

PROSPECTS FOR SUSTAINABLE DEVELOPMENT:
THE FUTURE OF PLANTS AND BUTTERFLIES
IN TRANSYLVANIA

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Prospects for sustainable development: The future of plants and butterflies in Transylvania

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Preface

This cumulative dissertation consists of three sections (Figure 0.1). Section A provides an introduction to relevant key concepts, identifies the overarching objective of this dissertation, summarizes the respective studies and discusses emerging cross-cutting themes (Chapter 1). The empirical research of this dissertation was based in Transylvania and is presented in Section B (Chapters 2-6). In Section B, I first develop a methodological background for the subsequent chapters by exploring an optimal survey strategy, allocating the available resources in a study design that enables high statistical power and covers a wide range of environmental conditions (Chapter 2). In Chapters 3-6, I empirically investigate the biodiversity and distribution patterns of plants and butterflies in response to different landscape structures. In Section C (Chapters 7 & 8), I conceptually embed socio-economic considerations into the local and international discourse on sustainable rural development. Chapters 2 to 8 represent a series of scientific articles which I have authored and which are either published or in revision in international peer-reviewed scientific journals. The corresponding references for each paper are listed on the title pages of the respective chapter. The content of each chapter is the same as the journal article, with figure and table labels adapted to the presentation of this dissertation. Because Chapters 2 to 8 were designed as stand-alone publications, there is some unavoidable repetition between chapters. All literature cited is presented in a single reference list at the end of the dissertation.

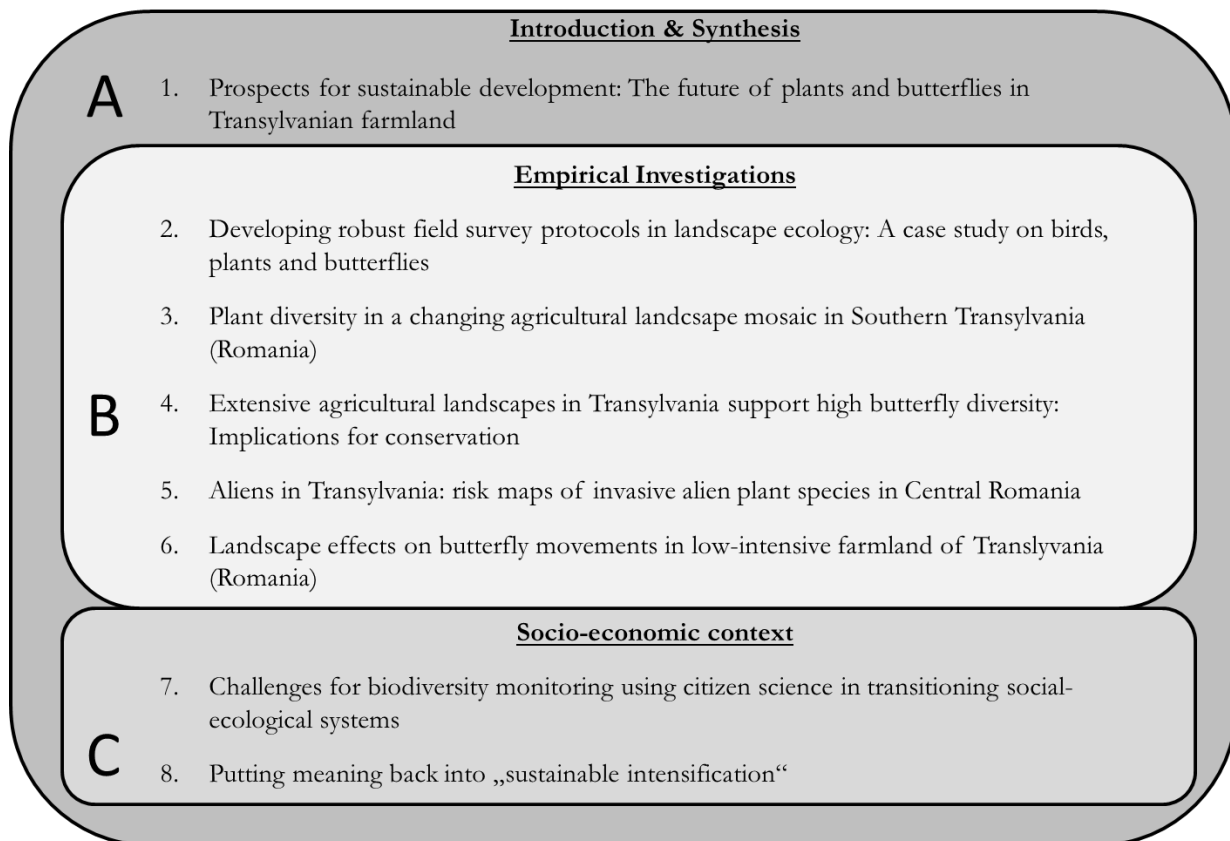


Figure 0.1: Structure of the dissertation

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Chapter 1

Prospects for sustainable development: The future of plants and butterflies in Transylvania



Fostering sustainable development in human-dominated systems

In the Anthropocene, humans dominate the world's ecosystems (Vitousek et al. 1997; Crutzen 2002). Effects of human activities include climate change, environmental pollution, the introduction of alien species, over-exploitation of natural resources as well as destruction and disruption of natural and semi-natural ecosystems (Steffen et al. 2004). Humans have already modified 75 % of the Earth's terrestrial surface (Ellis and Ramankutty 2008), primarily for agricultural purposes (Ramankutty and Foley 1999; Foley et al. 2011). Furthermore, fulfilling the needs, and desires, of a continuously growing human population (Foley et al. 2005; Godfray et al. 2010; Tilman et al. 2011) is exceeding planetary boundaries (Rockström et al. 2009). One of the biggest problems caused by these global changes is the worldwide and sometimes irreversible loss of biodiversity (Sala et al. 2000). Biodiversity includes genes, individuals, populations, species, communities, ecosystems, and the interactions between these entities (Lindenmayer and Franklin 2002). Accelerating species extinction rates exceed the natural background extinction rate by a factor of 100 or even 1000 (Chapin et al. 2000), so that scientists speculate we are close to the onset of the sixth mass extinction on Earth (Barnosky et al. 2011). This loss of biological diversity leads to biotic homogenization, which entails cascading effects on the multiple ecosystem functions and services which landscapes provide (De Groot et al. 2002; Hector and Bagchi 2007). Ultimately, the persistence of human well-being and of our socio-economic systems depends on these functions (Millennium Ecosystem Assessment 2005).

If these problems are to be solved there must be a directed and meaningful change towards environmentally sound and socially meaningful development (Lélé 1991). Such sustainable development involves the economic, social and biophysical dimensions of human well-being (Berkes et al. 2003). The best known expression of sustainable development is development that "meets the needs of the present without compromising the ability of future generations to meet their own needs" (WCED 1987). Hence, the notion of sustainable development creates an ethical framework that implies intra- and intergenerational distributive and procedural justice (Langhelle 2000).

International commitments, such as the Millennium Development Goals, incorporated the notion of sustainable development into their agenda, and the Convention on Biological Diversity (Convention on Biological Diversity 2010), declared conserving nature and wildlife as one of its major goals. However, in order to actually act within the framework of sustainable development, we urgently require well-informed governance and local solutions that build on interdisciplinary research which takes into account both the social and the ecological perspectives (Millennium Ecosystem Assessment 2005). This dissertation seeks to deliver insights into the links between biodiversity and sustainability from an ecological perspective, focusing on one of the last biocultural refugia of Europe: Southern Transylvania (Barthel et al. 2013; Hanspach et al. 2014).

Rural landscapes as social-ecological systems

Global change often has profound impacts on rural landscapes. Historically, rural landscapes are characterized by a low population density, distant from the more dynamic centres of political activity and decision making (Ambrosio-Albala and Delgado 2008). The social and economic structures of rural landscapes are often closely dependent on agriculture and forestry. The environment in these areas has often been highly influenced by human activities over centuries because the rural population extracted goods and services from the ecosystems (Fisher et al. 2009). In the context of sustainable development, rural landscapes need to function as a resource for future generations (inter-generational equity); therefore, the conservation of various important aspects of these landscapes, including their biodiversity, is crucial. Yet, despite the importance of rural landscapes in sustaining and enhancing human well-being, conservation is often neglected in management. Rural landscapes currently face tremendous transformations due to the modernization of agriculture and industrialization processes which triggers the migration of rural people from the countryside to the cities (Palang et al. 2006; Schouten et al. 2012). As a consequence, rural landscapes are undergoing profound social, economic and cultural changes (Antrop 2004) as well as shifts in land-use patterns.

Particularly in rural landscapes, humans directly influence and are influenced by the environment at several organizational scales. This close and dynamic interlink between human society and natural processes is characteristic of social-ecological systems (Berkes et al. 2000; Walker et al. 2004; Folke 2006). In these systems, human activities determine the ability of the system to adapt to ongoing and threatening environmental changes (Walker et al. 2004). This quality is also known as resilience, which is defined here as the ability to recover from external shocks and disturbances and retain the same essential functions and feedbacks (Holling 1973; Walker et al. 2004). A resilient rural system possesses a greater capacity to prevent undesirable changes in the face of external disturbances, and therefore a greater capacity to continue to provide the goods and services that support quality of human life (Walker and Salt 2006).

90 % of the European Union (EU) is comprised of rural landscapes, approximately half of it which are pastoral and cropping systems, henceforth called “farmland” (Geiger et al. 2010). Central and Eastern European rural landscapes integrate large natural and semi-natural areas, and have larger population rates than the Western parts of Europe (Geohive 2009). Many of these areas are now considered “traditional” cultural landscapes (Hartel et al. 2010). Besides the large amounts of biodiversity (Fischer et al. 2012), these traditional cultural landscapes also offer unique senses of place to many people (Palang et al. 2006; Plieninger et al. 2006). To ultimately put rural social-ecological systems on the pathway to sustainable development, a holistic approach is needed, which takes entire systems into consideration rather than optimizing individual components in isolation (Walker and Salt, 2006).

Impacts of land-use change on farmland biodiversity

Agriculture represents one of the foundations of modern human societies and the main activity in social-ecological systems– in order to produce agricultural products constant human interventions are required

(Lélé 1991; Altieri 1999). These interventions convert natural ecosystems into artificial ones at several intensities, thereby altering and destroying ecosystem functions as well as habitat and resources for many species. Such alterations in land use are one of the main reasons for the rapid global decline in biodiversity (Sala et al. 2000; Haberl et al. 2009).

Despite the detrimental impact of these changes in land use on the natural vegetation, many species have adapted to and depend on cultural landscapes (Kleijn et al. 2011). In fact, farmland harbours a large share of Europe's biodiversity (Geiger et al. 2010). However, this biodiversity has declined drastically over the last 50 years (Benton et al. 2003; Meyer et al. 2013), and there is increasing concern about the sustainability of agricultural systems (Kleijn and Sutherland 2003; Stoate et al. 2009; Butchart et al. 2010). Two processes which boost these concerns are agricultural intensification and land abandonment (Bignal and McCracken 2000). These are accelerating in many EU countries, and they both influence biodiversity and the multiple ecosystem functions that agro-ecosystems provide and affect (Young et al. 2005).

Agricultural intensification is the process of raising the agricultural output of land by increasing the intensity of cropping in existing fields (Boserup 1965). Conventionally, intensification increases the use of indirect and direct inputs, such as labour, water for irrigation, and agrochemicals. Land-use intensification takes places predominantly in flat and fertile areas. However, these interventions typically entail negative environmental impacts, for example environmental pollution, loss of habitat and loss of spatial heterogeneity (Weibull et al. 2000; Benton et al. 2003). Consequently, conventional intensification is seen as a threat to farmland biodiversity (Bignal and McCracken 2000).

Land abandonment, on the other hand, reflects a change in land use towards less intensive patterns or the total cessation of agricultural activities (Baudry 1991; Benayas et al. 2007). In Europe, this phenomenon occurs mostly in less accessible, marginal areas with less fertile soils (MacDonald et al. 2000). However, there is some debate as to the effects of land abandonment on biodiversity: Abandonment may lead to the structural simplification of a landscape through natural succession, and thus on the one hand it may cause a loss of biodiversity but on the other hand it may also offer opportunities for native ecosystems to recover (Navarro and Pereira 2012; Queiroz et al. 2014). Furthermore, it is not known whether land abandonment may also increase the risk of invasion by alien plant species, which would be an additional threat to biodiversity.

The case of Transylvanian farmland

Some of Europe's most notable examples of traditional farming landscapes are found in Romania (Fischer et al. 2012). Romania is known for its unique geography and exceptionally high levels of biodiversity, hosting species that are rare or endangered in the rest of the EU (Ioras 2003; Schmitt and Rákósy 2007; Page et al. 2012). In particular Transylvania, a region in the country's centre, represents a highly heterogeneous landscape mosaic, in which mainly small-scale farmland patches with low inputs of pesticides are scattered over large areas of semi-natural ecosystems. This cultural landscape is known as a

bio-cultural refugium that has maintained a uniquely rich flora and fauna (Ioras 2003; Akeroyd and Page 2006; Young et al. 2007; Wilson et al. 2012).

Historically, large parts of this landscape were managed over centuries by the ethnic group of Transylvanian Saxons, who were closely bound to their land (Akeroyd and Page 2006; Milcu et al. 2014). However, political and economic changes during the last century caused a fundamental transition of these ancient social-ecological systems (Fischer et al. 2012; Mikulcak et al. 2013). Land collectivization during the Communist period (1960-1989) led to agricultural modernization and intensification measures in the flat and fertile land of Romania. However, traditional, low-intensity semi-subsistence agriculture persisted in the hilly and less accessible areas of Transylvania (Kuemmerle et al. 2009).

The breakdown of Communism in the 1990s was accompanied by social, institutional and political instability (Fraser and Stringer 2009). During that period, previously nationalized parcels of land were handed back to their original owners, which re-created a small-scale mosaic of land parcels. In many cases, the farms were no larger than one hectare (Luca 2009), which is barely enough land to conduct subsistence farming. The farmers' poverty and the small size of their farms forced the remaining farmers to use manual labour instead of machines, horses instead of tractors, and manure instead of artificial fertilizers. In 2007, Romania became a member of the EU, which triggered further restructuring of land use and land ownership. Still nowadays, more than 70 % of all holdings in Romania are smaller than two hectares (Luca 2009). Emerging conflicts in land use include overgrazing by sheep (Akeroyd and Bădărău 2012) and encroachment by privatization and infrastructure measures on traditional grazing commons (Sutcliffe et al. 2013).

The ongoing transition exposes farmers to entirely new incentives and opportunities, so that small farms in flat areas are slowly converted into larger fields, and previously communally grazed areas become privatized or abandoned (Hartel et al. 2010). The speed and the number of changes are growing, with less time for agro-ecosystems to recover from disturbances. Overall, the traditional practices and small-scale structures of these farmlands are rapidly being lost (Palang et al. 2006). Thus, the future trajectory and consequences of land management for biodiversity and other ecosystem functions, goods and services is unclear.

Plants and butterflies as study groups

Biodiversity comprises the aspects species richness, species composition and functional diversity (Noss 1990; Cardinale et al. 2012). In this dissertation, I focus on species diversity, and more specifically on species richness and composition. Species diversity describes two basic principles: the number of species present in a specific area (species richness) and the absolute and relative number of individuals of different species (species composition). I chose to focus on plant and butterfly diversity, because these groups are relatively easy to identify and ubiquitous (Pollard and Yates 1993; Stohlgren 2007), which makes the comparison between different localities feasible. More importantly, plants and butterflies are particularly rich and abundant in Transylvania (Akeroyd and Page 2006; Schmitt and Rákósy 2007; Akeroyd and Page

2011; Page et al. 2012). Furthermore, these groups exhibit distinct sensitivities to environmental changes and are subject to critical rates of extinction worldwide (Thomas et al. 2004).

Plants are the primary producers in ecosystems and serve as a food resource for many (specialized) herbivores and nectarivores (Weibull et al. 2003). Furthermore, they create several layers of vegetation which determine the structure of the microhabitat and the soil conditions (Cardinale et al. 2012). Consequently, plants have a tremendous impact on ecosystems and their functions. In addition, plants are known to respond relatively slowly to environmental changes, meaning that they have a greater extinction debt than other organisms (Krauss et al. 2010). This vulnerability is especially interesting to study in the context of the quickly transforming landscapes under consideration, which may show differences in plant species richness and composition in varying systems with the same management regimes.

Butterflies, on the other hand, are known to react quickly to environmental changes due to their relatively short life cycles and their dependence on specific ecological conditions (Erhardt 1985; Thomas et al. 2004; Morris et al. 2008; Warren and Bourn 2011). Moreover, butterflies are one of the best described invertebrate species, and thus have already been used extensively as model organisms in spatial and population ecology (Hanski et al. 1994; Watt and Boggs 2003; Öckinger and Smith 2006).

The species compositions of plants and butterflies display a response to landscape structures (Steffan-Dewenter and Tschardt 1997; Weibull and Ostman 2003), since the two groups contain both relatively sedentary habitat specialists as well as more widespread generalist species. Increased nutrient input and structural simplification in farmland may therefore lead to a loss of diversity in species communities, mostly benefitting generalist species (McKinney and Lockwood 1999), as shown for birds (Devictor et al. 2008), butterflies (Warren et al. 2001; Börschig et al. 2013) and plants (Meyer et al. 2013). Such losses in species community diversity lead to a functional homogenization of the landscape (Jongman 2002; Antrop 2004). Often, generalist species are known to outcompete specialized species by their fast growth rate and their dispersal mechanisms (Stevens et al. 2012) – traits which are also common among invasive species (Catford et al. 2012).

Besides their ecological characteristics, it is easy to demonstrate the relationships between the chosen study groups and human beings. For example, humans value plants for medicinal purposes and for food (De Groot et al. 2002). Butterflies are charismatic and have cultural and aesthetic value for humans. Moreover, the life cycle of butterflies illustrates evolutionary and natural processes in biology and is often used as an example in environmental education. The use of charismatic flagship species is useful in holistic approaches to biodiversity conservation – a perspective which is still little explored in transitioning countries.

Overarching objective and specific research questions

This dissertation is embedded in the interdisciplinary research project “Fostering sustainable development in Southern Transylvania”, which aimed to develop a holistic, social-ecological understanding of the

ancient cultural landscapes in Central Romania and identify pathways to sustainable development. The overarching objective of this dissertation was to quantify the relationship between selected elements of biodiversity and different land uses and landscape structures – such as woody vegetation, topography and spatial heterogeneity – in order to understand current biodiversity patterns and their drivers. Insights from these studies create evidence from which to derive recommendations for sustainable development.

Specifically, I assessed the following research questions:

- (1) Which survey strategies are logistically efficient and also provide sufficient statistical power for this highly heterogeneous landscape to detect landscape-scale effects for butterflies and plants and also birds? (Chapter 2)
- (2) How do species richness patterns of vascular plants (Chapter 3) and butterflies (Chapter 4) respond to landscape structures at different spatial scales?
- (3) Which parts of the Transylvanian landscape are most prone to plant invasions? (Chapter 5)
- (4) How do different landscape structures in farmland facilitate or hinder butterfly movement? (Chapter 6)
- (5) What are the challenges and opportunities for biodiversity conservation related to the use of citizen science in Romania? (Chapter 7)
- (6) How could the wider scientific discourse on agricultural development affect land-use changes in Romania? (Chapter 8)

General approach and summary of included studies

The studies included in this dissertation cover a broad range of approaches. The empirical research (Section B) included methodological explorations and investigations of several aspects of biodiversity. The social-ecological research aspired to embed the processes in the case study area in the wider socio-economic context (Section C). In the following, I give a short overview of the general approach in the studies included here and briefly present the main findings.

Empirical investigations

The empirical research on several aspects of biodiversity in the wider farmland landscape forms the core of this dissertation. For this purpose, the study area was subdivided into village catchments, as these represent meaningful units for empirical investigations in a social-ecological system. Village catchments were defined as a given village and its surrounding land, using a cost-distance algorithm in ArcMap (ESRI, version 10.1), with the village centre as the reference point and the slope and the distance to the next village as the cost variables.

Chapter 2 aimed to provide an a priori assessment of survey requirements needed to derive reliable data on biodiversity distribution patterns. This study took place in five village catchments, which differed in their geomorphological and social characteristics. I tested several sampling schemes in order to optimize the allocation of survey effort per study site versus number of study sites included. I investigated the minimum requirements for the sampling of species richness, species turnover and species composition in birds and butterflies with respect to the number of visits per site, and estimated effect sizes when using different numbers of study sites. I also tested a sampling scheme for plants that was entirely based on randomly placed survey relevées and compared the results in species richness, species turnover and species composition patterns to outcomes applying a conventional (and often preferred) method of botanical assessments. I found that for birds and butterflies, at least three repeats per site were necessary to reliably characterize biodiversity patterns in the sites. For plants, I found that the alternative survey method was able to detect patterns similar to those detected by the conventional method, while simultaneously covering a smaller area of the site. In order to detect landscape effects on all three species groups, I determined how many sites had to be investigated and found that an influence of environmental variables could be detected even with small changes in species richness, when at least 100 sites were surveyed.

Based on the findings from Chapter 2, I surveyed the biodiversity patterns of plants (**Chapter 3**) and butterflies (**Chapter 4**) in response to landscape structures using a natural experimental design (Diamond 1986). For this, village catchments were stratified by a cross-combination of the protection status according to the EU Birds and Habitats Directives (Site of Community Importance, Special Protection Area and unprotected) and terrain ruggedness (low, medium, high; defined by quantiles), and thirty villages were then randomly selected. Within these villages, the three dominant land use types “arable land”, “grassland” and “forest” were broadly distinguished, and with the exception of forest, were further stratified along gradients of heterogeneity (measured by the standard deviation of SPOT satellite imagery within 1 ha squares) and percent cover of woody vegetation. By focusing on key gradients in land use, woody vegetation and heterogeneity, this design thus substituted space for time to anticipate the effects of future land-use intensification or land abandonment. Per village, five study sites were randomly selected according to a stratified survey design, so that in total, 150 study sites were investigated: 30 sites in forests, 60 on arable land and 60 on grassland. For logistical reasons, I actually surveyed 120 sites for diversity in butterflies and 139 sites for plants.

The survey methods applied in the field were those evaluated as meaningful in Chapter 2. Hence, I walked 200 m standard Pollard transects per one hectare site in a cross-shape for butterflies (Figure 2.1d), and eight one square meter relevées for plants in the same sites (similar to Figure 2.1c). Environmental variables, describing the topography, woody vegetation and several metrics of heterogeneity, were measured at the local (1 ha), the context (50 ha) and the landscape scale (catchment). In the analyses, species composition was analysed using ordination methods, and environmental variables were superimposed in order to identify significant correlations. The species richness of the respective groups

was also modelled using generalized linear mixed models with environmental variables from all spatial scales included as explanatory variables.

My main findings for plants were that the species richness did not substantially differ between arable land and grasslands (Chapter 3). This is interesting because arable land is often not considered as an important component for species diversity in a landscape, and the conservation focus is often on grasslands. For butterflies, species communities differed not as strongly as expected between grassland and arable land. This finding also reveals a high conservation value for both grasslands and arable land. Remarkably, heterogeneity had contrary effects on butterfly species richness in farmland: while heterogeneity had a positive effect for arable land, it appeared to have a negative effect for grasslands. I also found that structural and topographic conditions at multiple spatial scales affected butterfly species richness, the richness of functional groups and species abundances (Chapter 4).

Besides the distribution patterns of plants and butterflies, another issue to be investigated was which parts of the study area were most likely to be invaded by alien plant species. This is the topic of **Chapter 5**. For this investigation, I mapped presences of eight abundant invasive species by extended survey walks, covering the highest and lowest parts of valleys in the study area and including road margins and forests. The presence points allowed me to develop distribution maps for each species individually using the Maximum Entropy algorithm. These models were then correlated with environmental variables, such as distance to the road, remoteness, land use and heterogeneity. The findings of this study show that especially heterogeneous farmland at a large distance from roads appeared most prone to invasion by alien plant species. These areas are also most likely to have experienced abandonment in the past, because they mainly belonged to the Saxon villages of Transylvania, where emigration has been prevalent. Due to their remoteness and topography, these areas are also likely to continue to be abandoned in the future, thus providing further opportunities for invasive species to spread.

Loss of heterogeneity in the landscape often coincides with a homogenization of species communities, in many cases benefitting generalist species over specialists. **Chapter 6** aimed at finding out whether a causal relationship for butterfly declines in agricultural land can be seen in the changes in movement ecology of species with varying levels of mobility. To this end, I investigated butterfly movements in response to landscape structures. For this purpose, I recorded the individual movements of 563 individuals of nine butterfly species with varying mobility in 15 agricultural landscapes, covering a gradient of landscape heterogeneity and woody vegetation cover. All distinguishable land-use types – including arable land and all its surrounding elements – were included in this study, but in addition to the typology used in former studies, I also distinguished between cultivated and uncultivated patches. Each study site with a circular size of ten hectares was mapped in detail. Butterfly movements were characterized according to their flight duration, distance, speed and sinuosity, as well as number of boundary crossings between land-use sections. These variables were tested for difference in their response to landscape structures. The findings of this study showed that movement activities differed significantly between species, corresponding well

with expert-derived estimates of species-specific mobility. Interestingly, species of low and high mobility responded in opposite ways to increased levels of landscape heterogeneity. In relatively simple landscapes, the movement patterns of low- and high-mobility species were similar. By contrast, in complex landscapes, the flight paths of low-mobility species became shorter and more erratic, whereas the flight paths of high-mobility species became longer and straighter. Furthermore, most species avoided arable land but favoured the more heterogeneous parts of a given landscape.

Socio-economic context

Chapter 7 presents a short discourse on the obstacles to and opportunities for environmental conservation which arise when using citizen science, and describes as an example the establishment of a national butterfly monitoring scheme in Romania. Citizen science programmes have tremendous potential for environmental and scientific education, but they are rarely applied in Eastern European countries. Recommendations for the effective design of such programs are available in the literature, but the vast majority of existing work has focused on relatively rich and industrialized countries. Under more challenging socio-economic conditions, such as in Romania, there may be a need to adjust these general approaches. In this short study, I derive insights from my experience conducting several activities to strengthen citizen engagement and from synthesizing discussions with many stakeholders engaged in monitoring programs in and outside of Europe. This chapter highlights four general themes that may be worth considering when initiating new citizen science projects in Eastern Europe and other countries in which civil engagement is a relatively new idea. Firstly, I emphasize that it is important to balance formal and informal support in engaging volunteers. Secondly, I consider education as well as building capacity and confidence crucial to the establishment of a culture of volunteering. Thirdly, I argue for the active integration of both national experts and local stakeholders in volunteer programs; and fourthly, I conclude that successful volunteer programs require effective leadership.

Finally, growing concerns about global food security have led to recommendations to use “sustainable intensification” as a way to optimize agricultural production without compromising the environment.

Chapter 8 offers a critical appraisal of the notion of sustainable intensification in the context of global food security. In the current scientific discourse, sustainable intensification has been defined as the process of enhancing agricultural yields with minimal environmental impact and without expanding the existing agricultural land base. However, this notion does not engage with established principles that are central to sustainability and it may even be counterproductive for biodiversity conservation and the maintenance of ecosystem functions in farmland. In Transylvania, for example, intensification is possible because of the presence of yield gaps, but it would very likely undermine the long-term provision of other ecosystem services. Furthermore, without addressing issues related to food accessibility and individual empowerment in the intensification decision process, increased production cannot meaningfully contribute to improving global food security. Sustainable solutions for food security need to work from

regional to local scales, and truly sustainable food systems must consider the vital importance of governance and distribution issues.

Cross-cutting themes and synthesis

This dissertation is one of relatively few studies investigating a wide variety of approaches in landscape ecology. It provides new information on landscape characteristics that support biodiversity, with an emphasis on low-intensity farmland. The strength of this predominantly ecological work is that it determines the responses in terms of species richness and composition of two ecologically different groups at a landscape level. I used a stratified randomized survey approach along key landscape gradients that are likely to change in the future: relative amount of woody vegetation and heterogeneity. These responses were measured within survey units that are meaningful in a social-ecological context (i.e. village catchments). In the following, I discuss four interlinked themes that emerged from my investigations, and which span the different studies. The first of these is the impact of land use on biodiversity patterns. This is followed by a discussion of the roles of woody vegetation and spatial heterogeneity for biodiversity. I then discuss how prospective land-use change on Transylvanian farmland may influence biodiversity and finally as a synthesis of the previous points I describe how biodiversity conservation in Transylvanian farmland is intricately linked with sustainable development.

Responses of biodiversity patterns to land use

The empirical studies which form part of this dissertation revealed the widespread occurrence of high species richness in the low-intensity farmland of Southern Transylvania. All land-use types – forest, arable land and grassland – contributed to the overall species pool in the landscape. Grasslands carried significantly higher species richness of vascular plants (Chapter 3), but not of butterflies (Chapter 4). Despite this widespread species richness, I observed that some species of conservation interest occurred exclusively in grasslands. The findings derived from the butterfly movement study (Chapter 6) also showed that some low- and medium-mobility butterfly species preferred grassland or uncultivated patches in farmland, while all butterflies tended to use less arable land for their movements than was expected from random movement. A distinction in species communities between land-use types was most strongly pronounced for vascular plants. Butterfly communities on grasslands and arable land however, showed a broad overlap. This finding also holds true for bird diversity in these landscapes (see Appendix 1). In my analysis, land-use type played an important role in species composition and species richness of vascular plants. It was not, however, possible to fully distinguish the effect of land-use type on richness patterns of butterflies from that of other drivers since land use interacted with several environmental variables and at several spatial scales.

My main conclusion from these observations is that both arable land and grassland in Southern Transylvania have a high conservation value for plants and butterflies. However, this conclusion may only

be valid given landscape characteristics comparable to Southern Transylvania, where arable land and grassland are interspersed at a fine spatial scale and also contain uncultivated elements and scattered woody vegetation. Arable land, depending on its structure, can provide resources for butterflies (Ouin et al. 2003) and serve as habitat for some species of wild plants. Nonetheless, most crop fields are considered unsuitable as habitat for many species; certain features of crop fields may also function as a barrier to movements (Ricketts 2001) and the presence of a species may simply result from spillover effects (Dunning et al. 1992). Yet, the structure of the farmland in Southern Transylvania at present seems to display a high connectivity of natural and semi-natural elements and to support high presence and abundances of overall species richness across its different landscape elements. (Bennett et al. 2006; Simmering et al. 2006; Vrdoljak and Samways 2014). A mixture of land-use types and a variety of structural elements may complement the habitat requirements of a species on farmland. In order to understand patterns of species richness it is important to consider the entire farmland mosaic across a landscape.

Responses of biodiversity patterns to woody vegetation

The amount of woody vegetation cover was one of the two underlying gradients in the stratification of the study area. This dissertation showed differing reactions in species communities to the amount of woody vegetation present in farmland sites at several spatial scales. At the local and the landscape scale, woody vegetation was the most important driver of diversity in plant and bird communities (Chapter 3; Appendix 1). Woody vegetation also affected butterfly species composition, but was not as important as other environmental variables. Farmlands with larger amounts of woody vegetation were positively related to richness in all investigated species. The reason for this may be that patches with woody vegetation in general represent relatively undisturbed areas that provide shelter, a distinct microclimate and space for thermoregulation (Dover et al. 1997). The benefit of woody vegetation for biodiversity, however, may be restricted to moderate amounts of woody vegetation. Areas with a high amount of woody vegetation cover, such as forests, host comparatively low species richness of plants and butterflies in Europe (Balmer and Erhardt 2000; Bengtsson et al. 2000).

Not all functional groups considered in this dissertation showed a positive relation to woody vegetation: arable weeds benefitted from the presence of trees and shrubs on arable land, whereas grassland indicator species showed a negative unimodal relationship to woody vegetation on arable land, but a positive relation on grassland. Butterfly species with a low mobility also responded in a negative unimodal way to woody vegetation. These findings may indicate that these butterflies depend on shelter in open landscapes; thus, they may avoid both too open and too densely vegetated patches. Furthermore, the movement study (Chapter 6) showed that highly mobile generalists were more inclined to quickly fly straight through wooded and complex landscapes, while low-mobility species tended to follow shorter flight paths which were more erratic. A possible explanation for this is that low-mobility species were unable to cross woody elements in the landscape; alternatively, this movement behaviour may also exhibit a reaction to resources

that these butterflies were able to use in complex landscapes. Moreover, the presence of some butterflies may depend on the presence of trees and shrubs as their host plants.

In combination, these findings indicate that the presence of woody vegetation is an important component of a landscape supporting high biodiversity. However, woody vegetation also forms an integral part of spatial heterogeneity and it is difficult to interpret these phenomena separately. The presence of trees and shrubs can be part of the cultural landscape, but they can also grow as a consequence of natural succession after land abandonment. Hence, woody vegetation may reveal opposing effects on biodiversity patterns, and what is more, these can vary at different spatial scales. For instance, landscapes with a high proportion of forest cover were correlated with lower species richness in butterflies.

Effects of heterogeneity on biodiversity patterns

The second underlying gradient for stratification of the landscape was spatial heterogeneity, defined here as the structural variability of characteristic patterns of repetitive land cover types and linear landscape features in the landscape. In the empirical parts of this study, I included various measures of heterogeneity at several spatial scales. The response variables of interest, such as species richness, species presence and movement patterns, showed significant relations to several of these metrics at several spatial scales. Plants responded in a range of different ways to variables representing structural heterogeneity, as represented by woody vegetation cover at the local and the landscape scale, and to land-use heterogeneity at the landscape scale. Heterogeneity, as represented in this dissertation by topography, land cover types and spectral variance of the monochromatic channel of SPOT 5 satellite imagery, turned out to be an important driver of the species composition of plants. Land cover heterogeneity was generally beneficial for grassland indicator species, while topographical heterogeneity was the most important variable for plant species richness on arable land, but this applied only to a lesser extent to grasslands. Land-use heterogeneity at a landscape level was a driver of species composition in butterflies, with environmental variables such as the presence of woody vegetation and plant species richness being an indirect aspect of heterogeneity. Furthermore, heterogeneity played a role for species richness at the context level; that is within an area of 50 ha. However, the effects of heterogeneity variables on butterfly movements were relatively weak. These patterns can be understood as a proxy of land-use intensity and are inherently linked with the heterogeneity of a landscape. Arable land in Transylvania harbours large amounts of semi-natural elements which increase heterogeneity and provide niches for many species.

Overall, the heterogeneity of landscapes has been suggested as a major driver of farmland biodiversity (Benton et al. 2003; Tschardt et al. 2012). Heterogeneous landscapes, for example those with a high proportion of semi-natural habitat and organic farming systems are often associated with greater species richness than their counterparts (Rundlöf and Smith 2006; Batary et al. 2011; Tuck et al. 2014). Nonetheless, the relationship between heterogeneity and species richness may be more complex (Redon et al. 2014), since processes linked to heterogeneity are known to depend on the spatial scales at which they are measured (Pickett and Cadenasso 1995) and thus to describe more than one phenomenon.

Heterogeneity may reflect a high structural diversity, but it can also reflect a high amount of habitat fragmentation. Effects of heterogeneity depend furthermore on the species of interest, since different species perceive heterogeneity differently (Gustafson and Gardner 1996). Heterogeneity can be conceptualized in several ways, and as such heterogeneity may not *per se* be beneficial for biodiversity. In this dissertation, I showed that it was not only heterogeneity that explained biodiversity patterns, but that the wider surroundings also explain why some farmland is richer in biodiversity than others. I conclude that in order to compare different components of the landscape, heterogeneity should be considered jointly with the wider landscape context and include different metrics at several spatial scales (Wagner et al. 2000; Diacon-Bolli et al. 2012).

Potential impacts of land-use change on Transylvanian farmland

Transylvania maintained traditional land-use practices and small-scale structures over centuries, and farmland forms an integral part of the cultural landscape in the region. In this dissertation, I found significant correlations between biodiversity and environmental parameters which are likely to change in the course of projected changes in the future (see Chapters 3 and 4). In the following, I will touch on the drivers of these changes and describe the impacts they may have on the biodiversity of Transylvania's farmland. A limitation to this kind of approach is that, due to the necessarily short observation period, the effects of abandonment and intensification on biodiversity cannot be measured directly, but could only be based on the assumption that heterogeneity and the amount of woody vegetation would change over time with future land-use change. In other words, my surveys displayed snapshot investigations in which differences in spatial conditions were a substitute for temporal variation. Consequently, my conclusions are by necessity based on observations from the natural experiments that I conducted.

The traditional practices which create the small-scale farmland mosaic are currently at risk of developing towards either land abandonment or land-use intensification (Plieninger et al. 2006; Hanspach et al. 2014). These two processes are fostered by the decreasing profitability of agricultural practices in Romania (Kuemmerle et al. 2009; Robu et al. 2009) and will eventually lead to landscape simplification. Simplified or homogeneous landscapes typically include fewer structural elements, such as the amount of woody vegetation scattered throughout arable land, the area and configuration of uncultivated or fallow patches, and the sizes of individual arable fields (Tschardt et al. 2005; Stoate et al. 2009). This loss of landscape complexity will decrease species richness, change species composition and influence the diversity of functional groups (Baur et al. 2006; Sanderson et al. 2013; Rader et al. 2014). In particular, species with low dispersal abilities have been shown to be disadvantaged in such settings, whereas generalist and highly mobile species thrive. Hence, landscape simplification leads to a homogenization of species communities (Ekroos et al. 2010; Börschig et al. 2013).

Only recently, the exposure of yield gaps in Eastern European farmland led to recommendations to improve agricultural productivity (Mueller et al. 2012). Moreover, the industrialization of agriculture and the accompanying increase of field size and use of agrochemicals are being promoted as a way to improve

the economic situation in Romania (Robu et al. 2009). However, the application of agrochemicals on cropland as a means towards land-use intensification will probably have irreversible, negative effects on several species groups and on the surrounding ecosystems. Hence, boosting the intensification of farming in this area would very likely occur at a cost to biodiversity (Chapter 8). Furthermore, it may not be able to stop the current rural exodus trend, since it will only provide little employment in the rural landscape of Romania. Moreover, the operating costs and large investment sums involved are not likely to offer a perspective for small-scale farmers. They will ultimately be excluded from the markets and thus probably discouraged from participating in the traditional agricultural system. Hence, it is not the farming practices themselves but the current negative conditions, coupled with the exodus from the rural areas to the cities, which is culminating to detach the rural population from their land (Edelman et al. 2014).

Linking biodiversity conservation to sustainable development of rural social-ecological systems

Biodiversity conservation is at the core of Romania's rural development plan and of EU-wide interest. Biodiversity conservation supports multiple ecosystem functions that agricultural landscapes fulfil and enhances the resilience of the cultural social-ecological system by increasing the ability to buffer environmental changes (Hooper et al. 2005; Balvanera et al. 2006; Fischer et al. 2006). Often undervalued but crucial services that farmland provide are the delivering of valuable goods such as food, fibre, fuel and other collectables, recreational value, traditional knowledge, freshwater and carbon storage (Hartel et al. 2014). Land-use change towards agricultural intensification and land abandonment risk the loss of such functions and eventually have negative consequences for human well-being (Stoate et al. 2001; Millennium Ecosystem Assessment 2005). Hence, biodiversity conservation is intrinsically linked with the maintenance of the beneficial ecosystem functions which are needed for a sustainable transformation of Transylvanian rural social-ecological systems.

One currently implemented mechanism to protect species richness and ecosystems is the establishment of protected areas within the EU Habitats and Birds Directives. This dissertation revealed that species richness patterns in several species groups were not linked to areas designated as protected, but were widely distributed across farmland (Chapters 3 & 4). Hence, my findings present evidence that agricultural productivity and biodiversity do not necessarily have to be negatively correlated. Consequently, restricting biodiversity conservation to protected areas in Southern Transylvania may be useful for some species, but is not a panacea which safeguards the overall species diversity of the landscape. Instead of applying a fortress conservation approach for certain land-use types, the entire farmland mosaic and the species pool across the entire landscape should be integrated into conservation programs (Perfecto and Vandermeer 2010). Management strategies should account for a range of different and contrasting effects of environmental conditions on species richness and particular species groups inside and outside of protected areas and consider different strategies for various biotopes.

Other policy tools that aim at conserving the environment are agri-environment measures which are part of the EU Common Agricultural Policy. However, these tools have recently been evaluated as insufficient to prevent biodiversity loss (e.g. Kleijn et al. 2011; Pe'er et al. 2014). One reason for this may be that the employed measures stem from evidence based on research conducted in Western European countries, since a lack of knowledge has so far meant that they have not yet been adapted to the species-rich farmlands in Eastern Europe (Sutcliffe et al. 2014). Moreover, individual measures and field management cannot be evaluated separately from landscape effects (Rundlöf et al. 2008), which is why agri-environment measures need to be put into a wider context in order to be meaningful. Current shortcomings in EU regulations and worldwide recommendations for greening agricultural process risk a more extensive use of pesticides, increases in farm size and the use of technologies. Under the premise of improving food security and acting sustainably, research and management implications currently risk endangering the high biodiversity rates and disrupting ecosystem services on Transylvanian farmland (Chapter 8). Hence, holistic assessments on the effect of biodiversity are needed in order to evaluate the sustainability of mechanisms in sustainable agriculture.

Within the context of functioning social-ecological systems, it remains a major concern to understand and address the underlying system of values and the intrinsic motivation of local people to manage the land. Education can help to raise the interest of local people in the environment and support the goal of implementing biodiversity conservation at different societal levels (Chapter 7). Traditional farming practices, i.e. small-scale agriculture with low amounts of external input, seem to benefit biodiversity in the cultural landscape of Southern Transylvania thanks to the existing gradients of woody vegetation and heterogeneity at several spatial scales. However, this way of farming is increasingly becoming unviable and may not be a way of life that farmers desire to follow any longer. Currently, the rural exodus is leading to a loss of traditional agriculture, imposing uncertainty regarding the future of rural social-ecological systems (Poschlod et al. 2005). This process will most likely lead to land-use intensification and land abandonment, thereby compromising the biodiversity of the landscape. A holistic landscape-ecology perspective provides a useful framework with which to investigate the opportunities for a sustainable development which integrates biodiversity conservation, the well-being of humans and their economic interests (Opdam et al. 2013; Hanspach et al. 2014). Alternative forms of governance need to be found to navigate the transformation of the social-ecological system into a desirable state with a future (Martín-López and Montes 2014), which will benefit local people and at the same time safeguard the natural capital of the land, including its biodiversity.

Chapter 2

Developing robust field survey protocols in landscape ecology: A case study on birds, plants and butterflies

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Abstract

Sustainable land management requires scientists to provide reliable data on diversity distribution patterns. Resource restrictions limit the affordable sampling effort, both with respect to number of survey sites and amount of effort per site. We compared different levels of survey effort in a case study in Central Romania, varying the number of repeats per site and number of survey sites. Target taxa were plants, birds and butterflies. For plants, we surveyed three 10 m² plots and ten plots of 1 m² at each site. For birds, we used point counts and for butterflies Pollard walks, in both cases with four repeats. We fitted hierarchical community models to estimate true species richness per site. Estimates of true species richness per site strongly correlated with observed species richness. However, hierarchical community models yielded unrealistically high estimates of true species richness per site, hence we used observed richness for further analyses. For each species group, we compared diversity indices from subsets of the dataset with the full dataset. Findings obtained with a reduced survey effort reflected well those obtained with full effort. Moreover, we conducted a power analysis to assess how the number of survey sites affected the minimum detectable effect of landscape heterogeneity on species richness, and found there was an exponential decrease in the minimum detectable effect with increasing number of sites. In combination, our findings suggest that assessing broad diversity patterns in abundant and readily detectable organisms may be possible with relatively low survey effort per site. Our study demonstrates the utility of conducting pilot studies prior to designing large-scale studies on diversity distribution patterns.

Introduction

Human land use is a major driver of biodiversity loss (Sala et al. 2000). However, not all types of land use are equally threatening to biodiversity, and some strategies of land management can effectively sustain substantial biodiversity (Tscharntke et al. 2005; Rands et al. 2010; Mouysset et al. 2012). One of the prerequisites for appropriate land management is a thorough understanding of species distribution patterns, often across entire landscapes or regions (Gaston 2000; Dover et al. 2011). Quantifying distribution patterns, in turn, demands robust and reproducible field survey protocols for a range of different species (Lobo et al. 2010). Important variables in this context include patterns of local species richness (Yoccoz et al. 2001), species turnover (Tylianakis et al. 2005; Kessler et al. 2009), and species composition (Klimek et al. 2007).

Research projects investigating biodiversity distribution patterns are usually constrained by limited resources including money, personnel and time (Field et al. 2005; Baasch et al. 2010). These constraints pose limits on the affordable sampling effort, both with respect to the number of sites surveyed and the amount of effort per site. Scientists may opt for applying substantial effort at relatively few sites or for surveying a large number of sites with reduced effort. Collecting data in ways that allow the detection process to be modelled is often considered important to minimize the impact of false absences, especially in the case of animals (MacKenzie et al. 2002; Stauffer et al. 2002; Lahoz-Monfort et al. 2013). This is often done by repeatedly surveying a given site, but other methods are possible such as recording times to detection (Guillera-Arroita et al. 2011).

To collect reliable data using limited resources, ecologists thus face a trade-off between the number of survey sites and the number of repeated surveys at each sample site (Suarez-Seoane et al. 2002; Bailey et al. 2007; Guillera-Arroita et al. 2010; Bried et al. 2011; Reed et al. 2011; Reynolds et al. 2011; Guillera-Arroita and Lahoz-Monfort 2012). One tool to investigate tolerable information loss when survey effort is reduced is to evaluate the statistical power of the different survey designs (Field et al. 2005; Legg and Nagy 2006; Bailey et al. 2007; Vellend et al. 2008; Guillera-Arroita and Lahoz-Monfort 2012; Sewell et al. 2012). Power analysis calculates the size of an effect that is detectable with a certain level of confidence and significance for a given design. Power increases as more effort is spent per site (given that detectability increases), as well as when the number of sites is increased.

In this study, we examined how estimated species diversity patterns changed with varying survey intensity and a varying number of survey sites. We focused on a case study in Central Romania, a region that is characterized by low-intensity land use practices (Baur et al. 2006; Kuemmerle et al. 2008; Fischer et al. 2012), which have created a heterogeneous landscape that supports high biodiversity (Rakosy 2005; Fischer et al. 2012; Page et al. 2012). However, biodiversity in the region is threatened by a series of complex socio-economic changes, including potential changes in land use. These changes include land abandonment and agricultural intensification (Bouma et al. 1998; Stoate et al. 2009; Akeroyd and Page

2011), both of which have been observed to negatively affect biodiversity elsewhere in Europe (Suarez-Seoane et al. 2002; Verhulst et al. 2004).

We conducted surveys for three taxonomic groups, namely plants, birds and butterflies, which are particularly diverse in Romania compared to most other parts of Europe (Akeroyd 2006). Our study served as a pilot to design subsequent large-scale surveys for these groups. First, we investigated the effect of increasing survey intensity on diversity patterns, as represented by species richness, turnover and composition. Second, we calculated the statistical power of alternative plausible designs varying in survey intensity and number of survey sites for a specific relationship, namely the relationship between landscape heterogeneity, represented by the variability in land covers within a specific area, and species richness.

Methods

Study area

The study was conducted within a 50 km radius of Sighișoara, southern Transylvania, Romania (45°45'48 N - 46°40'17 N; 24°8'7 E – 25°26'40 E). The landscape is undulating, with altitudes between 266 and 1095 m above sea level. It is characterized by a heterogeneous and fine-grained mosaic of different land uses, including substantial amounts of semi-natural vegetation. Approximately 37 % of land is arable, 24 % is grassland (pastures and meadows), and 28 % is covered by forests. We initially identified a large number of potential survey points by comprehensively walking the land around each of five villages, covering all major land covers around each village in the process. Based on this initial reconnaissance survey, we randomly selected 35 points as survey sites, located in arable land (n= 17), grassland (n=13) and forest (n= 5). Each survey site was defined as a circle measuring one hectare. Sites were located with a minimum distance of 200 m from each other and a maximum distance of 6339 m within one village.

Field surveys

Plants

We used two different survey approaches to quantify plant species richness and composition. First, we used a 'classical' approach at all 35 survey sites from 1st May to 30th May 2011. We established three 30 × 30 m plots in each 1 ha site. Within each 30 x 30 m plot, we selected one representative 3.16 × 3.16 m subplot, in which we recorded the presence and percentage cover of all vascular plant species (Figure 2.1). Second, we used a 'cartwheel' approach to resample plants in a subset of 19 (n: arable land = 6, grassland = 8, forest = 5) of the 35 survey sites from 1st June to 15th July 2011. We decided to only resample sites that have remained largely unchanged since the first sampling round, i.e. in which no harvesting or mowing have occurred. In each 1 ha site, we distributed ten plots of 1 × 1 m at a random distance from the middle point, every 36 degrees. We alternated the random distances so that five plots were distributed within 40 m of the center (the inner 0.5 ha) and five were located between 40 and 56 m from the center (the outer 0.5 ha; Figure 2.1). We then recorded the presence and percentage cover of all vascular plant

species in each plot. Phenological changes over the two survey periods were minor, and did not cause systematic differences in the species detected.

Birds

Birds were surveyed at all 35 sites using 20 min point counts (Bibby 2000) between 1st May and 8th June 2011, on those days without rain or strong wind (Figure 2.1). At each site, four surveys were conducted between 05:30 and 11:00 AM, noting the presence of singing males. We controlled for temporal bias by rotating the site order, except for the forest sites which were always surveyed first in the morning to maximize detections.

Butterflies

Butterflies were surveyed four times at 26 sites (12 sites in arable land, 12 grassland sites and two forest sites) by walking Standard Pollard Transects (Pollard and Yates 1993) between 1st June and 15th July 2011. At each site, we sampled four transects with a length of 50 m to the east, south, north and west from the center (i.e. total of 200 m per site; Figure 2.1). Surveys were conducted at a pace of 10 m per minute when weather conditions were appropriate (no rain, <90 % cloud cover, >17°C, no strong wind). All butterflies within 2.5 m on either side of a given transect were caught with a butterfly net, identified and released. For identification, we used pan-European and eastern European guides (Tshikolovets 2003; Lafranchis 2004).

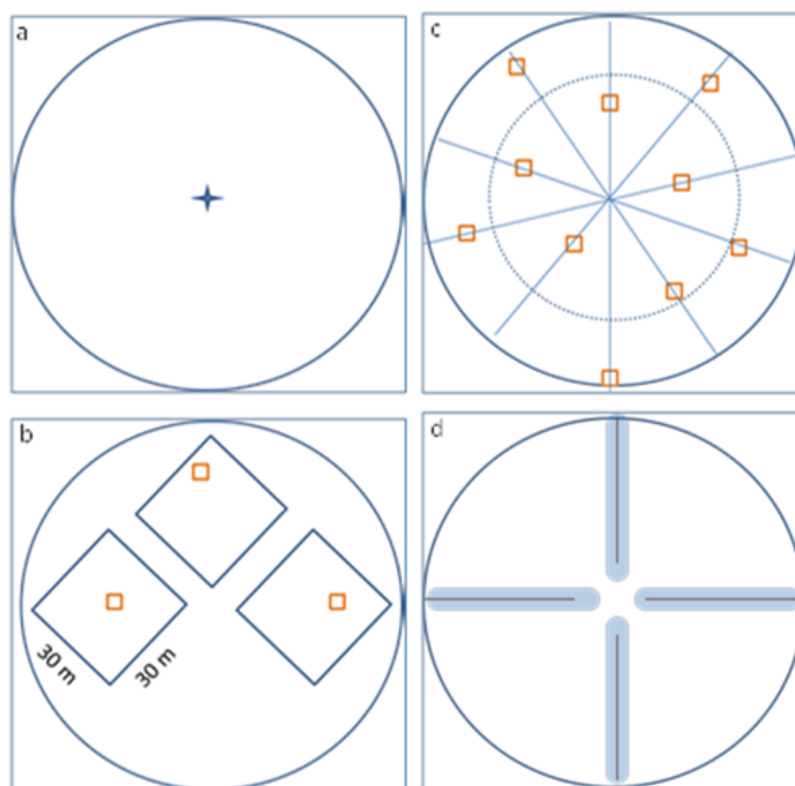


Figure 2.1: Illustration of the sampling scheme for (a) bird surveys; (b) plants surveys: classical approach; (c) plant surveys: cartwheel approach; and (d) butterfly surveys.

Analysis

Estimation of species richness and composition

We calculated species richness as the sum of all recorded species per taxonomic group over all plots or repeats in a given site. We calculated Whittaker's β - diversity index as a measure of species turnover among the sites and repeats in our dataset (Whittaker 1960; Anderson et al. 2011).

To compare plant survey methods, we correlated the species richness obtained by the two approaches using Spearman Rank correlation. In subsequent analyses, we considered data obtained by the cartwheel approach, since the randomized placement of plots within a site was more representative for the variation within a site.

We applied hierarchical community models to estimate true species richness at each site. Hierarchical community models can be used to estimate true species richness under consideration of the species specific detectability (Dorazio and Royle 2005; Dorazio et al. 2006). We considered the detectability of each species as a function of survey date and set the number of augmented species to 2/3 of the observed richness (Kéry and Royle 2009; Zipkin et al. 2009). Species augmentation accounts for the possibility that some species remained unobserved in a survey with imperfect detection. A community model with species augmentation will estimate the occupancy of unobserved species as a function of estimated detection probability of the observed species. The occupancy of observed and unobserved species, in turn, is used to calculate true species richness. Moreover, we assumed that detectability was constant and that populations were closed, that is, population sizes were constant and were not subject to processes such as recruitment, mortality or dispersal. Estimated true species richness at the site level was highly correlated with observed species richness (see results). However, the estimated values of true species richness were rather high for plants and butterflies (see results). This likely over-estimation probably resulted from the small number of sites and the fact that populations were not closed (for more details see: Kéry and Schaub 2012, pp. 414-461). Based on the high correlations with observed richness, but partly unrealistically high estimates for butterflies and plants, we continued further analyses using observed species richness rather than estimated true richness values as a baseline describing the outcomes of a “full survey effort”.

We described species composition using several multivariate analysis tools. To describe species composition we conducted detrended correspondence analyses (DCAs) with presence/ absence data for birds, and abundance data for plants. Abundance data of butterflies was analysed using principal component analyses (PCAs). We chose these ordination methods because the length of the gradient of the first DCA axis was > 3 for plants and birds and < 3 for butterflies (Ter Braak and Prentice 1988).

Assessment of the impact of survey effort reductions

For a given group of species, we were interested in comparing the data from a “full survey effort” with that of a “reduced survey effort”. Our full survey effort consisted of ten plots per site for plant surveys, four repeats per site for butterfly surveys, and four repeats per site for bird surveys. For each group, we

considered species richness, species turnover and species composition. We treated the results of species richness and species composition resulting from the full survey effort as “observed” richness and composition, respectively. We simulated subsets of the full survey effort by randomly dropping one to seven plots (for plants) or one to three repeats (for birds and butterflies) from the dataset. Random sampling of reduced datasets was repeated 100 times for each selection, and agreement of the reduced set was compared with the full dataset. Species richness and turnover of the reduced datasets was compared to the full dataset using Spearman Rank correlations.

We then assessed how strongly species composition changes when reducing the survey effort. This was done by using Procrustes analyses, which identifies differences of the locations of objects between two ordinations. Comparisons were performed between the ordination of the reduced dataset and the full dataset and differences were quantified by calculating a correlation based on the symmetric sum of squares between the two ordinations (Peres-Neto and Jackson 2001).

Power analysis of the effect of different survey designs

Study design and data quality fundamentally influence the statistical power in the analysis of survey data. We therefore investigated the effect of different designs on the power of linear models relating species richness with environmental variables. We used a simulation approach that reflects the nature of the variability in the field data, but in which the sample size can be varied. It is then possible to test how strong the actual effect of a specific variable needs to be, for a dataset with a certain sample size to detect such an effect.

Specifically, we applied power analyses to detect effects of landscape heterogeneity on species richness. The loss of landscape heterogeneity is a key concern in Europe’s agricultural landscapes (Benton et al. 2003), and is particularly relevant to our study area where low-input, small scale farming is increasingly replaced by industrialized high-input agriculture. We limited this analysis to arable sites, because this is where heterogeneity is most likely to be lost in the future due to land use intensification. We calculated heterogeneity as the standard deviation (SD) of the Normalized Difference Vegetation Index (NDVI) from 10 m monochromatic SPOT data (©CNES (2007), Distribution Spot Image SA) within each of the one hectare (arable) sites.

The methods used for the subsequent simulations are described in detail by Bolker (Bolker 2008), and are summarized here for our data. During the simulation we increased the sample size from the original number of 17 sites of arable land to a hypothetical maximum of 170 sites. We generated explanatory data from a uniform distribution spanning the range of heterogeneity values observed in the original 17 sites. We also varied effect size from no effect to a strong effect, that is, from no change in species richness along the heterogeneity gradient to a change in species richness that equaled the maximum number of species that was counted in a single site (32 species for plants, 12 species for birds and 22 species for butterflies). This effect was converted to 200 increasingly large hypothetical slopes for a regression line (from slope = 0 to increasingly steeper slopes). Based on a given slope, we simulated species richness for

each taxonomic group. To these simulated species richness values, we added a random variation. Random variation was generated by randomly drawing values from a normal distribution with a mean of zero and a standard deviation as large as in the original species richness data (10.27 for plants, 1.93 for birds, and 5.43 for butterflies). For this purpose, we used the plant richness data from surveying seven plots, and bird and butterfly richness data from three repeated surveys.

For each dataset thus generated, we fitted a simple linear model of simulated richness on simulated heterogeneity. We repeated this process 1000 times for each combination of number of survey sites and slope. For each combination of number of survey sites and slope, we noted how often we found a significant effect in the simulated data. Because data were simulated to be variable, sometimes the simulated effect was detected at the significance level of 0.05, and sometimes no effect was detected despite there being one (type II error). We were interested in how the incidence of type II errors varied with the number of survey sites and effect size (slope) – both more survey sites and steeper slopes will reduce the incidence of type II errors, that is, lead to greater statistical power. For each examined taxonomic group, and for a given number of survey sites, we noted the minimum slope (“minimum detectable effect” or MDE) at which the type II error rate was < 0.2 (i.e. power > 0.8). In a last step, the MDE was expressed as the difference in the number of species between the site with the lowest and highest heterogeneity.

Results

We detected 293 vascular plant species from 35 sites with the classical approach and 310 plant species from 19 sites with the cartwheel approach. We recorded 53 bird species (35 sites) and 81 butterfly species (26 sites) (Table 2.1). We found the highest values for species turnover between sites for plants with the classical approach (mean \pm SD: $\beta = 12.6 \pm 11.1$) and the cartwheel approach ($\beta = 8.8 \pm 5.9$), followed by birds ($\beta = 9.1 \pm 6.9$). Butterflies showed the lowest turnover ($\beta = 7.1 \pm 8.4$).

Plant species richness from the two different sampling methods was strongly positively correlated (Pearson correlation coefficient $r = 0.77$, $df = 17$, $P < 0.05$). Species richness differed between the two approaches most strongly within agricultural fields (Pearson correlation $r = 0.04$, $df = 5$, $P = 0.9$; non-arable sites: $r = 0.92$, $df = 12$, $P < 0.05$). Here, survey plots were selected to be within actual fields for the classical approach, while the random selection of plots in the cartwheel approach more frequently included weed and field edge vegetation. Consequently, estimates of richness were higher using the cartwheel method. There were positive correlations between the site-level richness of plants and butterflies (Pearson correlation $r = 0.42$, $df = 24$, $P < 0.05$; cartwheel approach $r = 0.71$, $df = 14$, $P < 0.05$), but no significant correlations between butterflies and birds ($r = -0.02$, $df = 24$, $P = 0.91$), and plants and birds (Pearson correlation $r = -0.004$, $df = 33$, $P = 0.98$; cartwheel approach $r = -0.39$, $df = 17$, $P = 0.1$).

Table 2.1. Mean species richness per site (and standard deviation) in the three land cover types surveyed. The most common species for each land cover type are also shown.

	<i>Plants</i>	<i>Birds</i>	<i>Butterflies</i>
Arable	47.4 ± 12.2	6.6 ± 3.2	18.0 ± 6.2
	<i>Festuca pratensis</i>	<i>Alauda arvensis</i>	<i>Maniola jurtina</i>
	<i>Taraxacum officinale</i>	<i>Acrocephalus palustris</i>	<i>Melanargia galathea</i>
	<i>Stellaria media</i>	<i>Sylvia communis</i>	<i>Plebeius argus</i>
	<i>Poa angustifolia</i>	<i>Saxicola rubetra</i>	<i>Coenonympha pamphilus</i>
	<i>Elymus repens</i>	<i>Lanius collurio</i>	<i>Polyommatus icarus</i>
	<i>Medicago sativa</i>	<i>Erithacus rubecula</i>	<i>Thymelicus sylvestris</i>
	<i>Rhinanthus rumelicus</i>	<i>Parus major</i>	<i>Leptidea sinapis/ juvernica</i>
	<i>Carex hirta</i>	<i>Fringilla coelebs</i>	<i>Thymelicus lineolus</i>
	<i>Capsella bursa-pastoris</i>	<i>Phylloscopus collybita</i>	<i>Everes argiades</i>
	<i>Symphytum officinale</i>	<i>Turdus merula</i>	<i>Aphantopus hyperantus</i>
Grassland	61.4 ± 13.1	7.4 ± 4.1	20.0 ± 6.1
	<i>Trifolium repens</i>	<i>Acrocephalus palustris</i>	<i>Maniola jurtina</i>
	<i>Festuca rupicola</i>	<i>Alauda arvensis</i>	<i>Melanargia galathea</i>
	<i>Achillea millefolium</i>	<i>Sylvia communis</i>	<i>Colias hyale/ alfajariensis</i>
	<i>Poa angustifolia</i>	<i>Saxicola rubetra</i>	<i>Everes argiades</i>
	<i>Taraxacum officinale</i>	<i>Saxicola torquata</i>	<i>Plebeius argus</i>
	<i>Festuca pratense</i>	<i>Passer montanus</i>	<i>Leptidea sinapis/ juvernica</i>
	<i>Anthoxanthum odoratum</i>	<i>Lanius collurio</i>	<i>Pieris rapae</i>
	<i>Crataegus monogyna</i>	<i>Motacilla flava</i>	<i>Polyommatus icarus</i>
	<i>Plantago lanceolata</i>	<i>Emberiza citrinella</i>	<i>Coenonympha pamphilus</i>
	<i>Trifolium pratense</i>	<i>Parus palustris</i>	<i>Aphantopus hyperantus</i>
Forest	20.2 ± 7.6	15.0 ± 2.6	2.5 ± 0.71
	<i>Carpinus betulus</i>	<i>Erithacus rubecula</i>	<i>Maniola jurtina</i>
	<i>Anemone nemorosa</i>	<i>Fringilla coelebs</i>	<i>Argynnis paphia</i>
	<i>Galium odoratum</i>	<i>Parus major</i>	<i>Inachis io</i>
	<i>Fagus sylvatica</i>	<i>Turdus merula</i>	<i>Pararge aegeria</i>
	<i>Viola reichenbachiana</i>	<i>Ficedula albicollis</i>	
	<i>Quercus petraea</i>	<i>Sturnus vulgaris</i>	
	<i>Dentaria bulbifera</i>	<i>Sylvia atricapilla</i>	
	<i>Astrantia major</i>	<i>Phylloscopus collybita</i>	
	<i>Stellaria holostea</i>	<i>Certhia familiaris</i>	
	<i>Helleborus purpurascens</i>	<i>Parus palustris</i>	

Mean observed species richness per site was 46.9 for plants; 17.7 for butterflies and 9.6 for birds. Observed species richness correlated highly with estimated true species richness from the hierarchical community models (plants $r = 0.83$, $df = 17$, $P < 0.001$; birds $r = 0.99$, $df = 33$, $P < 0.001$; butterflies $r = 0.99$, $df = 24$, $P < 0.001$). However, the absolute values of estimated mean richness per site were unrealistically high for plants and butterflies: Plants (mean; credible interval (2.5 % - 97.5 %): 92.6 (81.9 – 106.6); Butterflies: 60 (47.5 - 73.6); Birds: 9.4 (6.7 - 13.3). Hence, we continued all subsequent analyses using observed species richness. The average detection probabilities were estimated to be 0.25 for birds (± 0.15 SD), 0.17 for plants (± 0.12) and 0.16 for butterflies (± 0.17).

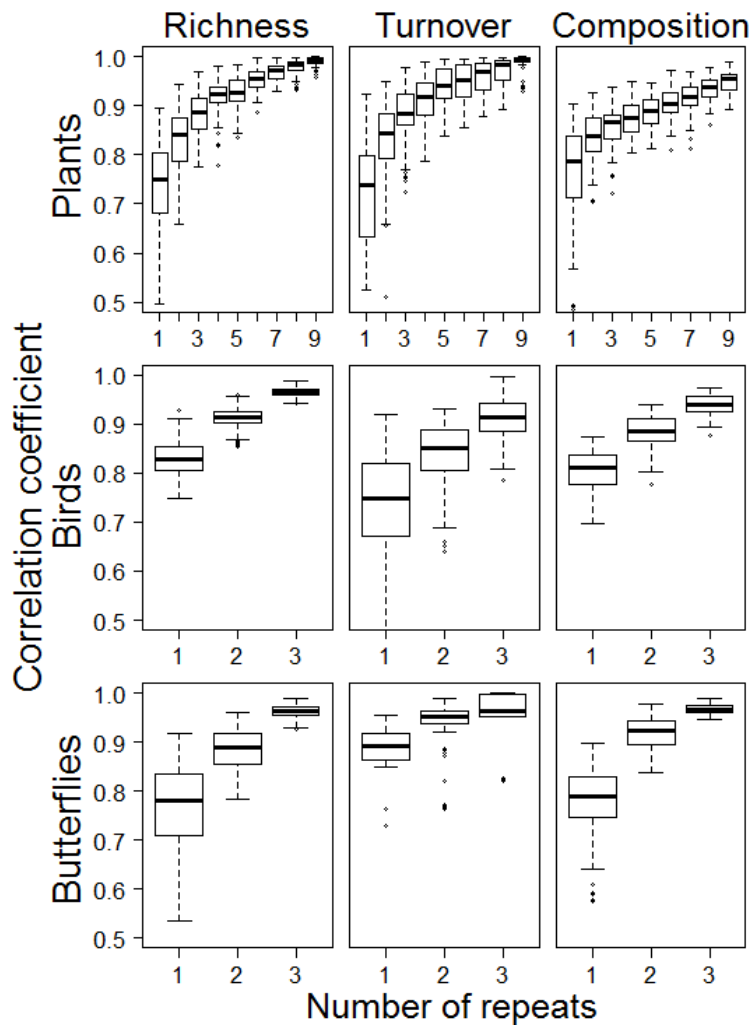


Figure 2.2: Correlations between data from reduced survey effort (1 to 9 plots for plants; 1 to 3 repeats for birds and butterflies) and the maximum survey effort (10 plots for plants; 4 repeats for birds and butterflies). Reduced survey effort was simulated by randomly sub-setting the full data set 1000 times for each level of data reduction.

Correlations between species richness from reduced survey effort and results from the full survey effort showed an overall pattern of asymptotic increase with increasing survey effort, especially for plants (Figure 2). For species turnover and composition, we also found consistently high correlations between estimates from reduced survey effort and full survey effort. For example, when considering seven plant plots per

site, three repeats for birds, and three repeats for butterflies, the mean correlations with estimates for the full dataset were > 0.9 , for species richness, turnover and composition (Figure 2.2).

Power analysis with simulated data showed an exponential decrease of the minimum detectable effect with increasing sample size. The marginal increase in statistical power per additional survey site was lower when the number of sites was already high (Figure 2.3). Minimum detectable effects were smallest for birds (1 species for 100 survey sites) and larger for butterflies and plants (approximately 3 species for 100 survey sites).

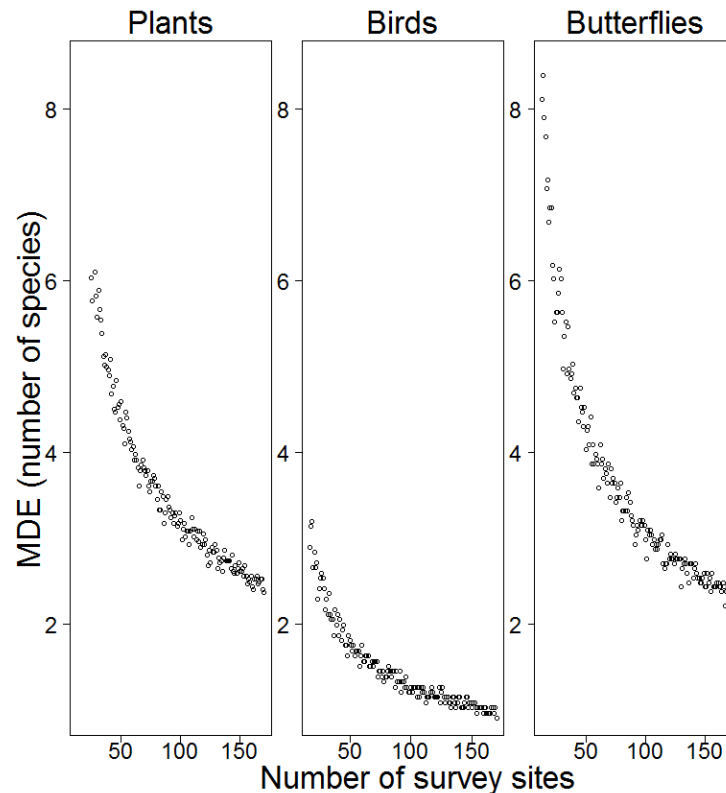


Figure 2.3: Power analysis with simulated data. Minimum detectable effect (MDE) is plotted as a function of the number of survey sites. MDE was defined as the absolute change in species richness along the observed heterogeneity gradient in arable fields that could be detected in a linear model with given sample size.

Discussion

Given the fast changes happening in human-dominated landscapes, ecologists need to use efficient survey protocols to be able to detect effects on wildlife. Field research projects face logistical, time and monetary constraints (Tyre et al. 2003), which inherently limit the affordable survey intensity. Dense sampling schemes – such as those that use survey protocols which aim to cover at least three percent of the area of a landscape with at least five repeats (Bried et al. 2011) – are rarely feasible. Typically, only small portions of the landscape can be surveyed (Stohlgren et al. 1997). A common approach therefore is to rely on a stratified random sampling design and then extrapolate data across the landscape (Stohlgren et al. 1997; Rosenstock et al. 2002).

Here, we present a protocol to assess the effects of survey effort on the detection of biodiversity patterns based on a case study. We show that for our data survey efforts per site could be moderately reduced, because the corresponding increase in bias was relatively small and relative biodiversity patterns remained stable. Such a reduction, however, needs to happen in a sensible and balanced way in order to assure sufficient statistical power to detect environmental effects on species richness. Also, this conclusion is based on the assumption that detection probability does not vary spatially.

Overall, our findings are broadly consistent with a range of previous works from different systems. For example, Stohlgren et al. (1997) tested reducing a larger set of plant sample replicates in different vegetation communities in the Rocky Mountains and found that already ten quadrats of one square meter per sampling unit provided sufficient information in order to detect fine-scale patterns of plant diversity. Similarly, other studies showed that in Australia and California, most animal species that were surveyed could be detected even if survey effort within a given sampling protocol was reduced to three repeat surveys (Field et al. 2005; Pellet 2008). Based on an assessment of birds, amphibians and invertebrates in Australia, Tyre et al. (2003) further suggested that with current survey methods, sampling from 100 sites and pooling data over three repeats yielded accurate results. This, too, is consistent with our findings – using 100 or more sites led to minimum detectable effects of changes in species richness in response to heterogeneity of three species for plants and butterflies, and one species for birds. Due to the coherences with findings from other studies, we assume our sampling protocol for landscape-scale surveys is applicable to other study systems as well.

Our results suggest that it can be reasonable to reduce survey effort per site when aiming at broad patterns of biodiversity and when the detectability of investigated taxa is high. Moreover, even a low survey effort per site can yield high statistical power provided that the survey effort per site is balanced in a meaningful way with the number of sites surveyed. A key advantage of using many sites is that data then is much more likely to be representative of the study area as a whole, which is valid at least for occurrence patterns of organisms with relatively high abundance and detectability. Abundance greatly influences detectability, and both factors determine whether a species is actually recorded (Royle and Nichols 2003). Rare species and species with a low detectability are highly susceptible to false absences compared to common species or ones with a high detectability, which can lead to an underestimation of their distribution (MacKenzie and Royle 2005; Lahoz-Monfort et al. 2013). Therefore, higher levels of survey effort are often recommended for rare species (e.g. Bried and Pellet 2012). In summary, we demonstrated a useful sampling protocol for assessing broad diversity patterns of relatively abundant species in response to environmental gradients (Vellend et al. 2008). However, we caution that our method may be of limited use for rare or cryptic species. Eventually, the required survey effort depends on the study area and the investigated species (Bried et al. 2012). With our case study, we provide an example how to allocate project resources meaningfully to obtain a high statistical power.

Conclusions

Developing field survey protocols is a challenging task for ecologists and demands thorough consideration of both theoretical and practical issues. Our results suggest that in Southern Transylvania, at least three temporal replicates on at least 100 study sites appeared to be sufficient to study landscape effects on diversity patterns of birds and butterflies following our sampling methods. To model plant diversity patterns, a combination of seven one square meter plots per one hectare site at approximately 100 sites appeared to be sufficient.

Before implementing landscape-scale surveys, we recommend ecologists conduct pilot studies for several reasons: (1) to trial and customize different techniques and sampling schemes; (2) to identify what is the most efficient use of available resources; and (3) to estimate the statistical power of plausible alternative designs. Our findings suggest that under certain conditions, relative patterns of biodiversity can remain relatively stable, when survey effort is moderately reduced. This in turn, can help to allocate resources to sampling more sites and to more representatively survey large areas. The general procedure presented in this paper is transferrable to other study systems and may be used as a guideline to help develop reasonable survey designs.

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Chapter 3

Plant diversity in a changing agricultural landscape mosaic in Southern Transylvania (Romania)

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III



Abstract

Traditional agricultural landscapes represent mosaics of land use covers that often support high species diversity. Many Eastern European countries contain large areas of High Nature Value (HNV) farmland. However, these landscapes are likely to change under current EU regulations and global market pressure, with potentially negative consequences for biodiversity. The conservation value of Romania's grasslands is widely recognized, but the potential conservation value of other parts of the landscape mosaic has not been assessed to date. For this reason, we sought to assess patterns of plant diversity across the entire landscape mosaic. We sampled vascular plants at 139 sites (comprising 8 plots of 1m²/ ha) in forest (n=23), grassland (n=57) and within the arable mosaic (n=59). To examine potential differences in species richness and composition between these land cover types, we used Analysis of Variance and Detrended Correspondence Analysis. We also modeled total species richness, richness of HNV indicator plants and richness of arable weeds in response to variables representing topography as well as structural and configurational heterogeneity. Species composition differed strongly between grassland, the arable mosaic and forests. Richness was highest in grasslands, but surprisingly, the arable mosaic and grassland contributed similarly to the cumulative number of recorded species. Models of species richness revealed a wide range of responses of plant groups to topographical conditions and to structural and configurational heterogeneity, which often differed between land use types. Plants were affected by conditions measured at both local (1 ha) and landscape (50 ha) scales. Noting the substantial, and hitherto under-recognised, contribution of the agricultural mosaic to regional-scale plant diversity, we recommend consideration of the entire landscape mosaic in future conservation schemes.

Introduction

Many agricultural landscapes around the world are characterized by a mosaic of land covers (Forman 1995). With their various patches of land-use types and structures, mosaic landscapes often host a wide range of species (Bennett et al. 2006). However, unprecedented changes in agricultural mosaic landscapes are causing major biodiversity loss worldwide (Tschardt et al. 2005). Moreover, patterns of species richness and distribution in agricultural landscapes are affected by processes operating at multiple spatial scales, including both local and landscape-level variables (Vandvik and Birks 2002; Rundlöf et al. 2010; Costanza et al. 2011). Hence, effective management of biodiversity in agricultural landscapes requires an assessment of the drivers of species diversity across multiple spatial scales.

In many Eastern European countries, such as Romania, traditional practices have created small-scale mosaic landscapes. For example, 72 % of farms in Romania are smaller than 1 ha (Fundatia Adept 2012), and individual fields are typically smaller than that. However, Romania's farmland has been undergoing drastic changes since the collapse of communism in 1990 (Kuemmerle et al. 2009) and accession to the European Union (EU) in 2007. Ongoing land use changes comprise both intensification of land use in some areas, and land abandonment in others (Government of Romania 2010; Dahlström et al. 2013; Mikulcak et al. 2013). At present, twenty percent of Romanian farmland is considered to be High Nature Value (HNV) farmland, and ten percent is protected under the EU Birds and Habitats Directives (Natura 2000) (European Environment Agency 2010). Despite official recognition of the ecological values of large areas of farmland, the future of Romania's agricultural landscapes and their biodiversity is uncertain.

Some of Romania's most notable mosaic landscapes occur in the region of Southern Transylvania. A large part of Transylvania was recently designated one of the largest continuous (lowland) Natura 2000 sites in Europe (i.e. Târnavelor Plateau), partly in recognition of its outstanding grassland diversity (Jones et al. 2010; Akeroyd and Page 2011). The region's biodiversity includes various taxa that are rare or endangered in other parts of Europe, such as the yellow-bellied toad (*Bombina variegata*) (Hartel and von Wehrden 2013), *Maculinea* butterflies (Vodă et al. 2010) and several rare species of woodpeckers (Dorresteijn et al. 2013). Moreover, Transylvanian dry grasslands hold the world record for vascular plant species richness at the scales of 0.1 m² and 10 m² (Wilson et al. 2012). However, land use change is likely in Transylvania, and would pose major threats to its biodiversity. Modifications of land use will most likely consist of increasing cropland area, increasing the use of agrochemicals, structural homogenization, and conversion of traditional hay meadows to pastures, thus mirroring the patterns already apparent in Western Europe (McLaughlin and Mineau 1995; Benton et al. 2003; Billeter et al. 2008; Ernoult and Alard 2011).

In this study we focus on vascular plants and their distribution throughout the entire landscape mosaic in Southern Transylvania. Plants respond relatively slowly to environmental changes (Helm et al. 2006), but in agricultural landscapes, specialized species are highly prone to rapid decline (Davies et al. 2004; Clavel et al. 2010). Plant communities in agricultural landscapes are at risk of homogenization in composition because of nutrient inputs, which many species, and especially grassland specialists, are sensitive to. For

Transylvania, a specific set of sensitive grassland specialists has been proposed to indicate High Nature Value (HNV) grassland (Akeroyd and Bădărașu 2012). Furthermore, arable weeds are of particular interest. Many such weeds have persisted in Transylvania to date, but are under worldwide decline, and may react quickly to changes in the environment, both at local and landscape scales (Gabriel et al. 2005; Armengot et al. 2012; Storkey et al. 2012).

We sought to understand the responses of vascular plant diversity to key landscape features. To that end, we used a snapshot natural experiment (Diamond 1986; Lindenmayer et al. 2008) that spanned a wide range of environmental conditions with respect to heterogeneity and woody vegetation cover across local and landscape scales. We sampled vegetation and environmental conditions throughout the landscape mosaic and asked: (i) how current land use was associated with vascular plant diversity and species composition; and (ii) how landscape structure was related to total richness, richness of HNV indicator plants and richness of arable weeds.

Methods

Study area

Our study area covered approximately 7,000 km² in the lowlands of Southern Transylvania, Romania. The area consists of undulating terrain with altitudes from 300 to 700 m above sea level, and its climate is subcontinental-temperate. The area comprises a mosaic of land use types, including arable fields (40 % according to CORINE land cover), secondary grasslands and ancient dry steppe-like grasslands (30 %) and deciduous forests (30 %) (Dengler et al. 2012). The natural vegetation consists of oak-hornbeam forests (*Quercus petraea*-*Carpinus betulus*; Bohn et al. 2004).

Site selection

We followed the notion of a natural experiment (Diamond 1986), with randomised site selection in pre-defined strata at two levels: (i) village catchments and (ii) survey sites within village catchments. We delineated the study area into village catchments using a cost-distance algorithm that allocated each pixel to the village with the lowest travel cost to this pixel (slope-penalized distance, implemented in ArcGIS 10.1). We randomly selected a subset of 30 village catchments within three different strata cross-combined by a gradient of terrain ruggedness (low, medium, high; defined by quantiles) and protection status according to EU Birds and Habitats Directives (Site of Community Importance (SCI), Special Protection Area (SPA) and unprotected; Table S3.1). Within each village catchment, we assigned land to three different land use types using the CORINE land cover map (EEA 2010), namely forest, grassland or arable land. By “arable land”, we refer to the mosaic of arable land in its entirety, including semi-natural vegetation occurring within the mosaic, such as field margins, road verges, hedges and old fields. Throughout grassland and arable land (collectively termed “farmland”), we identified gradients of heterogeneity and woody vegetation cover. We quantified heterogeneity as the standard deviation of panchromatic SPOT 5 data (© CNES 2007, Distribution Spot Image SA) within a 1 ha moving window.

We calculated the percentage of woody vegetation within a 1 ha moving window by supervised classifications of the panchromatic channels of SPOT 5, using a support vector machine algorithm (Knorn et al. 2009). We used the upper, middle and lower thirds of these gradients to randomly select cross-replicated circular 1 ha survey sites – 59 within arable land and 57 within grassland (Table S3.2). An additional 23 sites (also measuring 1 ha) were randomly selected in forest without further stratification.

Vegetation surveys

We conducted vegetation surveys between 26 May and 26 August 2012. We sampled eight plots measuring 1 m x 1 m within each site, placed at a random distance from the center, and distributed every 45 degrees. We alternated between random distances > 40m and < 40m from the center to cover the inner and the outer 0.5 ha of the site equally. In each plot, we identified vascular plants to species level and recorded their percent cover.

Environmental parameters

We considered variables that were potentially related to plant species richness within circles of one hectare (henceforth: local level) and circles of 50 hectare (henceforth: landscape level) around a given site. At the local level, we considered heterogeneity, altitude, woody vegetation cover, a heat index (after Parker (1991): $\cos(\text{slope aspect} - 225) * \tan(\text{slope angle})$), a terrain wetness index (after Fischer et al. 2010), and land cover type. At the landscape level, we considered terrain ruggedness, woody vegetation cover, edge density to account for configurational heterogeneity (Fahrig et al. 2011), and a Simpson index of heterogeneity to account for compositional heterogeneity. Variables were calculated using ArcGIS 10.1 and Fragstats 4.1, and are described in more detail in Table 3.1.

Statistical analyses

The analyses consisted of three steps. First, we compared the means of alpha and beta richness (sensu Tuomisto 2010) between the different types of land use and different levels of protection status. Second, we investigated patterns in community composition. Third, we modelled richness of all plant species, richness of HNV indicator plants, and richness of arable weeds as a function of environmental predictors. To visualize the resulting diversity patterns at a regional scale, we predicted species richness across the entire study area.

Patterns of alpha and beta richness

For all analyses, we pooled individual plots ($n = 8$) within a given site (1 ha) to obtain a relative estimate of plant species richness at the local level. First, we compared species richness between the different land use types (arable, grassland, forest) and different levels of protection status (SCI, SPA and unprotected) using Analysis of Variance (ANOVA). Second, we illustrated additive beta richness (Lande 1996) using species accumulation curves, and calculated species turnover by additive partitioning of species richness (Veech et

al. 2002; Tuomisto 2010). We tested differences in beta richness between land use types using ANOVA and a post-hoc Tukey test of Honest Significant Difference (HSD).

Table 3.1 Definition and method description of the explanatory variables used to model plant species richness

Scale	Variable	Definition and method
local (1 ha)	Heterogeneity	Heterogeneity measured as the standard deviation of 2.5 m panchromatic SPOT 5 data ^a
	Altitude	Altitude above sea level derived from ASTER DEM ^b
	Woody vegetation cover (woody 1ha)	Proportion of woody vegetation cover based on supervised classification 10m SPOT 5 data ^a
	Heat index	Potential for ground heating calculated after Parker (1991): Heat index = $\cos(\text{slope aspect} - 225) * \tan(\text{slope angle})$
	Terrain wetness index	Measure of potential soil wetness, estimated as the topographic position in the landscape and the slope ^b (after Fischer et al. 2010)
	Land cover	Land use classification as arable land, grassland or forest based on CLC ^c
landscape (50 ha)	Ruggedness	Terrain ruggedness, calculated as standard deviation of altitude ^b
	Woody vegetation cover (woody 50ha)	Proportion of woody vegetation cover based on classified 10m SPOT 5 data ^a
	Edge density	Configurational heterogeneity of different land covers, based on CLC ^{c,d}
Random effects	Village catchment	Classification of the landscape into social-ecological units according to a cost distance algorithm of proximity to the nearest village as reference point and the slope of the terrain as cost factor
	Level	Observation level random effect

Species composition analysis

We conducted Detrended Correspondence Analysis (DCA) to describe species composition at the local level and to assess its relation to possible underlying environmental gradients. We first performed DCA including all survey sites. To more clearly capture patterns in species composition within farmland, we performed a second DCA excluding forest sites. For both DCAs, we used a permutation test with 1000 permutations to correlate environmental variables with the ordination.

Species richness models

We used generalized linear mixed effects models (GLMMs) to assess the effects of environmental variables on richness of (i) all plant species, (ii) HNV indicator plants, and (iii) arable weeds. In all cases, we specified village catchment and site (to account for overdispersion) as random effects. Only farmland sites (i.e. arable land and grassland) were used in this analysis, because forests differed fundamentally in structure and composition. Prior to the modelling procedure, we tested the predictor variables for collinearity. Based on this, we excluded the Simpson index of heterogeneity, because it was highly correlated with edge density. Furthermore, we log-transformed local heterogeneity, local and landscape woody vegetation cover and landscape edge density to (near-) normal distribution and standardized all continuous variables to zero mean and unit variance. We calibrated the models using a randomly selected subset of 75 % of the data. We included interactions of land use with all environmental variables, because we considered responses may differ substantially between arable land and grassland. We derived the final minimum adequate models using stepwise backward model selection ($P \leq 0.1$). To validate the final models, we predicted species richness on the remaining 25 % of the dataset and compared the predicted species richness with observed species richness using Pearson correlations.

Finally, to obtain a regional-scale overview of species richness patterns, we predicted total plant species richness throughout the farmland of the study area, based on the fixed effect estimates of the final model. For this purpose, we used a raster of data points with a grid size of 1 ha that lay within the calibration range of the environmental variables as measured in our field samples ($\pm 5\%$). We plotted the results in a cumulative richness density curve to visualize what proportion of the study area's farmland supported species richness values above or below particular thresholds. All analyses were performed in R, using the packages *vegan*, *lme4* and *bbmle* (R Core Team 2013).

Results***Diversity patterns***

In total, we identified 603 vascular plant species in 139 sites, of which 25 % occurred exclusively in pastures, 20 % exclusively in arable land and 7 % exclusively in forests (Figure 3.1a). Of all species, 30 % occurred in more than one land use type. We found a maximum of 50 species per $1\text{ m} \times 1\text{ m}$ plot (mean \pm standard deviation: 14 ± 9) and a maximum of 84 species per 1 ha site (42 ± 21). Species richness differed significantly between the three land use types (ANOVA: $F_{2, 136} = 81.47$, $P < 0.001$), but not between Natura 2000 and unprotected sites (ANOVA: $F_{2, 136} = 0.07$, $P = 0.93$). A comparison of beta richness revealed significant differences between land use types (ANOVA: $F_{2, 136} = 81.47$, $P < 0.001$). Species accumulation curves illustrated that grasslands had the highest beta richness, closely followed by arable land (Figure 3.1b).

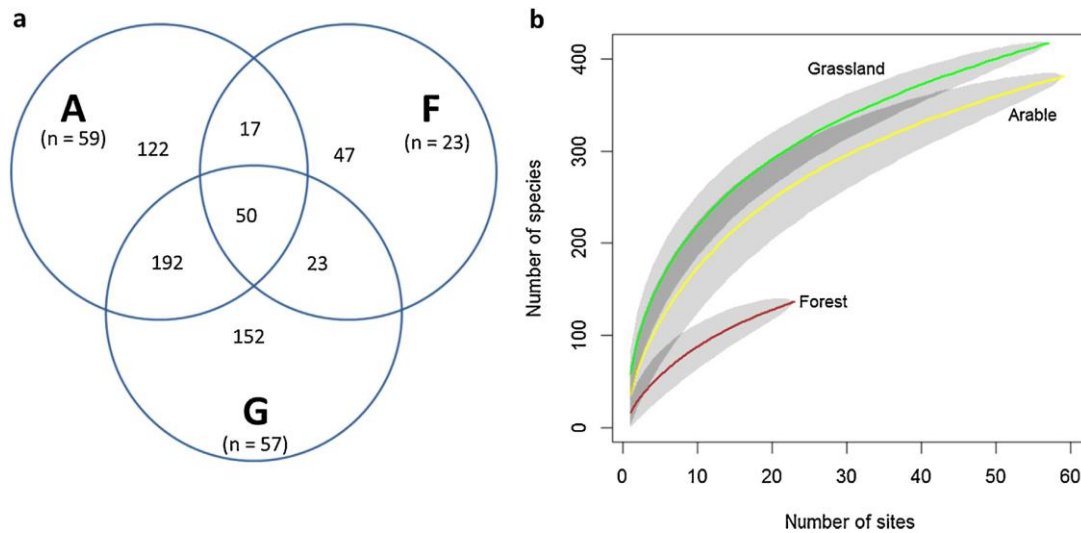


Figure 3.1. (a) Number of plant species that occurred exclusively in or were shared by the different landuse types, arable land (=A), grassland (=G), and forest (=F). (b) Species accumulation curves in the three different landuse types.

Species composition

DCA ordination with all land use types showed a clear separation of the three land use types (Figure 3.2a). It revealed woody vegetation at the local and the landscape scale as the strongest underlying environmental gradients and both correlated with the first axis (length of axis 1= 4.92, Figure 3.2a), which indicated more than one full species turnover. The second axis (length = 3.48) described gradients in topography and heterogeneity, represented by the terrain wetness index and heterogeneity at the local scale, and ruggedness and edge density at the landscape scale. The DCA ordination restricted to farmland sites showed a separation of grassland and arable sites, with only a small overlap of sites (Figure 3.2b).

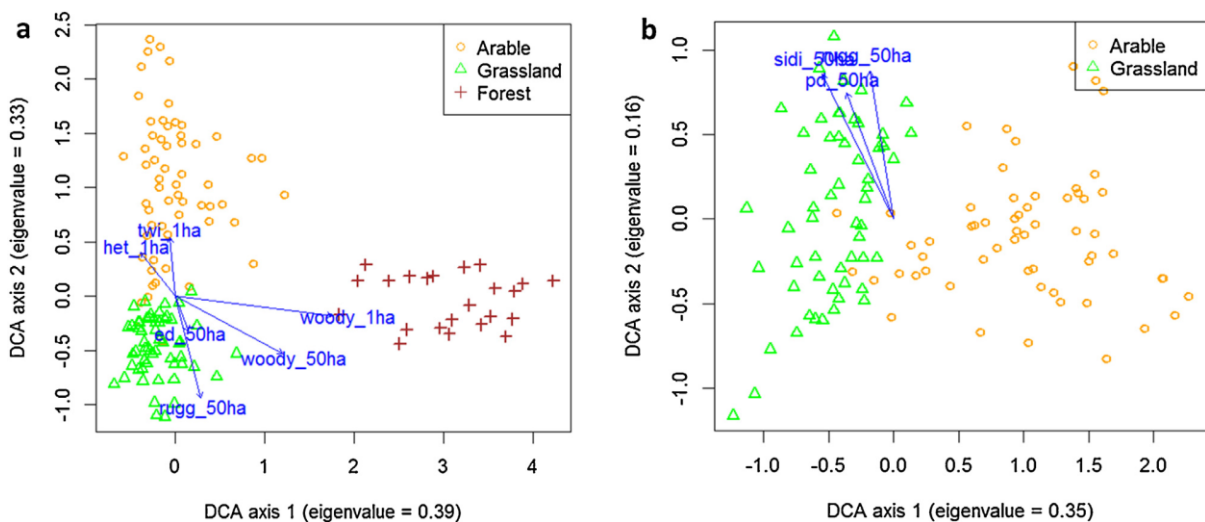


Figure 3.2. (a) Detrended correspondence analysis including all survey sites; (b) DCA with agricultural sites only. Significantly correlated environmental variables are superimposed (p < 0.05) (abbreviations: TWI_1 ha = local terrain wetness index; het_1 ha = local heterogeneity, ed_50_ha = landscape edge density; rugg_50 ha = landscape terrain ruggedness; woody_50 ha = landscape woody vegetation cover; woody_1 ha = local woody vegetation cover; SIDI_50 ha = landscape compositional heterogeneity; pd_50 ha = landscape configurational heterogeneity).

None of the measured environmental variables were significantly correlated with the first axis (length = 3.51), which corresponded to approximately one full species turnover. The second axis of the DCA (length = 2.24) correlated with landscape variables, including both topography and configurational and compositional heterogeneity.

Species richness models

Independently of the land use type, local woody vegetation cover was positively related to total species richness (Figure 3.3a). Total plant species richness was higher in grassland than in arable land (Table 3.2). Terrain ruggedness at the landscape scale affected species richness positively in arable land, but negatively in grasslands. The terrain wetness index had a negative effect on species richness in arable land, but a slightly positive effect in grasslands (Table 3.2).

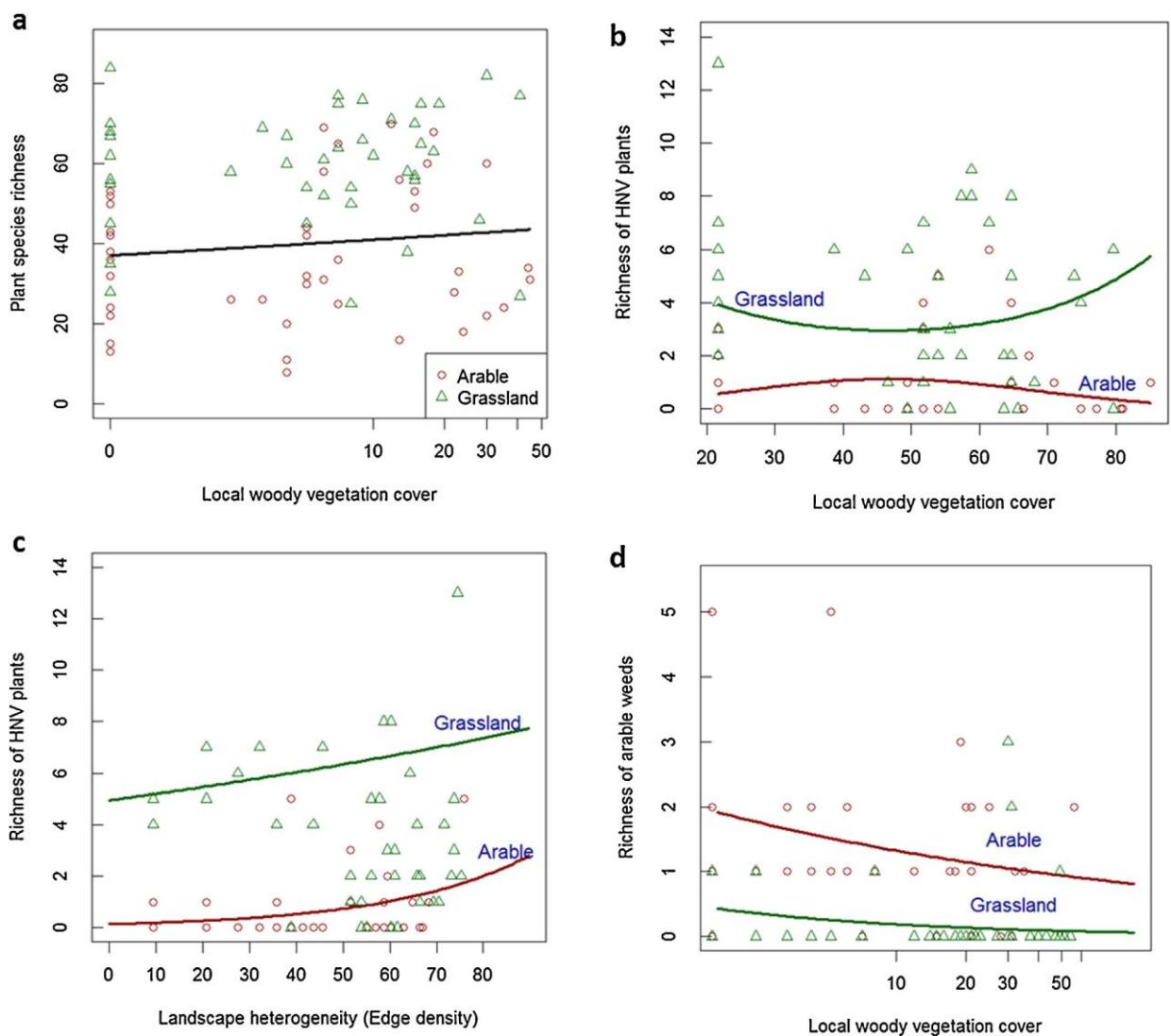


Figure 3.3. Results of generalized linear mixed effect models for relative richness of total species, HNV indicator species, and arable weeds. Relationships are based on the final models summarized in Table 3.2.

Table 3.2. Results of generalized linear mixed models for total plants species richness, richness of grassland specialists, High Nature Value (HNV) indicator plants and arable weeds. Parameter estimates are shown, with significance levels indicated by: † P<0.1; *P<0.005; **P<0.01; ***P<0.001

Explanatory Variable	Response Variable	Total plant richness	HNV plants	Arable weeds
Intercept		3.648	0.178	0.277
Grasslands		0.453 ***	0.822 *	- 2.292 ***
Arable: altitude				
Arable: edge density			0.969 ***	
Arable: heat index				
Arable: heterogeneity				
Arable: ruggedness		0.215 **	0.933 **	
Arable: terrain wetness index		-0.136 **	-0.347 †	
Arable: woody1ha				-0.249 *
Arable: (woody 1ha)^2			-0.722 *	
Arable: woody 50ha				
Grassland: altitude				
Grassland: edge density			-0.918 **	
Grassland: heat index				
Grassland: heterogeneity				
Grassland: ruggedness		-0.234 **	-0.879 *	
Grassland: terrain wetness index		0.163 †	0.45 †	
Grassland: woody 1ha				-0.106
Grassland: (woody 1ha)^2			0.931 **	
Grassland: woody 50ha				
Altitude				
Edge density				
Heat index				
Ruggedness				
Woody 1ha		0.077 †	-0.146	
Woody 50ha				

Predicting total species richness across the study area highlighted that the results from the training model correlated well with our field observation (total species richness: Pearson's $r = 0.75$; grassland specialists: $r = 0.76$; HNV plants: $r = 0.69$; arable weeds: $r = 0.76$). Predictions for total plant species richness throughout the farmland mosaic of our study area resulted in predicted values between 12 and 77 species per hectare (Figure 4). The distribution of predicted values illustrated the widespread occurrence of high species richness throughout the farmland mosaic, with approximately half of this mosaic supporting at least 50 species per hectare (Figure 3.5).

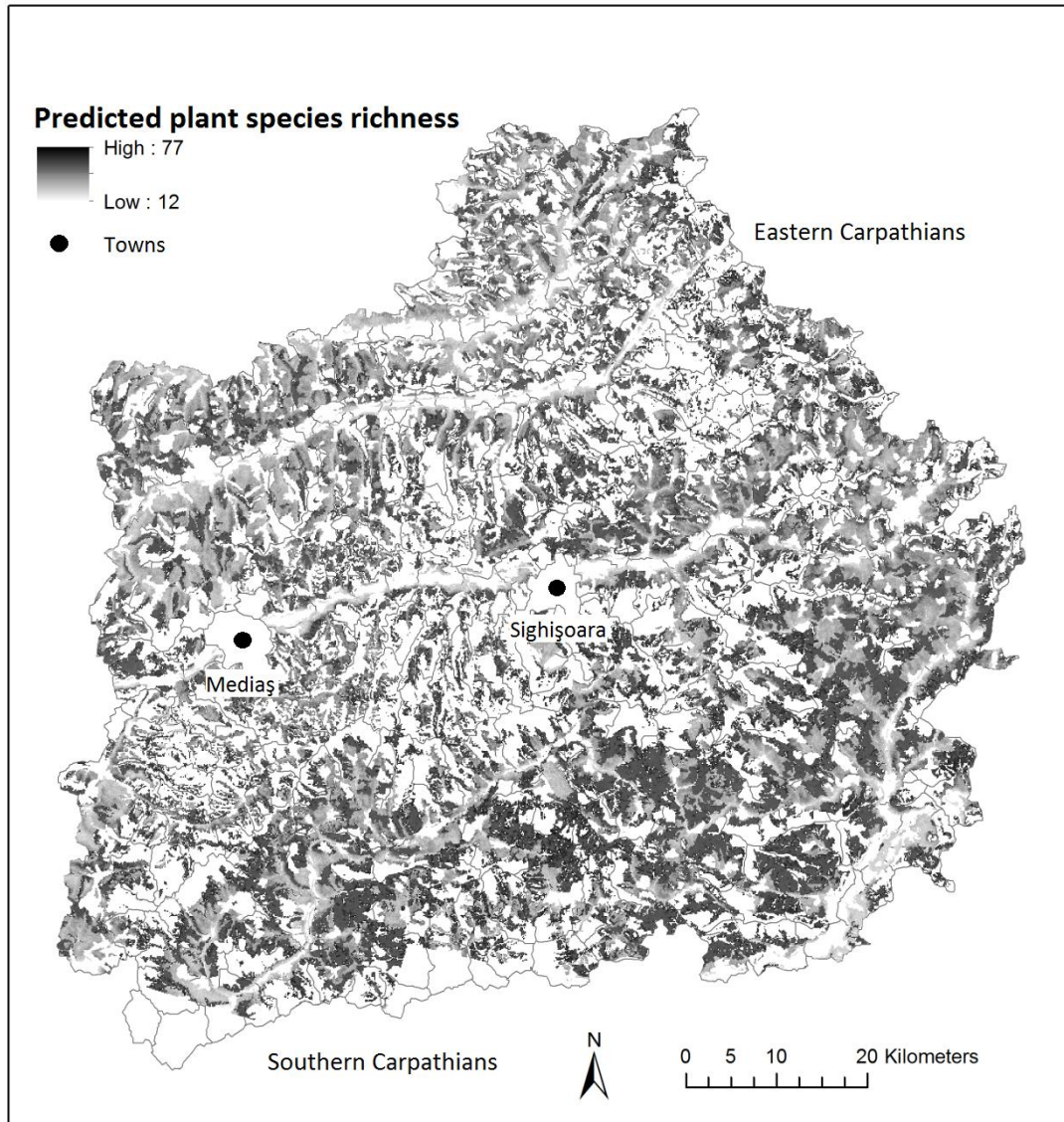


Figure 3.4. Map of predicted plant species richness for 1 ha pixels in agricultural land in the study area, based on the final generalized linear mixed model summarized in Table 3.2. Areas that are displayed in white were excluded from predictions, because they were either outside of the calibration range of our dataset or represented land cover types other than farmland.

Discussion

Besides notable exceptions (Wagner et al. 2000; Waldhardt et al. 2004; Simmering et al. 2006), this work is one of few studies on plant diversity patterns in Europe applying a sampling approach that covers a large extent of an agricultural landscape, and at the same time investigates environmental variables at different spatial scales. Our results illustrate the considerable contribution of arable land to total vascular plant diversity in a low-intensity traditional agricultural landscape. Our case study may well reflect a situation that is typical for other Eastern European countries whose agricultural landscapes are still structurally complex and rich in biodiversity (Young et al. 2007). Based on our findings, we argue that maintaining the extraordinary plant diversity of low-intensity farming landscapes calls for a conservation vision and for management plans that consider the entire farmland mosaic.

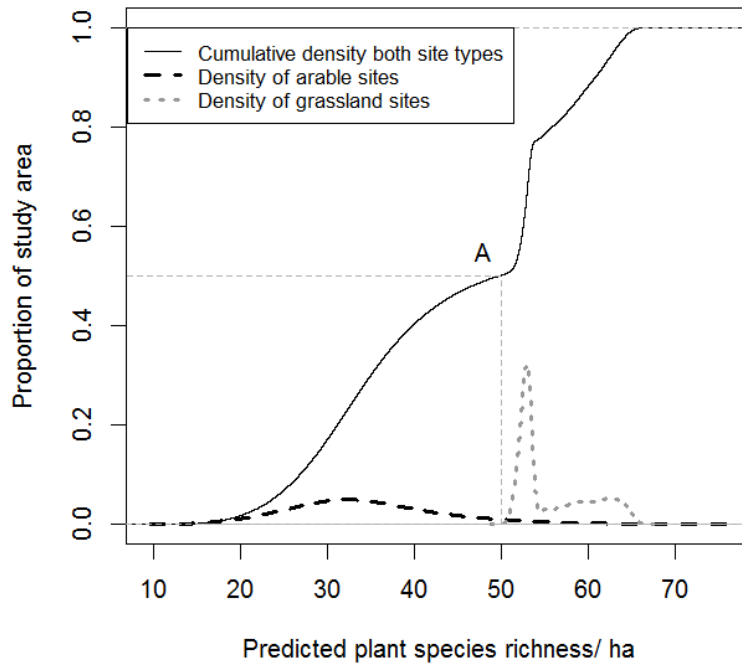


Figure 3.5. Density curves of predicted plant species richness in the farmland mosaic of the study area, separated for arable land (black dashed line) and grassland (grey dashed line). The two lines illustrate different distributions of species richness, which explains the two humps in the cumulative density curve (solid line). For example, point A indicates that 50 % of the landscape contains 50 or fewer plant species per hectare.

To date, biodiversity conservation in Europe has often targeted specific sites or local “hotspots” of biodiversity, instead of considering species pools across entire landscapes (Tscharntke et al., 2012). In Romania, such hotspots are represented by extensively and traditionally managed grasslands (Jones et al. 2010; Akeroyd and Page 2011; Dahlström et al. 2013). Some of these are among the world’s most species-rich biotopes (Wilson et al. 2012), and often support a range of species that are rare or endangered especially in Western European countries (Cremene et al. 2005; Peter et al. 2009). Hence, it is not surprising that in our case study, we found 69 % of all observed plant species in grasslands. However, we also found 63 % of all species were present within the arable mosaic of our study area. Although site-level species richness was significantly lower in arable land than in grassland, arable land also supported a considerable amount of species. Furthermore, plant communities in arable land differed strongly from those in grasslands and forests. In combination, these findings suggest that grassland, small-scale arable land and forests all make important contributions to the landscape species pool. Hence, conservation management in farmland would be most effective if it considers both arable land and grassland as integral parts of the landscape (Matson and Vitousek 2006; Perfecto and Vandermeer 2010).

Our study unraveled several key drivers of species richness, which occasionally differed between grassland and in arable land. In both land use types, total species richness responded positively to woody vegetation at the local scale. Woody vegetation may provide relatively undisturbed refuge areas, which provide niches

for several species (Ernault and Alard 2011). Woody vegetation therefore is an important part of structural heterogeneity, which is often lost as a result of land use intensification.

In grasslands, species richness was higher in locations with low ruggedness, higher terrain wetness and higher woody vegetation cover. This might indicate the importance of continuous areas of grasslands on species richness. Reasons why we may find lower species richness on rugged terrain might be that (i) rugged land is vulnerable to erosion if the grazing pressure is high; and (ii) rugged land is prone to land abandonment, because it is less accessible and less valuable for agriculture than flat areas. Typically, abandonment induces re-growth of woody vegetation. While the positive effect of a certain amount of shrub encroachment on species richness is known (and is consistent with our findings; see above), later successional stages that are dominated by woody vegetation do not support high grassland species diversity (Baur et al. 2006; Ruprecht et al. 2010). Consistently with this, our findings indicate the importance of land cover heterogeneity on species richness of HNV indicator plants. For woody vegetation and edge density, we found contrasting effects for HNV indicator plants between arable land and grassland. Specifically, greater heterogeneity appeared to be more beneficial in arable land than in grassland. This indicates the importance of maintaining structural elements within the arable mosaic while simultaneously keeping grasslands free from woody encroachment and fragmentation in order to maintain the richness of specialized and sensitive species (see also: Zulka et al. 2014).

We presume that high plant diversity at the landscape scale in our study area results from agricultural practices that are still dominated by semi-subsistence farming and labor-intensive, traditional techniques, with low levels of agrochemical inputs (van Elsen 2000; Oppermann et al. 2012). In Southern Transylvania, arable land in particular contains many semi-natural elements, including woody vegetation, which create high heterogeneity and provide different niches for a variety of species. However, these traditional systems are being lost rapidly, and EU legislation is likely to inadvertently foster the abandonment of traditional systems and intensification of land use (Kleijn and Baldi 2005; Strijker 2005; Fischer et al. 2012). It is well known from Western Europe that modernization in the agricultural sector, including farm consolidation and agrochemical application, has caused a drastic decline of plant species richness in arable land, with flow-on effects of other taxa and areas (Feest et al. 2014). Application of nitrogen, for example, has been known for decades to affect plant communities, and its negative impacts on species richness are sometimes irreversible (Strengbom et al. 2001; Stevens et al. 2004). Given existing trends towards rural exodus, it is likely that traditionally used grasslands in Southern Transylvania will also decrease in extent (Government of Romania 2010). In the long term, both abandonment and intensification imply structural simplification of the landscape, and typically cause declines in species richness in many different taxa (Weibull et al. 2000; Benton et al. 2003; Diacon-Bolli et al. 2012; Sanderson et al. 2013).

Preventing biodiversity loss is at the core of Romania's national rural development plan (Government of Romania 2010). It is not only an important goal in its own right, but also necessary to secure the delivery

of important ecosystem services and maintain landscape multi-functionality (Tschardt et al. 2012b). Moreover, protection of biodiversity in farmland is economically far more effective than expensive restoration management in hindsight, which is being applied in many more intensively used farmland areas in Western Europe (Kleijn et al. 2011). To counteract loss of species diversity in agricultural landscapes, the Common Agriculture Policy includes a series of agri-environment schemes, which provide opportunities to promote HNV farming practices, especially in semi-natural grasslands (Page et al. 2010). Existing agri-environment schemes, however, are largely derived from experiences in Western Europe, and their effectiveness in new EU member states is questionable (Gorton et al. 2009; Dahlström et al. 2013).

At the moment, 20 % of Romania's farmland is of High Nature Value (European Environment Agency 2010), and 10 % is protected under Natura 2000 regulations. In our study area, a management plan for the Natura 2000 area "Tarnava Mare" is currently being developed, but to date, it remains unclear how much effective support there will be for small-scale farmers and other decision makers to use land in a way that promotes biodiversity. Our results indicate that management strategies are needed that account for a range of different and contrasting effects of environmental conditions on species richness and particular species groups. The diversity of plants across the landscape thus appears to result from there being a wide range of different conditions available that suit different plant species – suggesting that the mosaic character of the region as a whole is important.

Conclusions

Despite many initiatives to conserve biodiversity in agricultural landscapes, it is highly likely that existing policy settings, coupled with rural exodus, will cause land use changes in many parts of Eastern Europe. The negative effects of land use intensification, in particular, are known to be especially pronounced in species-rich, extensively managed agricultural landscapes (Kleijn et al. 2009), such as in Southern Transylvania. Our study showed that plants responded in a range of different ways to variables representing structural heterogeneity, as represented by woody vegetation cover at the local and the landscape scale, and to land use heterogeneity at the landscape scale. To effectively safeguard the extraordinary biodiversity of this and other biodiverse farming landscapes of Eastern Europe, we suggest it would be useful to broaden the focus of conservation strategies to encompass entire agricultural mosaics. Such strategies should be developed both within and outside protected areas, and need to consider different management measures for grassland and arable land.

Acknowledgements

The study was funded through a Sofja Kovalevskaja Award by the Alexander von Humboldt Foundation to Joern Fischer, financed by the German Ministry for Research and Education. Sincere thanks to the farmers, landowners, mayors and the Mihai Eminescu Trust for their support. We warmly thank Doreen Hoffmann and Laura Sutcliffe for help in the field, Dave Abson and Pascal Fust for analytical support and Tibor Hartel for valuable discussions.

Supplementary Material

Table S3.1. Number of the 30 focal villages within different strata

		Protection status ^b		
		No	SCI	SPA
TRI^a	Low	4	1	4
	Medium	3	4	3
	High	4	4	3

^a Terrain ruggedness index, calculated as standard deviation of altitude within one village catchment, based on the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model with 30 m resolution Version 2 (GDEM V2)

^b Protection status is according to the EU Habitats and Birds Directives

Table S3.2. Number of survey sites (n=116) cross-combined along the two gradients local heterogeneity and local woody vegetation cover

		Heterogeneity ^b					
		low		medium		high	
		arable land	grassland	arable land	grassland	arable land	grassland
Woody vegetation cover^a	Low	8	5	7	8	0	0
	Medium	6	7	8	7	7	8
	High	8	7	7	8	8	7

^a Proportion of woody vegetation cover based on supervised classification 10m SPOT 5 data, © CNES (2007), ISIS programme, Distribution Spot Image SA

^b Heterogeneity measured as the standard deviation of 2.5 m panchromatic SPOT 5 data, © CNES (2007), ISIS programme, Distribution Spot Image SA.

Table S3.3: Plants included in the three different groups of plants modeled separately (arable weeds, grassland specialists and HNV indicator plants)

Grassland specialists	HNV indicator plants	Arable weeds
<i>Achillea millefolium</i>	<i>Asperula cynanchica</i>	<i>Adonis aestivalis</i>
<i>Acinos arvensis</i>	<i>Anthyllis vulneraria</i>	<i>Amaranthus retroflexus</i>
<i>Agrostis gigantea</i>	<i>Campanula sibirica</i>	<i>Apera spica-venti</i>
<i>Agrostis stolonifera</i>	<i>Coronilla varia</i>	<i>Armoracia rusticana</i>
<i>Ajuga genevensis</i>	<i>Dorycnium</i> <i>pentaphyllum</i>	<i>Asclepias syriaca</i>
<i>Ajuga laxmanii</i>	<i>ssp. herbaceum</i>	<i>Avena sativa</i>
<i>Anthyllis vulneraria</i>	<i>Dianthus carthusianorum</i>	<i>Brassica oleracea</i>
<i>Arrhenatherum elatius</i>	<i>Galium verum</i>	<i>Consolida regalis</i>
<i>Artemisia campestris</i>	<i>Inula ensifolia</i>	<i>Cucurbita pepo</i>
<i>Asperula cynanchica</i>	<i>Linum flavum</i>	<i>Echinochloa crus-galli</i>
<i>Asperula tinctoria</i>	<i>Linum hirsutum</i>	<i>Eruca vesicaria</i>
<i>Astragalus monspessulanus</i>	<i>Onobrychis viciifolia</i>	<i>Fallopia convolvulus</i>
<i>Astragalus onobrychis</i>	<i>Polygala major</i>	<i>Galeopsis ladanum</i>
<i>Astrantia major</i>	<i>Scabiosa ochroleuca</i>	<i>Lathyrus tuberosus</i>
<i>Avenula pratensis</i>	<i>Prunella grandiflora</i>	<i>Oxalis corniculata</i>
<i>Bellis perennis</i>	<i>Teucrium chamaedrys</i>	
<i>Bothriochloa ischaemum</i>	<i>Thymus glabrescens</i>	
<i>Briža media</i>	<i>Veronica austriaca</i>	
<i>Bromus erectus</i>	<i>Trifolium montanum</i>	
<i>Bupleurum falcatum</i>	<i>Viola hirta</i>	
<i>Campanula patula</i>		
<i>Campanula sibirica</i>		
<i>Carex humilis</i>		
<i>Carex pallescens</i>		
<i>Carex spicata</i>		
<i>Carex tomentosa</i>		
<i>Carlina vulgaris</i>		
<i>Centaurea jacea</i>		
<i>Centaurea biebersteinii</i> ssp. <i>biebersteinii</i>		
<i>Centaurea phrygia</i>		
<i>Cephalaria radiata</i>		
<i>Cerastium holosteoides</i>		
<i>Cerastium pumilum</i>		
<i>Chaerophyllum aromaticum</i>		
<i>Chamaespartium sagittale</i>		
<i>Chrysopogon gryllus</i>		
<i>Cirsium canum</i>		
<i>Cirsium pannonicum</i>		
<i>Colchium autumnale</i>		
<i>Crepis biennis</i>		
<i>Cynosurus cristatus</i>		
<i>Cynodon dactylon</i>		
<i>Dactylorhiza incarnata</i>		
<i>Danthonia alpina</i>		

Dianthus armeria
Dianthus carthusianorum
Dorycnium pentaphyllum ssp. *herbaceum*
Elymus hispidus
Erysimum odoratum
Euphorbia cyparissias
Euphrasia officinalis
Festuca ovina
Festuca pratensis
Festuca rubra
Festuca rupicola
Festuca valesiaca
Filipendula vulgaris
Fragaria viridis
Galium verum
Gypsophila muralis
Helianthemum nummularium
Hieracium pilosella
Hypochoeris radicata
Juncus conglomeratus
Juncus effusus
Juncus inflexus
Juncus tenuis
Koeleria macrantha
Lathyrus nissolia
Lathyrus pratensis
Leontodon crispus ssp. *crispus*
Leontodon autumnalis
Leontodon hispidus
Linum austriacum
Linum catharticum
Linum flavum
Linum hirsutum
Lolium perenne
Lotus corniculatus
Luzula campestris
Lychnis flos.cuculi
Lythrum salicaria
Medicago minima
Melampyrum pratense
Nardus stricta
Oenanthe aquatica
Onobrychis viciifolia
Ononis arvensis
Orchis coriophora
Parnassia palustris
Pastinaca sativa
Phleum pratense
Pimpinella major

Plantago lanceolata
Plantago major
Poa angustifolia
Poa pratensis
Polygala comosa
Polygala major
Polygala vulgaris
Potentilla argentea
Potentilla cinerea
Potentilla erecta
Potentilla recta
Prunella laciniata
Prunella vulgaris
Ranunculus acris
Ranunculus bulbosus
Ranunculus polyanthemos
Rhinanthus rumelicus
Rhinanthus angustifolius ssp. angustifolius
Rhinanthus minor
Rumex acetosa
Rumex acetosella
Salvia glutinosa
Salvia nemorosa
Salvia pratensis
Salvia transsylvanica
Sanguisorba minor
Scabiosa ochroleuca
Serratula radiata
Seseli annuum
Seseli peucedanoides
Silene nutans
Silene vulgaris
Stachys recta
Stellaria graminea
Stipa capillata
Teucrium montanum
Thalictrum lucidum
Thymus glabrescens
Thymus pannonicus
Thymus pulegioides
Tragopogon pratensis ssp. orientalis
Trifolium alpestre
Trifolium arvense
Trifolium campestre
Trifolium hybridum
Trifolium montanum
Trifolium pratense
Trifolium repens
Veronica arvensis

Veronica austriaca

Veronica prostrata

Veronica spicata

Vinca herbacea

Viola canina

Chapter 4

Low-intensity agricultural landscapes in Transylvania support high butterfly diversity: implications for conservation

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IV



Abstract

European farmland biodiversity is declining due to land use changes towards agricultural intensification or abandonment. Some Eastern European farming systems have sustained traditional forms of use, resulting in high levels of biodiversity. However, global markets and international policies now imply rapid and major changes to these systems. To effectively protect farmland biodiversity, understanding landscape features which underpin species diversity is crucial. Focusing on butterflies, we addressed this question for a cultural-historic landscape in Southern Transylvania, Romania. Following a natural experiment, we randomly selected 120 survey sites in farmland, 60 each in grassland and arable land. We surveyed butterfly species richness and abundance by walking transects with four repeats in summer 2012. We analysed species composition using Detrended Correspondence Analysis. We modelled species richness, richness of functional groups, and abundance of selected species in response to topography, woody vegetation cover and heterogeneity at three spatial scales, using generalised linear mixed effects models. Species composition widely overlapped in grassland and arable land. Composition changed along gradients of heterogeneity at local and context scales, and of woody vegetation cover at context and landscape scales. The effect of local heterogeneity on species richness was positive in arable land, but negative in grassland. Plant species richness, and structural and topographic conditions at multiple scales explained species richness, richness of functional groups and species abundances. Our study revealed high conservation value of both grassland and arable land in low-intensity Eastern European farmland. Besides grassland, also heterogeneous arable land provides important habitat for butterflies. While butterfly diversity in arable land benefits from heterogeneity by small-scale structures, grasslands should be protected from fragmentation to provide sufficiently large areas for butterflies. These findings have important implications for EU agricultural and conservation policy. Most importantly, conservation management needs to consider entire landscapes, and implement appropriate measures at multiple spatial scales.

Introduction

Almost half of Europe's terrestrial surface consists of farmland, and many species, including rare and endangered ones, depend on farmland as habitat (Stoate et al. 2009; Kleijn et al. 2011). The loss of cultural-historic landscapes through intensification or abandonment of farming practices is causing declines of farmland biodiversity (Benton et al. 2003; Thomas et al. 2004; Cremene et al. 2005; Foley et al. 2005; Stoate et al. 2009). To effectively design conservation strategies, knowledge is needed about which variables influence species richness and distribution at different spatial scales (Weibull et al. 2003; Kumar et al. 2009; Brückmann et al. 2010).

In Western Europe, species loss in farmland has been associated with an increase of agricultural productivity (Maes and Van Dyck 2001; Weibull et al. 2003; Van Dyck et al. 2009), most likely caused by the use of agrochemicals (McLaughlin and Mineau 1995) and the loss and fragmentation of semi-natural patches, especially grasslands (Bergman et al. 2004; Brückmann et al. 2010). In Eastern Europe, socio-economic conditions and land use have been rapidly changing since the breakdown of communism and accession of new member states to the European Union (EU) (Klúvánkóvá-Oravská et al. 2009; Kuemmerle et al. 2009; Mikulcak et al. 2013). Current changes involve a dual threat to biodiversity, with a trend towards structural simplification on the one hand and abandonment of low-intensity practices on the other hand (Schmitt and Rákósy 2007; Young et al. 2007). The current situation in Eastern Europe thus differs in important ways from Western European countries (Pullin et al. 2009; Stoate et al. 2009; Tryjanowski et al. 2011), and a better understanding is needed of how organisms respond to landscape features within low-intensity farming areas of Eastern Europe.

Heterogeneous landscapes typically harbour greater species richness than homogenous landscapes (Benton et al. 2003; Tschardt et al. 2005; Ekroos et al. 2013), most likely because of their greater niche diversity, as well as spillover effects and habitat complementation (Dunning et al. 1992). Agricultural simplification and land abandonment typically lead to a loss of landscape connectivity, which may not only dissect the habitats for species, but also causes flow-on effects on the composition and configuration of the landscape as a whole (Persson et al. 2010; Fahrig et al. 2011).

A particularly interesting cultural-historic region in Eastern Europe is Transylvania, which supports extraordinarily high levels of farmland biodiversity (Fischer et al. 2012; Page et al. 2012). Especially in its South, Transylvania is characterised by a small-scale mosaic of different low-intensity land-uses that provide many different, well-connected structures such as field margins and roadside vegetation. The historic management of the area has created heterogeneity at multiple spatial scales: within tens of metres (hereafter termed the local scale), in the immediate surroundings around any given location (the context scale), as well as over thousands of metres (the landscape scale) (Akeroyd and Page 2006; Hartel et al. 2008).

Here, we focus on butterflies as a taxonomic group that rapidly responds to environmental changes (Erhardt 1985) and is known to be sensitive to land use change worldwide (Thomas et al. 2004). In

Europe, many butterflies use anthropogenic landscape elements (van Swaay et al. 2006), but species with different traits are expected to respond differently to land use change (Krauss et al. 2003; Brückmann et al. 2010). For example, Öckinger & Smith (2006) found that the effects of landscape composition differed between species of different mobility classes, and Börschig et al. (2013) found that intensively used agricultural landscapes mostly support generalists. Yet, evidence on the responses of butterflies to gradients of spatial heterogeneity is sparse, and more thorough studies at multiple scales are needed (Öckinger et al. 2009; Ekroos et al. 2013).

We sought to understand the responses of butterfly diversity to key landscape gradients in Southern Transylvania, using a snapshot natural experiment (Diamond 1986; Lindenmayer et al. 2008) that spanned the full range of environmental conditions with respect to heterogeneity and woody vegetation cover across multiple scales. Our overarching aim was to understand drivers of species richness and composition. Specifically, we asked (i) how landscape structures affect the composition of butterfly communities; (ii) which landscape structures explain butterfly species richness at various spatial scales; and (iii) which landscape structures affect abundance patterns of selected species. We discuss our findings in the context of possible landscape changes that may take place in Transylvania.

Materials and methods

Ethics Statement

We obtained the necessary permit for surveying butterflies within the EU *Natura 2000* network from Progresul Silvic, the organization officially entrusted with the custody of the protected area by the Romanian government. The survey procedure was approved beforehand by the ethics committee of Leuphana University Lueneburg.

Data Availability Statement

All data underlying the findings reported in this study are available from the Dryad Digital Repository (<http://doi.org/10.5061/dryad.97s1k>).

Study area and experimental design

The study area covered approximately 7,000 km² in the lowlands of Southern Transylvania, Romania (Figure 4.1). We followed the notion of a natural experiment (Diamond 1986), with randomised site selection in pre-defined strata at two levels: study villages and survey sites within villages.

To select study villages, we first allocated each raster pixel of the study area to different “village catchments”. These were calculated using a cost-distance algorithm in ARCGIS with the village centre as the reference point and the slope and the distance to the next village as the cost variables. Information about village locations was extracted from CORINE land cover data 2006 (<http://www.eea.europa.eu>), and slope was calculated from the digital elevation model ASTER (Advanced Spaceborne Thermal Emission and Reflection Radiometer). Topographically based village catchments were used instead of

administrative boundaries because administrative boundaries were only available at the commune level (typically 3-5 villages). However, we found that the resulting polygons accurately reflected historical land use responsibilities. Second, we stratified village catchments along a gradient of terrain ruggedness and according to their protection status under the EU Birds and Habitats Directives. Terrain ruggedness was calculated as the standard deviation of the altitude of the catchment, and we used quantiles to classify ruggedness as either low, medium or high. Protection status of the catchments was either unprotected, SCI (Site of Community Importance) or SPA (Special Protection Area). Third, we randomly chose 30 villages, covering all combination of ruggedness and protection status (Table S3.1).

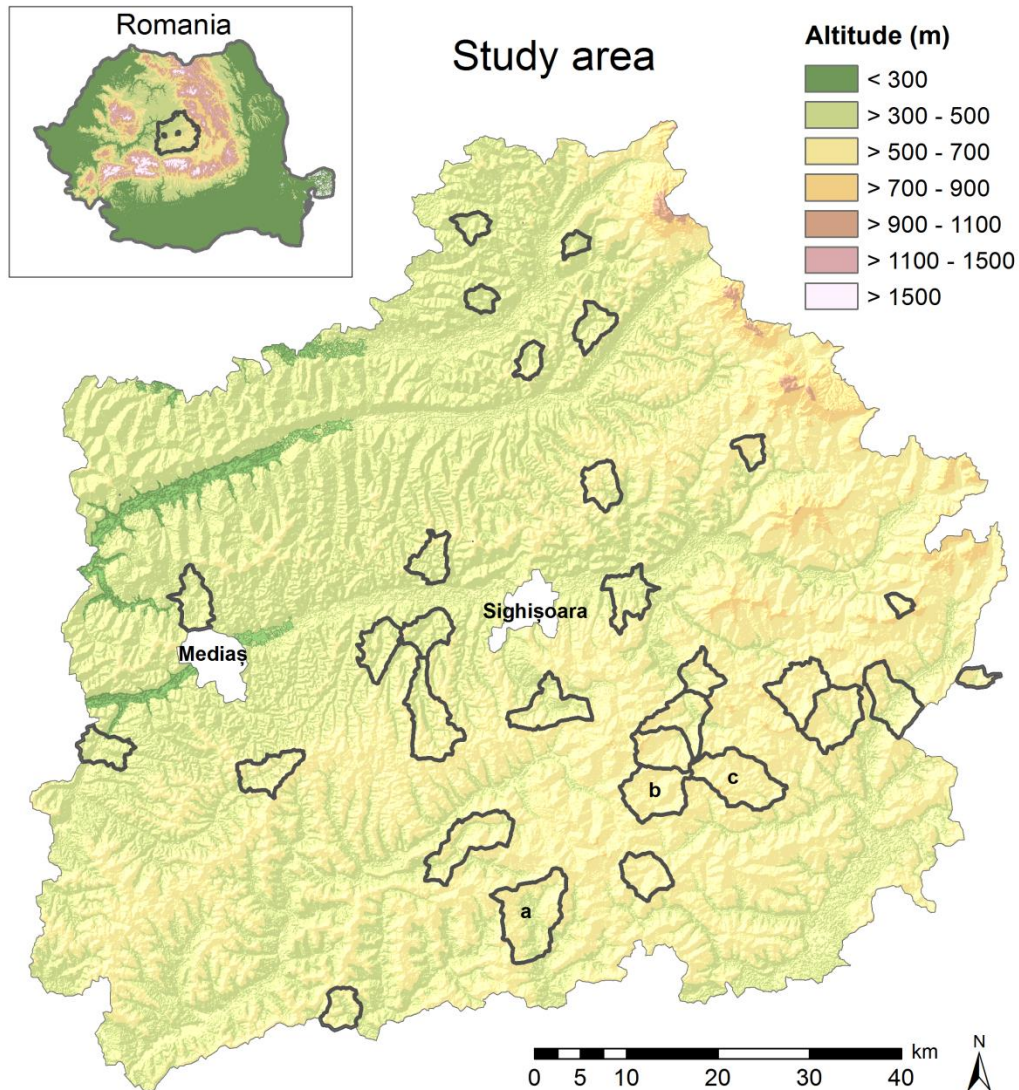


Figure 4.1. Location of the study area with investigated village catchments in Transylvania, Romania. The small letters indicate the village catchments illustrated for predictions in Figure 4.4 (a= Cincu, b= Granari, c= Viscri).

To select survey sites, we stratified the agricultural area within these 30 villages according to CORINE land cover as grassland or arable land and excluded other land cover classes. Within these strata, we spanned two gradients that we assumed sensitive to change in the future as a result of structural simplification, namely woody vegetation cover and heterogeneity. We estimated woody vegetation cover

in a circular one hectare area based on classified 10 m SPOT data (CNES, ISIS programme). To assess heterogeneity, we used the standard deviation of 2.5 m panchromatic SPOT data within a one hectare circle. We assigned each hectare of the agricultural landscape to a combination of three classes of woody vegetation cover by three classes of heterogeneity. We distinguished low (0-5 %), medium (>5-15 %) and high (>15 %) woody vegetation cover and used the lower, middle and upper third of percentiles to classify heterogeneity. Within these combinations, we randomly selected replicates for each cross-combination (except for the combination of high heterogeneity and low woody vegetation cover, which did not exist (Table S3.2)). In total, we selected 120 circular 1 ha survey sites, with 60 in grassland and 60 in arable land, and an average of four survey sites per village catchment. Notably, sites in arable land in this context were consciously placed not to represent only arable fields specifically, but rather to capture the whole range of conditions within the mosaic of arable land (Bennett et al. 2006), including field margins and fallow land.

Data collection

Butterfly surveys (response data)

We assessed species richness and abundance of butterflies (Rhopalocera) and diurnal burnet moths (Zygaenidae) by walking four transects of 50 m length per survey site (Pollard and Yates 1993). We included burnet moths because they are comparable to butterflies in their ecology (Naumann et al. 1999; Öckinger and Smith 2006). These transect pointed north, east, south and west, and started 6 m from the centre of a given site. In a given transect walk, each butterfly observed within 2.5 m of each side of the transect and 5 m in front of the observer was identified and counted. Species that we could not identify in the field were treated as compound species: *L. sinapis/ juvernica*, *C. alfacariensis/ hyale* and *Zygaena minos/ purpuralis*. *Adscita*, *Jordanita* and *Carcharodus* occurred within the study region, and are represented by two, two and three species, respectively (Rakosy et al. 2003). However, these species are difficult to distinguish and therefore were only identified to the genus level. Surveys were repeated on four occasions between May and August 2012 by four different, trained observers. Surveys were conducted under suitable weather conditions (no rain, <90 % cloud cover, >17°C, no strong wind), between 9 am and 5 pm.

Environmental data (explanatory variables)

We followed a multi-scale approach and included explanatory variables that could potentially explain butterfly distribution at the local (1 ha), context (50 ha) and landscape scale (i.e. village catchments, ranging from 430 to 4963 ha). An overview of all variables included in the analysis is presented in Table 4.1.

At the local scale, we collected data on vascular plant species richness in eight randomized quadrants (1x1 m). We used cumulative plant species richness per site as an explanatory variable. We also calculated indices for heatload (after (Parker 1991)) and terrain wetness as a measure of potential soil wetness, and included heterogeneity assessed by the spectral variance of SPOT data (see Table 4.1 for details).

Table 4.1. Definition of environmental variables used in the study at three different scales and method of obtaining those. Abbreviations are used in Figure 4.2 and Table 4.2.

Scale	Variable (abbreviation)	Definition and method
local (1 ha)	Number of plant species (NoPlant)	Vascular plant species richness assessed by eight randomly distributed quadrants of one by one meter
	Heterogeneity (het_1ha)	Heterogeneity measured as the standard deviation of 2.5 m panchromatic SPOT picture (© CNES, ISIS programme)
	Woody vegetation cover (woody_1ha)	Proportion of woody vegetation cover based on classified 10m SPOT satellite image (© CNES, ISIS programme)
	Heat index (heatload)	Potential for ground heating calculated after Parker (1991): Heat index = $\cos(\text{slope aspect} - 225) * \tan(\text{slope angle})$
	Terrain Wetness Index (TWI)	Measure of potential soil wetness, estimated as the position in the landscape and the slope from ASTER digital elevation model with 30m resolution.
	Land Cover (LU_type)	Land use classification as arable land, grassland or forest based on CORINE land cover
context (50 ha)	Ruggedness (rugg_50ha)	Terrain ruggedness, calculated as standard deviation of altitude
	Woody vegetation cover (woody_50ha)	Proportion of woody vegetation cover based on classified 10m SPOT satellite image
	Configurational heterogeneity (ED_50ha)	Configuration of different land covers, calculated as the edge density with FRAGSTATS v4.2 based on CORINE land cover
landscape (village catchment)	Amount of pasture (past_catch)	Proportion of pasture, based on CORINE land cover
	Woody vegetation cover (woody_catch)	Proportion of forest cover based on CORINE land cover
	Ruggedness (catch_rugg)	Terrain ruggedness, calculated as the standard deviation of the altitude
	Compositional heterogeneity (SIDI)	Composition of different land covers, calculated as Simpson index of diversity with FRAGSTATS v4.2 based on CORINE land cover
	Configurational heterogeneity (ED)	Configuration of different land covers, calculated as edge density with FRAGSTATS v4.2 based on CORINE land cover
Random effects	Village catchment	Classification of the landscape into social-ecological units according to a cost distance algorithm of proximity to the nearest village as reference point and the slope of the terrain as cost factor
	Level	Observation level random effect

We calculated percent woody vegetation cover at local and context scales, and used CORINE land cover to calculate percent forest at the landscape scale. For the context and landscape scales, we calculated the terrain ruggedness as the standard deviation of altitude. We also quantified compositional or configurational heterogeneity of the different land covers grassland, arable land and forest as provided by CORINE land cover data. At the context scale, our chosen heterogeneity measures (Simpson index of land cover diversity, edge density) were correlated ($r = 0.76$). Hence, we included only edge density as an explanatory variable (following Kumar et al. 2009). At the landscape scale, we used both edge density and the Simpson index of diversity and added the amount of pasture and forest per village catchment, based on CORINE land cover data. Variables on compositional and configurational heterogeneity were calculated using FRAGSTATS v4.2 (McGarigal et al. 2012) and all other variables using ARCGIS 10.1 (ESRI Inc., Redland, CA).

Analysis

We pooled all observed butterfly species and individuals from the four survey rounds for each survey site. First, we tested for differences in species richness and abundance between different levels of official protection by using Analysis of Variance (ANOVA). Second, we conducted a detrended correspondence analysis (DCA) to describe species composition and its relation to environmental variables. We used a permutation test to fit and test the correlation of environmental variables with the ordination.

Third, we used generalized linear mixed effects models (GLMMs) to assess effects of environmental variables on butterfly species richness. Beforehand, we tested the explanatory variables for collinearity (all $r < 0.7$; Table S4.2; (Dormann et al. 2013)). We log-transformed woody vegetation cover at local and context scales and heterogeneity at the local scale because these variables were highly skewed. All numerical explanatory variables were scaled to mean zero and unit variance. We included the variables listed in Table 4.1 to model species richness of butterflies. To test for a unimodal relationship in response to woody vegetation cover, we included a quadratic term of local woody vegetation cover. We furthermore expected that the effect of heterogeneity may differ between grassland and arable land and therefore included an interaction term between land cover type and heterogeneity. Grasslands are also interesting to look at separately because they are among the most species rich biotopes for butterflies in Europe (van Swaay et al. 2011). We assessed the variance inflation factor (VIF) of the generalized linear model (GLM) and tested for spatial auto-correlation in the residuals. We included the village catchment as a random effect and corrected for overdispersion by adding an observation level random effect. We simplified the model by stepwise backwards selection retaining all variables with $p < 0.1$. For GLMMs, significance levels are only approximations, hence many statisticians suggest using a significance level of $p < 0.1$ (Bolker et al. 2009).

Likewise, we modelled species richness of functional groups. To this end, we distinguished between species of low mobility (Bink's mobility classes 1 and 2) and high mobility (Bink's mobility classes 7, 8 and 9; (Bink 1992)). Highly mobile species were *Colias crocea*, *Pieris brassicae*, *Vanessa atalanta* and *Vanessa*

cardui. Low-mobility species were *Brenthis daphne*, *Brenthis ino*, *Coenonympha glycerion*, *Cupido minimus*, *Euphydryas aurinia*, *Hamaeris lucina*, *Heteropterus morpheus*, *Lopinga achine*, *Melitaea britomartis*, *Melitaea diamina* and *Satyrrium acaciae*. As a third group we modelled the richness of grassland specialists, namely *Euphydryas aurinia*, *Polyommatus coridon*, *Cyaniris semiargus*, *Lysandra bellargus*, *Pbengaris arion*, *Cupido minimus* and *Erynnis tages* (van Swaay et al. 2013).

We also modelled the abundance of individual species considered to be declining in Western and Northern Europe, but that are widespread or even increasing in Eastern Europe (van Swaay and Warren 1999; Konvicka et al. 2003; Franzén and Ranius 2004; van Swaay et al. 2013). We only used species that were common enough in the study area to obtain reliable models, namely *Maniola jurtina*, *Coenonympha pamphilus*, *Polyommatus icarus*, *Lycaena dispar* and *Glaucopsyche alexis*. We performed all statistical analyses in R (R Core Team 2013), using the packages MASS, ade4, vegan, gdata and lme4.

Results

In total, we counted 19,878 individuals of 112 species of butterflies (Table S4.1). Site-level species richness varied between three and 45, and the number of individuals between seven and 452. Eighty-five percent of all individuals belonged to 12 species: *Colias alfacariensis/hyale*, *Minois dryas*, *Aphantopus hyperantus*, *Pieris rapae*, *Everes argiades*, *Coenonympha glycerion*, *Leptidea sinapis/juvernica*, *Melanargia galathea*, *Coenonympha pamphilus*, *Maniola jurtina*, *Polyommatus icarus*, and *Plebeius argus*. SCI, SPA and unprotected sites did not differ in species richness ($F=0.54$, $p=0.58$) but SCI sites appeared to have a slightly lower abundance of individuals than unprotected sites ($F=2.37$, $p=0.09$). Arable land and grassland did not differ in species richness ($F=1.32$, $p=0.25$) nor abundance of individuals ($F=1.51$, $p=0.22$).

Multivariate analysis showed substantial overlap in species composition between arable land and grassland (Figure 4.2), with less than one complete species turnover (length of first axis = 2.9). The first axis (Eigenvalue = 0.21) described a gradient from sites with a low terrain wetness index in homogenous landscapes to sites with a high terrain wetness index within highly heterogeneous landscapes. The second DCA axis (Eigenvalue = 0.18) described a gradient from low to high richness of vascular plants, ruggedness, woody vegetation cover and context-level heterogeneity and landscape-level woody vegetation cover.

Butterfly species richness was positively related to local plant species richness and local woody vegetation cover, but negatively to local heatload (Table 4.2). It increased in response to local heterogeneity in arable sites, but not in grasslands (Figure 4.3). Species richness furthermore increased with configurational heterogeneity and ruggedness at the context scale, but decreased with landscape woody vegetation cover. The models show suitable areas for species of conservation interest exist throughout village catchments, especially in large grassland areas and boundary areas of arable land (Figure 4.4).

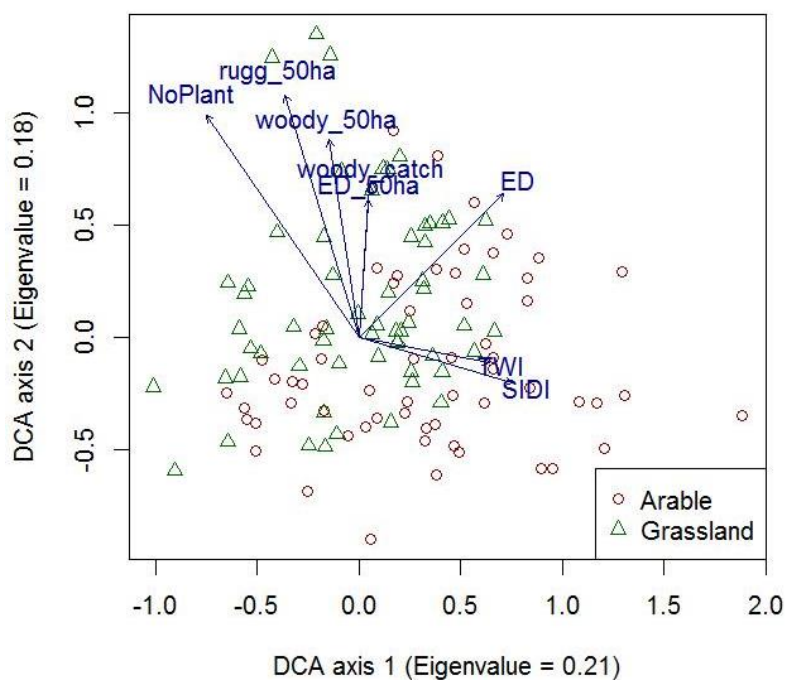


Figure 4.2. DCA ordination plot of butterfly species, with significant environmental variables superimposed ($p, 0.05$) (Abbreviations: NoPlant = Local plant species richness; TWI = Local terrain wetness index; rugg_50 ha = context terrain ruggedness; woody_50 - ha = context woody vegetation cover; ED_50 ha = context edge density; woody_catch = landscape woody vegetation cover; SIDI = landscape compositional heterogeneity; Table 4.1).

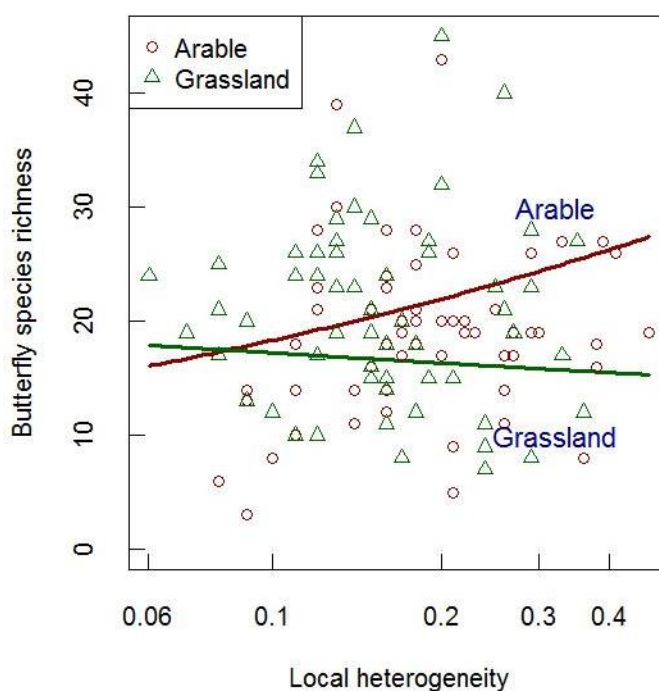


Figure 4.3. Predicted effect of local heterogeneity on species richness in arable land versus grassland, based on the simplified generalized linear mixed model (Table 4.2).

Species richness of mobile butterflies was highest in arable land, and responded positively at the landscape scale to both compositional heterogeneity and ruggedness. By contrast, richness of low-

mobility species was negatively related to landscape configurational heterogeneity, but responded positively to local-scale plant species richness and context heterogeneity (for additional details, see Table 4.2). Richness of specialist species was higher in grassland, in landscapes with high terrain ruggedness and at sites with high plant species richness.

For individual species, both *L. dispar* and *G. alexis* were more abundant in arable land, and were positively related to local plant species richness. *L. dispar* also responded positively to local woody vegetation cover, but negatively to local heatload, whereas *G. alexis* showed a positive response to context ruggedness and the amount of grassland in the landscape. The abundances of *P. icarus*, *M. jurtina* and *C. pamphilus* increased with heterogeneity in arable land, but not in grassland, and decreased with increasing heatload.

Abundance of *M. jurtina* and *C. pamphilus* were positively related to local plant species richness, and negatively to landscape woody vegetation cover. *P. icarus* responded positively to the amount of grassland in the landscape. Abundance of *C. pamphilus* was unimodally related to local woody vegetation cover.

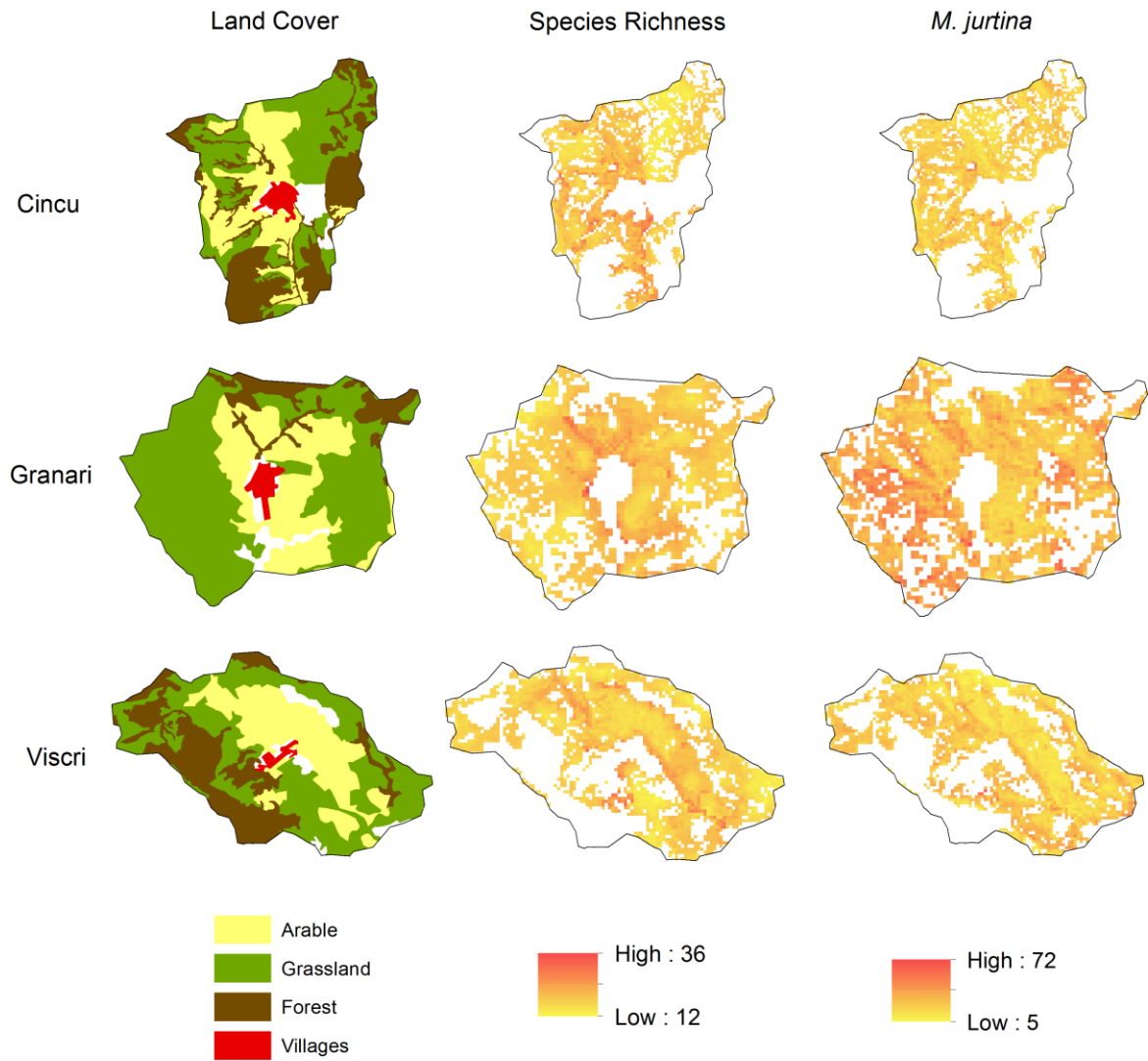


Figure 4.4. Maps of predicted butterfly distributions in three example villages. Left: Land cover map according to CORINE 2006; middle: predicted species richness for arable and grassland areas within each village catchment; right: predicted abundance of the Meadow Brown (*Maniola jurtina*).

Table 4.2: Parameter estimates of the species distribution models with significance levels indicated by: † P<0.1; *P<0.05; **P<0.01; ***P<0.001. Arable land was used as the baseline land cover in all models. See Table 4.1 for abbreviations. Arable land was used as the baseline land cover in all models. See Table 1 for abbreviations.

	Species Richness	High mobile species	Low mobile species	Specialists	<i>L. dispar</i>	<i>G. alexis</i>	<i>P. icarus</i>	<i>M. jurtina</i>	<i>C. pamphilus</i>
Intercept	3.026	-0.739	0.681	-0.436	0.581	-1.172	2.914	2.637	1.959
NoPlant	0.261***		0.600***	0.685***	0.581*	0.941**		0.597***	0.313***
LU_type	-0.243**	-1.250***		0.052†	-2.059***	-1.554*	-0.040	0.046	0.210
het_1ha	0.109*						0.278**	0.235*	0.224*
LU_type*het_1ha	-0.140*						-0.326*	-0.415**	-0.387*
TWI									
woody_1ha	0.072*		-0.054		0.443†				0.102
woody_1ha^2			0.232†						0.177*
heatload	-0.057*				-0.622†		-0.167*	-0.321***	-0.207**
rudd_50ha	0.064†					0.511*			
woody_50ha									
ED_50ha	0.077*		0.261*						
woody_catch	-0.079*							-0.412***	-0.232†
past_catch						0.721**	0.256.		
rudd_catch		-0.423*	0.249*	0.051***					
ED			-0.374**						
SIDI		0.448*							

Discussion

We found a high diversity of butterflies in the cultural-historic landscape of Southern Transylvania. This is especially the case considering that we did not seek out sites expected a priori to harbour great diversity, but rather surveyed randomly selected sites within the agricultural matrix. An even greater diversity of butterflies, including rare and endangered species, would be expected to occur in dry grassland patches and traditionally managed hay-meadows, which occur within our study area but which we did not specifically target. Our findings suggest that some types of land use change could pose serious threats to butterfly diversity in Transylvania. Our findings can be summarised within four themes, which we discuss in the following: (i) both grassland and arable land have conservation value; (ii) low-intensity landscapes provide important resources for butterflies; (iii) heterogeneity has a different effect in arable land than in grassland; and (iv) it is important to consider multiple scales for effective butterfly conservation.

Both grassland and arable land have conservation value

Our findings revealed a high conservation value for butterflies of the small-scale farming system in the lowlands of Transylvania. Interestingly, butterfly species richness and abundance were similar in arable land and grassland. This is a surprising result and suggests a need to broaden the emphasis of conservation activities from grassland protection towards the maintenance of heterogeneous mosaic farmland, including cropland (Bennett et al. 2006). This is particularly important in the context of criticisms that the recent reform of the European Union's Common Agricultural Policy, for example, falls far short of what is needed in terms of biodiversity conservation (Pe'er et al. 2014). Throughout Europe, grasslands are considered most important for butterfly conservation (e.g. Brückmann et al. 2010; van Swaay et al. 2011). Arable land, on the other hand, has received far less attention. In Western Europe, arable land has been found to support lower species richness and more homogenous butterfly communities than grassland (Weibull and Ostman 2003; Weibull et al. 2003). Our results indicate that this situation may be different in Eastern Europe, and that certain types of arable land can in fact support similar levels of butterfly diversity as grasslands. A possible explanation for the similar species richness in arable land and grassland in Transylvania may be spillover effects (Dunning et al. 1992), which may be more likely in small-scale mosaics of land covers. The mosaic character of the landscape also could explain the strong overlap in butterfly communities between arable land and grassland.

Low-intensity landscapes provide important resources for butterflies

The fine-grained mosaic nature of arable land and the low-intensity nature of grassland in Southern Transylvania emphasize that low-intensity land use practices have major benefits for butterfly conservation. Semi-natural elements occur throughout the landscape, and are a likely reason why species richness is high throughout different land covers (Ekroos et al. 2013). Furthermore, species richness of vascular plants can be high in field margins, which in turn may indicate high quality habitat for butterflies (Steffan-Dewenter and Tschardtke 2000). Consistent with the findings of Kumar, Simonson & Stohlgren (2009), we found plant species richness strongly related to butterfly species richness. Currently,

Transylvania contains some of the world's most species rich areas for plants (Wilson et al. 2012), which is partly linked to the low use of fertilizers (Jones 2009). Agricultural intensification, by contrast, would likely lead to increased use of fertilizers and hence reduced plant species richness (Zechmeister et al. 2003; Van Landuyt et al. 2008; Kleijn et al. 2009). Furthermore, intensification is typically associated with the use of fewer, high yielding crop varieties. Interestingly, many butterflies in Transylvania use the common crop *Medicago sativa* ssp. *sativa* (Alfalfa), a leguminous species that provides nectar and that we also observed to serve as a host plant for several butterfly species (e.g. *Glaucopsyche alexis*). Alfalfa is grown in small parcels, is primarily used as winter fodder for livestock, and may easily be lost as a result of intensification. However, high amounts of floral resources are critically important to maintain butterfly diversity. Similarly, woody vegetation offers important resources for butterflies, including shelter and space for thermoregulation (Dover et al. 1997). At present, Transylvania contains many scattered trees and hedgerows, and we found that butterfly species richness responded positively to these structures at the local scale. By contrast, a large amount of woody vegetation at the landscape scale may lead to decreased species richness, probably due to a lack of open habitat.

Heterogeneity has a different effect in arable land than in grassland

We considered heterogeneity and woody vegetation cover at the local scale as two potentially important gradients describing the structure of the landscape. Interestingly, our results showed that the effect of local heterogeneity on species richness depended on land cover. In arable land, species richness increased with heterogeneity, supporting our hypothesis that small-scale farming benefits biodiversity by providing a range of different resources for butterflies. Notably, our land use class of "arable land" reflected the highly heterogeneous nature of traditional farmland, and included cropped areas as well as fallows and uncultivated field margins. These non-cropped areas are likely to be particularly important to maintain butterfly diversity in arable land. By contrast, in grassland, high heterogeneity was associated with reduced butterfly diversity. A possible explanation for this pattern is that heterogeneity of grassland may correspond to a higher degree of fragmentation of butterfly habitat, with likely negative consequences for species diversity (Krauss et al. 2004). Our study thus confirms that heterogeneity per se is not universally beneficial for species richness (see also (Ekroos et al. 2008)), although most work to date has focused on its positive effects (e.g. (Kerr et al. 2001)).

The importance of considering multiple scales

To date, results from studies investigating multiple scales have been disparate and difficult to generalize (Flick et al. 2012). We included three spatial scales in our study which we considered relevant for butterfly diversity and distribution. Our study revealed that all investigated scales affected butterfly community composition. Previous studies found local factors affecting butterfly species composition, with local heterogeneity in land cover being a good predictor for species composition in Canada (Kerr et al. 2001; Weibull and Ostman 2003). Butterfly species composition in Transylvania also showed a significant correlation with local factors, but was explained by heterogeneity and woody vegetation cover only at the

two larger scales. Butterfly species richness also responded to variables at all different spatial scales, especially at the local scale, but also at the two larger scales (see also (Weibull et al. 2003)). This suggests that local habitat conditions are particularly important, yet these cannot be considered in isolation from the surrounding landscape (Steffan-Dewenter et al. 2002; Öckinger and Smith 2006).

Our models also showed that the different functional groups of butterflies were affected by variables from different spatial scales. For example, landscape heterogeneity appeared to benefit mobile species but not low-mobility species. Furthermore, we found that woody vegetation cover was related to species richness. Land abandonment induces natural succession, whereas intensification leads to loss of scattered woody vegetation, and both have negative effects on butterfly richness in the long term (Baur et al. 2006). Both processes decrease structural heterogeneity, which is important for viable butterfly populations in agricultural landscapes. In our study, only *Coenonympha pamphilus* showed a unimodal relationship to local woody vegetation cover. For such low-mobile species, presence of woody vegetation is crucial for wind shield and thermoregulation. *C. pamphilus* is abundant in Transylvania, however its population state in other European countries is declining (Conrad et al. 2007). Habitat heterogeneity from different spatial scales, including the presence of woody vegetation, should be further investigated as possible key elements in landscapes to halt biodiversity loss in farmland.

Conclusion

Collapse of communism and accession of Romania to the European Union have accelerated land use change in the rural areas of Transylvania, in particular towards land abandonment and agricultural intensification. The two key gradients considered in this study, namely woody vegetation cover and heterogeneity, would fundamentally change as a result of these two land use change processes. Along the gradients of woody vegetation cover and heterogeneity, we were able to show that butterfly abundance and distribution were affected by a range of different variables operating at multiple spatial scales. Not only local conditions, but the composition and configuration of the landscape as a whole need to be considered for effective conservation management of butterflies in low-intensively managed farming landscapes such as in Transylvania.

Our results showed that, unlike in Western Europe, species richness of butterflies was not only high in grassland, but also in arable land. This suggests that more emphasis needs to be placed on low-intensity farming practices and management of the landscape mosaic, and that arable land needs to be actively considered in butterfly conservation strategies. In our study area, butterfly richness would likely benefit from (1) the continuation of small-scale farming; (2) the production of a variety of crops, including legume species; and (3) the maintenance of broad field margins and uncultivated ruderal areas. New payment schemes under the Common Agricultural Policy have recently been criticised as grossly inadequate (Pe'er et al. 2014). Our findings suggest that even measures considered adequate in Western Europe may not be directly transferable to Transylvania – in low-intensity landscapes, it will be particularly important to consider the high nature value that entire agro-ecosystems provide, both inside

and outside of protected areas (see also (González-Estébanez et al. 2011)). Ultimately, the continued existence of historic-cultural landscapes such as those in Transylvania hinges on the successful transfer of its appreciation and historic management to future generations of farmers. Substantial efforts are therefore needed in environmental education and in developing alternative ways for local people to make a living, for example through the development of cultural and ecological tourism.

Acknowledgements

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Supplementary Material

Table S4.1. Species list of butterfly species observed in the transects

<i>Adscita</i> sp	<i>Hesperia comma</i>	<i>Plebejus idas</i>
<i>Aglais urticae</i>	<i>Heteropterus morpheus</i>	<i>Polygonia c-album</i>
<i>Antocharis cardamines</i>	<i>Hipparchia fagi</i>	<i>Polyommatus amandus</i>
<i>Apatura ilia</i>	<i>Inachis io</i>	<i>Polyommatus coridon</i>
<i>Apatura iris</i>	<i>Ipbiclides podalirius</i>	<i>Polyommatus dorylas</i>
<i>Aphantopus hyperantus</i>	<i>Issoria lathonia</i>	<i>Polyommatus icarus</i>
<i>Aporia crataegi</i>	<i>Jordanita</i> sp	<i>Polyommatus thersites</i>
<i>Araschnia levana</i>	<i>Lasiommata megera</i>	<i>Pontia edusa</i>
<i>Argynnis adippe</i>	<i>Leptidea morsei</i>	<i>Pseudophilotes vicrama</i>
<i>Argynnis aglaja</i>	<i>Leptidea sinapis/ juvernica</i>	<i>Pyrgus armoricanus</i>
<i>Argynnis laodice</i>	<i>Limenitis camilla</i>	<i>Pyrgus alveus</i>
<i>Argynnis niobe</i>	<i>Limenitis populi</i>	<i>Pyrgus malvae</i>
<i>Argynnis paphia</i>	<i>Lopinga achine</i>	<i>Rhagades pruni</i>
<i>Aricia agestis</i>	<i>Lycaena alciphron</i>	<i>Satyrium acaciae</i>
<i>Aricia artaxerxes</i>	<i>Lycaena dispar</i>	<i>Satyrium ilicis</i>
<i>Boloria dia</i>	<i>Lycaena phleas</i>	<i>Thymelicus lineola</i>
<i>Boloria euphrosyne</i>	<i>Lycaena thersamon</i>	<i>Thymelicus sylvestris</i>
<i>Boloria selene</i>	<i>Lycaena tityrus</i>	<i>Vanessa atalanta</i>
<i>Brenthis daphne</i>	<i>Lycaena virgaureae</i>	<i>Vanessa cardui</i>
<i>Brenthis hecate</i>	<i>Lysandra bellargus</i>	<i>Zygaena angelicae</i>
<i>Brenthis ino</i>	<i>Pbengaris arion</i>	<i>Zygaena carniolica</i>
<i>Brinthesia circe</i>	<i>Maniola jurtina</i>	<i>Zygaena ephialtes</i>
<i>Cacharodus</i> sp	<i>Melanargia galathea</i>	<i>Zygaena filipendulae</i>
<i>Callophrys rubi</i>	<i>Meleagera daphnis</i>	<i>Zygaena loti</i>
<i>Celastrina argiolus</i>	<i>Melitaea athalia</i>	<i>Zygaena minos/ purpuralis</i>
<i>Coenonympha arcania</i>	<i>Melitaea aurelia</i>	<i>Zygaena viciae</i>
<i>Coenonympha glycerion</i>	<i>Melitaea britomartis</i>	
<i>Coenonympha pamphilus</i>	<i>Melitaea cinxia</i>	
<i>Colias alfacariensis/ hyale</i>	<i>Melitaea diamina</i>	
<i>Colias crocea</i>	<i>Melitaea didyma</i>	
<i>Cupido decoloratus</i>	<i>Melitaea phoebe</i>	
<i>Cupido minimus</i>	<i>Melitaea trivia</i>	
<i>Cupido osiris</i>	<i>Minois dryas</i>	
<i>Cyaniris semiargus</i>	<i>Neptis sappho</i>	
<i>Erebia medusa</i>	<i>Nymphalis antiopa</i>	
<i>Erynnis tages</i>	<i>Ochlodes sylvanus</i>	
<i>Eumedonia eumedon</i>	<i>Papilio machaon</i>	
<i>Euphydryas aurinia</i>	<i>Pararge aegeria</i>	
<i>Everes alcetas</i>	<i>Pieris brassicae</i>	
<i>Everes argiades</i>	<i>Pieris napi</i>	
<i>Glaucopsyche alexis</i>	<i>Pieris rapae</i>	
<i>Gonepteryx rhamni</i>	<i>Plebejus argus</i>	
<i>Hamearis lucina</i>	<i>Plebejus argyrognomon</i>	

Table S4.2 Correlation matrix of the variables used in the study

	NoPlant	het_1ha	woody_1ha	heatload	TWI	rug_50ha	woody_50ha	ed_50ha	past_catch	woody_catch	catch_rugg	SIDI	ED
NoPlant	1.00	-0.22	0.07	0.03	-0.25	0.39	0.27	0.06	-0.09	0.14	-0.02	-0.17	-0.11
het_1ha	-0.22	1.00	0.22	0.15	0.09	0.02	0.09	0.12	-0.18	0.15	0.03	0.02	0.11
woody_1ha	0.07	0.22	1.00	0.00	0.25	0.10	0.29	0.02	0.02	0.22	-0.04	-0.20	-0.15
heatload	0.03	0.15	0.00	1.00	-0.04	0.12	0.00	0.06	0.00	-0.01	0.13	0.15	0.18
TWI	-0.25	0.09	0.25	-0.04	1.00	-0.13	-0.02	0.02	-0.05	0.17	0.10	0.04	-0.04
rug_50ha	0.39	0.02	0.10	0.12	-0.13	1.00	0.49	0.27	-0.29	0.38	0.24	-0.07	0.15
woody_50ha	0.27	0.09	0.29	0.00	-0.02	0.49	1.00	0.42	-0.29	0.61	0.01	-0.27	0.14
ed_50ha	0.06	0.12	0.02	0.06	0.02	0.27	0.42	1.00	-0.29	0.30	0.20	-0.12	0.31
past_catch	-0.09	-0.18	0.02	0.00	-0.05	-0.29	-0.29	-0.29	1.00	-0.46	-0.10	-0.11	-0.11
woody_catch	0.14	0.15	0.22	-0.01	0.17	0.38	0.61	0.30	-0.46	1.00	0.09	-0.29	-0.05
catch_rugg	-0.02	0.03	-0.04	0.13	0.10	0.24	0.01	0.20	-0.10	0.09	1.00	0.25	0.09
SIDI	-0.17	0.02	-0.20	0.15	0.04	-0.07	-0.27	-0.12	-0.11	-0.29	0.25	1.00	0.29
ED	-0.11	0.11	-0.15	0.18	-0.04	0.15	0.14	0.31	-0.11	-0.05	0.09	0.29	1.00

Chapter 5

Aliens in Transylvania: risk maps of invasive alien plant species in Central Romania

Heike Zimmermann, Jacqueline Loos, Henrik von Wehrden & Joern Fischer

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Abstract

Using the MAXENT algorithm, we developed risk maps for eight invasive plant species in southern Transylvania, Romania, a region undergoing drastic land-use changes. Our findings show that invasion risk increased with landscape heterogeneity. Roads and agricultural areas were most prone to invasion, whereas forests were least at risk.

Introduction

Species distribution models are a useful tool in biological invasion risk management (Jimenez-Valverde et al. 2011). They allow a rapid assessment of the distribution of alien species, which may serve to identify areas of high invasibility and to understand the mechanisms behind the establishment and spread of alien species (Zimmermann et al. 2011).

We focused our study on southern Transylvania, in Central Romania, where temporary or permanent abandonment of agricultural land is common. Knowledge on the introduction history of invasive plant species and their current distribution in this region is largely missing, although several common alien plant species are among the world's 100 worst invaders (DAISIE 2013; GISD 2013). To address this knowledge gap, we aimed to identify predictors of the distribution of eight highly invasive species.

Methods

Study area

Our study area comprised an area of 7,440 km² (Figure 5.1). It is a heterogeneous, hilly, rural landscape, at elevations from 230 to 1100 m, and characterized by a mosaic of different land cover types supporting high farmland biodiversity (Loos et al. 2014a). Small-scale semi-subsistence farming with little use of machinery or agrochemicals, as well as extensively used hay meadows and grasslands are typical for the region.

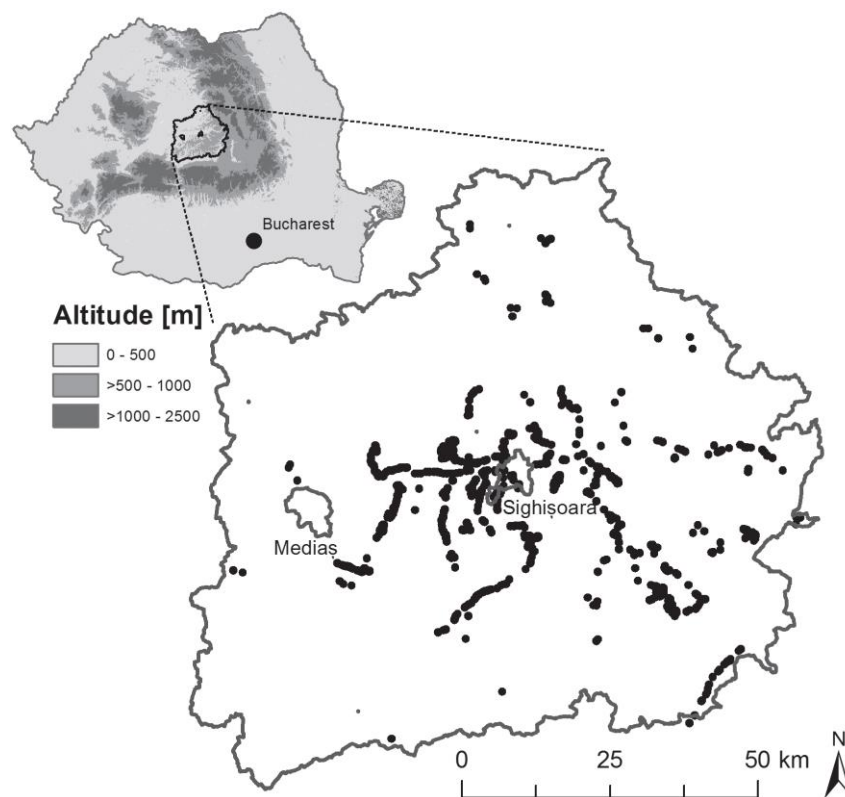


Figure 5.1. Location of our study area in Romania. Inside the enlarged map of our study area the cities Mediaș and Sighișoara are outlined and black points represent the presence points of all eight study species.

The small-scale mosaic pattern of different land cover types prevails throughout the study area, although the North-West has a relatively higher percentage of arable land, the South has a relatively higher percentage of pastures, and the central part a higher percentage of forests (Hanspach et al. 2014). Like many other parts of Eastern Europe, Romania has experienced drastic socio-economic changes, with the collapse of the communist regime in 1989, and its accession to the European Union in 2007 (Kuemmerle et al. 2009). Among other changes, the communist regime and its collapse triggered mass emigration from some areas, resulting in widespread farmland abandonment (Figure 5.2).

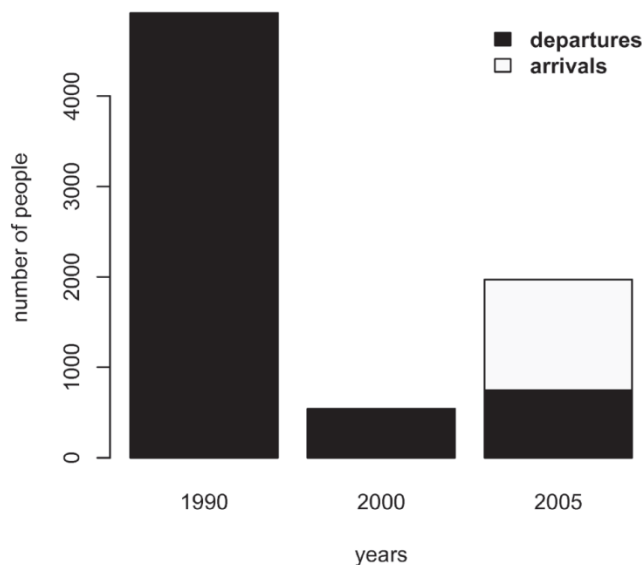


Figure 5.2. Population census data from 1990, 2000 and 2005 for a subsample of 22 communes across the study area. One commune typically includes four villages. In Romania the communist regime and its collapse in 1989 triggered mass emigration from these areas.

Sampling

In summer 2013, we mapped presences of eight prominent alien plant species across the study area using a handheld global positioning system (Table 5.1). Our sampling covered a large variety of landscape elements within 50 km of the town of Sighisoara (Figure 5.1). In each local valley, we undertook at least two extended survey walks that lasted between 30 and 180 minutes. We sampled along roads, but also tracked species off-road, by walking towards the top of the hills bordering a given valley. Furthermore, we took sample points whenever we observed an invasive species during our other field activities. For *Robinia pseudoacacia* we did not record planted trees, but only naturally dispersed individuals. We did not measure the distance to the next adult tree, but the minimum distance was approximately 100 m and for most recordings adult trees were not in sight. We also included vegetation sampling data from 2012, which was based on a randomized stratified design. The minimum distance between sampling points was 30 m. In combination, our sampling approach covered a wide range of environments across the study area.

Table 5.1. Overview of study species and number of sampling points (N Am = North America).

Species	Family	Common name	Life strategy	Origin	Reproduction/dispersal	Presence points
<i>Amaranthus retroflexus</i> L.	Amaranthaceae	Redroot amaranth	annual herb ~1 m	N Am	monoecious, wind pollinated, dispersed by wind, water and animals	45
<i>Asclepias syriaca</i> L.	Apocynaceae	Common milkweed	perennial herb ~1-2 m	N Am	insect pollinated, seeds wind dispersed, and vegetative reproduction (rhizomes)	65
<i>Conyza canadensis</i> (L.) Cronquist	Asteraceae	Canadian horseweed	annual herb ~1 m	N Am	insect pollinated, self- and cross-fertilization, seeds wind dispersed	35
<i>Erigeron annuus</i> (L.) Pers.	Asteraceae	Annual fleabane	annual herb ~1 m	N Am	insect pollinated, self- and cross-fertilization, winged achenes dispersed by wind and animals	475
<i>Fallopia japonica</i> (Houtt.) Ronse Decr.	Polygonaceae	Japanese knotweed	perennial herb ~3 m	Asia	insect pollinated, dioecious, winged achenes dispersed by wind, water, animals, and reproduces vigorously by rhizomes	69
<i>Robinia pseudoacacia</i> L.	Fabaceae	Black locust	deciduous tree ~30 m	N Am	insect pollinated, seeds wind dispersed, reproduces vigorously by root suckering and stump sprouting	264
<i>Solidago canadensis</i> L.	Asteraceae	Canadian goldenrod	perennial herb ~2.5 m	N Am	insect pollinated out-crossing, wind dispersed achene with pappus, and vegetative reproduction (rhizomes)	298
<i>Xanthium strumarium</i> L.	Asteraceae	Common cocklebur	annual herb ~1 m	N Am	wind-pollinated, monoecious, self- and cross-fertilization, apomixis, seeds dispersed by animals and water	236

Analysis

We derived invasion risk maps for each species individually. To this end, we applied the Maximum Entropy algorithm (MAXENT), which is based on presence only data to map the likely current distribution for each species in our study area (Phillips et al. 2006; Elith et al. 2011; Merow et al. 2013).

Our approach to model the likely current distribution based on presence only data is in line with our assumption that the expansion of our species has not yet reached equilibrium, making the use of observed absences misleading (Jimenez-Valverde et al. 2011). Clamping was activated as well as random seed, and we made an internal validation with 50 replicates and 20 % random test percentage. Predictors encompassed information on the topography, land use and potential distribution corridors (Table 5.2). Slope and terrain ruggedness (the variation in altitude) did not improve any of the models. Our final models therefore included four predictors (road and village distance, heterogeneity, and land cover classes). Each of these predictors was re-sampled to a cell size of 30 x 30 m within ArcGIS, which thus equals the resolution of our risk maps. To calculate the potential areas suitable for each species a threshold rule was applied to convert continuous suitability surfaces into binary outputs. We selected the threshold “maximum training sensitivity plus specificity logistic threshold”, which focuses on the correct classification of presences and background points (Jimenez-Valverde and Lobo 2007). For each grid cell, we then calculated the mean probability of occurrence over all eight species. This resulted in a map of general invasion risk for the study area, referred to “the invasibility map” hereafter.

Table 5.2. Predictors for the MAXENT model. All predictors have a 30 x 30 m resolution. (h.s. = habitat suitability).

Predictor	Description	Relative importance in the MAXENT model
Road distance	minimum distance to the closest road	18 to < 40 % (<i>A. retroflexus</i> , <i>A. syriaca</i> , <i>C. canadensis</i>) 45 - 48 % (<i>E. annuus</i> , <i>R. pseudoacacia</i> , <i>S. canadensis</i>) >50 % - 56 % (<i>F. japonica</i> , <i>X. strumarium</i>) for all species h.s. high with decreasing distance
Village distance	minimum distance to the closest village	15 % (<i>S. canadensis</i>) high h.s. at 3-4 km for remaining species values <10%
Heterogeneity (CNES 2007, Distribution Spot Image SA)	variation in the panchromatic channel of SPOT 5 satellite imagery	>20 % - 35 % (<i>A. syriaca</i> , <i>C. canadensis</i> , <i>E. annuus</i> , <i>F. japonica</i> , <i>S. canadensis</i> , <i>X. strumarium</i>) >40 % - 46 % (<i>A. retroflexus</i> , <i>R. pseudoacacia</i>) for all species h.s. high with increasing heterogeneity
Corine land cover classes (Corine 2006 Land Cover Map, EEA (2006) Corine land cover 2000 -- A seamless vector database (European Environment Agency, Copenhagen)	(1) broad leaved forest (2) coniferous and mixed forest (3) water (4) inland marshes (5) natural areas (sparsely vegetated, bare rocks, natural grasslands) (6) transitional woodland-shrub habitats (7) artificial surfaces (8) agriculture (9) pasture (10) Land principally occupied by agriculture with significant areas of natural vegetation	15 % (<i>X. strumarium</i> high h.s. for class 8) 22 % (<i>A. retroflexus</i> high h.s. for class 4) 23 % (<i>A. syriaca</i> high h.s. for classes 8, 9) 35 % (<i>C. canadensis</i> high h.s. for classes 8, 10) for remaining species values <15 %

Results

Single distribution models of the eight study species all had high discrimination performances with AUC values ranging from 0.8 to 0.9 (Elith 2002). Standard deviation of the output grids showed no signs of autocorrelation. Road distance and heterogeneity were the most important predictors (Table 5.2). Corine land cover classes substantially improved the MAXENT model of three species, with agricultural areas, pastures and land principally occupied by agriculture with significant areas of natural vegetation, having the highest risk of invasion. Forest was at least risk of being invaded. With 31 % potential habitat, *Erigeron annuus* has the largest potential distribution and with 8 %, *Asclepias syriaca* had the lowest (Figure 5.3a, b). Risk maps of all species show a high invasibility of distribution corridors such as roads and rivers. The overall invasibility map therefore shows a network structure with the highest invasibility close to distribution corridors stretching across the whole study area (Figure 5.3c). However, the invasibility was highest in heterogeneous areas, which is where it also reached furthest away from roads.

Discussion

Our risk maps show that the eight invaders considered have great potential to further expand their distributions. All except for one study species are wind dispersed, which is an effective long distance dispersal method (Cain et al. 2000). Roads serve as invasion corridors, enabling the species establishment inside disturbed road margins (Birdsall et al. 2012). Environments at greatest risk of invasion away from roads appeared to be heterogeneous agricultural areas. Landscape heterogeneity is beneficial for native species in farming landscapes, because it offers a greater variety of habitats (Fischer and Lindenmayer 2007). However, invasive species also appear to benefit from this variety. A positive correlation of native and invasive plant species richness in relation to landscape heterogeneity was also shown for the Rocky Mountain National Park in the USA (120-960 m radius scale; Kumar et al. 2006), for rural and urban areas in Germany (32 km² scale; Deutschewitz et al. 2003), as well as for rural areas and woodlands in Catalonia (100 km² scale; Bartomeus et al. 2012). Furthermore, heterogeneous landscapes offer more edge environments which are subject to higher levels of propagule pressure and disturbance, and therefore a higher abundance of invasive plant species (Vilà and Ibáñez 2011). Like many invasive species, our study species are adapted to disturbance through their short life cycles, rapid germination, persistent seed banks, or vegetative reproduction (Rejmánek and Richardson 1996; Kolar and Lodge 2001). We observed that areas with a high heterogeneity often coincide with areas that experienced the most widespread emigration following the collapse of communism. Socio-economic effects at regional or local scales are rarely considered in invasion science (Vilà and Pujadas 2001; Guo et al. 2012). This is a potentially important oversight. For example, farmland abandonment and land-use change can facilitate high abundances of alien plant species (Hobbs 2000; Cramer et al. 2008). Decades of cultivation may deprive native seed banks and altered soil conditions may no longer be suitable for native species (Cramer et al. 2008).

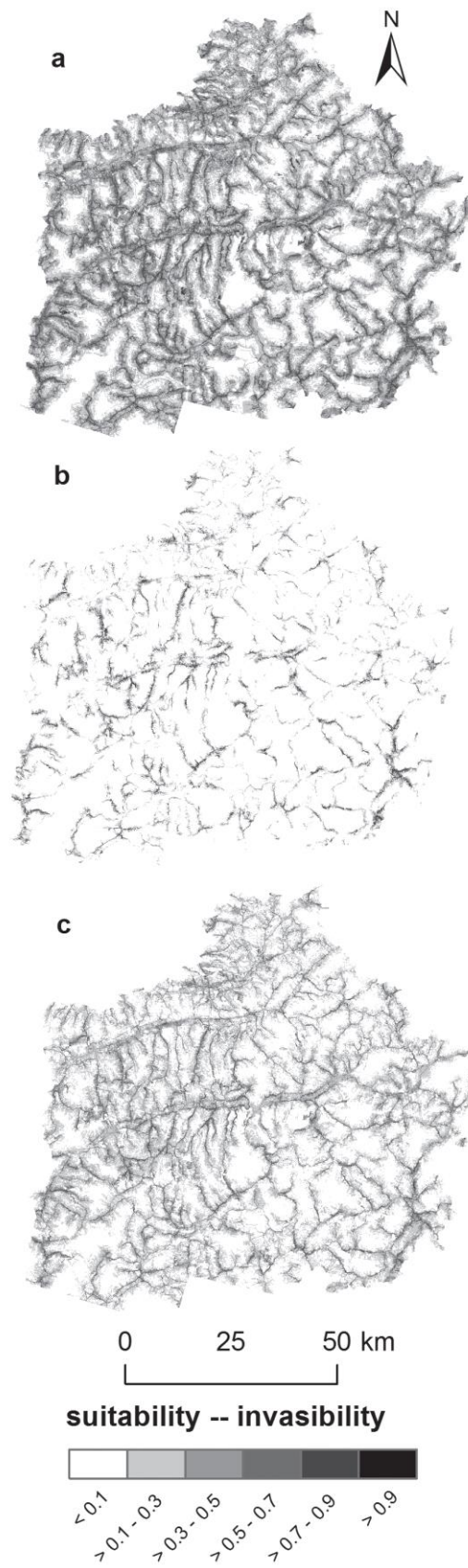


Figure 5.3. The likely current distribution for a *Erigeron annuus* and b *Asclepias syriaca* in our study area. c Shows the invasibility, calculated as the mean probability of occurrence over all eight study species.

In comparison to native species, species new to this region may possess traits that make them better colonizers of abandoned fields. They benefit from increased human mediated propagule pressure (propagule bias), are often stronger competitors (enemy release, novel weapons), and once established may further transform their environment, making it even less suitable for native species – thereby creating self-perpetuating alien monocultures (Catford et al. 2012). Our study area continues to undergo socio-economic changes. With our main project (“Fostering sustainable development in Eastern Europe” <http://peisajesostenabile.wordpress.com/>) we aim to provide leverage points for enabling sustainable land use practices. Based on the results of this study we recommend to preserve the remaining intact forests, which seem to be least in risk of invasions and to further investigate the role of land abandonment and land use change in our study area.

Acknowledgments

We thank all the people in the field who helped us to track down aliens in Transylvania. We are also thankful to P. Brandt and P. Fust for their technical advice. This study was funded by a Leuphana small research grant (HZ) and through a Sofja Kovalevskaja Award by the Alexander von Humboldt Foundation (JL, JF).

Chapter 6

Landscape effects on butterfly movements in low-intensive farmland of Transylvania (Romania)

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Abstract***Context***

Agricultural transformation and increased land use intensity often lead to simplified landscapes and biodiversity loss. For animals, one possible mechanism underpinning biodiversity loss in agricultural landscapes is the disruption of movements. The disruption of movements may explain, for example, why butterfly communities in agricultural landscapes are often dominated by generalist species with high mobility.

Objectives

Here, we investigated how the movement patterns of butterflies characterised by different levels of mobility changed along a gradient of agricultural land use intensity.

Methods

To this end, we studied 15 landscapes in low-intensity farmland in Central Romania, measuring 10 ha each and covering a gradient of landscape heterogeneity and woody vegetation cover. In these landscapes, we tracked movements of 563 individuals of nine butterfly species.

Results

Our findings showed that overall movement activities differed significantly between species, corresponding well with expert-derived estimates of species-specific mobility. Interestingly, species of low and high mobility responded in opposite ways to increasing levels of landscape heterogeneity. In relatively simple landscapes, the movement patterns of low and high mobility species were similar. By contrast, in complex landscapes, the flight paths of low-mobility species became shorter and more erratic, whereas the flight paths of high-mobility species became longer and straighter. An analysis of the land covers traversed showed that most species avoided arable land but favoured the more heterogeneous parts of a given landscape.

Conclusions

In combination, our results suggest that non-arable patches in agricultural landscapes are important for butterfly movements, especially for low-mobility species.

Introduction

Human activities have altered the structure and composition of landscapes worldwide, especially through the conversion of natural habitat to agricultural land (Benton et al. 2003; Foley et al. 2005; Lindenmayer and Fischer 2006). In traditional, low-intensity agricultural areas, many species can persist (Fahrig et al. 2011; Wright et al. 2012). However, farmland biodiversity in such areas has increasingly come under threat from land use intensification (Stoate et al. 2009).

Low-intensity agricultural landscapes often consist of a mosaic of habitat patches (Bennett et al. 2006), in which different landscape structures facilitate or impede ecological flows such as animal movements (Taylor et al. 1993; Tschardt et al. 2012b). The persistence of many species in mosaic landscapes depends on the capacity of species to move and disperse within a network of suitable patches (Nathan et al. 2008; Bergerot et al. 2012). In this context, butterflies are useful model organisms (Watt and Boggs 2003) because of their relatively short life cycles, their quick responses to environmental change (Erhardt 1985; Warren and Bourn 2011), and because they are relatively well-studied (Stevens et al. 2010). In general, the responses to landscape structures vary between butterfly species, depending on differences in ecological traits (Öckinger et al. 2009), including the innate capacity for movement (Stevens et al. 2010; Sekar 2012). Intensification of land use has shown effects on butterfly communities by causing an increase of ecological generalists and a decrease in ecological specialists and species with poor mobility (Ekroos et al. 2010; Börschig et al. 2013). To anticipate and manage the responses of butterflies to landscape change, it is important to understand the ecological mechanisms driving species decline (Bowne and Bowers 2004), including disruptions to movements.

Movements can be distinguished as routine movements versus dispersal movements. In butterflies, routine movements represent daily behavior, such as foraging, shelter-seeking, or territorial displays (Wickman and Wiklund 1983; Van Dyck and Baguette 2005). Such movements occur mainly within the same vegetation patch and are often characterized by higher sinuosity than directed flights (Kuefler et al. 2010; Stevens et al. 2010). In contrast, dispersal movements include shifts from one vegetation patch to another, for colonization or to obtain complementary resources (Dunning et al. 1992; Hovestadt and Nieminen 2009). Dispersal can occur through directed movements, but also as a by-product of routine movements (Van Dyck and Baguette 2005; Delattre et al. 2013),

While several studies have investigated dispersal (Stevens et al. 2010; Sekar 2012; Driscoll et al. 2014), a clear understanding of how landscape heterogeneity facilitates or impedes routine movements of butterfly species with different levels of mobility is still lacking (Dennis et al. 2013). Differing abilities of species to move between and across different kinds of closely located habitat patches may, in turn, depend on the size of the landscape grain and the perceptual range of different species (Baguette and Van Dyck 2007). Hence, movement is a response that differs between species (Komonen et al. 2004; Stevens et al. 2010; Sekar 2012), resulting from the interaction of species-specific movement capacity with landscape characteristics, such as habitat composition and configuration (Mennechez et al. 2003; Dover and Settele

2009). The movements of butterflies have been characterized by measures such as flight duration, the length of separate flights or step lengths (Kallioniemi et al. 2014), and the frequency of crossing boundaries between patch types (Ries and Debinski 2001; Conradt and Roper 2006; Schultz et al. 2012). However, empirical studies to date typically have considered very few species at the same time (Kallioniemi et al. 2014; Kuussaari et al. 2014), thus limiting their capacity to reach general conclusions.

To systematically investigate the effects of landscape heterogeneity on the movements of multiple butterfly species, we conducted a detailed case study in Central Romania (Fischer et al. 2012). We investigated how butterflies adjusted their movement patterns in response to landscape simplification by tracking butterfly movements in landscapes strategically selected to cover a broad gradient in heterogeneity. We expected that species characterized by low mobility would adjust their movement patterns along the gradient of landscape heterogeneity in a different manner than highly mobile species. Specifically, the concept of landscape functional grain (Baguette and Van Dyck 2007) suggests that the flight paths of habitat specialists should be shorter and more erratic in resource-rich, heterogeneous landscapes than in resource-poor, simplified landscapes. If this is the case, it may explain at least partly why low-mobility species are selected against during the process of landscape simplification (Dormann et al. 2007). Our specific aims were (i) to compare the observed mobility of a set of species with a priori estimates based on expert opinion; (ii) to test whether landscape heterogeneity differentially affected movement patterns of butterflies with different levels of mobility; and (iii) to examine which landscape elements were preferentially selected for in the flight paths of different butterfly species.

Methods

Study area

This study was conducted within farmland of Southern Transylvania, Romania (Figure 6.1a). Undulating terrain characterized this area (266-900 m ASL altitude), of which grassland (meadows and pastures) covered approximately 24 % and arable fields 37 %. Arable land was largely embedded within a fine-grained mosaic including semi-natural vegetation, such as field margins and hay meadows (Akeroyd and Page 2006).

Selection of butterfly species

To make sure that we would track a set of species with different levels of innate mobility, we asked local experts to estimate the relative mobility of a wide range of butterfly species. To this end, we used the responses to a questionnaire completed by eight experienced Lepidopterists from Romania and Eastern Europe. Experts were asked to assign a rank between one and nine, representing low and high mobility, respectively, to 110 species occurring in the study area. Based on the responses, we averaged the mobility scores provided by the experts and grouped species into three classes of mobility (1-3: low; 4-6: medium; and 7-9: high). For each class, we then selected three species that we knew from a previous study to be relatively widespread and abundant in our study area (Loos et al. 2014a; Loos et al. 2014b). We considered

Pieris rapae, the species complex *Colias hyale/alfacariensis*, and *Pontia edusa* as mobile species; *Pieris napi*, *Coenonympha pamphilus*, and *Melitaea phoebe* as species of intermediate mobility; and *Glaucopsyche alexis*, *Aphantopus hyperantus*, and *Minois dryas* as species of low mobility. *Colias alfacariensis* and *Colias hyale* represent two different species that could be considered having a too high intraspecific variation in their movement behaviour to be treated as a species complex in analyses such as ours. However, none of the used movement variables in this study does indicate a higher intraspecific variation in this species complex than in other species (Fig. S6.3), even though all movement variables showed significantly different species-specific variance (as stated in the Results). Finally, we ranked these nine species from one (i.e. lowest mobility) to nine (i.e. highest mobility), again drawing on the experts' assignments.

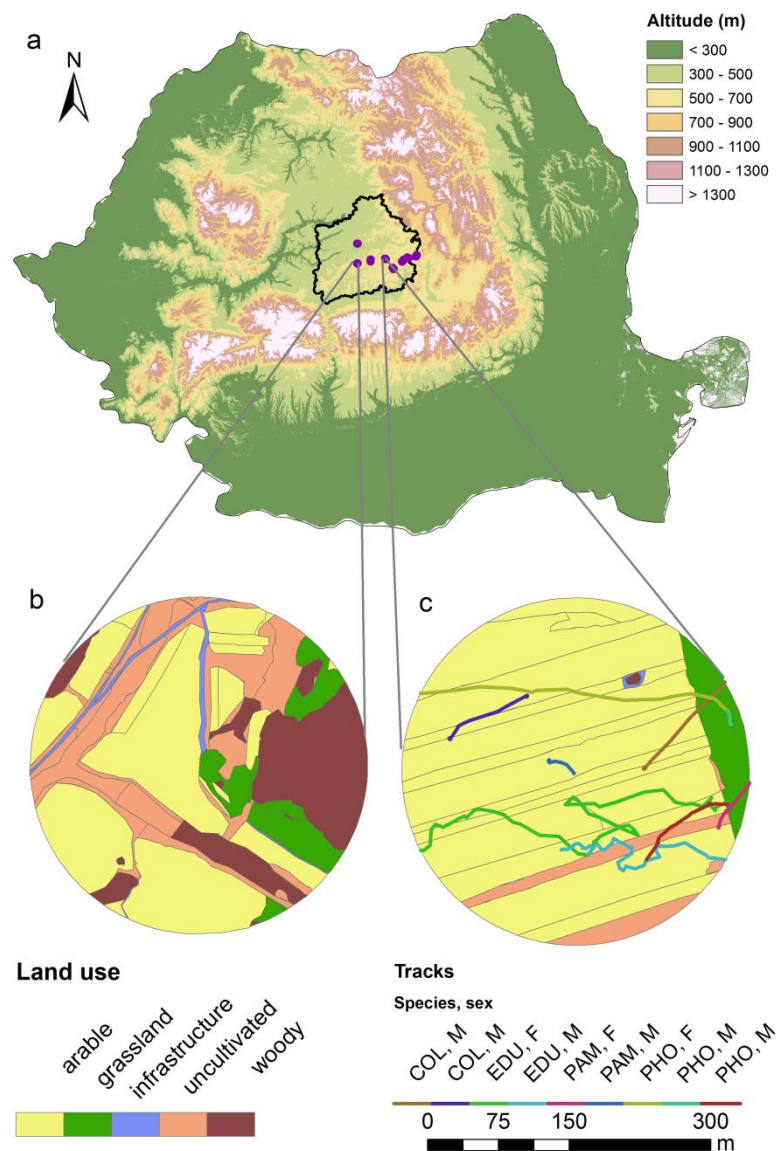


Figure 6.1: a) Location of the study area within Romania; b) location of the 15 study sites; c) example of a ground-map in a highly heterogeneous site; and d) example of butterfly tracks within a low-heterogeneity site. Abbreviations of species names: *Pieris rapae* (rap), *Colias hyale/alfacariensis* (col), *Pontia edusa* (edu), *Pieris napi* (nap), *Coenonympha*

pamphilus (pam), *Melitaea phoebe* (pho), *Glaucopsyche alexis* (ale), *Aphantopus hyperantus* (hyp), *Minois dryas* (dry).

Selection of landscapes

We investigated 15 different landscapes which were represented by circles with an area of 10 hectares each. These landscapes were specifically selected to cover a broad gradient in woody vegetation cover and landscape heterogeneity. The minimum percentage of woody vegetation cover in a landscape was 0 % and the maximum was 53 % (median: 6 %). We defined landscape heterogeneity as the spectral variance (i.e. the standard deviation) of the panchromatic channel of SPOT 5 satellite imagery (©CNES 2007, Distribution Spot Image SA), henceforth called “spot heterogeneity” (for more details see Hanspach et al. 2014). In the landscapes selected, the minimum value of spot heterogeneity was 0.14 and the maximum was 0.32 (median: 0.24), with higher values representing higher heterogeneity. Woody vegetation cover and spot heterogeneity were not correlated (Pearson's $r = 0.05$, $p = 0.85$).

Field sampling

Based on a previous study on butterfly species composition (Loos et al. 2014a), we knew that each of our focal landscapes was likely to support at least five of our target species. We conducted field work during five visits to each landscape, at regular interval of two weeks between 25 May and 5 August 2013. We collected data with pairs of two surveyors based on the following three steps.

First, we conducted ground mapping of a given site, subdividing it into sections representing one of five general land uses, namely arable land, grassland, woody vegetation (e.g. trees, hedgerows), uncultivated land, or anthropogenic infrastructure (e.g. roads, buildings). Ground mapping was repeated at each visit to account for changes in land-cover which occurred throughout the course of the season (e.g. through ploughing or mowing). At each visit, each land cover type was further sub-classified and described more precisely, for example by crop type, function (e.g. side strip, infrastructure), and status (e.g. mown or abandoned). Within each section, we estimated the height of the dominant vegetation as well as floral abundance and flower diversity. We transferred this information for each visit into ArcGIS 10.1 in order to create ground maps, which we used as a reference for the subsequent visit and later in the analyses (Figure 6.1b).

Second, we searched for the target butterfly species between 9.00 am and 5.00 pm and tracked individuals. We started searching from the center and continued in a systematic way to cover the entire study site. We organized our search routes in a way to enter forested patches later during the day, as we expected butterflies to move in or into the shaded areas when the temperature in open sections would be higher. When a suitable butterfly was found, we caught it, determined its sex, estimated its age by wing wear, marked it with a permanent marker to avoid re-capture of the same individual, transferred it to a plastic jar and placed it in a cooler box for five minutes. We then released the butterfly and tracked its flight path by following it with a handheld GPS device (Garmin etrex 20), keeping a minimum distance of 2 m (Figure

6.1c). We stopped individual tracking after 30 minutes, or alternatively when the butterfly was lost or when it flew out of the study site. For each track, we also recorded weather conditions and temperature.

Third, we recorded butterfly behavioural activities as sitting, basking, feeding on nectar, egg-laying, flying, or interacting with other individuals during the tracking period, every time the butterfly changed behaviour. To summarize each flight path thus recorded, we quantified six variables that described butterfly movement patterns: (i) flight duration (i.e. total time of all flying movements of the individual butterfly), (ii) the number of boundary crossings between sections, (iii) the distance between start and end of the observation (henceforth “air distance”), and (iv) total track length. Based on this, we calculated (v) mean speed and (vi) track sinuosity (ratio of track length to air distance).

Environmental variables

We assessed several environmental variables to quantify the heterogeneity and land use intensity of each site. Based on our ground maps, for each individual visit, we quantified landscape heterogeneity by calculating patch density based on the number of distinct landscape elements per site. Also based on the results of our on-ground mapping, we extracted edge density and the Shannon index of diversity as measures of landscape heterogeneity, using the software Fragstats 4.2 (McGarigal et al. 2012). In addition, we calculated the proportions of the different land cover types, classified as arable land, grassland, uncultivated patches, woody vegetation and human infrastructure. Finally, we imported the individual GPS-tracks into GIS and buffered each individual track with a distance of 20 m (to each side of the track). Within these buffers, we again noted the proportions of different land covers and again calculated patch density, edge density, and percent land cover.

Analyses

We first assessed the degree of congruence between expert evaluations of mobility and our measurements of mobility by first ranking all species according to the six observed movement variables (i.e. flight duration, boundary crossings, air distance, track length, mean speed, and sinuosity) and averaging the rank for these six movement variables for each species to derive an observed species-specific mobility rank. We correlated our observed mobility rank with the estimated mobility ranks provided by experts with Spearman correlations.

Second, we explored the quantitative differences in mobility between species by comparing linear mixed-effect models for each log_e-transformed movement variable as a response. To this end, we performed two models for each mobility variable with species identity as a fixed factor and site as a random [blocking] variable using the nlme package in the R statistical environment (Pinheiro et al. 2014). One model included an individual variance estimate for each species, whereas the other assumed equal variances between species. We then compared the performance of these two models with likelihood ratio tests to test for evidence of uneven variance in mobility between species. Having selected the better performing

model, we then conducted Tukey's Honestly Significant Difference post-hoc tests to quantify which species differed from one another in terms of their average mobility.

Third, we analyzed the relationship between butterfly mobility and landscape attributes using two separate analytical approaches. To obtain an overview of movement patterns in response to landscape structure, we simplified our data using two ordinations: (1) we fed all six movement variables described above into one Principal Component Analysis (PCA; henceforth “movement PCA”); and (2) we fed six selected environmental variables (patch density, edge density, Shannon index of diversity, percent arable land, percent forest, and spot heterogeneity) into another PCA (henceforth “environment PCA”). We normalized and scaled all heterogeneity and movement variables beforehand. We used the first axis of the movement PCA as a response variable in a generalized linear mixed model using the `lmer` function in the library `nlme`, including as fixed effects (i) the species-specific mobility rank, (ii) the first two axes of the environment PCA, (iii) the interaction between the mobility rank and the two environment variables, and (iv) temperature. We included two sets of random effects into the model: (i) visit nested within site, and (ii) a factor derived from all possible combinations of the species identity and its sex (e.g. *G. alexis* male, *G. alexis* female, etc.).

Finally, we investigated whether butterfly species preferentially selected certain land-cover types over others. For this purpose, we considered each individual flight path and its buffer as a presence point, and the whole site as the background data from which the individual chooses. Based on this, we calculated species-specific generalized linear mixed models with binomial error distribution. Fixed effects included percent land cover type for each buffered track versus percent land cover type for the entire ten hectare site. Species were included as random effects. All analyses were performed in R v.2.15.2 (R Core Team 2013).

Results

In total, we obtained tracks for 563 individual butterflies (Table S6.1). All movement variables showed significantly different species-specific variance (likelihood ratio ≥ 106.55 ; $p \leq 0.0001$) and significant differences in mean mobility between species ($p < 0.001$, Figure S6.1 and Table S6.2). The species-specific movement ranking based on observed mobility showed a high congruence with the independent expert opinions (Spearman's $\rho = 0.9$; Figure S6.2).

Regarding butterfly movement, the first two components of the movement PCA explained 67.1 % of the variance (Figure 6.2a). The first axis showed strong negative correlations with the movement variables air distance (Pearson's $r = -0.92$), track length ($r = -0.88$), number of boundary crossings ($r = -0.73$), and flight duration ($r = -0.67$), and a weak positive correlation with sinuosity ($r = 0.38$). A correlation test of the number of crossing boundaries of individuals and the number of sections present in a site revealed no correlation pattern (Pearson's $r = 0.13$), which is why we only intrinsically accounted for the variation of the number of boundaries between sites by combining the environment PCA with the movement PCA. In the environment PCA, we accounted for the different number of sections present in a site through the

variables patch density and edge density. When comparing the two PCAs, it is apparent that sites with a larger number of sections had higher numbers in crossing boundaries than sites with fewer sections. Crossing boundaries correlated with sinuosity and the first axes of the PCA (Fig. 2a), which we later on used in our modelling approach. The second axis was strongly and positively correlated with flight speed ($r = 0.94$). Regarding landscape attributes, the first two components of the environment PCA explained 72.1 % of the variance (Figure 6.2b). The first axis correlated negatively with the landscape heterogeneity measures edge density ($r = -0.94$), patch density ($r = -0.90$), Shannon index of landscape diversity ($r = -0.73$), and spot heterogeneity ($r = -0.36$). The second axis described a gradient of land use intensity, being negatively correlated with cover of woody vegetation ($r = -0.75$) and positively correlated with percent cover with arable land ($r = 0.60$).

Our landscape model revealed that the first axis of the movement PCA was significantly explained by the mobility rank, temperature, and an interaction between mobility rank and the second axis of the environment PCA (Table 1). Hence, movement patterns were differently influenced by increasing cover of intensively managed arable land in the landscape depending on the mobility of the species. Increasing proportions of arable land per site corresponded with longer and straighter movements for species with low mobility, but with shorter and more erratic movements in mobile species (Figure 6.3).

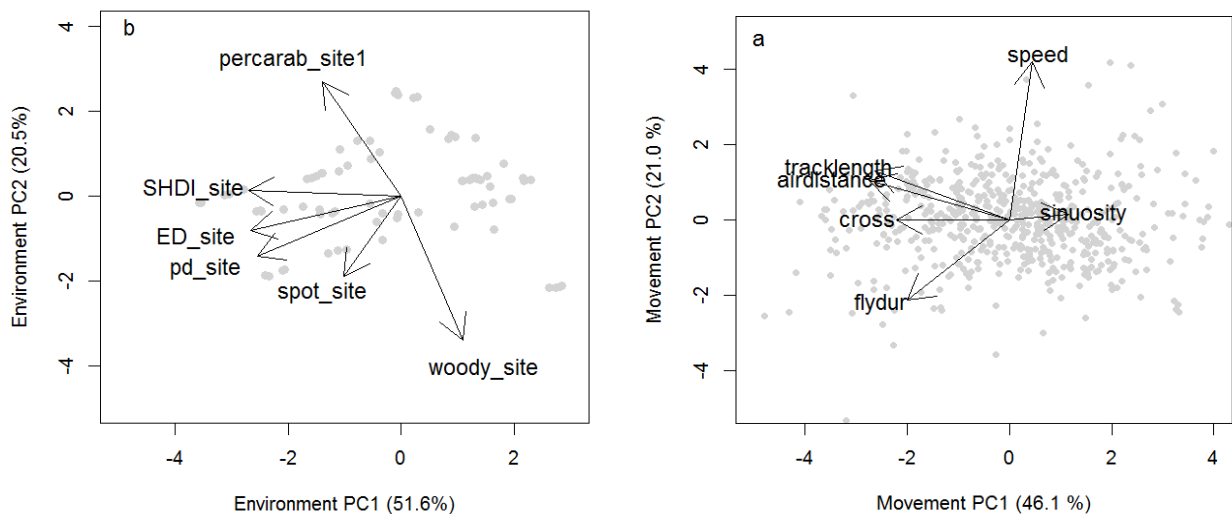


Figure 6.2. a) Movement PCA of all butterfly tracks, including the observed movement variables speed, air distance, track length, sinuosity, duration of flight (“flydur”), and number of boundary crossings (“cross”); b) environment PCA of all study sites and repeats, including the variables woody vegetation per site (“woody_site”), amount of arable land per site (“percarab_site”), heterogeneity variables measured by variance of panchromatic SPOT data (“spot_site”), Shannon index of landscape heterogeneity (“SHDI_site”), edge density (“ED”), and patch density (“pd”). The numbers in brackets in x- and y-axes display the explained variance of the PCA axis.

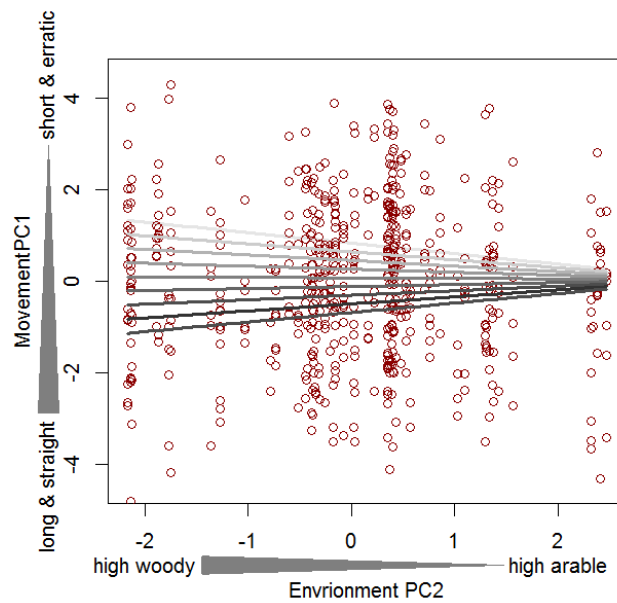


Figure 6.3: Result of the landscape model, in which the first axis of the movement PCA (Figure 6.2a), which represents movement activity of the individual butterfly, was explained by an interaction of species' mobility class and the second axis of the environment PCA (Figure 6.2b), which represented a gradient of land use intensity. The shade of the plotted regression line increases with mobility of the species, i.e. the darkest line refers to the most mobile species. The open circles are the empirical observation from the nine focal butterfly species.

Table 6.1: Results of the landscape model testing the effects of species mobility class and the two axes of the environmental PCA (env. PCA) on butterfly movement activity. The random effect "SpecSex" represented a factor combining the butterfly species and the sex of the individual (one level for each species-sex combination). Displayed are standard deviation (SD), estimates, standard errors and significance levels: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

	SD	Estimates	SE
Random effects			
Visit/ site	0.155		
SpecSex	0.302		
Site	0.229		
Residual	1.531		
Fixed effects			
Intercept		2.915***	0.564
Mobility class		-0.197***	0.038
1 st axis env. PCA		-0.001	0.098
2 nd axis env. PCA		-0.279	0.147
Mobility Class*1 st axis env. PCA		-0.003	0.015
Mobility Class*2 nd axis env. PCA		0.053*	0.023
Temperature		-0.069***	0.069

All butterfly species, except for the two highly mobile species *Colias* spp. and *P. rapae*, covered significantly lower areas of arable land in their flight paths compared to the available amount of arable land within the 10 ha site (Table 2). In addition, *G. alexis*, *M. dryas*, *A. hyperantus*, *P. napi*, and *M. phoebe* used significantly larger amounts of grassland relative to the whole study site. These species were characterized by low and medium mobility respectively. *M. dryas* and *P. napi* used significantly more uncultivated patches than would be expected at random based on the proportion of uncultivated patches in the entire 10 ha study sites, and

G. alexis used more infrastructure. *P. napi* avoided infrastructure but used significantly more woody vegetation than randomly available, as did *A. hyperantus*. All species except *G. alexis* preferably moved across areas with higher landscape heterogeneity compared to the heterogeneity characterizing the entire site (Table 2).

Table 6.2. Effects of specific landscape elements on butterfly flight paths. Abbreviations of species names: *Pieris rapae* (rap), *Colias hyale/alfacariensis* (col), *Pontia edusa* (edu), *Pieris napi* (nap), *Coenonympha pamphilus* (pam), *Melitaea phoebe* (pho), *Glaucopsyche alexis* (ale), *Aphantopus hyperantus* (hyp), *Minois dryas* (dry). The values are estimates based on species-specific generalized linear mixed models. Significant positive values indicate preference and negative values avoidance of a specific landscape element. Displayed are estimates and significance values: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Species	Arable (intercept)	Grassland	Unculti-vated	Infra-structure	Woody	Heterogeneity (ED)
Ale	-3.864 **	0.031 *	0.022	0.185 *	0.034	0.003
Col	-0.407	0.004	0.036	-0.057	-0.026	0.002 *
Dry	-7.325 ***	0.064 ***	0.075 **	0.005	0.029	0.006 **
Edu	-1.673 *	0.015	0.004	-0.032	-0.032	0.002 *
Hyp	-7.500 ***	0.061 ***	0.079	0.251	0.083 ***	0.003 *
Nap	-18.379 ***	0.071 *	0.204 **	-0.691 **	0.174 ***	0.022 ***
Pam	-2.195 **	0.014	0.014	0.022	0.002	0.002 *
Pho	-3.492 ***	0.032 **	0.026	-0.076	0.016	0.004 **
Rap	-0.739	0.008	-0.023	-0.272	-0.023	0.002 *

Discussion

To our knowledge, this is one of few studies in agricultural landscapes that have assessed butterfly movement responses in relation to landscape structure and land use intensity (see also Baguette et al. 2013). Unlike previous studies, we investigated multiple butterfly species across a strategically selected gradient of landscape heterogeneity. Our detailed measurements of flight paths showed that butterfly movements differed between species, and that species with differing mobility showed contrasting responses along the gradient of landscape heterogeneity. Our findings also confirmed that most species used proportionally less arable land than expected by random, and that heterogeneous, non-arable land was important for most species.

Assessing butterfly mobility

Our overall approach to assessing mobility acknowledged that overall “mobility” results from the interplay of many different movement characteristics. Because different movement variables are typically interlinked (Ries and Debinski 2001; Kallioniemi et al. 2014), we used a multivariate technique, and approaches similar to ours could also prove useful in future studies.

Although some butterfly species that were classified as having low mobility by independent experts showed a higher observed mobility than expected, overall the observed and estimated proxies of mobility were remarkably consistent (cf. Stevens et al. 2010). Expert assessments of mobility often represent the

only available estimates of butterfly mobility, but most expert opinions are based on conditions in Western Europe (e.g. Bink 1992). The mobility of a species can vary substantially over its geographical range, depending for example on landscape structure (Merckx et al. 2003) and the amount of suitable habitat available (Duplouy et al. 2013; Schtickzelle et al. 2006; Wang et al. 2011). Considering the possible dependence of mobility on environmental parameters, drawing on local expertise could be important, and may help to improve a priori estimations of butterfly mobility.

Landscape effects on butterfly movement patterns

Our initial hypothesis was that the movement patterns of low-mobility species would change in a different way along a gradient of landscape heterogeneity than those of high-mobility species. This hypothesis was confirmed, but the effect of landscape heterogeneity on butterfly movement attributes was relatively weak. General landscape heterogeneity (as expressed by environment PC 1; see Figure 6.2a) did not seem to affect butterfly movement, but we did find a significant relationship between movement attributes and environment PC 2, which described a gradient from sites with a high amount of woody vegetation cover to sites with a high amount of arable land. In response to this gradient, we found that in complex landscapes, flight paths of low-mobility species were short and erratic, whereas those of high-mobility species were long and straight; in simplified landscapes, these differences in movement patterns between mobile and less mobile species were less pronounced. The concept of landscape functional grain provides a plausible explanation for this finding (Baguette and Van Dyck 2007). That is, complex landscapes with a high amount of woody vegetation are likely to contain suitable resources for low-mobility species, which tend to be habitat specialists (Ekroos et al. 2010; Stevens et al. 2012). In contrast, highly mobile generalists are more inclined to quickly fly straight through wooded and complex landscapes. In simple landscapes, however, low-mobility species may need to fly longer distances to find resources. Generalist species, in contrast, are often more mobile and can adapt and include arable land as a part of their habitat, which may explain why their flight pattern shifts towards shorter and more erratic movements as the amount of arable land increases. These results are consistent with Delattre et al. (2013), and confirm that mobile species react differently in their movement patterns to landscape simplification (Börschig et al. 2013).

Movement patterns as a type of habitat filtering in arable land

Crops, depending on their characteristics, can provide resources for butterflies (Quin et al. 2003), but most crop fields are considered as unsuitable habitat or as barriers for movement for the species included in this study. Despite this, in the fine-scaled landscape mosaic structure in Transylvania, many butterflies were able to use arable land (especially alfalfa fields), even though low- and medium-mobility species showed a high tendency to preferentially use grassland patches. Most likely, butterflies frequently moved between land-use types in these landscapes because arable land and grassland patches are often interspersed at a fine spatial scale, and both land-use types included flowering resources. Agricultural intensification, however, could lead to homogenization of such landscape mosaics, reducing the availability of uncultivated patches and woody vegetation elements (Stoate et al. 2009). This, in turn,

would have negative impacts on low mobility species, especially if increasing land use intensity reaches a critical threshold that selects against sedentary species (Ekroos et al. 2010).

Conclusions

Fine-scaled landscape mosaics offer a variety of resources that benefit butterflies characterized by poor mobility, which still remain widespread in the Transylvanian lowlands. However, intensification of agriculture is likely to simplify landscape structure in the future. Species with low mobility are likely to be particularly vulnerable to landscape simplification, which could lead to the biotic homogenization of butterfly communities (Ekroos et al. 2010). To counteract such homogenization, we suggest that woody and grassy patches should be retained throughout the landscape, even if within-field intensification is unavoidable in some situations. Due to their greater ability to move longer distances, and potentially greater propensity to use arable land, mobile species are likely to be able to adapt more successfully to increasingly simplified landscapes. We believe that our approach of tracking butterflies provides a cost-effective way to quantify how landscape structure affects movement activity, and a similar approach could also be useful in other study systems.

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Chapter 7

Challenges for biodiversity monitoring using citizen science in transitioning social-ecological systems

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Abstract

Biodiversity monitoring requires sound data collection over large temporal and spatial scales in order to inform policy and conservation management. Citizen science programmes, if designed appropriately, can make valuable contributions to data collection and analyses. Moreover, citizen science has potential for both environmental education and civic participation. Recommendations on effective citizen science are available in the literature, but most existing work has come from relatively rich, industrialized countries. By contrast, there is very little knowledge on citizen science projects in transitioning economic, social and cultural settings. This paper seeks to adjust this deficit by contributing insights from our attempt to initiate a new monitoring scheme in Romania. We draw on our experience of conducting workshops, training events and camps to strengthen citizen engagement in a butterfly monitoring scheme, and discussions with many stakeholders engaged in other monitoring programmes inside and outside of Europe. We highlight four general themes that are worth considering when initiating new citizen science projects in socio-economically challenging settings: (i) engaging citizens requires a combination of formal and informal support; (ii) a culture of volunteering requires education as well as building capacity and confidence; (iii) citizen science needs active integration of both national experts and local stakeholders; and (iv) successful monitoring schemes require effective leadership. We conclude that particular attention should be paid to the cultural legacies of the target area.

Citizen science: an opportunity for long-term ecological monitoring

In light of global biodiversity decline, it is important to document the changing state of ecosystems in order to provide a solid evidence base for policy and management. Monitoring programmes, if designed appropriately, can deliver valuable data and results (Schmeller et al. 2009), but they require the long-term implementation of standardized survey designs (Legg & Nagy 2006; Yoccoz et al. 2001) – a demand that can rarely be met by conventional research projects and environmental agencies (Bell et al. 2008).

One cost-effective solution to this problem is to implement citizen science projects. Such projects involve volunteers with different levels of skill and engagement in monitoring activities (Bonney et al. 2009; Schmeller et al. 2009), such as gathering empirical data over large spatial and temporal scales (Bonney et al. 2014; Donald et al. 2007; Tulloch et al. 2013). The use of citizen science projects for monitoring purposes is, however, sometimes questioned due to its limited ability to contribute to scientific outcomes (Bell et al. 2008; Genet & Sargent 2003). By necessity, sampling designs are often more simplistic than in professional monitoring schemes (Danielsen et al. 2009; Engel & Voshell 2002), and may generate lower quality data. Nonetheless, citizen science can make a valuable contribution to long-term biodiversity monitoring, given an appropriate design and data validation. Furthermore, involving laypeople in science projects may enhance civic engagement and activity (Leach et al. 2005), and thus has the potential to raise public awareness (Bell et al. 2008; Silvertown 2009), for example, of the loss of biodiversity.

Successful volunteer-based monitoring schemes in industrialized countries have typically focused on charismatic species such as birds (Sullivan et al. 2009) or butterflies (Pollard & Yates 1993; van Swaay et al. 2008). Although valuable information on the establishment and organization of monitoring schemes exists for relatively rich (typically “Western”) countries, the specific challenges of initiating monitoring schemes in less wealthy countries, or ones with turbulent political histories, have received little attention (Danielsen et al. 2003).

Compared to “stable” Western economies, the process of implementing citizen science projects in transitioning countries should be expected to be different. This could be partly explained by a lack of money, time and taxonomic skills, but it is also due to mental, cultural and socio-economic differences arising from the overall context characterising transitioning countries. For example, the success of democracy is known to depend on changes in public mentality towards civic values (Sztompka 1993). However, in some Eastern European countries, such as Romania, recent studies point out that interpersonal trust and civic participation levels are very low (Mikulcak et al. 2015). In addition, people seem to favour more individualistic values, and social capital is often low (Badescu et al. 2004; Sztompka 1993). Although the civil society is relatively developed, the support it receives from citizens has yet to grow (Badescu & Sum 2005) and is facing difficulties in transferring democratic values to the larger population (Badescu et al. 2004). Finally, corruption is known to seriously affect investment rates in public and community goods, thus reinforcing mistrust in formal and even informal institutions (Mikulcak et al. 2013). All these factors combined make it challenging to engage Romanian citizens, and probably also

citizens from some other transitioning contexts (Anthony & Moldovan 2008). Filling the knowledge gaps on how to approach citizen science projects in such settings is important, because the countries of interest are often characterized by high biodiversity, which is likely to be threatened by economic transition.

Citizen science in challenging socio-cultural conditions: an example from Romania

Here, we summarize insights from a recent project aiming to initiate a volunteer-based butterfly monitoring scheme in Romania, Eastern Europe (Loos & Kirkland 2014). Citizen science could be a valuable participatory process in rapidly changing countries such as Romania (Stringer et al. 2009), which have high biodiversity, but (unlike some Western countries) may lack financial resources to employ professionals to conduct large-scale monitoring. However, in such settings, citizen science may also face some unique challenges, because it usually draws on an empowered and active civic perspective (Leach et al. 2005), which could be missing in societies that have only recently become democratic. Thus, the success of citizen science projects may depend on the support available from civic society as well as the degree of civic participation and engagement.

Romania has undergone a series of major changes in the past 30 years, including the collapse of communism in 1989. Despite recent improvements, Romania still has one of the weakest economies in the European Union (EU). The re-orientation of the post-communist country towards the EU has divided the society into “winners” and “losers” (Tucker et al. 2002). Many of the losers live in rural areas and continue to practice traditional semi-subsistence farming. The unstable conditions and the increased access to the free market may have encouraged utilitarian (Tucker et al. 2002) and opportunistic attitudes and excessive selfishness in society (Sztompka 1993), so that corruption, nepotism and low social capital are currently widespread (Newton 2001; Slangen et al. 2004). At the same time, Romania has high levels of cultural, ethnic and biological diversity and supports many endemic species (Ioras 2003), as well as species that are endangered or extinct in Western Europe. The conservation of Romania’s biodiversity is of high interest at the European level (Schmitt & Rákossy 2007), but Romania’s natural environment has come under intense pressure since its 2007 accession to the EU (Mikulcak et al. 2013). As in many other relatively poor countries, Romania has no official national biodiversity monitoring schemes.

In the following, we reflect on the successes and failures of our endeavours to establish a volunteer-based butterfly monitoring scheme in Romania (2011–2014). To recruit volunteers and experts we organized several workshops, species identification training events and butterfly camps, and promoted butterfly monitoring at national annual meetings of lepidopterists in 2012 and 2013. Throughout this time, we had open discussions with participants as well as with coordinators of other monitoring schemes from countries inside and outside of Europe. Based on our experiences, we summarize four key considerations that we believe to be critical when establishing citizen science projects in transitioning social–ecological systems.

Engaging citizens requires a combination of formal and informal support

Volunteers from countries with well-established economies often contribute their own financial resources to citizen-science activities (Dickinson et al. 2010). However, in poorer countries, people may not be able to afford materials and travel costs. Hence, financial support is needed to cover materials (such as field guides and butterfly nets) and travel costs. In the absence of government funding, external fundraising therefore becomes important. This, in turn, may require an official institution to be founded or involved, such as a legal association or a charity. Such an official body also can provide formal attendance certificates to participants of workshops or training events, which can be shown to employing institutions, thereby encouraging further collaboration and support.

Despite the likely need for an official institution to be involved, identifying (or even founding) a suitable institution can be difficult in countries experiencing economic challenges. For example, in Romania, socio-cultural legacies from the communist era have resulted in high levels of mistrust (Sztompka 1993), which hinders collaboration among established organizations. Setting up new institutions can also be problematic because of unclear bureaucratic structures and potential new actors being perceived as competition to established ones, even among non-governmental organizations. To gain trust, the process of setting up an official participatory network can benefit from building on informal social capital (Pichler & Wallace 2007), and from involving local stakeholders in a way that is transparent to existing interest groups.

A culture of volunteering requires education as well as building capacity and confidence

Romania does not have a pronounced culture of volunteering (Badescu et al. 2004), partly because the notion of volunteering was abused during communism, when people were coerced to carry out activities for the community. However, our activities have suggested that it is possible to improve the negative image of volunteering: after a relatively short time and a few workshops and meetings, we observed an emerging interest to participate in our initiative, as well as in other environmental projects. The desire of volunteers to contribute to conservation initiatives was related to a perception that these provided opportunities for socializing, learning and improving knowledge. The latter aspect appeared to be of particular importance to younger volunteers seeking careers in biodiversity conservation.

Ideally, monitoring should take place at random or stratified random sites (Snäll et al. 2011). However, at present, Romania lacks both lepidopterists and financial resources to pursue this ideal. Hence, the primary focus initially needed to be on recruiting and training more volunteers, increasing the number of monitoring transects, and enhancing general interest in butterfly conservation. Based on this foundation, future endeavours can then pursue more scientifically refined monitoring programmes.

Citizen science needs active integration of both national experts and local stakeholders

A successful volunteer-based monitoring scheme needs to overcome a slow starting phase by improving participation of and collaboration between experts and laypersons with little prior knowledge. Moreover,

in culturally diverse settings, we found it was important to organize activities in a way that overcame language and other cultural barriers. Indeed, our experience suggested that pursuing a common vision through a monitoring project helped to create a shared sense of belonging among participants, which in turn, was useful in overcoming social, historical and cultural differences.

Notwithstanding the important role of citizens, national experts can play a crucial role in ensuring data quality (Bonney et al. 2009) and helping with training (van Swaay et al. 2008). In Romania, the high species richness of butterflies was intimidating to novices entering lepidopterology, but appropriate support from experts helped to build confidence. In this context, finding the means to incentivize experts to devote time to the scheme was vital. Moreover, the idea of “ordinary people” doing scientific work can be unfamiliar to established experts, and it may take some time to develop a shared understanding that citizen science can in fact be useful and practical.

Successful monitoring schemes require effective leadership

As well as supporting and coordinating volunteers, those running monitoring projects must also take the responsibility for data collection and management. This is unlikely to be done solely by volunteers, especially in settings where many people prefer to follow rather than take proactive roles. Many volunteers we spoke with expressed the desire that specialists or scientists should take a leadership role. Once a leader emerges, a sympathetic personality and non-hierarchical approach to leadership are likely to be beneficial (Bell et al. 2011), especially in cultures where private connections are over-valued as was the case in many former communist countries (Sztompka 1993). It may prove necessary to employ a skilled person who can provide ongoing leadership and support, and can act as a central, dependable contact person.

The economic situation in Romania forces many people, including scientists, to commit their time almost entirely to paid activities. Furthermore, these pressures may force scientists and land managers to prioritize the production of short-term results rather than working on longer-term projects that require large amounts of time, work and personal investment – a trend that apparently also applied to natural resource management after privatization of land in the country in the early 1990s (Kuemmerle et al. 2009). As a response to unpredictable conditions, many people may take a short-term view and use up resources, letting the natural capital stock wear out rather than sustaining it (Hoff & Stiglitz 2004). This may be why, despite having shown a positive attitude towards our activities, many Romanian scientists were unable to attend our events. Eventually, good and reliable leadership can help citizen science to function as a system-stabilizing element by tackling various complex aspects that currently still hinder the prospering of a civil society (Berkes et al. 2003).

Conclusion

The collection of biodiversity data from citizen science projects requires substantial input by experts, reliable and responsible data management, effective coordination, sound leadership, and considerable

support for volunteers. Our activities in Romania showed that volunteer-based monitoring has the potential to foster civic engagement and raise environmental awareness. Based on our experience, in settings without an established culture of volunteering, the initial focus should be directed at training and at strengthening collaborations between stakeholders, with particular attention to informal exchange. As a next step, governmental or other significant support will then be required to scale up and formalize monitoring at larger scales. However, no single framework can fully address all societal and technical challenges occurring when fostering civil engagement (Irwin 1995). Hence we suggest paying particular attention to the cultural legacies of the region concerned.

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Chapter 8

Putting meaning back into “sustainable intensification”

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Abstract

In light of human population growth, global food security is an escalating concern. To meet increasing demand for food, leading scientists have called for “sustainable intensification”, defined as the process of enhancing agricultural yields with minimal environmental impact and without expanding the existing agricultural land base. We argue that this definition is inadequate to merit the term “sustainable”, because it lacks engagement with established principles that are central to sustainability. Sustainable intensification is likely to fail in improving food security if it continues to focus narrowly on food production ahead of other equally or more important variables that influence food security. Sustainable solutions for food security must be holistic and must address issues such as food accessibility. Wider consideration of issues related to equitable distribution of food and individual empowerment in the intensification decision process (distributive and procedural justice) is needed to put meaning back into the term “sustainable intensification”.

In a nutshell:

- In its current use, the term “sustainable intensification” is often weakly and narrowly defined, and lacks engagement with key principles of sustainability
- Without specific regard for equitable distribution and individual empowerment (distributive and procedural justice), agricultural intensification cannot legitimately claim to be “sustainable” nor does agricultural intensification address issues of food security
- Food security can be achieved only through a holistic agenda that looks beyond production, targets appropriate spatial and temporal scales, and considers regional conditions

Introduction

With a rising human population (projected to exceed 9 billion people by 2050), global environmental change, and changing dietary patterns (with a greater emphasis on meat and dairy consumption), global food insecurity is an emerging threat (Godfray et al. 2010). Food security exists when “all people, at all times, have physical and economic access to sufficient, safe, and nutritious food that meets their dietary needs and food preferences for an active and healthy life” (FAO 1996). Several recent high-profile papers (eg Benton et al. 2011; Tilman et al. 2011; Mueller et al. 2012) and policy documents (eg FAO 2011; Foresight 2011) have proposed “sustainable intensification” as one potential measure to address food security. Sustainable intensification, as currently framed, seeks to achieve food security through an increase in production, while minimizing negative environmental impacts and avoiding the expansion of land used for cultivation (Godfray et al. 2010; Garnett and Godfray 2012). Although the proposed “win–win” scenario of more food for more people with less impact on the environment is attractive, a major concern is the missing balance between “sustainable” and “intensification” (Garnett and Godfray 2012). Despite using the term “sustainable”, few advocates of sustainable intensification thoroughly engage with the goals and processes associated with sustainability. Although the concept of sustainability has many facets and interpretations (Panel 1; Lélé 1991; Kuhlman and Farrington 2010), there is broad agreement that it encompasses not only environmental integrity but also human well-being. Given the fundamental importance of food for human well-being, ensuring food security is an inherent objective of sustainability.

We argue that the current usage of the term “sustainable intensification” is potentially misleading because it inadequately addresses the central tenets of sustainability. In this paper, we: (1) highlight critical shortcomings in the definition of sustainable intensification that limit its ability to foster food security and sustainability, and (2) call for a more holistic characterization and assessment of sustainable intensification, including explicit regard for distributive and procedural justice.

Shortcomings in the current framing of sustainable intensification

Inappropriate terminology

As currently defined, sustainable intensification fails to address key aspects of sustainability. It is widely agreed that sustainability encompasses ecological, economic, and social concerns; considers intra- and intergenerational justice; and aims to maintain and improve human well-being from local to global scales (Panel 1; WCED 1987; Lélé 1991; Johnston et al. 2007). Yet the existing characterization of sustainable intensification primarily focuses on minimizing environmental impacts, and does not demonstrate how increased food production will improve human well-being – a crucial oversight given existing gaps between producing food for and providing food security to people (Chappell and LaValle 2011). This framing threatens to reduce the term “sustainable intensification” to a meaningless catch phrase that lacks theoretical rigor and is unable to provide practical guidance for achieving sustainability. Such careless use of the term “sustainable” could lead to misinterpretation or misuse in the context of environmentally destructive activities (Kates et al. 2005).

Panel 1. Definitions and history of sustainable development, sustainability, intensification, and sustainable intensification

Sustainable development and sustainability are often used as synonyms (Wu 2013) and both have various interpretations. The most widely accepted definition of sustainable development considers it to be development that “meets the needs of the present without compromising the ability of future generations to meet their own needs” (WCED 1987). Although this broad conceptual definition has led to many different operational definitions, most mainstream interpretations agree on the need to balance human development with environmental integrity. Central to sustainability is the maintenance of resources over time (Kuhlman and Farrington 2010), in order to ensure that future generations have access to at least the same level of resources (intergenerational justice) as the current generation (Pearce 1988). Here, we consider sustainable development as the process of moving toward sustainability.

Intensification of agriculture is the process of raising the yield output of land. Raising yields can be achieved by either expanding agricultural land or increasing the intensity of cropping in existing fields (Boserup 1965). Expanding land for agricultural purposes is undesirable in the context of biodiversity conservation. For this reason, increasing intensity of use within existing fields has been proposed as a more sustainable way of meeting rising demand for food. Conventionally, intensification has been achieved by shortening crop rotations and fallow times, using irrigation and agrochemicals, planting higher-yielding crop varieties, and introducing mechanization. These activities typically have negative environmental consequences. Alternatively, agro-ecological intensification focuses on “natural means” of increasing outputs, for example by incorporating legumes into fields or using agroforestry techniques.

Originating from sub-Saharan agriculture in the 1990s, the term sustainable intensification was used to describe the aim of raising agricultural yields while also benefiting the environment and the economy (Pretty 1997). This original definition emphasized local knowledge and the development of adaptive agricultural methods suited to local conditions. The participation of smallholder farmers was considered crucial for the development and extension of more productive technologies (Pretty 1997). A wide range of bottom-up, integrated methods and technologies were used to conserve water and soils, and to manage nutrient flows and pests. In its original formulation, sustainable intensification focused on building adaptable farming systems that support the livelihoods of the rural poor.

More recent framings of sustainable intensification have moved away from local approaches and instead focus on efficiency enhancement (Lang and Barling 2012), often at a global or national scale (eg Mueller et al. 2012). The main argument to promote sustainable intensification is the observation that a growing, wealthier human population is demanding more agricultural products. Current mainstream literature on sustainable intensification tends to focus on aggregate levels of food production rather than on patterns in the distribution and consumption of food.

Rather than a simple focus on minimizing environmental impacts, sustainability can be conceptualized in terms of intra- and intergenerational *distributive justice* – ensuring a socially just allocation of resources within and between different generations (Lélé 1991; Langhelle 2000). Moreover, sustainability requires fair and transparent decision-making processes that are adaptable to specific local conditions. Hence, *procedural justice* – the participatory governance by and empowerment of individuals, communities, and societies to decide how their needs are met – forms an additional pillar of sustainability (Agyeman and Evans 2004).

Inadequate treatment of ecological sustainability

In its current usage, sustainable intensification seeks to address ecological sustainability – that is, “the existence of the ecological conditions necessary to support human life at a specified level of well-being through future generations” (Lélé 1991) – primarily by minimizing the amount of land under agricultural production. By contrast, the consequences of intensifying agro-ecosystems have received less attention. For example, the targeted use of fertilizer has been proposed as part of a strategy for sustainable intensification (Tilman et al. 2011; Mueller et al. 2012), with the implicit assumption that yield gaps can be closed with little or no adverse impact on ecosystems. However, in some systems, even minimal fertilizer application could pose a severe threat to biodiversity (eg parts of Eastern Europe; Figure 8.1). Other aspects of intensification, including soil compaction, overuse of groundwater, or increasing application of broad-spectrum pesticides, could also degrade the multiple services and long-term ecological sustainability of low-intensity farming systems (Hector and Bagchi 2007; Maestre et al. 2012). While some recent work addresses these issues by specifically focusing on agro-ecological intensification (eg Bommarco et al. 2013), a coherent framework to assess the long-term impacts of different types of intensification is presently lacking.

Lack of attention to justice

The current manner in which sustainable intensification is framed also fails to consider justice, a fundamental component of sustainability (Hopwood et al. 2005). Food insecurity does not primarily stem from a lack of food production, but from a lack of access to food caused by the disempowerment of the world’s poor (Sen 1982; Chappell and LaValle 2011; De Schutter 2012). In many cases, food security could be enhanced without intensification, through improvements to justice. Increasing demand for food (which sustainable intensification seeks to address) disproportionately represents the wants of those with the financial resources to influence food markets, but greatly underrepresents the needs of those who are the most food insecure (Khan 1985). Although agricultural intensification does not necessarily imply a specific method to achieve higher yields, some of the most obvious interventions – such as the use of irrigation, agrochemicals, and modern machinery – are investment intensive. Without explicit regard to justice, there is a risk that certain types of supposedly “sustainable” intensification could lead to the dispossession of (capital poor) smallholder farmers, who represent the “true safeguards of global food security” (Tschardt et al. 2012a). For example, intensification can make previously marginal agricultural

land economically profitable, creating an incentive for landowners to evict subsistence tenant farmers and grow crops for sale on international markets (Shiva 1991).

Lack of attention to regional conditions

Global analyses of sustainable intensification have largely dismissed potential problems that intensification might cause regionally. Although useful in identifying the limits of global food production within the bounds of existing agricultural land, such analyses cannot generalize people's needs, which vary between different cultures and regions. Moreover, global analyses obscure a range of services beyond the production of food that agricultural landscapes may provide (eg cultural ecosystem services). Clearly, yield gains are important for food security in some regions, such as parts of sub-Saharan Africa (Pretty et al. 2011). Yet, in other regions, such as Eastern Europe (Figure 8.1), it is unclear how increasing yields would serve to offset hunger worldwide. If food security is the ultimate goal, regional approaches are needed that consider the multifunctionality of agricultural landscapes, and that focus on places where people are genuinely threatened by food insecurity.



Figure 8.1. A landscape in Transylvania, Romania. In this region, intensification is possible because of the presence of yield gaps, but it would undermine the long-term provision of other ecosystem services such as carbon storage and the build-up of nutrient pools. Intensification very likely would not benefit those in need of greater food security.

Missing links to other elements of food security

In its current mainstream use, sustainable intensification is poorly integrated with a broader set of documented strategies to improve food security. Many authors advocating sustainable intensification acknowledge the importance of other factors contributing to food insecurity, including gender inequality, food waste, poverty, and lack of power to access food (Godfray et al. 2010; Foley et al. 2011; Garnett and Godfray 2012; Mueller et al. 2012). However, there is a danger in assuming (implicitly or otherwise) that the multiple variables that influence food security are additive or independent, or that intensification is a useful goal, regardless of the state of these other confounding variables (Figure 8.2a; Hanspach et al. 2013).

Possible solutions

Reductions in food waste and more equitable distribution of existing food are logical first steps to improve food security. In those locations where agricultural intensification is necessary, whether such intensification is “sustainable” needs to be judged against a framework that explicitly considers key principles of sustainability.

Distributive justice and sustainable intensification

From the perspective of distributive justice, a coherent approach to sustainable intensification requires (1) adequate and equitable access to food within the current generation; (2) acknowledgment that heterogeneous, multifunctional agro-ecosystems meet more needs than simply the provision of food; and (3) maintaining the multifunctionality of agro-ecosystems for future generations.

Adequate and equitable access to food

Distributive justice requires an explicit focus on the allocation of food, which in turn requires addressing issues of power and food distribution. Food security must satisfy the “needs” of all people (FAO et al. 2012) but not necessarily all food “wants” – such as those related to the desire for a diet rich in animal proteins. Increased food production is not a guarantee of increased food security (Chappell and LaValle 2011; Sumberg 2012). Current literature on sustainable intensification often notes distributional issues but rarely addresses them in depth (eg Mueller et al. 2012). Such cursory treatment of food distribution implies that changes in food production can be meaningfully separated from issues of power and justice when addressing food insecurity. Yet land-use changes are inextricably linked to the multiple social and political contexts within which they occur (Turner and Robbins 2008). In the context of food security, food production and food distribution cannot be meaningfully analyzed separately. We believe a more appropriate way to conceptualize food security is to recognize that there are a series of filters that determine the extent to which intensification is sustainable and contributes to greater food security. That is, unless it meets the demands of both distributive and procedural justice, increased food production cannot be described as sustainable (Figure 8.2b).

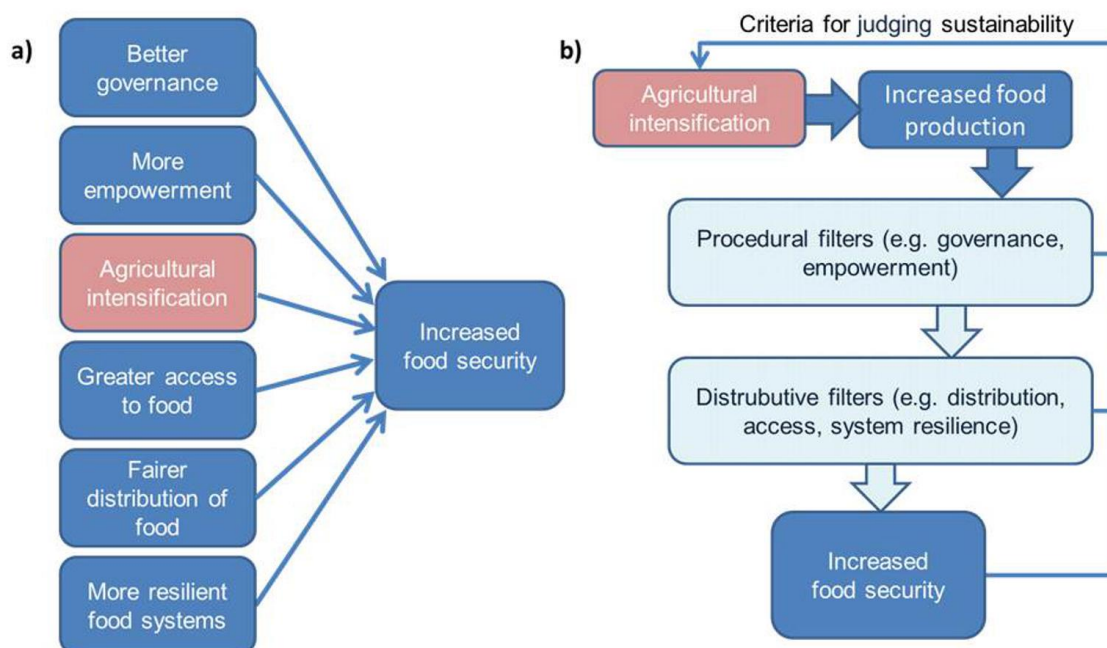


Figure 8.2. Contrasting ways to conceptualize the role of intensification for food security. (a) Conventional view of several variables influencing food security, implying that variables are independent and additive (additional variables may be considered important by some authors). (b) Alternative view, highlighting interactions and conditionality, with increased production increasing food security only if it passes through filters of distributive and procedural justice. According to this view, intensification can only be said to be sustainable if it successfully passes through these filters.

Multiple functions of agro-ecosystems

Beyond the allocation of food, distributive justice also needs to be considered for other socially valued goods and services associated with multifunctional agricultural landscapes. An increase in food production does not contribute to sustainability if it erodes other aspects of human well-being (Fish et al. 2013). One function of many traditional agricultural landscapes (other than the provision of food) is biodiversity conservation. Some landscapes characterized by low-intensity agriculture support high levels of biodiversity (Ranganathan et al. 2008). Conventional intensification in such landscapes not only negatively affects biodiversity in a given field but also has spillover effects on the wider landscape (Gibbs et al. 2009).

Another function of agro-ecosystems relates to their potential cultural value. In some settings, the ongoing persistence of cultural landscapes may be desirable from an ecological as well as a sociocultural perspective. Often, cultural landscapes represent co-evolved social–ecological systems with high natural and cultural heritage values (Figure 8.1; Fischer et al. 2012). Careful assessment and a thorough understanding of such systems is needed to maintain the indirect, unmanaged, underappreciated, and undervalued ecosystem services (Swinton et al. 2007) that intensification may otherwise erode.

Persistence of agricultural landscapes for future generations

Finally, distributive justice with a focus on future generations requires that agricultural landscapes are not irreparably damaged. To some extent, most agricultural landscapes are resilient to shocks and external inputs, from both social and ecological perspectives. That is, these landscapes are able to buffer and adapt to external influences up to a certain threshold level. However, exceeding such thresholds can cause major changes, known as regime shifts (Folke et al. 2004). While not inherently “good” or “bad”, regime shifts are likely to be undesirable in landscapes that are valued for the specific way in which humans and other organisms co-exist there.

Regional analyses of the impacts of yield improvements are required that consider the ability of particular social–ecological systems to persist under more intensive land use. In some regions with high potential for intensification, even moderate intensification (eg through minor increases in nutrient input) would cause severe ecological degradation (Stevens et al. 2004; Payne et al. 2012; Ceulemans et al. 2013), thereby reducing the ability of those systems to provide certain functions to future generations.

Procedural justice and sustainable intensification

A clear focus on procedural justice regarding where and how to close yield gaps would help identify possible conflicts between intensified production, access to food, and other services from agro-ecosystems that contribute to human well-being. In a food systems context, procedural justice can be characterized in terms of food sovereignty, which Patel (2009) described as calling for “new political spaces to be filled with argument...a call for people to figure out for themselves what they want the right to food to mean in their communities, bearing in mind the community’s needs, climate, geography, food preferences, social mix, and history”, and “the building of a sustainable and widespread process of democracy”. Allowing people to understand and engage in their food choices very likely will improve the sustainability of food systems, because people would be empowered to take control of their own lives – a key objective of sustainability (Panel 2; Lyons et al. 2001).

Crucially, concern for procedural justice would help to ameliorate conflicts that may otherwise arise during the course of agricultural intensification. Such strategies may include changes in land tenure, training for farmers, and better education for women. Smith and Haddad (2000) demonstrated a strong link between food security and procedural justice, and found that improved education for women reduced infant malnutrition to a greater extent than maximizing agricultural production.



Figure 8. 3. Garden of a MASIPAG rice cultivator in the Philippines. This garden contains 84 rice varieties and offers a seed bank for the farmers in the village. (Photo: L. Bachmann)

Panel 2. The MASIPAG network in the Philippines

The Farmer-Scientist Partnership for Development MASIPAG (Magsasaka at Siyentipiko para sa Pag-unladng Agrikultura) is a network of Philippine rice farmers that illustrates synergies between agricultural intensification and a wider set of aspects that are important for sustainability. The network grew from a bottom-up approach that involved a wide range of farmers to improve their access to safe, sufficient and nutritious food, while maintaining a sound ecological state of farmland. The network provides farmers with training facilities and with access to a seed bank harboring a wide range of traditional, locally developed rice varieties (Figure 8.3). This gives farmers the freedom to control their own management decisions. By doing so, the network integrates intra- and intergenerational aspects of sustainability and successfully improves food security of the rural poor (Bachmann et al. 2009; Sievers-Glotzbach 2014).

Conclusions

Despite its appeal, sustainable intensification as it is currently framed – as a vaguely defined global vision – cannot be a meaningful solution for food security in its own right. It is not our intention to dismiss the notion of sustainable intensification; instead, we are calling for greater engagement with the wider literature on sustainability, food security, and food sovereignty. This suggests moving beyond top-down, global analyses framed from narrow, production-oriented perspectives, and requires revisiting earlier, regionally grounded, bottom-up approaches (Panel 1). Appropriate governance, access, and distribution issues are foundational preconditions for – not additional concerns of – food security, without which

other measures to reduce hunger will remain futile (Figure 8.2). Therefore, producing more food in an (ecologically and economically) efficient way should be just one of several measures that must be embedded within holistic, regional-scale approaches to food security. Strategies aimed at enhancing food security must move away from a one-sided view that emphasizes narrowly defined land-use efficiency. Instead, these strategies must take into account food systems in their entirety, from production to consumption, including the desires and needs of those who live within and depend upon the multiple functions provided by agro-ecosystems. We suggest that an explicit focus on the notions of distributive and procedural justice in the framing of sustainable intensification would help to better align the term with key principles of sustainability.

Acknowledgements

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Appendix

Maintaining bird diversity in a traditional farming landscape in Eastern Europe

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Submitted Manuscript



Abstract

Traditional farming landscapes harbor high biodiversity worldwide. However, farmland biodiversity is increasingly threatened by agricultural intensification and land abandonment. We aimed to assess the drivers of biodiversity in a traditional farming landscape in order to gauge the likely effects of agricultural intensification and land abandonment on bird communities. We examined the responses of species composition, species richness, and richness within functional groups, to woody vegetation cover, land cover heterogeneity, and topography (each measured at local, context, and landscape scales). We conducted repeated point counts for breeding birds in a randomly selected set of 30 forest, 60 grassland, and 60 arable sites, which spanned stratified gradients in heterogeneity and woody vegetation cover. Species composition in forests differed from that in grassland and arable land. Species composition in grassland and arable land responded to gradients of woody vegetation cover at all three scales. Within grassland and arable land, total species richness, richness of farmland birds, and of forest specialists, asymptotically increased with local-scale woody vegetation cover. In contrast, richness of open-country species responded negatively to context-scale woody vegetation cover, and other farmland birds responded negatively to landscape-scale woody vegetation cover. Our results show that different groups of birds would be impacted differently by contrasting future land-use change scenarios. The regional bird community as a whole would benefit from the maintenance of gradients in woody vegetation cover across multiple scales.

Introduction

Agricultural expansion and intensification have caused biodiversity decline worldwide (Tilman et al. 2001; Foley et al. 2005), with the widespread loss of landscape heterogeneity identified as one of the major drivers (Benton et al. 2003). Agricultural land holds a large part of the world's biodiversity (Pimentel et al. 1992) and occupies 40 % of Earth's land surface (Foley et al. 2005). Growing recognition of the value of farmland biodiversity has sparked major national and international conservation initiatives, but nevertheless, farmland biodiversity continues to decline (Kleijn et al. 2011). In contrast, low-intensity land-use systems, such as traditional farming landscapes, often harbor exceptional biodiversity and are therefore of great conservation significance (Tscharntke et al. 2005; Kleijn et al. 2009).

Traditional farming landscapes occur in regions where farming practices have changed little over long periods of time, and are typically characterized by large amounts of semi-natural vegetation and high heterogeneity in land covers and structural elements (Plieninger et al. 2006). The value of traditional farming landscapes for biodiversity has been noted worldwide (Ranganathan et al. 2008; Takeuchi 2010; Robson and Berkes 2011; Liu et al. 2013), including in parts of Eastern Europe (Fischer et al. 2012). However, traditional farming landscapes have come under severe pressure from land-use intensification, and in economically marginal areas, from land abandonment (Lepers et al. 2005; Plieninger et al. 2006). Land-use intensification influences landscape structure via the loss of non-crop landscape elements (including semi-natural vegetation, shrub areas, and woodlands) and consequently, homogenization of the landscape (Benton et al. 2003). Land abandonment typically affects landscape structure by transforming agricultural land into shrubland, which may eventually turn into forest (Rudel et al. 2005; Kuemmerle et al. 2008). To effectively conserve biodiversity in traditional farmland facing potential land-use changes thus requires, first of all, a solid understanding of how different species respond to woody vegetation cover and landscape heterogeneity.

Here, we present a comprehensive, regional-scale case study on the drivers of bird diversity in a traditional farming landscape that is subject to land-use change. Our study investigated bird community responses to landscape structure in Southern Transylvania, Romania, and was specifically designed to cover the entire agricultural mosaic, spanning large gradients in heterogeneity and woody vegetation cover. Transylvania's farmland has changed relatively little since pre-industrial times, and traditional semi-subsistence farming has maintained a species-rich mosaic of arable fields, grasslands, and forests (Wilkie 2001; Cremene et al. 2005; Akeroyd and Page 2006). In recognition of its biodiversity, Europe's largest lowland protected area within the Natura 2000 network has been established in Southern Transylvania to conserve its farmland biodiversity. Yet, the region is undergoing rapid socio-demographic and land-use changes, which may significantly impact biodiversity in the future (Mikulcak et al. 2013). Traditional farming has become economically unviable, causing land abandonment by the rural population in some cases, and agricultural land-use intensification in others (Hanspach et al. 2014).

We used a snapshot “natural experiment” that substituted space for time (Diamond 1986) to gauge the likely effects of future land-use change on Transylvania’s bird community. Farmland is already intensified in parts of Transylvania, especially in the broadest valleys, whereas in remote or rugged areas, farmland is increasingly being abandoned. We used this opportunity of impending land-use change to strategically select survey sites along the full existing gradients of tree and shrub cover (from open landscapes to forests) and landscape heterogeneity (from low to high heterogeneity). Specifically, we assessed the responses of (1) bird community composition, and (2) overall species richness and richness of species with different habitat specializations, to gradients in woody vegetation cover, landscape heterogeneity, and topography, each measured at three different spatial scales.

Methods

Study area

The study area covered 7441 km² in the foothills (230 m to 1100 m above sea level) of the Carpathian Mountains in Southern Transylvania, Romania (Figure A.1a). The region contained 28 % forest, 24 % pasture, and 37 % arable land. The remaining land cover included villages (typically < 1000 inhabitants), towns, water bodies, and permanent crops. Forests were dominated by hornbeam (*Carpinus betulus*), oak (*Quercus* sp.), and beech (*Fagus sylvatica*). Most agriculture occurred at low intensities and small scales, with some exceptions, especially in the broader valleys. The major crops were maize, alfalfa and wheat. Pastures and hay meadows occurred on the slopes and were grazed by sheep, goats and cattle.

The landscape had an overall heterogeneous character, because of small farm sizes (often < 1 ha), a patchwork of small fields and field boundaries, and the occurrence woody vegetation throughout fields and grasslands. Woody vegetation occurred in linear features such as lines of trees and streamside vegetation, but also in small patches of shrubs and trees, small forest stands, and scattered shrubs or trees. The most common trees in farmland were similar to those in forest, but fruit trees (e.g. *Prunus* sp.) and *Robinia pseudoacacia* were also common. Common farmland shrub species were *Salix* sp., *Crataegus monogyna*, *Prunus* sp., *Corylus avellana*, and *Rosa* sp. Almost half of the study area was contained within Natura 2000 sites, including Sites of Community Importance (SCI, Habitats Directive) and Special Protection Areas (SPA, Birds Directive; Figure A.1b).

Study design

Our design followed the principles of a snapshot “natural experiment” in that we used randomly selected and replicated experimental units within pre-defined strata of ecologically relevant landscape gradients (Diamond 1986). We considered two spatial scales for stratification, namely village catchments (defined below) and survey sites. We selected 30 village catchments and within each selected five survey sites (Figure A.1c). Of a total of 150 sites, 30 were located in forest, 60 in grassland, and 60 in arable land. We collectively refer to grassland and arable land as “farmland”.

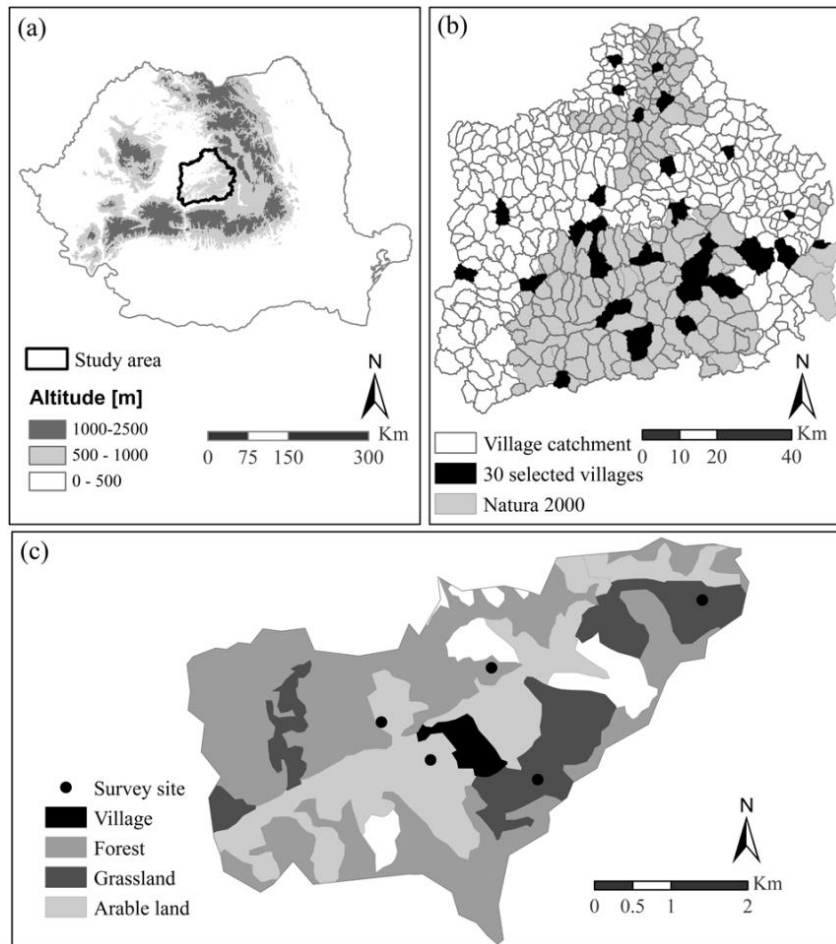


Figure A.1 Study area. (a) Romania with our study area highlighted, (b) our study area with selected village catchments highlighted, and (c) example of one of the village catchments showing different types of land cover and five survey sites

Village catchments were chosen for stratification at the landscape scale because they constitute both ecologically and socially meaningful units (Angelstam et al. 2003). We delineated village catchments using a cost-distance algorithm implemented in ArcGIS, which allocated each pixel to the village with the lowest travel cost (indicated by slope) to this pixel. These topographically based village catchments closely reflected historical land use responsibilities, and were more suitable than official administrative boundaries, which were available only at the commune level (with communes typically comprised of 3-5 villages). Of 448 village catchments, we randomly selected 30, stratified to cover full gradients in terrain ruggedness (standard deviation of the altitude; low, medium, high; defined by the upper, middle, and lower terciles) and protection level (SCI, SPA, no protection; see Table S3.1).

Sites were also randomly selected. For this, we used the Corine Land Cover Digital map 2006 (CLC) to identify three main land uses, namely forest, grassland and arable land. Sites were circular areas of one ha (i.e. radius of 56 m). To ensure that the entire site was located within a single land-use cover, we buffered all edges between land-use covers and all roads by 60 m. These areas were then masked prior to the random selection of sites. Furthermore, we only selected sites within an area of 400 m from the closest

track to ensure that all five sites within a village could be surveyed within one morning. Notably, arable sites included fields as well as fallow land and field margins. The median distance between neighboring sites was 606 m (the minimum was 200 m).

Grassland and arable sites were cross-stratified to cover full gradients in heterogeneity (low, medium, high; defined by terciles) and percent woody vegetation cover (low (0-5 %), medium (5-15 %), and high (15-60 %)). Within our sites, heterogeneity and woody vegetation cover were independent variables, and all possible cross-combinations were replicated, except for sites with low heterogeneity and high woody vegetation cover, which did not exist (see Table S3.2). Heterogeneity was measured as the standard deviation of 2.5 m monochromatic SPOT 5 satellite data (© CNES 2007, Distribution Spot Image SA). Percent woody vegetation cover was derived from a supervised classification of the 10 m panchromatic channels of SPOT 5 data (©CNES 2007, Distribution Spot Image SA) using a support vector machine algorithm (Knorn et al. 2009). The resulting high-resolution map of woody vegetation cover showed the vast majority of large shrubs, scattered trees, and linear features within the study area.

Environmental variables

We calculated environmental variables at three scales. The local scale covered the site (one ha), and approximately corresponded to the typical home range size of breeding passerines (Cramp 2000). The context scale covered an area of 50 ha (i.e. radius of 400 m), and was used because birds responded to landscape metrics at this scale elsewhere (Barbaro and Van Halder 2009). The landscape scale corresponded to the village catchment (mean \pm SD: 2046 \pm 1123 ha).

Within each scale we chose at least one variable for each of the following features: woody vegetation cover, landscape heterogeneity, and topography (Table A.1). Local variables included the proportion of woody vegetation cover (range: 0-59 %), remotely sensed compositional heterogeneity, and a topographic wetness index. Local heterogeneity and woody vegetation cover were calculated as described above. The topographic wetness index was calculated as a function of slope and topographic position (Fischer et al. 2010).

Context variables included the proportion of woody vegetation cover (range: 0-57 %), Simpson's diversity index of land cover (hereafter context land cover diversity), and terrain ruggedness. Simpson's diversity index of land cover was calculated using FRAGSTATS 4.2 (McGarigal et al. 2012), based on a raster of all land uses included in the CLC map (i.e. including land uses not considered for site selection). Terrain ruggedness was calculated as the standard deviation of altitude (based on the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model Version 2 (GDEM V2)).

Landscape variables again included the proportion of woody vegetation cover (range: 9-74 %), landscape edge density, and Simpson's diversity index of land cover, proportion of pasture cover, and terrain ruggedness. The proportion of woody vegetation at the landscape scale was primarily driven by the

amount of forest cover, and we therefore used percent forest cover as indicated by the CLC. Simpson's diversity index of land cover and terrain ruggedness were calculated as described above. Edge density (in m ha^{-1}) is a measure of configurational heterogeneity which standardizes edge per unit area; this meant it was comparable between village catchments of different sizes. Edge density was calculated using FRAGSTATS 4.2, based on all land-use types in the CLC map.

Table A.1. Overview of environmental variables used for generalized linear modelling.

Scale	Variable	Description
Local (LC)	Woody vegetation cover (WVC)	Percent woody vegetation cover derived from a supervised classification of the panchromatic channels of SPOT 5 Satellite data ^a
	Heterogeneity (HET)	Remotely sensed compositional heterogeneity indicated by the reflectance of land surfaces with a resolution of 2.5 m x 2.5 m measured using the monochromatic channel of SPOT 5 data ^a
	Topographic wetness index (TWI)	Measure of soil wetness, calculated as a function of slope and topographic position ^b
Context (CT)	Woody vegetation cover (WVC)	Percent woody vegetation cover derived from a supervised classification of the panchromatic channels of SPOT 5 data ^a
	Land cover diversity (LCD)	Simpson's diversity index of land cover, based on a raster of all land-use types derived from CLC ^{c,d}
	Terrain Ruggedness (TR)	Terrain ruggedness calculated as the standard deviation of the altitude ^b
Landscape (LS)	Woody vegetation cover (WVC)	Percent cover of forest derived from CLC ^c
	Land cover diversity (LCD)	Simpson's diversity index of land cover, based on a raster of all land-use types derived from CLC ^{c,d}
	Edge density (ED)	Edge density of land cover (in m ha^{-1}) based on a raster of land-use types derived from CLC ^{c,d}
	Pasture cover (PC)	Percent cover of pasture derived from CLC ^c
	Terrain Ruggedness (TR)	Terrain ruggedness calculated as the standard deviation of the altitude ^b

^a©CNES 2007, Distribution Spot Image SA

^bBased on the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model Version 2 (GDEM V2) with a spatial resolution of 30 m x 30 m

^cCLC: Corine Land Cover Digital map 2006

^dCalculated using FRAGSTATS 4.2 (McGarigal et al. 2012)

Bird surveys

Each site was surveyed three times during the breeding season by one of four experienced observers, using 10 minute point counts based on visual and auditory observations (Bibby 2000). Based on a pilot study, three surveys proved sufficient to representatively capture the species within a site (Loos et al. 2014b). Only singing males were recorded and included in the analysis – that is, we excluded non-singing birds, corvids, raptors and aerial foragers. Surveys were carried out in suitable weather conditions between 05:30 AM and 11:00 AM, between mid-April and mid-July 2012.

Statistical analysis

We analyzed the relationship between environmental variables and species presence, pooled across the three repeats, using multivariate methods and regression modelling. We first compared species richness using Analysis of Variance (ANOVA), and assessed patterns of beta diversity using species accumulation curves (Thompson and Withers 2003), between the three main land-use types (forest, grassland, arable land).

Second, we used detrended correspondence analysis (DCA) to compare bird community composition between the three land-use types, and visualized the relationship of species composition and environmental variables for farmland sites. DCAs were performed on bird species occurring in more than one site, and rare species were downweighted (Oksanen et al. 2013). Because forest communities strongly differed from farmland communities, further analyses were performed on farmland sites only.

Third, we modeled total species richness and species richness of forest specialists, farmland birds (defined here as farmland birds using shrubs and trees) and open-country birds, as response variables within generalized linear mixed effects models with Poisson error distribution. The models included the environmental variables and the quadratic term of local woody vegetation cover as explanatory variables (fixed effects), and village catchment and site-level (to account for overdispersion) as nested random effects. We also included the interaction terms of local woody vegetation cover and local heterogeneity with land-use type (arable versus grassland), because the effects of heterogeneity and woody vegetation cover may differ between arable land and grassland.

Prior to modeling, we log-transformed local and context woody vegetation cover and local heterogeneity; confirmed that variables were not strongly correlated ($\rho < 0.6$); and standardized all variables to zero mean and unit variance. The final models were obtained through a stepwise backward selection ($p \leq 0.01$) with model comparisons using Chi-square statistics (Zuur 2009), and did not exhibit spatial autocorrelation in the residuals. To visualize the effect of local woody vegetation cover, we plotted predicted total species richness (considering only fixed effects) as a function of local woody vegetation cover between 0 and 60 % cover (the observed range within the farmland sites) for arable and grassland sites separately. All analyses were implemented in the R-environment using the packages “vegan” and “lme4” (R Core Team 2013). Habitat specialization was assigned to all bird species by two Romanian experts (CIM and AD),

based on Birds of the Western Palearctic (Cramp 2000) and specific literature from Romania (Linția 1954, 1955; Ciochia 1992).

Results

Bird diversity

We identified 61 breeding bird species. Species richness was higher in forests (mean \pm SE: 10.6 ± 0.53) than grasslands (5.5 ± 0.35) and arable land (5.5 ± 0.52 ; $F_{2,147} = 28.18$, $p < 0.001$). Despite having the highest alpha diversity, forests had lower beta diversity than arable and grassland sites (Figure A.2).

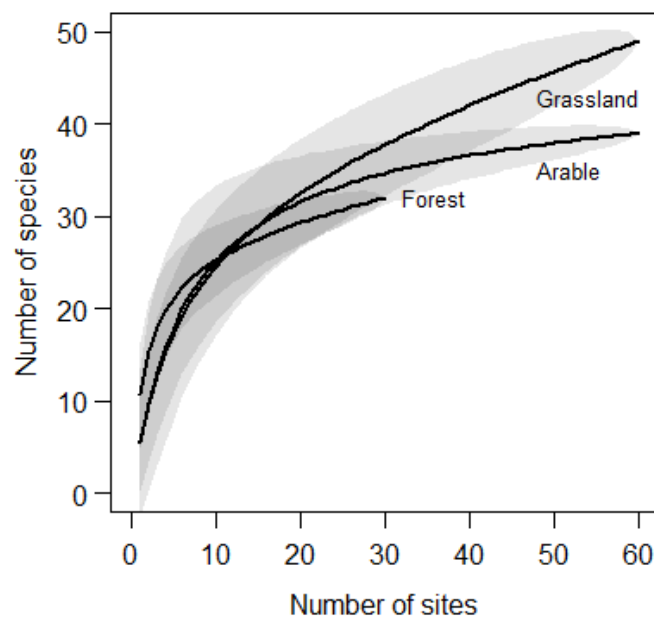


Figure A.2 Bird species accumulation curves for forest, grassland and arable sites. Ninety-five percent confidence intervals are indicated by grey shading.

Community composition

Species composition in forest sites differed from grassland and arable sites, and forest sites were more homogenous in species composition than grassland and arable sites (Figure A.3a). Bird community composition strongly overlapped in grasslands and arable sites, but exhibited clear gradients (both axes approximately covered one species turnover; length of gradient first DCA axis = 5.34, second DCA axis = 3.82; Figure A.3b, see Figure S1 for species scores of the ordination). The gradients of bird composition in farmland were related to environmental variables at all three scales. The first axis of community composition followed a gradient from high to low cover of local woody vegetation (Figure A.3b). The second axis described a gradient from sites with high woody vegetation cover at the landscape and context scales, and high context land cover diversity, to sites in less heterogeneous, pasture-dominated landscapes with low woody vegetation cover (Figure A.3b).

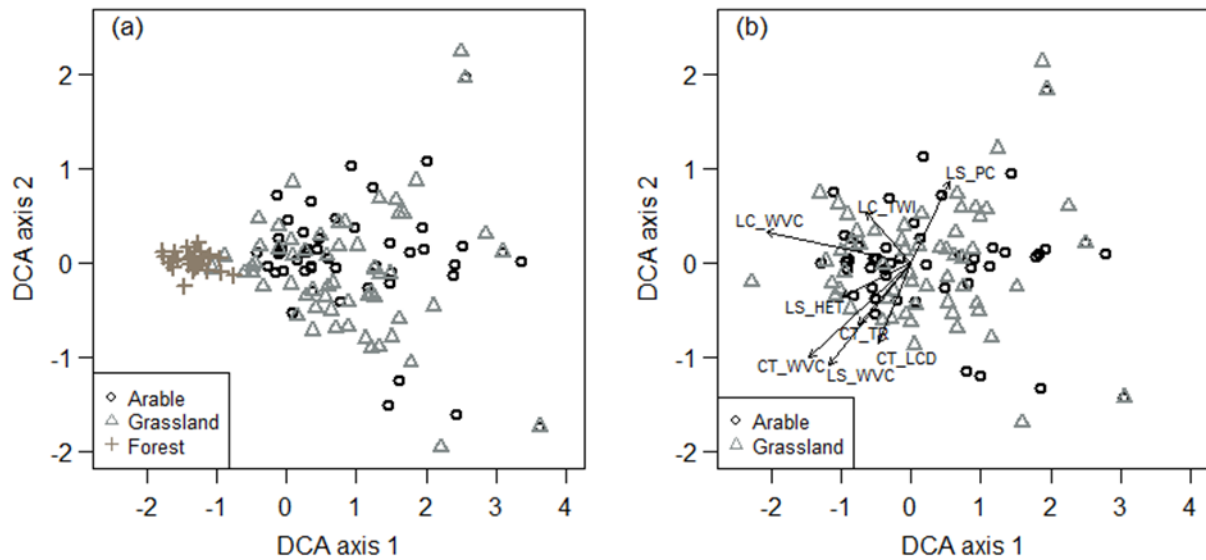


Figure A.3 Detrended correspondence analysis (DCA) of bird species composition in: (a) all three land-use types sampled, and (b) in farmland sites only, with significant environmental variables superimposed on the ordination plot. Abbreviations for the spatial scales: LC = local scale, CT = context scale, LS = landscape scale; and for environmental variables: WVC = woody vegetation cover, HET = Heterogeneity, TWI = Terrain Wetness Index, LCD = Land Cover Diversity, TR = Terrain Ruggedness, PC = Pasture Cover

Species richness

Species richness increased with increasing local woody vegetation cover, but reached an asymptote at high woody vegetation cover (Table A.2; Figure A.4). Furthermore, the positive effect of local woody vegetation cover on species richness was more pronounced in arable fields than in grasslands (Table A.2; Figure A.4). Richness of species groups with different habitat specialization showed different and sometimes opposite responses to the environmental variables (Table A.2). Richness of farmland birds and forest specialists (in farmland) peaked at intermediate levels of local woody vegetation cover. In contrast, richness of farmland birds decreased with increasing landscape woody vegetation cover, whereas the richness of forest specialists increased in response to this variable. Additionally, richness of forest specialists was positively related to local heterogeneity. Richness of open-country birds decreased with context ruggedness and woody vegetation cover (Table A.2).

Table A.2. Final generalized linear mixed effects models obtained through backward selection (threshold of $p < 0.1$) for total species richness and for species richness of groups with different habitat specialization in arable land and grasslands. The top row for each parameter represents the estimate \pm SE.

		Total richness	Forest specialists	Farmland birds	Open-country birds
Local	(Intercept) ^a	1.64 \pm 0.08 $p < 0.001$	0.42 \pm 0.12 $p < 0.001$	0.76 \pm 0.12 $p < 0.001$	
	Land-use: grassland	0.13 \pm 0.09 $p = 0.152$		0.48 \pm 0.14 $p < 0.001$	
	Woody vegetation cover	0.60 \pm 0.07 $p < 0.001$	1.13 \pm 0.15 $p < 0.001$	0.84 \pm 0.13 $p < 0.001$	
	Woody vegetation cover ²	-0.13 \pm 0.05 $p = 0.017$	-0.43 \pm 0.11 $p < 0.001$	-0.31 \pm 0.13 $p < 0.001$	
	Land-use Grassland * woody vegetation cover	-0.29 \pm 0.10 $p = 0.003$		-0.75 \pm 0.17 $p < 0.001$	
Context	Heterogeneity		0.24 \pm 0.09 $p = 0.004$		
	Terrain ruggedness		0.16 \pm 0.08 $p = 0.035$		-0.19 \pm 0.11 $p = 0.089$
	Woody vegetation cover				-0.22 \pm 0.10 $p = 0.026$
Landscape	Woody vegetation cover		0.19 \pm 0.08 $p = 0.020$	-0.20 \pm 0.06 $p = 0.001$	
Random effect	Village catchment ^b	0.000	0.000	0.000	0.000
	Site-level ^b	0.021	0.085	0.000	0.000

^aResults are given with arable land-use as baseline (i.e. the intercept shown is associated with the regression line for arable land)

^bThe rows "Village catchment" and "Site-level" show the variance associated with the random effects

Discussion

To the best of our knowledge, this is the first regional-scale study on birds in a transforming traditional farming landscape that is based on a stratified, randomized design with replicated survey sites spanning the entire agricultural mosaic. Our study shows the high conservation value of traditional farmland: although alpha diversity of birds was higher in forests than in farmland, the opposite was the case for beta diversity. That is, forest sites appeared relatively homogenous in bird community composition, whereas

farmland sites showed larger differences between sites. Within farmland, bird distribution patterns were primarily driven by gradients in woody vegetation cover, and to a lesser extent by gradients of landscape heterogeneity – rather than by differences in land-use *per se* (i.e. grassland versus arable land). In combination, our findings suggest that gradients in woody vegetation cover (and to a lesser extent in heterogeneity) need to be maintained at multiple scales to conserve regional bird diversity.

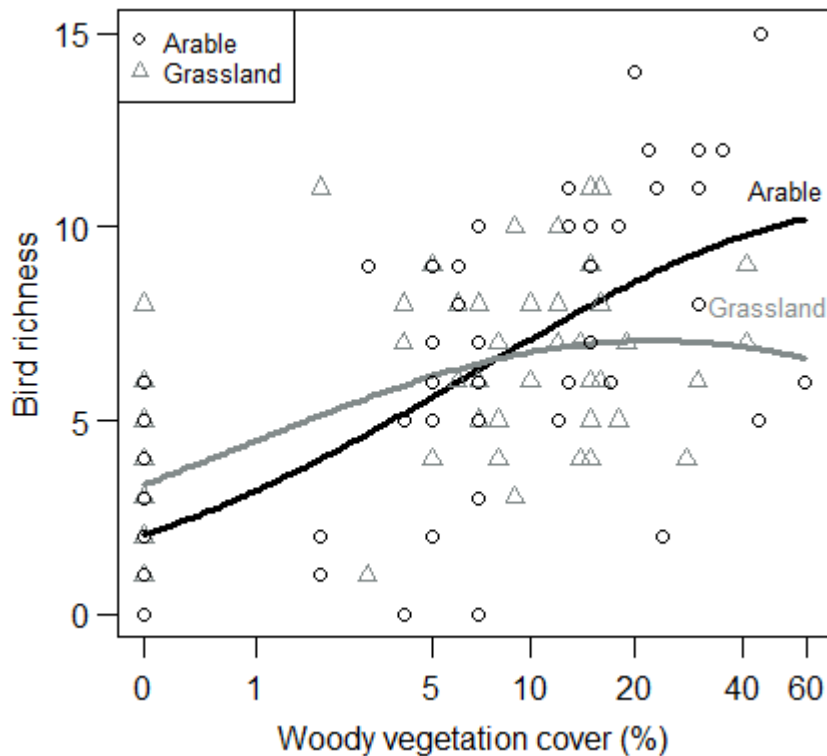


Figure A.4 Predicted total bird species richness (solid lines) in response to woody vegetation cover in arable versus grassland sites based on a generalized linear mixed effects model. Open circles (arable sites) and triangles (grassland sites) represent observed species richness

The most important driver of bird community composition in farmland was woody vegetation cover. As local woody vegetation cover decreased, farmland community composition changed from birds associated with forest and farmland birds (e.g. the Blue Tit, *Parus major*, and the Long-tailed Tit, *Aegithalos caedatus*), to a community mainly comprising open-country birds (e.g. the Whinchat, *Saxicola rubetra*, and the Quail, *Coturnix coturnix* (see Figure S1)). A similar change in community composition was observed along the gradient from high context-scale land cover diversity and woody vegetation cover to less heterogeneous, open pasture-dominated areas (see Figure S1). Gradients in woody vegetation cover are major drivers of bird community composition worldwide (Ranganathan et al. 2008; Hanspach et al. 2011), and within Europe, evidence continues to accumulate that both open farmland and farmland with woody vegetation need to be maintained and restored to conserve bird diversity in its entirety (Batary et al. 2011; Fischer et al. 2011).

Species richness followed similar patterns to community composition. Total species richness was positively related to local woody vegetation cover, although this relationship was less pronounced in grassland. This difference probably resulted from the greater prominence of several open-country specialists in grassland (e.g. *Saxicola sp.*), which avoid woody vegetation (Sanderson et al. 2013). Bird species richness has been observed to increase with high woody vegetation cover elsewhere in Europe (e.g. Sanderson et al. 2009), with most research focusing on edges and field margins (Herzon et al. 2008; Batáry et al. 2010; Wuczynski et al. 2011). The positive response to woody vegetation typically has been ascribed to a greater diversity of nesting, sheltering and feeding sites in areas with woody vegetation (Hinsley and Bellamy 2000). The strong effect of local woody vegetation cover in our study therefore may be related to the small home ranges (<1 to 4 ha, for most observed birds (Cramp 2000)) of breeding birds, with nesting and foraging site selection likely determined by fine-scale habitat characteristics. These findings suggest that retaining structures of woody vegetation at small scales could potentially ameliorate the negative effects of agricultural intensification on bird richness.

Despite the strong effect of local woody vegetation cover on species richness, this effect was found to level off at high levels of woody vegetation, or become negative in grassland. Land abandonment, and its subsequent transformation to shrubland and eventually forests, is a major threat to farmland in Eastern Europe (Kuemmerle et al. 2008) and is expected to expand in the future (Renwick et al. 2013). This is concerning, because many farmland birds, such as the Red-backed Shrike (*Lanius collurio*), need both open areas for foraging and trees or shrubs for breeding, and thus require landscapes with scattered woody vegetation cover (Brambilla et al. 2010). Thus, although an increase in woody vegetation might initially enhance bird diversity, a major expansion of shrubland will likely have negative impacts on farmland bird richness, especially in grasslands.

Context and landscape woody vegetation cover also had significant effects on the richness of birds with different habitat requirements. Unsurprisingly, open country-specialists were negatively affected by high woody vegetation cover at the context scale. These species often breed or forage in open landscapes, and dense cover of woody vegetation could also increase nest predation of ground nesting birds (Morris and Gilroy 2008). Forest specialists and farmland birds showed opposite patterns to landscape woody vegetation cover, with farmland birds responding negatively and forest specialists positively. Thus, besides a general decrease in species richness following local land abandonment, the abandonment of larger farmland areas would be associated with the replacement of open-country farmland birds and farmland birds by forest specialists. Such a change in bird community composition would also encompass the loss of several Species of European Conservation Concern. Thus, although extensification through land abandonment may be a desirable conservation strategy in some intensively managed landscapes (Gregory et al. 2005; Wretenberg et al. 2007), it could be detrimental to the bird fauna of traditional low-intensity farming landscapes (Suárez-Seoane et al. 2002; Laiolo et al. 2004; Verhulst et al. 2004; Sirami et al. 2008).

Heterogeneity has been proposed as a major factor underpinning farmland biodiversity (Benton et al. 2003), and positive effects of land cover diversity and structural landscape features on bird assemblages have been widely reported (e.g. Atkinson et al. 2002; Piha et al. 2007; Sanderson et al. 2009; Wretenberg et al. 2010; Guerrero et al. 2012). The overall lack of an effect of heterogeneity in our study (except for the positive response of forest specialists to local heterogeneity) may therefore be surprising. However, unlike our study, most other studies to date have not decoupled the effects of woody vegetation cover and land cover heterogeneity. Our findings suggest that woody vegetation cover may be more important for bird species richness than other aspects of heterogeneity related to land cover. This possible explanation is consistent with Sanderson et al. (2009), who found a stronger positive response of bird richness and abundance to woody edge habitat than to compositional land cover heterogeneity in Poland.

Open-country birds in particular (such as the Skylark, *Alauda arvensis*) often prefer simpler landscapes dominated by agriculture and may be expected to respond negatively to heterogeneity (e.g. Fischer et al. 2011). Nevertheless, within agricultural landscapes, small field sizes, high crop diversity, and a high proportion of field margins provide better conditions for foraging, nesting, and shelter (Vickery et al. 2001; Guerrero et al. 2012; Josefsson et al. 2013; Kuiper et al. 2013). The lack of a response to heterogeneity in this group might be related to the coarse resolution of the CLC map, used to derive context and landscape heterogeneity measures, which only distinguishes between the main land-use types but not individual arable fields. Alternatively, the reduced invertebrate prey due to simultaneous application of fertilizers and pesticides in intensified landscapes may partly explain the loss of open-country farmland birds in the more homogenous intensified landscapes (Verhulst et al. 2004). In contrast, in our study area pesticide and fertilizer use is very limited even in the more intensified regions, and hence invertebrates may be rich throughout the landscape and dampen the effect of heterogeneity on open-farmland specialists.

In combination, our findings suggest that the key mechanism underpinning Transylvania's bird community is the availability of gradients in woody vegetation cover and, to a lesser extent, land cover heterogeneity across multiple different scales. Notably, we captured responses of bird richness and composition only to those landscape features we could readily quantify, namely woody vegetation cover and heterogeneity. While these features are important, many other characteristics of Transylvanian farmland may also be relevant. These include a high variety of crops and crop rotation within small fields (Guerrero et al. 2012), traditional livestock rotation (Söderström et al. 2001), occurrence of fallow land and semi-natural vegetation (Devictor and Jiguet 2007; Sanderson et al. 2013), low pesticide and fertilizer use (Kleijn et al. 2009; Geiger et al. 2010), a wide variety of different field margins (Wuczynski et al. 2011), and land-use that is not optimized for a single performance or to produce maximum yield (Donald et al. 2001). As observed in other regions (Doxa et al. 2010; Wretenberg et al. 2010; Sanderson et al. 2013), the loss of low-intensity mixed farmland from Transylvania very likely would have a negative impact on bird diversity.

Conservation implications

Conservation actions in traditional farming landscapes are urgently needed because farmland bird populations are declining in Central and Eastern Europe (Reif et al. 2008; Voříšek et al. 2010). Although national conservation efforts improve population trends, decreasing trends are not being reversed (Koleček et al. 2014). Research on farmland biodiversity in these traditional farming landscapes is lagging behind research in Western Europe, which is problematic because the conservation challenges here may be different from those in more intensified landscapes (Baldi and Batary 2011; Tryjanowski et al. 2011). Our findings suggest that the key to conserve Transylvania's bird diversity is to maintain broad gradients of woody vegetation cover across multiple spatial scales, and to a lesser extent, maintain small-scale compositional heterogeneity.

In Transylvania, land abandonment is most likely to occur in the grasslands of more remote, forested, and steep areas. Preventing abandonment in these areas could be achieved by providing incentives to maintain rotational livestock grazing and to remove shrubs in order to maintain landscapes with little to intermediate woody vegetation cover. Intensification, on the other hand, is more likely to occur in arable land, especially in the broader, accessible valleys. Here, conservation strategies should prioritize the retention of woody vegetation cover at intermediate levels, for example by maintaining various types of field margins (Wuczynski et al. 2011), and encouraging high land-cover diversity through mixed farming. Furthermore, care should be taken in both grasslands and arable fields that larger tracts of open landscape with low woody vegetation cover remain available for open-country birds.

In conclusion, there is no simple conservation recipe that can be implemented across traditional farmland, but rather, farmland bird communities will benefit most from policies targeted to either mitigate land abandonment or land-use intensification, depending on the specific location. Because traditional farming has become largely unviable, new strategies need to be identified that not only maintain farmland biodiversity but also benefit local people, thus preventing an exodus of the rural population and subsequent cessation of farming. In our study area, potential strategies could include the uptake of modern agro-ecological and organic farming methods instead of conventional land-use intensification (Hole et al. 2005; Gabriel et al. 2010), or the development of incentives for smallholder farmers to engage in (agro-)ecotourism (Young et al. 2010).

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Declaration

I hereby certify that the submitted dissertation entitled “Prospects for sustainable development: The future of plants and butterflies in Transylvania” has been written by me without using unauthorized aids. I did not use any aids and writings other than those indicated. All passages taken from other writings either verbatim or in substance have been marked by me accordingly.

I hereby confirm that in carrying out my dissertation project I have not employed the services of a professional broker of dissertation projects, nor will I do so in the future.

This dissertation, in its present or any other version, has not yet been submitted to any other university for review. I have not taken or registered to take another doctoral examination.

Lüneburg, 12.12.2014

Jacqueline Loos