Biodiversity conservation in traditional farming landscapes

The future of birds and large carnivores in Transylvania

Doctoral thesis by Ine Dorresteijn

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Acknowledgements

> *'Even the woodpecker owes his success to the fact that he uses his head and keeps pecking away until he finishes the job he starts'* – Coleman Cox

I quite often felt like this woodpecker during my PhD, and I would still be pecking away if it wasn't for the many people that helped from the start to the finish of my PhD.

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Preface

This dissertation is presented as a series of manuscripts based on empirical research carried out in Transylvania, Romania. Chapter I provides a general overview of the dissertation, including the overarching goal and specific aims, a summary of all included manuscripts, a synthesis of the results identifying system properties that facilitate biodiversity conservation in traditional farming landscapes, and finally an outlook for conservation priorities in traditional farming landscapes. Beyond Chapter I, the manuscripts included in this dissertation (Chapters II-IX) are divided into three sections (A, B, and C). Section A examines the effects of local and landscape scale land-use patterns on birds and large carnivores and how these animals may be affected by future land-use change (Chapters II-V). To gauge the role of traditional land-use elements for biodiversity, in Section B, I focus on wood pastures as one prominent example of such traditional elements (Chapters VI-VIII). Lastly, in section C, I use a social-ecological systems approach to understand social drivers underlying human-bear coexistence (Chapters IV and IX). With the exception of Chapter II, all manuscripts are either published, in revision, or under review in international scientific journals. I, the author of this dissertation, conducted the majority of the research presented in this dissertation and am the lead author of the manuscripts presented in Chapters II-V, VII, and IX. I provided important contributions to Chapters VI and VIII as a co-author. A reference to the journal each manuscript is submitted to and the contributing co-authors is presented on the title page of each chapter. The Appendix contains two published manuscripts that I co-authored during my PhD. The research of these two manuscripts was conducted in the same study area but with a focus on butterflies and plants; their similar research context provides additional insights for the general synthesis of this dissertation.

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Abstract

Traditional farming landscapes typically support exceptional biodiversity. They evolved as tightly coupled social-ecological systems, in which traditional human land-use shaped highly heterogeneous landscapes. However, these landscapes are under severe threats of land-use change, in particular through land-use intensification and land abandonment. Changing land-use practices fundamentally change the structure of traditional farming landscapes, which implies a direct threat to the biodiversity they support. Navigating biodiversity conservation in such changing landscapes requires a thorough understanding of the drivers that maintain the social-ecological system.

This dissertation aimed to identify system properties that facilitate biodiversity conservation in traditional farming landscape, focusing specifically on birds and large carnivores in the rapidly changing traditional farmland region of Southern Transylvania, Romania. In order to identify these properties, I first examined the effects of local and landscape scale land-use patterns on birds and large carnivores and how they may be affected by future land-use change. Bird diversity was supported by the broad gradients of woody vegetation cover and compositional heterogeneity. Land-use intensification, and hence the loss of woody vegetation cover and homogenization of land covers, would thus negatively affect biodiversity. This was especially evident from predictions on the distribution of the corncrake (*Crex crex*) in response to potential future land cover homogenization. Here, a moderate reduction of land cover diversity could drastically reduce the extent of corncrake habitat. Further results showed that the brown bear (*Ursus arctos*) would mainly be affected by land-use change through the fragmentation of large forest blocks, especially if land-use change would reduce habitat connectivity to the presumed source population in the Carpathian Mountains. Moreover, this dissertation revealed that large carnivores (brown bear and wolf, *Canis lupus*) may have important and often ignored roles in structuring the ecosystem of traditional farming landscapes by limiting herbivores.

Second, to gauge the role of particular traditional land-use elements for biodiversity this dissertation focused on the conservation value of traditional wood pastures, as one prominent example of such traditional elements. Wood pastures were found to have a high conservation value. The combination of low-intensity used grasslands with old scattered trees provided important supplementary habitat for different forest species such as woodpeckers and the brown bear. Worryingly, current management of wood pastures differed from traditional techniques in several aspects, which may threaten their persistence in the landscape.

Third, this dissertation took a social-ecological systems approach to understand how links between the social and ecological parts of the system affect human-bear coexistence. The majority of people had a positive perception on human-bear coexistence. The use of traditional sheep

herding techniques combined with the tolerance of some shepherds to occasional livestock predation facilitated coexistence in a region where both carnivores and livestock are present. More generally, the genuine links between people and their environment (i.e. where people value their natural surroundings) were important drivers of people's positive views on human-bear coexistence. However, perceived failures of top-down managing institutions could potentially erode these links and reduce people's tolerance towards bears.

Through the consideration of two different animal taxa, this dissertation revealed six important system properties facilitating biodiversity conservation in traditional farming landscapes. Biodiversity was supported by the heterogeneous character of the traditional farming landscape at multiple spatial scales. At the scale of the study area, *similar proportions of the main land-use types* (arable land, grassland, and forests) support species associated with farmland as well as with forests, through for example habitat connectivity and continuous spill-over between land-use types. Heterogeneous landscapes can further support biodiversity through *complementation and supplementation of habitat* at the landscape scale, where species can occur outside their considered core habitat. *Gradients of woody vegetation cover and heterogeneity*, supported biodiversity at both local and landscape scales, possibly through the provision of a wide range of resources or by facilitating cross-habitat movements and spill-over. The heterogeneous character of the landscape is tightly linked to *traditional land-use practices*, and thus these practices are key to maintaining biodiversity. In addition, specific traditional land-use elements such as wood pastures have high conservation value, while specific practices such is traditional livestock husbandry techniques facilitate human-carnivore coexistence. *Top-down limitation of large carnivores* on herbivores may facilitate biodiversity conservation through for example enhancing vegetation growth and tree regeneration. The genuine *links between humans and nature* supported human-bear coexistence, and these links may form the core of people's values and sustainable use of natural resources.

Maintaining or preserving these six system properties should be a priority for biodiversity conservation in traditional farming landscapes. However, to accomplish this, there is an urgent need to develop more holistic visions for biodiversity conservation in traditional farming landscapes that integrates the entire social-ecological system. Such a holistic approach may comprise 'broad and shallow' landscape-scale conservation measures targeting the heterogeneous landscape character of the forest-farmland mosaic at multiple spatial scales. Large scale conservation measures may be complemented with more 'deep and narrow' conservation measures targeting specific species, land-use types, threats, or traditional practices. Finally, conservation measures should encourage the integration of the entire social-ecological system by recognizing and incorporating important links between people and the environment. Traditional farming landscapes are rapidly disappearing worldwide and developing conservation visions to navigate such landscape through land-use change are now needed to prevent major biodiversity declines in these landscapes.

Chapter I

Chapter I

Biodiversity conservation in traditional farming landscapes

The future of birds and large carnivores in Transylvania

'The most effective way to save the threatened and decimated natural world is to cause people to fall in love with it again, with its beauty and its reality.' – Peter Scott

Introduction

Traditional farming landscapes often harbour exceptional biodiversity and have high conservation value. These landscapes evolved as tightly coupled social-ecological systems, which are now under severe pressure of land-use change. From a biodiversity conservation perspective this is worrying because land-use change may potentially erode the high levels of diversity these landscapes support. Navigating biodiversity conservation in such changing landscapes requires a thorough understanding of the drivers that maintain the social-ecological system. In this dissertation I focus on the ecological part of the system and aim to identify system properties that facilitate biodiversity conservation in traditional farming landscapes, focusing specifically on the traditional farmland region in Southern Transylvania.

Human impacts on ecosystems

Humans have shaped and impacted the natural environment for tens of thousands of years (Smith 2007). Humanity's dominance over virtually all ecological systems has created the urgent need to understand the impacts and consequences of this anthropogenic influence (Vitousek et al. 1997; Ellis & Ramankutty 2008). Human influences on the environment range from hunting-gathering activities to the modification of entire ecosystems, most notably through agriculture. Until the onset of industrialization, relatively low human population densities and limited technological progress constrained human development. However, with the dramatic population increase and technological advances of the last 200 years, human influences on the environment are now so pervasive that they have become the major drivers of environmental change, taking us into a new geological era, the Anthropocene (Crutzen 2002; Steffen et al. 2007). The Anthropocene is characterized by a series of rapid biophysical and socio-economic changes (i.e. global change) that are threatening ecosystems and human well-being. For example, during the last 50 years, the structure of many ecosystems changed more rapidly than at any time in history (Millennium Ecosystem Assessment 2005; Steffen et al. 2007). One of the most notable consequence is the global biodiversity decline, with current rates potentially leading to the sixth mass extinction event (Pimm et al. 1995; Pereira et al. 2010; Barnosky et al. 2011; Monastersky 2014). This rapid loss of biodiversity matters not just because of the intrinsic values ascribed to biodiversity, but also because current rates of biodiversity loss cannot be sustained without substantially eroding resilience of ecosystems around the world – that is their ability to continue functioning in the face of external shocks (Folke et al. 2004; Rockström et al. 2009). Ambitious goals to reduce human-induced biodiversity loss (e.g. the Convention on Biological Diversity) have not yet been reached (Butchart et al. 2010), and because of this failure, such goals have sometimes simply been postponed into the future (www.cbd.int). Thus, a central challenge to humanity is to understand, address and act on the underlying causes of human-induced biodiversity loss to safeguard biodiversity in the future.

Land-use change and biodiversity loss

In terrestrial ecosystems, land-use change has been one of the major drivers of biodiversity loss - although other drivers such as climate change, pollution, invasive species, and the synergistic effects between different drivers also significantly contribute to global biodiversity loss (Sala et al. 2000). Land-use change can transform land through the conversion of the natural environment into farmland or farmland can be transformed through a change in agricultural practices (Foley et al. 2005). Responses of biodiversity to land-use change are complex and dynamic and depend on the type of land-use change and the ecological setting (DeFries et al. 2004). The conversion of the natural environment into farmland caused biodiversity loss worldwide (Foley et al. 2005). Cropland and pasture are now the largest terrestrial biome occupying 40 % of the land surface (Foley et al. 2005), while the area of forests has been halved over the past three centuries (Millennium Ecosystem Assessment 2005).

Two of the most distinct effects related to the conversion of the natural environment into agricultural land are habitat loss and habitat fragmentation for many species (reviewed in Fahrig 2003; Fischer & Lindenmayer 2007), especially for birds and mammals (Andrén 1994; Monastersky 2014). The expansion of agricultural land induced a global loss of birds to between a fifth and a quarter relative to estimates of pre-agricultural numbers (Gaston et al. 2003). For large carnivores, typical life-history traits such as large body size, large area requirements, slow reproductive rates, and low population densities make them exceptionally vulnerable to habitat loss and fragmentation (Crooks 2002). Increased human-carnivore conflicts and a resulting persecution by humans pose additional threats to large carnivores in modified landscapes (Treves & Karanth 2003). Habitat loss and fragmentation in combination with human persecution have severely reduced large carnivore populations worldwide, which on average occupy only 47% of their historical distribution range (Breitenmoser 1998; Woodroffe 2000; Ripple et al. 2014). However, large carnivores play critical roles in structuring ecosystems through inducing trophic cascades, and the loss of large carnivores has caused undesirable changes to a diverse range of ecosystems and its associated biodiversity (Estes et al. 2011; Ripple et al. 2014).

Farmland biodiversity, in contrast, is to a large degree adapted to and dependent on the continuation of agricultural management (Tscharntke et al. 2005). Farmland is the dominant ecosystem in many places (e.g. in Europe) and holds a large part of the world's biodiversity (Pimentel et al. 1992). Yet, also farmland biodiversity can be adversely affected by land-use change, most notably land-use intensification and land abandonment (Tscharntke et al. 2005; Queiroz et al. 2014; Uchida & Ushimaru 2014). Hence, understanding how land-use change affects biodiversity in agricultural landscapes is important to mitigate global biodiversity loss.

Land-use change in European farmland

In Europe, most forests were cleared for agricultural land before the onset of the Anthropocene (Kaplan et al. 2009). This historic forest loss, in combination with direct persecution, caused dramatic declines of large carnivore populations in large parts of Western Europe during the 18th and 19th century (Breitenmoser 1998). Biodiversity loss as a consequence of agricultural intensification and land abandonment, in contrast, occurred mainly over the last decades and are now the major threats to European farmland biodiversity (Donald et al. 2001; Tilman et al. 2001; Stoate et al. 2009).

Agricultural intensification, with the aim to increase agricultural production, has caused declines of farmland biodiversity and resulted in a halving of the European farmland bird population (Donald et al. 2001; Voříšek et al. 2010). This decline is caused by ecosystem changes during intensification due to increased mechanization, increased use of agrochemicals (i.e. fertilizers and pesticides), loss of crop varieties and management techniques such as crop rotation and intercropping, and the decline of low intensity land-use. Overall, intensification usually entails homogenization (e.g. decrease in land cover diversity and woody vegetation cover) at multiple spatial scales, including entire landscapes (Benton et al. 2003; Tscharntke et al. 2005). These changes lead to decreased food availability and increased habitat loss and fragmentation for a wide range of species (Hinsley 2000; Weibull et al. 2003; Concepción et al. 2008; Guerrero et al. 2012). Species persistence in agricultural landscapes is highly dependent on landscape structure (Fischer & Lindenmayer 2007), and maintaining or restoring heterogeneity in agricultural landscapes has been suggested as one of the major strategies to halt farmland biodiversity declines (Benton et al. 2003). For instance, negative effects of habitat loss and fragmentation may be reduced if the landscape contains elements that provide habitat connectivity for a range of species, including birds and carnivores (Uezu et al. 2005; Donald & Evans 2006; Crooks et al. 2011).

In addition to intensification, abandonment of farmland is also becoming more pervasive globally, especially in marginal agricultural areas characterized by low-intensity farming and generating relatively low yields (MacDonald et al. 2000; Queiroz et al. 2014). Land abandonment typically changes the landscape by transforming agricultural land into shrubland, which eventually turns into forest (Rudel et al. 2005). Land abandonment is often viewed as a negative process for biodiversity because farmland biodiversity in low-intensity farming regions is often higher than in natural forests (Höchtl et al. 2005; Lindborg et al. 2008). Indeed, especially in Europe, land abandonment has been reported to negatively affect a range of taxa, with especially detrimental effects on farmland birds (reviewed by Queiroz et al. 2014). On the other hand, land abandonment has also been viewed to offer unique opportunities to restore the biodiversity of natural forest ecosystems including large carnivores (Navarro & Pereira 2012).

Although intensification and more recently also abandonment have been exacerbated by the European Union's Common Agricultural Policy (CAP), the recognition of the value of farmland biodiversity sparked national and international conservation measures to halt biodiversity loss on farmland (Young et al. 2005; Henle et al. 2008). Despite these measures, farmland biodiversity continues to decline and their effectiveness is questioned (Kleijn et al. 2011; Pe'er et al. 2014). Ongoing biodiversity decline highlights the need for more effective biodiversity conservation in Europe's agricultural landscapes. In this context, traditional farming landscapes are of great interest to conservation because they often harbour exceptional biodiversity (Tscharntke et al. 2005; Kleijn et al. 2009).

Traditional farming landscapes: values and challenges

Traditional farming landscapes are increasingly valued for their natural and cultural heritage. Their importance for biodiversity has been noted worldwide (Ranganathan et al. 2008; Takeuchi 2010; Robson & Berkes 2011; Liu et al. 2013), including in the traditional village systems of Eastern Europe (Palang et al. 2006; Fischer et al. 2012). Traditional farming landscapes are characterized by a long history of relatively persistent farming practices. Farming techniques in these landscapes are often of low-intensity with low levels of agro-chemical input and little mechanization, that is, a high degree of manual labour (Bignal & McCracken 2000; Plieninger et al. 2006). This way of farming has created mixed farming landscapes with a mosaic of different land-uses including specific traditional landscape elements like wood pastures (Plieninger & Schaar 2008), high land cover and structural heterogeneity, and relatively abundant semi-natural vegetation (Plieninger et al. 2006).

Another distinctive feature of traditional farming landscapes is that they are often tightly coupled social-ecological systems, that is, systems in which rural communities influence the ecosystems and vice versa (Folke 2006). Moreover, the long history of interactions within this system has created the opportunity for the different entities of the system to constantly co-evolve (Liu et al. 2007). People have shaped the ecosystem through their activities, such as land-use, and the ecosystem in turn provided people a variety of ecosystem services (i.e. the benefits people derive from nature; Millennium Ecosystem Assessment 2005). These ecosystem services range from provisioning services such as crops, water, and firewood, to cultural services such as the feeling of a 'sense of place', and have historically provided direct incentives for sustainable land-use (Fischer et al. 2012; Hartel et al. 2014). It is these centuries of co-evolving interactions between humans and the natural environment that created the high cultural and natural value of the landscape (Bignal & McCracken 2000). Moreover, landscapes shaped by traditional farming practices harbour many of the habitats and species that are valued for biodiversity today (Halada et al. 2011).

Despite their unique natural and cultural values, traditional farming landscapes are under increasing pressure from modernization and globalization. Rapid socio-economic, political, and cultural changes lead to the cessation of traditional farming practices in exchange for more intensive practices, or abandonment of farmland altogether (Henle et al. 2008). The persistence of these landscapes depends on how the social-ecological system navigates these profound changes while simultaneously fostering biodiversity conservation and human well-being. Nevertheless, current policies often fail to acknowledge the links between the social and the ecological parts of the system, and policies usually target either the social or the ecological part exclusively (Fischer et al. 2012). Such one-sided policies potentially erode the established historical connections between people and the land that maintain the character of these landscapes, and hence the structures supporting biodiversity. In addition, in Europe in particular, existing policies for farmland biodiversity are often poorly adapted to traditional farmland (Sutcliffe et al. 2014). This can be partly ascribed to a significant research gap, with the majority of European studies on farmland biodiversity conducted in (Western European) countries with more intensively used farmland, while biodiversity patterns in the more low-intensity traditional farmland regions (e.g. in Eastern Europe) remain poorly understood (Baldi & Batary 2011; Tryjanowski et al. 2011).

Therefore, fostering biodiversity conservation of traditional farming regions requires a thorough understanding of the drivers that maintain the social-ecological system. While this dissertation does not aim to understand the entire social-ecological system, it deals with some important aspects of the ecological system while acknowledging the significance of the other features. In particular, I aimed to identify system properties that facilitate biodiversity conservation in traditional farming landscapes, focusing specifically on birds and large carnivores in the rapidly changing traditional farmland region of Southern Transylvania, Romania.

Transylvania's traditional farmland region

Southern Transylvania in Central Romania (Fig. 1.1) is one of Europe's last regions that is dominated by traditional, small-scale farming systems. The study region was shaped by the culture and land-use of the Saxons, which settled in Transylvania in the 12th and 13th century. The Saxons came from different German-speaking European countries, and were the dominating ethnic group in the study region where Hungarians, Romanians, and Roma were also present. Saxon land tenure was based on communal management of pastures and forests, with individually owned arable fields (Sutcliffe et al. 2013). The rise and fall of communism influenced land-use in the region. During communism, agricultural land became collectivized under state ownership, but intensification was not severe enough to fundamentally change the landscape and its associated biodiversity. After the fall of communism in 1989 there was a large exodus of Saxons from the region as many resettled to Germany. This exodus led to an abandonment of part of the agricultural land, while restitution of small parcels of arable land to the remaining and new population prevented intensification of agriculture and stimulated semi-subsistence farming.

Despite these social changes, the characteristics of Southern Transylvania's farming landscape have changed relatively little since pre-industrial times, and traditional semi-subsistence farming has maintained a land cover mosaic of relatively similar proportions of forest (28%), arable land (37%), and grassland (24%; Fig. 1.1). Land-use is primarily determined by topography with forests occupying the hill-tops, arable fields being located mainly in the valleys, and pastures occurring on the slopes. Forests are dominated by hornbeam (*Carpinus betulus*), oak (*Quercus* sp.), and beech (*Fagus sylvatica*). Arable lands are characterized by farming techniques that are small-scale (most fields are smaller than two hectares) and are of low-intensity (most fields have low chemical input and are tilled manually). The semi-natural pastures are grazed by sheep (dominant livestock), goats and cattle. Hay meadows provide fodder for livestock and are often harvested by hand. The lack of large-scale mechanization and lack of homogenization has facilitated a high structural diversity, as evident for example in different sward heights during spring and summer and a high abundance of hedgerows, streamside vegetation and scattered trees. Overall, these features maintain a uniquely high level of biodiversity across multiple taxa in the landscape (Cremene et al. 2005; Akeroyd & Page 2007; Wilson et al. 2012).

Furthermore, the region is still rich in traditional land-use types like the grazing systems of wood pastures. Wood pastures were established through ancient silvo-pastoral practices, often consist of open grasslands with scattered old trees, and are one the oldest European land-use types. This combination of the high ecological value of scattered trees with structural attributes resembling old-growth forests may support biodiversity of both open-country and forest species (Bauhus et al. 2009; Fischer et al. 2010). Apart from forest, arable land and grassland, the landscape mainly harbours scattered small villages (i.e. with usually less than 1000 inhabitants) and orchards. Part of Southern Transylvania's farmland is protected through Europe's largest lowland protected area, the Târnava Mare - Podisul Hârtibaciului area, within the Natura 2000 network, although no management plan is in effect to date. However, profound on-going societal and economic changes since Romania's inclusion into the EU in 2007 are leading to significant land-use changes in Southern Transylvania (Mikulcak et al. 2013; Fig. 1.2). Because traditional farming techniques have become economically unviable, the rural population increasingly either intensifies or abandons land. These changes, in turn, may significantly impact biodiversity in the future.

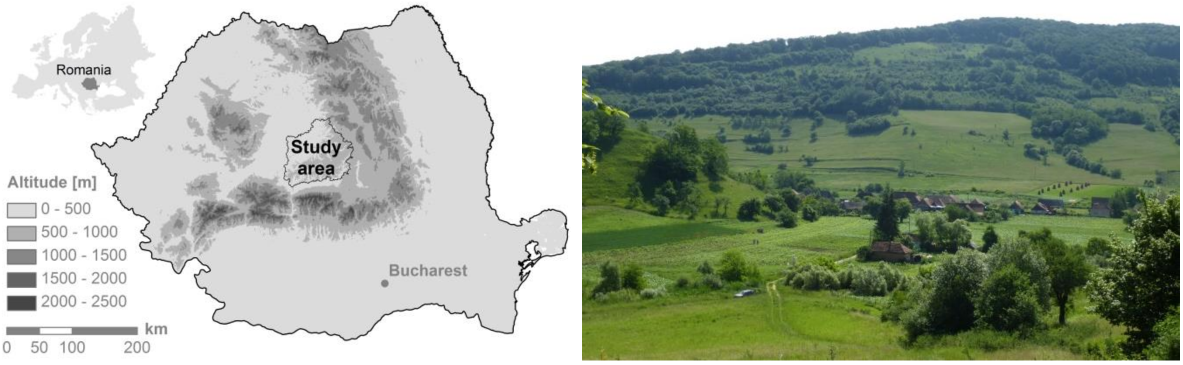

Figure 1.1 The study area was located in the foothills (230 m to 1100 m above sea level) of the Carpathian Mountains in Southern Transylvania, Romania (right). The picture shows the main land-use types of the study area (left).

Birds and large carnivores in Southern Transylvania

Different animal taxa may be affected by land-use change in distinct ways, and thus working on multiple taxa may provide a more complete picture of land-use change effects. The traditional farmlands of Transylvania harbour high densities of different farmland bird species, including several protected and rare species such as the corncrake (*Crex crex*) and several woodpecker species (I. Moga, unpbl. data; Moga et al. 2010). The current trends in land-use intensification and land abandonment in this region, however, may cause farmland bird declines comparable to those observed in the more intensified countries of Western Europe (Voříšek et al. 2010). Considering the effects of land-use change on the entire bird community beyond protected species is highly necessary since common European birds are declining at high rates while populations of rare species are slowly increasing (Inger et al. 2015).

Unlike most European countries, Romania sustains large and stable populations of large carnivores (Salvatori et al. 2002), and the study area harbours relatively high densities of the brown bear (*Ursus arctos*) and lower densities of the wolf (*Canis lupus*). In contrast to birds, large carnivores may be affected especially by changes in forest cover, and may thus be positively affected by land abandonment. In addition, large carnivores may not only be affected by land-use or land-use change, but also by the tolerance levels of the rural population towards carnivores. The reliance of people on forest products (e.g. firewood; Hartel et al. 2014), and the use of traditional practices such as shepherding and beekeeping are potential areas of conflicts with carnivores. Thus, large carnivore conservation in traditional farming landscapes does not only depend on the biophysical environment, but also on the willingness of people to live with carnivores (Treves & Karanth 2003; Dickman 2010).

Aims

As described above the overarching goal of this dissertation was to '*identify system properties that facilitate biodiversity conservation in traditional farming landscapes*' using birds and large carnivores in the rapidly changing traditional farmland region of Southern Transylvania as a study system (Fig. 1.3).

In order to identify these properties this dissertation is divided into three sections. In Section A, I focus on the effects of local and landscape scale land-use patterns on birds and large carnivores. This Section also provides insights on the effects of potential land-use change on biodiversity. To gauge the role of traditional land-use elements for biodiversity, in Section B, I focus on wood pastures as one prominent example of such traditional elements. Here, we examined the structure of wood pastures, and their use by woodpeckers and bears. Lastly, in section C, I use a social-ecological systems approach to understand social drivers underlying human-bear coexistence. In this part, we assessed the level of human-bear conflicts and the factors shaping the willingness of people to live with bears. Thus, my specific aims were (Fig. 1.3):

A. How do local and landscape scale land-use and land-use change affect biodiversity (Chapters II-V)?
B. How do ancient wood pastures affect biodiversity (Chapters VI-VIII)?
C. How do links between the ecological system and the social system affect human-bear coexistence (Chapters IV and IX)?

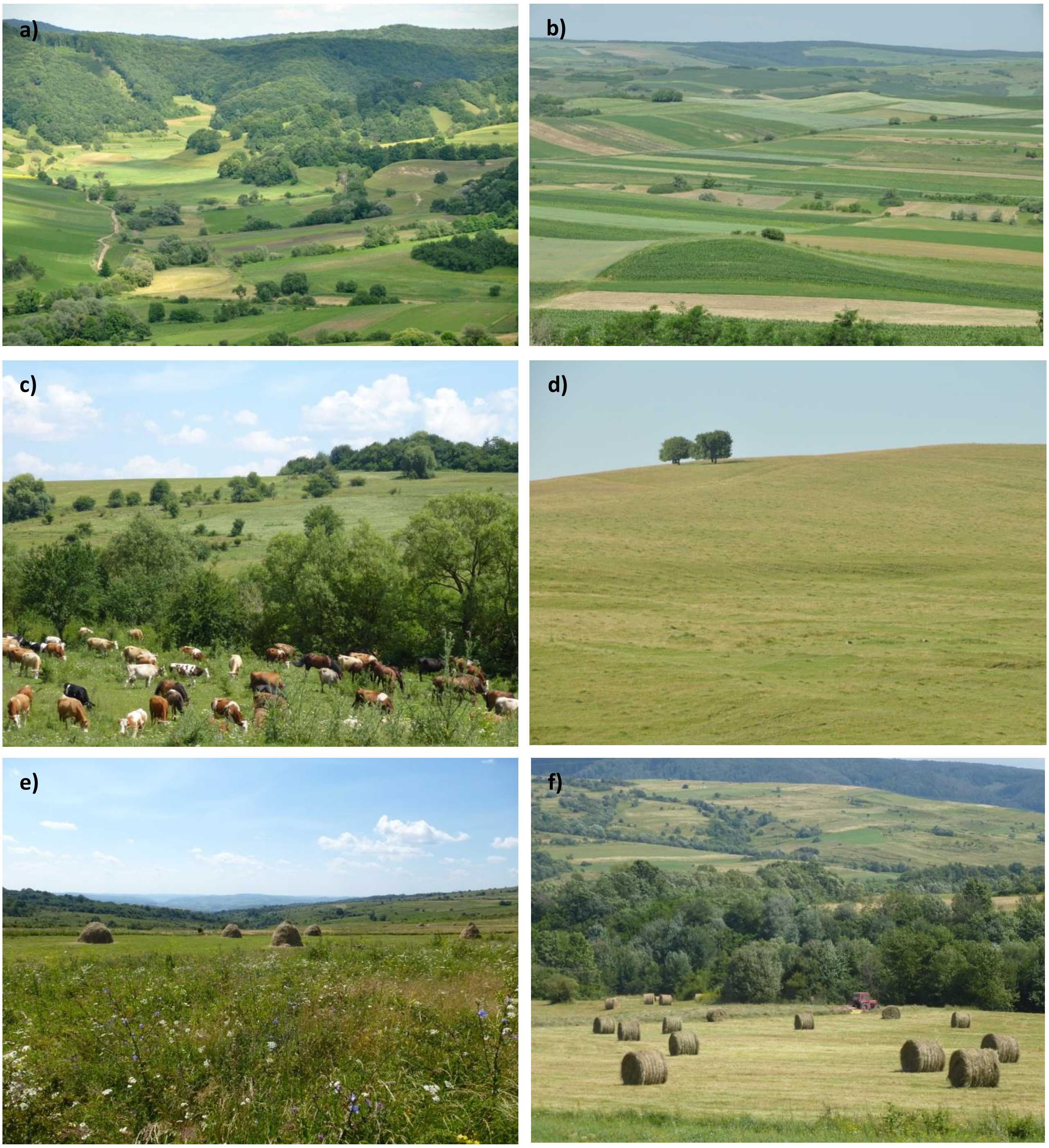

Figure 1.2 Examples of changes in land-use and land-use practices occurring in the study area. The pictures show the change from relatively low intensity land-use to higher intensity land-use in arable land (a and b) and in grassland (c and d). Intensification reduces the structural diversity of the landscapes through for example reduced woody vegetation cover and land cover diversity. Pictures e and f show a change from manual to mechanized hay harvest, reducing for example differences in sward heights throughout spring and summer.

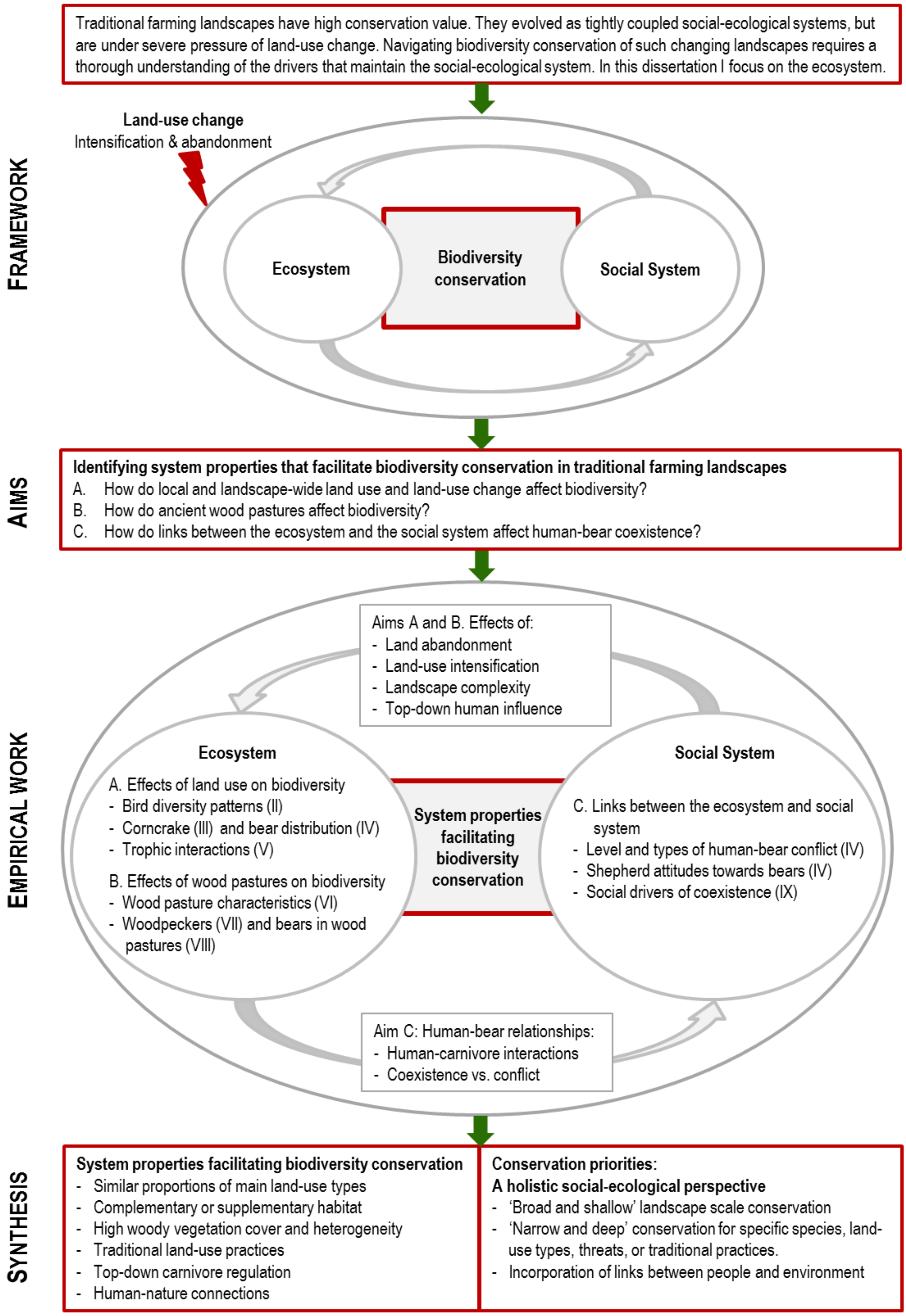

Figure 1.3 Overview of the dissertation. Starting from the top, the social-ecological framework for biodiversity conservation in traditional farming landscapes is presented, followed by the specific aims of this dissertation. The middle part summarizes the empirical work of the dissertation divided into three sections, each of these addressing a specific aim (A, B and C). The chapters contributing to the sections are indicated by Roman numbers (I-IX). The synthesis of the dissertation, namely the system properties facilitating biodiversity conservation and the conservation priorities for traditional farming landscapes, are presented at the bottom.

Summary of included chapters

Chapters II-V in **Section A** address how land-use and land-use change affect biodiversity. In **Chapter II**, we focused on the effects of land-use and land-use change on the passerine community. We conducted repeated point-counts for breeding males in the three main land-use types: arable fields, grasslands, and forests. While forest sites supported the highest bird species richness (alpha diversity), arable fields and grasslands supported a larger number of different species (beta-diversity) and communities were more heterogeneous than in forests. We used a snap-shot natural experiment to gauge how anticipated agricultural intensification and land abandonment would affect the bird community in farmland (arable fields and grasslands). Gradients in landscape heterogeneity and woody vegetation cover measured at three spatial scales, ranging from local to landscape-wide, were used to indicate anticipated changes in land-use and their effects on birds. We also included the effects of topographic variables on birds because they represent key biophysical gradients. Woody vegetation cover was the most important variable affecting the bird community. Species composition changed along gradients of woody vegetation cover at all three spatial scales. Total species richness asymptotically increased with local woody vegetation cover. In addition, woody vegetation cover negatively affected open-country specialists at an intermediate scale, and farmland birds at the landscape scale. Our study demonstrates the conservation value of traditional farming landscapes for birds. To maintain bird diversity it is important to uphold gradients of woody vegetation cover at multiple spatial scales, including open areas for open-country specialists. Both the decrease of woody vegetation through land-use intensification and the increase of woody vegetation through land abandonment, will negatively affect the farmland bird community as a whole, although the impact may differ between different functional groups. Thus, the landscape may benefit from different strategies aiming at mitigating either intensification or abandonment, with their implementation depending on the area.

Chapter III focused on the effects agricultural intensification on an EU-protected farmland bird species, the corncrake. Similarly to Chapter II we used changes in heterogeneity and woody vegetation cover, measured at three spatial scales, as measures to reflect changes associated with land-use intensification. In addition to heterogeneity and woody vegetation cover, we used topographic and human disturbance variables to explain corncrake presence in the landscape. The corncrake is typically considered a grassland species. However, we observed corncrakes in both grasslands (e.g. hay meadows) and in the arable mosaic (e.g. alfalfa fields). Furthermore, corncrakes were present more frequently in areas that were wet, flat and high in land cover diversity within a scale of 100 ha. This study shows the importance of the heterogeneous land cover mosaic of traditional farmland for the corncrake, where the loss of land cover diversity due to intensification could severely reduce the availability of corncrake habitat. To assess this impact, we predicted the distribution of suitable corncrake habitat under a scenario of land cover homogenization by simulating a reduction in land cover diversity. Importantly, the loss of land cover diversity and reductions of corncrake habitat were not linearly related, with even small losses in land cover diversity resulting in a high loss of suitable corncrake habitat. Thus, pro-active conservation measures for the corncrake should include the farmland mosaic beyond grasslands. Here it will be important to encourage the persistence of mixed farming.

We examined the effects of land-use patterns on bear distribution in **Chapter IV**. Bear distribution was indicated through a sign-based metric of bear activity, namely the proportion of anthills destroyed by bears relative to the total number of anthills in a transect. We were also interested in identifying specific hotspots for bears in the region, especially with regard to the Natura 2000 area. We modelled bear activity in relation to anthropogenic, biophysical, and connectivity variables, and based on this, predicted bear activity for the entire study area. Contrary to our expectations bears were not influenced by distance to the nearest settlement. Instead, connectivity to the Carpathian Mountains, where the source population resides, was the most important variable explaining bear activity. This measure of connectivity was indicated through a cost-distance metric, where the 'cost' for a bear to move through each possible land cover type was scored by a local bear expert. In contrast, connectivity between forest patches contained within the study area did not affect bear activity. Connectivity of the different forest patches was indicated through 'betweenness centrality', which represents how well connected a forest patch is within the forest patch network regardless of the other land covers between these patches. Furthermore, bear activity was higher in more rugged areas with large forest blocks and low pasture cover. We did not find particular hotspots of activity in the Natura 2000 area. Rather, predicted bear activity showed a gradual increase toward the Carpathian Mountains, but was otherwise relatively homogenous throughout the study. Our results suggest that conservation management for bears should primarily maintain the connectivity to the Carpathian Mountains, which would require land-use management beyond the Natura 2000 region. The lack of importance of connectivity between forest patches at more local scales indicates that forest fragmentation has not yet reached a level that would affect bears and that high connectivity remains throughout the study area. Therefore, emphasis should be placed on preserving large connected forest blocks, especially in rugged areas where bears can find shelter. In contrast to birds, reduced pasture cover and an increase in woody vegetation as result of land abandonment is likely to positively affect bears.

Chapter V explored the role of large carnivores in a human dominated ecosystem by analysing trophic interactions between forest mammals, including humans as apex predators. We aimed at assessing the top-down effects of large carnivores on herbivores and mesopredators in relation to direct and indirect human top-down effects and bottom-up effects. Wolves, bears, domestic dogs (*Canis familiaris*), and humans represented apex predators, red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) represented the herbivores, and the red fox (*Vulpes vulpes*) represented the mesopredator. Bottom-up effects were indicated by pasture and forest cover. We combined data on species encounter rates from camera traps and bear and wolf densities from hunting records to assess trophic interactions with piecewise structural equation models. We found that bears and wolves exert top-down control, especially on herbivores, and thus maintain their ecological role in human-dominated landscapes. Nevertheless, direct and indirect human-top down effects at multiple trophic levels affected species encounter rates more strongly. Furthermore, herbivores were also limited by dogs brought into the system by humans. The importance of top-down herbivore control was even more evident through the relatively weak effect of the land cover (i.e. bottom-up) variables. On the other hand, through their limiting effect on predators, humans may reduce the predators' top-down control. Although not accounted for in this study, humans may further affect trophic cascades by mediating bottom-up effects through landscape modification. Thus, bears and wolves are important for the regulation of the ecosystem, but human direct and indirect top-down effects are currently higher. The persistence of bears and wolves should therefore be ensured in order to conserve the ecological character of these valued traditional landscapes. We also believe that further understanding of the different human effects on trophic interactions in modified landscapes should be a major research priority.

Chapters VI-VIII in **Section B** focus specifically on the conservation value of traditional wood pastures to gauge the role of particular traditional land-use elements for biodiversity. To gain a better understanding of wood pastures we first of all explored the characteristics, management, and status of wood pastures in **Chapter VI**. Wood pastures were mainly dominated by oak and several species of fruit trees, which differed from the tree community composition in forests. Wood pastures also contained more ancient trees (trees of which the age can reach centuries) compared to forest sites, but were relatively low in dead tree abundance and shrub cover. These characteristics reflect the traditional management of wood pastures, which were created from forests by grazing and selective tree removal. Remaining trees were not only valued for their shade, but oaks provided timber and acorns for livestock, while fruit trees provided fruits. Specific characteristics of wood pastures were determined by variables such as topography, distance to village, management, and surrounding forest cover. For example, fruit trees were more prevalent close to villages, while many dead trees were found in wood pastures surrounded by forests. A detailed study on the biodiversity of one specific wood pasture showed the high potential of wood pastures to support high levels of biodiversity. Worryingly, current management of wood pastures differed from traditional techniques in several aspects, which could potentially threaten their persistence. First, most wood pastures were grazed by sheep only, whereas mixed livestock grazing used to be the common management type. Second, many large trees suffered from (anthropogenic) burning. Although pasture clearing through controlled burning has been used for centuries, the current trend towards uncontrolled burning is a major threat to wood pastures. Third, we found some evidence of (illegal) tree cutting, while historically only branches were cut and the trunk remained ('pollarding'). Wood pastures are not consistently formally protected within the EU, and our results show that their persistence in Transylvania is in danger. Therefore, a solid ecological understanding in combination with knowledge on cultural and human livelihood importance of wood pastures needs to be developed to further their recognition for formal conservation.

The role of wood pastures for biodiversity was explored in more detail in Chapters VII and VIII. In **Chapter VII** we assessed the habitat value of wood pastures for an assemblage of six woodpecker species. Woodpeckers are considered to be highly sensitive to changes in forest management due to their large home ranges and their requirement of large trees and dead wood for nesting and foraging. Since wood pastures retain elements of natural forests they may provide additional habitat for the more forest-associated woodpeckers. Indeed, we found that species richness in wood pastures was similar to forests, although species composition differed slightly. Wood pastures were especially important for the green woodpecker (*Picus viridis*), which is considered an open-country species, while forests were more important for the lesser-spotted woodpecker (*Dendrocopos minor*), which typically avoids foraging in open areas. In contrast, the other four woodpecker species occurred in both wood pastures and forests. Two of the protected species were especially prevalent in wood pastures with a higher surrounding forest cover. Thus, wood pastures provide valuable supplementary habitat for woodpeckers. Favourable characteristics of wood pastures may be high food availability (e.g. ants and insects), nesting cavities in large trees, and the provision of connectivity between different forest patches.

Chapter VIII showed that wood pastures also provide valuable supplementary habitat for the brown bear. We found evidence for bear activity in 87% of the surveyed wood pastures (indicated through destroyed anthills). Similarly to Chapter IV, bear activity was higher at a close proximity to the Carpathian Mountains and in more rugged and forested areas. Bears may find wood pastures suitable for foraging because of the availability of multiple food sources and the shelter provided by woody vegetation. Grassland ant species are not found in forests, but form an important source of protein for the mainly vegetarian bear. During autumn, wood pastures further provide fruits and hard mast, although the use of these food sources by bears could not be assessed within the time-frame of our study. These two studies show the high potential of wood pastures for biodiversity conservation. We suggest to explicitly consider wood pastures in major EU conservation policies, for example by stimulating the maintenance of scattered trees in extensively managed pastures.

Section C takes a social-ecological systems approach to understand how links between the social and ecological parts of the system affect human-bear coexistence. In **Chapter IV** we used questionnaires to obtain an overview on human-bear conflicts in the study area, and correlated perceived levels of conflicts with observed bear activity. Conflicts with bears occurred across the study area. People reportedly suffered from damage to crops, orchards, and beehives, as well as predation on livestock, while attacks on humans were rare. Cow herders had little problems with bears. In contrast, about half of the shepherds suffered bear attacks on sheep during the past three years. Interestingly, perceived level of damage to orchards and crops was positively correlated with bear activity, while bear activity did not correlate to the number of sheep attacks or perceived level of damage to beehives. These differences may be explained by differences in guarding management. Orchards and crops are often left unguarded, whereas, sheep are actively guarded by both shepherds and sheep guard dogs. The lack of a correlation between bear activity and perceived damage to beehives may be more related to the low abundance of this technique among participants. These results indicate the importance of local factors other than bear activity on the prevalence of livestock predation and highlight the possibility for conflict mitigation (e.g. through location of the sheep camp). We asked shepherds several additional questions to examine whether livestock predation affected their attitudes towards bears. There was some tolerance towards bears, despite occasional sheep predation. Shepherds suffering from a higher rate of bear attacks nevertheless expressed a strong dislike of bears more frequently. About half of the shepherds were unsupportive of immediate killing of bears after a sheep attack. Thus, the use of traditional sheep herding techniques combined with the tolerance of some shepherds is likely to facilitate human-bear coexistence in the region.

In **Chapter IX**, we combined questionnaires with semi-structured interviews for a more holistic understanding of the social drivers underlying human-bear coexistence. The majority of participants had a positive perception of coexistence. The questionnaires revealed general patterns on social drivers underlying coexistence such as past negative interactions, perceived risks of damage, attitude, and age. The interviews revealed three coexistence pathways highlighting the causal mechanisms driving people's willingness to coexist with bears. These pathways show different ways in which ongoing interactions between the ecological system and the social system shape the willingness of people to coexist with bears. The three pathways were defined by three major themes, namely bears, humans, and management. The landscape had important mediating effects on the pathways centred on bears and humans. For example, in the landscape-bear coexistence pathway, people's perceptions and beliefs about bears were largely shaped through direct interactions and experiences with bears. The importance of direct interactions was further emphasized in the landscape-human coexistence pathway where people's tolerance towards bears increased following positive encounters with bears, while livestock predation by bears decreased people's tolerance. Nevertheless, negative perceptions on coexistence were more likely to be shaped by the perception of a high risk of potential conflicts with bears than by the actual experience of damage caused by bears. Furthermore, the landscape-human-coexistence pathway showed that genuine links between people and their environment (i.e. where people value their natural surroundings) were important drivers of people's positive attitudes towards bears and an ascription of non-use values to bears. However, the management coexistence pathway revealed that perceived inadequate management may erode the rural population's tolerance for bears. Management related to bear population management, conflict mitigation and compensation payments, and trophy hunting was often perceived unsatisfactory by the participants. In addition, the feeling of distrust towards management bodies and dis-empowerment further widened the gap between management bodies and local stakeholders. We conclude that to avoid the escalation of human-human conflicts over bears, where bears represent disagreements between local stakeholders and management bodies, coexistence may be maintained or facilitated through: (i) participation of local stakeholders to enhance the information flow and reduce distrust towards management bodies; (ii) targeted education programs to address people's specific beliefs and concerns regarding bear-related issues; and (iii) the development and increased transparency of current and alternative solutions for conflict mitigation.

Synthesis: System properties facilitating biodiversity conservation

This dissertation provides important insights on biodiversity drivers and patterns in traditional farming landscapes. To start with, it demonstrates the large biodiversity value of traditional farming landscapes in general, and calls for an increased recognition of these systems for biodiversity conservation. This is especially urgent since anticipated land-use change and the loss of traditional farming practices may cause significant biodiversity declines in traditional farming landscapes. Undoubtedly, there are many system properties of traditional farming landscapes that potentially facilitate biodiversity conservation. Some of these are beyond the focus of this dissertation such as traditional livestock and crop rotation schemes, diverse crop systems, low agro-chemical input, and land-use that is not optimized to produce maximum yields. However, through the consideration of two different animal taxa, this dissertation reveals six important system properties that support high biodiversity in Transylvania's traditional farming landscape.

1. Similar proportions of main land-use types

Biodiversity was supported by the heterogeneous character of the traditional farming landscape at multiple spatial scales. At the scale of the study area, relatively similar proportions of the three main land-use types likely support high biodiversity. Habitat loss and fragmentation are considered major drivers of mammal and bird declines (Andrén 1994; Monastersky 2014). However, fragmentation effects usually become visible below a threshold of 30% of available habitat (Andrén 1994; Hanski 2011), which is close to the proportional cover of the study area's three main land-use types. The approximately one-third of forest cover also seemed to provide sufficient habitat connectivity for the brown bear (Chapter IV). Habitat connectivity at large scales is an important system property as it can facilitate species' movements and dispersal in fragmented landscapes and maintain gene flow and metapopulation dynamics (Fischer & Lindenmayer 2007; Kopatz et al. 2012). For the brown bear in Southern Transylvania, the existing connectivity between the study area and the source population in the Carpathian Mountains, provided by configuration and composition of land covers, was found to be particularly important (Chapter IV). In other parts of the brown bear's European range, in contrast, forest connectivity is degraded to a degree that limits the species' expansion (Fernández et al. 2012).

Within farmland, bird species composition was not determined by land-use *per se* (e.g. arable land *vs* grassland), but was influenced by different environmental gradients (Chapter II). The availability of both grassland and arable land in relatively large proportions may support the similar species composition of birds (Chapter II) and butterflies (Appendix I) in both land-use types, for example through constant spill-over (Tscharntke et al. 2012). These processes may prevent the divergence of distinct grassland and arable land communities but maintain more diverse communities at the landscape scale. Although plant species composition differed between grasslands and arable land, a substantial number of species was shared and both land-use types were important contributors to the total species pool (Appendix II). In addition, a forest-farmland mosaic facilitates spill-over effects from forests to farmland (Tscharntke et al. 2012), and we observed a considerable number of forest bird species in farmland (Chapter II). Thus, the observed proportions of land-use types in the study area support species associated with farmland as well as with forests, with all three major land-use types contributing to high regional biodiversity.

2. Complementary or supplementary habitat

Heterogeneous landscapes can further support biodiversity through complementation and supplementation of habitat at the landscape scale (Dunning et al. 1992). Landscape complementation is provided in landscapes in which species encounter all required spatially separated habitats containing necessary resources, while landscape supplementation is provided in landscapes in which species encounter additional habitats that contain similar resources (Dunning et al. 1992). We observed several species in land-use types outside their core habitat. For example, wood-pastures were extensively used by different woodpecker species and the brown bear (Chapters VII and VIII). The retention of forest structures across the landscape in traditional farming landscapes thus provides supplementary if not complementary habitat for forest species (Mikusinski & Angelstam 1998). Similarly, the corncrake was present throughout the arable mosaic despite being considered a grassland species (Chapter III). Uncropped arable land in combination with field margins or ditches may be important in providing resources similar to grasslands, such as safe breeding and sheltering sites and high insect availability (Corbett & Hudson 2010; Budka & Osiejuk 2013; Josefsson et al. 2013).

3. High woody vegetation cover and heterogeneity

At a more specific level, traditional farming landscapes supported biodiversity through the presence of gradients in woody vegetation cover, including semi-natural vegetation, and through heterogeneity, measured as the composition and configuration of land cover. High woody vegetation cover supported bird (Chapter III), butterfly (Appendix 1) and plant (Appendix 2) species richness locally, possibly by providing a range of resources such as refuge areas, nesting, sheltering, and foraging sites (e.g. Benton et al. 2003; Ernoult & Alard 2011), or by facilitating cross-habitat movements and spill-over (Tscharntke et al. 2012). Importantly, not all taxa respond linearly to woody vegetation cover or heterogeneity. For example, bird richness increased asymptotically with woody vegetation cover, which was especially evident in grasslands (Chapter II) which harbours a large number of open-country species that disappear beyond certain levels of woody vegetation cover (Sanderson et al. 2013). These findings demonstrate the need to also maintain relatively homogenous, open areas (Batary et al. 2011b). Another case of important non-linearity was revealed by the simulated severe reduction of corncrake habitat at relatively modest levels of land cover homogenization (Chapter III).

We also identified the significance of the landscape context for effects of woody vegetation cover and heterogeneity. Woody vegetation cover and heterogeneity influenced different species or groups of species of birds (Chapter II), butterflies (Appendix 1), and plants (Appendix 2) at larger spatial scales, and sometimes with effects opposite to those at smaller scales. Furthermore, we found biodiversity to be affected not only by processes at multiple spatial scales, but effects also differed between species, which may depend on their specific resource needs (Lindenmayer & Fischer 2006). To conclude, the availability of woody vegetation cover and heterogeneity at different spatial scales are important drivers of biodiversity in traditional farming landscapes. Moreover, we demonstrated the need to further understand the scale dependence of different species and across different taxa.

4. Traditional land-use practices

The presence of high woody vegetation cover and heterogeneity is linked to traditional semi-subsistence farming practices. Such farming, including high degree of manual labour and few agro-chemical inputs, is thus key to maintaining biodiversity. The manual cutting of hay in a mosaic pattern, for example, provides a variety of sward heights throughout the breeding season of corncrakes, thereby facilitating their presence in agricultural land (Chapter III). Wood pastures were created by traditional silvo-pastoral practices but current management techniques differ from the traditional ones and may severely threaten the persistence of wood pastures in the landscape (Chapter VI). This change in management is likely to have a negative effect on the biodiversity supported by wood pastures. As another example, the use of traditional livestock husbandry techniques allowed coexistence between humans and large carnivores (Chapter IV and IX). The combination of shepherds, livestock guard dogs, and nightly confinement of livestock are successful in reducing livestock conflicts worldwide (Rigg 2001; Gehring et al. 2010), as well as in Romania, as demonstrated here. This provides an important insight for European regions into which large carnivores return after their earlier extirpation, but in which the loss of these husbandry techniques and resulting conflicts hamper their successful establishment (Enserink & Vogel 2006; Chapron et al. 2014).

5. Top-down carnivore regulation

The presence of large carnivores in the landscape can benefit biodiversity through top-down control on mesopredators and herbivores (Estes et al. 2011; Ripple et al. 2014), which induce trophic cascades that affect species at multiple trophic levels (Letnic et al. 2009). The importance of trophic cascades for biodiversity have mainly been observed in wilderness areas (Ripple & Beschta

2012b), whereas the role of large carnivores in structuring human-dominated ecosystems remains unclear (Sergio et al. 2014). We found limited evidence for top-down control on a mesopredator (the red fox; Chapter V), which may be explained by large differences in body size (Donadio & Buskirk 2006; Ritchie & Johnson 2009), or by densities of wolves and bears too low to effectively limit foxes. In contrast, we found top-down limitation of wolves and bears on herbivores (Chapter V), which indicates the importance of their persistence for the ecosystem (for example by limiting overgrazing, enhancing vegetation growth, and maintaining biodiversity in general; Terborgh et al. 2001; Estes et al. 2011). Still, to fully understand the role of carnivores in traditional farming landscapes future research should aim to understand (i) the extent and effects of possible trophic cascades induced by carnivore top-down herbivore control; and (ii) the role of human bottom-up and top-down effects on trophic cascades in combination with the effects induced by carnivores.

6. Human-nature connections

Large carnivore persistence does not only depend on the biophysical environment, but also on the degree to which the rural population is willing to coexist with large carnivores (Treves & Karanth 2003). People in our study area had a general positive perception of human-bear coexistence (Chapter IX). Their ability to tolerate carnivores partly stemmed from genuine links between humans and nature, with people valuing the natural heritage. People's culture shapes the landscape, but the landscape in turn also shapes the culture of people (Pretty 2011). The centuries of co-occurrence of humans and bears in Southern Transylvania probably shaped human culture to accept and adapt to living with carnivores (see also Glikman et al. 2012). These strong ties between people and the landscape possibly form the core of people's values and sustainable use of natural resources. Disconnecting these bonds could potentially destroy people's culture and with it the associated natural heritage (Pretty 2011). In the case of large carnivores, for example, perceived failures of top-down managing institutions may harm carnivores through reduced tolerance and increased poaching (Chapter IX; Bell et al. 2007; Liberg et al. 2012; Gangaas et al. 2013).

Conservation priorities for traditional farming landscapes

Traditional farming landscapes have a high conservation value, and facilitating biodiversity conservation in these landscapes should be of priority worldwide. The maintenance or preservation of the six system properties highlighted in this dissertation should be a central part of conservation measures targeting traditional farming landscapes. Biodiversity was greatly supported through the heterogeneous character of the forest-farmland mosaic. This heterogeneous character, however, is tightly linked to the historical multi-functionality of the landscape and the practice of small-scale semi-subsistence farming. Yet, it is these features that will vanish under anticipated land-use change in form of agricultural intensification or land abandonment. Agricultural intensification will cause major declines in biodiversity. Although land abandonment may benefit certain forest species (e.g.

bears and forest birds), the associated decline of farmland species will significantly reduce the overall species pool. Moreover, we found that humans and bears can coexist in the landscape at current conditions, without the need to set additional land aside for carnivore conservation. Thus, conservation priorities should integrate farming and biodiversity conservation through encouraging farming that maintain the heterogeneous character of the landscape (i.e. land sharing; Fischer et al. 2008).

Conservation initiatives that prevent biodiversity loss in heterogeneous farmland are considered to be more (cost-) effective than restoration initiatives after biodiversity declines driven by land-use change (Kleijn et al. 2011). Yet, current conservation measures in the EU are poorly adapted to support biodiversity in heterogeneous traditional farming landscapes, which face very different conservation challenges from more intensified landscapes (Tryjanowski et al. 2011; Mikulcak et al. 2013; Sutcliffe et al. 2014). The two main measures to mitigate farmland biodiversity loss in Europe are agri-environment schemes (AES) of the Common Agricultural Policy and the Natura 2000 network. The effectiveness of AES for farmland biodiversity conservation has been questioned because biodiversity continues to decline (Kleijn et al. 2006; Kleijn et al. 2011; Pe'er et al. 2014). Through the voluntary uptake of AES by farmers, implementation of AES is often restricted to small field or farm scales and may be one of the reasons why AES can be unsuccessful (Whittingham et al. 2007). Furthermore, local-scale AES are generally considered to be ineffective in highly heterogeneous landscapes (Tscharntke et al. 2005; Concepción et al. 2008; Batary et al. 2011a). The Natura 2000 network, on the other hand, designates sites at larger scales that protect specific habitats and species listed under the Habitats and Birds Directives, and can have positive biodiversity impacts (Gruber et al. 2012; Brodier et al. 2013; Pellissier et al. 2013). Nonetheless, these measures also may be limited in their effectiveness, due to for example missing cooperation between EU member states and a lack of trans- and interdisciplinary research to obtain a holistic social-ecological understanding of the selected sites (Apostolopoulou & Pantis 2009; Albuquerque et al. 2013; Popescu et al. 2014). In our study area, the implementation of the management plan for the Natura 2000 area is pending, and it remains unclear how successful the forthcoming plan will be in maintaining the heterogeneous character of the landscape. Furthermore, the brown bear (listed under the Habitats Directive) depends on connectivity to the Carpathians Mountains outside the Natura 2000 area, which is threatened by Romania's increasing deforestation rates (Knorn et al. 2012; Griffiths et al. 2013), also in places where the Natura 2000 management plan will not apply. Thus, there is a need to develop more holistic visions for biodiversity conservation in this and other traditional farming landscapes, which include areas inside and outside protected areas.

Building upon the identified system properties such a holistic approach may firstly comprise 'broad and shallow' landscape-scale conservation strategies targeting the entire forest-farmland mosaic. Secondly, large scale conservation measures may be complemented with more 'deep and narrow' conservation measures targeting specific species, land-use types, threats, or traditional practices. Third, conservation initiatives should encourage the integration of the entire social-ecological system by recognizing important links between people and the environment.

The application of AES at the landscape scale has already proven beneficial for a range of species (Merckx et al. 2009; Dallimer et al. 2010). In the case of traditional farming landscapes, large-scale conservation measurements could provide the more 'broad and shallow' landscape perspective to maintain the heterogeneous landscape character at multiple spatial scales (Concepción et al. 2008). These measures could focus on maintaining similar proportions of land-use types, large-scale habitat connectivity, complementary and supplementary habitat of different species, and the gradients in land cover heterogeneity and woody vegetation cover. Applying this landscape perspective may, for example, prevent the under-valuation of certain habitats (e.g. wood pastures) and allow the inclusion of conservation strategies for supplementary species habitat (e.g. arable land for the corncrake and butterflies).

'Deep and narrow' conservation measures need to complement landscape-scale conservation measures to ensure the persistence of specific species (Koleček et al. 2014). Here, it seems vital to advance our understanding of scale-dependent responses of different species to woody vegetation cover and land cover heterogeneity (Pickett & Siriwardena 2011; Tscharntke et al. 2012). Biodiversity responses in our study also differed between land-use types indicating the need for distinct and more detailed strategies for grasslands and arable fields. Similarly, biodiversity may benefit most from policies targeted to mitigate either abandonment or intensification. For example, abandonment may be more prevalent in remote grasslands on steep slopes and could be mitigated by providing incentives to maintain rotational livestock grazing to remove shrubs. In contrast, intensification is more likely to occur in accessible arable land where the retention of woody vegetation cover should be prioritized. Lastly, these conservation measures could focus on the preservation of key elements of traditional land-use and practices (e.g. livestock herding techniques) and on strategies for their future integration in new land-use systems (Plieninger et al. 2006).

The above-mentioned priorities aim to support biodiversity conservation. However, ultimately, the persistence of biodiversity in traditional farming landscapes will depend on navigating social-ecological change so that it does not only maintain biodiversity but also benefit local people. Traditional farming practices have become largely unviable, and standard conservation policies take a 'preservation approach' where financial incentives are provided for people to maintain traditional farming practices (Fischer et al. 2012; Plieninger & Bieling 2013). These strategies, however, may only be successful in the short term, because human-environment bonds are not primarily driven by economic incentives (Milcu et al. 2014). In our study, people did not tolerate bears for their economic benefits but because of non-use values people ascribed to bears. Understanding and addressing these values and links between people and the environment could reduce conflicts between rural populations and conservation initiatives (Ives & Kendal 2014). Moreover, the links between people, their activities, and the environment could form the base for a more integrated 'transformation approach' (Fischer et al. 2012). Such an approach should foster new links between the social and the ecological parts of the system aimed at maintaining the system properties of traditional farming landscapes that support biodiversity but also fosters human-well-being. Alternative development pathways could be created through, for example, the uptake of agro-ecological and organic farming or the development of agro-ecotourism (Hole et al. 2005; Young et al. 2010). Because people may have aspirations for the future different from those prioritized by conservation (Milcu et al. 2014), community participation and the support of bottom-up driven initiatives are essential for the development of holistic conservation strategies. Importantly, biodiversity conservation of traditional farming landscapes can only be facilitated if initiatives to support other capitals (e.g. social, human, financial, physical) are developed simultaneously (Mikulcak et al. 2015). In the end, the future of traditional farming landscapes in a globalized world will depend on how well people can capitalize on the available opportunities (Hanspach et al. 2014), and thus successful biodiversity conservation will hinge on the integration of the entire social-ecological system.

Conclusion

The unique natural heritage of traditional farming landscapes is under severe pressure from the regional impacts of globalization, with land-use intensification and land abandonment threatening to erode regional biodiversity. The future of traditional farming landscapes and its associated biodiversity depends on the navigation route of the social-ecological system through these profound changes. Using the example of birds and large carnivores in the changing traditional farming region of Southern Transylvania, this dissertation revealed six important system properties that facilitate biodiversity conservation. Drawing on the identified properties this dissertation highlighted several conservation priorities that can help to maintain biodiversity in traditional farming landscapes. There is a clear need to develop a conservation vision for traditional farming landscapes that takes a holistic approach and complements 'broad and shallow' landscape-scale conservation of the entire forest-farmland mosaic with more 'deep and narrow' conservation initiatives targeting specific species, land-use types, threats, or traditional practices. More importantly, integration of the entire social-ecological system within this vision is necessary to maintain biodiversity and simultaneously foster the well-being of the rural population whose livelihoods are strongly interconnected with the natural environment. There is an urgent need to develop visions that navigate traditional farming landscapes through ongoing land-use change because these landscapes are rapidly disappearing worldwide. Ensuring the persistence of traditional farming landscapes in the future would contribute considerably to the challenging yet crucial goal to halt global biodiversity decline.

Section A: Land-use effects on biodiversity

This Section includes Chapters II-IV and examines the effects of local and landscape scale land-use patterns on birds and large carnivores, and how future land-use change may affect them. Chapter II aims to gauge the likely effects of future land-use change on the passerine community, with emphasis on land-use intensification and land abandonment. Chapter III aims to assess the sensitivity of an EU-protected farmland bird species, the corncrake, to possible future land-use intensification. Chapter IV examines the effects of land-use patterns on brown bear distribution. Chapter V explores the role of large carnivores in the ecosystem by analyzing the top-down effects of large carnivores on herbivores and mesopredators in relation to direct and indirect human top-down effects and land-use bottom-up effects.

Chapter II

Chapter II

Maintaining bird diversity in a traditional farming landscape in Eastern Europe

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Manuscript

'Farmland birds are at their lowest levels since records began.' – BBC News 2014

'We know that wildlife is bleeding from the countryside, we know the reasons behind it and we know how to fix it. We just aren't fixing it because government isn't bothered. No news there then.' – Mark Avery

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 & 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 & Page 2007). 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 (Fig. 2.1a). 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 occured 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; Fig. 2.1b).

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 (Fig. 2.1b & 2.1c). 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'.

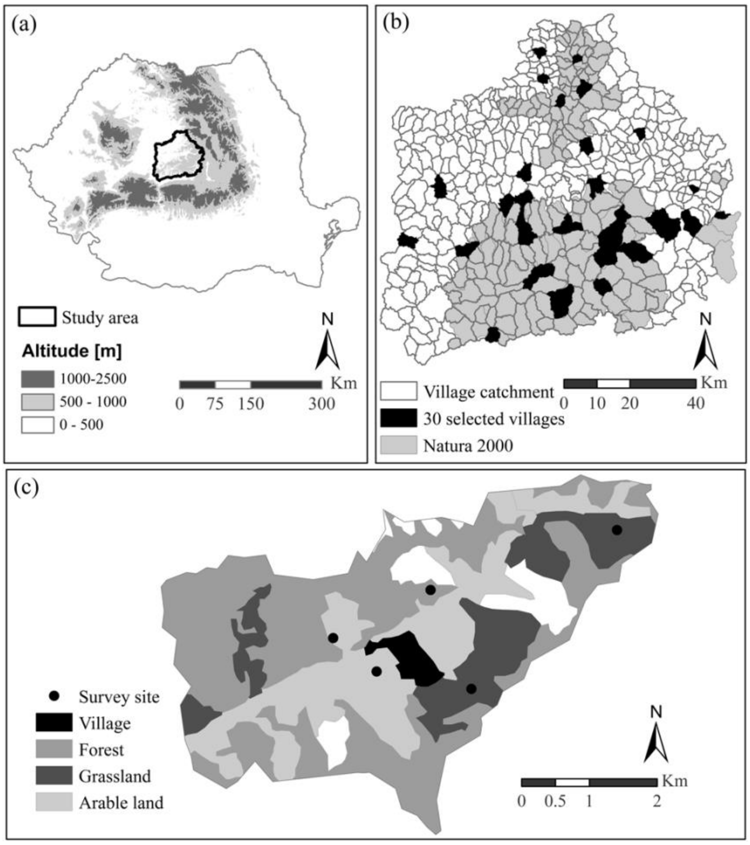

Figure 2.1 Study area. (a) Romania with our study area highlighted, (b) our study area with selected village catchments highlighted, and (c) example of one of the village catchments showing different types of land cover and five survey sites

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 S2.1 in Supplementary Material).

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 S2.2). 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 & Van Halder 2009). The landscape scale corresponded to the village catchment (mean ± SD: 2046 ± 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 2.1). 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. 2009).

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-use type 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 2.1 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

[b] Based 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

[c] CLC: Corine Land Cover Digital map 2006

[d] Calculated 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 et al. 2000). Based on a pilot study, three surveys proved sufficient to representatively capture the species within a site (Loos et al. 2014). 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 & 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 ($\varrho < 0.6$); 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 Development 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 (Linţia 1954, 1955; Ciochia 1992).

Results

Bird diversity

We identified 61 breeding bird species (see Table S2.3). Species richness was higher in forests (mean ± 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 (Fig. 2.2).

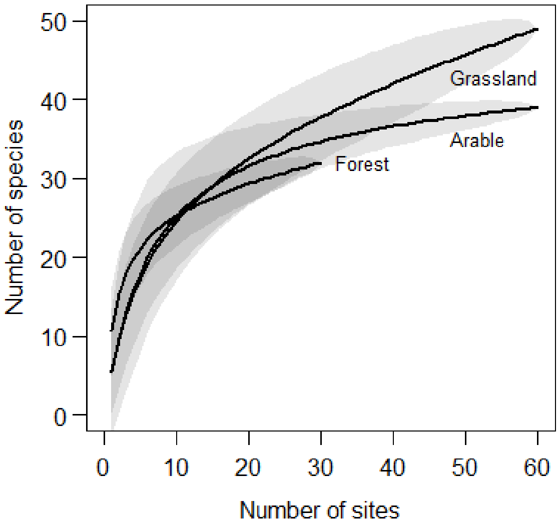

Figure 2.2 Bird species accumulation curves for forest, grassland and arable sites. Ninety-five percent confidence intervals are indicated by grey shading.

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 (Fig. 2.3a). 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; Fig. 2.3b, see Fig. S2.1 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 (Fig. 2.3b). 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 (Fig. 2.3b).

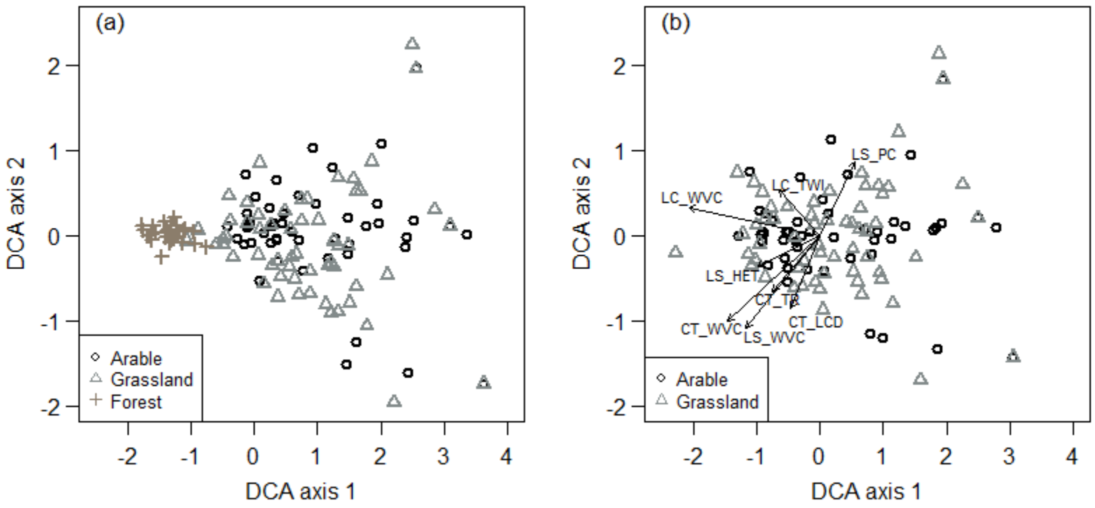

Figure 2.3 Detrended correspondence analysis (DCA) of bird species composition in: (a) all three land-use types sampled, and (b) in farmland sites only, with significant environmental variables superimposed on the ordination plot. Abbreviations for the spatial scales: LC = local scale, CT = context scale, 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 2.2; Fig. 2.4). Furthermore, the positive effect of local woody vegetation cover on species richness was more pronounced in arable fields than in grasslands (Table 2.2; Fig. 2.4). Richness of species groups with different habitat specialization showed different and sometimes opposite responses to the environmental variables (Table 2.2). 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 2.2).

Table 2.2 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 ± SE.

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

[a] Results are given with arable land-use as baseline (i.e. the intercept shown is associated with the regression line for arable land)

[b] The rows 'Village catchment' and 'Site-level' show the variance associated with the random effects

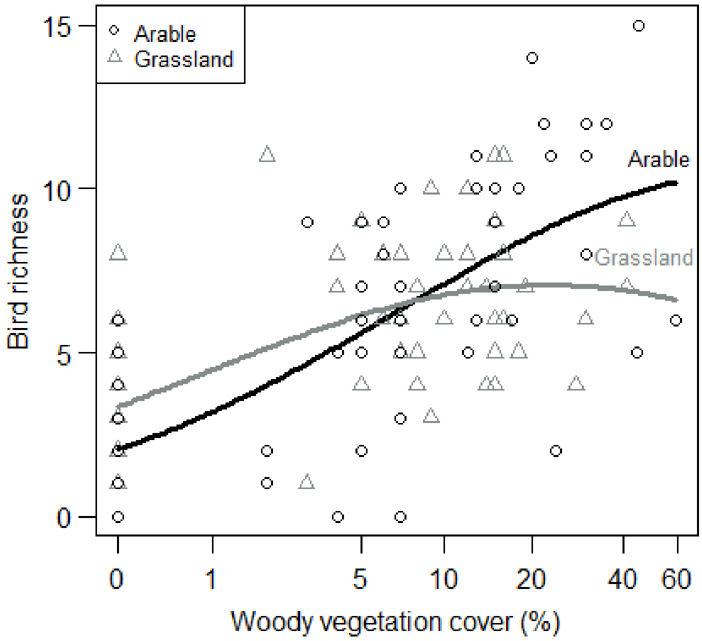

Figure 2.4 Predicted total bird species richness (solid lines) in response to woody vegetation cover in arable versus grassland sites based on a generalized linear mixed effects model. Open circles (arable sites) and triangles (grassland sites) represent observed species richness.

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.

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 caudatus*), to a community mainly comprising open-country birds (e.g. the Whinchat, *Saxicola rubetra*, and the Quail, *Coturnix coturnix* (see Fig. S2.1)). 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 Fig. S2.1). 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. 2011b; 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 & 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 & 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 (Table S2.3). 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 (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 & 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 & 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).

Acknowledgements

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Supplementary Material for Chapter II

Table S2.1 The number of replicated combinations of villages according to stratification by landscape terrain ruggedness and protection status. Terrain ruggedness was classified into three groups based on terciles covering the entire study area. Sites located within the protected Natura 2000 network are indicated by Sites of Community Importance (SCI, according to the EU Habitats Directive) and Special Protection Areas (SPA, according to EU Birds Directive).

		SCI	**SPA**	**Non-protected**
Terrain ruggedness	Low	1	4	4
	Medium	4	3	3
	High	4	3	4

Table S2.2 The number of replicated combinations of sites according to stratification by local heterogeneity and woody vegetation cover in arable (A) and grassland (G) sites. Heterogeneity and woody vegetation cover were classified into three groups based on terciles covering the entire study area.

		Heterogeneity					
		Low		**Medium**		**High**	
		A	**G**	**A**	**G**	**A**	**G**
Woody vegetation cover	Low	11	8	6	8	10	6
	Medium	6	7	7	7	6	9
	High			6	8	8	7

Table S2.3 List of recorded bird species, their associated SPEC category, and their habitat specialization. SPEC 1 represents European species of global conservation concern classified as Critically endangered, Endangered, Vulnerable, Near Threatened or Data Deficient under the IUCN Red List Criteria at a global level; SPEC 2 represents species whose global populations are concentrated in Europe and which have an Unfavorable Conservation Status in Europe; SPEC 3 represents species whose global populations are not concentrated in Europe but which have an Unfavorable Conservation Status in Europe; and SPEC 4 represents species whose global populations are concentrated in Europe (more than 50% of their global population or range in Europe) but which have a Favorable Conservation Status in Europe.

Latin	**English**	**SPEC**	**Habitat**
Aegithalos caudatus	Long-tailed Tit	NON	Forest
Certhia familiaris	Eurasian Treecreeper	NON	Forest
Coccothraustes coccothraustes	Hawfinch	NON	Forest
Columba oenas	Stock Pigeon	4	Forest
Columba palumbus	Wood Pigeon	4	Forest
Cuculus canorus	Common Cuckoo	NON	Forest
Dendrocopos major	Great Spotted Woodpecker	NON	Forest
Dendrocopos medius	Middle Spotted Woodpecker	4	Forest
Dendrocopos minor	Lesser Spotted Woodpecker	NON	Forest
Dryocopus martius	Black Woodpecker	NON	Forest
Erithacus rubecula	European Robin	4	Forest
Ficedula albicollis	Collared Flycatcher	4	Forest
Fringilla coelebs	Chaffinch	4	Forest
Garrulus glandarius	Eurasian Jay	NON	Forest
Oriolus oriolus	Golden Oriole	NON	Forest
Parus caeruleus	Blue Tit	4	Forest
Parus major	Great Tit	NON	Forest

Parus palustris	Marsh Tit	NON	Forest
Phylloscopus collybita	Chiffchaff	NON	Forest
Phylloscopus sibilatrix	Wood Warbler	4	Forest
Picus canus	Grey-headed Woodpecker	3	Forest
Picus viridis	Green Woodpecker	2	Forest
Sitta europea	Nuthatch	NON	Forest
Strix uralensis	Ural Owl	NON	Forest
Sturnus vulgaris	Common Starling	NON	Forest
Sylvia atricapilla	Blackcap	4	Forest
Troglodytes troglodytes	Eurasian Wren	NON	Forest
Turdus merula	Common Blackbird	4	Forest
Turdus philomelos	Song Thrush	4	Forest
Anthus trivialis	Tree Pipit	NON	Farmland
Carduelis cannabina	Linnet	4	Farmland
Carduelis carduelis	Goldfinch	NON	Farmland
Carduelis chloris	Greenfinch	4	Farmland
Emberiza citrinella	Yellowhammer	4	Farmland
Hippolais pallida	Eastern Olivaceous Warbler	3	Farmland
Lanius collurio	Red-backed Shrike	3	Farmland
Lanius excubitor	Great Grey Shrike	3	Farmland
Lanius minor	Lesser Grey Shrike	2	Farmland
Locustella fluviatilis	River Warbler	4	Farmland
Lullula arborea	Woodlark	2	Farmland
Luscinia luscinia	Thrush Nightingale	4	Farmland
Passer montanus	Tree Sparrow	NON	Farmland
Phylloscopus trochilus	Willow Warbler	NON	Farmland
Pica pica	Magpie	NON	Farmland
Sylvia borin	Garden Warbler	4	Farmland
Sylvia communis	Common Whitethroat	4	Farmland
Sylvia curruca	Lesser Whitethroat	NON	Farmland
Sylvia nisoria	Barred Warbler	4	Farmland
Turdus viscivorus	Mistle Thrush	4	Farmland
Upupa epops	Hoopoe	NON	Farmland
Acrocephalus palustris	Marsh warbler	4	Open-country
Alauda arvensis	Skylark	3	Open-country
Anthus campestris	Tawny Pipit	3	Open-country
Coturnix coturnix	Common Quail	3	Open-country
Crex crex	Corncrake	1	Open-country
Emberiza calandra	Corn Bunting	4	Open-country
Motacilla alba	White Wagtail	NON	Open-country
Motacilla flava	Yellow Wagtail	NON	Open-country
Saxicola rubetra	Winchat	4	Open-country
Saxicola torquata	Stonechat	3	Open-country
Passer domesticus	House Sparrow	NON	Sinantropic

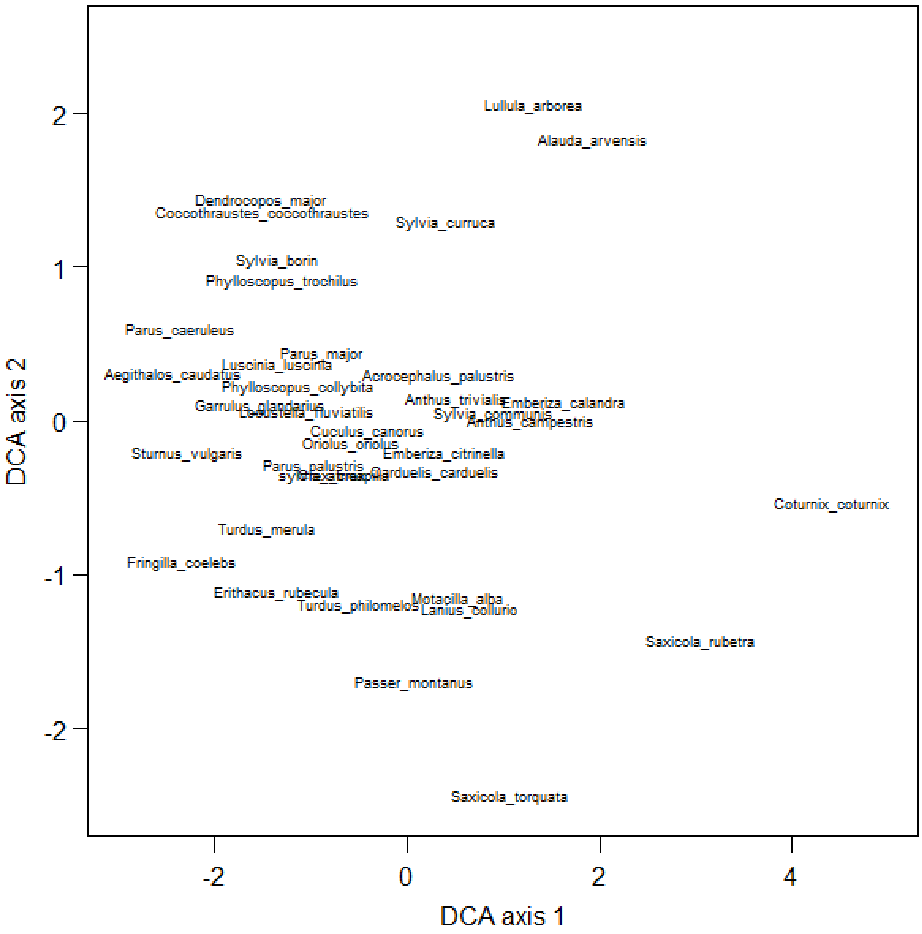

Figure S2.1 Species score of the detrended correspondence analysis (DCA; Figure 2.3b) of bird species composition in arable and grassland sites.

Chapter III

Chapter III

Impact of land cover homogenization on the Corncrake (*Crex crex*) in traditional farmland

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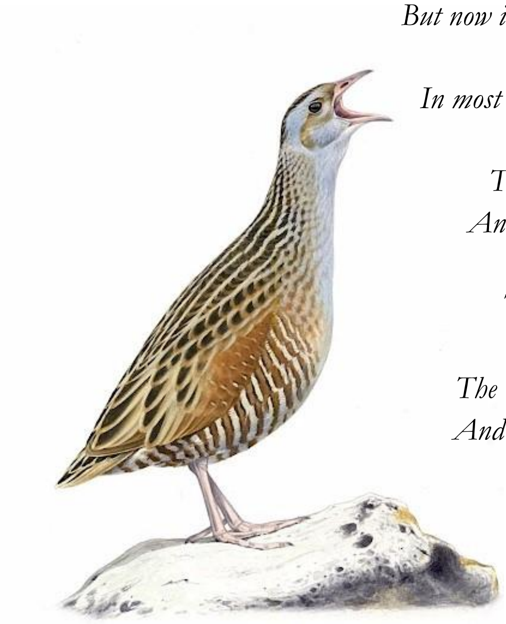
The Corncrake Heard No More

My memory take me back long years to when I was young boy
To evenings in mid-Summer in June and in July
The corncrake called in darkened mead the same notes o'er and o'er
But now in part of Ireland where I lived the corncrake heard no more.

In most of their old breeding grounds the corncrakes now don't breed
The earlier cutting of the grass stripped cover they did need
The silage harvester took its toll their nests and eggs destroyed
And in green meadow near my home the voice of corncrake died

The corncrake's voice no longer heard in meads of Duhallow
And I've not heard their familiar calls for thirty years or so
The earlier cutting of the grass left the birds with nowhere to hide
And the corncrakes have disappeared from my native countryside

On summer evenings long ago some hours after nightfall
In darkened meadows near my home the corncrakes did call
But the migrant rail no longer heard lost to posterity
And that voice I loved when I was young now just a memory
– Francis Duggan



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Abstract

Context.

The loss of landscape heterogeneity is causing declines of farmland biodiversity around the world. Traditional farmland regions are often highly heterogeneous and harbor high biodiversity, but are under threat of land cover homogenization due to changing agricultural practices. One species potentially affected by landscape homogenization is the Corncrake (*Crex crex*), which is threatened in Western Europe but remains widespread in the traditional farmland regions of Eastern Europe.

Objectives.

In this study we present a case study aiming to assess the potential threat of landscape homogenization for the Corncrake in Romania. We first examined current Corncrake distribution in relation to woody vegetation cover, landscape heterogeneity, and topography (measured at three different spatial scales), as well as human disturbance, throughout the existing agricultural mosaic. Second, we predicted potential future distribution of suitable Corncrake habitat in response to land cover homogenization by simulating a reduction in land cover diversity.

Results.

Corncrakes were present in grassland and arable fields, and preferentially occupied remote areas that were wet and flat, and had high land cover diversity at the 100 ha scale. The simulation of land cover diversity loss revealed that even a moderate reduction of land cover diversity could drastically reduce the extent of suitable Corncrake habitat.

Conclusions.

Our findings show the high conservation value of traditional heterogeneous farmland for the Corncrake. Therefore, to protect the Corncrake in traditional farmland, pro-active policy measures should encourage the continuation of mixed farming practices to maintain a diversity of land covers.

Introduction

Agricultural intensification since the mid-1900s has caused worldwide declines of farmland biodiversity (Donald et al. 2001; Tilman et al. 2001; Stoate et al. 2009). The process of agricultural intensification typically involves a combination of changes in management practices to increase production, such as increased mechanization and use of agrochemicals, loss of crop varieties and crop rotation, and the decrease of fallow land, non-cropped areas, and natural and semi-natural vegetation (e.g. Tilman et al. 2002; Tscharntke et al. 2005) . One of the defining consequences of agricultural intensification is the homogenization of the agricultural mosaic at multiple spatial scales, for instance through the loss of land cover diversity and structural heterogeneity (Benton et al. 2003; Tscharntke et al. 2005). Such land cover homogenization has severely reduced the suitability of farmland for numerous species across multiple taxa through reducing (nesting) habitat, food availability, and causing habitat fragmentation (Hinsley 2000; Weibull et al. 2003; Concepción et al. 2008; Guerrero et al. 2012; Tscharntke et al. 2012).

To mitigate the loss of farmland biodiversity, a range of national and international conservation policies are being implemented. In the European Union, agri-environment schemes (AES) of the European Common Agricultural Policy (CAP; Pillar 2) are a particularly prominent strategy (Skogstad and Verdun 2010). Farmers can take up AES voluntarily and receive financial support to improve habitat quality and promote certain species. However, the effectiveness of AES for biodiversity conservation has been questioned, and European farmland biodiversity continues to decline (Kleijn et al. 2006; Kleijn et al. 2011; Pe'er et al. 2014). The apparent ineffectiveness of AES partly could be explained by the lack of effective tools to assess the outcomes of AES (Kleijn & Sutherland 2003), or by a poor fit of AES to the ecological requirements of specific farmland bird species (Princé et al. 2012). Moreover, the effectiveness of AES is likely to be dependent on context conditions, including levels of land-use intensification (Princé et al. 2012) and landscape complexity. For example, local-scale AES may be more effective in relatively homogenous landscapes than in highly heterogeneous landscapes (Tscharntke et al. 2005; Concepción et al. 2008; Batary et al. 2011a). However, highly heterogeneous landscapes are threatened as a whole (Tscharntke et al. 2005). To more effectively protect the ecological values of heterogeneous landscapes, a key challenge therefore is to scale up AES, from local-level measures to landscape-level measures (Concepción et al. 2008).

The increasing shift in focus from local to larger scale agri-environment measures (e.g. Dallimer et al. 2010; McKenzie et al. 2013) could thus be of particular interest for heterogeneous landscapes, such as the traditional farming landscapes in Eastern Europe (Fischer et al. 2012). Traditional farmland is typically characterized by high heterogeneity in land cover and structural elements (Plieninger et al. 2006), and subsequently often harbors high levels of biodiversity, including threatened species (Tscharntke et al. 2005; Kleijn et al. 2009). However, traditional farming landscapes are under severe pressure of landscape homogenization from changes associated with agricultural intensification (Lepers et al. 2005). Nevertheless, empirical research to inform conservation management is lacking from the traditional farming regions in Eastern Europe, and therefore current measures within the CAP are poorly adapted to Eastern European conditions (Baldi & Batary 2011; Tryjanowski et al. 2011; Sutcliffe et al. 2014). Given this context, understanding the potential effects of land cover homogenization on biodiversity in traditional landscapes is an important research priority.

Here, we present a case study highlighting the potential consequence of homogenization of a traditional farmland mosaic for the Corncrake (*Crex crex*) in Transylvania, Romania. The Corncrake is a protected bird species in the European Union that primarily occurs in low-intensity grasslands and wet meadows with tall vegetation (Green et al. 1997). Agricultural intensification caused major declines in Corncrake populations in Western Europe (Green et al. 1997), although recently, some populations have begun to recover (Koffijberg & Schäffer 2006; Koleček et al. 2014). In contrast, large populations persist in former USSR and Eastern European countries. However, most populations in this region are declining (Koffijberg & Schäffer 2006; Koleček et al. 2014), and current trends in economic development are expected to enhance landscape homogenization and thus further exacerbate existing declines (Fourcade et al. 2013). To date, Romania has persisted as a major stronghold of the Corncrake, supporting an estimated 60,000 individuals (Koffijberg & Schäffer 2006).

With this study, we sought to understand the drivers underpinning Corncrake distribution in traditional Romanian farmland to gauge its sensitivity to possible future land cover homogenization. Specifically, (1) we assessed the response of Corncrake presence to human disturbance, and different features of landscape structure at three spatial scales; and (2) based on this, we simulated the possible effects of land cover homogenization on the distribution of suitable Corncrake habitat.

Methods

Study area and design

The study area covered 3100 km^2 and was located in Southern Transylvania, Romania, at altitudes between 230 and 1100 m (Fig. 3.1a). Transylvania is one of Europe's last regions dominated by traditional, small-scale farming systems. The landscape supports a heterogeneous farmland mosaic with similar amounts of forest and farmland: 47% forest, 20% pastures, and 25% arable land (Corine Land Cover Digital map 2006). Arable land is used mainly for low-intensity semi-subsistence farming, with most fields smaller than two hectares. Most fields are still tilled by horses and people, and agrochemical use is low by European standards. Considering all farmland, the use of inorganic fertilizer was only 16 kg/ha on average in 2013 in the four counties in which our study was carried out (INS 2015), while the average use in Romania is 28 kg/ha and 76 kg/ha for the entire European Union (www.ec.euopa.eu). Hay meadows provide fodder for livestock and many are still cut by hand. This, in turn, provides a variety of different sward heights throughout the spring and summer. The semi-natural pastures are grazed by sheep (dominant livestock), goats and cattle. Semi-natural vegetation is present throughout the landscape as hedgerows, streamside vegetation, and scattered trees. About half of the study area (1500 km^2) was located within the EU protected Natura 2000 network, including both Sites of Community Importance (SCI, Habitats Directive), and Special Protection Areas (SPA, Birds Directive; Fig. 3.1a).

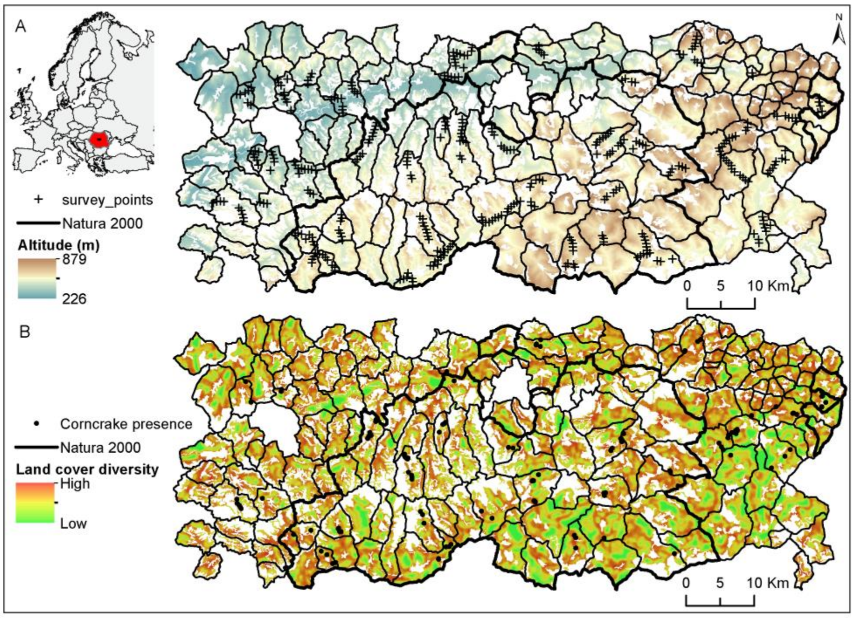

Figure 3.1 A) The inset shows the location of Romania in Europe (red) and the location of the study area in Romania (black). The close-up of the study area shows the 42 focal villages, location of the survey sites, and the area protected in the Natura 2000 network. The altitude is given for the area occupied by farmland (arable land and pastures), and represents the area for predicted Corncrake habitat suitability in Figure 3.3. B) The location of Corncrake presences in relation to land cover diversity at the context scale (100 ha).

To select our survey sites, we divided the study area into 'village catchments', defined as villages including their surrounding land. Such village catchments have been identified as both ecologically and socially meaningful landscape units (Angelstam et al. 2003). We delineated the area belonging to a given village catchment using a cost-distance algorithm that allocated each pixel to the village with the lowest travel cost (defined by slope) to this pixel in ArcGIS 10.1. The study area contained 172 villages. We randomly selected a subset of 42 villages (Fig. 3.1a), stratified to cover the full gradients of terrain ruggedness (low, medium, high) and protection level (Natura 2000, no protection). Terrain ruggedness was divided into three categories based on terciles of ruggedness values across the entire study area. The standard deviation ranged from 32.5 m to 47.8 m, with a mean altitude of 491 m for the low category; from 47.8 m to 57.7 m with a mean altitude of 500 m for the medium category; and from 57.7 m to 97.2 m, with a mean altitude of 518 m for the high category. Thus, seven villages were selected for each possible cross-combination of ruggedness level and protection status. Within each village, survey sites were placed along all drivable roads with a distance of 500 m between sites (Moga et al. 2010; Fig. 3.1a), resulting in 331 survey sites in total. The number of sites varied between 2 and 18 per village catchment.

Corncrake surveys

Corncrake surveys were performed under suitable weather conditions in the breeding season of 2013, from May 15 to June 30, from 23:00 to 3:00 hours, which is the most active calling period (Moga et al. 2010). Each site was surveyed twice, using five minute point counts from the road based on auditory observations (Bibby et al. 2000). The Corncrake typically calls loudly and frequently, and is often heard over several hundred meters. Five minutes appeared to be an appropriate time span, with 82% of all males detected within one minute and 98% within four minutes. The location of each singing (male) Corncrake was calculated by triangulation, based on two to three GPS points and their respective compass bearing towards the singing bird. Triangulation was implemented in ArcGIS using the tool 'Bearing distance to line'; Corncrake locations were defined as the crossing of two lines in case of two GPS points or as the center of the polygon in case of three GPS points.

To broadly characterize the landscape surrounding Corncrake locations we identified the land cover of all Corncrake locations from the road within the following categories: arable land, fallow land, hay meadow, pasture, and marginal elements (e.g. reed patches and field margins). No further habitat measurements were taken because detailed microhabitat requirements of the Corncrake in this region were previously described by Moga et al. (2010).

Variables used to model Corncrake presence

We modelled Corncrake presence/absence around each site in relation to two indices of human disturbance as well as to environmental variables that may explain Corncrake occurrence. The indices of *human disturbance* were human population density and distance to village. Environmental variables were measured at three spatial scales. The *local scale* (circular area of 10 ha, radius of 178 m) covered the approximate home range of the Corncrake (Grabovsky 1993; Van Weperen 2009), which rarely moves more than 250 m between calling sites (Peake & McGregor 2001). The *context scale* (circular area of 100 ha, radius of 564 m) and *village catchment scale* (mean ± SD: 18.2 km^2 ± 10.7 km^2) represented scales beyond the typical daily movements of male Corncrakes (Sklíba & Fuchs 2004).

At each scale, we quantified environmental variables expressing woody vegetation cover, land cover heterogeneity, and topography (Table 3.1). Both woody vegetation cover and land cover heterogeneity are likely to be affected by possible land cover homogenization (Benton et al. 2003; Tscharntke et al. 2005). In contrast, topography controls key biophysical gradients within the landscape, but is not subject to medium-term changes.

At the *local scale* we included the variables: (i) proportion of woody vegetation cover, (ii) spectral variance of monochromatic SPOT imagery (©CNES 2007, Distribution Spot Image SA) as an index of local structural heterogeneity, and (iii) Topographic Wetness Index (TWI) to indicate topographic position and potential soil wetness. At the *context scale* we included: (i) Simpson's diversity index of land cover (assessed with FRAGSTATS 4.1, McGarigal et al. 2012), and (ii) terrain ruggedness. We excluded woody vegetation cover at this scale because it was positively correlated with terrain ruggedness ($\varrho = 0.63$). We also excluded edge density (see below) because it was positively correlated with the Simpson's diversity index of land cover ($\varrho = 0.75$). Finally, at the *village catchment scale* we included: (i) Simpson's diversity index of land cover, (ii) land cover edge density, (iii) proportion of arable land cover, and (iv) terrain ruggedness. Together, these (statistically independent) variables characterized major differences in land cover composition and configuration between village catchments. We did not include woody vegetation at this scale because it is dominated by forest cover which is unsuitable for Corncrakes. For a detailed description of human disturbance and environmental variables and their calculation, see Table 3.1.

Statistical analysis

We pooled Corncrake presence data over the two repeated surveys. Because some individual Corncrake locations were in very close proximity to one another, we did not attempt to distinguish between individuals between the two repeats. At sites where no Corncrake was detected ($n = 171$), one absence point was randomly allocated in farmland within a 1000 m circular buffer, which equals the maximum distance a Corncrake call can be heard (Moga et al. 2010).

All analyses were implemented in the R-environment using the packages 'MASS', 'raster', 'rgdal', 'maptools' and 'spatstat' (R Development Core Team 2013). We modeled Corncrake presence/absence using a generalized linear mixed effects model (function glmmPQL from the 'MASS' package) with a binomial error distribution. The models included all human disturbance and environmental variables as explanatory variables (fixed effects), village as a random effect to account for nested experimental units, and an autocorrelation structure of order 1, implementing geographic coordinates to account for spatial autocorrelation (Dormann et al. 2007). The final minimum adequate model was obtained through stepwise backward selection ($p \leq 0.1$), because AIC is not implemented in glmmPQL. The model was internally validated using AUC based on a model calibrated on a randomly selected training dataset (70% of the data) and predictions to the remaining validation dataset (30% of the data). Validation was repeated 100 times and AUC values were averaged. We confirmed that variables were not correlated ($\varrho < 0.6$), log-transformed local woody vegetation cover and population density, square-root transformed distance to village, and standardized all variables to zero mean and unit variance, prior to modelling.

	Variable	Description and calculation	Data source
Human disturbance	Population density (people per km^2)	Human population density; calculated as the number of people per each village catchment area	
	Distance to village (m)	Distance to the closest village; calculated as the distance from each point to the edge of the nearest village	
Local scale (10 ha)	Woody vegetation cover (%)	Proportion of woody vegetation cover; calculated as the percent cover based on a supervised classifications of the panchromatic channels of SPOT 5 data	CNES 2007, Distribution Spot Image SA; resolution of 10 m
	Heterogeneity	Remotely sensed compositional heterogeneity; calculated as the standard deviation of the monochromatic channel of SPOT 5 data	CNES 2007, Distribution Spot Image SA; resolution of 2.5 m
	Topographic wetness index	Relative position in the landscape and hence potential soil wetness; calculated as a function of upslope catchment area to local slope	ASTER digital elevation model; resolution of 30 m
Context scale (100 ha)	Land cover diversity	Compositional heterogeneity of different land covers; calculated as the Simpson's diversity index of land cover	Corine Land Cover Digital map 2006
	Ruggedness (m)	Terrain ruggedness; calculated as the standard deviation of the altitude	ASTER digital elevation model; resolution of 30 m
Village catchment scale (18.2 km^2 ± 10.7 km^2)	Land cover diversity	Compositional heterogeneity of different land covers; calculated as the Simpson's diversity index of land cover	Corine Land Cover Digital map 2006
	Edge density (m ha^{-1})	Configurational heterogeneity of different land covers; calculated as the edge density of land cover in meters per hectare	Corine Land Cover Digital map 2006
	Arable land cover (%)	Proportion of arable land; calculated as the percent cover	Corine Land Cover Digital map 2006
	Ruggedness (m)	Terrain ruggedness; calculated as the standard deviation of the altitude	ASTER digital elevation model; resolution of 30 m

Table 3.1 Description and calculation of human disturbance variables and the environmental variables used to model Corncrake distribution. Environmental variables were calculated at three spatial scales. The data source for the environmental variables and units for variables with a unit are given.

Based on the model outlined above, we simulated how the distribution of suitable Corncrake habitat would change under hypothetical scenarios of land cover homogenization. This was implemented by a stepwise reduction of context land cover diversity and subsequently predicting suitable Corncrake habitat for each step. Notably, we only altered context land cover diversity, because of the modelled variables it is the variable most likely to change under land cover homogenization. Other variables that influenced Corncrake occurrence are either not influenced by land cover change (e.g. ruggedness), or would change in unpredictable ways (e.g. human population density). We reduced land cover diversity incrementally by values of 0.01 for a given pixel in a given step (original dataset: min = 0, max = 0.84). Pixels with a value of zero were not reduced further. After each homogenization step, we predicted the probability of suitable Corncrake habitat in farmland (grassland and arable land) of the whole study area using the fixed effects estimates from the above described Corncrake model. Finally, the predicted probabilities of occurrence were converted into presence/absence data using a probability threshold of 0.5 to define suitable Corncrake habitat.

Based on the results of this simulation, we calculated percent loss in land cover diversity as the proportion of land cover diversity in a given step relative to the current situation and standardized to 100%. Similarly, we calculated the remaining proportion of suitable Corncrake habitat based on the area of predicted suitable Corncrake habitat in a given simulation step relative to the total area of suitable Corncrake habitat in the region. To visualize the effects of reducing land cover diversity, we plotted percent loss of land cover diversity against the percent of available suitable Corncrake habitat. Additionally, land cover diversity and Corncrake suitable habitat were mapped, both for current conditions and for habitat losses of 33 % and 66 %, corresponding to the loss of a third or two thirds of the available suitable habitat, respectively.

Results

We found 114 Corncrake presences pooled over the two repeats, of which 71 were located in the Natura 2000 area (Fig. 3.1b). Corncrakes occurred most frequently in arable land (n = 36; 25 in Alfalfa fields, *Medicago sativa* subsp. *sativa*), marginal elements (n = 31; mostly reed (*Phragmites australis*)), and hay meadows (n = 25), followed by fallow land (n = 13) and pastures (n = 9).

Corncrake presence was predicted by human disturbance variables and by environmental variables at the local and context scales (Table 3.2). The Corncrake was more likely to occupy remote locations at large distances from villages, and village catchments with a low human population density. Moreover, the species was more likely to occur in areas with low terrain ruggedness and high land cover diversity at the context scale, and a high topographic wetness index at the local scale (Table 3.2; Fig. 3.1b). Model validation indicated a good overall model performance (AUC mean ± SD: 0.84 ± 0.04).

Table 3.2 Model coefficient estimates ± Standard Error (SE) of the final generalized linear mixed effects model obtained through backward selection (threshold of $p < 0.1$). '--' indicates variables not contained in the final model.

Scale	**Variable**	**Estimate ± SE**	***p***
	(Intercept)	-0.57 ± 0.37	0.13
Human disturbance	Population density	-0.77 ± 0.40	0.06
	Distance to village	0.35 ± 0.15	0.02
Local	Woody vegetation cover	--	--
	Heterogeneity	--	--
	Topographic wetness index	0.31 ± 0.14	0.03
Context	Land cover diversity	0.49 ± 0.18	<0.01
	Terrain ruggedness	-0.95 ± 0.20	<0.01
Village catchment	Land cover diversity	--	--
	Edge density	--	--
	Arable land cover	--	--
	Terrain ruggedness	--	--

The simulation of Corncrake distribution in response to landscape homogenization showed that the extent of predicted suitable Corncrake habitat decreased rapidly with a simulated loss of land cover diversity at the context scale. Notably, a substantial contraction of suitable Corncrake habitat was already apparent at relatively small reductions in land cover diversity (Fig. 3.2, 3.3). For example, an 11% overall decrease in current land cover diversity (based on the complete range of the variable standardized to 100%) resulted in a 33% loss of suitable Corncrake habitat (Fig. 3.3; middle row); and a 35% decrease in current land cover diversity resulted in a 66% loss of Corncrake habitat (Fig. 3.3; bottom row).

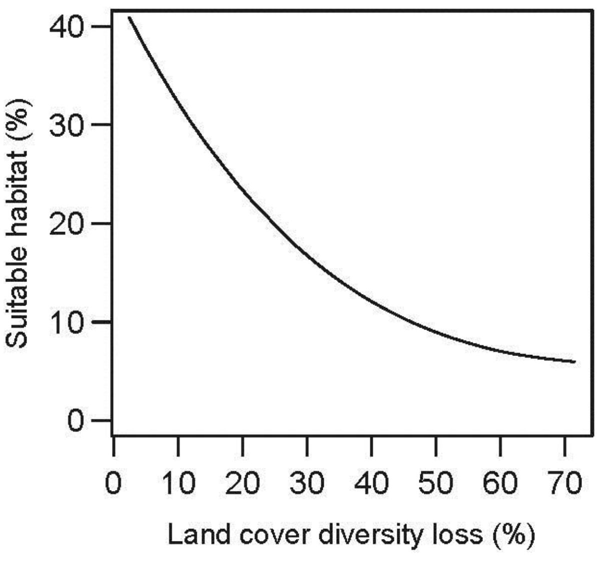

Figure 3.2 Predicted suitable Corncrake habitat as a function of land cover diversity loss within the context scale (100 ha). Land cover diversity loss was simulated through a step-wise reduction of current land cover diversity. Suitable Corncrake habitat was calculated as the remaining proportion of Corncrake habitat based on the area of predicted Corncrake habitat in a given simulation step relative to the total area of Corncrake habitat in the region.

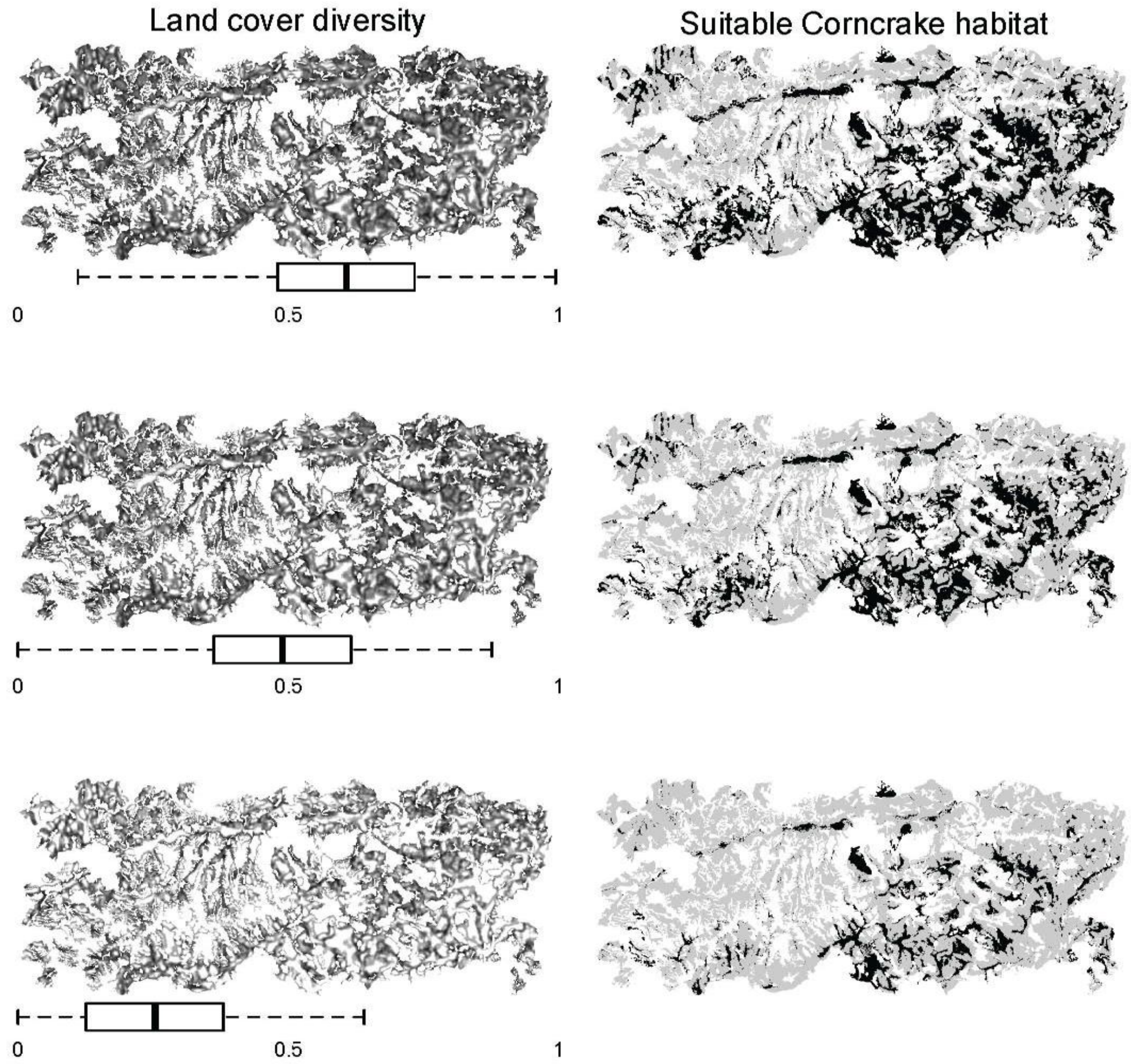

Figure 3.3 Predicted distribution of suitable Corncrake habitat under current and reduced land cover diversity in a 100 ha surrounding (resolution 27 m x 27 m). The left column shows changes in land cover diversity and the right column shows the predicted concurrent change in the distribution of suitable Corncrake habitat. The upper row represents the current situation. Thresholds for simulation of land cover diversity were selected to illustrate a habitat loss of 33% and 66% of the current habitat. These figures were chosen to exemplify the continuous pattern from Figure 3.2 and were purely based to show a third and two thirds of habitat lost. The middle row represents an 11% reduction in land cover diversity which reduces Corncrake habitat by 33%. The lower row represents a 35% reduction in land cover diversity which reduces Corncrake habitat by 66%. Land cover diversity varies from low (grey) to high (black) on a standardized scale between 0 and 1. The boxplot below each figure represents the distribution of land cover diversity for a given step. Suitable Corncrake habitat (black) was assumed by a predicted probability of Corncrake occurrence of 0.5 or higher.

Discussion

Our study adds to a growing body of knowledge on the effects of heterogeneity on farmland biodiversity, suggesting that the loss of heterogeneity, typically associated with land-use intensification, can negatively impact biodiversity (e.g. Stein et al. 2014). Furthermore, substantial losses of Corncrake habitat are likely to result from relatively small losses in land cover diversity, indicating a non-linear relationship between habitat loss and loss in land cover diversity. These findings have important implications for the management of heterogeneous farming landscapes. In Europe, the majority of studies on the effects of landscape homogenization on farmland biodiversity have been performed in countries with more intensively used farmland (Devictor & Jiguet 2007; Pickett & Siriwardena 2011), while more heterogeneous, low-intensity regions remain poorly understood (Baldi & Batary 2011; Tryjanowski et al. 2011). Our findings suggest that land cover homogenization in a traditional farming landscape could drastically reduce suitable habitat for farmland species such as the Corncrake. This underlines the need for conservation strategies that consider land cover diversity across entire landscape mosaics, and that are specifically geared towards traditional farmland supporting large populations of rare or threatened species.

Agricultural landscapes are increasingly recognized for their value for biodiversity conservation (Mendenhall et al. 2014). This is especially important for European landscapes, which reflect centuries of interactions between people and the natural environment (Bignal & McCracken 2000). Long-established traditional agriculture has created many of the habitats and niches for species valued for biodiversity today (Bignal & McCracken 2000). Nevertheless, traditional agricultural landscapes have declined dramatically over the last decades (Foley et al. 2005). The few remaining examples are under considerable threat from changes in agricultural management and their continued existence hinges on both national and international conservation policies (Henle et al. 2008).

Our study shows that land cover heterogeneity is a key feature to be addressed in conservation measures targeting traditional farmland. The positive effects of heterogeneity on biodiversity, including farmland birds, have been well-documented (e.g. Weibull et al. 2000; Benton et al. 2003; Diacon-Bolli et al. 2012; Stein et al. 2014). In particular, land cover diversity appears to positively affect bird richness and abundance in farmland (Sanderson et al. 2009; Pickett & Siriwardena 2011), suggesting that different land-use covers provide complementary resources, such as feeding, nesting, and sheltering sites. However, responses of farmland birds to heterogeneity are species-specific; especially ground nesting birds and open farmland specialists often prefer relatively homogenous landscapes (Filippi-Codaccioni et al. 2010; Fischer et al. 2011; Pickett & Siriwardena 2011; Guerrero et al. 2012). For such specialist species, management practices to increase heterogeneity may therefore reduce their populations, especially in low-intensity farmland (Batary et al. 2011b).

Also the Corncrake is a ground-nesting species in open farmland, and similar to other grassland species, it has been observed to occur in extensive areas of relatively homogenous, uncultivated meadows (Keišs 2005; Berg & Hiron 2012; Quinn et al. 2012). Nevertheless, a traditional farmland mosaic such as the one we studied evidently can provide important additional habitat for the Corncrake. Land cover homogenization at the context scale as consequence of intensification would have a substantial negative impact on the Corncrake in currently heterogeneous landscapes. To protect the Corncrake in traditional farmland, it is therefore important to ensure the persistence of mixed farming practices.

While the use of low-intensity grasslands and hay meadows by the Corncrake is well documented (Berg & Gustafson 2007; Budka & Osiejuk 2013), less is known about the complementary values of other land-use types to the species (but see e.g. Berg & Hiron 2012). For example, in a diverse land cover mosaic, uncropped arable land, and the high density of edges between different land covers (e.g. field margins or ditches) provide safe breeding or sheltering sites for the Corncrake (Green et al. 1997; Corbett & Hudson 2010; Budka & Osiejuk 2013). Such structures are especially important during the early breeding season when the height of surrounding spring-vegetation is short (Budka & Osiejuk 2013). In addition, field margins are often rich in invertebrates (Josefsson et al. 2013), and thus a higher abundance of field margins may increase food availability for the Corncrake.

Some studies have found that the Corncrake tends to avoid annually cropped arable fields (Keišs 2005; Berg & Hiron 2012; Budka & Osiejuk 2013). However, we found a considerable number of Corncrakes in arable fields, and in particular in Alfalfa fields. Corncrakes and other grassland species have also been observed in grass or clover fields used for silage and hay in other regions (Corbett & Hudson 2010; Berg & Hiron 2012; Quinn et al. 2012). Although this suggests that arable fields sown with grass or leguminous plants can provide important additional habitat for Corncrakes, care should be taken for appropriate management because hayed crops can create population sinks (Perlut et al. 2006). In contrast, pastures appeared to have little habitat value for the Corncrake, and similarly to other regions, the Corncrake was more likely to be present in hay meadows than pastures (Wettstein et al. 2001; Keišs 2005). The Corncrake may avoid grazed pastures for several reasons. For example, they are typically located on better drained, steeper slopes, whereas the Corncrake preferentially uses moist flat areas. In addition, the reduced vegetation height in pastures caused by grazing may reduce habitat suitability (Berg & Gustafson 2007).

Loss of hay meadows and the intensification of grassland management are currently viewed as the main threats to Corncrake populations (Koffijberg & Schäffer 2006). Therefore, current conservation strategies (including AES schemes) for the Corncrake relate primarily to the maintenance of hay meadows and low-intensity grasslands, with emphasis on specified mowing regimes (Koffijberg & Schäffer 2006; Berg & Gustafson 2007) and leaving unmown refuge strips (Tyler et al. 1998). These methods have been successful (Koffijberg & Schäffer 2006), and have also provided wider biodiversity benefits in countries with relatively intensive agriculture (Wilkinson et al. 2012). However, our results suggest that the implementation of grassland-focused strategies alone may not be sufficient for Corncrake conservation in Transylvania's traditional farmland. Moreover, at present, farmers in Transylvania mow their land in a way that creates a heterogeneous vegetation structure, including numerous unmown patches until late in the season. Delayed mowing regimes could potentially be counter-productive, because they may result in the synchronization of management and thus homogenization of vegetation height (Dahlström et al. 2013), which has negatively affected Corncrakes elsewhere (Brambilla & Pedrini 2013). Other specific CAP measures in Romania, such as sheep premium payments, also may pose a threat to the Corncrake. This is because such incentives may inadvertently encourage the conversion of hay meadows to pastures (Demeter & Kelemen 2012). These examples highlight the need to carefully adjust agri-environment schemes and other CAP measures to traditional farmland. Moreover, schemes particularly related to the Corncrake should primarily target core Corncrake habitat, such as remote, flat and wet areas, which are especially at risk of conversion to homogenous, intensified farmland.

Our findings thus underline that agri-environment management needs to be adapted to the context of the landscape (Batary et al. 2011a), and schemes designed for high-intensity landscapes cannot be readily transferred to traditional farmland (Sutcliffe et al. 2014). Given the affinity of the Corncrake with the heterogeneous farmland mosaic, there could be major benefits in agri-environment schemes specifically aiming at maintaining the heterogeneous character of low-intensity landscapes (Kleijn et al. 2011). Without pro-active policy measures to maintain land cover heterogeneity in traditional farmland, homogenization of the landscape will have negative effects on biodiversity in general, and on already threatened species such as the Corncrake in particular.

The successful implementation of measures that maintain land cover heterogeneity across entire landscapes will hinge on finding ways to coordinate actions across multiple farmers, rather than relying on local measures alone (McKenzie et al. 2013). Moreover, high heterogeneity in traditional farmland is tightly linked to the multi-functionality of semi-subsistence farm holdings of relatively small size (Tryjanowski et al. 2011). Thus, landscape-scale governance may be challenging because it depends on the involvement of many individual farmers (McKenzie et al. 2013). In traditional farmland, AESs could be used to support collaborations of specific target groups (Pe'er et al. 2014), such as small-scale farm holders which create the heterogeneous mosaic but are also particularly susceptible to selling land to large-scale farmers.

Conclusions

Our study showed that heterogeneous farmland has high complementary conservation value for the Corncrake, in addition to their core habitat of large areas of wet meadows. Furthermore, our simulations highlighted that in heterogeneous low-intensity farmland, conservation measures implemented on small scales by single farmers should be complemented with landscape-scale measures to maintain land cover heterogeneity. Although we highlighted the importance of landscape-scale conservation for a single protected species, a similar pattern appears to be emerging more generally (Merckx et al. 2009; Dallimer et al. 2010). More research is needed on the effectiveness of landscape-scale conservation in farmland; however, research should also focus on how conservation measures targeting whole landscapes rather than single farms can be implemented. This is especially important in traditional farming landscapes, many of which are complex but rapidly changing social-ecological systems that are threatened by land cover homogenization.

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Chapter IV

Chapter IV

Human-carnivore coexistence in a traditional rural landscape

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'There is no conservation without conservation.' – Luigi Boitani

Abstract

Facilitating human-carnivore coexistence is a major conservation concern in human-dominated landscapes worldwide. Useful insights could be gained by studying and understanding the dynamics of human carnivore-coexistence in landscapes in which carnivores and humans have coexisted for a long time. We used a two-pronged approach combining ecological and social data to study coexistence of the brown bear (*Ursus arctos*) and humans in Transylvania, Romania. First, we surveyed 554 km of walking transects to estimate activity via a bear sign index, namely the proportion of anthills disturbed by bears, and used spatially explicit predictive models to test which biophysical and anthropogenic variables influenced bear activity. Second, we interviewed 86 shepherds and 359 villagers and community representatives to assess conflicts with bears and attitudes of shepherds towards bears. Our interdisciplinary study showed that bears and humans coexisted relatively peacefully despite occasional conflicts. Coexistence appeared to be facilitated by: (1) the availability of large forest blocks that are connected to the source population of bears in the Carpathian Mountains; (2) the use of traditional livestock management to minimize damage from bears; and (3) some tolerance among shepherds to occasional conflict with bears. In contrast, bear activity was unrelated to human settlements, and compensation for livestock losses did not influence people's attitudes toward bears. Our study shows that coexistence of humans and carnivores is possible, even without direct economic incentives. A key challenge for settings with a discontinuous history of human-carnivore coexistence is to reinstate both practices and attitudes that facilitate coexistence.

Introduction

Facilitating coexistence between humans and carnivores is a conservation challenge worldwide (Woodroffe et al. 2005; Treves et al. 2006; Dickman et al. 2011), because carnivores have often been extirpated locally due to conflicts with humans (Breitenmoser 1998; Woodroffe 2000). Predators are important because they exert top-down control on ecosystem processes (Estes et al. 2011; Ripple et al. 2014), and provide emotional, recreational, and cultural benefits to society (Kellert et al. 1996). Due to increasing conservation efforts (Ray et al. 2005), some carnivore populations are growing again (Linnell et al. 2001; Enserink & Vogel 2006), but many continue to decline (Ripple et al. 2014). The two most frequently advocated strategies to counteract carnivore declines are: (i) to separate carnivores from settlements by establishing protected refuge areas (Karanth et al. 2010; Packer et al. 2013); and (ii) to promote human-carnivore coexistence in human-dominated landscapes through conflict mitigation programs (Woodroffe et al. 2005; Dickman et al. 2011).

Several studies have shown that humans and carnivores can coexist (Carter et al. 2012b; Schuette et al. 2013). However, coexistence is often hampered by human-carnivore conflicts, which can harm rural households especially (e.g. Holmern et al. 2007). Because many carnivores live in human-dominated landscapes, a key to their successful conservation is to better understand the dynamics of human-carnivore coexistence. To this end, one useful approach could be to learn from landscapes in which carnivores and humans have coexisted for a long time.

In Eastern Europe, large carnivores and humans have co-inhabited multiple-use landscapes for centuries. Romania sustains large, stable populations of the brown bear (*Ursus arctos*), wolf (*Canis lupus*) and lynx (*Lynx lynx*) (Salvatori et al. 2002), with the brown bear population being particularly large (estimated at 6000 individuals by the IUCN). Most of Romania's bears live in the Carpathian Mountains, but many also occur in the Transylvanian foothills of the Carpathian Mountains, which harbor hundreds of villages characterized by traditional semi-subsistence agriculture. This situation is exceptional because the majority of bear populations elsewhere in Europe are confined to remote mountainous areas – and where bears do range into human-dominated landscapes, they often damage livestock, orchards and beehives (Zedrosser et al. 2001). Thus, Transylvania offers an interesting model system that may help to facilitate greater understanding of the dynamics underpinning successful coexistence of humans and carnivores.

Gathering reliable data on carnivore distribution is notoriously difficult due to their elusive nature. Especially in Romania, long-term data is scarce, and the reliability of official data collected by hunting organizations may be questionable (Salvatori et al. 2002). Therefore, we used a new, sign-based metric, namely the proportion of anthills destroyed by bears relative to the total number of anthills in an area, being fully aware of the limitations of sign-based indicators (Barea-Azcon et al. 2007; Long et al. 2007). Although the proportion of destroyed anthills may be a less accurate sign than footprints or faeces, it offers the opportunity to survey large areas in a relatively short time, which we believe more than compensates the risks of potentially higher methodological uncertainty.

To understand long-term coexistence in multiple-use landscapes, both ecological and social variables are important (Treves & Karanth 2003; Treves et al. 2006; Carter et al. 2012a). Although the need for interdisciplinary work on human-wildlife coexistence has repeatedly been acknowledged (Redpath et al. 2012), few studies have combined ecological studies on habitat preferences of carnivores with social data on human-carnivore conflicts and tolerance levels towards carnivores (Glikman and Frank, 2011; but see Schuette et al. 2013). The overarching goal of our study was to assess how humans and bears coexist in Southern Transylvania. Our study had two specific objectives. First, we sought to understand spatial patterns of bear activity in response to anthropogenic variables, biophysical variables, as well as local connectivity between forest patches and regional connectivity to the Carpathian Mountains. Second, we examined the nature of human-bear conflicts in the region and related it to the spatial distribution of bear activity.

Methods

Study area and design

Our 7441 km^2 study area was located within a 50 km radius around the town of Sighisoara, in the foothills of the Carpathian Mountains in Southern Transylvania (Fig. 4.1a). Recently, one of the largest sets of non-mountainous EU protected Natura 2000 sites was established in this area (Fig. 4.1b). We selected transects inside and outside this protected area to provide data for the foundations of the brown bear management plan, and to provide reference data so the management plan can later be evaluated. A detailed description of the area is provided in Supplementary Material Text S4.1.

To quantify bear activity, we used the proportion of anthills destroyed by bears relative to the total number of anthills in each pasture transect. Destroyed anthills and other signs are rare in forests and therefore we walked transects on pasture adjacent to forest. Anthills are available on pastures across the entire landscape which allowed us to cover a large area in a standardized way. Ants form an important food source of protein for the brown bear (Dahle et al. 1998; Swenson et al. 1999). Ant larvae are particularly sought after by bears in spring and summer, and the incidence of destroyed anthills has been used in previous sign surveys for bear presence (Munro et al. 2006; Ciarniello et al. 2007). Anthills destroyed by bears are readily distinguishable from those destroyed by other animals (e.g. cattle) and humans because they have a characteristic 'crater' dug out of the top.

Our choice of transects was guided by three design considerations. First, we sought to obtain a broad overview of bear activity in the study area. We surveyed bear activity in 30 focal villages and their surrounding land, because villages have been identified as both ecologically and socially meaningful 'landscape' units (Angelstam et al. 2003). We delineated the area belonging to a given village 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, mean area ± SD: 20.5 ± 11.2 km^2). We randomly selected 30 villages from 448 villages in the study area, stratified to cover the full gradient in terrain ruggedness and to include Natura 2000 areas as well as unprotected areas (Fig. 4.1b). With few exceptions arising from logistical obstacles we surveyed four transects around each village (n = 113; described in detail below).

Second, we covered the focal conservation area (2675 km^2) in detail to inform the new management plan. We divided the Natura 2000 area into grid cells of 2 km x 2 km (n = 759). We surveyed one transect in each grid cell with more than 15% forest cover (n = 417), and we surveyed one transect per grid cell for 100 additional, randomly chosen cells with less than 15% forest cover. For these two considerations, all transects were chosen to cover the full gradient of available distances to the nearest village and amount of surrounding forest cover within a radius of 1500 m.

Third, to assess the connectivity from our study area to the assumed source population of brown bears in the Carpathian Mountains, we compared alternative cost-distance metrics to the mountains, so that the best cost-distance metric could be used in later analyses (see the section on variables used to model bear activity below). For this, we specifically surveyed 59 transects within 15-20 km from the mountains (Fig. 4.1b). These transects were chosen to cover a gradient from likely low cost to high cost by varying the sets of land cover types available between a given transect and the mountains.

All transects were walked once at the forest-pasture interface at approximately 10 m distance from the forest edge. Each transect was 800 m long and 6 m wide. All destroyed and undestroyed anthills within a transect were counted. We included both fresh (this year) and old (previous years but clearly visible) destroyed anthills. In total, we walked 692 transects (554 km) between April 28 and August 10, 2012. Three transects were excluded from analysis because they had no anthills. The mean number of anthills per transect was 139. All transects for the cost-distance analysis were surveyed in May and June, 2012.

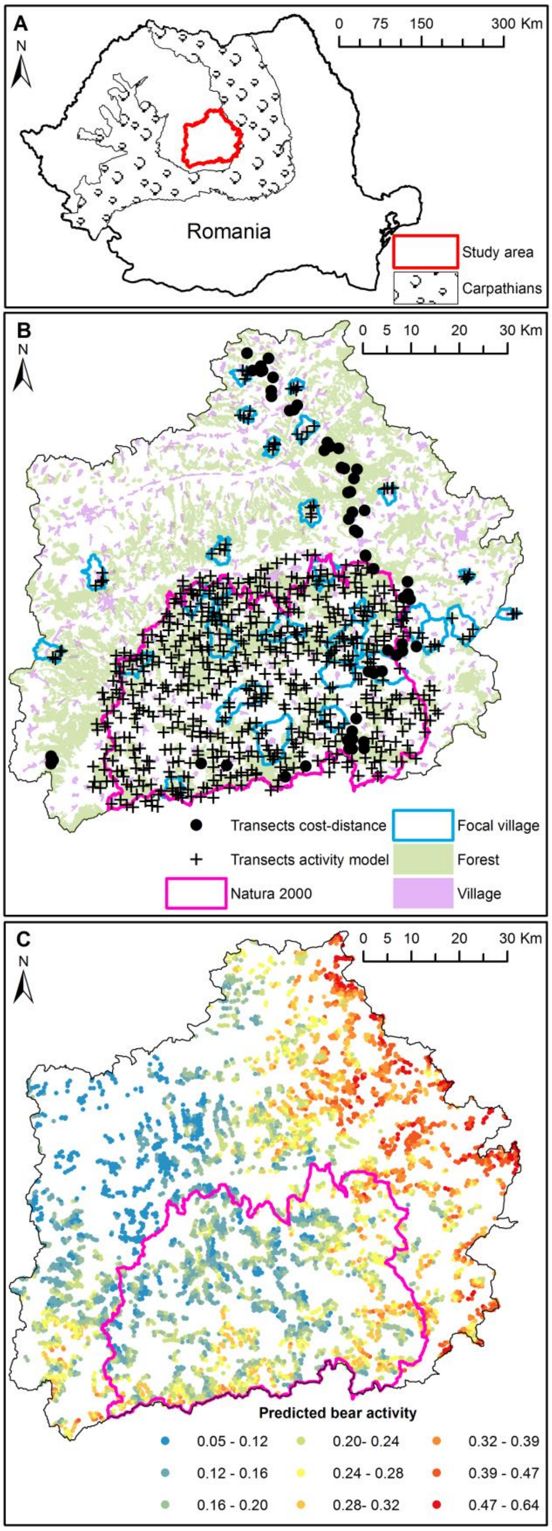

Figure 4.1 Study area, study design and predicted bear activity. (A) Study area in southern Transylvania, Romania, and location of the Carpathian Mountains used for the cost-distance analysis. (B) Close-up of the study area and study design and location of the transects used for the bear activity model (n = 630) and cost-distance analysis to the Carpathian Mountains (n = 59). The Natura 2000 area was surveyed for bear activity in detail. The study area was surveyed at a large scale for bear activity and human-bear conflict in 30 focal villages and their surrounding land. (C) Predicted bear activity in the study area, based on generalized linear modelling. Bear activity is indicated as the predicted proportion of destroyed relative to total number of anthills.

Variables used to model bear activity

We used four sets of variables to explain patterns in bear activity. First, anthropogenic disturbance was indicated by distance to settlements. Second, the biophysical environment within a radius of 1000 m from the midpoint of each transect was indicated by (i) terrain ruggedness calculated as the standard deviation of the altitude; (ii) percent pasture cover; and (iii) the shape and size of forest patches indicated by the forest edge to forest interior ratio. We did not include forest cover because it was correlated with forest edge to interior ratio (ϱ = - 0.71). Third, local connectivity between forest patches within the study area was indicated by betweenness centrality. Betweenness centrality is an index of how well connected a given forest patch is within the network of forest patches regardless of land-use between the different forest patches. Fourth, connectivity to the Carpathian Mountains (the presumed source population) was indicated by the cost-distance of each transect to the mountains. Cost-distance was based on a matrix with a resolution of 10 m x 10 m and combined distance to the mountains with weights between 1-10, assigned by experts to the different land-use types. Detailed descriptions of these variables are provided in Supplementary Material Text S4.1.

We accounted for possible effects of the total number of anthills per transect and survey date (bears might be more attracted to pastures with more anthills; and the number of destroyed anthills by definition accumulates with time) by including them as variables in the model. Because the effects of number of anthills and survey date were not necessarily linear, we included their quadratic terms (e.g. the number of destroyed anthills might level off before the end of the field season if bears shift to other food sources such as fruit). Protection level was not included in the models, because the recent establishment of the Natura 2000 area has not yet resulted in different natural resource use that could affect bear activity.

Statistical modelling

All analyses were performed with the proportion of destroyed vs. total number of anthills as the response variable within generalized linear models (GLM) with a quasi-binomial error structure to account for overdispersion. This model specification took into account that the precision of the response variable increased with an increasing total number of anthills found along a given transect (e.g. one destroyed anthill out of two total anthills is less precise information than 50 destroyed out of 100). The final GLM was obtained by using model averaging based on a 10-fold cross-validation (Fielding & Bell 1997). Validation was done by relating the predicted activity (based on a model using nine tenths of the data) with the activity observed in the remaining tenth via a binomial GLM (see Table S4.1 for the estimates and explained deviance for each of the validation steps). We calculated the amount of deviance explained as a measure of predictive performance of each of the ten models. We averaged the parameter estimates over the 10 models, weighting the estimates from each model by its predictive performance. The averaged estimates were used to predict bear activity in forest edges bordering pastures across the entire study area, at a resolution of 800 m, equalling the transect length of the field surveys. All statistical analysis were implemented in the 'R' environment (R Development Core Team 2013). Further details on statistical modelling and predictive mapping are provided in Supplementary Material Text S4.1.

Human-bear conflicts

Human-bear conflicts were assessed using questionnaires in the same 30 villages targeted for bear transects (Fig. 4.1b). We used a detailed questionnaire for shepherds that addressed attacks on livestock, attitudes towards bears, and the current compensation schedule; and a shorter one for villagers that addressed the types of damage caused by bears. To assess attitudes among different stakeholder groups relevant to coexistence dynamics, we used the same short questionnaire for mayors, hunters and local councillors. These groups are in charge of compensation payments after carnivore damage, and we therefore included several questions regarding compensation (questionnaires are available as Supplementary Material Text S4.2-4.4). We aimed to interview approximately three shepherds (on average a village had between one and four shepherds), ten villagers, one mayor and one hunter or councillor per village, but not everyone was available in all villages. Ultimately, we obtained questionnaires from 86 shepherds (73 sheep-herders, 13 cow-herders), 302 villagers, 22 mayors or vice-mayors, 20 local councillors and 15 hunters. (For ethical considerations see Supplementary Material Text S4.1.)

We expected a significant relationship between bear activity and perceived number of conflicts (e.g. higher bear activity could increase bear-related impacts), as well as livestock management (e.g. proactive measures prevent attacks by bears). To test for a possible relationship between bear activity and conflicts, we first averaged predicted bear activity within the land associated with each village. We then calculated Spearman rank correlations between average predicted bear activity and: (i) the mean number of bear attacks on sheep in the last three years; and (ii) perceived damage to orchards, crops and beehives. For the latter we used the proportion of local people who stated that bears caused damage to local orchards, crops or beehives. To assess whether certain herding techniques were more or less prone to attacks we used Spearman rank correlations between number of bear attacks on sheep and (i) the number of sheep in the herd; (ii) the number of sheep per guarding dog; (iii) total number of dogs, and (iv) the number of sheep per shepherd.

Results

Predictive model of bear activity

Bear activity was recorded in 52% of the 630 transects. Cost-distance to the Carpathian Mountains had the largest effect on bear activity (Table 4.1), which decreased with increasing cost-distance. Biophysical variables also were strongly related to bear activity (Table 4.1). Bear activity was highest in rugged terrain, near large forest patches with a low edge to interior ratio, and in areas with low pasture cover. The effects of distance to the village and local connectivity between forest patches were weak and not significant (Table 4.1; Table S4.1).

Table 4.1 Model-averaged coefficient estimates (weighted mean ± weighted SE) of the bear activity model. Ten separate models were initially calculated, and then a ten-fold cross-validation procedure was used. The ten models were largely consistent in terms of which variables were significantly related to the response.

		Number of times significant in the ten separate models	
Variable	**Estimate ± SE**	**$P < 0.05$**	**$P < 0.01$**
(Intercept)	-1.66 ± 0.099	10	10
Number of anthills	0.04 ± 0.113	0	0
Number of anthills^2	-0.29 ± 0.072	10	10
Time	0.58 ± 0.073	10	10
Time^2	-0.24 ± 0.069	10	9
Distance to village	0.02 ± 0.069	0	0
Ruggedness	0.17 ± 0.059	10	7
Pasture cover	-0.15 ± 0.069	8	3
Forest edge : forest area	-0.17 ± 0.065	10	5
Betweenness centrality	0.04 ±0.076	0	0
Cost-distance to Carpathian Mountains	-0.34 ±0.069	10	10

Predicted bear activity showed a gradient with proximity to the Carpathian Mountains but was otherwise relatively homogenous throughout the region (Fig. 4.1c). We found no obvious hotspots for bear activity inside the Natura 2000 area, but noted that predicted bear activity was particularly high just north-east of (i.e. outside) the focal Natura 2000 area.

Human-bear conflicts

Predicted bear activity did not correlate with the average number of bear attacks on sheep reported by shepherds (n = 73, *rho* = -0.1, p = 0.61). However, predicted bear activity was positively related to the damage perceived by local villagers to orchards (n = 302, *rho* = 0.61, p < 0.001) and fields (n = 302, *rho* = 0.5, p = 0.004), but not to beehives (n = 302, *rho* = 0.03, p = 0.86). All participants, except one, stated that bear attacks on humans happened rarely or never.

The median herd size of sheep was 500, the median number of sheep per dog (typically including one herding dog and several guarding dogs per herd) was 88, and the median number of sheep per shepherd was 400. Of 34 described attacks in 23 villages, 56% occurred at night, 79% in pastures, and 61% in shrubby places. In 69% of cases, less than three sheep were killed. Among the shepherds who had suffered attacks, there was no correlation between the number of attacks and the number of sheep per shepherd (*rho* = 0.13, p = 0.45), the number of sheep per dog (*rho* = 0.29, p = 0.11), the total number of dogs (*rho* = 0.18, p = 0.11), or the total number of sheep (*rho* = 0.34, p = 0.052). Many shepherds mentioned that having good dogs was the most important to avoid sheep predation (pers. comm.).

The majority of shepherds perceived bear populations to be increasing over the past decade, regardless of how many attacks they had suffered (Fig. 4.2a). However, shepherds who had suffered more bear attacks perceived more strongly that bear attacks had increased over the past decade (Fig. 4.2b). Despite these trends, approximately 50% of shepherds had neutral or positive feelings towards bears (Fig. 4.2c).The percentage of shepherds who strongly disliked bears was higher for shepherds who had suffered more attacks (Fig. 4.2c). Only six of 86 shepherds indicated that their feelings towards bears had changed over the past decade. Over 50% of shepherds did not support immediate killing of bears after attacks on livestock (indicated by 'no' and 'depends'). Shepherds who answered 'depends' supported the killing of a bear if livestock losses occurred repeatedly by the same bear. Support for immediate killing (indicated by 'yes') was slightly higher among shepherds who had suffered attacks than among those who had not (Fig. 4.2d).

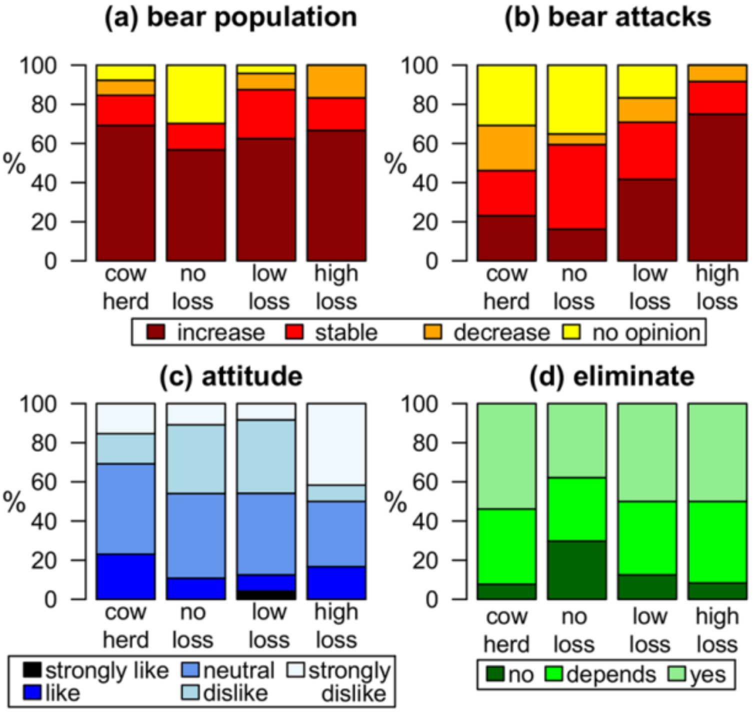

Figure 4.2 Perceptions of shepherds regarding the brown bear. (A) trend in bear populations over the last decade; (B) trend in attacks of bears on livestock over the last decade; (C) attitudes towards bears; and (D) immediate elimination of bears after attacks on livestock. Cow herd = cow herders; no loss = shepherd with no attacks by bears in the past three years; low loss = shepherd with fewer than ten attacks by bears in the past three years; high loss = shepherds with ten or more attacks by bears in the past three years.

Ninety-three percent of shepherds found compensation for damage to livestock important. However, 92% of shepherds agreed that compensation should be received only if appropriate measures were taken by herders to protect livestock from carnivores. Interestingly, 90% of shepherds were unaware of the (officially) existing compensation scheme. This finding, however, should be interpreted cautiously because two shepherds indicated they had tried to receive compensation, but were of the impression that no current compensation scheme was active. In stark contrast, 85% of mayors, hunters and local councillors thought the compensation scheme was readily accessible; but only 43% of mayors, hunter and councillors believed that the majority of the community was aware of the scheme.

Discussion

There is growing recognition of the need to conserve large carnivores outside protected areas (e.g. Athreya et al. 2013; Schuette et al. 2013), however, insights from human-dominated landscapes are still limited (e.g. Ghosal et al. 2013). Our approach drawing on both ecological and social data suggests an apparent balance between humans and bears in Southern Transylvania. The main factors contributing to this appeared to be: (i) the availability of large forest blocks connected to the presumed source population of bears in the Carpathian Mountains; (ii) the use of traditional livestock husbandry techniques to minimize damage from bears; and (iii) some tolerance among shepherds to occasional conflict with bears. Unlike elsewhere, avoidance of human settlements by bears (Posillico et al. 2004; Preatoni et al. 2005; Nellemann et al. 2007) and financial incentives (Maclennan et al. 2009; Banerjee et al. 2013) appeared to play negligible roles in facilitating human-bear coexistence.

Explaining coexistence

The Carpathian Mountains support the largest extant populations of the brown bear in Europe (Zedrosser et al. 2001). Consistent with this, the most important predictor of bear activity was proximity to the Carpathians. Higher bear activity was also found in rugged areas and near large blocks of forest, which is most likely related to better shelter and den sites in rough terrain, and potentially a wider variety of food resources (Nellemann et al. 2007; May et al. 2008; Güthlin et al. 2011). Local connectivity between forest patches, however, was unrelated to bear activity, suggesting that forest patches are well-connected throughout the region. Indeed, forest cover in our study area was close to the presumed 30% threshold below which the effects of habitat loss may be exacerbated by isolation effects (Andrén 1994). Alternatively, local connectivity may be related to shrub cover which was not accounted for in our analyses, and this may partly explain the lack of statistical significance of local connectivity. In contrast to other studies (Posillico et al. 2004; Preatoni et al. 2005; Nellemann et al. 2007), bears were not affected by distance to human settlements. This may be because, at present, vehicle traffic does not increase strongly near settlements, and major agricultural machinery is also relatively uncommon, although agricultural intensification is likely in the future (Mikulcak et al. 2013). In addition, human presence *per se* may not deter bears because local people are not a major threat, given that bears are protected by law and hunting is prohibited. Finally, retaliation killing is probably uncommon in the study area, though better knowledge on this would be useful to more fully understand human-bear coexistence.

Interestingly, observed bear activity was not related to the frequency of attacks on sheep, but was negatively related to perceived damage to orchards and fields. Unlike sheep, fields and orchards are often guarded less carefully and most lack (effective) fences, suggesting that the livestock husbandry techniques used by shepherds may effectively prevent bear attacks. The use of guarding dogs and nightly confinement appears to reduce livestock attacks worldwide (Gehring et al. 2010; Rigg et al. 2011). Indeed, most of the reported bear attacks occurred on the pasture, and not in the well-guarded sheepfolds. Similar to observations in the Romanian mountains (Mertens & Schneider 2005), we found no relationship between the frequency of bear attacks and the number of sheep per dog. This is surprising, given the shepherds' emphasis on the importance of good guarding dogs. The lack of a relationship between attacked and the number of dogs could arise from: (i) the use of an appropriately large number of dogs by the majority of shepherds; (ii) our sample size being too small to detect a significant relationship; or (iii) our model for bear activity only explaining bear distribution in spring and summer, while bear attacks occurred year-round.

The lack of a relationship between bear activity and frequency of attacks further suggests that local conditions may be more important than actual carnivore densities in determining rates of attack (Kaczensky 1999; Rigg et al. 2011). This supports the notion that human-carnivore coexistence is possible, but knowledge of local conditions is necessary for effective, proactive conflict management. In our case, relevant local conditions may include the quality of guarding dogs and vigilance of shepherds, but also the prevalence of woody vegetation in pastures. Because local conditions can, in principle, be managed, our findings indicate opportunities for proactive conflict mitigation.

Public attitudes towards carnivores are typically most positive in areas without carnivores (Kellert et al. 1996), or where people and carnivores have coexisted for a long time (Boitani 1995). The long-term coexistence of bears and shepherds may have led to the acceptance of occasional livestock loss by some shepherds, however, as observed elsewhere (Kaczensky et al. 2004), shepherds that were heavily affected by bears were also less tolerant to livestock loss. Tolerance could be further enhanced via compensation measures (Dickman et al. 2011) or the availability of lethal measures to local authorities to take care of occasional 'problem bears' (Lescureux & Linnell 2010). At present, coexistence was not artificially upheld by economic incentives, suggesting that in the absence of effective payment schemes, relatively cheap traditional, non-lethal methods can help facilitate coexistence. Thus, the key to successful human-bear coexistence could lie in limiting livestock losses to levels that are acceptable to a large proportion of the shepherd community, while also establishing an understanding between local authorities and people that authorities will increase efforts to prevent damage by bears. Developing such an understanding might be a difficult challenge in Romania, where trust between local people and authorities is low due to historical suppression, corruption and poverty (Hartel et al. 2014).

Local management priorities

To facilitate the ongoing coexistence of bears and humans in southern Transylvania, conservation measures should aim to maintain or improve: (i) connectivity between the foothills and the Carpathian Mountains; (ii) availability of large blocks forest; and (iii) acceptance of occasional losses to bears within the rural population. Maintaining regional connectivity and large forest blocks could be challenging because of increasing pressure on forests from illegal logging activities (Knorn et al. 2012), and because of new major highways planned to cut through the study area. Highways can negatively impact bear populations by causing habitat fragmentation and increasing the risk of collisions with vehicles (Kaczensky et al. 2003; Karamanlidis et al. 2012). Wildlife crossing structures could partly counteract these impacts, but research is needed to identify suitable locations for such structures (Clevenger & Waltho 2001). Furthermore, there is the danger that conservation efforts will focus on the protected Natura 2000 area, which does not extend all the way to the Carpathian Mountains, and does not capture all of the most important areas for the brown bear (Fig. 4.1c).

Compensation payments are often used to increase tolerance levels of people negatively affected by carnivores (Dickman et al. 2011). In Romania, damage caused by protected species should be compensated through the central public authority for environmental protection (law 407/2006). Yet, most shepherds indicated they found compensation payments important but did not know about the existence of the compensation scheme. Many officials dealing with compensation thought the scheme was still relatively unknown, but overall, despite a complicated application process (Mertens & Promberger 2001), they believed that the scheme was readily accessible. This suggests that the compensation payments need to be more transparent and accessible to local people. Importantly, monetary compensation is not the only plausible policy option. Proactive payments for preventive measures may be more successful in improving conditions for coexistence (Swenson & Andrén 2005), and subsidizing electric fences along forest edges and around sheepfolds could help reduce sheep predation. Moreover, given widespread mistrust in authorities, bottom-up compensation payments organized by local groups could be more effective. For example, contributions to a local livestock insurance program (Mishra et al. 2003) or replacements of lost livestock from a communal compensation herd may be worth considering.

Limitations

The proportion of destroyed anthills to total anthills turned out to be a low-cost and pragmatic, but evidently useful, index of bear activity. However, this metric has several limitations. First, bear use of anthills in a given pasture might be influenced by overall levels of anthill availability and by other pasture characteristics. Our large sample size and stratification of transects should minimize systematic biases caused by general pasture characteristics, and the availability of anthills was accounted for in the model. Therefore, we are confident that our indicator measured actual bear activity rather than bear exploitation of anthills. Second, ant larvae are a seasonal food source, and thus, other variables may explain bear distribution patterns in other seasons. The seasonal nature of our surveys could partly explain the lack of a correlation between bear activity and self-reported attacks of bears on sheep, which occurred year round. That said, we did find significant correlations between bear activity and perceived damage to orchards and fields, suggesting a certain level of cross-validation of methods – by definition, it is highly unlikely that a statistical significant correlation between our activity index and perceived damage would have arisen by chance if there was in fact no relationship between these two variables. Third, our data on damage caused by bears was based on the perceptions of shepherds and local people, and was not validated by official damage reports. Interview data therefore should be interpreted with care. While these limitations should be kept in mind, we do not believe they fundamentally undermine the validity of our overall findings.

Future research and conclusion

Although coexistence of humans and carnivores is a socially desired goal in many landscapes around the world, most research takes place in protected areas with few people (Ghosal et al. 2013). Our interdisciplinary approach demonstrated the usefulness of combining ecological and social data to highlight conservation priorities in carnivore conservation. Arguably, framing carnivore conservation in a social-ecological context would also be useful in other human-dominated landscapes.

Our study indicates that coexistence of humans and carnivores is possible, even without direct economic incentives. Continuous coexistence with large carnivores appears to foster the development of management tools and attitudes that effectively reduce conflicts. Nevertheless, this shared history of relationships between humans and bears has been eroded in many regions worldwide. Thus, a key challenge for settings with a broken history of human-carnivore co-occurrence is to reinstate both practices and attitudes that facilitate coexistence. While a history of continuous coexistence cannot be re-created in places where carnivores have been extirpated, it is noteworthy that in areas were carnivores are slowly re-colonizing landscapes, initially negative attitudes can become more neutral as people once again become accustomed to living with carnivores (Majić & Bath 2010).

Although our study indicates that coexistence is possible, the functional mechanisms facilitating this remain poorly understood. One recently discussed mechanism is that of behavioural adjustment on behalf of the carnivores, who may adjust temporal activity patterns (Martin et al. 2010; Carter et al. 2012b). Our study suggests that 'behavioural' mechanisms on behalf of people – that is, social mechanisms – also deserve more attention. Social mechanisms underpinning human-carnivore coexistence are acknowledged by several authors (e.g. Carter et al. 2012a; Athreya et al. 2013), but still remain poorly accounted for in many studies on human-carnivore conflicts, as well as in many mitigation programs (Dickman 2010; Glikman & Frank 2011). Future research should investigate the drivers of human attitudes towards carnivores, which may vary substantially in relation to the behaviour and ecology of the species in question, the prevalence of traditional ecological knowledge, dominant cultural values and beliefs, differences in social equity and distribution of carnivore impacts, and political context (Dickman 2010; Lescureux & Linnell 2010).

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Supplementary Material for Chapter IV

Text S4.1. Additional information on the study area and bear activity model.

Study area

The overall character of Transylvanian villages and the surrounding land has changed relatively little for decades (Wilkie 2001; Akeroyd & Page 2007). The on-going practice of low-intensity semi-subsistence farming has maintained exceptional levels of biodiversity (Cremene et al. 2005; Akeroyd & Page 2007). The study area had approximately equal amounts of the main land-use types forests (28%), pasture (24%), and arable land (37%), and altitudes ranged between 230 and 1100 m above sea level. Most forests are deciduous and dominated by hornbeam (*Carpinus betulus*), oak (*Quercus* sp.), and beech (*Fagus sylvatica*). Pastures occur on the slopes and are grazed by sheep (dominant livestock), goats and cattle. Forest edges usually abut pastures. Low-intensity small scale farming occupies the valleys. Recently, one of the largest sets of non-mountainous Natura 2000 sites in the EU has been established in the study area, including both Sites of Community Importance (SCI, Habitats Directive), and Special Protection Areas (SPA, Birds Directive; Fig. 4.1b).

Details on the variables used to model bear activity

Distance to the nearest settlement was measured as the distance from the midpoint of a given transect to the edge of the nearest village (min = 30 m, max = 4368.7 m, median = 1505.8 m) and was included because human activities often negatively affect bear presence (Nellemann et al. 2007; Fernández et al. 2012). We did not include the distance to roads nor human population density, because there are few big roads, and population density was relatively uniform across the region.

The biophysical variables were calculated within a radius of 1000 m from the midpoint of a given transect, which is slightly larger than the straight line daily distance travelled by brown bears in Croatia (Huber & Roth 1993). Variables included: (i) terrain ruggedness calculated as the standard deviation of the altitude (Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model Version 2 (GDEM V2)), because more rugged areas may offer more and better resting and sheltering sites (Naves et al. 2003); (ii) percent pasture cover as a general indicator of the extent to which the landscape was used for livestock grazing; and (iii) forest edge to forest interior ratio as an indication of the shapes and sizes of forest patches (patches with lower edge to interior ratios were both rounder and larger). We first calculated forest cover for the entire study area within a moving window with a radius of 1000 m. Second, we extracted all forest edges as polylines in ArcGIS, and converted them into pixels of 10 x 10 m to create a measure of forest-edge cover. Third, we used these two variables to calculate the forest edge to forest interior ration. Hence, no artificial forest edges were created by the circle itself. Forest and pasture variables were derived from the Corine Land Cover digital map 2006 (CLC). All variables were calculated and mapped for the entire study area with a resolution of 10 m x 10 m.

Due to the large home range of the brown bear (58 km^2 – 128 km^2; Huber & Roth 1993), habitat characteristics probably influence bear activity beyond a 1000 m radius. Therefore, we included a measure of local connectivity between forest patches, indicated by the betweenness centrality of the forest patch k that was closest to a given transect. Betweenness centrality is the sum of all shortest pathways between all pairs of patches that go through patch k: it measures how much patch k is involved in potential movements between other pairs of patches by serving as an intermediate stepping stone patch (Bodin & Saura 2010). Betweenness centrality was calculated with Conefor Sensinode 2.2 (Saura & Torne 2009), between the edges of individual forest patches using a dispersal distance of 2000 m (Huber & Roth 1993).

The presumed source population of brown bears resides in the Carpathian Mountains and thus proximity to the mountains is likely to affect bear activity. We used the cost-distance from the midpoint of a given transect to the mountains in our models, which we calculated using the cost-distance analysis tool in ArcGIS 10.0 at a resolution of 10 m x 10 m. Expert opinions are widely used in animal habitat suitability models and corridor analyses (e.g. Rathore et al. 2012), and therefore we asked two local bear experts in Romania to weight the different main land-use types of the Corine Land Cover Map 2006 on a scale from 1-10 with regard to their effects on bear movement (Table S4.2). Expert 1 has approximately 20 years of working experience with bears in Transylvania including basic research on bears, monitoring movement activities with radio-collars, conflict mitigation and non-invasive genetic monitoring. Expert 2 has approximately 10 years of working experience with bears in Transylvania including basic research on bears and conflict mitigation. Based on the weights provided by these experts, we developed two alternative cost surfaces for the cost-distance analysis in ArcGIS. To decide which cost-distance matrix performed best we compared three generalized linear models with a quasi-binomial error structure and the proportion of destroyed anthills as response variable. For this procedure, we used only those 59 transects at an approximately constant distance of 15-20 km from the Carpathians. The three different models included the same variables as the model used to predict bear activity; however, they differed in their cost-distance measures. Model 1 and 2 each reflected a cost-distance measure according to either of the experts, while model 3 did not include a cost-distance measure. In the latter case, we could have used 'raw distance' as an alternative (with no weightings for land cover types), but we did not deem this meaningful because raw distance to the mountains was held approximately constant during this calibration. The cost-distance measure associated with the model that explained most deviance was used in further analyses (Table S4.3).

Details on statistical modelling

Prior to modelling we log-transformed the number of anthills, distance to village, and forest edge to interior ratio; we confirmed that variables were not correlated (allowing only Pearson's $r < 0.5$); and we standardized all variables to zero mean and unit variance. We pooled transect data from the 30 villages with data from the Natura 2000 site. We used principal components analysis to confirm that the environmental variables spanned similar gradients in these two datasets to ensure they could be meaningfully combined.

All analyses were performed with the proportion of destroyed vs. total number of anthills as the response variable within generalized linear models (GLM) with a quasi-binomial error structure to account for overdispersion. We first included all data into a global model to check model assumptions and test for spatial autocorrelation. We found spatial autocorrelation in the first five bins using an increment of 4000 m, however, the correlation was low (first bin correlation = 0.13, $p < 0.001$). To correct for this (relatively mild) autocorrelation, we ran a mixed effects model (glmmPQL) with an exponential spatial correlation structure, using the R packages 'MASS'. Although the mixed model diminished spatial autocorrelation of the data, the model estimates were very similar to the estimates in the quasi-binomial GLM (Table S4.4). Therefore, we chose to present the modelling results from the simpler quasi-binomial generalized linear model, and also used it to predict bear activity for the whole study area.

The final GLM was obtained by using model averaging with a 10-fold cross-validation (Fielding & Bell 1997). This means we randomly divided our data into ten equally-sized groups, successively left out one tenth of the data to calibrate the models, and predicted and tested bear activity for the omitted tenth. Validation was done by relating the predicted activity (obtained from a model using nine tenths of the data) with the activity observed in the remaining tenth via a binomial GLM. We calculated the amount of deviance explained as a measure of predictive performance of each of the ten models. Finally, we averaged the parameter estimates over the 10 models, weighting each model by its predictive performance. The averaged parameter estimates then were used to predict bear activity. Table S4.1 shows the estimates and explained deviance used for each of the validation steps.

We predicted bear activity for all 800 m segments (n = 7536) of forest-pasture interface in the entire study area. We first extracted all forest-pasture interfaces as a polyline from the Corine Land Cover Map 2006 using ArcGIS 10.0. We divided all forest-pasture polylines into segments of 800 m, because this was equal to the length of our transects. Then we extracted the middle point from each segment. We used these points to extract the values for all variables used in the bear activity model to predict bear activity across the study area. To extract the variables we used the same maps (resolution 10 m x 10 m) we created for our bear activity model described above. The total number of anthills presumed to exist at any given forest edge was set to the mean observed, and time was set to the time when observed bear activity peaked. All statistical analysis were implemented in the 'R' environment (R Development Core Team 2013).

Ethical considerations for the interviews

Prior to all interviews, informed voluntary consent was obtained orally by all interviewees. Interviewees were provided with information about the research project before the interview. Interviewees had the opportunity to withdraw from interview at any time if they felt uncomfortable with the questions. The privacy of the interviewees was protected by keeping them anonymous. Data were not of a personal nature, and no interviewees expressed concerns.

Text S4.2. The questionnaire for the personal interviews with 86 shepherds (original in Romanian).

With this questionnaire we would like to learn more about the problems between people and bears and wolves.

Date: Village:
GPS point:

Please indicate how often you encounter:

	Never or very rarely	About once a year	Several times a year	About once a month	About once a week
Bears					
Wolves					

The following questions will ask about your experience with damage by bears and wolves

1. Have you ever lost livestock due to bears?
   a) yes b) no

2. How many times did bears attack your livestock in the last 3 years:

3. Have you ever lost livestock due to wolves?
   a) yes b) no

4. How many times did wolves attack your livestock in the last 3 years:

If you have ever suffered an attack by bears and/or wolves answer the following questions regarding the last attack for each species.

Bears

5. Date of the attack
   - Year:
   - Month:

6. Which livestock was present and approximately how many of each?
   - Sheep: present: a) yes b) no c) number:
   - Cows: present: a) yes b) no c) number:
   - Goat: present: a) yes b) no c) number:
   - Horse: present: a) yes b) no c) number:
   - Donkey: present: a) yes b) no c) number:

7. What were the losses?
   - Animal species 1:
   - Loss in numbers:

   - Animal species 2:
   - Loss in numbers:

   - Animal species 3:
   - Loss in numbers:

8. When did the attack happen? a) day b) night

9. Where did the attack happen?
   a) in the sheepfold c) in the forest
   b) on the pasture d) other, namely:

10. Did the attack happen in the location of this sheepfold?
    a) yes
    b) no, in another location, namely:

11. What did the surroundings look like?
    a) open landscape
    b) shrubby landscape
    c) other, namely:

12. How many shepherds were present?

13. What was the behavior of the shepherds present?

14. How many dogs were present?

15. What was the behavior of the dogs present?

16. Would you like to add anything else that could explain why the attack was successful or unsuccessful?

Wolves

17. Date of the attack
    - Year:
    - Month:

18. Which livestock was present and approximately how many of each?

Sheep:	present: a) yes	b) no	c) number:
Cows:	present: a) yes	b) no	c) number:
Goat:	present: a) yes	b) no	c) number:
Horse:	present: a) yes	b) no	c) number:
Donkey:	present: a) yes	b) no	c) number:

19. What were the losses?
    - Animal species 1:
    - Loss in numbers:

    - Animal species 2:
    - Loss in numbers:

    - Animal species 3:
    - Loss in numbers:

20. When did the attack happen? a) day b) night

21. Where did the attack happen?
c) in the sheepfold c) in the forest
d) on the pasture d) other, namely:

22. Did the attack happen in the location of this sheepfold?
b) yes b) no, in another location, namely:

23. What did the surrounding look like?
a) open landscape c) other, namely:
b) shrubby landscape

24. How many shepherds were present?

25. What was the behavior of the shepherds present?

26. How many dogs were present?

27. What was the behavior of the dogs present?

28. Would you like to add anything else that could explain why the attack was successful or unsuccessful?

This section will ask for your opinion about a list of statements on bears and wolves.
In your opinion:

29. Bear populations over the last 10 years have:
a) increased b) remained stable
c) decreased d) don't know

30. Wolf populations over the last 10 years have:
a) increased b) remained stable
c) decreased d) don't know

31. Sheep populations in my region over the last 10 years have:
a) increased b) remained stable
c) decreased d) don't know

32. Cow populations in my region over the last 10 years have:
a) increased b) remained stable
c) decreased d) don't know

33. Bear attacks on livestock over the last 10 years have:
    a) increased b) remained stable
    c) decreased d) don't know

34. Wolf attacks on livestock over the last 10 years have:
    a) increased b) remained stable
    c) decreased d) don't know

35. Which of the following describes your feeling towards bears?
    a) do not like at all b) do not like c) neutral
    d) I rather like e) I like very much

36. Has your attitude towards bears changed over the last 10 years? a) yes b) no

37. If yes, have you become a) more negative b) more positive

38. Why has your attitude changed?

39. Which of the following describes your feeling towards wolves?
    a) do not like at all b) do not like c) neutral
    d) I rather like e) I like very much

40. Has your attitude towards wolves changed over the last 10 years? a) yes b) no

41. If yes, have you become a) more negative b) more positive
42. Why has your attitude changed?

The following questions are about bear attacks on humans.

43. Bear attacks on humans happen:
    a) never b) rarely c) regularly d) very often

44. Bears only attack humans when they feel threatened by humans: a) yes b) no

45. I am afraid to be attacked by a bear: a) yes b) no

The following questions are about compensation schemes.

46. It is important to receive compensation for livestock losses:
    a) yes b) no

47. Compensation should only be paid when livestock is properly guarded, e.g. by dogs or fences
    a) yes b) no

48. Bears and wolves should be eliminated after damaging livestock:
    a) yes b) no

49. Compensation is currently being paid for livestock losses:
    a) yes b) no c) don't know

48. Have you ever asked for compensation for livestock losses: a) yes; b) no
    If yes:
    a. Was it easy to receive the compensation: a) yes b) no
    b. What did you need to do to receive compensation:

____
____
____
____
____

The following questions are about you.

48. Gender: a) M b) F

49. Age:______years

50. Ethnicity: a) Romanian b) Hungarian c) Roma d) Saxon e) Other, namely:

51. Which animals do you have in your camp and how many of each?
    - Sheep number:
    - Cows number:
    - Goat number:
    - Horse number:
    - Donkey number:
    - Dogs number:

Thank you very much for your participation!

Text S4.3. The questionnaire used for interviews with 302 local people, 15 hunters and 20 local councillors (original in Romanian).

With this questionnaire we would like to learn more about the problems between people and bears and wolves.

Date: Village:

The following questions will ask about your experience with damage by bears and wolves.

Please indicate how often you encounter:

	Never or very rarely	About once a year	Several times a year	About once a month	About once a week
Bears					
Wolves					

Please indicate if you agree or disagree.

1. My village suffers great damage to fields by bears? a) yes b) no

2. My village suffers great damage to orchards by bears? a) yes b) no

3. My village suffers great damage to beehives by bears? a) yes b) no

4. My village suffers great damage to livestock by bears? a) yes b) no

5. My village suffers great damage to livestock by wolves? a) yes b) no

The following questions are about bear attacks on humans.

6. Bear attacks on humans happen:
a) never b) rarely c) regularly d) very often

7. Bears only attack humans when they feel threatened by humans: a) yes b) no

8. I am afraid to be attacked by a bear: a) yes b) no

9. Do you have anything you would like to add regarding your opinion about bears or wolves?

____

____

____

____

The following questions are about compensation schemes and should only be filled in for *members of the local council* and *hunters.*

10. It is important that compensation is paid for livestock losses and/or damage to crops by wolves and bears
a) yes b) no c) don't know

11. In my village compensation for damage to livestock by bears and/or wolves is frequently requested
a) yes b) no c) don't know

12. In my village compensation for damage to crops by bears is often requested
a) yes b)no c) don't know

13. Most people in my village are aware of the existing compensation scheme for damage caused by bears and wolves
a) yes b)no c) don't know

14. Most applications for compensations are successful
a) yes b)no c) don't know

15. Could you briefly describe the steps that need to be taken to receive compensation for damage inflicted by bears and wolves?

____

____

____

____

16. Do you think the procedure you described is accessible to everybody?
a) yes b) no c) don't know

The following questions are about you.

17. Gender: a) M b) F

18. Age:______years

19. Profession

20. Ethnicity: a) Romanian b) Hungarian c) Roma d)Saxon e) Other, namely:

21. Do you have:

i)	Land with crops	a) yes	b) no
ii)	Orchards	a) yes	b) no
iii)	Beehives	a) yes	b) no
iv)	Livestock	a) yes	b) no

Thank you very much for your participation!

Text S4.4. The questionnaire used for interviews with 22 mayors or vice-mayors (original in Romanian).

Date: Commune:

In this questionnaire we would like to know about the problems between humans and bears/wolves in your commune.

The following questions are about damage caused by bears and wolves. Please indicate if you agree or disagree.

22. My commune suffers great damage to fields by bears? a) yes b) no

23. My commune suffers great damage to orchards by bears? a) yes b) no

24. My commune suffers great damage to beehives by bears? a) yes b) no

25. My commune suffers great damage to livestock by bears? a) yes b) no

26. My commune suffers great damage to livestock by wolves? a) yes b) no

27. Bear attacks on humans in my commune happen:
a) rarely b) regularly c) very often d) never

The following questions are about compensation schemes.

I. It is important that compensation is paid for livestock losses and/or damage to crops by wolves and bears
a) yes b) no c) don't know

II. In my village compensation for damage to livestock by bears and/or wolves is frequently requested
a) yes b) no c) don't know

III. In my village compensation for damage to crops by bears is often requested
a) yes b)no c) don't know

IV. Most people in my village are aware of the existing compensation scheme for damage caused by bears and wolves
a) yes b)no c) don't know

V. Most applications for compensations are successful
a) yes b)no c) don't know

VI. Could you briefly describe the steps that need to be taken to receive compensation for damage inflicted by bears and wolves :

VII. Do you think the procedure you described is accessible to everybody?
a) yes b) no c) don't know

VIII. Do you have anything you would like to add regerading your opinion about bears or wolves?

____

____

____

____

The following questions are about you.

8. Gender: a) M b) F
9. Age:______years
10. Ethnicity: a) Romanian b) Hungarian c) Roma d)Saxon e) Other, namely:

Thank you very much for your participation!

Table S4.1 Model coefficient estimates (± SE) of the ten models used in the 10-fold cross-validation and their explained deviance. An asterisk (*) indicates significant variables ($p < 0.05$). Explained deviance was calculated as the amount of deviance explained from a binomial GLM relating the modelled and observed bear activity.

Variable	**Model 1**	**Model 2**	**Model 3**	**Model 4**	**Model 5**
(Intercept)	-1.74 ± 0.101*	-1.68 ± 0.100*	-1.63 ± 0.100*	-1.72 ± 0.098*	-1.63 ± 0.101*
Number of anthills	0.04 ± 0.115	0.10 ± 0.118	0.01 ± 0.111	0.07 ± 0.113	0.02 ± 0.116
Number of anthills^2	-0.28 ±0.071*	-0.35 ± 0.078*	-0.25 ± 0.081*	-0.28 ± 0.069*	-0.29 ± 0.073*
Time	0.55 ± 0.071*	0.56 ± 0.071*	0.56 ± 0.071*	0.58 ± 0.071*	0.61 ± 0.077*
Time^2	-0.17 ± 0.069*	-0.23 ± 0.067*	-0.27 ± 0.069*	-0.23 ± 0.069*	-0.28 ± 0.072*
Distance to village	-0.02 ± 0.068	0.03 ± 0.070	0.06 ± 0.069	0.03 ± 0.069	0.02 ± 0.072
Ruggedness	0.15 ± 0.059*	0.21 ± 0.057*	0.18 ± 0.057*	0.16 ± 0.057*	0.19 ± 0.061*
Pasture cover	-0.14 ± 0.069*	-0.17 ± 0.070*	-0.20 ± 0.070*	-0.15 ± 0.068*	-0.15 ± 0.070*
Forest edge : forest	-0.18 ± 0.065*	-0.20 ± 0.064*	-0.15 ± 0.064*	-0.20 ± 0.066*	-0.16 ± 0.066*
Betweenness centrality	0.02 ± 0.076	0.08 ± 0.077	0.00 ± 0.078	0.03 ± 0.075	0.03 ± 0.077
Cost-distance to Carpathian Mountains	-0.29 ± 0.069*	-0.39 ± 0.070*	-0.38 ± 0.069*	-0.32 ± 0.070*	-0.34 ± 0.069*
Explained deviance	*0.35*	*0.12*	*0.19*	*0.24*	*0.27*

	Model 6	**Model 7**	**Model 8**	**Model 9**	**Model 10**
(Intercept)	-1.64 ± 0.100*	-1.61 ±0.093*	-1.62 ± 0.097*	-1.67 ± 0.100*	-1.65 ± 0.100*
Number of anthills	0.03 ± 0.112	0.03 ± 0.107	0.01 ± 0.110	0.09 ± 0.114	0.06 ± 0.115
Number of anthills^2	-0.30 ± 0.071*	-0.30 ± 0.067*	-0.28 ± 0.069*	-0.30 ± 0.071*	-0.29 ± 0.071*
Time	0.56 ± 0.073*	0.67 ± 0.073*	0.57 ± 0.071*	0.57 ± 0.073*	0.60 ± 0.075*
Time^2	-0.23 ± 0.070*	-0.32 ± 0.068*	-0.26 ± 0.068*	-0.24 ± 0.068*	-0.25 ± 0.070*
Distance to village	0.02 ± 0.070	-0.02 ± 0.068	0.07 ± 0.069	-0.01 ± 0.070	0.03 ± 0.070
Ruggedness	0.17 ± 0.060*	0.14 ± 0.057*	0.14 ± 0.058*	0.17 ± 0.057*	0.19 ± 0.059*
Pasture cover	-0.15 ± 0.068*	-0.18 ± 0.065*	-0.19 ± 0.070*	-0.13 ± 0.068	-0.12 ± 0.068
Forest edge : forest	-0.16 ± 0.066*	-0.16 ± 0.063*	-0.13 ± 0.065*	-0.20 ± 0.067*	-0.18 ± 0.065*
Betweenness centrality	0.06 ± 0.077	0.01 ± 0.074	0.06 ± 0.074	0.05 ± 0.074	0.05 ± 0.076
Cost-distance to Carpathian Mountains	-0.36 ± 0.069*	-0.39 ± 0.065*	-0.33 ± 0.068*	-0.35 ± 0.068*	-0.33 ± 0.071*
Explained deviance	*0.28*	*0.02*	*0.39*	*0.19*	*0.36*

Table S4.2 Weights assigned to different land-uses regarding bear movements by the two local bear experts. The weights spanned a gradient between 1 and 10, with 10 being difficult for bear movement and 1 being easy. The weights by Expert 1 were ultimately used in the activity model because they provided a better fit to the data (see Table S4.3).

Land cover type	**Expert 1**	**Expert 2**
Human settlement/industrial units	8	10
Agricultural land	3	8
Pasture	4	7
Forest	1	1
Woodland/scrubland	1	2
Major rivers	3	5
Orchards	2	4
Major roads	6	5

Table S4.3 Model coefficient estimates (± SE) of the three models used to choose the most appropriate cost-distance measure to be used in the main bear activity model. These models were constructed on the basis of the 59 transects located at 15-20 km from the Carpathians (see Figure 4.1a).

	Expert 1		**Expert 2**		**No cost-distance**	
Variable	**Estimate ± SE**	***p***	**Estimate ± SE**	***p***	**Estimate ± SE**	***p***
(Intercept)	-3.83 ± 0.846	<0.001	-2.88 ± 0.706	<0.001	-2.20 ± 0.491	<0.001
Number of anthills	-0.37 ± 0.274	0.184	-0.32 ± 0.282	0.267	-0.29 ± 0.283	0.317
Number of anthills^2	-0.13 ± 0.139	0.370	-0.08 ± 0.144	0.572	-0.09 ± 0.146	0.561
Time	0.89 ± 1.950	0.651	0.69 ± 1.989	0.729	0.30 ± 1.910	0.877
Time^2	1.30 ± 1.693	0.445	0.97 ± 1.704	0.571	0.41 ± 1.596	0.780
Distance to village	-0.33 ± 0.158	0.044	-0.28 ± 0.168	0.102	-0.22 ± 0.161	0.171
Ruggedness	-0.15 ± 0.227	0.502	-0.02 ± 0.243	0.918	0.21 ± 0.166	0.205
Pasture cover	0.16 ± 0.24	0.516	0.14 ± 0.253	0.582	0.09 ± 0.245	0.729
Forest edge : forest area	-0.31 ± 0.174	0.085	-0.36 ± 0.192	0.064	-0.29 ± 0.177	0.103
Betweenness centrality	0.15 ± 0.101	0.145	0.07 ± 0.124	0.581	0.17 ± 0.101	0.094
Cost-distance to Carpathian Mountains	-1.81 ± 0.764	0.022	-0.70 ± 0.512	0.175	- / -	- / -
Proportion of deviance explained by the model	0.33		0.28		0.25	

Table S4.4 Model coefficient estimates (± SE) of the global Generalized Linear Model (GLM) and the alternative Generalized Linear Mixed Model (GLMM) that included a correlation function to correct for spatial autocorrelation. Because parameter estimates were very similar, the simpler GLM was used as the final bear activity model.

	GLM		**GLMM**	
Variable	**Estimate ± SE**	***p***	**Estimate ± SE**	***p***
(Intercept)	-1.66 ± 0.09	<0.001	-1.71 ± 0.106	<0.001
Number of anthills	0.04 ± 0.11	0.675	0.02 ± 0.11	0.861
Number of anthills^2	-0.29 ± 0.068	<0.001	-0.26 ± 0.068	<0.001
Time	0.58 ± 0.069	<0.001	0.58 ± 0.074	<0.001
Time^2	-0.25 ± 0.065	<0.001	-0.26 ± 0.069	<0.001
Distance to village	0.02 ± 0.066	0.765	0.04 ± 0.072	0.536
Ruggedness	0.17 ± 0.055	0.002	0.15 ± 0.059	0.010
Pasture cover	-0.16 ± 0.065	0.016	-0.18 ± 0.069	0.010
Forest edge : forest area	-0.17 ± 0.062	0.006	-0.16 ± 0.066	0.017
Betweenness centrality	0.04 ± 0.072	0.580	0.07 ± 0.078	0.403
Cost-distance to Carpathian Mountains	-0.35 ± 0.065	<0.001	-0.38 ± 0.073	<0.001

Chapter V

Chapter V

Incorporating anthropogenic effects into trophic ecology: Predator-prey interactions in a human-dominated landscape

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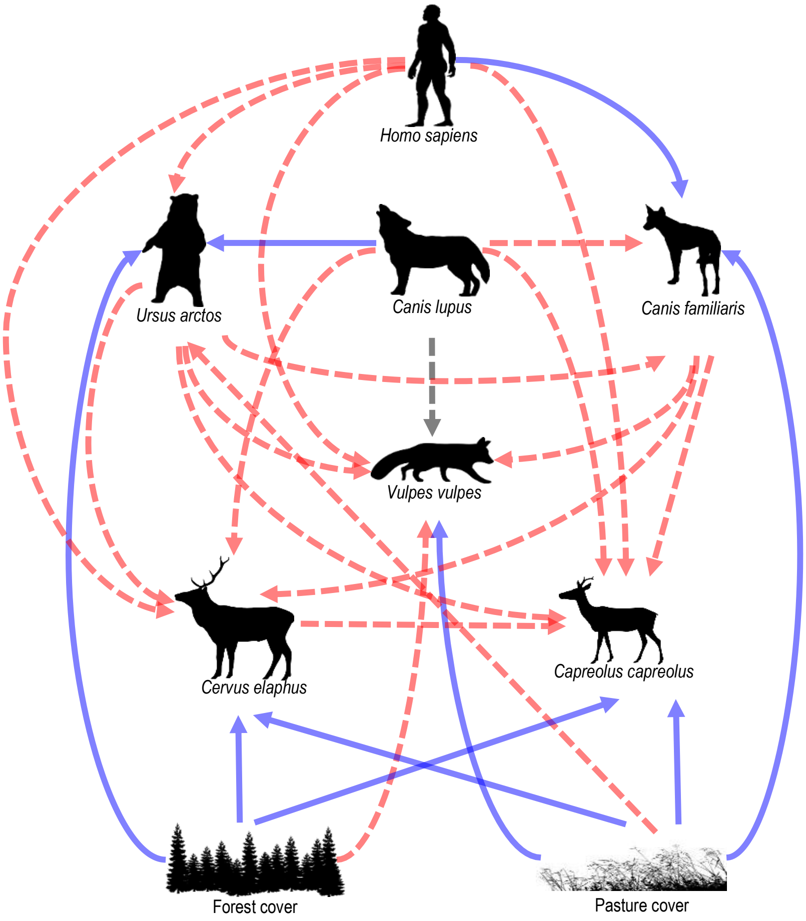

> *‘What escapes the eye…is a much more insidious kind of extinction: the extinction of ecological interactions.’*
> *–Daniel H. Janzen*

> *‘The last word in ignorance is the man who says of an animal or plant: 'What good is it?’ – Aldo Leopold*

Abstract

Apex predators perform important functions that regulate ecosystems worldwide. However, little is known about how ecosystem regulation by predators is influenced by human activities. In particular, how important are top-down effects of predators relative to direct and indirect human-mediated bottom-up and top-down processes? Combining data on species' encounter rates from camera traps and hunting records, we aimed to understand and quantify the relative effects of top-down and bottom-up processes in shaping predator and prey distributions in a human-dominated landscape in Transylvania, Romania. By global standards this system is diverse, including apex predators (brown bear and wolf), mesopredators (red fox) and large herbivores (roe and red deer). Furthermore, humans and free-ranging dogs represent additional predators in the system. Using structural equation modelling we found that apex predators maintained their ecological role by suppressing lower trophic levels, especially herbivores. However, direct and indirect human top-down effects at multiple trophic levels affected the ecosystem more strongly, influencing species at all trophic levels. Our study highlights the need to explicitly embed humans and their influences within trophic cascade theory. This will greatly expand our understanding of species interactions and ecosystem dynamics in human-modified landscapes, which compose the majority of Earth's terrestrial surface.

Introduction

There is increasing recognition of the critical role apex predators play in structuring ecosystems globally (Estes et al. 2011; Ripple et al. 2014). They do so by killing or instilling fear in competitors and prey (Creel & Christianson 2008; Ritchie & Johnson 2009), thereby inducing trophic cascades that flow through entire ecosystems (Letnic et al. 2009). Despite 40% of the Earth's terrestrial surface being dominated by agriculture (Foley et al. 2005) and human's effects permeating into more natural areas (Sanderson et al. 2002), most research on trophic cascades has focused on relatively intact wilderness and conservation reserves. However, top-down processes (i.e. the structuring of the ecosystem by high trophic levels) and bottom-up processes (i.e. control through productivity and low trophic levels) in largely pristine areas may differ substantially from those in human-dominated landscapes. Thus, a key question remains: what role do humans play in the trophic networks of modified ecosystems (Sergio et al. 2014)? Answering this question is important for a number of reasons. Firstly, many large carnivore populations exist outside protected areas and are embedded within human-dominated landscapes (Crooks et al. 2011; Carter et al. 2012b; Vanak et al. 2013). Secondly, there is increased focus on using large carnivores in the context of ecosystem restoration (Ritchie et al. 2012). And thirdly, in parts of the world such as Europe and North America, large carnivores are returning through active rewilding efforts and conservation initiatives (Enserink & Vogel 2006; Navarro & Pereira 2012; Morell 2013). Together this highlights the urgent need to better understand relationships between apex predators, people, and ecosystem components in human-dominated landscapes.

In terrestrial ecosystems, apex predators have been linked to two major trophic cascades. First, apex predators limit herbivores through direct predation and behaviourally mediated changes in habitat use, thereby promoting vegetation growth (i.e. tri-trophic cascades; Beschta & Ripple 2009; Ripple & Beschta 2012b; Kuijper et al. 2013). Second, apex predators limit smaller predators through interference competition, including in its most extreme form, intraguild predation (Polis & Holt 1992; Palomares & Caro 1999; Brook et al. 2012). Mesopredator suppression by apex predators can thereby increase the abundance of small mammals and birds (i.e. mesopredator cascades; Crooks & Soulé 1999; Ritchie & Johnson 2009). Such cascading effects could differ in human-dominated landscapes in at least two main ways. For example, humans influence species abundances through bottom up processes such as land-use, agriculture, and forestry, which may translate into a wide range of changes in ecosystem properties and functions (Foley et al. 2005), including ecosystem productivity (Haberl et al. 2007), or food and habitat availability (Muhly et al. 2013). Such changes in productivity can significantly modify predator-prey relationships (i.e., the Ecosystem Exploitation Hypothesis; Oksanen & Oksanen 2000). Also, humans directly (e.g. harvesting of both predators and prey; Barnosky et al. 2004) or indirectly (e.g. by creating an anthropogenic landscape of fear; Ordiz et al. 2013) affect top-down processes and it remains unclear if apex predators can achieve high enough densities outside wilderness areas and protected areas to be 'ecologically effective' (Soulé et al. 2003; Letnic et al. 2012; Mech 2012; Ordiz et al. 2013). These latter effects in particular have been overlooked in literature on trophic cascades.

Useful insights into the role of humans could be gained by studying ecosystems in which both humans and carnivores have coexisted for extended periods. Traditional farming regions in Romania form an ideal system in this respect. The forests surrounding the villages cover a third of the area and are well-connected (Dorresteijn et al. 2014). The heterogeneous landscape harbors cervid herbivore and mesopredator populations, but also relatively high densities of brown bears (*Ursus arctos*) and lower densities of the grey wolf (*Canis lupus*). The use of free-ranging large-bodied livestock guard dogs (*Canis familiaris*) to protect livestock against carnivores adds a third non-human, predator to the system.

Wolves are the most important cervid predator in the Northern Hemisphere (Peterson et al. 2003), and are involved in both tri-trophic and mesopredator cascades (Berger et al. 2008; Ripple & Beschta 2012b). Bears are omnivorous and may not be able to limit herbivore populations alone (Ripple & Beschta 2012a), and their effects on mesopredators remain unclear. However, bears can limit cervid densities in combination with wolves, and their predation on cervid calves may affect the recruitment of juveniles (Berger et al. 2001; Barber-Meyer et al. 2008; Ripple & Beschta 2012a). Dogs are the most common predator of wildlife worldwide (Ritchie et al. 2014); nevertheless, their effects on structuring ecosystems remain largely unknown (Hughes & Macdonald 2013; Lescureux & Linnell 2014).

Here, we aimed to understand (1) the relative top-down effects of apex predators on mesopredators and herbivores relative to the indirect effects of humans via their land-use; and (2) the direct and indirect effects of human presence throughout the landscape on the interactions between apex predators, mesopredators, and herbivores. We tested specific *a priori* expectations within a conceptual framework using piecewise structural equation modelling as outlined below.

Methods

Study area and design

Our study area covered 4900 km^2 in the foothills of the Carpathian Mountains in Southern Transylvania, Romania (Fig. 5.1). The region contains 28% forest, 24% pasture, and 37% arable land. The remaining land cover included villages, water bodies, and permanent crops. Forests are dominated by hornbeam (*Carpinus betulus*), oak (*Quercus* sp.), and beech (*Fagus sylvatica*). Pastures occupy the hills and are grazed by sheep (dominant livestock), goats and cattle, which are guarded by shepherds and guard dogs. Small semi-subsistence farming villages of up to several hundred inhabitants are scattered throughout the study area (Fig. 5.1).

We surveyed wild mammal, human, and dog presence in forests using remote, heat and motion, passive infra-red Bushnell Trophy Cam HD Max cameras between May and August 2013. Camera locations were selected according to two considerations. First, we divided the study area into grid cells of 5 km x 5 km, and excluded all grid cells with less than 20% forest cover (n = 120).

We placed one camera in the middle of each grid cell or in the nearest forest patch if no forest was present there (Fig. 5.1). Cameras were rotated in 4 consecutive rounds with grid-cells randomly allocated to each round. Second, an additional set of cameras in round 3 and 4 were placed within 24 out of 35 hunting blocks with known lowest and highest wolf densities (n = 59, for hunting blocks see below; Fig. 5.1). Camera locations were chosen randomly but in proportion to forest cover within each block (one camera per 5-7 km² forest). For both designs, cameras were spaced with a minimum distance of 1.5 km to minimize spatial autocorrelation.

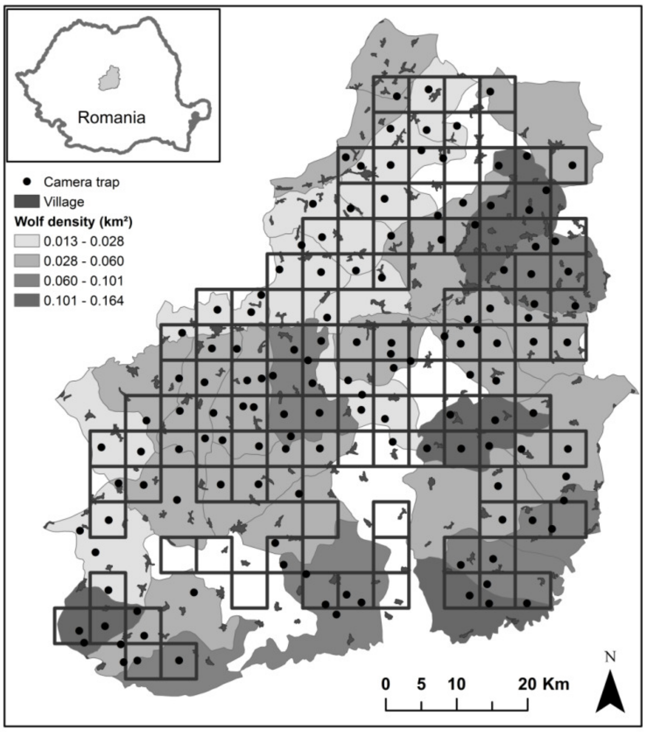

Figure 5.1 Study area in Southern Transylvania, Romania, camera trap locations, and wolf densities (km²) for each hunting block. The white areas indicate hunting blocks for which no data was available.

We used a total of 179 camera locations, with individual cameras operating between 15 and 29 days. However, only 138 locations were used for modelling because we excluded all cameras that operated for less than 20 days (n = 28; Hamel et al. 2012) or were located in hunting blocks for which no predator density data could be obtained (n = 12). In addition, seven cameras were stolen and one camera recorded 26 bear presences and was removed as a statistical outlier.

To increase the chance of predator detection, we placed cameras alongside animal and human paths, and used a lure of honey and wolf urine to attract bears and wolves, respectively. Lures were deployed at 75% of the locations (selected randomly), while the other 25% served as controls to assess whether wolf urine deterred herbivores. Since the presence of lures did not affect species occurrence of predator and prey (Fig. S5.1), we did not consider lures in further analyses.

Variables used for modelling

We modelled the occurrence of five species in relation to top-down and bottom-up variables: bears and dogs (apex predators), foxes (mesopredator; *Vulpes vulpes*), and red and roe deer (herbivores; *Cervus elaphus* and *Capreolus capreolus*, respectively). Species occurrence was derived from data collected by the cameras, and calculated as a cumulative abundance index or encounter rate by summing all individuals for each species at each camera location, and corrected for camera days during modelling (see below). Due to insufficient wolf records (two presences), wolves were not included as a response variable.

Explanatory variables included (i) top-down variables which were represented by apex predators (wolves, bears, dogs) and humans; and (ii) bottom-up variables which were represented by land-use variables (forest and pasture cover). Bear and dog variables were calculated from the camera data as the number of presences per camera day. Because of insufficient wolf records and surprisingly little spatial variation in bear presences across camera locations, we obtained additional information on large-scale wolf and bear densities within the 35 hunting blocks from 2010 (http://www.mmediu.ro/paduri/vanatoare.htm-accessed 01.02.2014). Although absolute densities are most likely overestimated (Salvatori et al. 2002), this data provided a useful general indicator for regional-scale differences in predator pressure. Notably, reported predator densities had been largely stable between 2006 and 2010 (Supplementary Material Fig. S5.2, S5.3), suggesting that the 2010 data was likely to be indicative of bear and wolf densities, despite not being from the same year as our camera data. The local density of humans near camera traps was calculated as the number of presences per camera day. As an additional approximation of human pressure, we also calculated the total number of people within the three nearest villages to each camera location. For bears, we used *either* reported hunting block bear density *or* bear encounter rate from the camera as an explanatory variable, and for humans, nearby village population size *or* human encounter rate from the camera. The choice between these two variables was based on which provided the better fit for a given response variable, based on Akaike information criterion, AIC (i.e. lower AIC values). Pasture cover (range 0 - 50%; median: 13%) and forest cover (range 15 - 100%; median: 59.5%) were derived from the Corine Land Cover map (2006) within a radius of 1000 m around camera locations. Forest cover also indicated fragmentation because it was highly correlated with the forest edge to area ratio (ϱ = -0.83).

Modelling

We used piecewise structural equation modelling (SEM) to model the importance of top-down and bottom-up effects for the five target species. SEMs are used to analyse both direct and indirect relationships in ecosystem processes, where *a priori* knowledge of relationships between components is available (Grace 2006). In contrast to classical SEM, a piecewise approach does not calculate global estimates for the entire network of relationships, but calculates local estimates for each 'node' or response variable (Grace et al. 2012). This approach has been applied in recent studies of trophic cascades (Pasanen-Mortensen et al. 2013; Colman et al. 2014).

First, generalized linear mixed-effect models with a Poisson error distribution were built for each species. Depending on the species, fixed effects included human variables, natural predators and competitors, and bottom-up variables (see *Model description*). All fixed variables were scaled, and log-transformed where transformation led to a better explanation of the response variable (based on Akaike information criterion, AIC). Random effects included hunting block, study round, and – in cases of overdispersion (i.e. $\varphi > 1.5$) – individual site identity (Elston et al. 2001). We included camera days as an offset in all models to account for differences in exposure time for response variables.

Next, we performed model averaging across the set of models with all possible combinations of fixed variables. We calculated averaged parameter estimates, averaged standard errors, and the relative importance of explanatory variables (i.e. the sum of AIC weights over all models including the explanatory variable) on the subset of models within dAIC<4 of the best model. We also calculated marginal R^2 for the full model to assess the explained variance of the fixed factors (Nakagawa & Schielzeth 2013). Finally, composite graphs of all local estimates were generated to visualize the relative importance of relationships between ecosystem components. All statistical analyses were performed in R using the packages lme4 and MuMIn (R Core Team 2013).

Model description

The pathways between top-down and bottom-up variables were determined by *a priori* knowledge on trophic cascade theory and included the following assumptions (Fig. 5.2). Apex predators (brown bear, wolf, dog) were assumed to potentially limit the main mesopredator, the red fox, through interference competition or intraguild predation (Elmhagen & Rushton 2007; Ritchie & Johnson 2009), as well as to limit red deer and roe deer through direct predation (Peterson et al. 2003; Ripple & Beschta 2012a). Bottom-up factors were assumed to be strong for the brown bear with an expected positive effect of forest cover and a negative effect of pasture cover (Dorresteijn et al. 2014). We did not assume a relationship between dogs and forest cover, but expected a strong positive link with pasture cover because dogs are commonly used for shepherding in our study area. We assumed bottom-up factors would play a role in mesopredator and herbivore encounter rate, but that top-down would be stronger than bottom-up effects as expected for productive ecosystems (Ecosystem Exploitation Hyoptthesis; Oksanen & Oksanen 2000). We expected the fox encounter rate to be negatively affected by forest cover and positively affected by pasture cover since this species prefers fragmented and open farmland (Kurki et al. 1998; Panek & Bresiński 2002). Herbivores were expected to be positively affected by both forest and pasture cover (Godvik et al. 2009; Morellet et al. 2011). We assumed that there would be no intraguild competition between wolves and bears due to different diets, but that wolves would positively affect bear encounter rate through increasing carrion (Wilmers et al. 2003). In contrast, we assumed that wolves and bears potentially limit dog encounter rate through interference competition. In addition, we expected that roe deer would be limited by red deer through interspecific competition (Torres et al. 2012).

Humans were expected to limit all other species, except dogs, through habitat modification and disturbance (including instilling fear), or direct killing by hunting or poaching. Humans were expected to indirectly limit red fox and herbivore encounter rate through their positive effects on dogs. We did not include a link between humans and wolves because of too few camera records of wolves. We did not attempt to explain wolf or bear densities obtained for hunting blocks, because these were at a much larger scale than species encounter rates obtained from cameras or human population size in nearby villages.

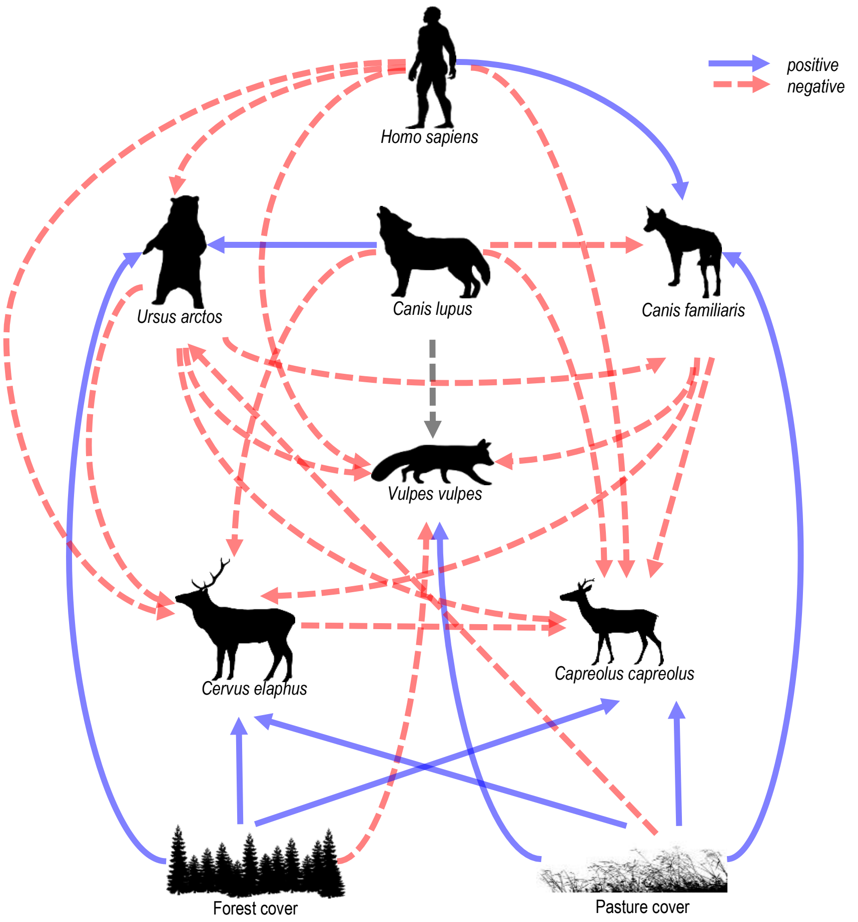

Figure 5.2 *A priori* piecewise structural equation model describing hypothesized predator-prey interactions in a human-dominated rural landscape. Positive links are indicated by solid blue lines and negative links are indicated by dashed red lines.

Results

Across 3042 camera days at 138 locations we obtained 2197 detections of roe deer, 388 of red foxes, 275 of humans, 120 of dogs, 94 of red deer, 76 of bears, and 2 of wolves.

Top-down and bottom-up effects on species encounter rates

In accordance with our *a priori* SEM, wolves and bears had a negative effect on foxes (Fig. 5.3a). Bottom-up effects were similar in strength as top-down effects on fox encounter rates with the strongest negative effect found for forest cover (Fig. 5.3a). Nevertheless, both top-down and bottom-up effects were fairly weak with standard errors indicating a high degree of uncertainty, and explained less variance as compared to all other species (Fig. 5.3a). Positive bottom-up effects of forest cover and negative effects of pasture cover were strong determinants of bear encounter rates (Fig. 5.3a). Within the apex predator guild, bears were negatively related to wolves (Fig. 5.3a).

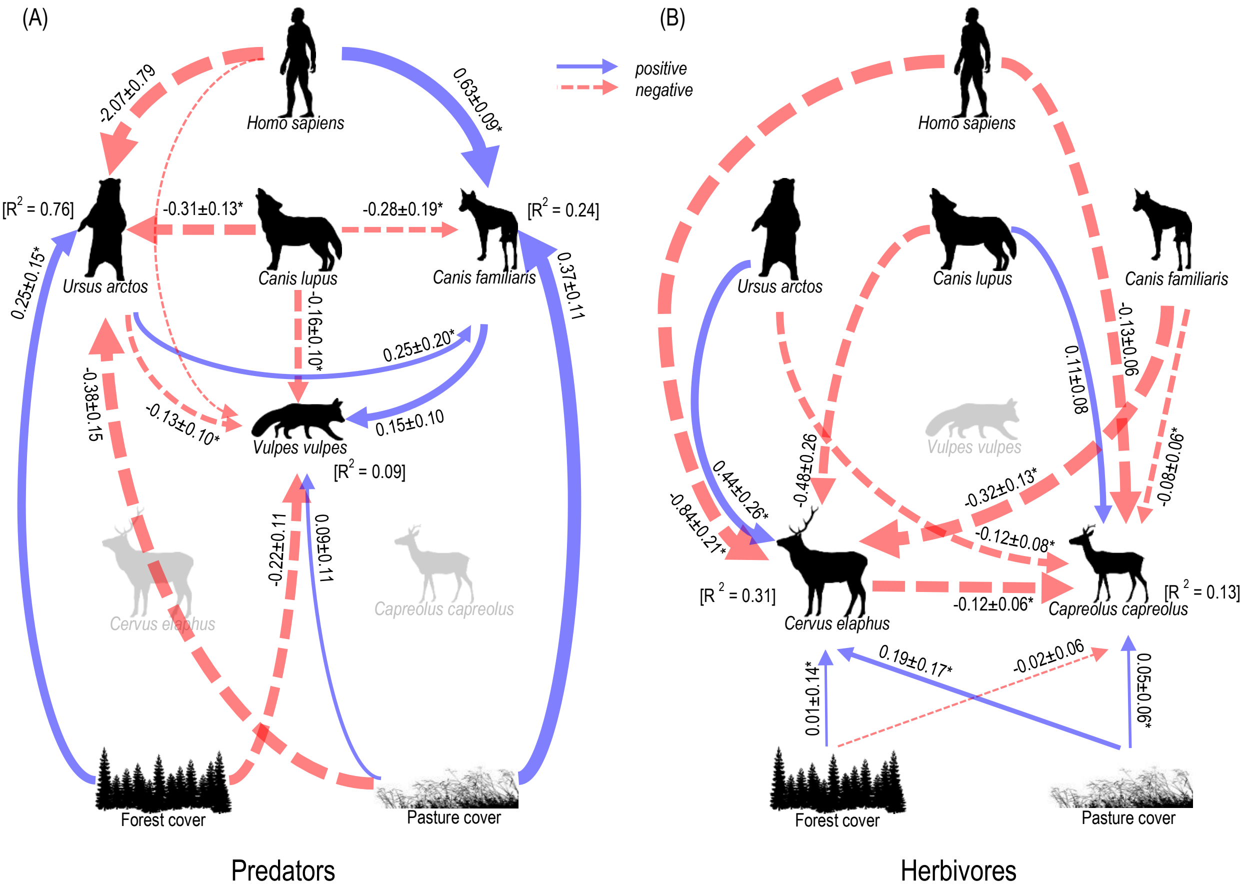

Figure 5.3 Final structural equation models showing top-down and bottom-up pathways for encounter rates of (A) predators, and (B) herbivores. Co-efficient estimates and standard errors are presented for each interaction and marginal R^2 are given for all response variables (i.e. brown bear, domestic dog, red fox, red deer, and roe deer). The line thickness of the arrows refers to the Akaike weights and can therefore only be compared within a species and not between species. Positive links are indicated by solid lines and negative links are indicated by dashed lines. The * indicates log-transformed variables

For herbivores, we also found a negative effect of wolves on red deer and of bears on roe deer. In contrast, a positive effect was found for wolves on roe deer and bears on red deer (Fig. 5.3b). Bottom-up effects were positive (except for forest cover on roe deer) and very weak with a larger degree of uncertainty compared to top-down effects for both red deer and roe deer (Fig. 5.3b). For example, the negative coefficient indicating the effect of wolves on red deer was 2.6 times larger than the positive coefficients of pasture cover. Roe deer appeared further limited through competition with red deer with its coefficient similar to the coefficients of top-down predator effects (Fig. 5.3b).

Top-down control by humans and their dogs

As predicted, humans limited all other species (Fig. 5.3a, b). While the effect was negligible for foxes, human top-down control on bears, dogs, and herbivores was relatively strong (Fig. 5.3a, b). For example, the coefficient describing the effect of humans on bears was 5.6 to 8.3 times larger than the coefficients of the bottom-up effects. Human effects on red deer and roe deer were also larger than top-down predator effects (red deer coefficients were 1.7 - 2.5 times larger; roe deer coefficients were 1.1 - 1.6 times larger) and much larger than the very weak bottom-up effects.

Additionally, humans had significant indirect effects on species' encounter rates due to a strong positive effect on dogs and their subsequent flow-on effects (Fig. 5.3a). The top-down limiting effect of dogs on red deer and roe deer was only slightly weaker than that of natural predators but stronger than bottom-up processes (Fig. 5.3b). In contrast, dogs were positively correlated with fox encounter rates; however, the SEM showed a negative effect of wolves on both dogs and foxes (Fig. 5.3a). All model selection tables are available in Supplementary Material Tables S5.1- S5.5

Discussion

Despite growing interest in using apex predators for ecological restoration (Ritchie et al. 2012), and although agriculture covers 40% of the world's ice-free land surface (Foley et al. 2005), few studies have examined and quantified the ecological role of apex predators in human-dominated landscapes. Our study addressed (1) the relative contributions of top-down limitation by apex predators and (2) direct and indirect human bottom-up and top-down processes on mesopredator and herbivore encounter rates in a multiple-predator, human-dominated landscape. In accordance with trophic cascade theory, apex predators appeared to be important in structuring the ecosystem, particularly through the suppression of herbivores. However, the extent of human direct and indirect top-down effects at multiple trophic levels notably had a stronger effect on the ecosystem than apex predators. Our results suggest that human factors need far greater consideration in trophic ecology research and associated theory, because excluding humans could lead to incomplete understanding of ecosystem structure and function.

Mesopredator limitation by apex predators and human-mediated bottom-up effects

The mesopredator release hypothesis predicts top-down control of mesopredators by apex predators, with bottom-up factors mediating mesopredator abundance, but not regulating it (Crooks & Soulé 1999; Elmhagen et al. 2010). We found limited evidence of suppression of foxes by wolves and bears in our study, therefore questioning the mesopredator release hypothesis in this human-dominated landscape. The suppressive effects of apex predators, although present, were generally weak, and similar in strength to bottom-up control. There are large differences in body-size and diet between foxes, omnivorous bears, and large ungulate-predating wolves, and body size differences may be too pronounced to provide ecological benefits to bears and wolves by killing foxes (Donadio & Buskirk 2006; Ritchie & Johnson 2009). Similarly, foxes were not suppressed by wolves in Europe (Pasanen-Mortensen et al. 2013), but were limited by the smaller-sized dingo, *Canis lupus dingo*, in Australia (Johnson & VanDerWal 2009), and lynx, *Lynx lynx*, in Europe (Elmhagen et al. 2010; Pasanen-Mortensen et al. 2013). An alternative explanation is that, at currently low apex predator densities, mesopredators may not be significantly suppressed. Indirect effects of interference competition, such as restricting habitat use and prey availability by instilling fear, could also have contributed to the limiting effects of apex predators but were unaccounted for in this study (Creel & Christianson 2008; Shirley et al. 2009; Brook et al. 2012).

Human-mediated bottom-up effects were apparent through a preference of foxes for less forested areas that are more fragmented (see also Kurki et al. 1998). Nevertheless, this effect was also weak, probably because generalist foxes can thrive in both forested and open landscapes (Panek & Bresiński 2002; Payne et al. 2014), and their densities increase along a natural-urban environmental gradient (Šálek et al. 2014). Thus, our gradients in land-use may not have been strong enough to capture fox habitat preferences, or fox distribution may be more affected by other human-mediated bottom-up effects such as the presence of anthropogenic food sources (Panek & Bresiński 2002). Furthermore, increased spatial heterogeneity in more complex habitats could have mediated interference competition and dampened top-down suppression of foxes through reduced encounter rates (McGee et al. 2006; Ritchie & Johnson 2009). More importantly, bottom-up effects influenced foxes and bears, and most likely wolves (Jedrzejewski et al. 2004), in opposite ways and thus, human-mediated bottom-up processes could further reduce interference competition between foxes and apex predators through increasing forest loss and fragmentation in Romania (Knorn et al. 2012; Griffiths et al. 2013).

Herbivore limitation by apex predators and human-mediated bottom-up effects

Despite human presence, apex predators still exerted substantial top-down limitation on herbivores. This is consistent with the Ecosystem Exploitation Hypothesis for systems with tri-trophic-cascades, where herbivores should be top-down limited and apex predators bottom-up limited (Oksanen & Oksanen 2000). Top-down control of wolves and bears on red deer and roe deer showed varying patterns. The observed negative effect on red deer and not on the roe deer encounter rate by wolves can be explained by wolves' preference for red deer over roe deer when both species are present (Jędrzejewski et al. 2000). Wolf extirpation caused eruptions of deer populations in European and American national parks (Jedrzejewski et al. 2002; Ripple & Beschta 2012b), and our results suggest that similar wolf reductions and extirpations could have led to increased red deer populations elsewhere in Europe (Lovari et al. 2007). By contrast, roe deer populations were only suppressed by apex predators in unproductive landscapes, and were more affected by foraging needs and competition for food in Europe (Melis et al. 2009; Samelius et al. 2013).

In contrast, bears had a negative effect on roe deer and not on red deer. Bears are known to predate young cervids (Berger et al. 2001; Swenson et al. 2007), and may either have predated preferentially on fawns of roe deer over those of red deer, or the positive relationship between bears and red deer is a likely indirect effect of the strong negative impact of humans on both species. However, since the diet of bears in our region does not include a lot of meat (Bojarska & Selva 2012), deer could alternatively have been suppressed by apex predators through a landscape of fear where deer alter their behaviour in response to predation risk (Laundré et al. 2001; Creel & Christianson 2008).

Although our results confirm theoretical predictions of weak bottom-up effects on deer species, they contrast with a recent study where human-mediation of forage quality influenced herbivores more strongly than top-down predator effects (Muhly et al. 2013). A lack of bottom-up effects may be due to the present land cover composition, which features forest and pasture cover close to the 30% threshold below which fragmentation effects become severe (Andrén 1994). Alternatively, the resolution of the Corine Land Cover (25 ha minimum mapping unit) may have been too coarse to pick up deer habitat preferences. Although human-mediated processes through land-use may not determine deer encounter rates in our study area; other human-mediated bottom-up processes such as supplemental feeding of deer may affect their populations (Schmidt & Hoi 2002). Moreover, similar to mesopredators, an increase in deforestation in the area would reduce apex predator presence and ultimately reduce top-down control of deer.

Humans as apex predators in the system

Direct and indirect human top-down impacts were more important in shaping patterns of species encounter rates compared to the effects of apex predators and human-mediated bottom-up effects. Thus, our study shows that humans themselves are an apex predator in the system, indicating that they should not be ignored in predator-prey studies (Sergio et al. 2014), particularly given the pervasive impacts of humans across the globe (Steffen et al. 2007; Goudie 2013). Humans are perhaps unique amongst apex predators in their ability to influence ecosystems through simultaneously directly reducing large carnivore, mesopredator and herbivore populations and, impacting their behaviour by creating a landscape of fear for all three trophic levels (Ordiz et al. 2013).

Direct human effects on foxes were negligible in our study. This is consistent with Baker & Harris (2006) who showed that fox culling through hunting does not necessarily reduce fox numbers. In contrast, direct human negative effects on deer were relatively large. Hunting of deer could have directly reduced deer populations (see e.g. Jędrzejewski et al. 2000), however, the observed pattern could also be a response to an anthropogenic landscape of fear where deer avoid areas where hunting and other human activities are prevalent (Theuerkauf & Rouys 2008). In addition, humans also suppressed deer through the use of livestock guard dogs, which are kept on the pasture and thus in proximity to preferred deer foraging areas. Although the effects of dogs on wildlife are relatively unknown, they can reduce herbivore populations through the same mechanisms of direct predation and behaviourally induced changes as other apex predators (Ritchie et al. 2014).

Indirectly, humans suppression of bears and possibly wolves (Jedrzejewski et al. 2004; Llaneza et al. 2012) could lift top-down control and lead to increased herbivore populations and possibly further mesopredator release. Herbivore and mesopredator population increases after anthropogenic extirpations of apex predators are widely documented (Terborgh & Estes 2010). For example, in Europe, the loss of lynx due to a combination of anthropogenic pressures (Breitenmoser et al. 2000), caused large scale mesopredator release in Europe (Elmhagen et al. 2010), perhaps even in our study area. However, here we found that in a system where both humans and other apex predators are present, top-down control by humans and predators and indirect release due to human suppression of apex predators act simultaneously, particularly on herbivore populations. Further studies that disentangle the effects of humans and predators on lower trophic levels will be key to advancing our understanding of the drivers and dynamics of ecosystems, trophic cascade theory, and ultimately how these affect biodiversity conservation. This is especially important since humans may not replicate the exact nature of indirect effects caused by other apex predators, highlighting that the ecological roles of apex predators are not always interchangeable (Ordiz et al. 2013). This may explain in part why humans are often unsuccessful at preventing or reversing negative impacts such as overgrazing, reduced vegetation recruitment, and biodiversity loss caused by altered predator-herbivore-plant trophic cascades or mesopredator release (e.g. Terborgh et al. 2001; Estes et al. 2011; Kuijper 2011; Ripple et al. 2013).

Conclusions

To date, ecological theory on trophic cascades has not explicitly included human effects, despite humanity's pervasive impacts on the globe (Sanderson et al. 2002). Our study adds to a growing recognition that humans play vital roles in influencing ecosystems through mediating and altering trophic cascades as well as through direct landscape modification. Apex predators maintained their ecological role by suppressing lower trophic levels in a human-dominated landscape, but both direct and indirect anthropogenic top-down effects dominated over natural processes. Improving our understanding of human impacts on trophic cascades in human-dominated landscapes is especially important because apex predators are declining rapidly in much of the world, but just as importantly they are also being encouraged to recover and are reintroduced to other areas. There are ample possibilities for restoring ecosystems through rewilding efforts or carnivore reintroduction programs, but especially in this context, it is important to anticipate the implications of simultaneous effects of humans and apex predators on multiple trophic levels. Our results and conclusions are presented with caution, as we acknowledge the limitations of correlative studies and the need to test conceptual understanding via experiments, and in doing so establish mechanistic causation underpinning the patterns observed. Given the extent and speed of global anthropogenic environmental change, elucidating how humans directly and indirectly alter bottom-up and top-down processes should receive increased consideration by future studies.

Acknowledgements

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Supplementary Material for Chapter V

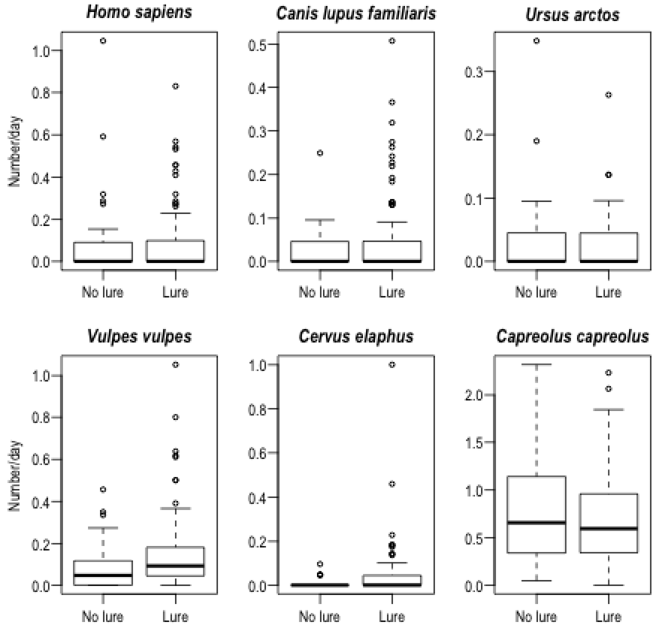

Figure S5.1 Boxplots of species encounter rates per camera day at camera locations with and without lure. The boxplots show that the presence of the lure did not affect species encounter rates appreciably and was therefore not included as a random factor in the models.

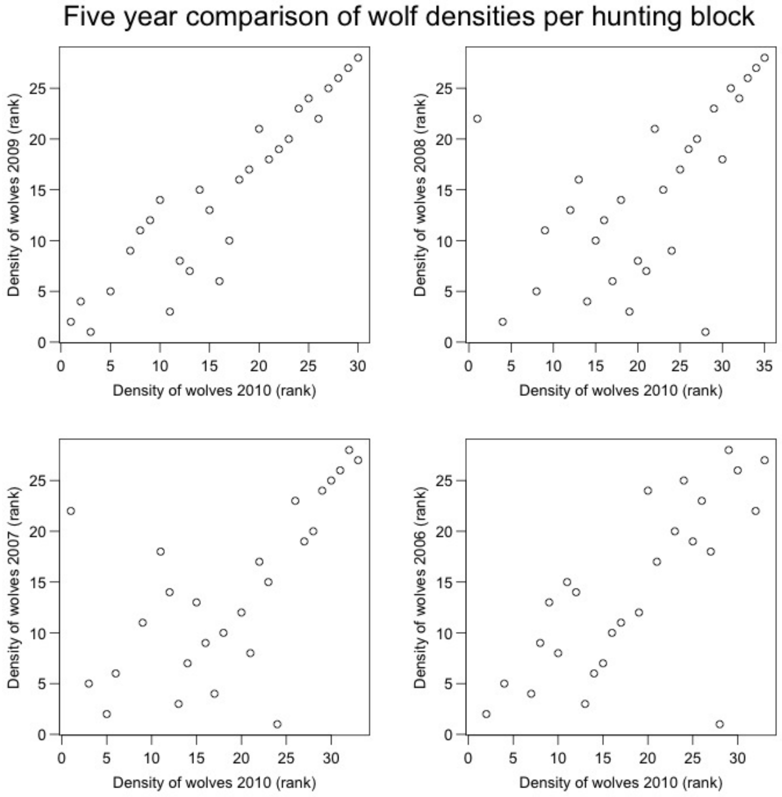

Figure S5.2 5 year comparison of reported wolf densities per hunting block. Wolf densities per hunting block (i.e. number of reported wolves divided by hunting block size; http://www.mmediu.ro/paduri/vanatoare.htm - accessed 01.02.2014) were ranked within each year (high rank = low density, low rank = high density). Ranks of hunting blocks for 2006-2009 were then plotted against 2010 ranks. Overall, the ranks of hunting block wolf densities were similar throughout years.

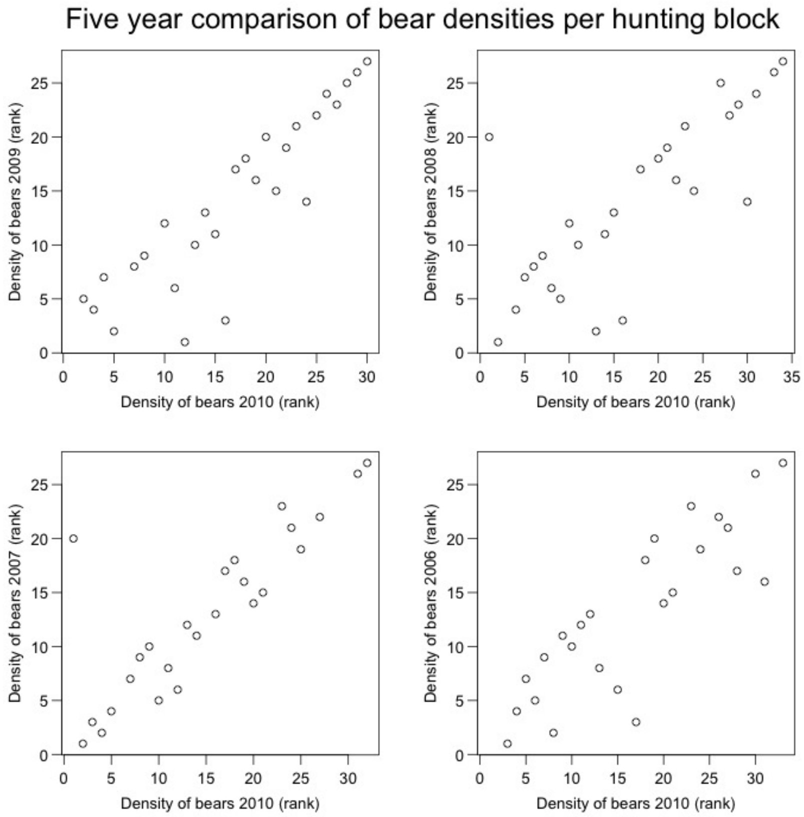

Figure S5.3 5 year comparison of reported bear densities per hunting block. Bear densities per hunting block (i.e. number of reported bears divided by hunting block size; http://www.mmediu.ro/paduri/vanatoare.htm - accessed 01.02.2014) were ranked within each year (high rank = low density, low rank = high density). Ranks of hunting blocks for 2006-2009 were then plotted against 2010 ranks. Overall, the ranks of hunting block bear densities were similar throughout years.

Table S5.1 Model selection table for all candidate models for brown bear. Average estimates are given for each variable. Log stands for log-transformation of the variable. Human (B) indicates human population size in the nearest three villages.

Rank	Forest (log)	Pasture	Human (B)	Wolf (log)	df	Log likelihood	AICc	delta AICc	weight
1	+	+	+	+	7	-131.09	277.00	0.00	0.42
2		+	+	+	6	-132.66	278.00	0.92	0.26
3	+	+	+		6	-133.42	279.50	2.42	0.12
4		+	+		5	-134.81	280.10	3.02	0.09
5	+		+	+	6	-133.79	280.20	3.17	0.09
6	+		+		5	-136.89	284.20	7.19	0.01
7			+	+	5	-137.10	284.70	7.61	0.01
8			+		4	-140.05	288.40	11.36	0.00
9	+	+		+	6	-138.58	289.80	12.75	0.00
10	+	+			5	-139.74	289.90	12.88	0.00
11	+			+	5	-140.82	292.10	15.05	0.00
12		+			4	-142.44	293.20	16.13	0.00
13	+				4	-142.52	293.30	16.29	0.00
14		+		+	5	-141.61	293.70	16.63	0.00
15				+	4	-145.40	299.10	22.04	0.00
16					3	-146.84	299.90	22.81	0.00
Coefficient	*0.25*	*-0.38*	*-2.07*	*-0.30*					

Table S5.2 Model selection table for all candidate models for domestic dog. Average estimates are given for each variable. Log stands for log-transformation of the variable. Bear (B) indicates bear densities from the hunting blocks. Human (L) indicates number of humans from the camera traps.

Rank	Bear (log, B)	Human (log, L)	Pasture	Wolf (log)	df	Log likelihood	AICc	delta AICc	weight
1		+	+		5	-190.23	390.90	0.00	0.37
2		+	+	+	6	-189.63	391.90	1.00	0.22
3	+	+	+		6	-189.83	392.30	1.39	0.19
4	+	+	+	+	7	-188.77	392.40	1.50	0.18
5		+			4	-194.16	396.60	5.71	0.02
6	+	+			5	-193.87	398.20	7.28	0.01
7		+		+	5	-193.94	398.30	7.43	0.01
8	+	+		+	6	-193.41	399.50	8.54	0.01
9	+		+	+	6	-209.17	431.00	40.07	0.00
10			+		4	-211.40	431.10	40.20	0.00
11			+	+	5	-210.49	431.40	40.53	0.00
12	+		+		5	-210.78	432.00	41.11	0.00
13					3	-215.07	436.30	45.42	0.00
14	+			+	5	-213.37	437.20	46.28	0.00
15				+	4	-214.48	437.30	46.36	0.00
16	+				4	-214.50	437.30	46.39	0.00
Coefficient	*0.25*	*0.63*	*0.37*	*-0.27*					

Table S5.3 Model selection table for all candidate models for red fox. Average estimates are given for each variable. Log stands for log-transformation of the variable. Bear (B) indicates bear densities from the hunting blocks. Human (L) indicates number of humans from the camera traps.

Rank	Bear (log, B)	Dog	Forest	Human (log, L)	Pasture (log)	Wolf (log)	df	Log likelihood	AICc	delta AICc	weight
1			+			+	6	-295.73	604.10	0.00	0.06
2		+	+			+	7	-294.75	604.40	0.27	0.05
3			+				5	-297.00	604.50	0.36	0.05
4	+		+				6	-295.95	604.50	0.44	0.05
5	+	+	+				7	-294.84	604.50	0.45	0.05
6		+	+				6	-296.02	604.70	0.59	0.05
7	+		+			+	7	-295.22	605.30	1.21	0.03
8		+				+	6	-296.37	605.40	1.29	0.03
9	+	+	+			+	8	-294.16	605.40	1.33	0.03
10		+			+	+	7	-295.48	605.80	1.72	0.03
11			+		+	+	7	-295.56	606.00	1.88	0.02
12		+	+		+	+	8	-294.44	606.00	1.90	0.02
13	+	+					6	-296.81	606.30	2.16	0.02
14			+	+		+	7	-295.71	606.30	2.19	0.02
15		+	+	+		+	8	-294.61	606.30	2.24	0.02
16	+	+				+	7	-295.78	606.40	2.32	0.02
17	+	+	+		+		8	-294.67	606.50	2.35	0.02
18						+	5	-298.02	606.50	2.39	0.02
19			+		+		6	-296.94	606.50	2.43	0.02
20		+	+		+		7	-295.87	606.60	2.50	0.02
21			+	+			6	-296.99	606.60	2.53	0.02
22	+		+		+		7	-295.88	606.60	2.53	0.02
23		+	+	+			7	-295.91	606.70	2.58	0.02
24	+	+	+	+			8	-294.79	606.70	2.60	0.02
25		+					5	-298.14	606.70	2.63	0.02
26	+		+	+			7	-295.95	606.80	2.66	0.02
27	+	+			+	+	8	-294.91	606.90	2.84	0.02
28	+	+			+		7	-296.10	607.10	2.97	0.01
29	+	+	+		+	+	9	-293.87	607.10	3.04	0.01
30					+	+	6	-297.28	607.20	3.10	0.01
31	+		+		+	+	8	-295.08	607.30	3.17	0.01

32		+			+		6	-297.45	607.50	3.43	0.01
33	+	+	+	+		+	9	-294.07	607.60	3.45	0.01
34	+		+	+		+	8	-295.22	607.60	3.46	0.01
35		+		+		+	7	-296.37	607.60	3.50	0.01
36	+					+	6	-297.54	607.70	3.62	0.01
37	+						5	-298.72	607.90	3.80	0.01
38		+	+	+	+	+	9	-294.28	608.00	3.87	0.01
39		+		+	+	+	8	-295.44	608.00	3.91	0.01
40							4	-299.90	608.10	3.99	0.01
41			+	+	+	+	8	-295.54	608.20	4.10	0.01
42	+	+		+			7	-296.80	608.50	4.35	0.01
43				+		+	6	-297.93	608.50	4.40	0.01
44	+				+	+	7	-296.83	608.50	4.42	0.01
45		+	+	+	+		8	-295.75	608.60	4.51	0.01
46	+	+	+	+	+		9	-294.61	608.60	4.53	0.01
47	+	+		+		+	8	-295.78	608.70	4.57	0.01
48			+	+	+		7	-296.93	608.70	4.63	0.01
49	+		+	+	+		8	-295.88	608.90	4.78	0.01
50		+		+			6	-298.13	608.90	4.81	0.01
51	+				+		6	-298.17	609.00	4.87	0.01
52					+		5	-299.35	609.20	5.05	0.01
53	+	+		+	+	+	9	-294.90	609.20	5.11	0.01
54	+	+	+	+	+	+	*10*	*-293.77*	*609.30*	*5.18*	*0.01*
55				+	+	+	7	-297.23	609.30	5.22	0.00
56	+	+		+	+		8	-296.10	609.30	5.22	0.00
57	+		+	+	+	+	9	-295.07	609.60	5.46	0.00
58	+			+			6	-298.46	609.60	5.46	0.00
59	+			+		+	7	-297.39	609.60	5.54	0.00
60		+		+	+		7	-297.44	609.70	5.64	0.00
61				+			5	-299.73	609.90	5.82	0.00
62	+			+	+	+	8	-296.73	610.60	6.48	0.00
63	+			+	+		7	-297.97	610.80	6.70	0.00
64				+	+		6	-299.23	611.10	7.01	0.00
Coefficient	*-0.13*	*0.15*	*-0.22*	*-0.03*	*0.09*	*-0.16*					

Table S5.4 Model selection table for all candidate models for red deer. Average estimates are given for each variable. Log stands for log-transformation of the variable. Bear (B) indicates bear densities from the hunting blocks. Human (B) indicates human population size in the nearest three villages.

Rank	Bear (log, B)	Dog (log)	Forest)log)	Pasture (log)	Human (log, B)	Wolf	df	Log likelihood	AICc	delta AICc	weight
1	+	+			+	+	7	-160.84	336.50	0.00	0.18
2	+	+		+	+	+	8	-160.14	337.40	0.86	0.11
3		+			+	+	6	-162.62	337.90	1.34	0.09
4		+			+		5	-163.79	338.00	1.49	0.08
5	+	+			+		6	-162.96	338.60	2.02	0.06
6	+	+	+		+	+	8	-160.84	338.80	2.25	0.06
7		+		+	+	+	7	-162.03	338.90	2.39	0.05
8		+		+	+		6	-163.24	339.10	2.58	0.05
9	+	+		+	+		7	-162.35	339.60	3.02	0.04
10	+	+	+	+	+	+	9	-160.10	339.60	3.07	0.04
11		+	+		+	+	7	-162.62	340.10	3.56	0.03
12		+	+		+		6	-163.78	340.20	3.67	0.03
13	+				+	+	6	-164.02	340.70	4.14	0.02
14	+	+	+		+		7	-162.96	340.80	4.23	0.02
15		+	+	+	+	+	8	-162.02	341.20	4.61	0.02
16		+	+	+	+		7	-163.24	341.30	4.79	0.02
17					+	+	5	-165.45	341.40	4.81	0.02
18					+		4	-166.53	341.40	4.83	0.02
19	+	+	+	+	+		8	-162.35	341.80	5.27	0.01
20	+				+		5	-165.89	342.20	5.68	0.01
21	+			+	+	+	7	-163.92	342.70	6.16	0.01
22	+		+		+	+	7	-163.95	342.80	6.22	0.01
23				+	+	+	6	-165.37	343.40	6.83	0.01
24				+	+		5	-166.47	343.40	6.85	0.01
25			+		+	+	6	-165.40	343.40	6.91	0.01
26			+		+		5	-166.51	343.50	6.94	0.01
27	+			+	+		6	-165.81	344.30	7.73	0.00
28	+		+		+		6	-165.86	344.40	7.83	0.00
29	+		+	+	+	+	8	-163.79	344.70	8.16	0.00

30			+	+	+	+	7	-165.28	345.40	8.88	0.00
31			+	+	+		6	-166.42	345.50	8.94	0.00
32	+		+	+	+		7	-165.76	346.40	9.84	0.00
33	+	+		+		+	7	-169.15	353.20	16.62	0.00
34	+	+	+	+		+	8	-168.73	354.60	18.03	0.00
35	+	+		+			6	-171.56	355.80	19.22	0.00
36		+		+			5	-173.11	356.70	20.14	0.00
37		+		+		+	6	-172.04	356.70	20.17	0.00
38	+	+	+	+			7	-171.26	357.40	20.85	0.00
39	+	+				+	6	-172.56	357.80	21.21	0.00
40		+	+	+		+	7	-171.63	358.10	21.58	0.00
41		+	+	+			6	-172.79	358.20	21.68	0.00
42	+	+					5	-174.56	359.60	23.04	0.00
43	+	+	+			+	7	-172.37	359.60	23.06	0.00
44		+					4	-176.01	360.30	23.78	0.00
45		+				+	5	-175.15	360.80	24.22	0.00
46	+	+	+				6	-174.44	361.50	24.99	0.00
47		+	+				5	-175.87	362.20	25.66	0.00
48		+	+			+	6	-174.97	362.60	26.04	0.00
49	+		+	+		+	7	-174.82	364.50	27.97	0.00
50	+			+		+	6	-176.02	364.70	28.14	0.00
51	+					+	5	-177.52	365.50	28.96	0.00
52	+		+			+	6	-176.83	366.30	29.76	0.00
53	+			+			5	-178.02	366.50	29.96	0.00
54				+			*4*	*-179.18*	*366.70*	*30.12*	*0.00*
55	+		+	+			6	-177.04	366.70	30.18	0.00
56			+	+		+	6	-177.04	366.70	30.19	0.00
57			+	+			5	-178.16	366.80	30.23	0.00
58	+						4	-179.27	366.80	30.30	0.00
59				+		+	5	-178.22	366.90	30.35	0.00
60							3	-180.43	367.00	30.50	0.00
61						+	4	-179.64	367.60	31.04	0.00
62	+		+				5	-178.71	367.90	31.32	0.00
63			+				4	-179.84	368.00	31.44	0.00
64			+			+	5	-178.95	368.40	31.82	0.00
Coefficient	*0.44*	*-0.32*	*0.01*	*0.18*	*-0.84*	*-0.48*					

Table S5.5 Model selection table for all candidate models for roe deer. Average estimates are given for each variable. Log stands for log-transformation of the variable. Bear (B) indicates bear densities from the hunting blocks. Human (B) indicates human population size in the nearest three villages.

Rank	**Bear (log, B)**	**Dog (log)**	**Forest**	**Pasture (log)**	**Human (B)**	**Red deer (log)**	**Wolf**	**df**	**logLik**	**AICc**	**delta**	**weight**
1					+	+		6	-494.92	1002.50	0.00	0.05
2	+				+	+	+	8	-492.70	1002.50	0.02	0.05
3	+				+	+		7	-493.95	1002.80	0.26	0.04
4		+			+	+		7	-494.01	1002.90	0.39	0.04
5	+				+		+	7	-494.28	1003.40	0.94	0.03
6	+	+			+	+		8	-493.27	1003.60	1.16	0.03
7	+	+			+	+	+	9	-492.19	1003.80	1.30	0.03
8					+	+	+	7	-494.52	1003.90	1.40	0.02
9		+		+	+	+		8	-493.59	1004.30	1.80	0.02
10				+	+	+		7	-494.73	1004.30	1.82	0.02
11		+			+	+	+	8	-493.65	1004.40	1.93	0.02
12	+			+	+	+	+	9	-492.54	1004.50	1.99	0.02
13	+			+	+	+		8	-493.74	1004.60	2.10	0.02
14	+		+		+	+	+	9	-492.62	1004.60	2.15	0.02
15			+		+	+		7	-494.92	1004.70	2.20	0.02
16		+				+		6	-496.05	1004.70	2.26	0.02
17		+	+		+	+		8	-493.88	1004.90	2.39	0.01
18	+				+			6	-496.14	1004.90	2.43	0.01
19	+						+	6	-496.17	1005.00	2.49	0.01
20	+		+		+	+		8	-493.94	1005.00	2.50	0.01
21	+					+	+	7	-495.08	1005.00	2.53	0.01
22	+	+			+		+	8	-493.96	1005.00	2.54	0.01
23	+	+		+	+	+		9	-492.87	1005.10	2.65	0.01
24	+		+		+		+	8	-494.10	1005.30	2.82	0.01
25					+			5	-497.43	1005.30	2.82	0.01
26		+		+		+		7	-495.23	1005.30	2.83	0.01

27						+		5	-497.45	1005.40	2.86	0.01
28	+			+	+		+	8	-494.15	1005.40	2.92	0.01
29	+	+		+	+	+	+	10	-491.89	1005.50	3.02	0.01
30	+	+				+	+	8	-494.20	1005.50	3.03	0.01
31	+	+	+		+	+	+	10	-491.96	1005.70	3.16	0.01
32	+	+	+		+	+		9	-493.16	1005.70	3.24	0.01
33	+	+				+		7	-495.44	1005.70	3.24	0.01
34	+					+		6	-496.58	1005.80	3.30	0.01
35				+	+	+	+	8	-494.35	1005.80	3.32	0.01
36	+	+					+	7	-495.54	1005.90	3.45	0.01
37		+		+	+	+	+	9	-493.28	1006.00	3.47	0.01
38		+				+	+	7	-495.56	1006.00	3.49	0.01
39			+		+	+	+	8	-494.48	1006.10	3.59	0.01
40					+		+	6	-496.74	1006.10	3.63	0.01
41		+			+			6	-496.76	1006.20	3.67	0.01
42	+	+			+			7	-495.67	1006.20	3.72	0.01
43		+	+		+	+	+	9	-493.44	1006.30	3.80	0.01
44	+	+		+		+		8	-494.63	1006.40	3.89	0.01
45						+	+	6	-496.87	1006.40	3.89	0.01
46		+	+			+		7	-495.79	1006.40	3.94	0.01
47	+			+		+	+	8	-494.68	1006.50	3.98	0.01
48		+	+	+	+	+		9	-493.54	1006.50	4.00	0.01
49	+	+		+		+	+	9	-493.55	1006.50	4.02	0.01
50	+			+			+	7	-495.83	1006.50	4.03	0.01
51			+	+	+	+		8	-494.73	1006.60	4.08	0.01
52				+		+		6	-496.97	1006.60	4.09	0.01
53	+	+	+		+		+	9	-493.59	1006.60	4.10	0.01
54	+		+				+	*7*	*-495.91*	*1006.70*	*4.19*	*0.01*
55	+		+	+	+	+	+	10	-492.51	1006.70	4.26	0.01
56		+		+		+	+	8	-494.82	1006.80	4.27	0.01
57	+			+	+			7	-495.96	1006.80	4.30	0.01
58	+							5	-498.17	1006.80	4.31	0.01
59	+	+		+	+		+	9	-493.72	1006.80	4.36	0.01
60	+		+	+	+	+		9	-493.73	1006.90	4.39	0.01
61								4	-499.32	1006.90	4.44	0.01
62	+		+			+	+	8	-494.92	1007.00	4.46	0.01
63		+						5	-498.25	1007.00	4.46	0.01
64	+	+	+			+	+	9	-493.78	1007.00	4.48	0.01
65	+			+		+		7	-496.08	1007.00	4.53	0.01
66	+		+		+			7	-496.09	1007.00	4.56	0.01
67		+			+		+	7	-496.11	1007.10	4.58	0.01
68	+	+	+				+	8	-494.99	1007.10	4.61	0.01
69	+	+		+			+	8	-495.02	1007.10	4.66	0.01
70				+	+			6	-497.27	1007.20	4.70	0.01
71	+	+						6	-497.33	1007.30	4.82	0.00
72		+	+	+		+		8	-495.13	1007.40	4.89	0.00
73			+		+			6	-497.38	1007.40	4.90	0.00
74	+	+	+	+	+	+		10	-492.83	1007.40	4.91	0.00
75							+	5	-498.50	1007.40	4.96	0.00
76			+			+		6	-497.41	1007.50	4.97	0.00
77		+	+			+	+	8	-495.17	1007.50	4.97	0.00
78	+		+	+	+		+	9	-494.03	1007.50	4.97	0.00
79	+	+	+			+		8	-495.20	1007.50	5.02	0.00
80	+	+	+	+	+	+	+	11	-491.76	1007.60	5.12	0.00
81		+					+	6	-497.49	1007.60	5.14	0.00
82		+		+	+			7	-496.43	1007.70	5.23	0.00
83				+		+	+	7	-496.45	1007.80	5.28	0.00
84	+	+		+	+			8	-495.36	1007.80	5.34	0.00
85		+		+				6	-497.60	1007.80	5.36	0.00
86		+	+		+			7	-496.54	1007.90	5.44	0.00
87	+		+			+		7	-496.54	1007.90	5.45	0.00
88		+	+	+	+	+	+	10	-493.17	1008.10	5.59	0.00
89				+	+		+	7	-496.61	1008.10	5.60	0.00
90			+	+	+	+	+	9	-494.34	1008.10	5.60	0.00
91			+		+		+	7	-496.62	1008.10	5.61	0.00
92	+	+	+		+			8	-495.50	1008.10	5.62	0.00
93	+			+				6	-497.76	1008.20	5.67	0.00
94	+	+		+				7	-496.69	1008.20	5.74	0.00
95				+				5	-498.94	1008.30	5.84	0.00
96			+			+	+	7	-496.77	1008.40	5.91	0.00

97	+	+	+	+		+	+	10	-493.34	1008.40	5.92	0.00
98		+	+					6	-497.89	1008.40	5.94	0.00
99	+		+	+			+	8	-495.70	1008.50	6.02	0.00
100	+	+	+	+		+		9	-494.55	1008.50	6.02	0.00
101		+	+		+		+	8	-495.76	1008.60	6.14	0.00
102	+		+	+		+	+	9	-494.62	1008.70	6.16	0.00
103	+	+	+	+	+		+	10	-493.46	1008.70	6.17	0.00
104		+	+	+		+	+	9	-494.65	1008.70	6.21	0.00
105		+		+			+	7	-496.93	1008.70	6.22	0.00
106		+		+	+		+	8	-495.82	1008.80	6.27	0.00
107	+	+	+	+			+	9	-494.68	1008.80	6.28	0.00
108			+	+		+		7	-496.97	1008.80	6.31	0.00
109	+		+					6	-498.09	1008.80	6.32	0.00
110		+	+				+	7	-496.98	1008.80	6.33	0.00
111			+					5	-499.22	1008.90	6.41	0.00
112	+	+	+					7	-497.02	1008.90	6.42	0.00
113				+			+	6	-498.17	1009.00	6.50	0.00
114	+		+	+	+			8	-495.95	1009.00	6.53	0.00
115			+				+	6	-498.31	1009.30	6.77	0.00
116	+		+	+		+		8	-496.08	1009.30	6.78	0.00
117			+	+	+			7	-497.26	1009.40	6.89	0.00
118		+	+	+				7	-497.43	1009.70	7.23	0.00
119		+	+	+	+			8	-496.30	1009.70	7.23	0.00
120	+	+	+	+	+			9	-495.26	1009.90	7.44	0.00
121			+	+		+	+	8	-496.44	1010.00	7.50	0.00
122	+	+	+	+				8	-496.54	1010.20	7.71	0.00
123			+	+	+		+	8	-496.54	1010.20	7.72	0.00
124	+		+	+				7	-497.75	1010.40	7.86	0.00
125		+	+	+			+	8	-496.62	1010.40	7.87	0.00
126			+	+				6	-498.92	1010.50	7.99	0.00
127		+	+	+	+		+	9	-495.59	1010.60	8.10	0.00
128			+	+			+	7	-498.09	1011.00	8.55	0.00
Coefficient	*-0.12*	*-0.08*	*-0.02*	*0.05*	*-0.13*	*-0.12*	*0.11*					

Section B: Traditional wood pastures

This Section includes Chapters VI-VIII and focuses specifically on the conservation value of traditional wood pastures to gain insights on the role of particular traditional land-use elements for biodiversity. Wood pastures are one of the oldest land-use types in Europe. They were established through ancient silvo-pastoral practices and often consist of open grasslands with scattered old trees. Chapter VI explores the characteristics, management, and status of wood pastures, but also the current threats to wood pastures. The role of wood pastures for biodiversity is assessed in more detail in Chapters VII and VIII: Chapter VII examines the habitat value of woodpeckers for an assemblage of six woodpecker species, Chapter VIII aims to assess the extent of wood pastures use by the brown bear.

Chapter VI

Chapter VI

Wood-pastures in a traditional rural region of Eastern Europe: Characteristics, management, and status

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'Someone's sitting in the shade today because someone planted a tree a long time ago.' – Warren Buffett

'Many a genius has been slow of growth. Oaks that flourish for a thousand years do not spring up into beauty like a reed.' – George H. Lewis

Abstract

Wood-pastures are among the oldest land-use types in Europe and have high ecological and cultural importance. They are under rapid decline all over Europe because of changes in land-use, tree cutting, and lack of regeneration. In this study we characterized the structure, condition and threats of wood-pastures in a traditional rural region in Romania. Forty-two wood-pastures were surveyed, as well as 15 forest sites for comparison. All wood-pasture sites were described via four groups of variables: condition, management, site, and landscape context. Forest sites were dominated by Hornbeam (*Carpinus betulus*) and Beech (*Fagus sylvatica*), whereas wood-pastures were dominated by Oak (*Quercus* sp.) and various species of fruit trees. Most wood-pastures contained trees classified as 'ancient' but no such trees were found in forests. The proportion of dead trees was positively related to forest cover within 300 m around the wood-pasture. Models that included management, site and landscape-related variables best explained the prelevance of Oak, Beech, Hornbeam and Pear trees in wood-pastures. Large oaks and hornbeams were more likely to be dead or affected by uncontrolled pasture burning than small oaks and other tree species. Our results show that ancient wood-pastures are common in this rural region, and they may be more common in Eastern Europe than previously thought. There is an urgent need for research, legal recognition and conservation management of wood-pastures as distinct landscape elements for their cultural, ecological and agricultural importance.

Introduction

Wood-pastures represent an important part of European cultural–natural heritage (Bergmeier et al. 2010), and are one of the oldest land-use types in Europe, being known since the Neolithic (Luick 2008). Although the concept of wood-pastures is broad (Spencer & Kirby 1992; Caledonian Partnership 2003; Goldberg et al. 2007), it characteristically refers to environments that are defined by trees scattered through an open area, generally grassland. Appropriate livestock grazing regimes applied through centuries have been crucial for the formation of wood-pastures and will be important for their further persistence (Quelch 2002).

Ancient wood-pastures bring together several important components that make them attractive for ecologists and conservationists. First, wood-pastures contain scattered trees. The age of these trees can reach centuries; such trees are sometimes referred to as 'veteran' or 'ancient' trees (Read 2000; Quelch 2002). Old, scattered trees provide a broad range of habitat features such as dead branches or hollows (Gibbons & Lindenmayer 2003). For this reason, old trees represent local 'biodiversity hotspots' in ecosystems around the world (Fischer et al. 2010; Lindenmayer et al. 2014). Moreover, scattered trees (regardless of their age) significantly influence microclimatic conditions and soil humidity, and consequently vegetation structure (Manning et al. 2006) and may help to facilitate adaptation to anthropogenic climate change in the future (Manning et al. 2009). Second, the open habitat throughout which trees are scattered is managed mostly as pasture (Quelch 2002; Mountford & Peterken 2003; Bergmeier et al. 2010). Traditional pasture management has typically been low in intensity, thus supporting a rich flora and fauna, including many species of conservation interest (Rosenthal et al. 2012). Low intensity grazing, together with scattered, often old trees, makes many wood-pastures regional hotspots of biodiversity (Bugalho et al. 2011).

Wood-pastures have received increasing scientific attention throughout Europe in recent years. Studies on the biodiversity of wood-pastures and the ecological value of old trees have been conducted in the Czech Republic (Vojta & Drhovská 2012; Horák & Rébl 2013), Portugal (Gonçalves et al. 2012), Romania (Moga et al. 2009; Dorresteijn et al. 2013), and Sweden (Paltto et al. 2011; Widerberg et al. 2012). Vegetation dynamics and landscape change related to management regimes are available, for example, from the Swiss Jura Mountains (Buttler et al. 2008), the Italian Alps (Garbarino et al. 2011), Belgium (Van Uytvanck et al. 2008), the Netherlands (Smit & Ruifrok 2011; Smit & Verwijmeren 2011), Spain (Plieninger & Schaar 2008) and Sweden (Brunet et al., 2011). Studies exploring the recruitment of trees in wood-pastures are available from Spain (Plieninger 2007); and research about the vegetation structure and conservation status of wood-pastures is available from Romania (Öllerer 2012, 2013), Turkey (Uğurlu et al. 2012), and Greece (Chaideftou et al. 2011). Finally, the crucial importance of low intensity human use for the maintenance of biodiversity and ecosystem services in Mediterranean wood-pastures and their provisioning ecosystem services was reported by Bugalho et al. (2011).

Existing studies highlight that wood-pastures have been undergoing major changes in the past few decades. These changes threaten the existence of wood-pastures and are mostly driven by changing land-use (e.g. land abandonment and changing farming practices), policies, changing attitudes toward old trees, and lack of tree regeneration (reviewed in Bergmeier et al. 2010).

While until recently Britain was considered as one of the main locations in Europe for large (veteran) trees in wood-pastures (Rackham 1998; Mountford & Peterken 2003), information from Central and Eastern European (CEE) countries about ancient wood-pastures is scarce. Some national level evaluations exist for example in Hungary (e.g Haraszthy et al. 1997), suggesting that wood-pastures are among the most threatened ecosystems in this country.

Here, we present research on wood-pastures in a traditional rural region of Central Romania. Our study had three aims: (i) to compare the structure of tree communities and tree sizes between forests and wood-pastures, (ii) to describe the main characteristics and current management of wood-pastures and (iii) to model wood-pasture condition using a number of site, landscape and management related variables. Although our study has a regional focus and is partly descriptive in nature, we discuss our findings broadly in the context of international wood-pasture conservation. Drawing on our findings, we argue that some Eastern European wood-pastures have particularly high, but largely unrecognised, conservation values.

Methods

Study area

The study was conducted in Southern Transylvania, Romania and covered ca 3600 km^2, of which ca 860 km^2 were covered by Natura 2000 regulations (Site of Community Importance, hereafter SCI) (Fig. 6.1). The region is dominated by traditional land-use practices and has low levels of infrastructure development. The most important land cover types based on CORINE land cover classes (see Table 6.1 for reference) are forest (ca. 30%), pasture (ca. 26%), heterogeneous agricultural areas (including agro-forestry areas; ca. 15%) and arable fields (ca. 14%). The urban area cover is low (ca. 3%). Other minor land covers include wetlands and vineyards. The climate in the region is continental and moderate. Annual temperature averages 8.2 ºC, with an average temperature of -4.3 ºC in January and 18.6 ºC in July. The yearly mean amount of precipitation is between 650 and 700 mm (Hartel and Moga, 2010).

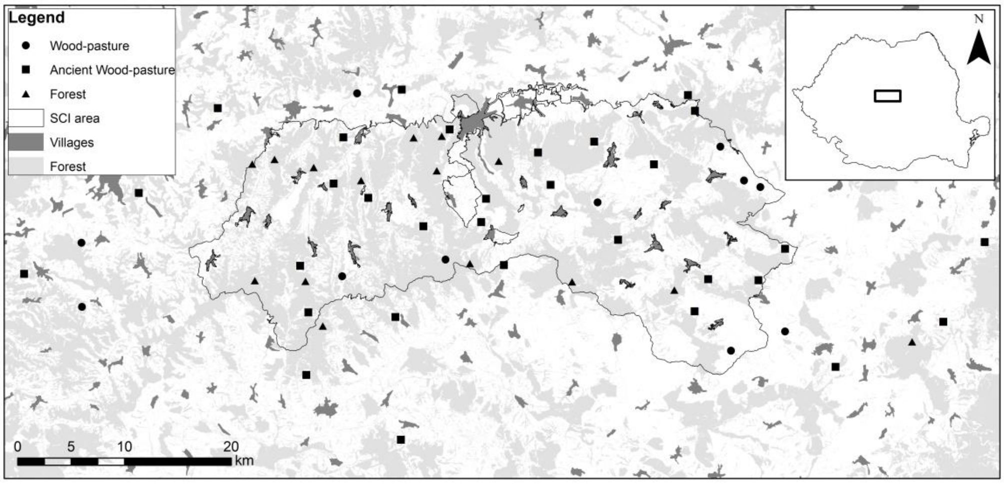

Figure 6.1 Map of the study area. All survey sites, including wood-pastures, ancient wood-pastures, and forests are shown. The Natura 2000 site (SCI) is delineated (see study area in Central Romania description).

Field methods and variables

Data were collected in 2012. Forty-two wood-pastures and 15 forest sites were studied (see Supporting Information 6.1 and 6.2). We sampled a larger number of wood-pastures than forests because forests are relatively homogenous, whereas wood-pastures differ substantially in structural elements and adjacent forest cover. Furthermore, we were especially interested in the description of wood-pastures and thus chose more sites to comprehensively cover existing gradients within wood-pastures.

We used five groups of variables to characterize wood-pastures: condition variables (tree density per ha, number of scattered trees per ha, proportion of dead trees per, tee size, scrub cover and woody vegetation cover), composition variables (prevalence of oak, hornbeam, beech and pear), site (area, elevation and ruggedness) and landscape (forest cover and distance to nearest village) related variables and management (evidence for scrub cleaning related to Agency for Payments and Intervention in Agriculture (hereafter APIA), livestock and burning) related variables. Descriptions of these variables and their units of measurement and sources (for data other than field data) are summarized in Table 6.1. The tree diameter at breast height (DBH) was calculated from the circumference, which we measured with a tape for standing trees. Tree measurements were made in February–March (2012) in the following way: (1) all trees in wood-pastures were measured within a radius of 80 m around a central survey point (i.e. within a 2 ha site). In forest sites, 50 trees were selected randomly in a spiral from the centre of the site to the edge of the 2 ha, to obtain a representative sample of trees. (2) Additional trees were measured within four strip transects of ca. 10 m width between 80 m and 300 m from the central survey point in the four cardinal directions (N, S, E, W). In the case that three or fewer trees were found within the wood-pasture transects we measured up to five trees close to the transect. The resulting data provided indications of the diameter distribution within 2 ha around a central point and in the immediate surroundings. We used the DBH of trees as a proxy for their age categorization and conservation value (i.e. 'truly ancient', 'ancient', 'of conservation value', and 'potentially interesting', following Read (2000) and Farm Environment Plan Guide (2006)). We also recorded if the measured trees were burned (i.e. the tree showed signs of fire but was alive), dead (for standing dead trees), healthy (no visible injury on the trunk of the tree) and injured (when the trunk was injured by cutting – coppicing and pollarding were not considered as injuries).

Tree density within 2 ha was assessed in wood-pastures as the count of all trees within 80 m of the central survey point. All dead trees from the two hectare sites were counted, both in wood-pastures and forests. Trees were identified to genus level. According to a previous study (Hartel & Moga 2010), the vast majority of the Oaks in wood-pastures in this region belong to the species *Quercus robur* (90% out of 339 Oaks measured), or to *Q. petraea* and hybrids between the two species. Due to the similarities of the ecology and habit of these two oaks, we believe that considering them together was reasonable and facilitated meaningful comparison with the other dominant tree genera.

Scrub cover was assessed for the entire wood-pasture using 400 m long and 6 m wide transects which were placed subjectively so that they covered all representative locations of the wood-pasture. This assessment was made in the period of May-July. The number of transects in each wood-pasture was chosen according to the size of the wood-pasture: two transects were used in wood-pastures with an area of up to 30 ha, three transects in those measuring 30–80 ha, four transects in those of 80–130 ha area, five transects in those of 130–180 ha area, and six in those measuring more than 180 ha. On average there were 3.7 transects per site. In each transect, the percent of scrub cover was assessed visually every 100 m. Scrub cover values were averaged for the entire wood-pasture to obtain a single representative estimate.

Furthermore we recorded the presence/absence of livestock based on direct observation of the animals and/or their faeces. Pasture burning was recorded in March–April period (when this activity usually takes place as management intervention to remove excessive biomass from pastures), and the presence of scrub removal was recorded in March–July (Table 6.1). We further recorded if we observed tree cutting activities in wood-pastures in 2012.

Table 6.1 The description of the environmental variables used to characterize wood-pastures from Southern Transylvania and to model wood-pasture condition and composition. Variables highlighted in italics are those that were used in statistical models as explanatory or response variables (see section on Analysis).

Variable name	**Description**
(a) Condition variables	
Tree density per ha	Calculated from the overall number of standing trees (dead and alive) counted in the 2 ha sites.
Number of scattered trees	The overall number of scattered trees in the entire wood-pasture based on counts of trees using Google Earth satellite images.
Proportion of dead trees (2 ha)	The percent of dead trees (standing or fallen) in the 2 ha site.
Tree size	The median value was computed for each wood-pasture based on the diameter at breast height (DBH) in cm of trees higher than 3 m. These median values across all wood-pastures were then averaged.
Scrub cover	The percent cover of scrub in the wood-pasture. Scrub was defined in our study as vegetation dominated by woody perennials (shrubs and young trees), usually exceeding the height of the grass layer, and being between 0.2 m and ca 3 m in height. Characteristic shrub species were: Hawthorn (*Crataegus monogyna*), Blackthorn (*Prunus spinosa*), Blackberry (*Rubus* sp.) and the Dog Rose (*Rosa canina*). The most common young tree was the Hornbeam (*Carpinus betulus*).
Woody vegetation cover	The percent coverage of woody vegetation (trees and shrubs) in the whole wood-pasture. Source: data derived from a supervised classification of the monochromatic channels of SPOT 5 data (©CNES 2007, Distribution Spot Image SA) using a support vector machine algorithm (Knorn et al. 2009).
(b) Composition variables	
Prevalence of Oak, Hornbeam, Beech and Pear	Defined as the proportion of Oak, Hornbeam, Beech and Pear in relation to the complete number of trees measured in a given site.
(c) Site related variables	
Area	The size of the wood-pasture (ha). Source: satellite imagery and GIS.
Elevation	In meters (m). Source: recorded *in situ* with a Global Positioning System.
Ruggedness	The ruggedness of the terrain for the whole wood-pasture and was calculated as the standard deviation of elevation in a 25 m x 25 m grid (Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model Version 2 (GDEM V2))
(d) Landscape related context	
Forest cover	Percentage of forest cover within a 300 m buffer from the edge of wood-pasture based on CORINE Land Cover classes. Source: European Environmental Agency (2011): (http://www.eea.europa.eu/publications/COR0-landcover).
Distance to nearest village	The Euclidean distance from the centre of the wood-pasture to the edge of the closest village calculated in GIS (in m).
(e) Management related variables	
Scrub cleaning (APIA)	The presence of scrub clearance. Cut scrub collected in piles was considered evidence for APIA activities at the site.
Livestock	Cattle, sheep, buffalo, horses or a mixture of these. The percent of wood-pastures grazed by each of these livestock was calculated.
Burning	Presence of burning in the wood-pasture.

Analysis

Raw data were summarized using descriptive statistics. Due to the different scaling of the data the Coefficient of Variation (CV) was used as dimensionless measure of variability, allowing a meaningful comparison among different variables. Illustration of tree communities was based on genera composition from forests versus wood-pastures using detrended correspondence analysis (DCA), using the number of stems belonging to different genera. The DBH of burned and dead trees was compared against that of healthy trees using t-tests. Prior to this, DBH data were log-transformed to meet assumptions about the distribution of the data. Density of dead trees per hectare was compared between forests and wood-pastures using a t-test.

To model indicators of condition and composition we used an information-theoretic model selection approach based on the Akaike information criterion (AIC) to identify models best supported by the data (Burnham & Anderson 2002). We separately considered six different response variables: the proportion of dead trees and the proportion of scrub cover were variables from the 'condition' group (see above and Table 6.1). The prevalence of Oak, Hornbeam, Beech and Pear were 'compositional' variables (see above and Table 6.1). We selected the condition variables as responses because (i) they directly influence the quality of the (wood-) pasture (scrub cover, proportion of dead trees); and (ii) they are highly dynamic variables – both increased after the 1989 Romanian revolution, but since the entry of Romania into the European Union (2007 hereafter EU), financial incentives (i.e. APIA payment, see above) have been used to clean pastures of scrubs. We selected the compositional variables because these tree species were abundant and some of them (e.g. Oak, Pear) historically have a strong cultural importance for local communities (Dorner 1910). Each response variable (see above) was modelled separately as a function of six explanatory variables from the following categories (detailed in Table 6.1): 'Site related' (S) variables (altitude and ruggedness), 'Management related' (M) variables (evidence of sheep grazing or not, evidence of 'APIA' related scrub removal) and 'Landscape related' (L) variables (forest cover and distance to nearest village).

We constructed seven candidate models arising from all combinations of the groups of explanatory variables listed above (M, S, L, M + S, M + L, S + L, M + S + L). All continuous variables were standardized to an average of zero and a standard deviation of one in order to make the effects comparable. For each model, the AIC value was calculated using correction for small samples sizes (AICc, Burnham and Anderson, 2002). The models were ranked according to their AICc, where the best model has the smallest AICc value. Delta AICc (D AICc) was calculated to express the difference between each model and the best model. Akaike weights (w) were used to estimate the relative evidence for each model, which could be interpreted as the probability that the model i was the best model for the observed data, given the candidate set of models.

Results

Tree community composition in wood-pastures and forests

We measured 6739 trees, including 4870 in forests and 1869 in wood-pastures. Twelve tree genera were found in forests and 14 in wood-pastures (Table 6.2). Tree communities differed between wood-pastures and forests (Fig. 6.2). Forest sites were dominated by Hornbeam (*Carpinus betulus*) and Beech (*Fagus sylvatica*), while wood-pastures were dominated by Oak (*Quercus* sp.) (Fig. 6.2).

Table 6.2 Tree genera identified in the forest and wood-pasture sites. The fourth column shows which species are known to occur in our region for each genus (based on Coldea 1992). A plus denotes presence, minus denotes absence.

Genus	Forest	Wood-pasture	Species from the region
Acer	+	+	*Acer campestre,* *A. platanoides,* *A. pseudoplatanus,* *A. tataricum,* *A. negundo*[3]
Betula	+	+	*Betula pendula*
Carpinus	+	+	*Carpinus betulus*
Fagus	+	+	*Fagus sylvatica*
Fraxinus	+	+	*Fraxinus excelsior*
Juglans	-	+	*Juglans regia*
Larix	+	+	*Larix decidua*[1]
Malus	-	+	*Malus domestica*[2] *M. sylvestris*[2]
Pinus	+	+	*Pinus nigra*[3] *P. sylvestris*[3]
Populus	+	+	*Populus alba* *P. tremula*
Prunus	+	+	*Prunus avium,* *P. spinosa* *P. cerasifera* [2] *P. domestica*[2]
Pyrus	-	+	*Pyrus communis*[2] *P. pyraster*[2]
Quercus	+	+	*Quercus petraea* *Q. pubescens* *Q. robur* *Q. robur* × *Q. petraea* *Quercus rubra*[3]
Robinia	+	+	*Robinia pseudoacacia*[1]
Salix	-	+	*Salix alba* *S. caprea,* *S. cinerea,* *S. fragilis,* *S. purpurea,* *S. triandra*
Tilia	+	+	*Tilia cordata*

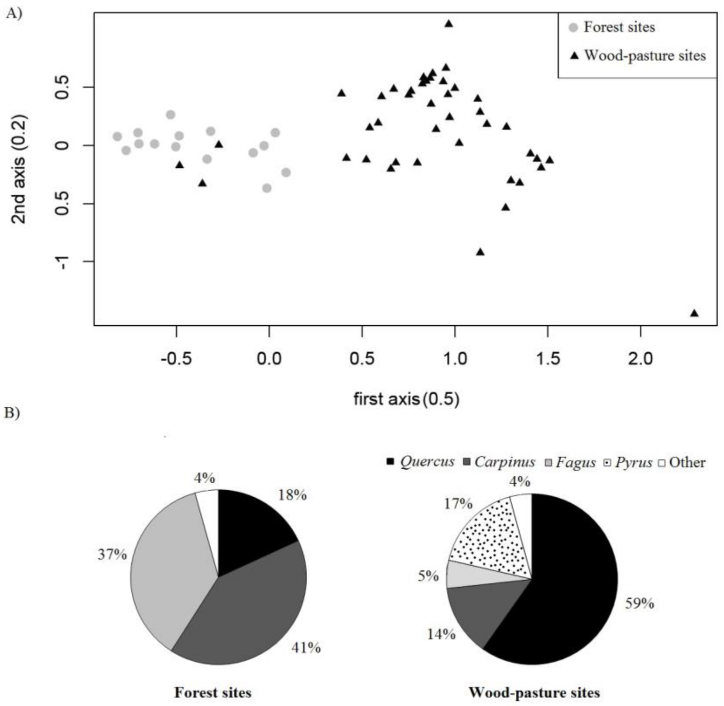

Figure 6.2 Tree community composition in forests versus wood-pastures. A) Illustration of tree communities based on genera composition from forests versus wood-pastures using detrended correspondence analysis. Eigenvalues are given in brackets for each axis. The length of first axis is 3.1 and that of the second axis is 1.7. B) Percentage of the most common tree genera found in forests and wood-pastures.

Smaller (and presumably younger) trees were better represented in forests than in wood-pastures, while larger (presumably older) trees were better represented in wood-pastures (Fig. 6.3). Wood-pastures contained more ancient trees and more trees of conservation value, while only two individuals of such trees were found in forests (Table 6.3). Dead trees were observed in every forest site but 64% of wood-pastures contained no dead trees. The average number of dead trees per hectare for the remaining wood-pastures was 2 (min–max: 1–6) while forest sites contained on average 7 (min–max: 1–16) dead trees per hectare, this difference being significant (t-test, $P < 0.05$).

Table 6.3 The number of ancient trees and trees of conservation value found in the wood-pastures (n = 42) and forests (n = 15). The most common tree genera are presented. Numbers in brackets are sites (i.e. wood-pastures) where trees from that category were observed.

	Truly ancient[a] (DBH ≥ 2 m)	**Conservation value[a] (DBH ≥ 1.5 m)**	**Potentially interesting[a] (DBH ≥ 1 m)**	**Ancient[b]**
Wood-pastures				
Oak (n = 1113)	3 (2)	73 (11)	175 (32)	251 (31)
Hornbeam (n = 255)	1 (1)	0	9 (4)	37 (16)
Beech (n = 100)	0	0	23 (8)	0
Forests				
Oak (n = 883)	0	0	1	1
Hornbeam (n = 1994)	0	0	0	1
Beech (n = 1782)	0	0	0	0

[a] Read (2000)

[b] Farm Environment Plan Guide (2006): DBH ≥ 75 cm for Hornbeam, ≥ 100 cm for Oak, ≥ 150 cm for Beech

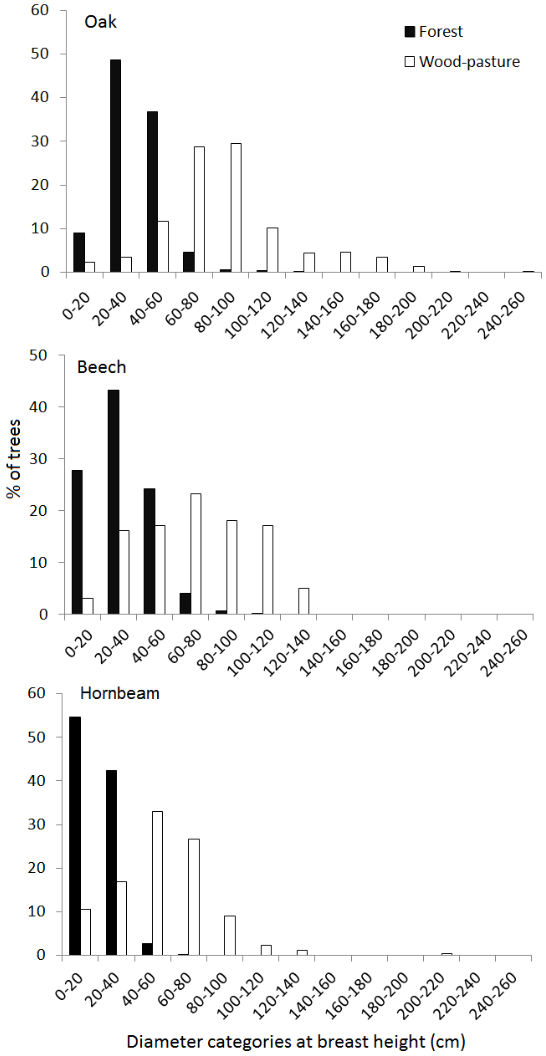

Figure 6.3 The percent representation of the tree size categories in forests and wood-pastures. Only Oak, Hornbeam and Beech are shown because these were the most common trees present in both forests and wood-pastures.

The characteristics and current management of wood-pastures

The 42 wood-pastures covered a total area of 42.21 km^2. Descriptive statistics describing wood-pastures are presented in Table 6.4. Sixty percent of wood-pastures were grazed only by sheep, 21% only by cattle and 14% were grazed by a mixture of livestock (i.e. cattle, sheep, buffalo) (Table 6.4). Evidence for scrub removal (APIA) was found in 88% of wood-pastures (Table 6.4). Management by burning in 2012 was observed in 50% of the wood-pastures (Table 6.4). Comparison of the size of burned versus unburned trees was possible only for Oak and Hornbeam due to insufficient sample sizes for other species. Burned Oaks (mean DBH = 123.93, SD = 39.99, n = 76) and dead Oaks (mean DBH = 123.28, SD = 48.73, n = 13) were significantly larger than healthy Oaks (mean DBH = 83.56, SD = 32.59, n = 1014) (t-tests, $P < 0.001$ and $P < 0.05$ respectively; 10 trees injured by humans and struck by lightning were not included). Burned Hornbeams (mean DBH = 70.95, SD = 28.51, n = 10) were larger than unburned Hornbeams (mean DBH = 53.03, SD = 26.03, n = 243 two dead trees were not included) (t-test, $P < 0.05$). Across all wood-pastures sampled (though not necessarily within our survey sites), we observed that more than 40 ancient Oaks (sensu Farm Environment Plan Guide 2006) collapsed following uncontrolled pasture fires in 2012. In 2012 we recorded tree (Oak and Hornbeam) cutting activities in five wood-pastures, two of them being ancient (sensu Farm Environment Plan Guide 2006).

Table 6.4 Descriptive statistics for variables used to characterize the wood-pastures. CV = coefficient of variation.

Variable	Mean	SD	CV
Condition variables			
Tree density	7.60	4.80	0.63
Number of scattered trees	260.64	230.44	0.88
Proportion of dead trees	0.06	0.10	1.72
Tree size	74.25	23.11	0.31
Scrub cover	0.06	0.12	1.90
Woody vegetation cover	0.19	0.14	0.73
Site related variables			
Area	100.50	90.97	0.90
Elevation	543.65	68.21	0.12
Ruggedness	62.75	14.54	0.29
Landscape context			
Forest cover	61	0.23	0.37
Distance to nearest village	1225.17	804.17	0.65
Management related variables			
Scrub cleaning (APIA)	Observed in 88% of wood-pastures		
Livestock	Cattle: 21%, Buffalo: 7% (always mixed with other livestock), *Sheep: 60%*, Mixed: 14.28. No grazing: 5%		
Burning	50%		

Models of wood-pasture condition and composition

For condition-related response variables, the models best supported by the data contained either management variables (M; scrub cover) or variables describing the landscape context (L; proportion of dead trees) (Table 6.5). For the prevalence of particular genera, the best models always included all three groups of variables (M + S + L) (Table 6.5). GLM analysis showed that the proportion of dead trees was positively related to surrounding forest cover (Table 6.6). Moreover the prevalence of Oak, Hornbeam and Beech was positively and the prevalence of Pear was negatively associated with forest cover (Table 6.6). Oak prevalence was negatively and Beech prevalence was positively related to ruggedness (Table 6.6). Distance to the nearest village was related negatively to the prevalence of Pear and positively to the prevalence of Beech (Table 6.6). Oak prevalence was negatively and Pear prevalence was positively associated with elevation (Table 6.6).

Table 6.5 Model selection results for response variables describing different aspects of wood-pasture condition and composition. The best ranked models ($\Delta i \leq 2$) are shown. Log(L) = maximised log-likelihood, K = number of estimable parameters, ΔI = difference in AICc compared with the model with the lowest AICc, *wi* = Akaike weights; S = site variables, M = management variables, L = landscape variables. Variables are defined in the Methods section.

Response variables	Model	Log (L)	K	AICc	Δ_i	w_i
Proportion of dead trees	L	-71.14	4	151.37	0.00	0.60
Scrub cover	M	38.53	4	-67.98	0.00	0.54
Oak prevalence	M+S+L	-254.81	7	526.92	0.00	0.66
	S+L	-258.34	5	528.36	1.43	0.32
Beech prevalence	M+S+L	-114.72	7	246.47	0.00	0.99
Hornbeam prevalence	M+S+L	-173.62	7	364.54	0.00	0.98
Pear prevalence	M+S+L	-169.81	7	356.92	0.00	1.00

Table 6.6 The relationship between the response variables (first column) and the explanatory variables, separately tested using GLMs.

	Livestock type	**APIA clearing**	**Altitude**	**Ruggedness**	**Forest cover**	**Village distance**
Proportion of dead trees	NS	NS	NS	NS	0.47 (0.21)*	NS
Scrub cover	NS	NS	NS	NS	NS	NS
Oak prevalence	NS	-0.50 (0.19)	-0.19 (0.06)*	-0.45 (0.06)**	0.23 (0.06)***	NS
Hornbeam prevalence	-0.92 (0.16)***	0.66 (0.23)**	NS	0.24 (0.06)***	0.67 (0.09)***	NS
Beech prevalence	-1.26 (0.26)***	1.61 (0.53)**	NS	0.56 (0.08)***	0.66 (0.16)***	0.30 (0.13)*
Pear prevalence	0.56 (0.16)***	0.70 (0.28)*	0.39 (0.07)***	NS	-0.61 (0.08)***	-0.17 (0.08)*

NS = non-significant.

*** = $P<0.001$.

** = $P<0.01$.

* = $P\leq 0.05$.

Discussion

In this paper we showed that forests and wood-pastures differed with respect to their tree community structure, typical tree sizes and the prevalence of dead trees. We also showed that sheep grazing dominated wood-pastures while the other livestock (cattle, horse and buffalo) were scarcely used. Burning as a management tool was widely applied, and large trees appeared to be particularly affected by this. Scrub clearance induced by the EU level financial incentives was applied in most wood-pastures. Finally, the prevalence of different species and of dead trees in wood-pastures was related to management, site and landscape related variables.

Wood-pastures versus forests

While wood-pastures were dominated by Oak and fruit trees (mostly Pear), forests had a more balanced proportion of Beech, Oak and Hornbeam. Differences between the tree communities of forests and wood-pastures can be explained the ecology of the trees (Vera 2000), natural prerequisites and the traditional preferences of local people for Oak and fruit trees. The potential primary vegetation in the study region is represented by mixed Oak and Hornbeam, and mixed Beech and Hornbeam forests. Mixed Oak and Hornbeam forests (*Quercus petraea*, *Q. robur*, *C. betulus*) were found on shaded and semi shaded hills while mixed Beech and Hornbeam forests (*F. sylvatica*, *C. betulus*), have a more zonal distribution on valley slopes (Coldea 1992). Historical information suggests that many wood-pastures from Southern Transylvania originate from forest grazing and selective tree removal from forests (Teşculă & A. 2007; Hartel & Moga 2010). Transylvanian Saxons traditionally valued Oak not only for timber production but also (and especially) for the acorns, which were eaten by domestic pigs and sometimes sheep (Dorner 1910; Oroszi 2004). The importance of grazing for wood-pasture formation and their maintenance is well known for other European wood-pastures (Mountford & Peterken 2003).

Our results highlight that the largest trees in Southern Transylvania occurred in wood-pastures: the majority of the surveyed wood-pastures contained ancient Oaks while forest sites contained virtually no such trees. Within the same bioclimatic conditions large trees of a given species are typically older than smaller ones (Gibbons & Lindenmayer 2003; Holzwarth et al. 2013), and hence the relative proportion of young trees appeared to be higher in forests than in wood-pastures. Age estimations for Oaks from the 'Breite' ancient wood-pasture (situated close to the centre of the study region) suggest that a tree with a DBH of ≥100 cm may be at least 200 years old, and the largest Oaks may be up to 700–800 years old (Hartel & Moga 2010; Patrut 2011). The main reason for these size (and age) differences could be the long term management of forests and wood-pastures. In our region trees were maintained on pastures mostly to provide shade for livestock and for their fruit (TH, unpublished results of 110 semi structured interviews in Southern Transylvania). Timber extraction occurred also in wood-pastures, but it was done mainly by pollarding (i.e. cutting branches while maintaining the trunk) (Rackham 1980; Hartel & Moga 2010). This allowed trees to grow and eventually to become large (old). By contrast, forests were traditionally managed for timber production (see Oroszi 2004 for and overview of forest managament by Transylvanian Saxons), and the economic value (in a monetary sense) of trees was and still is important in determining management actions. Old trees were and are removed from forests because their economic value is decreasing as the amount of dead elements and hollows increase with age. Assuring sustainability of the forests by regeneration (naturally 'from seed' or by replanting the cleared parcels) was important both traditionally (Oroszi 2004) and continues to be common practice nowadays (Codul Silvic (Forest Code of Romania), Law 46/2008). However, no mechanisms to re-plant trees (or otherwise support their regeneration) occur in the vast majority of wood-pastures.

Management of wood-pastures

Sixty percent of wood-pastures surveyed in 2012 were grazed only by sheep and 14% by a mixture of livestock (Table 6.4). This is in sharp contrast with traditional grazing systems: Saxons preferred cattle, horses, buffalo and pigs, and typically each of these had its own pastures with specific management practices around a given village (Dorner 1910; and also Heinlein et al. 2005 for selected areas of Bavaria, Germany). Pig grazing stopped in the late 1940s and 1950s, and the number of buffalo dropped after the Romanian revolution in 1989, partly because of mass emigration of Saxons and partly for economic reasons. Cattle grazing also declined sharply in many wood-pastures after 1989 (although less so than for buffalo), and the number of sheep is now higher than ever before in the Saxon region of Transylvania (TH, unpublished results of 110 semi structured interviews in Southern Transylvania). Changes to the traditional grazing systems also have been reported from many European wood-pastures throughout Europe (Plieninger & Schaar 2008; Bergmeier et al. 2010; Costa et al. 2011; Garbarino et al. 2011; Chételat et al. 2013).

Half of the wood-pastures were burned in 2012, and large trees (Oak and Hornbeam) appeared to be most likely to be permanently damaged from this. Fire has been used as a method for pasture clearing in the region since the 16th century (Dorner 1910). However, uncontrolled pasture burning appears to have increased in recent years, even in protected areas, despite being illegal (TH, personal observation).

Wood-pasture condition

Our model selection approach showed that the prevalence of Oak, Beech, Hornbeam and Pear trees in wood-pastures was best explained by models containing management, site and landscape related variables. Oak dominated in wood-pastures with low terrain ruggedness while Beech dominated in areas with high ruggedness. This result can be explained partly by the ecology of these species (see above) and partly by human influence. For example, it is possible that Oak was retained in flatter terrain where accessibility for livestock was high and which contained wet areas often preferred by these animals (especially cattle, domestic pigs and buffalo). Fruit trees (especially Pear) dominated in wood-pastures close to villages (suggesting that accessibility for people was important in creating them) with little forest cover in their surroundings. By contrast, forest cover was an important positive predictor for the abundance of all three forest tree species. A likely explanation is that many, if not most, thinning existing forests created wood-pastures in our region. The pear prevalence was positively associated with the elevation; this is most likely a result of the slight increase of the average elevation toward the Eastern part of the region, where this tree is more abundant. Our result regarding the significant relationship found between the management related variables and prevalence of different tree genera (Table 6.5) is not straightforward: the relationship is likely caused by the fact that local conditions shaped human activity (this being recorded in 2012) and not the other way round. For example, it is possible that wood-pastures where beech and hornbeam dominated were less attractive for grazing, possibly because of steeper slopes or higher woody vegetation density. The grazing system in our region is undergoing rapid changes, and therefore this relationship is likely to change in the future.

The percentage of dead trees was significantly related to forest cover around the wood-pasture. Wood-pastures surrounded by forests may be less accessible for people than the wood-pastures from open landscapes. Traditional rural communities from this region carefully cleared the pastures of dead wood and scrub to maintain pasture quality (Dorner 1910; TH, unpublished results of 110 semi structured interviews in Southern Transylvania). Based on this, it is reasonable to assume that wood-pastures in traditional societies contained dead wood only accidentally and if the scrub was present, it was deliberately maintained (e.g. as occasional firewood or as source of fruits). It is possible that the increase of the dead wood on pastures is the result of the abandonment of pastures, which was very pronounced after the 1989 Romanian revolution. As the continuation of use of pastures and hay meadows is promoted by EU agro-environment incentives, it is likely that abundance of dead wood will decline again in the future in most of wood-pastures from this region.

The biodiversity of the 'Breite' ancient wood-pasture

In the context of wood-pasture conservation, it is important to note that some wood-pastures in our study area have been shown to support a very rich diversity of plants and animals. A wide range of studies have been conducted on one of the wood-pastures also surveyed by us for this paper, namely the 'Breite' wood-pasture, situated near the centre of our study area, near the town Sighisoara. The Breite measures 133 ha and is completely surrounded by deciduous forest. It is dominated by Oaks (mostly *Q. robur*), many of which are over 200 years old (Patrut 2011). Overall, 476 species of vascular plants (Öllerer, 2012), 121 species of macromycetes (from which over 50 species were found on ancient Oaks - Bucşa 2007; Bucşa & Tăuşan 2010), 281 species of Lepidoptera, 40 species of xylophagous beetles (i.e. insects to which wood represents the primary diet), eight species of amphibians, four species of reptiles, 27 species of nesting birds and 38 species of mammals (including Gray Wolf, *Canis lupus,* and Brown Brear, *Ursus arctos*) have been identified in this wood-pasture (synthesized in Hartel & Moga 2010; Hartel et al. 2011). The overall number of species considered rare or protected at national (e.g. Red List) and international (e.g. IUCN, Habitats and Birds Directives) level exceeds 50.

Conclusions and conservation implications

We showed that there were differences between the tree communities in wood-pastures and forests. Ancient trees were found only in wood-pastures, and most of the surveyed wood-pastures contained ancient trees. Historical and current management, traditional preferences of local people, and natural environmental gradients are likely explanations for these differences. Fire appears to be regularly used in pasture management, but our data suggest that uncontrolled fires can negatively affect (or even kill) trees, especially large ones. Further, our data, in combination with historical records, suggest that major changes are underway regarding patterns of livestock grazing in Southern Transylvania, implying that the management of wood-pastures is shifting from traditional practices. Demographic and economic factors are the likely drivers of these recent shifts. Data from one of the wood-pastures in the centre of our study area suggest that the presence of scattered, old trees, in combination with dead trees, scrub and extensively managed grassland, results in a high biodiversity, with species rich communities of woodland and grassland related organisms. To maintain the ecological value of wood-pastures, at least some of the dead trees and scrub need to be maintained - although this runs counter to both traditional practices and current policy incentives. Wood-pastures are currently managed as pastures (or occasionally as hay meadows) and are formally recognized as such at the national level (Romanian Law No. 214/2011). While tree cutting from wood-pastures without a formal institutional agreement is illegal in Romania (Law 214/2011), there is no legal framework that specifically targets the maintenance and regeneration of wood-pastures and the conservation of old (including ancient and veteran) trees. With very few exceptions, wood-pastures are not recognized in the nature conservation policies of the EU and are not protected as distinct land cover types with special management history, ecological and cultural value. Therefore their maintenance as such is not promoted at policy level. Our study shows that ancient wood-pastures are common in our region, and we suggest that they also may be common in other CEE countries. We urge for more wood-pasture inventories and research in other parts of CEE, to develop the knowledge base that is needed for their formal recognition and legal protection.

Acknowledgements

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Appendix A. Supplementary material

Figure 1. KML-file of the surveyed wood-pasture sites shown in Google Earth Map
Figure 2. KML-file of the surveyed forest sites shown in Google Earth Map

Chapter VII

Chapter VII

The conservation value of traditional rural landscapes: The case of woodpeckers in Transylvania, Romania

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'When a dead tree falls, the woodpeckers share in its death.' – Malayan proverb quote

Abstract

Land-use change is a major threat to global biodiversity. Forest species face the dual threats of deforestation and intensification of forest management. In regions where forests are under threat, rural landscapes that retain structural components of mature forests potentially provide valuable additional habitat for some forest species. Here, we illustrate the habitat value of traditional wood pastures for a woodpecker assemblage of six species in southern Transylvania, Romania. Wood pastures are created by long-term stable silvo-pastoral management practices, and are composed of open grassland with scattered large, old trees. Because of their demanding habitat requirements, woodpeckers share habitat with many other bird species, and have been considered as possible indicator species for bird species diversity. We first compared woodpecker assemblages between forests and wood pastures. Second, we grouped features of wood pastures into three spatial contexts and addressed how these features related to the occurrence of three woodpecker species that are formally protected. Woodpecker species composition, but not the number of species, differed between forests and wood pastures, with the green woodpecker occurring more commonly in wood pastures, and the lesser spotted woodpecker more commonly in forests. Within wood pastures, the intermediate context (especially surrounding forest cover) best explained the presence of the grey-headed and middle spotted woodpecker. By contrast, variables describing local vegetation structure and characteristics of the surrounding landscape did not affect woodpecker occurrence in wood pastures. In contrast to many other parts of Europe, in which several species of woodpeckers have declined, the traditional rural landscape of Transylvania continues to provide habitat for several woodpecker species, both in forests and wood pastures. Given the apparent habitat value of wood pastures for woodpeckers we recommend wood pastures be explicitly considered in relevant policies of the European Union, namely the Habitats Directive and the EU Common Agricultural Policy.

Introduction

Human-induced landscape change poses a major threat to global biodiversity (Fahrig 2003; Foley et al. 2005). Forest species face the dual threat of deforestation and intensification of forest management. Woodpeckers are especially sensitive to these changes because they require large home ranges and depend on large trees for nesting and dead wood for foraging (Angelstam & Mikusinski 1994). Consequently, changes in forest structure and cover have caused woodpecker declines worldwide (Conner & Rudolph 1991; Roberge et al. 2008; Lammertink et al. 2009). Because of their demanding habitat requirements, woodpeckers share habitat requirements with many other bird species. Therefore, woodpeckers have been considered as potential indicator species for bird species diversity (Roberge & Angelstam 2006).

In Europe, six out of ten species of woodpeckers are protected under the EU Birds Directive Annex I. While several woodpecker species have declined in Western Europe, Eastern European woodpecker assemblages have remained diverse and stable due to the persistence of large forest tracts (Mikusinski & Angelstam 1998). However, Eastern European forest landscapes are increasingly coming under pressure from more intensive and widespread logging operations (Knorn et al. 2012). Against this background, it is important to understand to what extent the landscape context surrounding forest patches could provide complementary habitat for woodpeckers in Eastern Europe. Many agricultural landscapes in Eastern Europe are characterized by low-intensity subsistence farming that still contain semi-natural vegetation cover, including transitional elements between forest patches such as scattered trees (Tryjanowski et al. 2011). Such relatively complex landscapes have the potential to support high biodiversity. However, the links between biodiversity and land-use are still relatively poorly understood in Eastern Europe (Tryjanowski et al. 2011). Mikusinski and Angelstam (1998) proposed that rural landscapes retaining remnant structures of natural forests could provide valuable additional habitat for species otherwise confined to forests, but little work has specifically tested this claim to date.

One of the most intact traditional rural landscapes in lowland Europe occurs in southern Transylvania (Romania). In this area, traditional wood pastures are of particular interest in terms of their potential habitat value for woodpeckers. Many wood pastures in southern Transylvania are several centuries old; they are composed of open grassland with scattered trees and result from ancient silvo-pastoral management practices. Wood pastures bring together three ecologically important components. First, scattered trees have a disproportionate ecological value, that is their effect on ecosystem functioning is disproportionately large relative to the small area occupied by an individual tree, both locally (Fischer et al. 2010) and at a landscape scale (Manning et al. 2006; Manning et al. 2009). Second, many wood pastures contain large and old trees (Robles et al. 2007; Hartel & Moga 2010), and therefore incorporate structural attributes that support biodiversity elements typical of old-growth forests (Bauhus et al. 2009). Third, wood pastures can provide habitat for both open-country and forest species. Despite their high potential to support biodiversity, the ecological importance of wood pastures, especially in Eastern Europe, remains poorly understood (but see e.g. Mountford & Peterken 2003; Taboada et al. 2006; Bergmeier et al. 2010). However, existing evidence from Western Europe suggests that wood pastures can provide habitat for a range of bird species including woodpeckers and secondary cavity-nesting birds (Robles et al. 2007; Robles et al. 2011).

Here, we document the habitat value of wood pastures for an assemblage of six woodpecker species in Transylvania, Romania. Our specific objectives were to (1) compare woodpecker communities between wood pastures and forests; and (2) assess which features of a wood pasture are particularly important for different woodpecker species. Our findings highlight the conservation value of wood pastures in traditional rural landscapes in Eastern Europe.

Methods

Ethics statement

All necessary permits were obtained for the described study. Permission to survey woodpeckers within the EU *Natura 2000* network was granted by Progresul Silvic, the organisation officially entrusted with the custody of the protected area by the Romanian government. The survey procedure, including the use of playback calls for protected species, was cleared by the ethics committee of Leuphana University Lueneburg.

Woodpeckers were surveyed in 28 wood pastures and 12 forests in Southern Transylvania, Romania (Fig. 7.1a). We sampled a larger number of wood pastures than forests because forests are relatively homogenous, whereas wood pastures differ substantially in structural elements and adjacent forest cover. Furthermore, we were especially interested in which features of a wood pasture affected woodpecker presence and thus chose more sites to comprehensively cover existing gradients within wood pastures. Wood pastures were chosen on the basis of availability and access, and to cover a gradient in surrounding forest cover (min. = 3.3%; max. = 96.8%; mean ± SE = 59.7 ± 4.8%). Within each wood pasture we choose one survey site, located approximately in the centre of the wood pasture, for woodpecker point counts. Forests were chosen on the basis of accessibility, and each forest site was located randomly at a distance of at least 600 m from the forest edge. Wood pastures and forests differed in tree species composition: forests were dominated by oak (*Quercus robur* and *Q. petrea*), hornbeam (*Carpinus betulus*) and beech (*Fagus sylvatica*), whereas wood pastures were dominated by oak and had more fruit trees (mainly pear, *Pyrus pyraster*) (Table 7.1). Trees were larger (and typically older) and occurred at a lower density in wood pastures than in forests (Table 7.1).

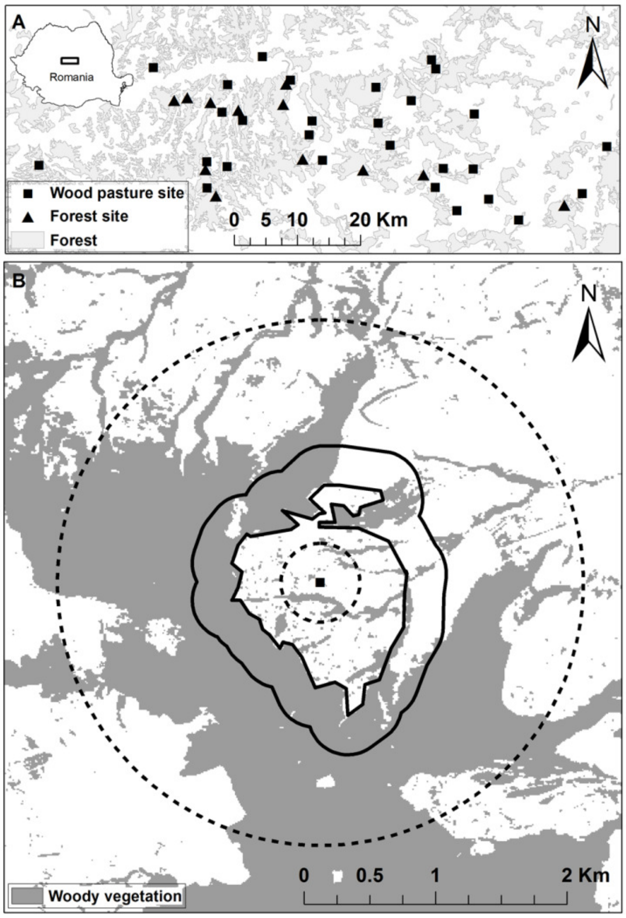

Figure 7.1 Study area and design. A) The location of the study area in southern Transylvania, Romania, and location of the 12 forest and 28 wood pasture sites. B) Example of a survey site, showing the three different landscape extent groups considered in the analyses. The small dashed circle (a 300 m radius around the survey point) represents the local context; solid lines represent the intermediate context (a 300 m buffer from the border of the wood pasture); and the large dashed circle represents the broader landscape context (a 2000 m radius around the survey point).

Table 7.1 Habitat characteristics (mean ± SE) of the two surveyed habitat types: forests (n = 12) and wood pastures (n = 28). The number of trees was calculated as the number of trees in 2 ha; median dbh (cm) was calculated as the mean of the medians measured within 2 ha and between 80 and 300 m; the proportion of a tree species was calculated as the mean of the proportion of a species in 2 ha and between 80 and 300m.

Habitat variables; mean ± SE	**Forest**	**Wood pasture**
Number of trees	1345 ± 255.89	16.54 ± 1.77
Median DBH	25.97 ± 2.69	76.52 ± 4.86
Proportion of oak	0.20 ± 0.03	0.63 ± 0.04
Proportion of hornbeam	0.44 ± 0.05	0.12 ± 0.03
Proportion of beech	0.33 ± 0.07	0.05 ± 0.02
Proportion of fruit trees	0.003 ± 0.001	0.15 ± 0.03

We surveyed the six most common woodpecker species, namely great spotted woodpecker (*Dendrocopos major*), middle spotted woodpecker (*D. medius*), lesser spotted woodpecker (*D. minor*), green woodpecker (*Picus viridis*), grey-headed woodpecker (*P. canus*), and black woodpecker (*Dryocopus martius*). The middle-spotted woodpecker, grey-headed woodpecker and black woodpecker are protected under the EU Birds Directive Annex I. We did not include the Syrian woodpecker (*Dendrocopos syriacus*) and white-backed woodpecker (*Dendrocopos leucotos*) into our study because they are very rare in our study area, and we did not encounter these species during our surveys. We used unlimited point counts enhanced by the use of playbacks of woodpecker drummings and/or calls with an audible range of approximately 150 m. Following 5 minutes of initial listening, playbacks were used in a sequence from smallest to largest species (Kumar & Singh 2010). For each species, a sequence of drummings and/or calls was played three times for 15 seconds, with 15 seconds of silence between playbacks and 1.5 minutes of silence between species. All sites were surveyed three times during appropriate weather conditions between 10 March and 6 April 2012.

To characterize the structure of sites, we recorded the species and diameter at breast height (dbh) of: (1) within 80 m of the survey point (= 2 ha), all trees in wood pastures (1 to 34 trees) or 50 trees in forests (selected randomly in a spiral from the survey point to the edge of 2 ha); and (2) in four strip transects of 10 m width between 80 and 300 m from the survey point in the four cardinal directions (N, S, E, W). In case that no or too few trees were found on a transect we measured between one and four trees close to the transect. For forest sites, we estimated tree density in 2 ha by doubling the count of all trees in two opposite quarters of a 2 ha circle; in wood pastures we counted all trees within 2 ha around the survey point.

All analyses were performed on presence/absence data, pooled across the three repeats, and implemented in the 'R' environment (R Development Core Team 2013). First, we assessed differences in woodpecker species composition and the number of species between forest sites and wood pastures. We conducted nonmetric multi-dimensional scaling based on Sørensen dissimilarity to assess the differences in woodpecker composition between forests and wood pastures using the R package 'Vegan'. We used analysis of similarity (ANOSIM; Sørensen dissimilarities) with 1000 permutations to test for differences in woodpecker composition between forests and wood pastures. In a last step, we modelled the number of woodpecker species as a function of site type using a generalized linear model with Poisson error structure. Although using playbacks and three repeat surveys presumably decreased the incidence of false absences, they cannot be ruled out. This is especially the case for the species that were relatively uncommon (number of times a species was observed at least twice compared to total number of sites present: great spotted woodpecker: 21/33; middle spotted woodpecker: 7/15; lesser spotted woodpecker: 1/9; grey-headed woodpecker: 9/22; green woodpecker: 23/30; black woodpecker: 4/10). Importantly, however, we are confident that detectability did not differ between forests and wood pastures. Potential differences in visibility between forests and wood pastures were of minor importance because: (1) most woodpeckers were identified using calls; and (2) trees did not yet have leaves and visibility in forests was therefore good.

Second, we assessed which features of a wood pasture were important for different species of woodpeckers. The response of the three species protected under the EU Birds Directive to environmental variables was analysed using generalized linear models with a binomial error structure. We did not include the forest sites in these analyses because their habitat characteristics were very different from wood pastures (Table 7.1), and we were specifically interested in which features of wood pastures affected woodpecker occurrence. We did not analyse the three unprotected species because they occurred too rarely or too frequently to be modelled (site occurrence of great spotted woodpecker: 23/28; green woodpecker: 26/28; lesser spotted woodpecker: 5/28)

We hypothesized that different site-specific and landscape variables might influence woodpecker presence, and we therefore grouped our explanatory variables as follows: local context (L) represented by a circle with a 300 m radius around a site; intermediate context (I) represented as an irregular buffer of 300 m around a particular wood pasture; and broader landscape context (B) represented by a circle with a 2000 m radius around a site (Fig. 7.1b). Scales were selected both to match the scale of the wood pastures and to be ecologically meaningful to woodpeckers.

Local variables included the proportion of oak, median dbh, and percent woody vegetation cover. Woodpeckers generally prefer older trees for nesting, with several species showing a particular preference for oak (Kosiński & Kempa 2007; Barrientos 2010). Proportion of oak was estimated by calculating the mean of the proportion of oak in 2 ha and between 80 and 300 m, and median dbh was estimated by calculating the mean of the median diameters measured within 2 ha and between 80 and 300 m. Percent woody vegetation was derived from a supervised classifications of the panchromatic channels of SPOT 5 data (©CNES 2007, Distribution Spot Image SA) using a support vector machine algorithm (Knorn et al. 2009).

Intermediate context variables were related to specific structures of the wood pasture and included the area of the wood pasture and percent woody vegetation cover within a 300 m buffer from the edge of the wood pasture (as a measure of how much of the perimeter of a given wood pasture was adjacent to forest). Adjacency to forest cover was considered important because it may positively or negatively affect the use of wood pastures by woodpeckers.

Landscape variables related to compositional heterogeneity and terrain ruggedness within a radius of 2000 m around the survey point. This radius corresponds to the approximate average valley width of the study area. Birds occurring in farmland mosaics have been observed to respond strongly to landscape heterogeneity (Benton et al. 2003). Compositional heterogeneity was calculated as the standard deviation of the monochromatic channel of SPOT 5 data (©CNES 2007, Distribution Spot Image SA). Terrain ruggedness was calculated as the standard deviation of the elevation. It indicated the geomorphology of the surrounding landscape, and also functioned as a proxy for forest cover because highly rugged landscapes tended to be densely forested.

Prior to modelling we log transformed percent woody vegetation within 300 m of the survey point, as well as area of the wood pasture; we standardized all variables by subtracting their mean and dividing by their standard deviation; and we confirmed that variables were not correlated. We then used an information theoretic approach for model selection to identify models that best explained woodpecker presence (Burnham & Anderson 2002). We constructed eight alternative candidate models arising from all possible combinations of the three groups of variables (I, I+L, I+B, I+L+B, L, L+B, B) and the null model. We used the R package 'AICmodavg' to rank the candidate models, based on AICc values to account for small-sample bias (Burnham & Anderson 2002). Models considered best had an AICc difference (ΔAICc) of less than two from the model with the lowest AICc.

Results

We found differences in species composition between wood pastures and forests in the ordination and the analysis of similarity (NMDS: two axes, stress = 15.1, see Fig. 7.2; ANOSIM: R = 0.141, *P* = 0.009). The R-statistic from the analysis of similarity was only slightly larger than zero indicating that compositional dissimilarity between groups was only slightly larger than within groups. Only two species showed a clear habitat preference: the green woodpecker for wood pastures and the lesser spotted woodpecker for forests (Fig. 7.2). The number of species ranged from two to six in wood pastures, and from zero to four in forests. The mean number of species did not differ significantly between wood pastures (mean: 3.14 ± 0.25) and forests (mean: 2.58 ±0.38) (GLM, z = 0.91, *P* = 0.34).

We detected the middle-spotted woodpecker in 11, the grey-headed woodpecker in 16, and the black woodpecker in 7 of our 28 wood pasture sites. The best ranked models for individual species included the intermediate context group and the null model for the middle spotted woodpecker, and the intermediate context and broader landscape context groups for the grey-headed woodpecker (Table 7.2). Within the intermediate context, the amount of woody vegetation within 300 m from the edge of the wood pasture (i.e. a proxy of the amount of perimeter that was forested) had the largest effect on both species, with both responding positively to a more forested perimeter (Table 7.3). For the black woodpecker only the null model was selected as the best-ranked model (Table 7.2).

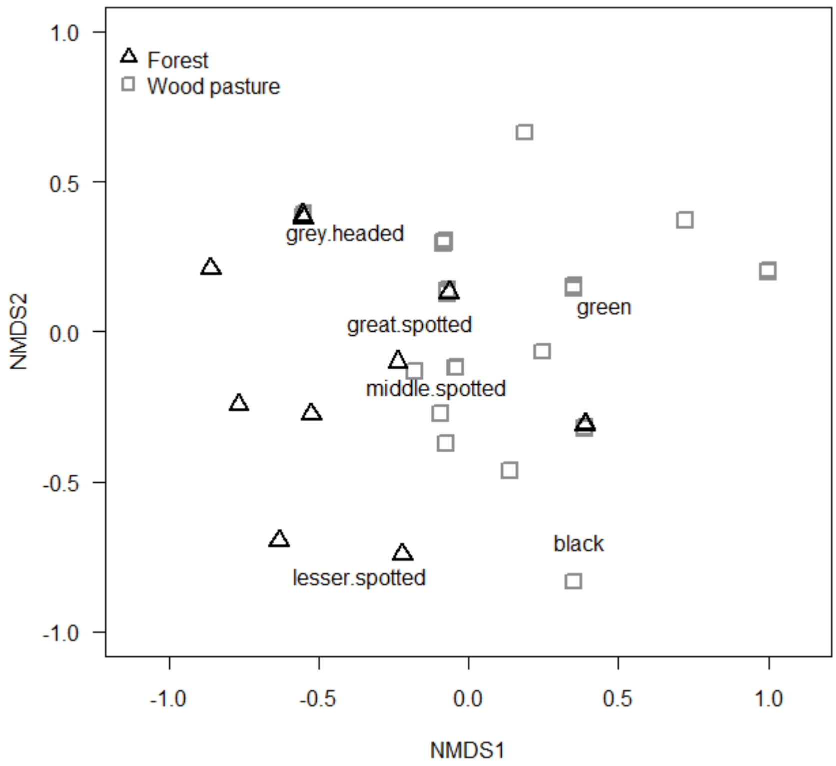

Figure 7.2 Woodpecker species composition in forests and wood pastures. Non-metric multidimensional scaling of woodpecker composition in both forests and wood pastures, based on a Sørensen dissimilarity matrix (two axes; stress = 15.1).

Table 7.2 Full model summary of all the candidate models for the three woodpecker species protected under the EU Bird Directive Annex I.

Species	**Model**	**Log(L)**	**K**	**AICc**	**Δ AICc**	**W_i**
Middle spotted woodpecker	I*	-15.69	3	38.39	0.00	0.479
	Null*	-18.76	1	39.67	1.29	0.252
	B	-16.86	3	40.73	2.34	0.149
	B+I	-15.05	5	42.83	4.44	0.052
	L	-16.77	4	43.28	4.89	0.041
	L+B	-14.28	6	44.58	6.19	0.021
	L+I	-15.73	6	47.47	9.08	0.005
	L+I+B	-13.94	8	51.46	13.07	0.001
Grey-headed woodpecker	I*	-15.06	3	37.12	0.00	0.606
	I+B*	-13.12	5	38.97	1.85	0.241
	Null	-19.12	1	40.40	3.27	0.118
	B	-18.94	3	44.87	7.75	0.013
	L+I	-14.65	6	45.05	7.92	0.012
	L	-18.05	4	45.54	8.42	0.009
	L+I+B	-12.41	8	48.39	11.26	0.002
	L+B	-17.95	6	51.65	14.53	0.000
Black woodpecker	Null*	-15.75	1	33.64	0.00	0.701
	L	-13.91	4	37.56	3.91	0.099
	I	-15.33	3	37.66	4.02	0.094
	B	-15.60	3	38.21	4.56	0.072
	L+B	-12.65	6	41.31	7.67	0.015
	I+B	-14.52	5	41.76	8.12	0.012
	L+I	-13.56	6	43.12	9.48	0.006
	L+I+B	-11.62	8	46.76	13.12	0.001

Best ranked models ($\Delta_i < 2$) are marked with *.

Model: L = local context; I = intermediate context; B = broader landscape context; Null = null model

Model summary: Log(L) = the maximised log-likelihood, K = number of estimated parameters; AICc: Akaike's Information Criterion corrected for small sample bias; ΔAICc: difference in AICc compared with the model with the lowest AICc; W_i: Akaike weights.

Table 7.3 Model coefficients (and standard errors) of the environmental variables included in the best ranked models in binomial GLMs for the middle spotted and grey-headed woodpecker.

		Model terms				
Species	**Model**	***(Intercept)***	**Size wood pasture**	**Woody vegetation in perimeter**	**Hetero-geneity**	**Ruggedness**
Middle spotted woodpecker	I	-0.58 ± 0.45	0.40 ± 0.48	1.03 ± 0.52		
	Null	-0.44 ± 0.39				
Grey-headed woodpecker	I	0.34 ± 0.45	-0.25 ± 0.43	1.31 ± 0.55		
	I + B	0.48 ± 0.51	-0.47 ± 0.51	2.41 ± 0.98	0.001 ± 0.51	-1.27 ± 0.72

Model: I = intermediate context; B = broader landscape context; Null = null model

Discussion

Our findings highlighted that traditional wood pastures, as well as forests, provide useful habitat for woodpeckers in southern Transylvania. The value of wood pastures was particularly evident for the green woodpecker, which was more likely to occupy wood pastures than forests. This finding is consistent with earlier work by Rolstad et al. (2000) who suggested that home ranges of the green woodpecker were often confined to meadows and pastures. The diet of the green woodpeckers consists of ants, and it actively selects foraging sites with a high ant biomass (Rolstad et al. 2000; Alder & Marsden 2010). High ant abundance occurs in grazed semi-natural grasslands (Dauber et al. 2006), whereas forests typically support lower ant abundances than open areas (Rolstad et al. 2000). Furthermore, the green woodpecker avoids foraging in areas with tall and dense vegetation (Alder & Marsden 2010). Thus, the structure and management of wood pastures support optimal foraging habitat for the green woodpecker (and possibly for other species specialized on ants).

The lesser-spotted woodpecker was more strongly associated with forests than wood pastures. Although the home ranges of the lesser spotted woodpecker sometimes include open areas, the species typically avoids open areas for foraging (Wiktander et al. 2001). The lesser spotted woodpecker feeds on insects such as aphids, beetle larvae and ants, which are often found in dead wood (Angelstam & Mikusinski 1994). This suggests that wood pastures could provide potential foraging habitat for the lesser spotted woodpecker, and foraging requirements therefore cannot explain why the species appeared to avoid wood pastures. A possible alternative explanation is that the lesser-spotted woodpecker may avoid wood pastures to reduce predation risk. Other authors have suggested that the lesser spotted woodpecker appears to select locations with lower predation risk (e.g. forests compared to more open wood pastures) over locations with higher energetic profitability (Olsson 1998 cited in Wiktander et al. 2001).

However, wood pastures may be used by other woodpecker species typically associated with forest environments, as demonstrated in Spanish dehesas for the middle spotted woodpecker (Robles et al. 2007). Indeed, we found no difference in the number of species between wood pastures and forests, and all three woodpecker species protected by the EU Bird Directive Annex I (and typically considered to be forest-associated) were present in both types of sites.

Surprisingly, environmental variables at different spatial scales had little effect on the presence of protected woodpecker species. The only environmental variable positively related to the presence of two species was surrounding forest cover (especially evident for the grey-headed woodpecker; Table 7.3). The grey-headed woodpecker may preferentially occupy forest stands containing beech (Shurulinkov et al. 2012), which in our study area more frequently occurred in forests rather than wood pastures. It is possible, therefore, that the grey-headed woodpecker selects nest sites in beech trees within forest patches (Kosiński & Kempa 2007) but uses nearby wood pastures for foraging. We observed the grey-headed woodpecker twice or more in only 9 out of the 22 sites in which it was ultimately detected, which may support the notion that it uses wood pastures for foraging rather than breeding. The grey-headed woodpecker forages on ants, although it is less specialized compared to the green woodpecker (Angelstam & Mikusinski 1994) – it is primarily a ground feeder when the ground is free of snow or forages on bark-dwelling insects on dead trees during winter (Rolstad & Rolstad 1995). While it appears that wood pastures should provide good foraging habitat for the grey-headed woodpecker, data on breeding locations would be required to further scrutinize this explanation of occurrence patterns.

Similarly to the grey-headed woodpecker, the black woodpecker also may preferentially select beech trees for nesting (Kosiński & Kempa 2007), and its diet also includes ants (Angelstam & Mikusinski 1994). However, the black woodpecker is likely to use the landscape at a different spatial scale compared to the other two species. It moves over larger areas (Tjernberg et al. 1993) and the intermediate spatial scale chosen in our study may have been too small for this species to show an effect of adjacent forest cover.

Local vegetation structure, including the availability of large trees, is known to influence woodpecker presence elsewhere (e.g. Pasinelli 2000). The lack of association of woodpecker species with local variables in our study may reflect that wood pastures contain enough old trees to provide critical habitat elements such as dead wood and food resources (Angelstam & Mikusinski 1994) - the amount of old-growth elements thus apparently did not limit woodpecker distribution.

Habitat fragmentation by loss of forests has been hypothesized to be one of the major causes of forest bird declines (Robinson et al. 1995). Because woodpeckers have large home ranges, they may be highly sensitive to forest fragmentation (Pettersson 1985; Wiktander et al. 1992). Given the widespread occurrence of woodpeckers throughout our study area, our results suggest that woodpeckers are likely to perceive the landscape as largely unfragmented: (1) we found no difference in the number of species between forests and wood pastures; and (2) environmental variables such as ruggedness (a proxy for landscape level forest cover) had little effect on the three threatened woodpecker species. Broad-leaved forest cover in our study area is approximately 42%, and existing evidence suggests that fragmentation effects becomes severe only well below this threshold (Tjernberg et al. 1993; Andrén 1994; Wiktander et al. 2001). For example, the black woodpecker was largely insensitive to fragmentation in a highly fragmented landscape with only 26% of forest cover (Tjernberg et al. 1993). Moreover, scattered trees are available throughout the agricultural mosaic, very likely providing effective functional connectivity between forest patches (Manning et al. 2006). Because we lack information on reproductive performance of woodpeckers in wood pastures compared to forests, we cannot make inferences about the quality of wood pastures as breeding habitat for woodpeckers. Nevertheless, our results suggest that wood pastures provide important feeding habitat for woodpeckers and probably provide connectivity between different forest patches.

Conservation implications

Despite their high cultural and natural values, wood pastures are declining rapidly throughout Europe (Bergmeier et al. 2010). Considering their important values for a range of species (Taboada et al. 2006; Paltto et al. 2011; Robles et al. 2011; Horák & Rébl 2013), the conservation of wood pastures should be addressed in relevant policies and directives. For woodpecker conservation specifically, we recommend that conservation policies focus not only on maintaining mature forests but also recognize the complementary value of wood pastures that have retained old-growth structures. There are a few national conservation policies for wood pastures (e.g. Goldberg et al. 2007), but to date there is no pan-European conservation policy (Bergmeier et al. 2010).

To improve the conservation status of European wood pastures we suggest they should be considered explicitly in two major EU policies: (1) the EU Habitats Directive; and (2) the EU Common Agricultural Policy, specifically with respect to agri-environment payments. Currently, wood pastures are inconsistently considered in the EU Habitats Directive, and the Directive does not include Romanian wood pastures (Bergmeier et al. 2010). Although the ecological effect of some agri-environment payments is still debated (Kleijn et al. 2006), when appropriately targeted, they can provide a useful tool for farmland biodiversity conservation (Donald & Evans 2006). In many member states of the EU, agri-environment payments exist for management of extensive pastures, which typically provide subsidies for clearing woody vegetation to maintain extensive grassland environments. However, such payments may inadvertently pose a threat to wood pastures, because scattered tress can fall victim to the clearing process (legally or accidentally, pers. obs.; (Blom 2012)). More carefully specified agri-environment schemes could stimulate the conservation of trees in extensively managed pastures, thereby recognizing their keystone role for a wide range of organisms (Manning et al. 2006).

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Chapter VIII

Chapter VIII

Brown bear activity in traditional wood-pastures in Southern Transylvania, Romania

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Ursus (2014), 25:43-52

'We're going on a bear hunt!
We're gonna catch a big one!
I'm not afraid!
Are you?
Not me!'
– Children's song,
Michael Rosen

Abstract

During the past century, habitat fragmentation and increased human impacts have reduced populations of large carnivores throughout the world. Although bears have been extirpated from human-dominated landscape in most parts of Europe, they still occur in multiuse cultural landscapes in Southern Transylvania, Romania. Wood-pastures - grazed permanent grasslands with scattered or clumped trees and shrubs - are important elements of these cultural landscapes and provide habitat for a wide range of species. However, wood-pastures are under threat from land-use change, including intensified agricultural use and land abandonment. In 2012 we assessed the level of activity of brown bears (*Ursus arctos*) and environmental factors influencing bear activity in 54 wood-pastures in Southern Transylvania. As an index of bear activity, we measured the proportion of anthills that were destroyed by bears. The variables were combined in 3 groups (anthropogenic effects, local variables, and landscape context) to test which group most strongly influenced bear activity. Bear activity was found in 47 (87%) wood-pastures. Bear activity was best explained by variables describing the landscape context, with proximity to the Carpathian Mountains, terrain ruggedness, and amount of surrounding woody vegetation positively related to bear activity. Local variables (distance to forest edge and anthill density) had no effect, and surprisingly, variables related to anthropogenic features (distance to major roads, distance to villages) were positively related to bear activity (albeit weakly). Most of the wood-pastures in Southern Transylvania were used by bears for foraging on ant larvae. For the conservation of brown bears in Southern Transylvania, it is important to maintain large areas of forest but also consider cultural landscape elements such as wood-pastures. To conserve European wood-pastures, we suggest they be explicitly considered in national nature conservation policies and in major European Union (EU) policies such as the EU Habitats Directive.

Introduction

Habitat fragmentation and increased human impact have reduced populations of large carnivores throughout the world (Breitenmoser 1998; Woodroffe 2000). The brown bear (*Ursus arctos*) is Europe's largest carnivore, but has been displaced from human-dominated landscapes in most parts of Europe (Swenson et al. 1995; Zedrosser et al. 2011; Kopatz et al. 2012). Most remaining populations are confined to mountainous regions and heavily depend on major conservation efforts (Swenson et al. 2000; Zedrosser et al. 2001). Thus, the need to protect the brown bear in Europe remains a priority (Zedrosser et al. 2011; Krofel et al. 2012), even though the species has been listed in Annex II and Annex IV of the European Union (EU) Habitats Directive (92/43/EEC) since 1992. Although bear populations are now increasing in some areas (Zedrosser et al. 2011), agricultural intensification and habitat fragmentation, resource extraction, road development, recreation development, and urban expansion still threaten Europe's remaining bear populations (Swenson et al. 1995; Breitenmoser 1998; Zedrosser et al. 2001).

Romania has the largest national brown bear population in Europe (excluding Russia; Chestin 1999; Spassov & Spiridonov 1999), estimated by the International Union for Conservation of Nature, to be stable at approximately 6,000 individuals (Huber 2007). In Transylvania, bears occur not only in large forest patches, but also in multi-use cultural landscapes. However, potential landscape changes such as intensified agriculture, deforestation, and planned new highways could negatively affect Transylvania's bear population (Swenson et al. 2000; Ministry of Agriculture Forestry and Rural Development and the Ministry of Environment and Water Management [MAPDR and MMGA] 2005).

Changes in land-use also pose a major threat in multi-use cultural landscapes such as the traditional grazing systems of wood-pastures (Plieninger 2007; Bergmeier et al. 2010). Wood-pastures are grazed permanent grasslands with scattered trees and shrubs or with groups of trees and shrubs, and important elements of cultural landscapes in Europe (Bergmeier et al. 2010). Wood-pastures are used by a wide range of species, including many threatened species (Tucker & Evans 1997; Wegener 1998; Olea & San Miguel-Ayanz 2006; Bergmeier et al. 2010; Dorresteijn et al. 2013). Plants, invertebrates, and birds are the most commonly studied species in wood-pastures but, apart from some publications mentioning use of the Spanish dehesas by Iberian lynx (*Lynx pardinus*; Olea & San Miguel-Ayanz 2006; Bergmeier et al. 2010), relatively little is known about the use of wood-pastures by large carnivores. To our knowledge, this is the first ecological study focusing on the use of wood-pastures by large carnivores.

Wood-pastures in Southern Transylvania (Fig. 8.1) are generally open, with a density of approximately 8 trees/ha (Hartel et al. 2013). Some wood-pastures are surrounded by forest, while others are situated within open pastures or, more rarely, arable fields. Wood-pastures in Southern Transylvania are mainly grazed by sheep, cattle, and sometimes goats and buffalos in moving herds. The main tree species are oak (*Quercus* spp.) and beech (*Fagus sylvatica*), but also fruit trees such as wild pear (*Pyrus silvestris*) and hornbeam (*Carpinus betulus*). Characteristic shrub species are hawthorn

(*Crataegus monogyna*), blackthorn (*Prunus spinosa*), blackberry (*Rubus* spp.) and dog rose (*Rosa canina*; Hartel et al. 2013). Most of these trees provide potential food sources (mast and fruits) for brown bears.

Anthills are also typical elements of woodpastures, and the larvae within these provide an important source of protein for brown bears in spring (Swenson et al. 1999). The most common antspecies in grasslands (such as the wood-pastures in Southern Transylvania) include yellow meadow ants (*Lasius flavus*), black garden ants (*L. niger*), *L. paralienus*, and pavement ants (*Tetramorium* cf. *caespitum*; B. Markó and K. Erös, Babes-Bolyai University, Cluj-Napoca, Romania, unpublished data). Three of these (*L. flavus*, *L. niger*, and *T.* cf. *caespitum*) are probably consumed by bears, based on the abundance of nests in the field, the abundance of individuals in the nests, and the amount of larvae and pupae (B. Markó , personal communication).

Wood-pastures in Southern Transylvania thus contain several useful elements for brown bears: (1) their heterogeneous character provides a wide variety of food sources including ant larvae in spring, fruits and berries in the summer, and hard mast during autumn; (2) groups of trees or shrubs provide immediate refuge for bears (Swenson et al. 2000); and (3) they are used extensively by grazing livestock in moving herds (Hartel et al. 2013), meaning that pastures are not fenced and are accessible for bears.

To date, it is largely unknown which environmental variables explain bear activity in cultural landscapes such as wood-pastures, and at which scales these variables are important. To fill this knowledge gap, we investigated bear activity in wood-pastures in Southern Transylvania. We aimed to ascertain (1) whether, and to what extent, wood-pastures were used by brown bears; and (2) which environmental variables, and at which scale, could explain bear activity in wood-pastures.

Figure 8.1 Typical wood-pasture in southern Transylvania, Romania.

Methods

Study area and site selection

We conducted the study in Southern Transylvania, Romania. Southern Transylvania is a plateau surrounded by the Carpathian Mountains. We investigated bear activity in 54 wood-pastures around the town of Sighisoara (Fig. 8.2). The study area was chosen because of the widespread occurrence of wood-pastures and available information about them (Hartel & Moga 2010).

We defined wood-pastures as pastures with scattered trees and shrubs, or with groups of trees and shrubs (Bergmeier et al. 2010). To locate wood-pastures, we used published literature (Hartel & Moga 2010) as well as CORINE pasture distribution data (CORINE landcover; European Environment Agency [EEA] 2006) and satellite images of the area (Google Earth). We selected wood-pastures with a broad gradient in percentage surrounding forest cover. Within each wood-pasture, we established 2–6 transects, depending on the size of the wood-pasture (<30 ha = 2 transects; 30–80 ha = 3 transects; 80–130 ha = 4 transects; 130–180 ha = 5 transects; >180 ha = 6 transects). At each site, we placed one transect 7 m from, and parallel to, the forest edge and one in the centre of the pasture. Additional transects were placed randomly via Geographic Information System and were typically separated by several hundred meters. Each transect was 400 m long and 6 m wide.

To quantify bear activity, we documented the proportion of anthills disturbed by foraging activity (i.e., we counted all destroyed and intact anthills in each transect). This method was developed and successfully used by the Mammal Conservation Workgroup of the "Milvus Group" Bird and Nature Protection Association for monitoring bear activity in Transylvania (http://milvus.ro/Mammal_Conservation). In each transect, we noted the coordinates in longitude and latitude using a Global Positioning System at 100-m intervals, and recorded the number of intact anthills (diam > 25 cm, ht > 15 cm) and destroyed anthills in the previous 100-m segment. All surveys were conducted from 1 May to 24 June 2012.

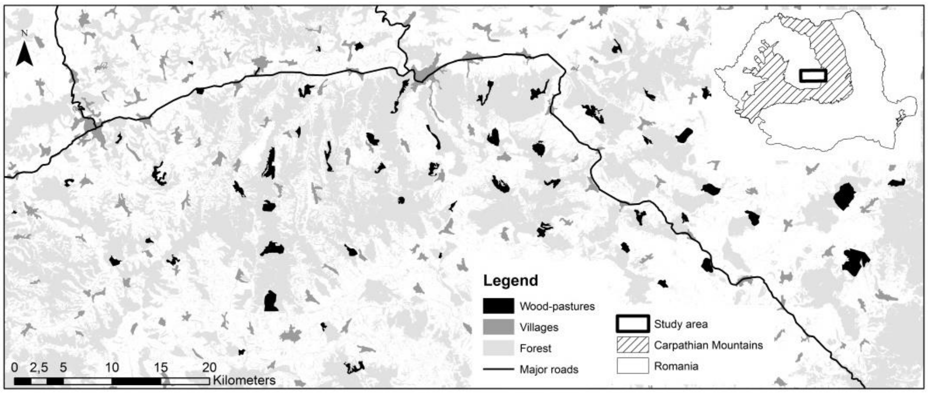

Figure 8.2 Study area in southern Transylvania, showing Romania, the Carpathian Mountains, forest areas, villages, major roads, and locations of the 54 wood-pasture sites.

Environmental variables

Bears are known to react to both human activity (e.g. Clevenger et al. 1992; Nellemann et al. 2007; May et al. 2008) and environmental conditions (Slobodyan 1974; Swenson et al. 2000), and we assumed based on their large range size (Preatoni et al. 2005) that they are sensitive to multiple spatial scales. Therefore, to investigate which combination of variables best explained bear activity in wood-pastures, we grouped our explanatory variables as follows: (1) anthropogenic variables (AV), (2) local variables (LV), and (3) variables describing the (broader) landscape context (LC). Each of the variables was calculated based on the midpoints of each 100-m segment.

We used anthropogenic variables to describe disturbance, measured as the shortest distance to village limits and major roads, based on each midpoint. For local variables, we estimated the proportion of woody vegetation cover within a 300-m-radius circle and measured the distance to forest edge (using CORINE forest data from 2006 [EEA 2006]), as a proxy for distance to shelter, from each segment's middle point. We also accounted for possible effects of the total number of anthills/100 m by including them as a local variable, because bears might be more attracted to pastures with more anthills. Finally, landscape-context variables included woody vegetation cover and terrain ruggedness within a 3-km radius around each segment's midpoint, as well as distance to the Carpathian Mountains, measured from each segment's midpoint to the edge of the Carpathian Mountains. Both woody vegetation cover and ruggedness may be important with respect to the availability of sheltering habitat and a wider variety of food for bears. Woody vegetation and distance to the Carpathian Mountains may be important for connectivity to a larger (source) population and to dens at the higher altitudes. We derived woody vegetation from a supervised classification of the monochromatic channels of SPOT 5 data (ECNES 2007; Distribution Spot Image SA, Toulouse, France) using a support vector machine algorithm (Knorn et al. 2009). We calculated terrain ruggedness as the standard deviation of the elevation (Advanced Spaceborne Thermal Emission and Reflection Radiometer [ASTER] Global Digital Elevation Model Version 2 [GDEM V2]; Land Processes Distribution Active Archive Center, Sioux Falls, South Dakota, USA).

Modelling bear activity

As an index of bear activity, we quantified the proportion of destroyed anthills relative to the total number of anthills in each 100-m segment of each transect. The resulting data structure therefore was nested, with 4 segments/transect, and several transects per site (i.e., pasture). Thus, we modelled activity at the transect level to simplify the structure of random effects to 2 nested levels (transect/site). We used a binomial error distribution for the response data. All statistical analyses were implemented in the R environment (R Development Core Team 2013), and generalized linear mixed models were fitted using the package 'lme4' (Bates et al. 2014).

To account for the nested data structure, we initially included site as a random intercept in the model, while in a second model we accounted for potential changes in activity over time by including Julian date as a random slope. Using both date and site as random factors at the same time was not meaningful because they were redundant, meaning each site was sampled on a specific date. Because site explained a greater amount of variance and arrived at more parsimonious models based on initial Akaike Information Criterion (AIC) comparisons, we used the model that included site only as a random intercept.

Distance to forest and anthill density were strongly skewed; therefore, we log-transformed these variables before modelling. Furthermore, we standardized all predictors by subtracting their mean and dividing by their standard deviation to make the estimates comparable. Because of a strong correlation between distance to forest edge and woody vegetation within a 300-m-radius circle (Spearman rank correlation; r = -0.68), we removed woody vegetation from the group of local variables.

We used an information theoretic approach for model selection to identify models that best explained bear activity (Burnham & Anderson 2002). We constructed 7 alternative candidate models, which considered all possible combinations of the 3 groups of variables (AV, LV, LC). We used the R package AICmodavg (Mazerolle 2012) to rank the candidate models, based on AICc values to account for small-sample bias (Burnham & Anderson 2002). The AICc values of the best models were compared with the AICc values of the null model (which only included the random effects). Marginal and conditional R^2 values were calculated following the procedure outlined by Nakagawa and Schielzeth (2013), using the package 'arm' (Gelman et al. 2013).

Results

The size of wood-pastures ranged from approximately 11 ha to 475 ha, but most were 30 - 130 ha (<30 ha, n = 8; 30–80 ha, n = 19; 80–130 ha, n = 15; 130–180 ha, n = 6; >180 ha, n = 6). We surveyed 199 transects, with a mean of 3.6 transects/wood-pasture. Anthills were found in all pastures; only 1 of the transects and 21 of the 100-m segments contained no anthills.

We detected destroyed anthills in 87% of wood-pastures and in 42% of transects. We found 29,236 total anthills, including 1,771 destroyed anthills (6%). Within a given 100-m segment, we recorded up to 300 anthills, and up to 127 destroyed anthills (mean total no./100 m ≈ 37; mean destroyed/100 m ≈ 2).

Mean distance to nearest village was 2 km (range = approx. 150 m to approx. 5 km). The distance to the major roads averaged 35 km (120 m to 100 km). The average distance to the Carpathian Mountains was 30 km (11 - 64 km) and average distance to forest edge was 0.2 km (7 m to 1.8 km). The woody vegetation cover within 3,000 m averaged 44% (7% - 84%). Terrain ruggedness averaged 57 m (32 - 105 m). All models including explanatory variables performed better than the null model (Table 8.1). The best supported model (w_i = 0.66) included anthropogenic variables (AV) and landscape context variables (LC). Despite the low difference in AIC values (<2) between the best supported and the second-ranked model, we selected the most parsimonious one (i.e., containing AV and LC), because the contribution of the third group of variables (local variables; LV) was unlikely to contribute meaningful explanatory power to the model (Burnham & Anderson 2002; Arnold 2010), given the low estimates of the local variables (Table 8.2). The marginal (i.e., only explaining the fixed effects) R^2 value for the top model was low, but the conditional R^2 value (explaining the random and fixed effects) was 70% (Table 8.1).

Table 8.1 Summary of candidate models influencing brown bear activity in wood-pastures, southern Transylvania, Romania, including the maximised log-likelihood (Log(L)), number of estimable parameters (K), AICc, difference in AICc compared with the model with the lowest AICc (Δi), and Akaike weights (w_i). Also shown are the marginal and conditional R^2 values for all models. (AV = Anthropogenic variables, LV = Local variables, LC = Landscape context).

Model Summary

Model	**Log(L)**	**K**	**AICc**	**Δi**	**W_i**	**Marginal R^2**	**Conditional R^2**
AV+LC	-1778.81	7	3571.77	0.00	0.66	0.125	0.695
AV+LV+LC	-1777.46	9	3573.16	1.39	0.33	0.117	0.686
LC	-1785.53	5	3581.15	9.38	0.01	0.179	0.754
LV+LC	-1784.27	9	3582.68	10.90	0.00	0.167	0.7434
AV+LV	-1801.77	6	3615.64	43.87	0.00	0.017	0.451
AV	-1804.16	4	3616.36	44.60	0.00	0.014	0.446
LV	-1811.37	4	3630.78	59.00	0.00	0.003	0.429
Null Model	-1813.90	2	3631.81	60.04	0.00		

Landscape context was the most important variable group related to bear activity. Within this group, the distance to the Carpathians Mountains had the strongest effect. Bear activity increased with decreasing distance to the mountains. Also terrain ruggedness and percentage of woody vegetation cover in the surrounding area were positively related to bear activity in wood-pastures (Table 8.2). Bear activity was slightly correlated with the anthropogenic variables: we found higher bear activity in wood-pastures that were closer to villages, but almost no relationship between bear activity and proximity to roads.

Table 8.2 Best-supported model describing which variables explained bear activity in wood-pastures, southern Transylvania, Romania. The table shows the model coefficients (and standard errors) that were included in the best ranked models. Also shown is the second ranked model to highlight the low estimates for both variables of the group 'local variables' (AV = Anthropogenic variables, LV = Local variables, LC = Landscape context).

		Model terms						
Model	**(Intercept)**	**Distance to villages (km)**	**Distance to roads (km)**	**% Woody vegetation 3km**	**Terrain Rugged-ness**	**Distance to mountains (km)**	**Distance to forest edge (km)**	**Anthill density (no./0.06ha)**
AV+LC	3.67±0.33	-0.26±0.07	-0.05±0.06	0.29±0.10	0.74±0.11	-0.90± 0.30		
AV+LC +LV	3.72±0.34	-0.26±0.07	-0.05±0.6	0.30±0.10	0.72±0.11	-0.82±0.30	-0.02±0.03	-0.14±0.09

Discussion

Our findings show that most of our studied wood-pastures in Southern Transylvania were used by brown bears, confirming the relevance of non-forest habitats (Slobodyan 1974; Swenson et al. 2000). In the following, we reflect on the survey method used, the variables related to bear activity, and potential conservation implications arising from our work.

Survey method

Ants are a well-known food resource for bears (Swenson et al. 1999), and several previous studies have used destroyed anthills as a sign for the presence of bear activity (Munro et al. 2006; Ciarniello et al. 2007). Using the proportion of destroyed anthills to total anthills turned out to be a pragmatic, but apparently useful, index of bear activity in our study, despite the unequal distribution of anthills across wood-pastures. Ideally, we would have compared our activity estimation with some other measure of bear activity known to be reliable. No such validation was possible during the study period; however, a similar study in 2012 in the same study area also used destroyed anthills as an index for bear activity and generated ecologically consistent results (I. Dorresteijn et al., Leuphana University, Lueneburg, Germany, unpublished data). Studies on the foraging behavior of bears have shown that bears often target ants during spring when numbers of pupae increase (Noyce et al. 1997; Swenson et al. 1999). Because of the harsh winter of 2011 - 2012, ant larvae were available later in the season than expected, and bear foraging activity increased rapidly a few weeks after we started our surveys. Additionally, it is plausible that activity may increase over time because we considered anthills during a period of 2 months. Both of these issues could result in a positive effect of time on observable foraging activity; however, such effects were corrected for by including site (and thus implicitly survey date) into our model as a random intercept. We did not take into account potential selection by bears for different ant species, but we acknowledge that this may occur and warrants addition research.

Variables influencing bear activity in wood-pastures

Bear activity in wood pastures was primarily driven by environmental variables at the landscape level and to a lesser extent by anthropogenic variables. The importance of the landscape variables is consistent with previous studies, which also identified mountainous regions (Posillico et al. 2004), as well as rugged and forested areas, as being preferred by bears for shelter, denning sites, and food (Clevenger et al. 1992; Preatoni et al. 2005; Nellemann et al. 2007; May et al. 2008). The relative lack of importance of local variables was surprising because we hypothesized that distance to the forest edge could be an important element of escape over (Swenson et al. 2000) and expected higher bear activity closer to forests. However, the relatively small size and complex shape of many of the studied wood-pastures may have ensured that the forest edge was generally within close proximity. Alternatively, the structurally rich wood-pastures could have provided adequate shelter. Anthill density also did not appear to influence bear activity; fewer anthills than were available in our study area are potentially still sufficient in number to attract bears.

Bear occurrence has been shown to be negatively affected by human presence (Clevenger et al. 1992; Preatoni et al. 2005; Nellemann et al. 2007; May et al. 2008). However, bear activity in our study was slightly positively associated with the anthropogenic variables we measured. This unexpected finding may be explained by most villages in Southern Transylvania being small and characterized by low human density (approx. 34 inhabitants/km^2; Arion et al. 2011). Elsewhere in Europe, bears inhabit areas with human densities up to 80 people/km^2 (Linnell et al. 2001). In Scandinavia, female brown bears avoided human activity, but used human-dominated landscapes for foraging when human density was low, especially at night (Martin et al. 2010). Such temporal niche partitioning between humans and bears may also occur in Southern Transylvania. Major roads were generally several kilometers from the wood-pastures we studied, which may explain their lack of influence on bear activity.

Conservation and management implications

Although bears typically require large, relatively undisturbed areas, we showed that they also use wood-pastures within the cultural landscapes of Southern Transylvania. This is likely because they represent a source of protein (ants), which is critically important in the otherwise mainly vegetarian diet of the brown bear in temperate latitudes (Bojarska & Selva 2012). Wood-pastures likely provide fruits and hard mast as food sources for brown bears in summer and autumn, but our investigations were confined to the spring season when ants and their larvae were most abundant and sought after by bears.

Wood-pastures in Southern Transylvania face several threats. Land abandonment leads to forest succession, which will eventually displace species linked to the semi-open character of wood-pastures, including fruit trees and invertebrates such as the grassland ant species (both food sources for bears). On the other hand, intensified agricultural use, including clearing of tree cover or fertilization, will destroy the semi-open and semi-natural character of the wood-pastures, which is also a threat to animal and plant species (Manning et al. 2006). Additional threats to wood-pastures are illegal burning in spring, which often leads to the destruction of trees, and legal and illegal cutting of trees. These factors, in combination with occasional overgrazing and clearing the pastures of shrubs as part of the requirements for EU agricultural subsidies, leads to a lack of regeneration (Hartel et al. 2013). Within Europe, some types of wood-pastures (such as the dehesas in Spain and the Fennoscandia wooded pastures in Scandinavia) are protected under the EU Habitats Directive, but there is no consistent conservation approach across Europe (Bergmeier et al. 2010). A loss of Transylvania's wood-pastures could mean the loss of some food sources for bears, but also the loss of a buffer between forest patches and villages, which could increase conflicts between people and bears. The protection and management of wood-pastures in Southern Transylvania thus could make a positive contribution to bear conservation.

Finally, a critical aspect of bear conservation in Southern Transylvania is the maintenance of a network of large and well-connected forest patches. Southern Transylvania has approximately 30% forest cover, which offers several potential corridors to nearby mountains and source populations. We did not observe a negative effect of roads on bear use of wood-pastures. However, other studies have shown the negative impact of highways, and newly planned major highways could negatively impact bear activity by causing habitat fragmentation (Kaczensky et al. 2003; Karamanlidis et al. 2011). Further research is needed on the importance of connectivity of forest patches to the mountains and how it may be affected by improvements and/or alterations to the local road network.

Zedrosser et al. (2011) suggested that bear conservation in Europe should not be restricted to only wild and remote areas, because few such areas remain (Linnell et al. 2005), and because other landscape elements can provide useful complementary conservation opportunities. Our findings suggest this is the case for our study area, where bears also use wood-pastures within multi-use cultural landscapes.

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Section C: Human-bear coexistence

This Section includes Chapters IV (see Section A) and IX and takes a social-ecological systems approach to understand how links between the social and ecological parts of the system affect human-bear coexistence. Chapter IV aims to obtain an overview on human-bear conflicts in the study region. Chapter IV also examines whether the level of perceived conflict relates to bear activity and whether it influences attitudes of shepherds towards bears. Chapter IX aims to gain a more holistic understanding on the social drivers shaping the willingness of people to coexist with bears.

Chapter IX

Chapter IX

Social factors mediating human-carnivore coexistence: Understanding coexistence pathways in Central Romania

Ine Dorresteijn, Andra Ioana Milcu, Julia Leventon, Jan Hanspach, Joern Fischer

In revision in AMBIO

'Nature is not a place to visit, it is home.'
– Gary Snyder

'Well, for us the bear is like our neighbor. Like the neighbor at home. There's no difference between my neighbor and the bear that comes every second evening. We're somehow used to him.' – Shepherd from Vidacut, Southern Transylvania

Abstract

Successful carnivore conservation depends on the degree to which humans and carnivores can coexist. Facilitating human-carnivore coexistence does not only depend on the biophysical environment but also on understanding the social factors that shape human-carnivore coexistence. Focusing on Central Romania, we aimed to understand social drivers of coexistence by applying a combined approach of questionnaires (n = 252) and inductive semi-structured interviews (n = 70) to examine human-bear (*Ursus arctos*) coexistence. The majority of respondents had a positive perception of coexistence. The questionnaires revealed general patterns on the most important social drivers, and highlighted four distinct groups of respondents. Perceptions of coexistence were negatively influenced by negative attitudes towards bears, past negative interactions with bears, and perceived risks of damage. Qualitative content analysis of interviews identified three coexistence pathways. These pathways showed different (but not mutually exclusive) ways in which ongoing interactions between the ecological system and the social system shape the willingness of people to coexist with bears. While the connection between humans and the landscape had important mediating effects on perceived coexistence, the generally positive perception of coexistence could be undermined by perceived flaws in official bear management. We suggest that the concept of coexistence pathways, coupled with a comprehensive approach to their analysis, can help landscape managers identify drivers that facilitate or hinder coexistence, and thus target interventions accordingly. This conceptual framework, in turn, may help facilitate human-carnivore coexistence worldwide.

Introduction

Where humans and large carnivores share the same landscape, there are inevitable conflicts: humans experience attacks and predation on livestock, with resultant economic impacts (Thirgood et al. 2005; Holmern et al. 2007); and carnivore populations decline as a result of persecution and growing human pressure on carnivore habitat (Woodroffe 2000; Ripple et al. 2014). Therefore, successful carnivore conservation depends not only on the biophysical environment but also on understanding the social factors that shape human-carnivore coexistence (Treves & Karanth 2003). Importantly, human tolerance towards carnivores is not only shaped by the experience of damage (Hazzah et al. 2009; Dickman et al. 2014; Kansky et al. 2014). Rather, it is constructed through a variety of factors related to economic, aesthetic, ecological, cultural, religious, and intrinsic values ascribed to carnivores (Zinn et al. 2000; Dickman 2010). For example, traditional and cultural differences between pastoralist and agriculturalists lead to differences in their tolerance towards lions in South Africa (Gusset et al. 2008; Lagendijk & Gusset 2008). Moreover, in many places the political environment has added an additional factor influencing human-carnivore interactions, for example through the implementation of top-down conservation management, financial incentives, or tight legislation (Redpath et al. 2012), which may clash with the priorities of rural populations (Skogen et al. 2008; Majić et al. 2011).

To design effective tools that facilitate coexistence, studies need to account for the complexity of social factors that shape it (Dickman 2010). Despite an increasing recognition of the need to integrate social science into understanding the extent of human-carnivore conflicts (Carter et al. 2012a; Inskip et al. 2014), the majority of studies to date have described conflicts or patterns of attitudes towards carnivores, whereas fewer studies have focused on the underlying drivers and impacts of conflict, or on conflict resolution and coexistence (Lescureux & Linnell 2010; Barua et al. 2013; Can et al. 2014). In Europe, such knowledge is particularly important because recent expansions of brown bear (*Ursus arctos*) populations have caused conflicts (Enserink & Vogel 2006; Can et al. 2014), and illegal killing could undermine the recovery of bear populations (Ciucci & Boitani 2008; Kaczensky et al. 2011). To understand coexistence, regions where humans and carnivores have successfully co-occurred for a long time could provide particularly useful case studies (Boitani 1995).

In this study, we aimed to elicit the social drivers of coexistence by taking a combined approach of questionnaires and inductive semi-structured interviews to examine human-brown bear coexistence. We focused on the foothills of the Carpathian Mountains in Transylvania, Romania. Here, people and bears have co-occurred for extended periods of time, and the close proximity of the forest to villages and farmland, as well as the reliance of people on forest ecosystem services (e.g. firewood) provide ample opportunities for human-bear interactions. Furthermore, traditional practices such as shepherding and bee keeping are potential areas of conflict with bears (Zedrosser et al. 2001).

Our specific objectives were (i) to obtain a general overview of how social drivers affect people's perception of human-bear coexistence; and (ii) to generate a deeper understanding of the mechanisms and causal factors underlying people's perceptions of coexistence. One of our key outcomes is the concept of coexistence pathways, which show how ongoing interactions between elements of the ecological system and the social system shape the willingness of people to coexist with carnivores. We outline specific coexistence pathways for our case study, and discuss their potential general relevance for carnivore conservation. In addition, we discuss how the concept of co-existence pathways could be extended to other species and locations by providing a general framework for unpacking the social factors mediating human-carnivore co-existence.

Methods

Our research design was based on a sociological triangulation approach which combined quantitative and qualitative methods to broaden understanding rather than to validate each other (Olsen 2004). In particular, we used quantitative questionnaires to identify general patterns, and inductive, semi-structured qualitative interviews to gain a deeper understanding of the social factors mediating human-carnivore coexistence. We used an inductive approach to generate insights on human-carnivore coexistence, rather than a deductive approach to test specific theories or hypotheses (Pratt 2009). This approach was chosen to construct a holistic framework of understanding that would account for a wide range of social factors that shape co-existence. Indeed, inductive research has previously been useful in gathering detailed information for understanding human-carnivore relationships (Inskip et al. 2014).

Questionnaires for an overview

We used questionnaires to identify general patterns in the social drivers underlying coexistence (objective i), by assessing how combinations of predefined social factors influenced people's perception of current and future coexistence. Questionnaires are useful when the researchers know what they are seeking, give the opportunity to sample many individuals and thereby obtain an impression of average opinions, and simplify the comparison between respondents by enabling quantitative analyses (Huntington 2000). We utilised these strengths by basing questions on social factors we deemed relevant to our study area, including socio-demographic factors, interactions and conflicts with bears, general attitudes, knowledge acquisition and culture, perceived benefits and disadvantages of bears, and bear management (e.g. Kaczensky et al. 2004; Dickman 2010; Redpath et al. 2012; Dickman et al. 2014). For all questions on perceptions we used a 5-point Likert scale (from strongly disagree to strongly agree), whereas for all other questions we either used multiple choice or yes/no answers (46 questions total; Supplementary Material Text S9.1). Questions that could not be answered by the respondent were noted as 'don't know'.

We randomly selected 30 villages of the over 400 villages scattered throughout the 7441 km^2 study area spanning the full range of biophysical and social conditions (Dorresteijn et al. 2014).

The average number of inhabitants per village was 584 (min–max cc. 30–1900) (INS 2011). We aimed to ask 7-10 persons per village for the questionnaires in all 30 villages, based on chance encounters, and obtained 252 responses.

General patterns on how social drivers influenced people's perception of coexistence were analysed using hierarchical agglomerative cluster analysis (Wards clustering based on Euclidean distances: agglomerative coefficient of 0.95) and principal component analyses (PCA). First, we used a cluster analysis to identify groups of people that were similar in their perceptions of the importance of different social factors (questions based on a 5-point Likert scale). We characterized these groups based on their perceptions of coexistence, interactions and conflicts with bears, and socio-demographic factors. Second, we used PCA to extract the main social drivers of coexistence and related these to four groups previously obtained from the cluster analysis. We calculated four separate PCAs for each of the following themes: (i) attitudes towards bears; (ii) cultural values and bear knowledge acquisition; (iii) benefits and disadvantages related to bears; and (iv) bear management (Supporting information Fig. S9.1-S9.4). For each theme, we plotted the first two axes and overlayed them with the four groups from the cluster analysis. Twenty individuals missed one question, and their responses were replaced with imputed values (i.e. the average of the total sample pool). All questions that were answered with 'don't know' where scored with a 3 (neutral opinion about a statement). All statistical analysis were implemented in the 'R' environment (R Core Team 2013).

Semi-structured interviews for in-depth analysis

In contrast to questionnaires, semi-structured interviews give the opportunity to go deeper into certain topics by guiding participants into discussions but allowing the interview to follow the thoughts of the participant (Huntington 2000). Therefore, interviews can generate insights into the mechanisms and causal factors underlying people's perception of human-bear coexistence (objective ii), and can help interpret the patterns derived from questionnaires. Although the interviews were guided to prompt discussions, we allowed for discussions on unanticipated themes. The themes covered were the same as in the questionnaire (Supplementary Material Text S9.2). All interviews were conducted by a local Romanian and Hungarian speaker, digitally recorded, and later transcribed and translated into English.

We aimed to interview 3-4 people per village in a total of 20 villages, and selected the 10 villages with the highest and 10 with the lowest perceived human-bear conflicts as indicated by previous research (Dorresteijn et al. 2014) to ensure a broad gradient in perceived conflicts, and thus a broad range of responses on conflict and coexistence. We purposefully sampled for shepherds, foresters and hunters to obtain a wide variety in human-bear interactions. In total, we conducted 70 interviews.

We analysed the interview transcripts by first grouping all interview participants into three groups regarding their perception of human-bear coexistence (positive, negative and neutral). For ease of communication we only show the results here for people with positive or negative perceptions. We applied qualitative content analysis by coding the interviews for themes using '*NVivo 10*' (QSR International Pty ltd 2012). Coding was conducted in an exploratory way to extract themes that related to those covered in the interview guide as well as to unprompted content or emerging themes. To gain a deeper understanding of the mechanisms driving coexistence, we combined themes in an emergent conceptual framework that included three coexistence pathways. These coexistence pathways reflected how different elements of the social and ecological systems interacted to create mechanisms that shaped human-bear coexistence according to local people. Each coexistence pathway consisted of different themes, and in a second round of coding, we categorized the statements of the participants to the different themes within each pathway.

Results

Social drivers affecting perceptions, based on questionnaires

The cluster analysis revealed four distinct groups of respondents (Fig. 9.1), which differed in their perception of coexistence, interactions with bears, and socio-demographic factors (Table 9.1). The majority of people clustered in groups 1 and 2 and had a more positive perception of current and future human-bear coexistence compared to groups 3 and 4. Respondents from group 1 had the fewest interactions with bears, and respondents from groups 3 and 4 most frequently experienced damage to crops and predation on livestock. The largest proportion of women was in group 1 and the largest proportion of men was in group 2. Respondents in group 4 were oldest on average.

The identified groups revealed that attitudes towards bears, culture and knowledge acquisition, perception of damages and threats, and opinion of management, may be important social drivers influencing people's perceptions of human-bear coexistence. The four groups of respondents were characterized by their position along the main gradients of the four themes (see PCAs in Fig. 9.1; full ordinations can be found in Supporting Information, Fig. S9.1-S9.4). Overall patterns were more similar between groups 1 and 2, who had a more positive attitude towards bears and between groups 3 and 4, who held a more negative attitude (Fig. 9.1). Similarly, groups 1 and 2 perceived bears to be less harmful than groups 3 and 4, while in contrast different beliefs regarding the benefits provided by bears were not reflected in the grouping (Fig. 9.1). Also, responses on the influence of culture, knowledge acquisition, and management had relatively little influence on the grouping. However, group 4 ascribed low cultural importance to bears, and group 3 acquired most knowledge through experience (Fig. 9.1). Opinions on management most importantly were characterized by the desire to be more actively involved, which was especially high for group 2, whereas the overall satisfaction with bear management differed only slightly between the groups (Fig. 9.1).

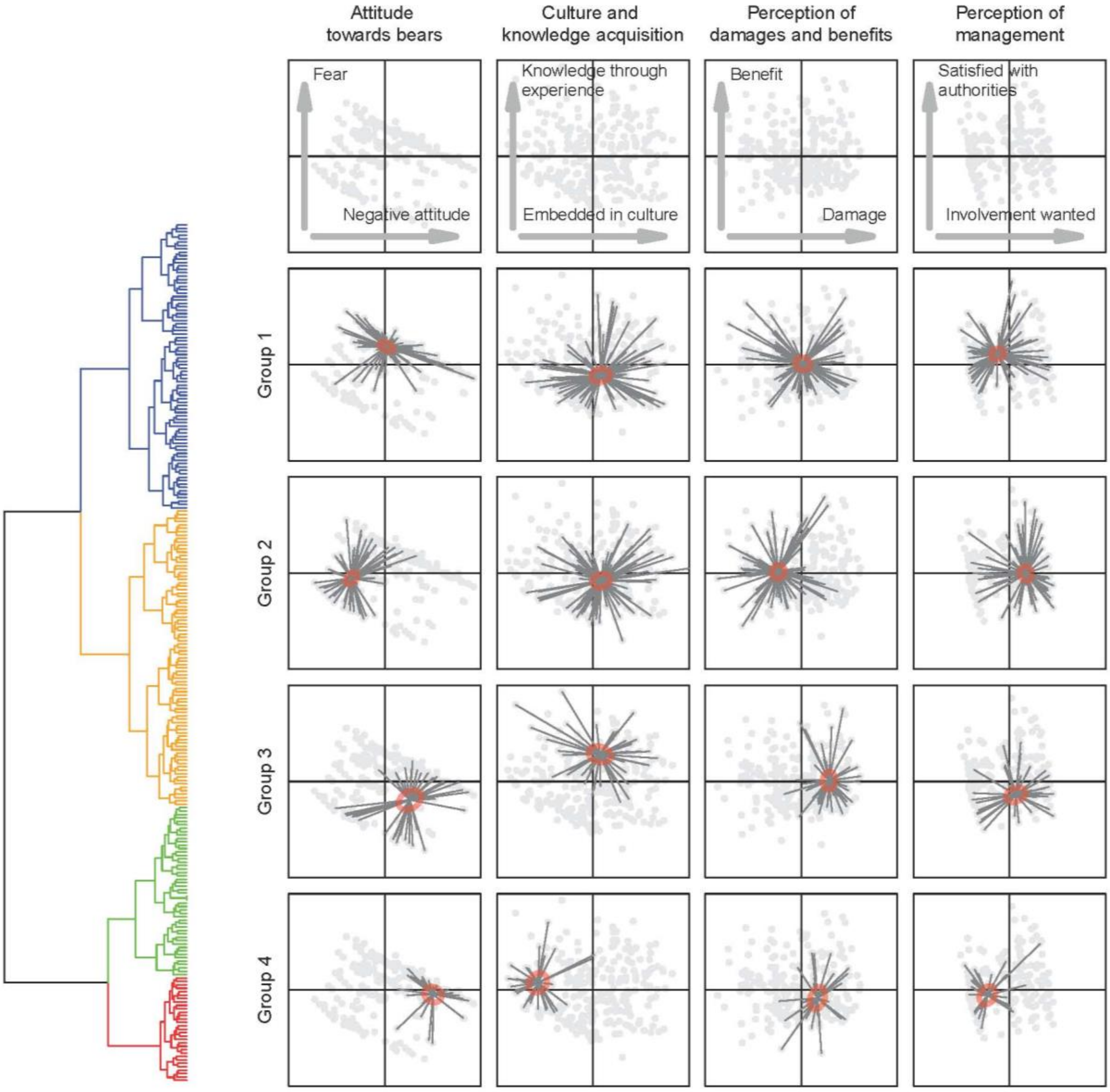

Figure 9.1 Classification and ordination of the 252 questionnaire respondents according to their perceptions of bear-related themes. The left panel shows the dendrogram and the four groups of people derived from hierarchical agglomerative cluster analysis. The other panels show the principal components analyses of the four different themes. The upper row shows the main gradients, whereas the lower four rows show the loadings for each group on the different PCAs. The legs of the spider diagrams indicate each person belonging to a given group and the circle indicates the standard deviation of the weighted average of each group.

Table 9.1 Perception of current and future coexistence, socio-demographics, frequency of actual bear encounters and conflicts, and average knowledge score, of the four different groups derived from the cluster analysis based on the questionnaires. The number of people and the percentage in parentheses within a certain group are given.

	Group 1 (n = 84)	**Group 2 (n = 87)**	**Group 3 (n = 50)**	**Group 4 (n = 31)**
Current Coexistence				
Positive	70 (83)	82 (94)	24 (48)	18 (58)
Negative	14 (17)	4 (5)	25 (50)	13 (42)
Future Coexistence				
Better	9 (11)	20 (23)	2 (4)	2 (6)
No change	35 (42)	44 (51)	15 (30)	7 (23)
Worse	23 (27)	13 (15)	29 (58)	15 (48)
Gender				
Male (n = 181)	46 (55)	78 (90)	34 (68)	23 (74)
Female (n = 71)	38 (45)	8 (9)	16 (32)	8 (26)
Average age	47	46	47	62
Frequent bear observations	7 (8)	22 (25)	19 (38)	9 (29)
Frequent damage to crops, orchards and hives	6 (7)	5 (6)	21 (42)	6 (19)
Frequent attacks on livestock	1 (1)	2 (2)	8 (16)	2 (6)

Mechanisms that shape perceptions, derived from interviews

Coexistence pathways

Similar to the questionnaires, the majority of respondents in the interviews had a positive perception of human-bear coexistence (61%; n = 50), whereas 18 people (25%) had a negative perception, and 10 people (14%) did not have a very strong opinion. Three coexistence pathways emerged from the data and showed how people's attitudes towards different aspects of bears, the human community, and management support or oppose their willingness to live with bears (Fig. 9.2). Furthermore, the pathways related to bears and humans were affected through interactions with the landscape (Fig. 9.2). However, the identified pathways do not predict perceptions of coexistence, and each pathway can lead to both positive and negative perceptions of coexistence, depending on the respondent. Rather, a pathway refers to the mechanisms that create a person's relationship with bears, and how that relationship is perceived depends on how the respondent experiences those mechanisms.

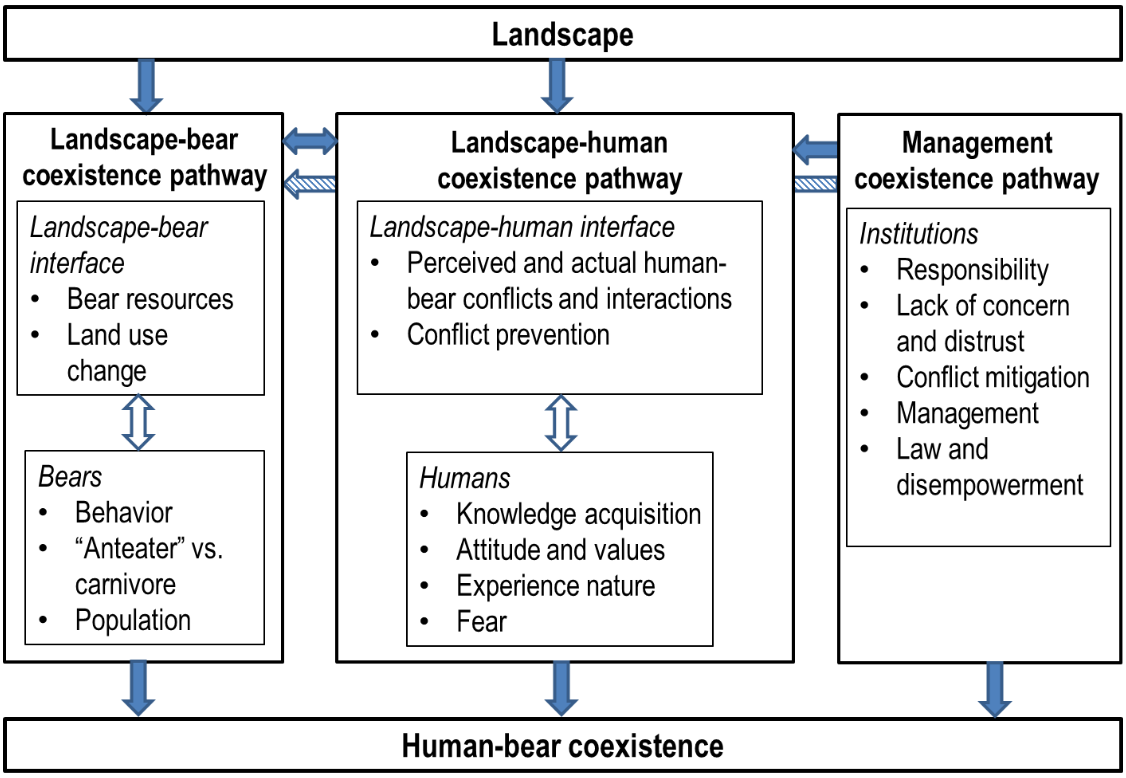

Figure 9.2 Conceptual framework showing three identified coexistence pathways based on qualitative content analyses of 70 interviews. A coexistence pathway shows how ongoing interactions between elements of the ecological system and the social system shape the willingness of people to coexist with bears.

Landscape-bear coexistence pathway

The landscape-bear coexistence pathway contained two components. The first component was related to how people conceptualise interactions between bears and the surrounding landscape, while the second component described people's opinion on bear behaviour and ecology. The pathways demonstrated that coexistence was supported by people's understandings of bear behaviour, and hindered by concerns about inadequate bear habitat, deforestation, and increasing bear populations. The make-up of the surrounding landscape played an important role in people's perception of current and future coexistence (Table 9.2, row a). People with a positive perception deemed forest size and food supply in the region sufficient, while people with a negative perception deemed it insufficient. Deforestation and land-use change were major concerns of both groups because they expected an increase in future conflicts with increasing disturbance to bear habitat (Table 9.2, row b).

The 'peaceful' behaviour of bears and their relatively low damage compared to other species (e.g. wolf) were character traits considered important to coexistence by both groups (Table 9.2, row c). The importance of perceptions of bear behaviour to coexistence was further expressed through the local belief of the existence of two types of bears, namely the primarily vegetarian 'ant-eating bear', and the 'carnivorous bear' (Table 9.2, row d). Coexistence with the ant-eating bear was perceived to be unproblematic, whereas the carnivorous bear was perceived as a dangerous animal. Despite the view of bears being relatively harmless, the perceived increase in the bear population was considered a major problem to coexistence (Table 9.2, row e). Several people even mentioned that bears were only present recently and that they either came down from the mountains or had been brought to the area from overpopulated areas or for hunting purposes.

Table 9.2 Characterizing quotes for the themes within the landscape-bear coexistence pathway. The respondents were grouped into two groups based on their perception of coexistence (positive or negative). The number of people mentioning a given theme is reported and the percentage within each group is given in parentheses. The 'P' or 'N' behind each quote indicates whether the person had a positive or negative perception of coexistence.

	Landscape-bear coexistence pathway		
	Perception of coexistence		
	Positive (n = 43)	**Negative (n = 18)**	**Characterizing quotes**
a. Bear resources	17(40)	6(33)	So long as forests remain I don't think something bad can happen, I don't think the bear will come down in the village (ALM4; P); As long as it has food in the forest it won't eat up the people's potatoes or corn. Then it has no reason to come into the village (SAC2; P); We have only a few, small forests here! There's no place for the bear to stay there (BLA3; N).
b. Land-use change	17(40)	4(22)	The bear typically stays far from humans. Only when it is being attacked or when it has cubs they are dangerous (ALM1; P); I'm thinking about deforestation. You destroy the bears' habitat. It needs to adapt as well. It can't hide anymore; it gets more and more in contact with humans, its hunting area disappears and that becomes a problem. This is how the bear may become a problem! (MAL1; N).
c. Bear behaviour	21(72)	14(78)	The bear is not an animal that attacks without being provoked (BLA1; P); The shepherd was always saying: 'Hey, the bear is coming, the bear is coming!' [I answered]: 'Let it come, man! Let it come' When it comes, it takes [one/ a few]... It's not like the wolf! A wolf, once it jumps into a compound, it kills 4-5-10 sheep, and then it takes one and leaves! But the bear takes one under its arm and leaves (DEA1; N).
d. The anteater vs. the carnivore	12(28)	5(28)	There are only ant-eating bears. They don't attack the sheep (MAL2; P); Doesn't matter what point of view we take on them: As long as they eat plants, there's no problem with them, but once it gets to taste meat, it'll get aggressive (SAC1; N).
e. Bear population	25(58)	12(67)	No, there aren't 'urgent' problems – it's just that they appear more and more often! (VAD3; P); Because there are more of them, it attacks animals and man more often! (SAC4; N); We have knowledge about the fact that bears have been brought here. There haven't been that many bears in the past, by far (ALE1; P); It has been brought here. And then it reproduced (VAL3; N).

Landscape-human coexistence pathway

The landscape-human coexistence pathway also contained two components. The first component described the relationships between people and the landscape (including interactions with bears), while the second component related to people's values. Experiencing bears and nature, and the values ascribed to them, were key in shaping people's perceptions of coexistence. The perception of coexistence was especially positive for people that had positive interactions with bears, while negative perceptions were related to higher livestock predation and the levels of perceived damage and danger by bears (Fig. 9.3a). Interestingly, such damage beliefs appeared to have more influence on coexistence than actual conflict (Fig. 9.3a). In contrast, crop damage and indirect knowledge of conflicts had little effect on the perception of coexistence (Fig. 9.3a). Moreover, preventing conflicts by adjusting human behaviour or using traditional shepherding techniques was seen as an integral component of coexistence by both groups and was mentioned in 62% and 23% of the cases respectively.

Family, community members, and education all played a role in acquiring knowledge on how to live with bears, but people with a positive perception mentioned more often that they learned through experience (Fig. 9.3b). Attitudes towards bears were especially positive for people with a positive perception of coexistence (88% positive attitude; 0% negative attitude), compared to people with a negative perception (19% positive attitude; 28% negative attitude). Non-use values, such as cultural, existence, and historical values, were more often associated with bears than use values by both groups, although these values were more prominent among people with a positive perception (Fig. 9.3c). The genuine and continuous relations between people and nature, where they experience and value nature, seemed to be more important to support coexistence than financial incentives or other use-values: 'Well, for us the bear is like our neighbour. (…) like the neighbour at home. There's no difference between my neighbour and the bear that comes every second evening. We're somehow used to it. (VID4)'; 'When you love nature I don't think that you need a lesson, necessarily, to live with them [bears] (CIN3)'; You don't want to see a dead forest [without animals], right? It's different when you see a bird on a tree, a bear, a deer. 'That makes the difference! You see life in nature! Dead nature is like a village without inhabitants (LAS4)'. Fear was one of the emergent themes but only mentioned by several people (afraid: n = 6; not afraid n= 9), without large differences between the two groups.

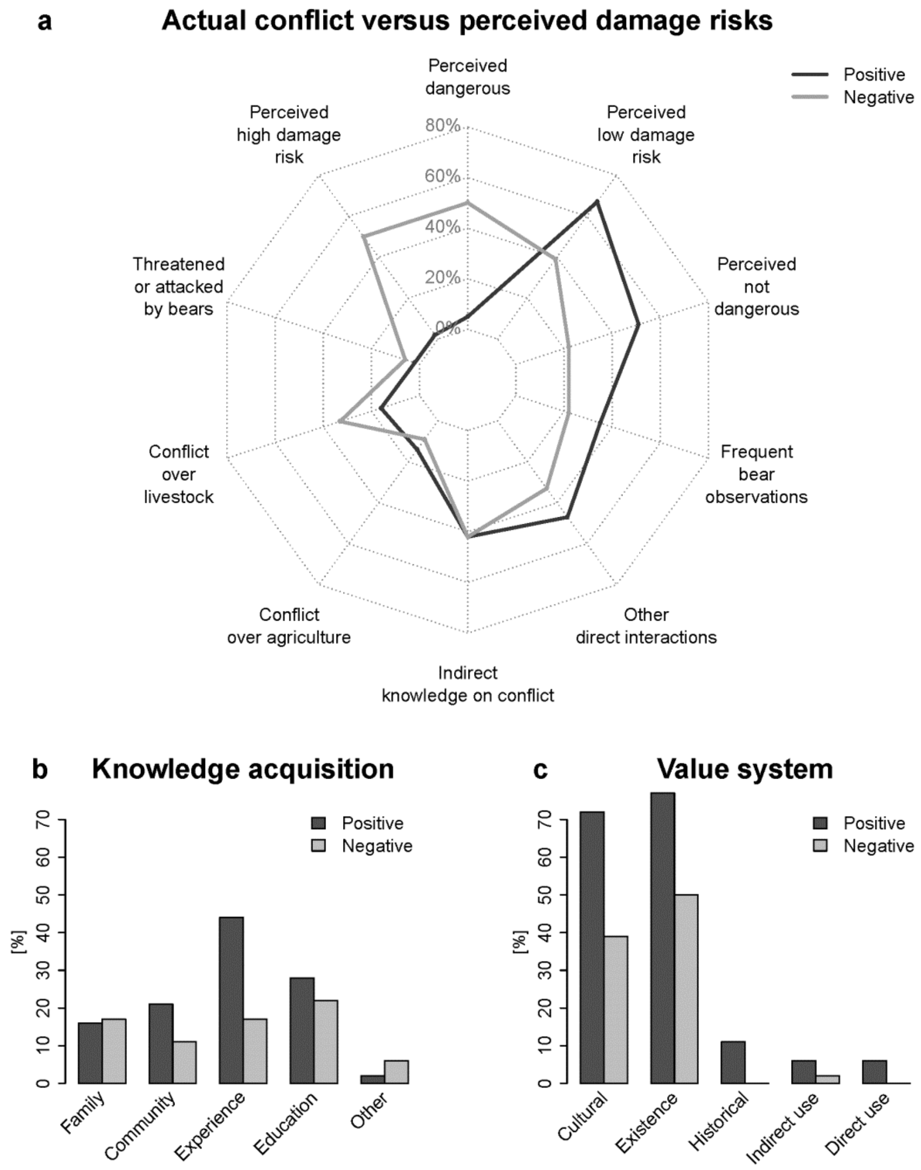

Figure 9.3 Human-bear interactions, bear knowledge acquisition, and values ascribed to bears between two groups of respondents – those with a generally positive perception (n = 43) of human bear-coexistence versus those with a generally negative perception (n = 18). a) The difference between actual conflicts, bear interactions and perceived damage risks. The actual conflicts and bear observations were derived from direct questions asked at the beginning of the interview (see S9.2), while perceived damage risk, other direct interactions, and indirect knowledge of conflicts was interpreted from the interviews. b) Sources where people acquire knowledge on how to live with bears. c) Values ascribed to bears. The importance of cultural values was a question in the interview guide (see S9.2) whereas all other types of values emerged from the interviews.

Management coexistence pathway

The management-coexistence pathway was related to the institutions managing bears and how people perceived these institutions. The majority of people were dissatisfied with current bear management mainly due to a lack of concern for their problems with bears, disinterest from the management authorities, distrust towards them, lack of conflict mitigation, and perceived bad management (Table 9.3). The only 12 people that were satisfied with management believed that the provision of supplemental or divisionary feeding was enough to prevent conflict (Table 9.3, row c). However, the majority of people believed that authorities and hunting organizations failed to mitigate conflict by not feeding the bears (enough), by not controlling the bear population, and by not providing compensation after damage (Table 9.3, rows i-k). Furthermore, six people expressed concerns about trophy hunting, indicating that common people carried the burden of living with bears so that hunting organizations could earn money from trophy hunting (Table 9.3, row l). Although the law and protection status was perceived to aid coexistence by people with a positive perception of coexistence, people with a negative perception viewed it as an artificial tool that they could not influence or even felt disempowered by, because they were not able to take care of problem animals themselves (Table 9.3, row g and m).

Table 9.3 Characterizing quotes for the themes within the management coexistence pathway. The respondents were first grouped into two groups based on their perception of coexistence (positive or negative), and second, based on their opinion whether they were satisfied with current bear management. The number of people mentioning a given theme is reported and the percentage within each group is given in parentheses. The 'P' or 'N' behind each quote indicates whether the person had a positive or negative perception of coexistence.

	Management coexistence pathway		
	Perception of coexistence		
	Positive (n = 11)	**Negative (n = 1)**	**Characterizing quotes**
Satisfied with current bear management			
a. Lack of concern and distrust			
b. Conflict mitigation: compensation	1(9)		Yes, there is the principle when an animal caused damage, the person affected will be compensated. (…)There is this principle of compensation at local level (BLA1;P).
c. Conflict mitigation: feeding	9(82)	1(100)	Yes, they feed them – the 'paznic de vanatoare'. This has been done in the past as well, when they brought them dead animals in a big open pit (CIN1; P).
e. Management: control bear population	1(9)		I'm against their killing and wiping them out, but I think that their population growth should be controlled a bit, as well as their spreading (CIN3; P).
f. Management: legal and illegal hunting	6(55)		Every year we shoot one bear which is pretty ok. That's the money of the hunting association. They pay something to the state as well. Don't know if they pay something to the local community (VAN2; P).
g. Law and disempowerment	5(45)		They'd almost disappeared and [you can shoot them today] only with a special permit where the cause big damage. The wolf, the wild cat, the bear – they're all protected (GRA1; P).

	Positive (n = 21)	Negative (n = 13)	
Dissatisfied with current bear management			
h. Lack of concern and distrust	11(52)	3(23)	But they don't do anything. Nobody cares for nothing! Nothing. I've been to the mayor and he said: 'Should I come and guard them instead of you?'(VID4; P). A bear values four human lives. Yes! Once it has killed four humans, you're allowed to shoot it. Therefore, it is worth four human lives. (VAL3; N).
i. Conflict mitigation: compensation	5(24)	5(38)	The one who has the damage, stays with the damage. Only when the damage is bigger. Only then. Otherwise nobody cares/makes an effort (ALM1; P); I guard the fields that I have paid for, otherwise the wild animals destroy the harvest and nobody pays me the damage. Nobody pays for it! Because we don't have such a big output (...).We don't have a big production but we're living of it. The damages aren't big for them [authorities], but we have to live from this (GHI1; N).
j. Conflict mitigation: feeding	8(38)	4(31)	When there are many bears, they should guarantee them feed so they don't come and attack…I2: They don't guarantee them the feed, that's why they attack! (CRI2; P). They must be fed as well! It's not enough to let them free in the forest, but to feed them as well. The forest authority has fed them in the past! (PRO3; N)
k. Management: control bear population	3(14)	3(23)	Let the bear population grow but keep it under control (AGA1; P). The population management is a bit out of control. I don't think there is a true population management. (…) But the true control was in the past the fact that the bears were kept under a certain number/density in a certain area (MAL1; N)
l. Management: legal and illegal hunting	13(62)	8(62)	For the locals it's just disadvantages, cause the hunters are not from this region so that we can say: 'We keep the earnings from the hunting!' In case they shoot a bear. The problem is that those who shoot the bears are not locals and the truth is that, as far as I see, they don't even care for compensating for losses that locals might have (SAC3; P); The management of bears by the state is not working properly. This could be improved – but as long as a hunter may come to shoot a bear for a certain amount of Euros, without caring that this causes to others a double amount of damage or even a human's life... We'd need to think about all this! Then bears and humans would get along well (MAD1; N).
m. Law and disempowerment	8(38)	5(38)	How should I say: They could live together. Cause you can't do them anything! You can't go in the forest and shoot them. What can you do else, but live next to them (BLA2; P); A human life is worth more than a bear's, Sir. Protecting bears is good, but it's somehow overprotected, Sir (MIH1; N).

Discussion

Our methodological approach provided two different perspectives on the social drivers to human-bear coexistence. First, questionnaires revealed general patterns of the most important drivers within groups of people. Grouping people with similar perceptions may be beneficial for the design of more specific conservation programs targeted at different groups or societal concerns. Second, semi-structured interviews identified coexistence pathways highlighting the causal mechanisms driving people's willingness to coexist with bears. Our research showed that perceptions of coexistence were negatively influenced by negative attitudes, past negative interactions with bears, perceived risks of damage, and respondents' age, which is in line with previous studies (e.g. Naughton-Treves et al. 2003; Kaczensky et al. 2004; Carter et al. 2012a). Nevertheless, other factors such as culture and management were also found to be important.

Our study showed that human-carnivore coexistence is possible, and we identified three major pathways consisting of different social drivers that influenced human-carnivore coexistence from the perspective of the rural population. These pathways serve as a framework for identifying the drivers that shape co-existence and how they interact. Identifying such drivers is essential in shaping management approaches, but also to linking the drivers to broader theoretical and research areas that help to understand how these factors are shaped. Thus the concept of coexistence pathways and the research approach to elicit them offers a conceptual framework to assist in facilitating human-carnivore facilitation worldwide.

Factors mediating coexistence

The two landscape-mediated coexistence pathways showed that conservation management geared towards facilitating coexistence needs to address the beliefs shaping people's tolerance towards carnivores, and maintain or re-establish people's connections to carnivores and nature. Similar to other regions (Lescureux et al. 2011), direct interaction with bears and experiential knowledge acquisition was particularly important in shaping perceptions and beliefs about bears (e.g. behaviour, anteater vs. carnivore, population size).

The importance of direct interactions was further emphasized through reduced tolerance of people that experienced livestock predation, while positive direct interactions were distinctively higher among people with a positive perception of coexistence. Nevertheless, beliefs about bear-related conflicts and damage risk more strongly determined people's perception of coexistence than the actual negative experiences, which has also been observed elsewhere (Kaczensky et al. 2004; Carter et al. 2012a). More importantly, a stronger impact of affective risk perceptions compared to cognitive risk perceptions can influence human behaviour and has been associated to motivations of tiger killing (Inskip et al. 2014). To fully comprehend human-carnivore coexistence therefore requires an understanding of the links between beliefs and risk perceptions.

The landscape-human coexistence pathway also showed that key social drivers for people's perceptions of human-bear coexistence were landscape-mediated attitudes and non-use values.

These were constructed through the existence of genuine links between people and nature, where people valued their surrounding landscape and considered bears as part of their natural heritage. Thus, human-carnivore coexistence may be influenced by factors such as sense of place, and understanding which specific dimensions of sense of place affect human-carnivore coexistence could be an important domain for further research (Williams & Stewart 1998). Such values may be more important drivers of people's perceptions towards carnivores than damage risks (Lagendijk & Gusset 2008; Glikman et al. 2012; Dickman et al. 2014). Tolerance may have been further facilitated by low fear levels, most likely resulting from sharing the landscape with bears (Roskaft et al. 2003; Majić et al. 2011). Moreover, in intact social-ecological systems cultural tolerance to carnivores is not uncommon (Lagendijk & Gusset 2008) and can reduce carnivore extinction risk (Karanth et al. 2010). Such a genuine link to nature is perhaps facilitated by the continuous coexistence with large carnivores over long periods of time. Such long-term coexistence most likely also influenced human behaviour to avoid conflict with bears and prevent livestock predation by using traditional livestock husbandry techniques. Thus, the continuous coexistence with large carnivores presumably shaped the emotional component of human culture to accept and adapt to human-bear coexistence (Glikman et al. 2012). While a history of continuous coexistence cannot be re-created in places where carnivores were once extirpated, a key conservation challenge for settings without a continuous history of human-carnivore coexistence is to (re-)connect people to nature and carnivores.

The management coexistence pathway underlined the perceived gaps in current management and showed that perceptions of (mis-)management could become a major obstacle to coexistence. Consistent with the varying responses to management in the questionnaire, strong negative opinions about current management did not necessarily lead to a negative perception of coexistence. Nevertheless, people's negative opinions on various aspect of current bear management and the feeling of being treated unfairly have the potential to erode the build-up tolerance towards carnivores through human-human conflicts. For example, a perception of inadequate governance can compel people to retaliatory killing (Treves et al. 2002), and poaching in Greece is partly motivated by a desire to defy the authorities (Bell et al. 2007). The approach of seeking coexistence pathways was particularly useful to detect where people perceived mitigation as necessary, which strategies were culturally accepted, and whether current efforts were satisfactory. For example, the beliefs and concerns around an increasing bear population and its control should receive high priority because increasing carnivore populations, rumours about 'secret' carnivore introductions, and inequality over benefits and disadvantages, could reduce people's tolerance towards carnivores (Skogen et al. 2008).

Managing coexistence

To avoid such disagreements between management bodies and local stakeholders, management may facilitate coexistence through participation and education. Distrust and the feeling of disempowerment can be reduced by including people in carnivore management through participatory processes or active management (Treves et al. 2006), and conflicts could be reduced through a holistic set of mitigation strategies geared towards the needs of both humans and bears (Can et al. 2014). Although the interviewed respondents did not express the wish to be involved in bear management, several respondents to the questionnaires showed this aspiration. This potential for co-management of different local stakeholders may increase or maintain tolerance through shared responsibilities, accepted management and good relationships between local people and management bodies (Treves et al. 2006; Lagendijk & Gusset 2008).

Such participation or collaboration could also provide an education component or function. Under the landscape-mediated pathways, experience and education were mentioned as the most important sources to acquire knowledge about bears, and conservation could use these tools to address people's beliefs and concerns to facilitate coexistence. For example, by fostering positive interactions with bears, people may feel less threatened and their tolerance towards bears may increase (Majić et al. 2011). Education can help to foster tolerance towards large carnivores by targeting specific (local) beliefs (Zinn et al. 2008).

Finally, direct actions such as well-regulated and managed options for local people to react against certain 'carnivorous' problem animals could increase empowerment of people (Lescureux & Linnell 2010; Majić et al. 2011). Yet, non-lethal interventions are still more effective in reducing livestock predation rates (Bergstrom et al. 2014), and socially accepted methods like divisionary feeding need more attention. The anger around compensation payments may be harder to resolve when it is governed by perceived 'weak' institutions (Ferraro & Kiss 2002). Although compensation payments or other financial benefits can aid conservation (Dickman et al. 2011), they often do not improve tolerance (Naughton-Treves et al. 2003; Hazzah et al. 2009) or are distributed unequally among society (Hemson et al. 2009). Therefore it could be worthwhile to explore other alternatives for social-ecological systems to manage human-carnivore conflicts such as bottom-up community organized payments like contributions to a local livestock insurance program (Mishra et al. 2003).

Conservation implications

Facilitating human-carnivore coexistence is a conservation goal worldwide. By highlighting the existence of coexistence pathways, and then unpacking these pathways, it is possible to derive meaningful recommendations for approaches to manage coexistence. In our case study, the content of conservation programs should be designed to target these mechanisms in a way that meaningfully engages with people's coexistence perceptions, both in terms of content and how it is delivered. In particular, we advocate for a more collaborative, participatory approach to carnivore management in this area. The approach should foster people's connection to their landscape, provide education on bears and management approaches, and provide transparency around management.

More broadly, we believe that our approach of combining questionnaires for large scale patterns with the concept of coexistence pathways could be extended to regions worldwide. In particular, the inductive approach of generating an understanding of coexistence pathways could be used to understand human-carnivore coexistence for different regions and species. Whether the specific pathways and their outcomes are transferable to other regions remains yet to be tested in future studies. However, by constructing co-existence pathways through inductive research, a broad range of factors that influence co-existence can be identified, and how these factors interact with each other can be understood. We therefore encourage scientists to use interdisciplinary research to obtain a comprehensive understanding of social drivers to human-carnivore coexistence, and thus to work towards holistic conservation efforts. Through the framework concept of coexistence pathways, and a comprehensive analysis of such pathways, landscape managers can identify factors that facilitate or hinder coexistence, and thus target interventions accordingly.

Acknowledgements

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Supplementary Material for Chapter IX

Text S9.1. The questionnaire used for 252 people (original in Romanian).

Please indicate how often:

1. You see a bear
   a) never b) rarely c) several times a year d) often

2. A bear damages your fields/orchards/beehives
   a) never b) rarely c) several times a year d) often e) not applicable

3. A bear attacks your animals
   a) never b) rarely c) several times a year d) often e) not applicable

The following questions will ask if you use any protective measures against bears

Please indicate:

4. Do you use protective measures to prevent damage to fields/orchards/beehives
   a) no b) occasional c) yes d) not applicable

5. Do you use protective measures to prevent bear attacks on your animals
   a) no b) occasional c) yes d) not applicable

6. I go into areas where bears are present
   a) no b) occasional c) yes

7. In my daily life I try to prevent getting into conflict with bears
   a) no b) occasional c) yes

The following questions are general questions about bears

Please answer the following statements to your best knowledge:

8. Bears mainly feed on meat	a) yes	b) no
9. Female bears have young every year	a) yes	b) no
10. Most bears weigh more than 150 kg	a) yes	b) no
11. Bear cubs leave the mother in their first year of their life	a) yes	b) no
12. Bears are protected animals in Romania	a) yes	b) no

The following questions will ask about how you achieve knowledge about bears

Please indicate the extent to which you disagree or agree with the following statements:
1 = strongly disagree; 2= disagree; 3 = neutral; 4 = agree; 5 = strongly agree

13. My parents told me how to live in a landscape with bears	1	2	3	4	5
14. At school we learned about bears and how to live with them	1	2	3	4	5
15. Local authorities provide information on how to live with bears	1	2	3	4	5
16. Local NGO's provide information on how to live with bears	1	2	3	4	5

17. What I know about bears, I learned from experience 1 2 3 4 5

The following questions will ask about bears in your culture

Please indicate the extent to which you disagree or agree with the following statements

18. Bears are important in our culture 1 2 3 4 5
19. Hunting bears is important in our culture 1 2 3 4 5
20. I grew up hearing stories about bears 1 2 3 4 5
21. In the stories I know, bears mainly have a positive character 1 2 3 4 5
22. It is important for our culture that bears persist in the landscape 1 2 3 4 5

The following questions are regarding your feelings towards bears in general

Please indicate the extent to which you disagree or agree with the following statements

23. I generally like bears 1 2 3 4 5
24. It is bad to have bears in Transylvania 1 2 3 4 5
25. Bears should remain part of our landscape in the future 1 2 3 4 5
26. I am afraid to meet a bear 1 2 3 4 5
27. Bears do not have the same rights as humans to exist in the landscape 1 2 3 4 5

The following questions are regarding the usefulness of bears in the landscape

Please indicate the extent to which you disagree or agree with the following statements

28. Bears have a negative impact on hunting opportunities 1 2 3 4 5
29. In areas where there are bears and sheep, bears kill a lot of sheep 1 2 3 4 5
30. Bears damage a lot of orchards and fields 1 2 3 4 5
31. Bears are dangerous to humans 1 2 3 4 5
32. Bears increase the value of a hunting area 1 2 3 4 5
33. Having bears increases tourism in the area 1 2 3 4 5
34. Bears keep the forest clean of dead and sick animals 1 2 3 4 5
35. Bears keep nature in balance 1 2 3 4 5

The following questions are regarding the management of bears

Please indicate the extent to which you disagree or agree with the following statements

36. Bears should be completely protected 1 2 3 4 5

37. Local authorities put in enough effort to prevent damage by bears 1 2 3 4 5

38. Hunting associations put in enough effort to prevent damage by bears 1 2 3 4 5

39. I would like to be involved in the management of bears in the area 1 2 3 4 5

40. We receive compensation for damage by bears 1 2 3 4 5

41. Trophy hunting benefits the entire community 1 2 3 4 5

42. Hunting bears should be possible to everybody in the community 1 2 3 4 5

The following questions are about your opinion on how humans and bears share the landscape

43. In your opinion, how do bears and humans live together in this region
    a. Peacefully without conflicts
    b. Relatively peacefully with tolerance for occasional conflicts
    c. Relatively unpeacefully due to occasional conflicts
    d. Unpeacefully due to escalating conflicts

44. In your opinion, how do you see the relationship between humans and bears in the future?
    a. Better
    b. Worse
    c. No change

45. Explain shortly your answer under question 44

____
____
____

46. Would you like to add any additional information about bears?

____
____
____

The following questions are with respect to you

IX. Gender: a) M b) F
X. Age:______years
XI. Profession
XII. Ethnicity: a) Romanian b) Hungarian c) Roma d)Saxon e) Other, namely:
XIII. Where did you grow up: a) this region b) a different region, but with bears present c) a different region without any bears present

Thank you very much for your participation!

Text S9.2. The interview guide used for semi-structured interviews with 70 people (original in Romanian).

1. The following questions will ask about your experience with bears

Please indicate how often:

1.1 You see a bear
a) never b) rarely c) several times a year d) often

1.2 A bear damages your fields and/or orchards, and/or beehives
a) never b) rarely c) several times a year d) often e) not applicable (no fields/orhards/beehives)

1.3 A bear attacks your animals
a) never b) rarely c) several times a year d) often e) not applicable (no animals)

1.4 Which other animals cause problems in the village? Do you think these problems are worse than the problems caused by bears?

____

____

____

2. (Traditional ecological) knowledge on how to live with bears

Romania is a special country regarding bears because it has one of the largest populations in Europe. Furthermore, Transylvania is especially unique, because people and bears live alongside each other and share the same landscapes. This is very different from Western Europe. There are few bears in Western Europe, and in many places they have been hunted to extinction. However, at the moment in many places bears are returning to Western Europe. Therefore, we would like to know and learn more on how you manage to live together with bears in Transylvania.

2.1 How do you manage to live together with bears?

2.2 Where and how do you learn to share a landscape with bears?

3. Which factors could disturb human-bear relationships

The Transylvanian country side has changed rapidly over the last years. For example, tourism from foreign countries has increased and the architecture of the houses has changed. In your opinion, are there certain changes that have changed or might change the relationships between humans and bears?

3.1 Do you think the way people and bears live together now is different from the past?

3.2 Do you think people and bears can live together in this region in the future?

3.3 What do you think are the major factors that could change the way people currently live with bears?

4. Cultural values and attitudes towards bears

In some countries bears are important for their culture and there are stories and believes around bears. For example, Sleeping Bear Dunes, a huge sand dune in America, is named after a Native American legend. A female bear and her cub swam across a big lake (Lake Michigan). Exhausted from their journey, the bears rested on the shoreline and fell sound asleep. Over the years, the sand covered them up, creating a huge sand dune. Or for example, in Finland and Russia the bear is the national animal. In your opinion, does the bear play an important role in your culture?

4.1 Are bears an important part of your culture?

4.2 Can you remember any particular stories that include bears? Which one and what kind of character did the bear have?

Germany and Switzerland have had similar recent experiences with bears. In both countries one bear came back and lived in the country for a while. However, in both countries they decided to shoot the bear as it was classified as a problem bear and a threat to human safety. How do you feel about this approach?

4.3 What would you do in this case? What are your feelings in general towards bears?
4.4 Do you think it is important that bears persist in the Transylvanian landscape in the future?

5. Management of bears

Not everybody in a country, region or village is affected in the same way by sharing the landscape with bears. Do you think that there are any benefits or disadvantages of sharing the landscape with bears?

5.1 Are these benefits or disadvantages equally distributed between community members?

5.2 Do local authorities/hunting associations help to prevent damage caused by bears? Do they take care to close the difference in the distributions of benefits/disadvantages indicated in the previous question?

People living in countries that lack large carnivores such as bears are often very impressed by the presence of these animals. Therefore, many countries have developed tourism based on large carnivores. This includes guiding tourists around the landscape with the chance to see and photograph carnivores, or tourists pay for a license to hunt for carnivores and they can take home the fur and parts of the skeleton (trophy hunting). Are there any of these examples present in your village?

5.3a If yes, are they managed well and does the community benefit from this? Who benefits?
5.3b If no, do you see a future for tourism based on bears in this region?

The following questions are with respect to you

I. Gender: a) M b) F
II. Age:
III. Profession
IV. Ethnicity: a) Romanian b) Hungarian c) Roma d)Saxon
V. Where did you grow up: a) this region b) a different region, but with bears present
c) a different region without any bears present

Thank you very much for your participation!

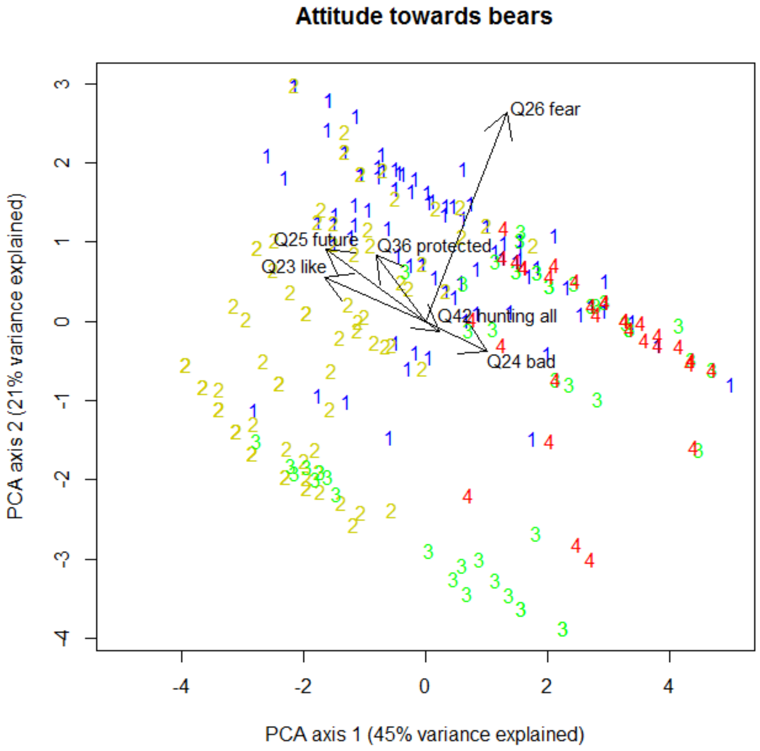

Figure S9.1 Principal Component Analyses of all questions reflecting the participant's attitudes towards bears. The numbers reflect the four different groups derived from the hierarchical agglomerative cluster analysis. The 'QX' indicates the question from the questionnaire in Supporting Information Text S9.1. The PCA was based on the following six questions: 23-26, 36, 42.

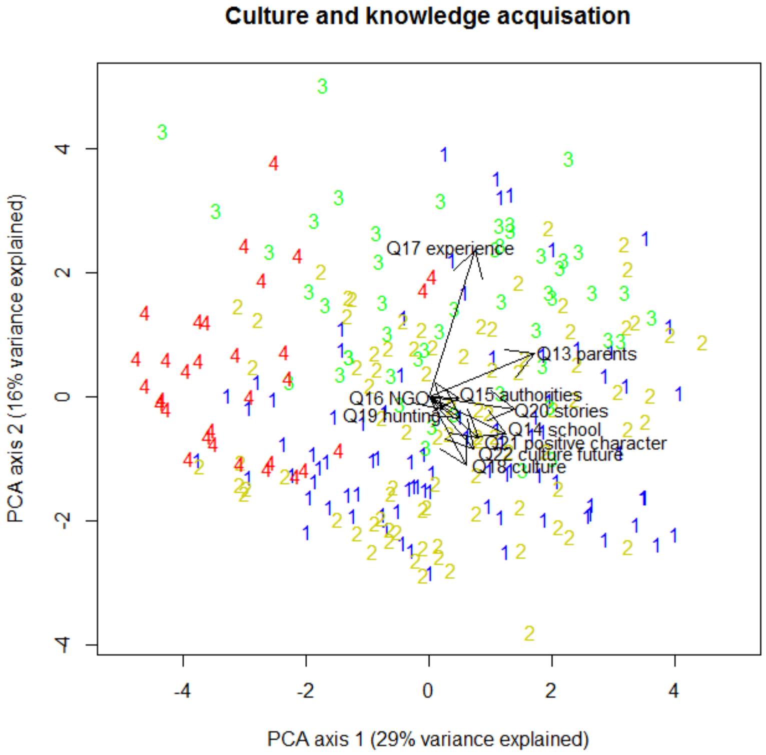

Figure S9.2 Principal Components Analysis of all questions reflecting the participant's perception of cultural values of bears and knowledge acquisation about bears. The numbers reflect the four different groups derived from the hierarchical agglomerative cluster analysis. The 'QX' indicates the question from the questionnaire in Supporting Information Text S9.1. The PCA was based on the following six questions: 13-22.

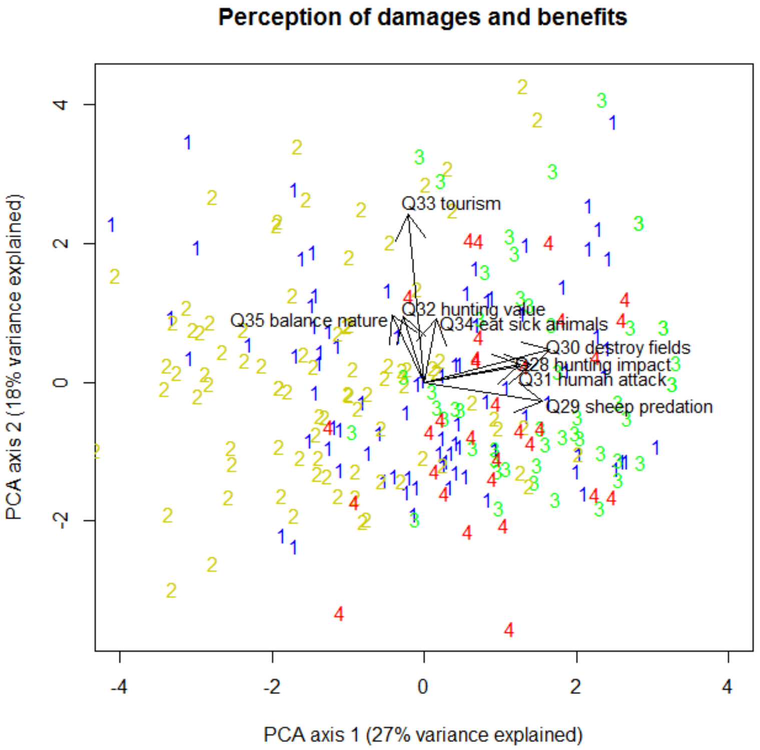

Figure S9.3 Principal Components Analysis of all questions reflecting the participant's perception of bear-related benefits and disadvantages. The numbers reflect the four different groups derived from the hierarchical agglomerative cluster analysis. The 'QX' indicates the question from the questionnaire in Supporting Information Text S9.1. The PCA was based on the following six questions: 28-35.

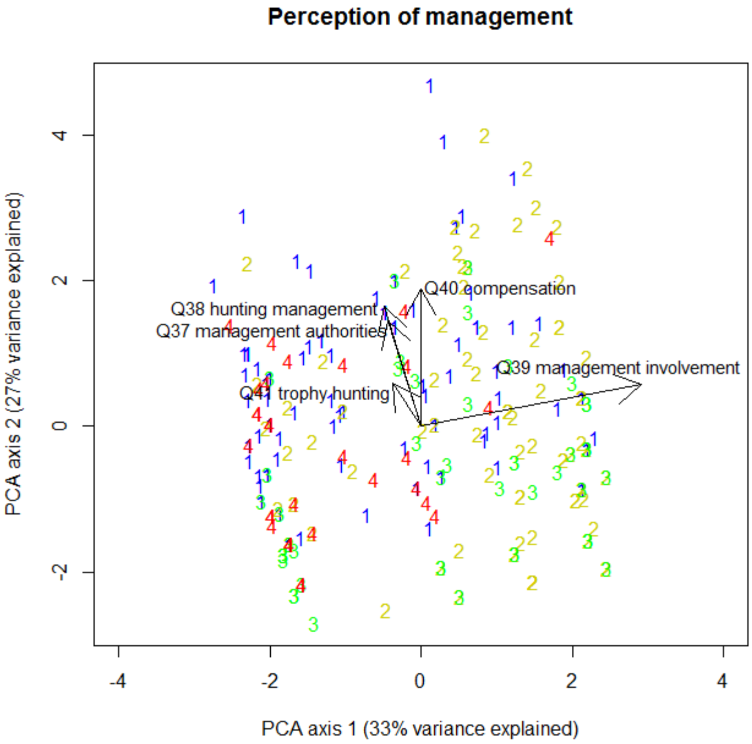

Figure S9.4 Principal Components Analysis of all questions reflecting the participant's perception of current bear management. The numbers reflect the four different groups derived from the hierarchical agglomerative cluster analysis. The 'QX' indicates the question from the questionnaire in Supporting Information Text S9.1. The PCA was based on the following six questions: 37-41.

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Appendix I

Appendix I

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

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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 & Van Dyck 2001; Weibull et al. 2003; Van Dyck et al. 2009), most likely caused by the use of agrochemicals (McLaughlin & 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) (Kuemmerle et al. 2008; Kluvánková-Oravská 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 & Rákosy 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; Tscharntke 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 & 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 km^2 in the lowlands of Southern Transylvania, Romania (Fig. A1.1). 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/data-and-maps/data#c12=corine+land+cover+version+13&b_start=0&c17=CLC2006), 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 accurently 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 SA1.1).

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 SA1.2)). 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.

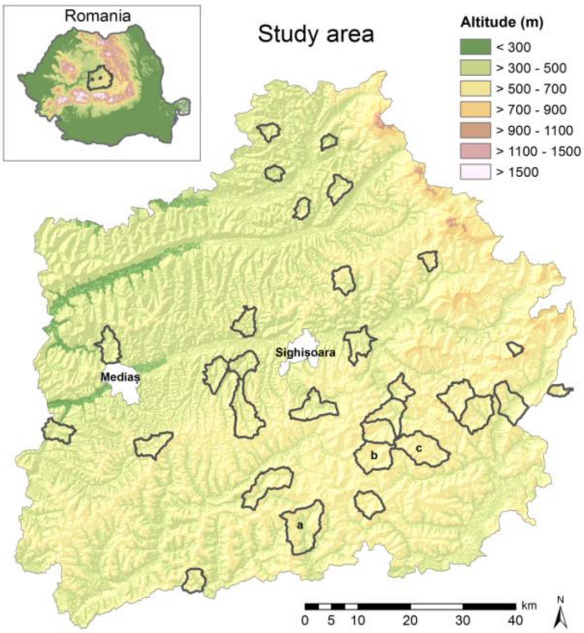

Figure A1.1 Location of the study area with investigated village catchments in Transylvania, Romania. The small letters indicate the village catchments illustrated for predictions in Figure A1.4 (a= Cincu, b= Granari, c= Viscri).

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 & Yates 1993). We included burnet moths because they are comparable to butterflies in their ecology (Naumann et al. 1999; Öckinger & 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 A1.1.

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 A1 for details). 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 (ϱ = 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).

Table A1.1 Definition of environmental variables used in the study at three different scales and method of obtaining those. Abbreviations are used in Figure A1.2 and Table A1.2.

Scale	Variable (abbreviation)	Definition and method
Local (1 ha)	Number of plants 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 (slope aspect -225) * tan (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

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 $\varrho < 0.7$; Table SA1.3; (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 A1.1 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 *Satyrium acaciae*. As a third group we modelled the richness of grassland specialists, namely *Euphydryas aurinia*, *Polyommatus coridon*, *Cyaniris semiargus*, *Lysandra bellargus*, *Phengaris 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 & Warren 1999; Konvicka et al. 2003; Franzén & 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 SA1.4). 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 (Fig. A1.2), 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.

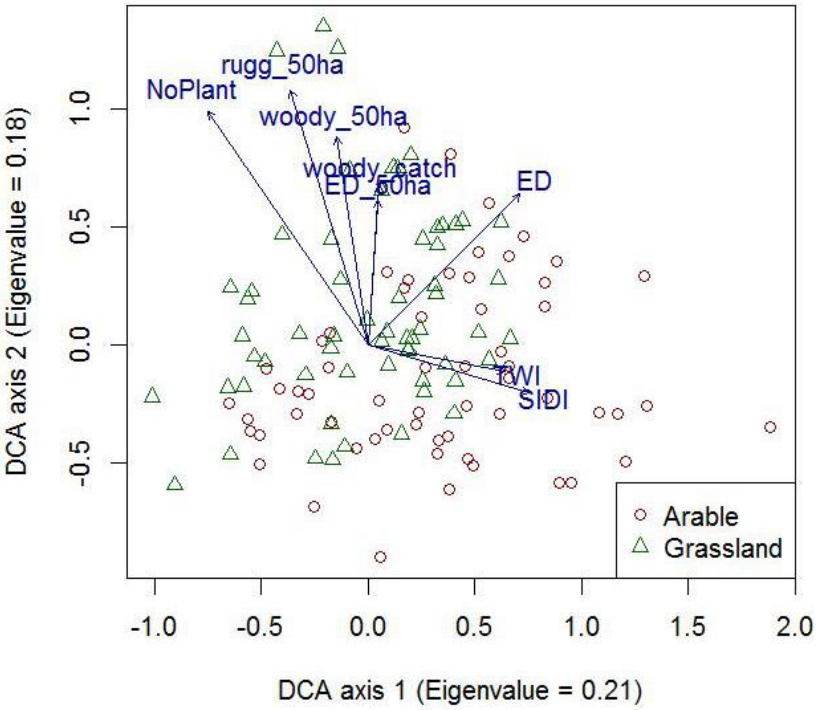

Figure A1.2 DCA ordination plot of butterfly species, with significant environmental variables superimposed ($p<0.05$) (Abbreviations: NoPlant = Local plant species richness; TWI = Local terrain wetness index; rugg_50ha = context terrain ruggedness; woody_50ha = context woody vegetation cover; ED_50ha = context edge density; woody_catch = landscape woody vegetation cover; SIDI = landscape compositional heterogeneity; Table A1.1).

Butterfly species richness was positively related to local plant species richness and local woody vegetation cover, but negatively to local heat load (Table A1.2). It increased in response to local heterogeneity in arable sites, but not in grasslands (Fig. A1.3). 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 (Fig. A1.4).

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 A1.2). Richness of specialist species was higher in grassland, in landscapes with high terrain ruggedness and at sites with high plant species richness.

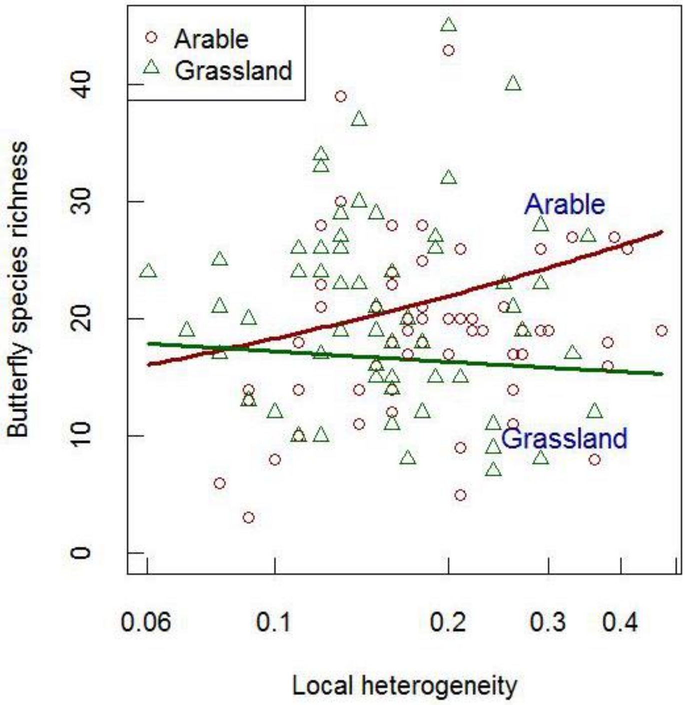

Figure A1.3 Predicted effect of local heterogeneity on species richness in arable land versus grassland, based on the simplified generalized linear mixed model (Table A1.2).

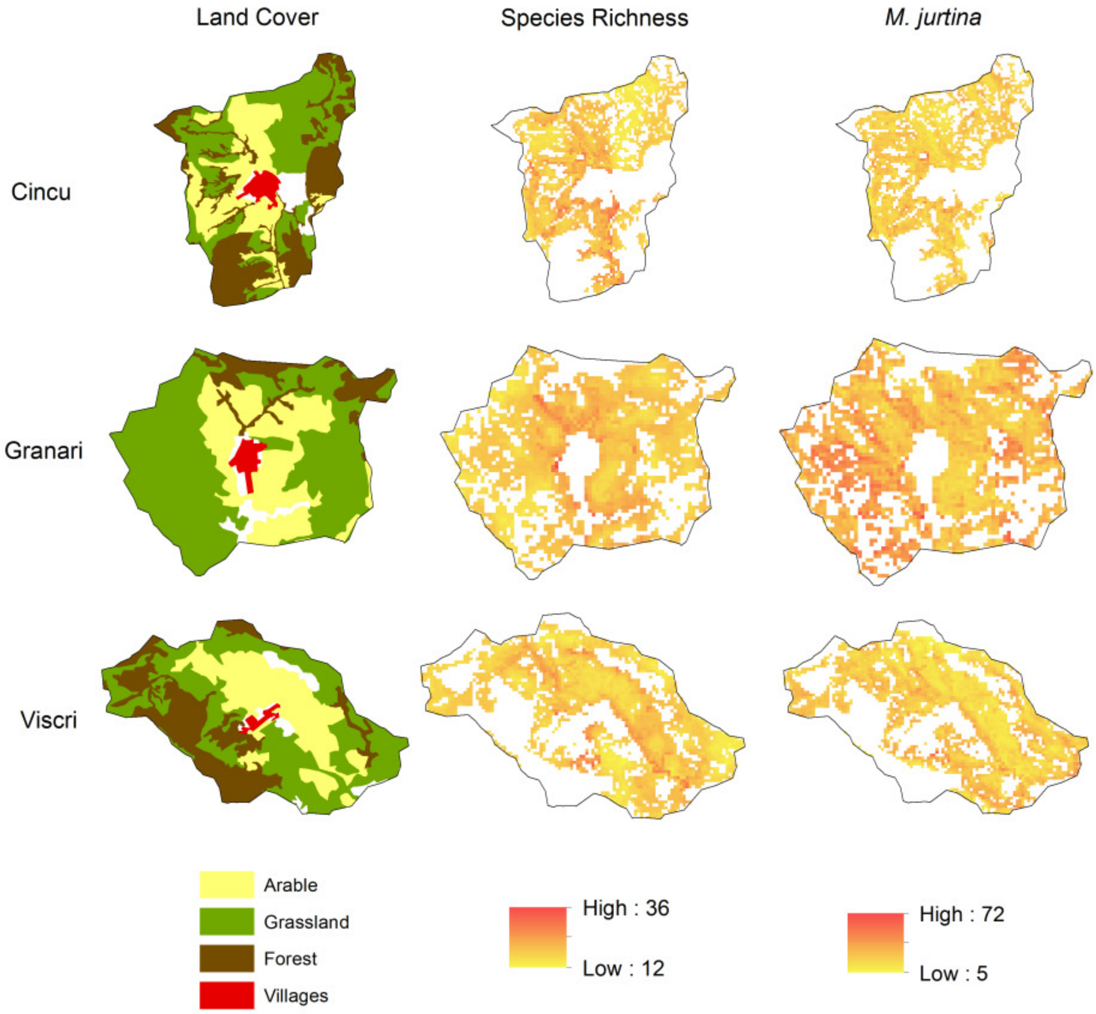

Figure A1.4 Maps of predicted butterfly distributions in three example villages. Left: Land cover map according to CORINE 2006; middle: predicted species richness for arable and grassland areas within each village catchment; right: predicted abundance of the Meadow Brown (*Maniola jurtina*).

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.

Table A1.2 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 A1.1 for abbreviations.

	Species Richness	**High mobile species**	**Low mobile species**	**Spec-ialists**	***L. dispar***	***G. alexis***	***P. icarus***	***M. jurtina***	***C. pam-philus***
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 **
rugg_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		
rugg_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 & 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 & Tscharntke 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 & 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 & 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.

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Supporting Information for Appendix I

Table SA1.1 Number of the 30 focal villages within different strata. TRI= Terrain Ruggedness index, Protection status is according to the EU Habitats and Birds Directives

		Protection status		
		No	**SCI**	**SPA**
TRI	Low	4	1	4
	Medium	3	4	3
	High	4	4	3

Table SA1.2 Number of survey sites along the two gradients local heterogeneity and local woody vegetation cover. A = Arable land and G = grassland

		Heterogeneity					
		Low		**Medium**		**High**	
		A	**G**	**A**	**G**	**A**	**G**
Woody vegetation cover	Low	8	7	7	8	0	0
	Medium	7	8	8	7	7	8
	High	8	7	7	8	8	7

Table SA1.3 Correlation matrix of the variables used in the study

	NoPlant	**het_ 1ha**	**woody_ 1ha**	**heatload**	**TWI**	**rugg_ 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
rugg_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

Table SA1.4 Species list of butterfly species observed in the transects

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

Appendix II

Appendix II

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

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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 1m^2/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 (Tscharntke 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 & 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. 2008) 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 & 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 & 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 m^2 and 10 m^2 (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 & Mineau 1995; Benton et al. 2003; Billeter et al. 2008; Ernoult & 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 & Bădărău 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 km^2 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 SA2.1). Within each village catchment, we assigned land to three different land-use types using the CORINE land cover map (EEA 2006), 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 SA2.2). 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 (slope aspect -225) * tan (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 A2.1.

Table A2.1 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 (slope aspect -225) * tan (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

[a] ©CNES (2007), ISIS programme, Distribution Spot Image SA

[b] Based on the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model with 30 m resolution Version 2 (GDEM V2)

[c] CLC: Corine Land Cover Digital map 2006

[d] FRAGSTATS 4.2 (McGarigal et al. 2012)

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).

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 (± 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 (Fig. A2.1a). Of all species, 30% occurred in more than one land-use type. We found a maximum of 50 species per 1 m × 1 m plot (mean ± 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 (Fig. A2.1b).

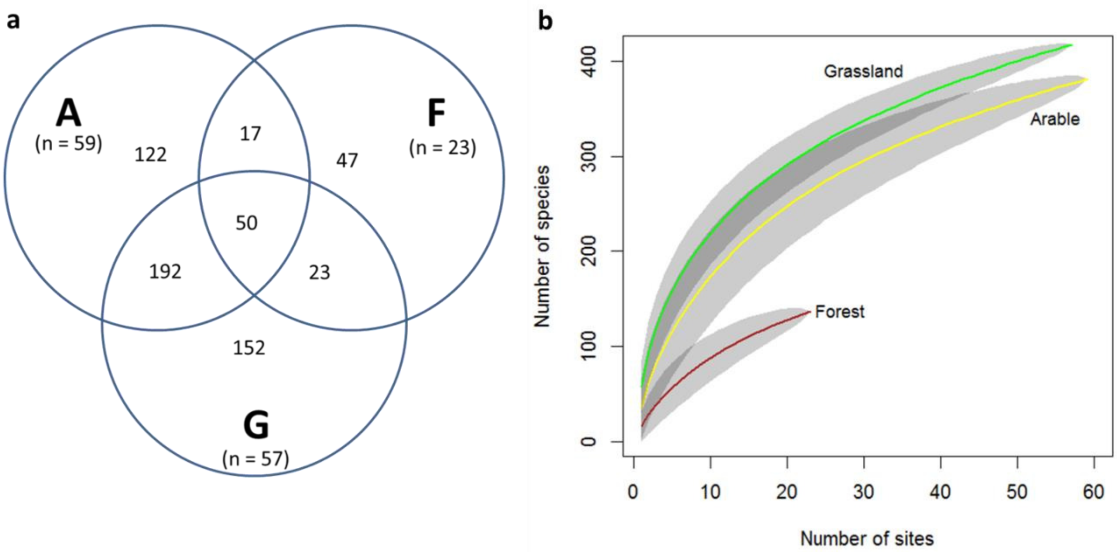

Figure A2.1a Number of plant species that occurred exclusively in or were shared by the different landuse types, arable land (=A), grassland (=G), and forest (=F). **b**: Species accumulation curves in the three different landuse types.

Species composition

DCA ordination with all land-use types showed a clear separation of the three land-use types (Fig. A2.2a). 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, Fig. A2.2a), 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 (Fig. A2.2b). 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.

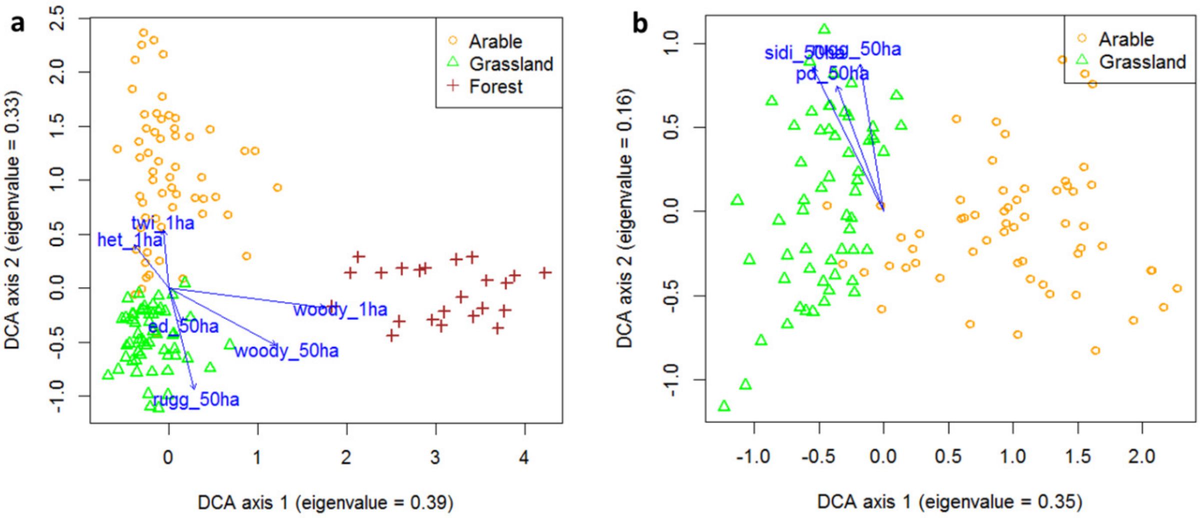

Figure A2.2a Detrended correspondence analysis including all survey sites; **b**: DCA with agricultural sites only. Significantly correlated environmental variables are superimposed correlated environmental superimposed (p<0.05) (Abbreviations: TWI_1ha = Local terrain wetness index; het_1ha = local heterogeneity, ed_50_ha = landscape edge density; rugg_50ha = landscape terrain ruggedness; woody_50ha = landscape woody vegetation cover; woody_1ha =local woody vegetation cover; SIDI_50ha = landscape compositional heterogeneity; pd_50 ha = landscape configurational heterogeneity.

Species richness models

Independently of the land-use type, local woody vegetation cover was positively related to total species richness (Fig. A2.3a). Total plant species richness was higher in grassland than in arable land (Table A2.2). 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 A2.2).

Unsurprisingly, richness of HNV indicator plants was higher in grasslands than in arable land. Especially in arable land, richness of this group was positively related to edge density (Fig. A2.3c). Terrain ruggedness had a positive effect on HNV plant richness in arable land and a weaker positive effect in grassland. The terrain wetness index was negatively related to the richness of HNV plants in arable land, but positively in grassland. We found a unimodal relationship with local woody vegetation cover, which was negative in arable land and positive in grassland (Fig. A2.3b). Richness of arable weeds was higher in arable land, where it decreased with increasing local woody vegetation cover (Fig. A2.3d).

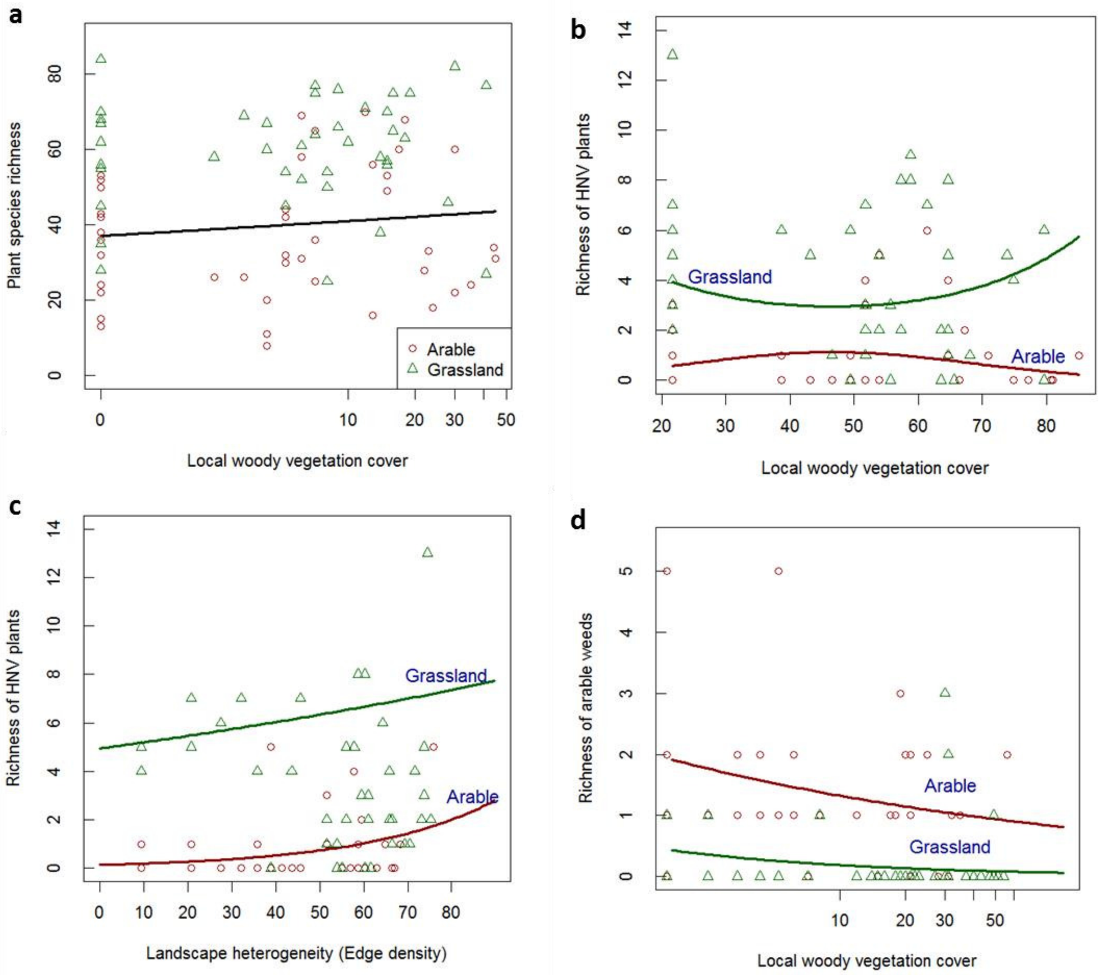

Figure A2.3 Results of generalized linear mixed effect models for relative richness of total species, HNV indicator species, and arable weeds. Relationships are based on the final models summarized in Table A2.2.

Table A2.2 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<0.05; **P<0.01; ***P<0.001

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 (Fig. A2.4). 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 (Fig. A2.5).

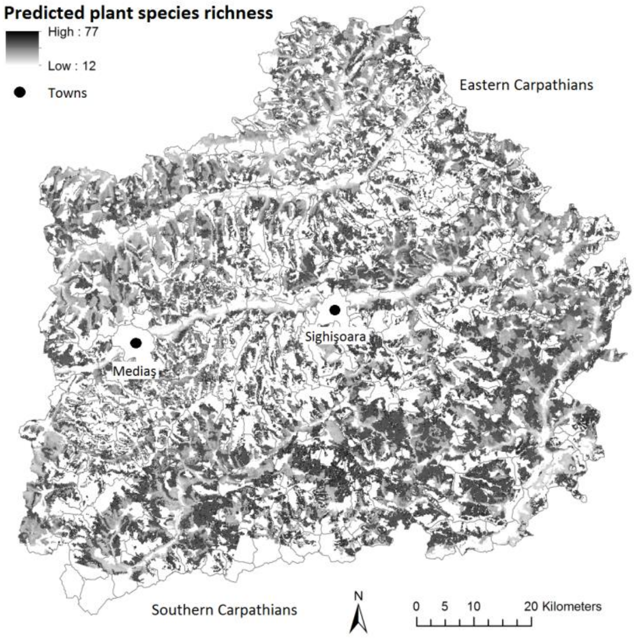

Figure A2.4 Map of predicted plant species richness for 1 ha pixels in agricultural land in the study area, based on the final generalized linear mixed model summarized in Table A2.2. Areas that are displayed in white were excluded from predictions, because they were either outside of the calibration range of our dataset or represented land cover types other than farmland.

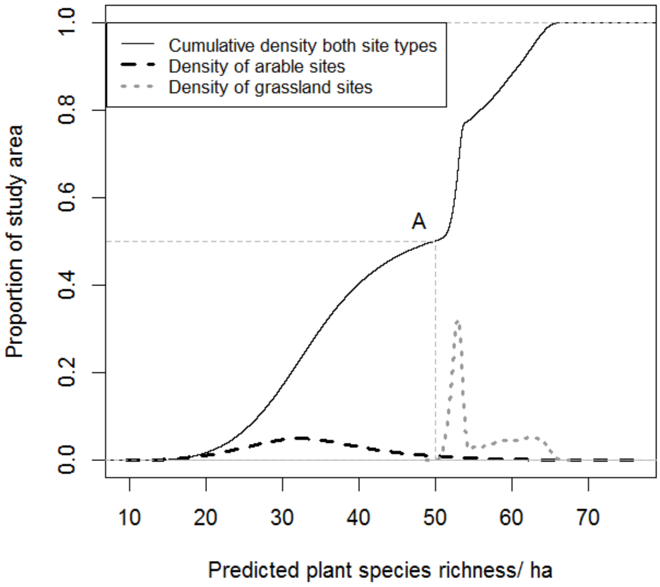

Figure A2.5 Density curves of predicted plant species richness in the farmland mosaic of the study area, separated for arable land (black dashed line) and grassland (grey dashed line). The two lines illustrate different distributions of species richness, which explains the two humps in the cumulative density curve (solid line). For example, point A indicates that 50 % of the landscape contains 50 or fewer plant species per hectare.

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.

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 & 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 & Vitousek 2006; Perfecto & 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 (Ernoult & 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 & 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 declines 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 (Tscharntke et al. 2012). 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.

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Supplementary Material for Appendix II

Table SA2.1 Number of villages sampled for a given combination of protection status and terrain ruggedness

		Protection status[b]		
		No	**SCI**	**SPA**
TRI[a]	Low	4	1	4
	Medium	3	4	3
	High	4	4	3

[a] Terrain ruggedness, 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 SA2.2 Number of survey sites (n=116) along the two local ecological gradients heterogeneity and woody vegetation cover. A = arable land and G = grassland

		Heterogeneity[b]					
		low		**medium**		**high**	
		A	**G**	**A**	**G**	**A**	**G**
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 SA2.3 List of plant species used for modelling the ecological groups, namely weeds, grassland specialists and HNV indicator species

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

Declaration

I hereby certify that the submitted dissertation entitled 'Biodiversity conservation in traditional farming landscapes: The future of birds and large carnivores 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, 09.01.2015

Ine Dorresteijn