loss, habitat deterioration, and habitat fragmentation are the main factors for species extinctions in cultural landscapes. Extinctions often follow landscape change with a time lag if species are able to maintain populations over periods of declining suitability of environmental conditions. In this study, we investigated the key factors for species richness of selected grasshopper species in north-western Switzerland. We compare the influence of habitat availability on multiple scales, as well as its historic dimension (time span of 20 years), with other site specific factors (e.g., local climate, topography). “Historic” habitat availability was found to explain more of the current richness pattern than more recent and more detailed habitat data. We identified three key factors for species richness of xerophilic grasshoppers: historic habitat availability on the site level, current habitat availability including a 100m buffer around the study sites, and precipitation. Our results show that even short-lived species like grasshoppers may respond with a time-lag to landscape change. However, landscape change does not necessarily lead to an extinction debt. In our study, the time-delayed response to landscape change can be connected with an “immigration debt” because habitat availability in our study sites has mostly increased over the last 20 years. We conclude that increasing the connectivity of habitats should be a primary goal in conservation practice, first to maintain species richness in sites with an extinction debt, but also to foster immigration to sites that have not yet reached equilibrium due to time-delayed immigration. Because all taxonomic groups may show a time-delayed response to environmental change we suggest discussing critically the use of species richness as an indicator for environmental change and to predict species richness across taxonomic groups.

**Keywords:** *extinction debt, immigration debt, habitat availability, connectivity, GAM*

## Introduction

During recent decades, the cultural landscapes of many countries have changed markedly. High levels of urbanisation and the spatial segregation of land-use intensity are the main developments to be observed (e.g., Leonard and Cobham 1977, Robinson and Sutherland 2002). Both developments have caused dramatic changes in habitat availability and habitat quality (e.g., Paoletti and Pimentel 1992, Lindblach 1999, Germann and Holland 2001, Dullinger et al. 2003, Haines-Young et al. 2003, Millán de la Peña et al. 2003, Veken et al. 2004). Today, habitat loss, habitat deterioration, and habitat fragmentation are the main factors behind species extinctions (e.g., Delis et al. 1996, Desender and Turin 1989, Köhler et al. 2003). Consequently, the conservation and the restoration of species-rich habitats play key roles in the sustainable development of cultural landscapes (Rio Convention, European Common Agricultural Policy).

One prerequisite for preserving species richness in the cultural landscape is the preservation of non-intensively used grasslands that feature exceptionally high numbers of species (Báldi and Vörös 2006). However, these habitats are threatened both by the intensification of land use in some areas and by land-use abandonment in other areas (Kleijn and Báldi 2005, Öckinger and Smith 2006). One possible strategy to prevent the loss of species is to create reserves and reserve networks. A promising alternative to creating reserves are agri-environmental schemes similar to those already implemented in many European countries (Kleijn and Sutherland 2003, Donald and Evans 2006).

In conservation planning, the number of species or the species pool of a specific site is what is mainly considered. Two well-known ecological processes are, however, generally not incorporated into conservation planning, one is the response of local populations to habitat connectivity and the other the time-delayed response of species to landscape change. Habitat connectivity is a function of habitat availability in the surrounding area and of the spatial configuration of these habitats (Hanski 1999). Low levels of habitat availability in the surroundings and many dispersal barriers are restricting immigration and therefore promote species extinctions (e.g., Pellet et al. 2004).

Habitat connectivity, especially in dynamic cultural landscapes, is not static. Focal habitats deteriorate and adjacent habitats may be completely lost over time. Species do often not respond immediately to changes in habitat quality and connectivity; several studies have shown that species exhibit a time-lagged response to landscape change (e.g., Lindborg and Eriksson 2004, Lunt and Spooner 2005, Helm et al. 2006). It may take centuries until a new equilibrium in species richness is reached (e.g., Brooks et al. 1999, Vellend et al. 2006).

Because of the extinction debt (Tilman et al. 1994), creating reserves and reserve networks will not be per se successful to conserve species richness (Hanski and Ovaskainen 2002, Lindborg and Eriksson 2004, Berglund and Jonsson 2005). Hence, for nature conservation, it is crucial to identify the key parameters that control species richness at the landscape level (Huston 1995), including the impacts of landscape change.

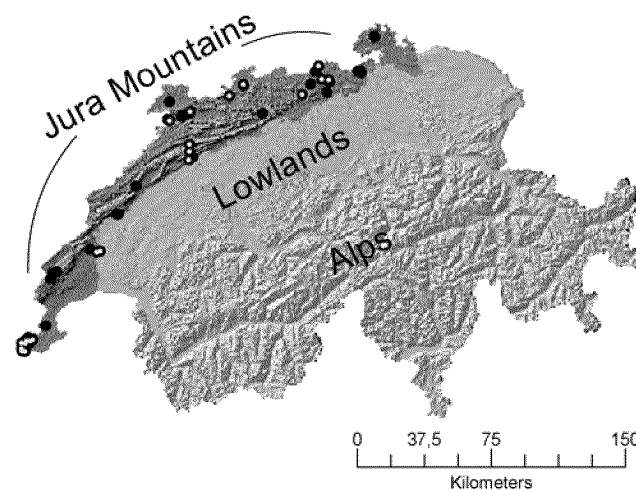
Time-lagged response to landscape change might not be so important for short-lived and relatively mobile species like insects and birds (as suggested by Lindborg and Eriksson 2004). To explore this question in this study, we investigated the key factors for species richness of selected

grasshopper species in Switzerland. We evaluated to what extent habitat area and the availability of habitats in the surroundings, as well as the historic dimensions of these factors, contribute to the current pattern of species richness in comparison to other site-specific variables (e.g., local climate). The primary goal of our study was to improve the empirical background for the conservation of grassland-related biodiversity in the European cultural landscape.

## Methods

### *Study area*

The study area covered the region between Geneva in the west of Switzerland and the Randen region in the north-eastern part of the country (Figure 1). The area stretches along the Jura Mountains (limestone) with an altitudinal range from 250 to 1'680 meters above sea level.



*Figure 1: The study area is situated in the north-western part of Switzerland, ranging along the Jura Mountains. All the plots studied are indicated by black dots. Black dots with grey centres represent the subset analysed with the multi-scale approach.*

### *Selected grasshopper species*

To identify the key factors for grasshopper species richness, we selected 18 species that have comparable habitat requirements (Table 1). In Central Europe, all selected species are xerophilic and prefer habitats that are dry, xerotherm and exhibit relatively low vegetation cover (e.g., gravel, steppe, very dry grassland; Thorens and Nadig 1997, Detzel 1998, Schlumprecht and Waerber 2003, Baur and Roesti 2006). These habitats are relatively rare in Switzerland and most of the selected species are threatened (Thorens and Nadig 1994; Table 1).

### Grasshopper surveys

Data-bases for our study were grasshopper surveys conducted between 2000 and 2004 by the Swiss Biological Records Centre (CSCF Neuchâtel) for the Red List Project with a spatial resolution of 1ha (100m x 100 m). In the surveys for the Red-List Project, professional entomologists sampled grasshopper species in selected quadrants of 1 km<sup>2</sup> all over Switzerland. Within these quadrants, they visited sites with highest quality as grasshopper habitats, where they recorded all the grasshopper species observed. Afterwards, they searched for additional species in the remaining area of the quadrant (Gonseth, personal communication). This approach ensured that at least the sites with the highest numbers of recorded grasshopper species within a 1km<sup>2</sup> quadrant were accurately sampled.

Table 1: Xerophilic grasshopper species selected to analyse the spatial distribution of species richness in north-western Switzerland. (Red-List categories: 1 = critically endangered; 2 = endangered; 3 = vulnerable; Thorens and Nadig 1994)

| Species                             | Preferred habitat type           | Red-List category |
|-------------------------------------|----------------------------------|-------------------|
| <i>Metriopectera bicolor</i>        | Dry grassland                    | 3                 |
| <i>Platycleis albopunctata</i>      | Dry grassland                    | 3                 |
| <i>Tetrix bipunctata bipunctata</i> | Gravel with low vegetation cover | -                 |
| <i>Tetrix bipunctata kraussi</i>    | Gravel with low vegetation cover | 3                 |
| <i>Calliptamus barbarus</i>         | Dry grassland                    | -                 |
| <i>Calliptamus italicus</i>         | Dry grassland                    | 3                 |
| <i>Aiolopus thalassinus</i>         | Gravel with low vegetation cover | 2                 |
| <i>Chorthippus brunneus</i>         | Gravel with low vegetation cover | -                 |
| <i>Chorthippus mollis</i>           | Dry grassland                    | 3                 |
| <i>Euchorthippus declivus</i>       | Dry grassland                    | 1                 |
| <i>Myrmeleotettix maculatus</i>     | Gravel with low vegetation cover | 2                 |
| <i>Oedipoda caerulea</i>            | Dry grassland                    | 3                 |
| <i>Oedipoda germanica</i>           | Gravel with low vegetation cover | 3                 |
| <i>Omocestus haemorrhoidalis</i>    | Dry grassland                    | 3                 |
| <i>Omocestus rufipes</i>            | Dry grassland                    | 3                 |
| <i>Psophus stridulus</i>            | Dry grassland                    | 3                 |
| <i>Sphingonotus caeruleus</i>       | Gravel with low vegetation cover | 1                 |
| <i>Mantis religiosa</i>             | Dry grassland                    | -                 |

### Plot selection for the analyses on the one-hectare scale

We analysed the key factors for the species richness of xerophilic grasshopper species on multiple spatial scales. First, we evaluated the influence of different variables at a resolution of 1 hectare (100m x 100m). For this hectare-level analysis, all plots featuring 6 to 8 xerophilic species were selected because these plots represented “hotspots” of xerophilic grasshopper species richness.

However, we excluded 2 plots that were less than 200m apart from another plot to reduce autocorrelation. Consequently, we analysed 7 plots with 6 to 8 xerophilic species each (Figure 2a). From the plots with 3 to 5 species, we selected those that were most species rich (all grasshopper species) in the related quadrant of 1km<sup>2</sup> (Figure 2a). Here, as well, plots that were less than 200m apart from another were excluded from the analyses. To minimise potential undersampling, we did not analyse plots for which less than three xerophilic species were recorded (Figure 2a). Altogether, we analysed 59 plots with 3 to 8 species on the hectare level.

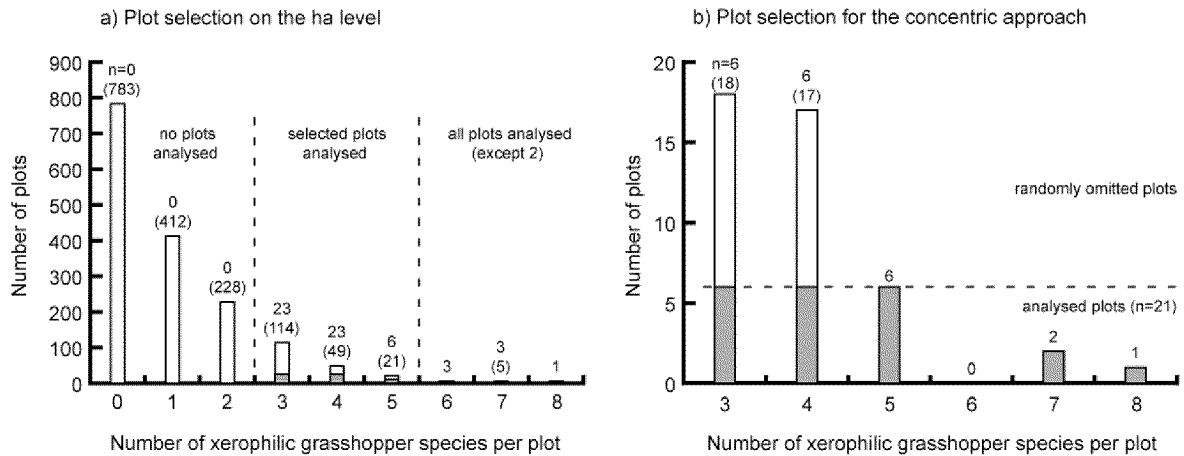


Figure 2: a) Frequency distribution of 1-ha plots with different numbers of xerophilic species in the study area (in brackets: total number of studied plots;  $n=1'616$ ). Due to the sampling strategy of the grasshopper surveys, we selected plots in order to get the most accurate data-bases for our analysis (see text for further explanations;  $n=59$ ).

b) For the multi-scale approach, we took only those plots into account, of which the 500m buffers did not overlap. From these 44 plots we excluded 23 plots to get a more even frequency distribution ( $n=21$ ).

#### Plot selection for the multi-scale approach

In a second step, we analysed the influence of habitat variables on xerophilic grasshopper species richness with a multi-scale approach. Here, we additionally measured variables in the surroundings of the study plots. We applied buffers with radii of 100 m, 200m, 300m, 400m, and 500m around the edge of the 1 ha plots. For this approach, the sample size was reduced because several 500m buffers around the previously selected 59 ha plots overlapped. If any of the 500m buffers around the study plots overlapped, we excluded the study plot(s) with the lower number(s) of xerophilic grasshopper species. Following this procedure reduced the number of plots to 44. To get a more even frequency distribution of the numbers of species, we randomly excluded 23 plots (12 plots with 3 species, 11 plots with 4 species) from the analyses (Figure 2b). We finally analysed 21 plots with the multi-scale approach.

#### Predictive variables

To evaluate the key factors for xerophilic grasshopper species richness, we chose the predictive variables summarised in Table 2. The geographic coordinates of the study plots were included to

test for spatial autocorrelation effects. To account for the preference of the selected grasshopper species for exceptionally warm and dry habitats we chose the environmental factors temperature, precipitation and northness (cosine of the aspect in radians) of each 1 ha plot as predictive variables. The variable slope indicates the management suitability of the site and therefore how suitable the land is for agricultural use. Land use on steep sites is more difficult and, therefore, generally less intensive. These variables were primarily chosen to compare their effects with the effects of habitat availability on xerophilic grasshopper species richness.

Table 2: Predictive variables used to model xerophilic grasshopper species richness.

| Predictive variables                   | Specifications  | Data source  |
|--|---|--|
| X                                      | X coordinates of the ha plots   | Coordinate system: CH1903_LV03   |
| Y                                      | Y coordinates of the ha plots   | Coordinate system: CH1903_LV03   |
| Temperature                            | mean temperature in July; in °C   | Zimmermann and Kienast (1999);<br>spatial resolution: 25m x 25m              |
| Precipitation                          | mean precipitation in July; in mm   | Zimmermann and Kienast (1999) ;<br>spatial resolution: 25m x 25m             |
| Northness                              | cosine (aspect in radians)  | DHM25 © Bundesamt für<br>Landestopographie; spatial resolution:<br>25m x 25m |
| Slope                                  | in %  | DHM25 © Bundesamt für<br>Landestopographie; spatial resolution:<br>25m x 25m |
| <b>Current habitat availability</b>    |   | <b>Orthophotos from 1998</b>   |
| Steppe1                                | number of points in dry grassland, disturbance level = 1                              |  |
| Steppe2                                | number of points in dry grassland, disturbance level = 2                              |  |
| Steppe3                                | number of points in dry grassland, disturbance level = 3                              |  |
| Steppe123                              | number of points in dry grassland, disturbance level = 1 or 2 or 3                    |  |
| Mixed1                                 | number of points in highly structured dry grassland, disturbance level = 1            |  |
| Mixed2                                 | number of points in highly structured dry grassland, disturbance level = 2            |  |
| Mixed3                                 | number of points in highly structured dry grassland, disturbance level = 3            |  |
| Mixed123                               | number of points in highly structured dry grassland, disturbance level = 1 or 2 or 3  |  |
| Bare ground1                           | number of points on bare ground, disturbance level = 1                                |  |
| Bare ground2                           | number of points on bare ground, disturbance level = 2                                |  |
| Bare ground3                           | number of points on bare ground, disturbance level = 3                                |  |
| Bare ground123                         | number of points on bare ground, disturbance level = 1 or 2 or 3                      |  |
| Smb1                                   | Sum of the number of points in all habitat types with disturbance level = 1           |  |
| Smb12                                  | Sum of the number of points in all habitat types with disturbance level = 1 or 2      |  |
| Smb123                                 | Sum of the number of points in all habitat types with disturbance level = 1 or 2 or 3 |  |
| <b>“Historic” habitat availability</b> |   | <b>Orthophotos from 1979-1981</b>  |
| Smb12_1980                             | Sum of the number of points in all habitat types with disturbance level = 1 or 2      |  |

To measure habitat availability, we divided up the studied areas using a grid with a cell size of 5x5 meters. Then we determined the habitat type in the centre of every grid cell by interpreting aerial photographs from 1998, which were the latest available aerial photographs (true colours; spatial resolution = 50 cm x 50 cm; average scale = 1:30'000). We mapped three different types of habitats: steppe-like grassland ("steppe"; e.g. dry meadows), bare ground (e.g. floodplains), and a mixture of these two types ("mixed"; e.g. highly structured dry grassland with a high proportion of bare ground). For each habitat type, the anthropogenic disturbance intensity was classified into three levels: low disturbance ("1"; e.g. natural riverbanks), intermediate disturbance ("2"; e.g. non-intensively used dry grassland), and high disturbance ("3"; gravel pits in use). For the analysis, we additionally collated all plots of identical habitat types (e.g. "sum\_steppe\_123"), as well as of identical disturbance levels ("sum\_smb\_1"; "sum\_smb\_12"; "sum\_smb\_123"). Our measure for habitat availability was the number of points with habitats of a given type.

To evaluate the influence of habitat history on the current spatial pattern of species richness, we additionally analysed aerial photographs from 1979-1982 (black and white; spatial resolution = 50cm x 50cm; average scale = 1:25 000), but in this text we refer only to the year 1980. Because habitat types were more difficult to distinguish in these photographs, we aggregated all habitat types with disturbance levels 1 and 2 into a single historic habitat variable ("steppe 1 and 2" + "mixed 1 and 2" + "bare ground 1 and 2" = "smb12\_1980").

### *Statistical analysis*

To compare the influence of the predictive variables on xerophilic grasshopper species richness, we used generalised additive models (Hastie and Tibshirani 1990). We used a quasipoisson model as we analysed count data and to account for the dispersion of the input data (Chambers and Hastie 1990). The smoother degree of freedom was set to 4, using a smoothing spline. All statistical analyses were conducted using the R software (R Development Core Team 2005).

## **Results**

### *Analyses on the one-hectare scale*

Seven variables influenced xerophilic grasshopper species richness most: the x and y coordinates, temperature, precipitation, northness, the amount of highly structured dry grassland with the disturbance level 3 ("mixed3"), and the sum of all mapped habitat types with the disturbance levels 1 or 2 ("hist\_smb12"; Figure 3). The "historic" habitat variable ("hist\_smb12") had the highest level of significance and its explained deviance exceeded all current habitat variables as well as the topographic variables.

These seven variables did mostly show low levels of collinearity (Table 3), but the x and y coordinates, temperature, precipitation, and northness showed high levels of collinearity. From these variables, precipitation had the highest value of explained deviance. Consequently, the x and y coordinates as well as temperature were excluded from further analyses on the one-ha scale.

Subsequently, we took to be precipitation, northness, mixed3, and smb12\_1980 the key explanatory variables.

Sites with low levels of precipitation were most favourable for xerophilic grasshopper species richness (Figure 4). Plots that are exposed to the south are also relatively favourable (variable “northness”: the value 0 represents exposure to the south). An increasing proportion of highly disturbed and highly structured dry grassland habitats (“mixed3”) influences species richness negatively, except at high levels of habitat availability. The “historic” habitat availability correlates positively with xerophilic grasshopper species richness up to approximately 12.5% (50 of 400 sample points) of the plot size. At higher levels the trend changes with a higher error, leading to a negative impact of historic habitat availability at values of more than 25% of the ha plot (Figure 4).

To analyse whether the significant influence of historic habitat availability on species richness reflects an extinction debt, we calculated the difference between “smb12\_1998” and “smb12\_1980”. This was done only for plots with “smb12\_1980” lower than 50 because the response of species richness was most clear for these 46 plots (78% of total sample size). In the majority of the plots, habitat availability for xerophilic grasshopper species increased between 1980 and 1998 (Figure 5). This increase in habitat availability was mainly caused by gravel-pit exploitation during this time. However, the number of xerophilic grasshopper species did not respond accordingly.

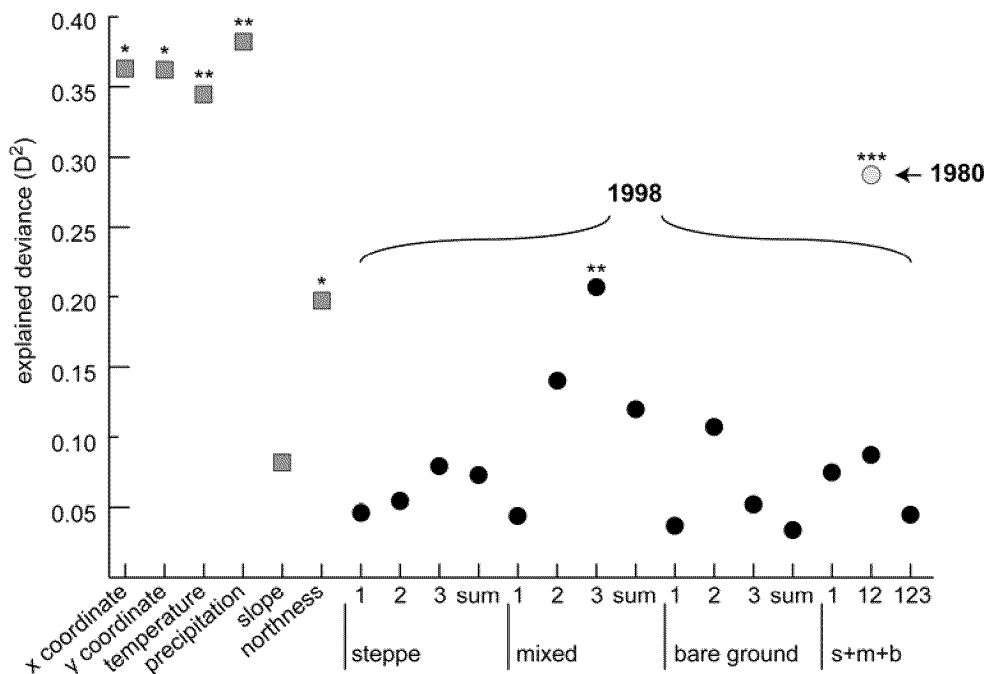


Figure 3: Explained deviance of the univariate models on the ha level (\*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ). Some of the abiotic factors (squares) explained more of the deviance than the habitat factors (circles). The historic habitat factor (smb12\_1980) exhibited a higher explained deviance than the more detailed current habitat data dating from 1998.



Table 3: Spearman's rank correlation coefficients for the variables with highest influence on xerophilic grasshopper species richness on the hectare level (n=59).

| Variables       | 1     | 2     | 3     | 4     | 5     | 6     | 7    |
|-----------------|-------|-------|-------|-------|-------|-------|------|
| 1 CX            | 1.00  |       |       |       |       |       |      |
| 2 CY            | 0.97  | 1.00  |       |       |       |       |      |
| 3 Temperature   | -0.51 | -0.53 | 1.00  |       |       |       |      |
| 4 Precipitation | 0.63  | 0.62  | -0.96 | 1.00  |       |       |      |
| 5 Northness     | -0.19 | -0.20 | 0.54  | -0.45 | 1.00  |       |      |
| 6 Mixed3        | -0.06 | -0.02 | 0.09  | -0.14 | 0.14  | 1.00  |      |
| 7 Hist12        | -0.02 | -0.05 | -0.25 | 0.26  | -0.13 | -0.35 | 1.00 |

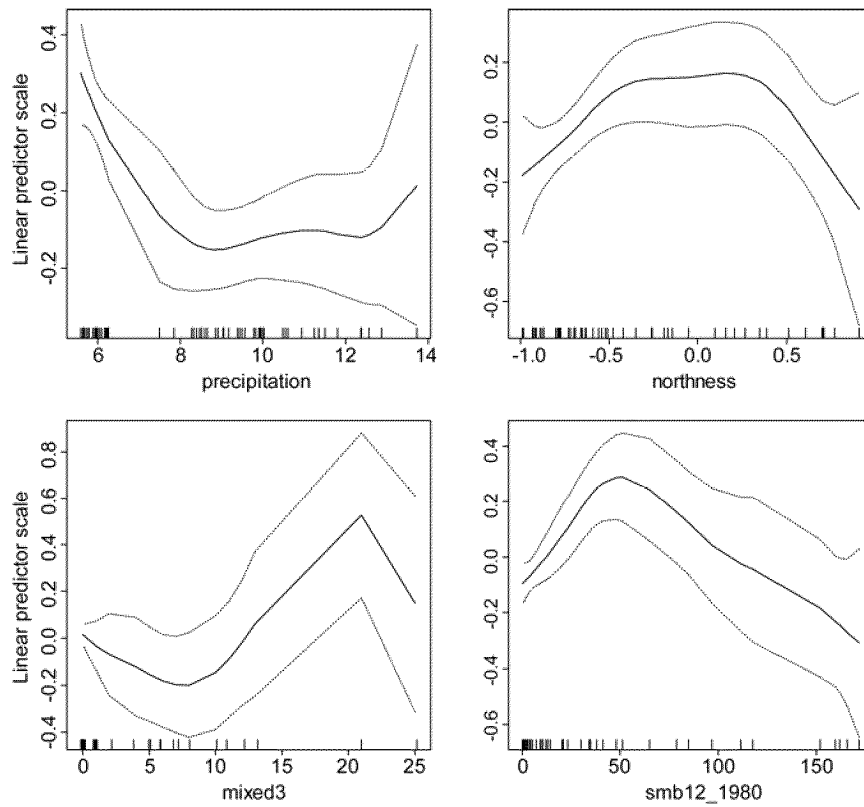


Figure 4: Response curves (additive logistic fit) of the univariate models to the identified key variables on the hectare level. "Mixed3" and "smb12\_1980" represent the number of sample points in the related habitat types (the dashed/grey lines are two times standard-error bands; the location of the individual data points is indicated on the x-axis).

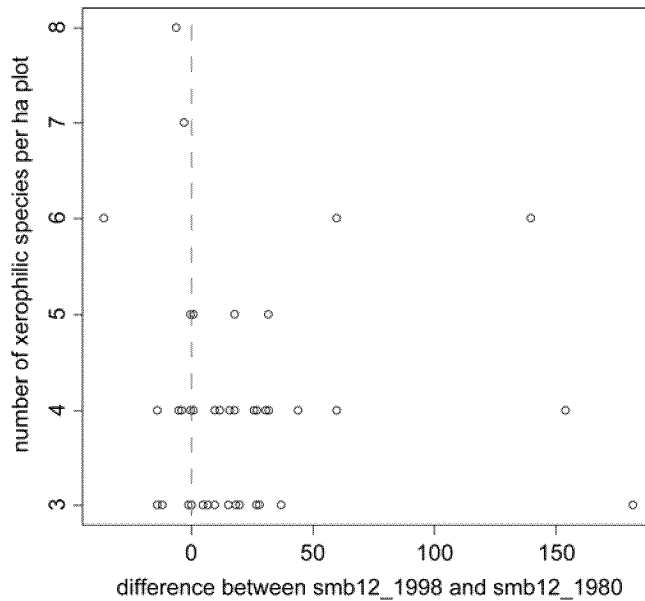


Figure 5: Difference in habitat availability of all mapped habitat types with disturbance levels 1 or 2 (“smb12”) between 1998 and 1980. In most ha plots, the proportion of habitats increased over the 20 years studied. (Positive values: 1998 higher proportion of habitats in ha plots than 1980; negative values: vice versa)

#### Multi-scale approach

We analysed a subset of 21 plots with a multi-scale approach, including buffers of up to 500 meters around the plots. The highest levels of explained deviance was revealed by seven variables: the x and y coordinates, precipitation (marginally significant), “smb12\_1980” (significant), and “smb12\_1998” including the 100m (significant), 200m and 300m buffers (Figure 6). The x and y coordinates and precipitation are highly correlated, as is “smb12\_1998” with the 100m, 200m, and 300m buffers. All other variable combinations exhibit low colinearities (Table 4). Subsequently, we identified precipitation, “smb12\_1980” at the ha level, and “smb12\_1998” with a 100m buffer as the key variables.

As in the ha-level analyses, the response of xerophilic grasshopper species richness to historic habitat availability (smb12\_1980) was a nearly linear positive relationship for low to intermediate levels of habitat availability (Figure 7). The same can be observed for the current habitat availability including a 100m buffer around the studied plots of 1 hectare (smb12\_1998 + 100m buffer).

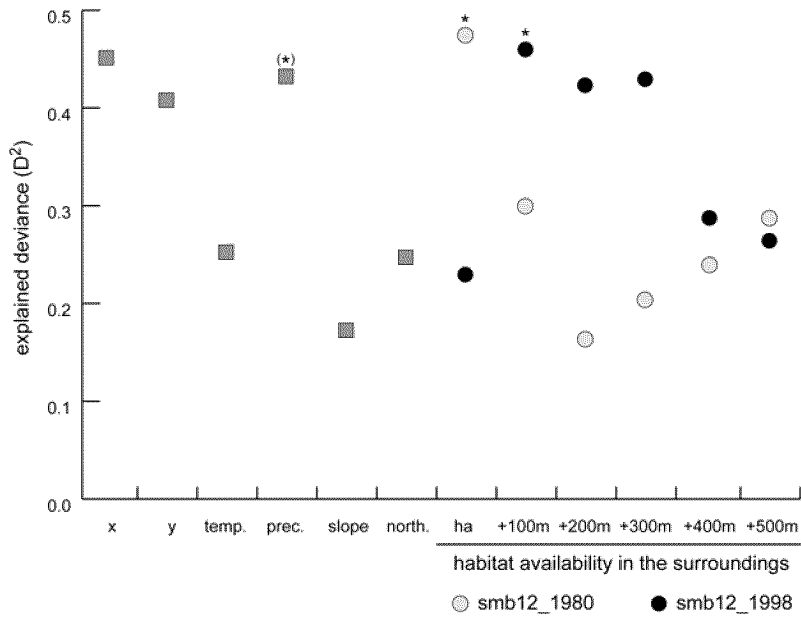


Figure 6: Explained deviance of the univariate models based on all variables included in the analyses with the multi-scale approach. ((\*)  $p < 0.08$ ; \*  $p < 0.05$ )

Table 4: Spearman’s rank correlation coefficients for the variables with highest influence on xerophilic grasshopper species richness with the multi-scale approach ( $n=21$ ).

| Variables         | 1     | 2     | 3     | 4    | 5    | 6    | 7    |
|-------------------|-------|-------|-------|------|------|------|------|
| 1 CX              | 1.00  |       |       |      |      |      |      |
| 2 CY              | 0.97  | 1.00  |       |      |      |      |      |
| 3 precipitation   | 0.72  | 0.72  | 1.00  |      |      |      |      |
| 4 smb12_1980_ha   | 0.05  | -0.04 | 0.13  | 1.00 |      |      |      |
| 5 smb12_1998_+100 | -0.11 | -0.15 | -0.20 | 0.34 | 1.00 |      |      |
| 6 smb12_1998_+200 | 0.03  | -0.02 | -0.11 | 0.26 | 0.93 | 1.00 |      |
| 7 smb12_1998_+300 | -0.03 | -0.11 | -0.21 | 0.31 | 0.31 | 0.95 | 1.00 |

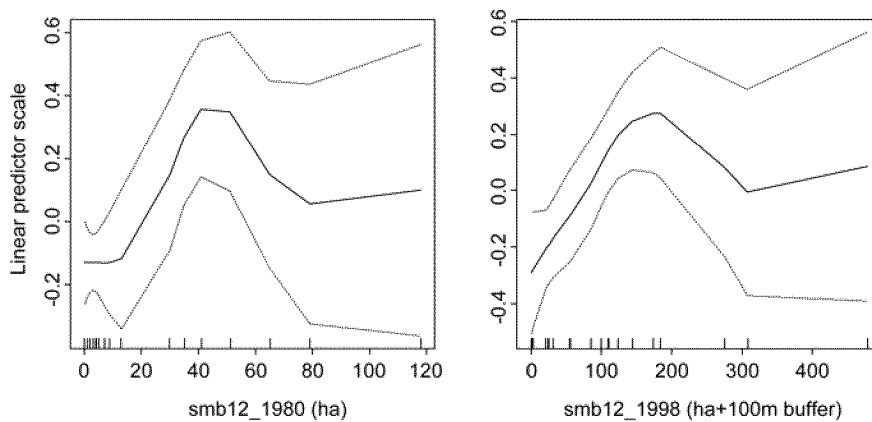


Figure 7: Response curves (additive logistic fit) of the univariate models to the two most important habitat variables with the multi-scale approach. (the dashed/grey lines are two times standard-error bands)

## Discussion

### *Analyses on the ha level*

The four variables that best explained the spatial distribution of xerophilic grasshopper species, namely precipitation, the x and the y coordinates, and temperature (in descending order), were highly correlated (Table 3). We, therefore, consider precipitation as the most important key factor. Precipitation is negatively correlated with xerophilic grasshopper species richness, which confirms the selected grasshopper's preference for dry and warm habitats. The importance of precipitation is also apparent for overall grasshopper species richness in Switzerland (C.E.S. et al., unpublished data). Interestingly, the "historic" availability of suitable habitats for the selected grasshopper species explained much more of the current richness pattern than more recent and more detailed habitat data.

The response of species richness to historic habitat availability must be interpreted carefully. At low levels of habitat availability (that is, sites with low numbers of suitable habitat patches) the response is a nearly linear positive relationship that reaches an optimum with a habitat cover of about 25%. But if more potential habitats become available, this trend is reversed. The negative impact on species richness at high levels of habitat availability is caused by just seven plots (Figure 4). Three of these plots are situated at altitudes of about 1300 meters above sea level. At 1300 meters habitat availability is clearly not as important for grasshopper species richness as climate is. The other four plots are also situated in unfavourable areas with relatively high precipitation, which turned out to be the most important factor affecting species richness of xerophilic grasshoppers. Stratifying the study area according to climatic conditions could have eliminated the effect of a negative correlation at high levels of habitat availability. Therefore, this negative correlation might be caused in part by abiotic factors.

At low levels of habitat availability, the species richness of xerophilic grasshoppers generally responds with a time-lag to landscape change. In contrast to the hypothesis of Lindborg and Eriksson (2004), our findings suggest that the history of habitat availability is an important factor for the current diversity of short-lived and relatively mobile species like xerophilic grasshoppers. But this time-lagged response is not exclusively an extinction debt. An extinction debt arises when habitats deteriorate without an immediate decrease of species richness but with a decrease after a certain time (Tilman et al. 1994, Chamberlain et al. 2000, Hanski and Ovaskainen 2002, Lindborg and Eriksson 2004, Piessens and Hermy 2006). In our study, most of the plots show an increase in habitat availability. A relatively high proportion of plots therefore seem to be more suitable than the number of species observed would suggest. These plots may become more species-rich in the future, if additional species are able to immigrate. Consequently, the lack of immigration exceeds the lack of extinction concerning the time-lagged response in xerophilic grasshopper species richness.

### *Multi-scale approach*

With this approach, we identified three key factors for xerophilic grasshopper species. The variable with the highest level of explained deviance was the historic habitat availability on the hectare level

("smb12\_1980\_ha"), followed by current habitat availability including a buffer of 100m around the study plots ("smb12\_1998\_+100"), and then by precipitation. This is an increase in relative importance of landscape history for xerophilic grasshopper species richness compared to the ha-level analysis.

The reason why landscape history becomes more important is probably the reduction of plots with low numbers of species. Most of these low-richness plots are likely to be situated in unfavourable climates. Therefore, we (by chance) reduced the plots where interacting abiotic factors reduced the importance of historic habitat availability. However, historic habitat availability seems to be influential only at the one-hectare level. Historic habitat availability in the surroundings did not have a significant influence on the current distribution of xerophilic grasshopper species richness.

It is the combination of site history and current connectivity that is most important for diversity. The current availability of suitable habitats within a radius of 100 meters around the studied plots was the current habitat factor with the most influence on species richness. Current connectivity is an additional key factor for grasshopper species richness because of the time-lagged response of xerophilic grasshopper species richness to landscape change. We suggest that the historic habitat availability of a site determines the basic potential for species richness, whereas the current habitat availability in the surroundings (that is, high connectivity) guarantees the survival of the populations due to the possible immigration of individuals or species.

A buffer radius of 100 meters seems to be a threshold for habitat availability in the surroundings of a site. This corresponds well with the results of Kindvall and Ahlén (1992), who observed that, for the bush cricket *Metrioptera bicolor*, the critical inter-patch distance is about 100 meters. We suggest, however, that at least for a few xerophilic grasshopper species the critical inter-patch distance is about 300 meters, even though the influence of habitat availability in the surroundings of 200 and 300m is not significant. This is indicated by a marked drop in explained deviance between the 300-meter and the 400-meter radii (Figure 6). A critical inter-patch distance of about 300 meters might be valid for highly mobile species like *Oedipoda caerulescens*, where the females can migrate up to 300 meters within short periods of time (Zöller 1995). However, the identification of connectivity thresholds for individual species was beyond the scope of this study as it requires species-specific modelling. In general, we recommend 300 meters as the minimum radius, in which habitat availability and habitat quality should be maintained or increased to conserve xerophilic grasshopper species.

#### *Mechanisms behind extinction debt and immigration debt*

In our study, we identified habitat history as a key factor for current grasshopper species richness. This contradicts the hypothesis of Lindborg and Eriksson (2004), who suggest that the diversity of short-lived species like insects does not reflect landscape history. We, in contrast, hypothesise that a time-lagged response to landscape change can be observed for all kinds of species if it reflects a time-delayed immigration in landscapes with increasing habitat quality and connectivity. This effect can be called "immigration debt". The duration of the time lag will then mainly depend on the species' dispersal ability and the level of habitat isolation.

Time-lag response of species to landscape change is, in general, to be connected with the extinction debt (e.g., Baldi and Vörös 2006, Helm et al. 2006, Vellend et al. 2006). Extinction debt is to be expected for long-living species and for species with life-cycles of several years because these species are likely to have the ability to survive despite diminishing habitat quality and connectivity. In this case, the crucial factor for the time-lag response should be the species' ability to maintain populations over periods of decreasing habitat quality and connectivity. Even generally short-lived species like insects may exhibit this ability because the life-cycles of many insect species may last for several years (e.g. grasshoppers; Ingrisch 1985).

Our results show that, even in cultural landscapes, environmental change per se is not necessarily a threat to biodiversity. Indeed, habitat availability and habitat suitability may increase with climate and landscape change (e.g., Lunt and Spooner 2005, Menéndez et al. 2006, C.E.S. et al. unpublished data). This may lead to an "immigration debt" if the present species distribution does not allow successful immigration although habitat quality or habitat availability has increased. Therefore, the role of landscape history differs markedly according to whether there is an extinction debt or an immigration debt. When an extinction debt occurs due to decreasing habitat quality and connectivity, both the historic habitat quality and historic connectivity are likely to be key factors for current species richness (Figure 8). In the case of an immigration debt, the historic habitat quality may also be more important for current species richness than current habitat quality. But the importance of the historic connectivity is lower than the importance of the current connectivity, because increasingly suitable habitats have to be connected to other populations to ensure immigration.

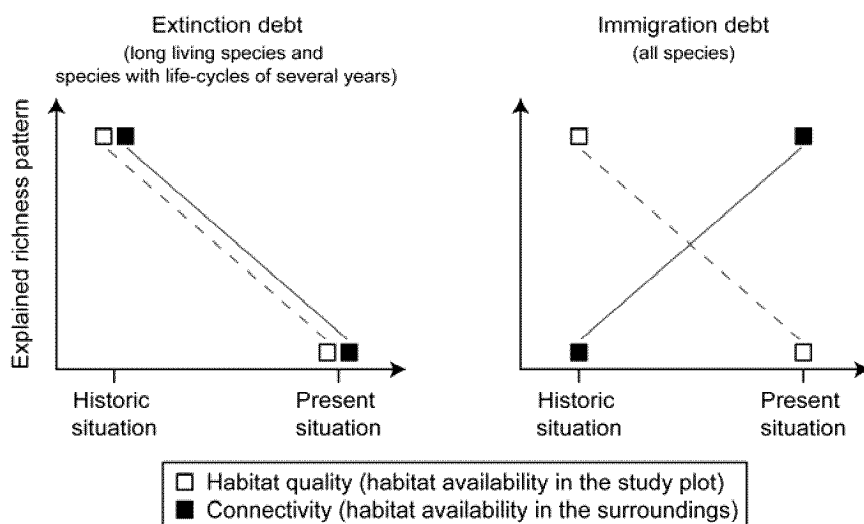


Figure 8: The importance of historic connectivity for species richness differs between the case of an extinction debt and the immigration debt, while historic habitat quality is likely to be important in both cases.

Our findings correspond with island theory (Mac Arthur and Wilson 1967) and the metapopulation concept (Hanski 1999), as well as with other studies (e.g., Wettstein and Schmid 1999, Steffan-Dewenter 2003, Dahlgren and Ehrlen 2005, Cousins 2006). Consequently, increasing habitat connectivity should be a primary goal in conservation practice because of two reasons. This will, first, maintain species richness in sites that exhibit an extinction debt, and second, foster immigration to sites that would be currently well suited for the species but that have not yet reached equilibrium due to an immigration debt.

#### *The use of focal species as surrogates*

The fact that all taxonomic groups may show a time-delayed response to environmental change has important implications for nature conservation. Studies of species richness that do not incorporate environmental change may be severely biased because the spatial distribution of species richness does not per se reflect the current environment. This fact complicates the task of conservation biology considerably. Incorporating changing environmental conditions may be important for, in example, identifying thresholds for species occurrences, for using focal species as indicators for environmental change or for overall species richness, and for developing reserve-selection strategies.

We recommend paying critical attention to reserve selection that is based on just a few indicator species. It is not only a question of scale and region (Hess et al. 2006), or of how strongly rare or endemic species correlate with overall species richness (Prendergast et al. 1993, Ricketts 1999, Bonn et al. 2002). It is also the different responses of different taxonomic groups to environmental changes that question the suitability of indicator species for predicting species richness across taxonomic groups. Indicator species can not reliably predict species richness across taxonomic groups if they are not affected in the same way by environmental changes. Consequently, prioritisation of areas based on species richness might not be a successful approach for maintaining biodiversity.

It might be more appropriate to select potentially species-rich reserves based on environmental surrogates and habitat structure than based on species richness alone (e.g., Margules and Pressey 2000, Sarkar et al. 2005, Hein et al. 2006, but see Lindenmayer et al. 2002). In a second step, current species richness or the spatial distribution of indicator species could be used as a measure to establish priorities for conservation practice. Top priority should be given to species-rich habitats because they might exhibit an extinction debt and because they may act as a source to enhance biodiversity in other habitats. Higher levels of connectivity could then be established, for example, by large-scale conservation programs including agri-environmental schemes. But still, species specific measures will be necessary for the conservation of critically endangered or endemic species.

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## **6. GENERAL CONCLUSIONS**

### **6.1. Data sources for large-scale analyses**

Analysing the spatial pattern of species richness on a large scale needs a large set of data. To sample species e.g. on a national scale for a single research project would require large resources. Therefore, large-scale studies are often based on data from databases of record centres or distribution atlases for analysing richness patterns (e.g., Prendergast et al. 1993, Lennon et al. 2004). Such databases are a very important source to increase the knowledge about the range size of species.

However, the use of data from record centres may bias scientific investigations due to unsystematic sampling. These data generally represent species presences but not absence of species. In general, most observations of species collected in national databases are delivered by specialists. It is not likely that certain species are systematically omitted or even determined wrongly.

However, the system of collecting data in databases may be improved. This is true even if the spatial precision of the location is documented and the persons who deliver data are known to be experts (e.g. Swiss faunistical database, CSCF Neuchâtel). Information on how the observations have been made could help to select the most accurate data for scientific investigations. Concerning grasshoppers, such information could encompass weather conditions or the time that was spent on a specific site looking for species. Collecting such information would certainly increase the database expenses. But, science might considerably profit from such an effort.

### **6.2. Effects of environmental change on species richness**

The results of this study show that future land-use change is potentially a threat to grasshopper species richness in the cultural landscape of Switzerland (chapter 4). Even if land-use change is mainly characterized by the increase of low-input habitats, which is an important measure in European agri-environmental schemes, some habitats may deteriorate in the future (at least as far as grasshoppers are concerned). Consequently, the recent trend of declining species richness in the European cultural landscape may continue in the future.

Like hotspots at the global scale, small scale hotspots are likely to be threatened by human-induced land-use change (e.g. Witt and Samways 2004, Sodhi et al. 2004). Species richness in small-scale hotspots of grasshopper species richness probably reacts more negatively to future land-use changes than an average site of Switzerland (chapter 4), because these hotspots represent outstanding habitats in the cultural landscape. They feature a high proportion of overall grasshopper species richness and they are likely relics of habitats that were created and maintained by traditional land-use practices (chapter 3). Surprisingly, the effects of different scenarios of land-use change were very similar for the rarity hotspots (hotspots of endangered grasshopper species) and the hotspots of common species (chapter 4). Therefore it is to conclude that hotspots of common species may be affected in a similar way by future environmental changes as rarity hotspots.

However, environmental change is not always a threat to biodiversity. Some animal species may adapt to environmental changes (e.g., *Myotis myotis*; Steck and Güttinger 2006), landscape change may lead to an increased availability of habitats (chapter 5), or species might profit from increasing temperatures due to climate change (chapter 4). Especially the positive short-term effects of climate change should not be neglected. In Central Europe, it is to be expected that climate change will foster especially thermophilic species like some grasshoppers (e.g., *Oedipoda germanica*), bats (e.g., *Myotis emarginatus*), or trees (e.g., *Quercus pubescens*). While today, these species are relatively rare in Central Europe, they might become more common in the future.

Consequently, credible nature conservation should not only focus on the threats of environmental change but also incorporate the potential positive effects, although the negative effects of environmental change are likely to dominate.

### **6.3. Challenges of using indicator species**

Species richness of selected taxonomic groups is often used as an indicator for biodiversity, as a decision metric for setting conservation priorities, and as a monitoring measure. The use of this estimate is problematic due to different basic assumptions (Fleishman et al. 2006). The dynamic nature of species richness is very difficult to incorporate into nature conservation. The spatial distribution of species is influenced by landscape and climate change (chapter 4). Furthermore, species richness frequently follows environmental change with a time lag (chapter 5, Brooks et al. 1999, Lindborg and Eriksson 2004, Lunt and Spooner 2005, Báldi and Vörös 2006, Helm et al. 2006, Paltto et al. 2006, Vellend et al. 2006). This means that the current species occurrences may not reflect today's environmental situation. Consequently, selected species may not be reliable predictors for other taxonomic groups after future environmental changes. Additionally, the use of specific indicator species is risky if they are used to predict species richness in different geographic regions (Hess et al. 2006).

Therefore, the conservation value of small-scale hotspots of grasshopper species richness (chapter 3) and the results of habitat-suitability models (chapter 4) are to be discussed carefully. Especially in chapter 3, the importance of the extinction debt might have been underestimated concerning "rarity hotspots", which seem to represent habitat relics. If those rarity hotspots exhibit an extinction debt, conservation practice should primary focus on these habitats and enhance quality and connectivity in order to preserve local species richness. In general, the potential time-lag response of species has to be considered in order to propose effective measures for conservation practice and to realistically predict the impact of potential environmental change on species richness.

Based on the results of this study I do not warn against the use of indicator species in general. But, I suggest using them with caution; their relevant characteristics, i.e. regarding dispersal ability and live-history traits, have to be considered. After a pre-selection of potential indicator species, e.g. applying the straightforward approach proposed by Duelli and Obrist (2003), this set of species has to be evaluated with regard to some crucial characteristics. These characteristics depend on whether the focus lies on the protection of species in an environment of decreasing quality, or the focus lies on the development of species richness in an environment of generally increasing quality.

If the species of interest rely on habitats that are generally deteriorating or lost, species presences might not reflect the “real” habitat suitability due to a time delayed response to environmental change (that is an extinction debt; Tilman et al. 1994). In this case, the persistence of species should be the key factor for the final selection of indicator species. Species with highest ability to persist to environmental change will exhibit the largest extinction debt; species with a low persistence will respond fast to changing conditions. It is evident that a group of species can reliably predict the occurrence of only those species that show a similar level of persistence. Consequently, in a deteriorating matrix, the most suitable set of indicator species for biodiversity will feature at least two groups of species: species exhibiting high levels of persistence, and species with a low ability to persist to declining habitat suitability.

In an environment that is characterized by increasing habitat quality and availability (e.g., due to agri-environmental schemes), species might show an “immigration debt” (chapter 5). Consequently, a considerable proportion of newly created habitats or of habitats, whose quality increased markedly, might not be reached by some species due to isolation effects. In this case, the chosen set of indicator species should ideally encompass taxonomic groups with different dispersal abilities or groups of different mobility, respectively.

Unfortunately, knowledge about persistence and dispersal ability is low, even for well studied taxonomic groups like grasshoppers. Further investigations on these parameters across environmental gradients are therefore needed. Especially the question of the dispersal ability should be investigated across environmental gradients and with different approaches. On the one hand, thresholds of connectivity, minimum inter patch distances, or the barrier effects of different landscape elements can be assessed with empirical studies on the spatial distribution of species richness (e.g., chapter 5, Kindvall and Ahlén 1992, Pelet et al. 2004). On the other hand, more qualitative investigations on the dispersal behaviour or the mobility of selected species can deliver important singular observations on these parameters that are generally not made with large-scale studies (e.g., Zöller 1995, Steck and Coch 2006). However, it will always be a difficult task to distinguish between the potential maximal dispersal distance and the behaviour in each singular case (the same problem in another context: Husak 2006).

#### **6.4. Implications for conservation practice**

Environmental change was not only a task for nature conservation in the past. It will also be a challenge in the future (chapters 3 and 4), even if some species might profit from future environmental change. A major challenge for nature conservation will be, on the one hand, the preservation of biodiversity in areas that are extraordinarily species rich (e.g., so-called “hotspots”) and in habitats that feature endemic or highly specialized species. On the other hand, the increase of habitat availability should be the main goal in the remaining areas. Both can be achieved by establishing habitat continuity. Habitat continuity is most often used statically as a synonym for the spatial and structural steadiness of a focus site (e.g., Wulf 2004). For effective nature conservation, habitat continuity has to be established in a broader sense (Coch et al. in press). On the landscape level, a functional continuum of habitat availability is to be established in order to maintain and

enhance species richness over time. To ensure sufficient habitat continuity by selecting sites for the application of conservation measures is a major task for conservation planning.

The selection of sites for the conservation of species richness is often based on present species occurrences. Because of the time-lag response of species richness to environmental change, environmental surrogates may be more appropriate for site selection than species presence (chapter 5). However, biodiversity hotspots or sites with populations of endemic and highly endangered species should get top priority in conservation planning. Species preservation in these sites is a great task if they exhibit an extinction debt. Therefore, past environmental changes should be investigated at different scales before conservation plans are developed.

In a next step, habitat availability should be enhanced in the surroundings of existing hotspots and around populations of endemic and highly endangered species. The populations of these sites may act as sources for the immigration of target species into previously uncolonized, but suitable areas. Ideally, current populations will be connected with previously uncolonized habitats to ensure migration of species and individuals. But, it may take decades or even centuries until species colonize new habitats (chapter 5). Monitoring programs should therefore be established at the long-term and conservation measures should not be judged without considering the time-lag response of species richness to environmental change.

Of course, the procedure described above is not a cure for all in nature conservation. Especially as reducing the isolation of populations may also be a threat to species richness. Invasive species may compete native species (e.g., Crivelli 1995), predators may immigrate (e.g., Scheffer et al. 2006), or parasites and pathogens may threaten populations of native species (e.g., Rachowicz et al. 2006). Consequently, reducing isolation by enhancing habitat connectivity might lead to reduced local species richness (see also Hubbell 2001).

It is a trade-off between the need for connectedness of habitats and populations and the threats of connectivity for the long-term conservation of species richness. In the case of grasshopper species richness in the Swiss cultural landscape, however, the advantages of reducing isolation effects are likely to exceed its threats. This is to be expected as there is no published evidence of the existence of species specific diseases, of direct competitors, or of species specific predators. The conservation of the most important habitat types should therefore be the most straightforward strategy in conserving grasshopper diversity in the European cultural landscape.

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