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Kaisa J. Raatikainen

Conservation of Traditional Rural Biotopes in Finland

A Social-Ecological Approach

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ABSTRACT

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This research focuses on conservation of traditional rural biotopes, which are biodiverse meadows and wood-pastures that are dependent on management through grazing or mowing. These low-intensity management actions have become rare as a result of agricultural modernisation. I have utilised a social-ecological approach in order to seek for the most critical factors hindering conservation of traditional rural biotopes in Finland. I also explore practical solutions that have the potential to improve their conservation status. The coverage of traditional rural biotopes has faced severe habitat loss during the last 150 years. This has led to endangerment of several habitat types and species that dwell in them. As a result of habitat loss and dynamic land use history, contemporary factors drive remnant biodiversity related to traditional rural biotopes in Central Finland. Therefore an emphasis on present, not past, better supports their conservation. On national level, the management actions are not targeted to ecologically most valuable sites. On site-level, management actions foster local biodiversity, but also cultural heritage and human–nature relationship. Understanding of this multiscale social-ecological complexity is crucial in promoting management actions among landowners according to conservation goals. Yet current agri-environmental policies treat the social-ecological interactions in a simplified manner, and therefore they do not self-evidently encourage management of traditional rural biotopes. My results show that the inefficiency in conservation of traditional rural biotopes largely follows from a scale mismatch between the extent and location of current management actions and the desired ecological response. More effective conservation of traditional rural biotopes calls for adoption of a new governance approach that aims for resilience through local focus and increased actor participation.

Keywords: Agri-environment schemes; high-nature-value farming; landscape; resilience; semi-natural grasslands; social-ecological systems; wood-pastures.

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I–IV.

I Kaisa J. Raatikainen, Anna Oldén, Niina Käyhkö, Mikko Mönkkönen & Panu Halme 2018. Contemporary spatial and environmental factors determine vascular plant species richness on highly fragmented meadows in Central Finland. Submitted manuscript.

II Anna Oldén, Kaisa J. Raatikainen, Kaisa Tervonen & Panu Halme 2016. Grazing and soil pH are biodiversity drivers of vascular plants and bryophytes in boreal wood-pastures. *Agriculture, Ecosystems and Environment* 222: 171–184. This paper has also been included as a chapter in Anna Oldén's thesis.

III Kaisa J. Raatikainen, Maija Mussaari, Katja M. Raatikainen & Panu Halme 2017. Systematic targeting of management actions as a tool to enhance conservation of traditional rural biotopes. *Biological Conservation* 207: 90–99.

IV Kaisa J. Raatikainen & Elizabeth S. Barron 2017. Current agri-environmental policies dismiss varied perceptions and discourses on management of traditional rural biotopes. *Land Use Policy* 69: 564–576.

The table below shows the contributions of the authors to the original papers. The contributions of non-authors are stated in the acknowledgments of the original papers.

	I	II	III	IV
Planning	KJR, AO, NK, MMö, PH	AO, KJR, KT, PH	KJR, MMu	KJR, ESB
Data	KJR, AO	AO, KJR, KT	KJR	KJR
Analyses	KJR, AO	AO, KJR	KJR	KJR
Writing	KJR, AO, NK, MMö, PH	AO, KJR, KT, PH	KJR, MMu, KMR, PH	KJR, ESB

KJR = Kaisa J. Raatikainen, PH = Panu Halme, MMö = Mikko Mönkkönen, ESB = Elizabeth S. Barron, AO = Anna Oldén, NK = Niina Käyhkö, KT = Kaisa Tervonen, MMu = Maija Mussaari, KMR = Katja M. Raatikainen

PREFACE

The Earth — our planet, living environment, habitat, and home — is facing an unprecedented biodiversity loss that is caused by us humans. This troubles me, and the feeling of responsibility to fix what we broke has been a strong motivator for this work. My chosen field of science, conservation biology, is a value-laden discipline. I do not want to hide this nor the fact that I have a personal connection to my research subject: traditional rural biotopes, i.e. different kinds of meadows and wood-pastures. On the verge of extinction these habitats still maintain a significant amount of Finnish biodiversity. I want to cherish them and wish that people could discover them and their miraculous nature and cultural value.

After this confession, I would like to introduce a central challenge related to conservation of traditional rural biotopes: agricultural modernisation. My generation has seen the disappearance of small-scale agriculture in Finland. With my roots in a small family farm, I want to be realistic on the possibilities to ensure the continuance of traditional farming practices in Finland. During the last 150 years, the role of traditional rural biotopes in Finnish agriculture has changed, and an adaptation to that change is needed in order to make their sustenance possible.

As agricultural land uses have intensified, grazing or mowing of traditional rural biotopes has lost its meaning as a basis for food production. With the endangerment of traditional rural biotopes and their species, their management has become a conservational effort. Despite this, it is tied to farming practices and cattle husbandry. This dependence on human action creates another challenge, because not all people consider traditional rural biotopes worth to conserve.

"What's the point in it?" is a question I have faced many times. Usually I have tried to explain the exceptional biodiversity, habitat loss and fragmentation, cultural heritage, and the importance of management actions to our human–nature relationship and place-bound identity in just 15 seconds.

This time I have a whole book, which is rather exciting.

In this thesis, I explore conservation of traditional rural biotopes through several lenses. From an ecological point of view, I study the spatiotemporal dynamism of meadows and the effects of grazing management vs. management abandonment on species communities living on wood-pastures. To achieve a deeper understanding on my research subject, I have adopted a social sciences approach. I discuss certain ways to improve current conservation policies, specifically through spatial targeting of management actions. I also explore what motivates people to manage traditional rural biotopes, and give suggestions on how traditional rural biotopes could be supported in this world of uncertainty in a resilient way.

But before we go into that, I want to begin with a travel back in time. Let's go and meet the mammoths.

1 INTRODUCTION

1.1 The ever-changing nature

1.1.1 A peek into biogeographical history of Finland

Nature is not static. It adapts to the prevailing conditions, and alters those conditions while adapting to them. This process is slow for humans to observe, and we often tend to ignore or forget it, but understanding the dynamism of nature is important for understanding nature itself.

Thirty thousand years ago Finland was covered with cold periglacial steppe grazed by woolly mammoths (*Mammuthus primigenius*) and other large herbivores (Ukkonen 1993, Koivisto 2004). Thirteen thousand years ago everything was covered with ice. This was the last glaciation, and it covered the whole country. All ecosystems we see now have developed after the Scandinavian ice sheet retreated (Koivisto 2004). The adaptation to ice-free conditions is still continuing; in the shallow coasts of Baltic Sea post-glacial rebound still rises the Earth crust that was depressed by the weight of the ice mass (Koivisto 2004).

Where did the plants, animals, and other species arrive from when they colonised Finland as the glacier retreated? How did those first ecosystems look like? Based on paleoecological analyses it was nothing like what we see now. First of all, Finland was mostly under water. Exposed land was rather calcareous but low in nitrogen (Koivisto 2004). It was colonised by a mix of periglacial tundra and steppe vegetation, and arctic fauna followed first from south and later from east (Ukkonen 1993, Koivisto 2004). Colonisation was rapid, as some arctic animal and plant species survived the last glaciation at high latitudes or were widely distributed throughout the steppes that were located south of the ice sheet (Hewitt 1999, Schmitt 2007). The period of primary successional ecosystems was soon replaced by fell heaths which were sparsely covered by birches (*Betula nana*) (Ukkonen 1993, Koivisto 2004). Heaths, in turn, were eventually replaced by forests with pines (*Pinus sylvestris*) and mixed oaks (*Quercus robur*) (Ukkonen 1993).

There were pronounced changes in the postglacial ecosystems during the period of warm climate that prevailed 11 590–6 000 years ago. These were caused by rapid amelioration of the climate, expansion of dry land, and eventual changes in soil properties (Koivisto 2004). At the end of that warm and moist period broadleaf forests with oak, elm (*Ulmus* spp.), linden (*Tilia cordata*), and hazel (*Corylus avellana*) dominated in southern Finland, pine forests occurred in Lapland, and current treeless tundra was covered with mountain birches (*Betula pubescens* spp. *czerepanovii*) (Seppä *et al.* 2002, Koivisto 2004, Miller *et al.* 2008).

After that, the climate started to cool. Expansion of coniferous forests and their associate, acidic podsol soil, benefited from this eventual change (Koivisto 2004). Norway spruce (*Picea abies*) arrived from east 8 000 years ago and spread slowly over the country during the following 6 000 years (Ukkonen 1993, Koivisto 2004). The driving or limiting factors for the changes in spruce distribution and abundance are still not fully understood (Miller *et al.* 2008). But, as a result of its advance, over the last 2 000 years the Finnish landscape has been dominated by taiga forest. And now the climate is warming again. This, however, may not result in re-expansion of broadleaf forests. Spruce is now wide-spread and as a strong competitor its presence may outweigh the effect that current climate warming has on the abundance of temperate species (Miller *et al.* 2008).

Although the current biogeography of Finland largely follows from contemporary climatic conditions, past ecosystems have left remnant habitats and relict species behind. These are met on sites with favourable soils and microclimate (Koivisto 2004, Uusitalo 2007). For example, populations of Siberian primrose (*Primula nutans* subsp. *finmarchica* var. *jokelae*) on the shore meadows along Bothnian Bay are likely relicts that originally spread to Finland from Russian Karelia after the last glaciation (Ryttäri *et al.* 2012). In Central Finland, hazel and Scots elm (*Ulmus glabra*) are considered as relicts from the period of warmer climate (Uusitalo 2007). As rare features, many relict plant species are red-listed and seen as important contributors to biodiversity in Finland (Ryttäri *et al.* 2012). But why and how do they persist?

1.1.2 Adaptive cycles

Changes in nature tend to be cyclic. This principle applies to large- and small-scale phenomena such as the glacial periods and the annual cycle of seasons, alike. Over distinct areas, during long or short periods of time, species can completely disappear and then reappear, raising questions concerning the conditions for their persistence (Holling 1973). All ecosystems experience disturbances that affect their structure and functions. The question is: how much disturbance is needed to surpass the limits of ecosystem recovery?

In many cases, the answer is “surprisingly much”. Ecosystems deal with disturbances through phases of release, renewal, growth, and conservation (so-called steady-state). These adaptive cycles are initiated by a disturbance event, and they either end up in regenerating the ecosystem to the pre-disturbance state or transforming it to some new state (Chapin *et al.* 2009, Allen *et al.* 2014). The long-term stability of ecosystems depends on changes that occur during critical phases of these long-term adaptive cycles (Chapin *et al.* 2009).

What would the adaptive cycle of a periglacial mammoth steppe look like? The environmental conditions maintaining a steppe ecosystem are cold and dry climate, grazing by large herbivores, and occasional fire outbursts (Dixon *et al.* 2014). Climate and grazing create the steady-state circumstances to which steppe species are adapted to. The conservation phase is eventually disrupted by fire, which burns the grassland vegetation and drives away the grazers. Such reduction in structural complexity of the ecosystem is typical for the rapidly occurring release phase (Chapin *et al.* 2009). Renewal follows as seedlings are established from the seed bank. Seeds also disperse from the surrounding undisturbed landscape. During renewal, the original species assemblage can regenerate, but there is little resistance for new communities to be established (Chapin *et al.* 2009). Resources such as nutrients and space were released through the fire event and are now freely available. The ecosystem enters the growth phase. Nutrients are assimilated into organisms and free space is colonised. At growth phase the ecosystem is relatively insensitive to disturbances (Chapin *et al.* 2009). Gradually the vegetation recovers and the grazers return, biotic and abiotic interactions become more complex and specialised, and the ecosystem develops again into the conservation phase.

Despite the severity of the disturbance event, the resulting ecosystem often is very similar to the pre-disturbed one (Holling 1973, Chapin *et al.* 2009). It almost seems that the nature remembered how it once was, and aimed back to that state. But the processes driving the adaptive cycle are not that simple.

1.1.3 Resilience and the “memory” of ecosystems

Species, their populations and evolutionary adaptations, and biotic interactions within species communities and ecosystems, are at the same time dynamic and resistant. This means that they often do not disappear easily but are able to adapt to changes in conditions. Although mammoths and other megafauna are extinct, Europe still has grassland species living in habitats that resemble the periglacial steppe ecosystem (Pykälä 2000, Fischer *et al.* 2012). Observed long-term persistence of ecosystems in the face of major environmental changes suggests that ecosystems have a high capacity to absorb change without dramatically altering (Holling 1973). This capability to adapt results in *resilience*, which is the amount of disturbance that an ecosystem can absorb without changing state between alternative regimes of relative stability, or local domains of attraction (Holling 1973, Berkes *et al.* 2003). Resilience, thus, is connected to the ecosystem’s adaptive cycle. It is distinct from stability[1], which is the ability of a system to return to an assumed equilibrium after a temporary

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1 Stability is commonly called as engineering resilience, and often confused with actual resilience (Berkes *et al.* 2003).

disturbance, and can be measured as the amount of time needed for such return (Holling 1973, Berkes *et al.* 2003).

Highly resilient ecosystems can have low stability and vice versa — both phenomena have been observed in nature (Holling 1973). The balance between resilience and stability is a product of evolutionary history of ecosystems in the face of random fluctuations they have experienced (Holling 1973, 1978). Over long time periods, dynamism maintains resilience and stability deteriorates it (Holling 1973). In other words, ecosystems need disturbances to maintain their resilience; otherwise they become vulnerable to changes.

Ecological resilience facilitates multiple steady-states (Folke 2006). These can be understood as alternative conservation phases in the adaptive cycle. Steady-states are detected as domains of attraction created by slowly changing variables such as climate, nutrient accumulation, species composition, or spatial connectivity of habitat patches (Berkes *et al.* 2003, Chapin *et al.* 2009). These definitive conditions express slow dynamics and ecosystems adapt to them; this potential to react to changes is called *adaptive capacity* (Berkes *et al.* 2003). Because periglacial steppe ecosystems had adaptive capacity, we still have grasslands that carry on their prehistoric abiotic and biotic patterns.

On the other hand, if an ecosystem loses its adaptive capacity, it loses opportunity to regenerate. Its options during periods of reorganisation and renewal become constrained (Resilience Alliance 2017), resulting in loss of resilience (Berkes *et al.* 2003). Adaptive capacity builds on genetic diversity, taxonomic diversity, functional diversity, and the heterogeneity of landscape mosaics (Berkes *et al.* 2003, Folke 2006, Resilience Alliance 2017). High biodiversity — in all its levels — therefore corresponds to a higher potential of an ecosystem to functionally adapt to change and resist disturbance (Berkes *et al.* 2003, Chapin *et al.* 2009). It is like having insurance in order to be prepared for a rainy day.

As I already discussed, some part of the biodiversity we see in a given location results from historical, not current factors. Many if not most of the species recorded in any survey seem unnecessary in terms of ecosystem functionality. Yet they are like the insurance policy; in case of accidence, they are able to step in and remedy the damage. This happens as the species take over the ecological niches or functions of other species that went locally extinct due to abrupt disturbance (Chapin *et al.* 2009).

Through temporal persistence species and their interactions form something that is called *ecological memory*. Ecological memory is the composition and distribution of organisms and their interactions in space and time, and it includes their evolutionary adaptation to environmental fluctuations (Nyström and Folke 2001). Although overlapping functional diversity may seem redundant, it actually increases the variation in possible alternative reorganisation patterns and pathways following disturbances, thus contributing to ecosystem resilience (Berkes *et al.* 2003).

One specific form in which ecological memory can be observed is *extinction debt*. The term refers to the existence of delayed extinctions of species (Kuussaari *et al.* 2009). After environmental disturbance, the populations of habitat specialist species are expected to become locally extinct, but this often happens after a temporal lag (Kuussaari *et al.* 2009, Hylander and Ehrlén 2013). This means that the species are resistant to change, and as long as their populations prevail, they contribute to the resilience of the ecosystem. If the disturbed habitat is restored before the remnant species disappear, the species community can reorganise itself.

Such biological legacies form only one component of ecological memory. In addition to persistent species and patterns, mobile links and support areas are of importance (Nyström and Folke 2001). Mobile links are species of functional groups that disperse and/or migrate between habitat patches, linking disturbed areas to undisturbed ones; support areas provide habitat for the mobile links within the landscape (Nyström and Folke 2001, Berkes *et al.* 2003). Large herbivores, for example, were important mobile links in the periglacial steppe. Their movement through the landscape most likely followed patterns of available food resources, i.e. grassland patches in growth and conservation phases of the adaptive cycle. In case of fire, grazers moved to undisturbed patches (support areas). Every time they found a renewed patch of steppe grassland, they restored some of the patterns and processes of the pre-disturbed ecosystem through grazing.

The grazers also are important vectors of seed dispersal, or zoochory, thus increasing functional connectedness of populations of grassland plants (Bruun and Fritzbøger 2002, Rico *et al.* 2014). This means that ecological memory connects an ecosystem's present state both to its past and to its neighbours (Berkes *et al.* 2003). It forms a spatiotemporal network through which ecosystem reorganisation becomes possible.

1.1.4 The ecological legacy behind traditional rural biotopes

Thus, current ecosystems are in many ways remnants of the times past. This is similar to the evolution of species' traits. Grassland plant species have adapted to grazing in many ways that evolved during the era of megafauna. Some of those species now live on Finnish traditional rural biotopes. They once lived on a plain of permafrost, tundra, and cold steppe that covered much of Eurasia during the last glaciation, and the agents that maintain their habitats now (cows, sheep, horses, scythes, and trimmers etc.) have taken on the ecological and evolutionary role of extinct browsers and grazers such as woolly mammoths, aurochs (*Bos taurus primigenius*), tarpans (*Equus ferus ferus*), and steppe bisons (*Bison priscus*).

This argument is not a new one. In Europe, many species that were dependent on natural grazing, fires, and floods — which are currently largely suppressed — now occur on complementary habitats that have similar kinds of intermediate disturbances created by traditional agricultural practices (Pykälä 2000, Fischer *et al.* 2012). Livestock grazing and mowing have made possible the continued existence of many species threatened by the human overkill of large herbivores (Pykälä 2000, Vera 2000).

In his pioneering and much debated work, Franciscus Vera argued that the vegetation dominating lowlands of Central and Western Europe after the end of the last glaciation much resembled that of current wood-pastures (Vera 2000). He presents another view on the adaptive cycle of prehistoric European ecosystems, one that complements the earlier concerning periglacial steppes. In his "theory of the cyclical turnover of vegetations", he states as follows (Vera 2000, pp. 377–378):

The synthesis of the findings leads to the conclusion that the original vegetation in the lowlands of Europe is a park-like landscape where the succession of species of trees is determined by large herbivorous mammals and birds such as the jay, which act as facilitators for certain species of trees. […] *Grazing is dominant in the system. It consists of three modules. Each module is in itself the result of an irreversible development brought about in the system by grazing. The first module is the grassland, where as a result of grazing by specialized grazers, bushes shoot up in which trees can grow protected from being eaten. The grazers cannot stop this formation of forest. On the contrary, they facilitate it by offering bushes and trees places to establish themselves, including the oak with the jay as vector. The second module is the formed grove, in which the bushes, in which the trees grew, disappear as a result of the shade of the canopy. Due to the presence of the large ungulates, there is no more regeneration of trees and bushes. A grove arises that only has a canopy storey.* […] *The third module is where the canopy in the centre of the grove becomes more and more open, due to trees decaying through age, possibly in combination with storms, drought and fungal damage, without being replaced by shadetolerant trees. As a result of the increased openness, more light reaches the ground, so that grasses and herbs can establish themselves. The grasses and herbs in turn attract the specialized grazers among the large ungulates. Due to the lack of protective bushes, there is no successful establishment of young trees as a result of this grazing. In this way, the grove changes to open grassland over time. Eventually, the surface area of the grassland becomes so large that light-demanding thorny bushes establish themselves there again and young trees can grow in among them. This closes the cycle. At a certain point in time, all the stages of this cycle of succession are present in one place in a large area. Therefore all the biotopes are always present, though not always in the same place.*

I will not take a stand on whether Vera's theory is correct or not in its claim of the extent of grazed ecosystems, but there are some interesting points to discuss. First is that grazing seems to have been an important driver of both ecological and evolutionary change in European grassland and forest ecosystems. In the tropics, grazing still is an important feature of savanna ecosystems. There tree savannas are extensive and overlap with open savannas or grassland (Dixon *et al.* 2014). Given that the numbers of large herbivores were high enough in postglacial Europe, similar open and semi-open landscapes may have evolved also here (Vera 2000). This argument is supported by recent reconstructions of vegetation changes during the Holocene epoch (since 11 560 B.P.) indicating that the proportion of unforested land has been strongly underestimated by earlier pollen studies (Gaillard *et al.* 2010).

Second point is that during the period of warm climate southern Finland was dominated by broadleaved forests with oak and hazel (Koivisto 2004, Miller *et al.* 2008). These are shade-intolerant species that do not survive in closed forests (Vera 2000, Gaillard *et al.* 2010). During the same time, grazing and/or browsing animals such as moose (*Alces alces*), roe deer (*Capreolus capreolus*), and reindeer (*Rangifer tarandus*) were present (Ukkonen 1993). It is thus possible that natural grazers maintained a patchy mosaic of grassland and grove patches also in Finland.

Third point is related to the importance of thorny bushes in tree generation in grazed ecosystems. On Finnish wood-pastures the number of young birches and pines is correlated with the number of junipers (*Juniperus communis*), likely because thorny junipers protect palatable seedlings from grazers (Oldén *et al.* 2016). This is another ecological interaction that may have its roots in the postglacial ecosystems.

Fourth point is the notion that grasslands and grazed forests can be seen as different phases of a single ecosystem cycle (Olff *et al.* 1999, Vera 2000). There is evidence on a long-term ecological transition of broadleaf and pine-dominated wood-pastures into open pastures (Oldén *et al.* 2016). If semi-natural grasslands and wood-pastures — or their intermediate forms — indeed are part of the same adaptive cycle, treating them as separate ecosystem types may prohibit deeper understanding of their ecological dynamism.

In my work, I have termed semi-natural grasslands (or meadows) and wood-pastures collectively as traditional rural biotopes. Based on literature, traditional rural biotopes can be defined through three characteristics:

1) they are dependent on disturbances created by low-intensity mowing or livestock grazing (Pykälä 2000, Mládková *et al.* 2015), often accompanied by other multifunctional actions such as coppicing, pollarding, and pruning (Hartel and Plieninger 2014);
2) they have a long-term history as pastures or meadows that has resulted in nutrient impoverishment (Pykälä 2000, Kumm 2003, Mládková *et al.* 2015); and
3) they host exceptional biodiversity (Pykälä 2000, Lindborg *et al.* 2008, Halada *et al.* 2011).

Finnish environmental administration has defined traditional rural biotopes as culturally influenced natural habitat complexes that are part of a traditional landscape formed through archaic rural livelihoods (Ministry of the Environment 1992). For conservational purposes, traditional rural biotopes often are perceived as species-rich semi-natural habitats maintained by human-induced intermediate disturbances (Pykälä *et al.* 1994, Raunio *et al.* 2008, Kemppainen 2017). On more general level, traditional rural biotopes can be seen as specific types of habitat belonging to high nature value farmland, which comprises those areas in Europe where agriculture is a major land use and where that agriculture supports or is associated with either a high species and habitat diversity or the presence of species of European conservation concern or both (Andersen *et al.* 2004). Despite their ecological emphasis, all these different definitions have the interaction between people and nature at their heart. This interaction dates back to the beginning of agrarian history, to the time when humans began cultivating and domesticated animals.

Although traditional rural biotopes bear the legacy of steppe ecosystem and grazing-induced grassland–forest mosaics, as ecosystems they are unique. Some differences between the contemporary and prehistorical ecosystems are structural. For example, the modern-day grazers are domestic herbivores bred according to agricultural purposes, and the vascular plant species community is a mix of "natural" species and archaeophytes (Pykälä 2001). Also the soil chemistry is altered because of millennia of vegetation-induced changes such as fixing of nitrogen (Koivisto 2004).

Other differences are functional: perhaps the most important being that traditional rural biotopes slowly lose nutrients as biomass is removed from the site through grazing or mowing (Mládková *et al.* 2015). Disturbance caused by anthropogenic management ecologically resembles natural disturbances, but its magnitude is generally low when compared to grazing of large wild herds, natural flooding, or fire outbursts. The intermediate-level disturbance and process of nutrient impoverishment benefits grassland species (Pykälä 2000, 2004, Mládková *et al.* 2015). The combination of management-induced disturbance and nutrient-poor conditions is what maintains the species richness of traditional rural biotopes. Shortage of nutrients and disturbance by grazing (or mowing) restrict competition among plants, thus allowing more species to co-exist (Grime 1974).

In terms of ecosystem continuity, there are "good" and "bad" disturbances. The former maintain resilience and the latter drive ecosystems beyond their adaptive capacity. Some disturbances result in sudden appearance or disappearance of populations, fluctuations in ecosystem state, and the establishment of new domains of attraction for ecosystem function and structure (Holling 1973). A meadow can become overgrazed, in which case its vegetation disappears and a bare soil is exposed for erosion. The resilient character of any ecosystem has its limits, and when those limits are passed, the ecosystem changes irreversibly (Holling 1973). These kinds of changes in ecosystem behaviour are not deterministic, but profoundly affected by random events (Holling 1973). Next, I will discuss the consequences of the chain of events that led to the formation of traditional rural biotopes as we know them today.

1.2 Human influence is everywhere

1.2.1 From ecosystems to social-ecological systems

After the Scandinavian ice sheet retreated from Finland, one of the species that colonised the land was *Homo sapiens*. First five thousand years or so were the time of hunter-gatherers. And hunt they could; at the end of the last glaciation, together with the pronounced warming of climate, human impact drove the megafauna to extinction throughout Northern Europe (Barnosky *et al.* 2004).

Five to four thousand years ago another fundamental change happened. It started with slash-and-burning and gradually developed into permanent, rotational field cultivation (Soininen 1974). Remains of domestic animals appeared ca. 3 200 years ago in the bone material collected from Finnish early Bronze Age dwelling sites (Ukkonen 1993). Even in its elementary forms agriculture provided people with more food and other resources; at the same time, it demanded labour to clear and cultivate the fields. The human population started to grow.

The pace of change was slow in the beginning. But during the past 300 years, the terrestrial landscape of Finland has gone through a transition from nearly pristine taiga forests and mire ecosystems into an anthropogenic mosaic of silvicultural forests, drained peatlands, and agricultural farmlands. As the permanent settlement of Finns spread towards the eastern and northern parts of the country in the 18th century, an extensive deforestation around the settlements followed (Björn 2000, Myllyntaus *et al.* 2002). The main livelihood at that time was still slash-and-burn cultivation, and wood-demanding tar burning was also common. The logging of naturally regrown forests for timber production started in the 19th century, and during 20th century, silvicultural practices including tree plantations and clear-cuts modified the structure of Finnish forests profusely (Uotila *et al.* 2002). At the same time, slash-and-burning was ceased and agricultural practices intensified due to innovation of machinery and new farming technologies (Soininen 1974).

Our ancestors were dependent on nature for food, shelter, clothing, and many other things. This has not changed. Our generation, and those yet to come, continue to live out of Earth. The interdependency of natural and social has become widely recognised in environmental and resource management. The provisional, supporting, regulating, and cultural dependencies of humans on nature are now called ecosystem services (Millennium Ecosystem Assessment 2005). Humans cannot exist without ecosystems. The use of ecosystems always has ecological consequences and it happens in a social context. This has raised the core idea of coupled natural and human systems, or *social-ecological systems* (Berkes *et al.* 2003). Similar to an ecosystem, a social-ecological system consists of physical (or abiotic) components and organisms (biotic components) and their interactions. In addition, a social-ecological system includes the products of human activities, such as food, money, and pollution (Chapin *et al.* 2009).

The main idea in social-ecological systems science is that delineation between social and natural is arbitrary (Berkes *et al.* 2003). Although the system components can be categorized as social or ecological, they are linked to each other (McGinnis and Ostrom 2014). Social-ecological systems theory conceptualises the environment as an open system consisting of natural and cultural components and processes, which are integrated through interactions such as management practices, adaptation, and resource use (Virapongse *et al.* 2016).

It seems that everything is connected to everything; a practical example of a social-ecological system is needed for clarification. During the time period between the Bronze Age and the early 19th century, Finns largely lived on grain produced by small-scale subsistence farming (Soininen 1974). Higher yields were gained from permanent plots through fertilisation; for this reason, cattle was kept for provision of manure to fertilize the fields (Soininen 1974, Ministry of the Environment 1992). Because fields were reserved for growing cereals, cattle grazed everywhere else but on fields, and forest grazing was common throughout the country (Multamäki 1916, Lampimäki 1939, Jäntti 1945) (Fig. 1).

FIGURE 1 A graphic arts excerpt from mid-19th century portraying a typical forest landscape in Humppila, Southern Finland (Lindeström, A.: En skogstrakt i Humpila kapell — In: Topelius (ed.) 1845: Finland framställdt i teckningar).

During winter, animals were kept indoors and had to be fed with winter fodder that had been collected by mowing from mineral soil and peatland meadows (Soininen 1974). Throughout the year, dung was collected and spread to the fields (Soininen 1974). These practices resulted in a nutrient flow from farm surroundings into cultivations (Luoto *et al.* 2003). In this traditional agricultural system extensive haying and pasturing on natural vegetation provided the basis for more effective food production on fields (Soininen 1974). As a side product, cattle husbandry created a diversity of wood-pasture and meadow habitats that were suitable for a variety of disturbance-dependent and disturbance-tolerant grassland species, but also many species of original habitats — forests, mires, and shores — were able to prevail on them (Schulman *et al.* 2008). The need for muck resulted in an unexpected accumulation of biodiversity on those habitat patches that we now call traditional rural biotopes.

The above example may be a coarse simplification, but it points out some key factors in traditional agricultural systems. It depicts complex interactions between several components (people, grain yield, cultivations, grazing animals, manure, pastures, meadows, and species). This leads us to another basic feature of social-ecological systems: they are inherently complex (Berkes *et al.* 2003).
Yet complexity is not enough. Social-ecological systems are also dynamic (Berkes *et al.* 2003). I have already discussed the dynamism of ecosystems; now I will further deepen the issue. Social systems are under constant change, and social change tends to be faster than the ecological change (Chapin *et al.* 2009). Let us explore this phenomenon by continuing with our example. For the early 19th century farmer cattle was important primarily in terms of producing manure to increase the grain yield (Soininen 1974). Milk, butter, and cheese were accompaniments (*särvin* in Finnish) for real food such as bread and porridge (Soininen 1974). But in less than a hundred years — two or three generations in those times — Finnish agriculture shifted strongly towards dairy production and intensified farming (Luoto *et al.* 2003). Fields that earlier provided cereals for people now grew grass for cows, and tractors began to replace horse and human power in many farming practices (Soininen 1974).

The main reason behind the change was that crop cultivation, which was still largely complemented by slash-and-burning, could not keep up with the rapid population growth (Soininen 1974) (Fig. 2). At the same time, it became profitable to produce exports such as butter and import grain from abroad (Soininen 1974, Luoto *et al.* 2003). Finally, cold weather caused three crop failures during 1860s, leading to wide-spread famine that killed ca. 10 % of the total human population (Soininen 1974). The crisis of traditional agriculture escalated, and the decade of 1880s marked its end and a beginning of market-based agriculture that emphasised cattle husbandry (Soininen 1974). This agricultural transformation reflects a reaction to changes in both social and ecological conditions: market-based agriculture was able to feed more people (who were increasingly migrating to cities and thus not farming for themselves), and dairy production was better suited for boreal climatic conditions (with grass being less vulnerable to frost than cereals).

FIGURE 2 The painting of slash-and-burners by Eero Järnefelt (1893: Raatajat rahanalaiset / Kaski) has become a symbol of misery involved in the fall of traditional agriculture in Finland. The painting was photographed by Daniel Nyblin. By courtesy of National Board of Antiquities, under CC BY-SA 3.0 license.

The history of Finnish agriculture has thus far presented several surprises. I doubt that no-one could have predicted that traditional agriculture promoted biodiversity in the way it did. The rapid development of agricultural production in the 19th century was astonishing. And, finally, the whole country was overtaken by the years of crop failures — not once, not twice, but three times within a decade. These unforeseeable twists in the story are, paradoxically, common in trajectories of social-ecological systems. As a result of their indivisibility, complexity, and dynamism, social-ecological systems do not behave deterministically but in unexpected ways (Berkes *et al.* 2003). The key in managing them is not to know what is coming, but to be prepared for whatever is coming.

Unfortunately, conventional resource and environmental management that utilises command-and-control and top-down approaches is ill-equipped to deal with the challenges of management of such complex systems (Berkes *et al.* 2003). To resolve this dilemma aid has been sought from resilience theory. *Social-ecological resilience* has been introduced as an organising concept that brings together the complexity of the social and ecological systems, and underlines that adaptability and flexibility can improve management processes (Berkes *et al.* 2003, Folke 2006).

In terms of resilience theory, the long period of slowly developing traditional agriculture represented one domain of dynamic stability of the Finnish agricultural system. Its practices — slash-and-burn cultivation, meadow haying, and extensive cattle grazing — adapted to the prevailing but fluctuating ecological and social conditions for centuries (Soininen 1974). Observed adaptive capacity and the resulting ability to persist indicates social-ecological resilience (Berkes *et al.* 2003). But, during the 19th century, traditional agriculture fell into a crisis and collapsed (Soininen 1974). The system had eventually lost its ability of renewal, and a regime shift in agricultural production, practices, and livelihoods followed.

To retain resilience, social-ecological systems need to confront disturbances on regular basis. Apparent instability of a system, in the sense of fluctuations, fosters adaptive capacity, whereas stability reduces it (Holling 1973, 1978). It can be hypothesised that because of the growing demand for food, traditional agriculture became constrained to maximising sustained yield, thus losing its dynamism and variability (Soininen 1974, Chapin *et al.* 2009). It could no more persist in the face of shocks and disturbances, such as wars, crop failures, and human population growth.

1.2.2 Conservation science and traditional agriculture in the Anthropocene

Today the number of people is still continuously growing, and this underlies most if not all of our environmental problems. Need to support human population has led to land-use changes that have been destructive to ecosystems (Millennium Ecosystem Assessment 2005). Land-use conversion is the main driver of change in terrestrial ecosystems (Sala *et al.* 2000). Agriculture is now the dominant land use and cultivations cover a quarter of Earth's terrestrial surface (Millennium Ecosystem Assessment 2005). The green revolution introduced new high-yielding crop varieties, chemical fertilisers, pesticides, irrigation, and machinery that enabled global intensification of agriculture during 20th century (Millennium Ecosystem Assessment 2005). As a result, traditional small-scale farmlands have been replaced by large intensively farmed monocultures (Lindborg *et al.* 2008). Combined with other wide-spread human impacts, such as climate change, biotic exchange, and nitrogen deposition to mention but a few, our influence is seen everywhere (Sala *et al.* 2000).

In order to concretise the extent of human impact on Earth, certain scientists have proposed that we have entered into a new geological epoch called *Anthropocene*. Anthropocene marks the era during which humans and our societies have become a global geophysical force, starting from industrialisation in early 19th century (Steffen *et al.* 2007). During the beginning of the Anthropocene, local traditional agricultural systems were transformed into industrial food production chains that are driven by global market forces.

Anthropocene requires scaling social-ecological systems theory up to the planetary level.

Given the current conditions, a question arises: is systematic management of social-ecological systems possible? Natural, undisturbed systems are likely to be continually in a transient state; they will be equally or more so under the influence of humans (Holling 1973). Are we able to sustain our planet and ourselves, if the very facts that we are basing our deeds upon are constantly changing? Global change has been so vast and fast that nature has not been able to adapt to it. As a result, we have induced the sixth mass extinction of species (Pimm *et al.* 1995). Is there room for conservation of traditional rural biotopes in this world plagued by such immense environmental issues?

I argue that a better understanding on social-ecological character of traditional rural biotopes can offer valuable insight for both sustainable resource management and biodiversity conservation. After all, management of traditional rural biotopes is one of the rare contemporary human actions that benefit nature. As long as it continues, we can learn from it.

There seems to be significant resilience in some traditional farming systems; both in the species composition that partly goes back to the era of last glaciation, and in the farming practices that are able to adapt to the context of modern agriculture and still retain their traditionalistic character. In rare locations within Europe traditional agricultural practices are still continued and they maintain a significant amount of biodiversity (Halada *et al.* 2011, Fischer *et al.* 2012). Knowledge on such self-sustaining or stabilising social-ecological systems is essential in order to understand how to manage natural resources sustainably (Berkes *et al.* 2003, Chapin *et al.* 2009). Although traditional agriculture cannot feed the global human population, it certainly can provide lessons for environmentally-friendly farming and enhancing local food security.

The conservational value of traditional rural biotopes is not trivial, either. Traditional agriculture supported rich biodiversity for centuries; this biodiversity is now under threat of agricultural modernisation (Halada *et al.* 2011). In Finland alone, over 99 % of the total coverage of traditional rural biotopes disappeared during the 20th century (Salminen and Kekäläinen 2000, Luoto *et al.* 2003). Over 90 % of habitat types categorised as traditional rural biotopes have become threatened (Raunio *et al.* 2008). Either the traditional management practices have seized or management is carried out in a way that no longer maintains the characteristics of the sites (Salminen and Kekäläinen 2000, Raunio *et al.* 2008). Furthermore, many sites have been destructed due to land-use changes (Salminen and Kekäläinen 2000, Raunio *et al.* 2008). Habitat loss has resulted in severe decline in species dependent on traditional rural biotopes. They are now the second most important habitat for threatened species, providing habitat for a total of 1 807 red-listed species in Finland (Rassi *et al.* 2010).

Finally, traditional rural biotopes lend themselves to studies on evidence-based conservation because they represent a mutual relationship between people and nature. Modern conservation science explicitly recognises the tight coupling of social and natural systems (Kareiva and Marvier 2012). There is a wide acceptance of the notion that people are part of ecosystems (Mace 2014). This emergent framing of tight human–nature-relationship succeeds the earlier conservation approaches that portrayed nature first as a place of sublime wilderness, then as threatened and in need of protection, and finally as a system providing goods for people (Cronon 1996, Mace 2014). These views co-exist, and the latter view is evident in the ecosystem services framework (Millennium Ecosystem Assessment 2005). The most recent framing envisages a multi-layered and multidimensional relationship between people and nature that is difficult to conceptualise (Mace 2014). For that reason, we need to study social-ecological systems such as traditional rural biotopes: they are able to inform us how nature conservation as an ideology, a practice, and a discipline can navigate through the ambivalence of Anthropocene.

1.3 Traditional rural biotopes as a social-ecological study system

There are several frameworks that can be used for analyses of social-ecological systems (for a comparison, see Binder *et al.* 2013). In my work, I have utilised Elinor Ostrom's framework that is specifically designed for analysis of sustainability in social-ecological systems (Ostrom 2007, 2009, McGinnis and Ostrom 2014). The framework guides identification of basic working parts and critical relationships among the elements that are essential for the functionality of the social-ecological system (McGinnis and Ostrom 2014).

The core subsystems in the framework are resource system(s), resource units, actors, and governance system(s); these all interact together in order to create outcomes that feed back to the subsystems, and impact also other related ecosystems outside of focal social-ecological system (Ostrom 2009). The system is understood as inherently open; influences to and from other ecosystems or social, economic, and political settings can affect any of its components (McGinnis and Ostrom 2014).

In the case of contemporary management of traditional rural biotopes in Finland, the social-ecological system framework can be applied as follows. To start with the system's ecological components, traditional rural biotopes are seen as resource systems, which consist of identifiable abiotic and biotic features and are managed in certain ways in order to derive desired resource units. Key features of a resource system include variables such as their size and location, productivity, and the predictability of their ecosystem dynamics (McGinnis and Ostrom 2014). Thus, it matters how extensive traditional rural biotopes are, where they are, what goods they provide, and how certain the provision of these goods or resource units is.

Resource units can be directly derived, such as hay from meadows; or indirect products such as milk or meat from pasturing animals. Traditional rural biotopes can also be managed in order to create or maintain intangible benefits, for example aesthetic landscapes with open sceneries (Birge and Herzon 2014). Because of the conservational value of traditional rural biotopes, farmers and civic associations are eligible for agri-environmental payments in return of management actions (Ministry of Agriculture and Forestry 2014). This monetary compensation can also be considered as a resource unit.

The social subsystems include actors and governance systems. Managers — people who manage traditional rural biotopes — are an important actor group, but also landowners, other community members, administrative officers etc. are included. Actors include those people that participate in management of traditional rural biotopes in one way or another.

Organisations (governmental or non-governmental) are parts of the governance system that defines and sets rules for actors, thus setting conditions for how management can be conducted (Ostrom 2009, McGinnis and Ostrom 2014). Rules, norms, and policies are also important features of the governance system. In Finland, management of traditional rural biotopes is part of the national conservation agenda and agri-environmental programme (Heikkinen 2007, Ministry of Agriculture and Forestry 2014). As most of the resources for management and its governance are channelled through agri-environmental policies, the national agri-environment scheme forms the main governance system for management (and conservation) of traditional rural biotopes.

Large-scale social, economic, and political settings comprise an important framework that controls and directs the way traditional rural biotopes are managed. The above description is quite different from the previously introduced situation that prevailed before the end of the 19th century. What happened after that? In short: traditional rural biotopes lost their position as the basis of food production (Fig. 3). The rural society started to dissolve as people moved to cities. Agriculture (and forestry) intensified and extensive land uses such as wood-pasturage or haying of meadows were ceased as unprofitable. Domestic and foreign trades started to define the prices and volume of supply and demand of agricultural products.

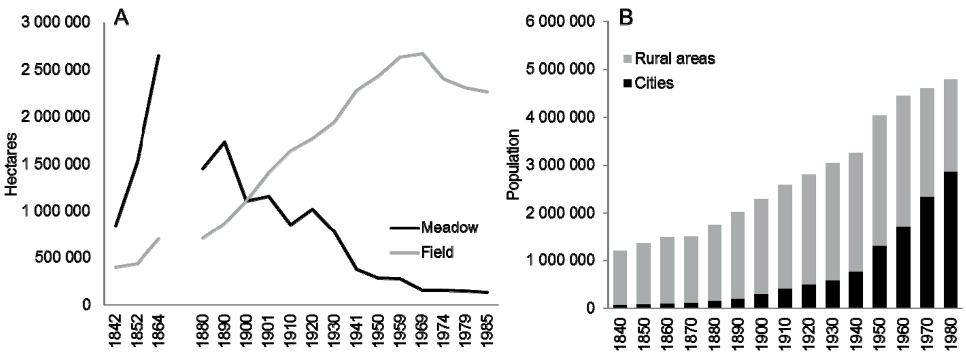

FIGURE 3 The decrease in meadows and increase in field coverage (A) and the population growth (B) in Finland from mid-19th century to 1980s. The data were compiled from Official Statistics of Finland. Figures concerning the province of Vyborg (Viipurin lääni) were removed from the data of years 1840–1940. Most of the province was yielded up to the Soviet Union during World War II. Note that the areal records from years 1842–1864 are rough estimates.

Finland joined the European Union in 1995 and since then the European Common Agricultural Policies have guided the way in which Finnish agriculture is practiced. This change, however, provided a new role for traditional rural biotopes; their conservational value was acknowledged through agri-environmental policies, and their management was included as a measure in the national agri-environment scheme.

Along with these overall changes, farmers have made decisions on continuation of management of traditional rural biotopes on farm level. When their individual decisions are scaled up the resulting general pattern has been the large-scale abandonment of traditional rural biotopes (Raunio *et al.* 2008). The social change has been rapid, occurring in just one hundred years (Salminen and Kekäläinen 2000). Nature has been much slower in reacting to it. Many species that are dependent on grazing or mowing still persist on habitat patches that are no longer managed. These species populations are prone to extinction debt following habitat loss or degradation (Kuussaari *et al.* 2009).

The above description provides a general overview on contemporary situation of traditional rural biotopes. One particular aspect that I yet want to highlight is the multidimensionality hidden in the narrative. In ecology and geography, spatial and temporal dimensions form important scales of research (Cash *et al.* 2006, Cumming *et al.* 2006). Studies on social-ecological systems often include an additional sociological scale which adds ideas about organisation and representativeness of social structures (Cumming *et al.* 2006). Phenomena of interest can range across many scales (e.g., be spatiotemporal). If these scales interact, a cross-scale research approach is recommended (Cash *et al.* 2006). When several levels within a single scale are included, studies are conducted in a multilevel fashion (e.g. certain attributes of individual persons vs. organisations are compared). Studies that take all possible dimensional interactions into account are termed as cross-scale and cross-level (Cash *et al.* 2006). This kind of research is needed to develop a better understanding of structure, function, and dynamism of social-ecological systems.

In case of traditional rural biotopes, time is the first essential dimension. I have spent quite much time explaining the historical changes that have led to the formation of traditional rural biotopes as we see them today. Temporal changes are cumulative, and if we are to picture the future of traditional rural biotopes, we need to take the history into account.

Another important dimension is space; the species that make up traditional rural biotopes once were wide-spread, and now they are confined into a sparse and fragmented network of habitats. Spatial scale is important in any conservation effort. Management actions are conducted on site level, but to be ecologically effective, they need to be coordinated on a wider level. This is because ecosystem functions — and social-ecological system functions — operate across a range of spatial levels (Chapin *et al.* 2009).

Finally, there is a managerial scale that weaves together the temporal change, spatial scale, and action. It encompasses the site-specific management decisions and broader coordination (or lack of it). Managerial scale ranges from tasks to strategies; from farm-level decision-making to national agri-environmental programme to European Common Agricultural Policy.

Inclusion of such governance perspective is important. Conservation of traditional rural biotopes has not improved, and it is termed as one of the most difficult challenges in Finnish conservation agenda (Heikkinen 2007). One possible reason for this inefficiency in conservation policies is a scale mismatch between the extent and location of management actions and the desired ecological response. In a cross-scale and cross-level manner we can ask, for example, why are local populations of endangered meadow plants declining despite the management effort mediated through national agri-environmental policies that should support meadow habitats?

Similar mismatches between ecological processes and agricultural management are common also elsewhere: biodiversity management at patch or farm levels often ignore the large-scale ecological functions they aim to secure (Pelosi *et al.* 2010). If allowed to continue, scale mismatches lead to a loss of adaptive capacity in social-ecological systems (Cumming *et al.* 2006). This means loss of species, functions, and other system components, processes, or relationships that contribute to the systems' resilience (Cumming *et al.* 2006).

1.4 Aims of this thesis

The broad aim of this study is to find out the most critical factors hindering conservation of traditional rural biotopes in Finland. In relation to this main question, I seek for practical solutions for enhancing the management effort in order to improve the conservational status of traditional rural biotopes. As a result, I provide insight into current challenges in conservation of traditional rural biotopes, and propose sustainable means to facing those challenges in a more resilient way.

My research consists of ecological and social studies, and an integrative synthesis. Each chapter of my thesis focusses on different aspects of conservation of traditional rural biotopes on a specific level within spatial and managerial scales, and using a particular temporal focus (Fig. 4).

I connect the partial studies from different chapters with each other through a governance perspective. This interdisciplinary multiscale approach enables me to detect cross-level and cross-scale social-ecological interactions that are important in improving conservation of traditional rural biotopes.

In chapters I–IV, I focus on following specific research questions:

1. How changes in land use have affected traditional rural biotopes in Central Finland, particularly in terms of meadow coverage? What is the effect of historical meadow connectivity on vascular plant species richness and community composition? (I)

2. How do grazed and abandoned wood-pastures differ in their species assemblages of vascular plants and bryophytes (mosses and liverworts)? What factors drive biodiversity on wood-pastures? (II)
3. What is the current coverage of managed traditional rural biotopes, and where management actions should be directed to? How the current network of traditional rural biotopes can be spatially complemented in terms of conservation value based on known ecological characteristics? (III)
4. What kinds of social-ecological factors underlie maintenance of traditional rural biotopes in the context of current Finnish agriculture? What are the landowners' motivations for site management or abandonment, and what is the role of the national agri-environment scheme in conservation of traditional rural biotopes? (IV)

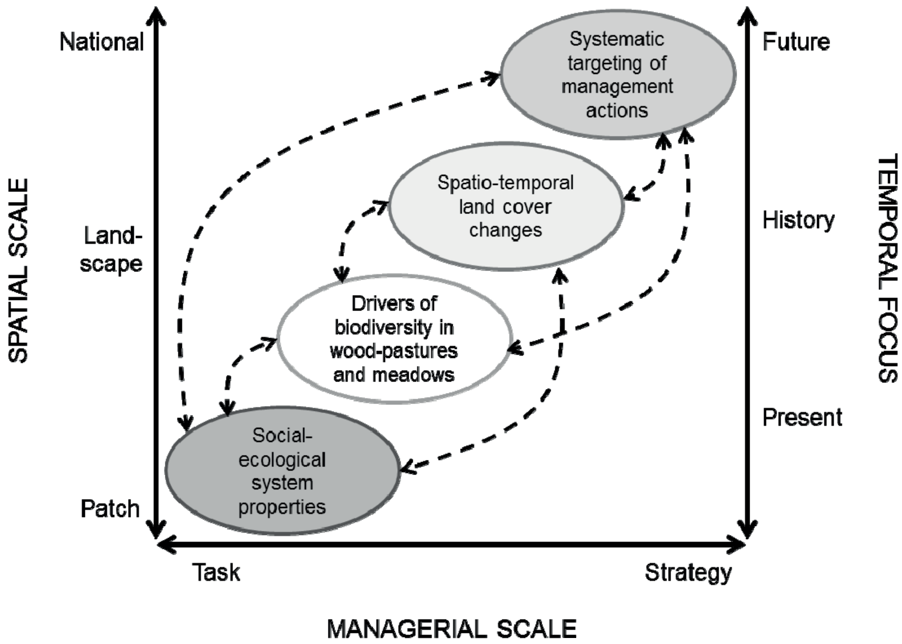

FIGURE 4 A schematic illustration of temporal foci and spatial and managerial scales utilised in the study. Levels on each axis refer to the units of analysis. Central themes of research are within ovals, which are located according to their approximate positions on the axes. Transition from white to grey background corresponds to a shifting focus between ecology and the social sciences. Cross-level and cross-scale interactions are depicted as dotted arrows.

2 MATERIALS AND METHODS

2.1 Caught between disciplines and mixed methods

I have adopted an interdisciplinary approach in my research. This has resulted in a mix of different methodologies. Most of the ecological case studies included spatial data, and for that reason GIS (Geographic Information System) -based analyses played an important role in my work (especially in chapters I and III). Species occurrence and abundance data were analysed with generalised linear models (GLMs) combined with ordination analyses (I, II). Social context of contemporary management of traditional rural biotopes was explored through discourse analysis (IV). In addition, I interviewed landowners of traditional rural biotopes and analysed the content of this data in a qualitative manner (IV).

This variety of descriptive research methods has allowed me to gain a broader understanding on my research subject. This principle is concordant with the post-positivistic theoretical perspective that I relate myself to; it underlines the importance of using multiple methods to identify a valid belief because all research methods are imperfect (Moon and Blackman 2014).

Next, I will give an overview on the application of the research methods according to the central research themes. For detailed descriptions, I refer the reader directly to chapters I–IV.

2.2 Spatio-temporal land cover changes

In order to gain an overall understanding of the dynamism of meadow coverage, land-cover changes throughout the province of Central Finland were quantified. Contemporary spatial data and mid-20th century maps covering the region were acquired for two time steps: topographical maps from 1958–1973 and topographical database from year 2010. The older maps were in raster format and they were georeferenced and rectified in ArcGIS (ESRI® ArcMAP™ version 10.3) to match spatially with the more recent vector-format database.

Buffer zones with a two-kilometre radius were created around 211 meadow sites. The sites were selected based on surveys conducted by environmental authorities during years 1992–2012[2]. From the buffers, which covered a total of 2,283.5 km^2 per time step, six semantically corresponding land cover types were interpreted based on the topographical map data: meadows, fields, built areas, wetlands, forests, and lakes. The studied land cover classes were digitised into geospatial data.

The data from the time steps were rasterised, overlaid, and summed together in order to detect the land cover changes. Based on the results, a spatially explicit land change matrix was formed (Eriksson and Skånes 2010).

To gain a more comprehensive understanding on the temporal change of meadow coverage, a subset of 24 meadow sites was selected for further analysis (I). All of these sites were located in the southern half of the province. For these sites, also cadastral maps from years 1841–1855 were acquired, georeferenced, and rectified. Since the cadastral maps had gaps and missing land cover information in some places, only the coverage of meadows and areas with missing data were digitised using the 2 km buffers. The cadastral maps also had substantial spatial inaccuracies, which made them inapplicable for the overlay analysis on land cover changes. Instead, the data was used to calculate descriptive statistics and index values concerning the spatial extent and configuration of meadows within the buffers.

In order to gain information on the functional connectivity of meadow patches, integral index of connectivity (IIC; Pascual-Hortal and Saura 2006) was calculated for each site in every time step. In addition to regular IIC, which takes into account patch sizes and inter-patch distances, also a distance-based index was calculated. In it, a fixed patch size attribute was used; therefore, the index value reflected the variation in patch distances and number of patches. Both indices were calculated using Conefor 2.6 (Saura and Torné 2009). In this part of the study also a 1 km buffer radius was used to include a second spatial level to the analysis.

Corresponding information (total amount of meadows, regular IIC, distance-based IIC, and distance to nearest-neighbouring meadow patch) was derived from the more recent data layers. The data were used to compare the three time steps with each other in terms of meadow loss and fragmentation (I).

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2 *Surveyed traditional rural biotopes* refer to sites that have been verified of being ecologically valuable based on a field survey conducted by officers working for national or regional environmental administration. During the survey, vascular plant species occurrences, habitat types, management status, and quality of management are mapped. Sites are classified as nationally, regionally, and locally valuable. If the criteria for locally valuable class are not fulfilled, sites can be categorized as restorable if they have the potential to develop more value through management. The original national inventory of traditional rural biotopes was conducted in Finland during the 1990s (Vainio *et al.* 2001). After that, additional surveys and monitoring visits have been done regionally (Kemppainen and Lehtomaa 2009). The current guidelines for the survey method are described by Kemppainen (2017).

2.3 Drivers of biodiversity in meadows and wood-pastures

To examine the ecological effects of historical changes in meadow coverage, vegetation of the subset of 24 meadow sites was surveyed in the field (I). We hypothesised that due to the loss and fragmentation of meadows remnant species communities express extinction debt, observable as a causal relationship between species richness and the historical amount and/or connectivity of meadow habitat. In addition to the meadow coverage variables, also current environmental factors were recorded and their effects on species assemblages were estimated. These factors were soil pH and management type: either mowing or grazing (n = 12 and 12, respectively).

Data on vascular plant species richness and community composition was collected between late June and early July 2014. In each site, a 44 meter long edge-to-centre study transect was established with a randomised compass course determining the starting point. A study plot sized two by two metres was located in every ten meters along the transect. A total of five plots, comprising together 20 m^2, were sampled on each meadow. Within each plot all vascular plant species and their abundances (as percentage cover) were recorded. In the subsequent analyses, we included only meadow species (*sensu* Pykälä 2001).

Meadow plant species richness and community composition were modelled according to contemporary environmental factors (management type and soil pH) and present and past historical meadow coverage attributes (calculated within the 1 km and 2 km radiuses for the three time steps: 1841–1855, 1958–1973, and year 2010). The richness of meadow species was analysed using GLMs with Poisson distribution. We built seven models, each including one of the meadow coverage variables (for details, see chapter I). The community data consisting of species abundances were analysed with canonical correspondence analysis (CCA), using model-building approach that corresponded to the GLMs. Finally, the results of the models were compared in order to determine the ecological effects of past and present habitat amount, connectivity, and isolation together with contemporary environmental factors (I).

In the second field study, two species groups, vascular plants and bryophytes, were compared in order to achieve a more comprehensive understanding of biodiversity patterns in traditional rural biotopes (II). Here the focus was on boreal wood-pastures and their land uses. We studied the ecological impacts of a social phenomenon (land abandonment) by exploring how grazing management vs. management abandonment affected wood-pasture plant biodiversity when compared to other environmental factors.

Also this study was conducted within southern Central Finland. A total of 48 wood-pastures were selected from 33 farms according to their tree structure and management status (grazed or abandoned). The study set-up was balanced so that each grazed site had an equivalent abandoned site in terms of dominant tree species (birch, pine, spruce, or mixed deciduous and coniferous).

Within each study site, three plots of ten by ten meters were surveyed for their tree structure and sampled for soil moisture and pH. Vascular plants, bryophytes, and grazing and trampling intensities were recorded from four subplots of two by two meters placed inside the corners of every plot. Thus, plant data was collected from a total of twelve subplots (48 m^2) from each site. In addition, to derive information on historical land-use, the number of farms during mid-19th century was counted within one kilometre buffer zone around each study site from old cadastral maps (that were used also in chapter I; wood-pastures are not recorded in the maps so direct information on their extent was not available). This estimate reflects historical grazing intensity as during 19th century farms typically had cattle that grazed freely in forests surrounding the farm (Lampimäki 1939, Jäntti 1945, Soininen 1974).

The data were analysed on site-level using either species richness or community composition as a dependent variable. Vascular plants and bryophytes were analysed separately. Species richness was measured as the number of observed species, and the effects of management and other environmental variables on richness were estimated using negative binomial GLMs with log link function. Community composition (including species abundances) was analysed through Nonmetric Multidimensional Scaling (NMDS) ordination with Bray-Curtis dissimilarities. For both species groups, separate GLM and ordination analyses were done for all sites, grazed sites, and abandoned sites (II).

In chapters I and II, statistical analyses were done with R (version 3.1.1 in I and 3.4.0 in II; R Core Team 2016). We used packages "MASS" (Ripley *et al.* 2017), "spdep" (Bivand *et al.* 2017), and "vegan" (Oksanen *et al.* 2017).

2.4 Systematic targeting of management actions

The governance perspective was introduced by exploring if and how conservation of traditional rural biotopes could be improved by directing restoration and management actions and funding spatially (III). Here the scope of research was broadened to the scale of ecological networks and to a national-level conservation planning perspective.

First, the current management status of traditional rural biotopes in Finland was evaluated. Then it was explored how management effort on surveyed traditional rural biotope sites could be complemented based on known ecological values residing outside of their network. It was assumed that the most important aim of network expansion is to secure the maintenance of threatened habitats and species dependent on management of traditional rural biotopes. An ultimate objective for the analysis was to inform the national goal of securing management of all valuable surveyed sites and increasing the total cover of managed traditional rural biotopes to 60,000 ha (Salminen and Kekäläinen 2000, Kemppainen and Lehtomaa 2009, Kotiaho *et al.* 2015).

The current spatial extent of management effort was determined using GIS data on agri-environmental payment contracts targeted for management of traditional rural biotopes in year 2014. Moreover, the shares of surveyed vs. unsurveyed, protected vs. unprotected, and state-owned vs. privately-owned managed traditional rural biotopes were calculated. These categories correspond to the administrative classification often used by Finnish environmental authorities (e.g. Vainio *et al.* 2001, Kemppainen and Lehtomaa 2009). The data were handled with ArcGIS 10.3.1.

To inform targeting of future management effort, a spatial prioritisation analysis was conducted using Zonation software. Zonation yields an optimised prioritisation solution that takes issues such as irreplaceability and complementarity of data features into account (Moilanen *et al.* 2005). Starting from a full landscape, Zonation iteratively removes locations (cells or planning units) of least contribution to remaining biodiversity while minimising marginal loss of overall conservation value following from the removal (Moilanen *et al.* 2005). It also can account for different connectivity measures, weights given for each data layer, and works well with large data sets (Moilanen *et al.* 2014).

The prioritisation analysis was done with Zonation 4.0 (C-BIG Conservation Biology Informatics Group 2014). In the prioritisation, a total of 35 nation-wide GIS data layers derived from five different sources contributed to the conservation value of a given location. The database included information on survey, protection, and management statuses, habitat types, and occurrences of red-listed vascular plants specialised in traditional rural biotopes. When calculating the distribution of conservation value over the landscape individual data layers were weighted according to their conservational importance. Also connectedness of unsurveyed sites to surveyed sites was included in order to produce an ecologically meaningful result that takes species dispersal better into account.

As Zonation proceeds iteratively, the final spatial prioritisation solution was sequenced into four nested management scenarios (A: surveyed sites, B–D: surveyed sites with a progressive addition of managed area). In each consecutive scenario, ca. 4,000 managed hectares were added, thus forming a realistic step-wise plan for expansion of the management network. The most extensive scenario (D) yielded a spatial allocation of nearly 45,000 ha of managed traditional rural biotopes. Finally, maps of management scenarios were generalised to a resolution of 100 km^2 in order to inform management allocation regionally (III).

Implementation of a spatially targeted management plan is often complicated by the fact that a range of factors not taken into account in the prioritisation affect local land use (Knight *et al.* 2011). To create a tighter connection between the prioritisation results (III) and site-level management decision-making (IV), the analysis was planned and conducted alongside the development of an official management agenda for protected traditional rural biotopes in Finland (Raatikainen 2017). The agenda corresponds to an implementation strategy as defined by Knight *et al.* (2011). In the agenda, the same ecological parameters that were used to produce the management scenarios by the Zonation analysis were translated into site-level management prioritisation guidelines. These included also additional criteria that had to be excluded from the analysis due to lack of spatial data (e.g. management continuity, availability of grazing animals, and cultural value; Raatikainen 2017).

2.5 Social-ecological system properties

Further insight into social context of contemporary management and conservation of traditional rural biotopes was acquired through a site-level analysis (IV). Social-ecological structure and resilience of traditional rural biotope systems was explored through landowners' perceptions and discourses on the sites and their management. In this case study, the focus was on the contemporary decision-making on whether to continue or to abandon management (grazing or mowing) on site level. Informed by social-ecological systems theory, key social-ecological variables that are attendant to landowners' decision-making strategies for successful conservation action were detected.

A mixed methods approach was used to gather complementary quantitative and qualitative data sets. Quantitative analysis was used to derive shared discourses that guide the site-level management decision-making on general level. The qualitative methodology, on the other hand, made it possible to gain a better understanding on landowners' personal motivations for managing traditional rural biotopes. Their personal perceptions on management of traditional rural biotopes were explored by analysing repetitive, emergent meanings related to the management from data collected through semi-structured interviews.

The interviews were conducted in January and February 2015. Twenty landowners of 16 traditional rural biotope sites that were located in Central Finland were interviewed. Participants needed not be farmers nor live within Central Finland. They were grouped into "managers" or "non-managers" based on whether they actively managed their traditional rural biotope themselves.

The interview was divided in two parts. First part was a semi-structured discussion around three themes: Farm property and its history, change in surrounding landscape, and the traditional rural biotope site itself. In the second part, participants sorted a set of general statements related to management of traditional rural biotopes according to their level of agreement or disagreement with each statement. The interviews were audio-recorded with participants' permission and later transcribed for further analysis, and the sorts were recorded by writing down ordinal ranks of individual statements.

Transcribed data were used in a qualitative content analysis of interviews that explored landowners' personal perceptions on traditional rural biotope management or abandonment. Specific repetitive meanings that emerged from the interviews were derived first and used to code all data accordingly. After this inductive phase of analysis, these emergent perceptions were deductively related to a social-ecological system framework. For those key framework variables that corresponded to the perceptions, detailed insights were derived from the interview transcripts.

Elinor Ostrom's social-ecological system framework (*sensu* McGinnis and Ostrom 2014) was chosen to provide the theoretical background for four reasons: firstly, it gives equal value for ecological and social perspectives (Binder *et al.* 2013); secondly, the framework is well suited for exploring the role of policies and other governance arrangements because it is rooted in institutional analysis (McGinnis and Ostrom 2014); thirdly, its aim for sustainability resonates with the resilience theory[3]; and fourthly, its focus on action situations corresponds to the idea of the centrality of management practices in both conservation and ecology of traditional rural biotopes.

Data from statement sorting were analysed using Q method, a quantitative method to assess subjectivity (Stephenson 1935, Webler *et al.* 2009). This analysis aimed to detect discourses on contemporary management of traditional rural biotopes that were shared among the landowners. Q methodology is an invert of a traditional statistical approach that seeks for patterns in variables across study subjects (so-called R methods) (Stephenson 1935). In Q, patterns are sought across the study variables for each subject, i.e. correlations are computed between persons instead of their traits (Danielson 2009, Webler *et al.* 2009). In a Q study, typically a small group of people rank a set of statements about some issue based on how well the statements reflect their own thinking (Danielson 2009). When patterns are found across these rankings, it suggests that there are inter-subjective perspectives that are shared among people (Webler *et al.* 2009).

Q methodology applies multivariate statistical methods in detecting the similarities in participants' statement sorts. In this study, factor analysis was run on statement ranks in order to derive latent patterns in the way the landowners had sorted the statements. The sorts were clustered into a meaningful set of factors, and a descriptive narrative was synthesised for each factor on the basis of analysis results, participants' comments, and interview records. These were translated into discourses (IV).

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[3] To be precise, the framework is not fully compatible with the theory. Ostrom preferred to consider resilience as one of the possible ecological outcomes of the system's interactions rather than a property of the overall social-ecological functionality of the system. However, the connection between sustainability and social-ecological resilience is widely acknowledged (Berkes *et al.* 2003, Chapin *et al.* 2009).

2.6 Synthesis: planning of future scenarios

As described above, different research questions need to be answered through certain ways; they demand specific types of data, which are suited for particular analytical methods. I used scenario planning technique to synthesise results from studies that utilised different methodologies. A scenario is a structured account of a plausible future; scenarios are alternative, dynamic stories that capture key ingredients of the uncertainty about the future of a study system (Peterson *et al.* 2003). Scenario planning can incorporate a variety of quantitative and qualitative information in a systemic way, and it usually involves a diverse group of people in constructing the scenarios (Peterson *et al.* 2003). In this case, I based the scenarios on my research, which was conducted with collaboration with other scientists (I–IV), representatives of environmental administration (III), and private landowners (IV).

Scenario planning complements the social-ecological system analysis (described in chapter IV). Although the latter provides an understanding of the current state of a system and its functional relationships, it does not necessarily describe the system's plausible future pathways or people's aspirations to alter the system (Hanspach *et al.* 2014). The motivation for scenario planning lies in that it offers conservationists a method for developing more resilient conservation policies by facilitating decision-making in the face of uncontrollable, irreducible uncertainty (Peterson *et al.* 2003).

The aim of the synthesis was to produce a few contrasting scenarios that illustrate the future consequences of different decision paths in conservation of traditional rural biotopes. I concentrated on the regional context of Central Finland, as most of my data originates from there. I started developing the scenarios on the basis of the observed land cover changes. Then I identified the main agents of change that contributed to the results of each case study (I–IV).

After the identification of change factors, I grouped them according to their relative importance. I concentrated on a few main drivers and started to structure the possible futures for an average managed traditional rural biotope site in Central Finland within a time frame of next 20–50 years. I also assessed whether that outcome was likely or not in terms of biodiversity conservation. As different paths converged into roughly similar visions of plausible future landscapes, I chose two factors that were the most important contributors to the scenarios and visualised a double dichotomy based on them. The main guidelines behind the visualisation exercise were that 1) a social-ecological system is either maintained or driven towards change by interactions between its inner and outer structures (Ostrom 2007), and 2) the main force behind change is the reorganisation of the existing structure to optimise their functioning (Antrop 1998). In creating the scenarios, I imagined alternative ways for traditional rural biotope systems to reorganise given the prevailing drivers of change. To make the causal relationships within each scenario more implicit, I also created narratives for them.

3 RESULTS AND DISCUSSION

3.1 The history

3.1.1 Land cover changes drive meadow dynamics

The dominant land covers of Central Finland are forests and lakes, of which forested area has increased by 7.3 % between mid-20th century (time step 2) and early 21st century (time step 3) (Table 1). Changes in lake coverage result mainly from water levels' regulation. Wetlands, namely mires and bogs, are also common, but their share of the landscape has slightly declined mainly due to silvicultural drainage. The result is a change into forest.

TABLE 1 Transition matrix of land cover changes between time steps 2 and 3 (1958–1973 and year 2010) in circular local landscapes surrounding meadow sites (n=211, r=2 km). Values denote the share of the studied landscape changing from time step 2 to time step 3 land cover class (rows to columns; in percent). Also total proportions of each land cover class in both time steps are shown (for time step 2 in a column and for time step 3 in a row). Similarly, gross losses and gains are presented. Time step 1 (1841–1855) was excluded.

	Time step 3							
Time step 2	Meadow	Field	Built	Wetland	Forest	Lake	Total, time step 2	Gross loss
Meadow	0.04	0.18	0.12	0.14	0.86	0.04	1.37	1.34
Field	0.21	6.91	0.63	0.09	3.28	0.01	11.14	4.22
Built	0.01	0.13	1.19	0.02	0.43	0.01	1.79	0.59
Wetland	0.00	0.18	0.13	8.60	2.61	0.03	11.55	2.95
Forest	0.03	0.79	1.31	1.20	54.24	0.16	57.74	3.49
Lake	0.00	0.00	0.01	0.08	0.12	16.19	16.41	0.22
Total, time step 3	0.29	8.20	3.39	10.12	61.55	16.45	100.00	
Gross gain	0.25	1.29	2.20	1.52	7.30	0.26		

Large changes are seen in agricultural land-uses: the proportional coverages of fields and meadows have decreased (Table 1). Gross loss of fields is largely resulting from afforestation, which has additionally increased the forest cover. Similar transition to a more forested landscape between years 1939 and 2008 has also been observed in a case study conducted in South-Western Finland archipelago (Pitkänen *et al.* 2014). On the studied islands, which belong to a national park, the increase in forest coverage was mainly due to secondary succession of overgrowing semi-natural grasslands (Pitkänen *et al.* 2014).

The transition matrix (Table 1) summarises the share of the landscape that changes between land cover classes, and thus it represents the overall landscape structure but tells only little about the changes within individual classes (Eriksson and Skånes 2010). For this reason the changes in meadow coverage were examined in more detail. During 50 years' time, only 2.6 % of time step 2 meadows have remained. Comparison of meadow transitions between the two time steps revealed that a substantial share (63.0 %) of meadow coverage has been afforested, following with 13.0 % cleared into arable fields (Fig. 5). Further 9.8 % — mainly moist meadows — have returned to wetlands, and 8.4 % have been transformed by human constructions.

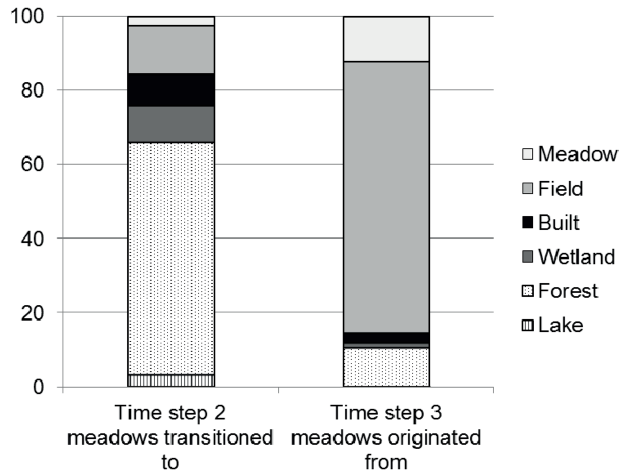

FIGURE 5 Dynamics of meadow coverage in Central Finland between time steps 2 (1958–1973) and 3 (year 2010). Data are from circular local landscapes surrounding 211 meadow sites with a 2 km radius.

On the other hand, retrospective examination of contemporary meadows shows that 72.4 % of them were cultivated during time step 2 (Fig. 5). Also on other occasions, a long-term land-use history of meadow patches has been observed to be interrupted by tilling for agricultural production (Käyhkö and Skånes 2006). Although the patches were returned to meadows again, the ecological effects of such trajectories may be irreversible in regions with poor soils (Käyhkö and Skånes 2006).

As a result, it can be concluded that meadows as a land-cover type have been highly dynamic in Central Finland. This finding is contrasting when compared to the observations from the SW Finland archipelago. There, depending on the studied island, meadow continuity was much more prevalent, and restoration actions had on some occasions increased semi-natural grassland coverage between years 1963 and 2008 (Pitkänen *et al.* 2014). Another case study from Sweden found that as much as 67 % from the recorded grassland coverage in year 1993 had been grassland also in year 1946 (Käyhkö and Skånes 2006). Compared to that, the agricultural landscapes of Central Finland have been more susceptible to change, as only 10 % of the present meadow coverage has a longer history as traditional rural biotopes (Fig. 5).

The observed landscape change was discussed also during interviews with landowners (IV). They described the transformation of meadows and wood-pastures into fields and forests, thus confirming the results from the land cover change analysis. Landowners explained how socioeconomic drivers behind loss of traditional rural biotopes have become visible through land-use changes. Meadows were ploughed to fields as a result of agricultural intensification. Landowners also described how urbanisation is depopulating rural areas, as young people move to cities to gain education and work. This leads to abandonment of traditional rural biotopes and launches the reforestation process (IV).

Also elsewhere in Europe changes in economic conditions for farming drive both land-use intensification and agricultural land abandonment (Kumm 2003, 2004, Plieninger *et al.* 2006, Lindborg *et al.* 2008, Beilin *et al.* 2014). Relative decline of rural working opportunities creates an important pressure to abandon agriculture (Beilin *et al.* 2014). There is a general understanding on the fact that people's responses to economic opportunities drive land cover changes (Lambin *et al.* 2001). The effect of such drivers is related to social and historical contexts, and the process of abandonment can be counteracted for example by individual-level idealism and place-bound identity (Kumm 2003, 2004, Beilin *et al.* 2014). In Central Finland, there seems to be a limited number of factors that would encourage the young to stay and keep on farming. Despite this, some young farmers choose to continue farming (IV). More work is needed to clarify what types of rural livelihoods are seen in positive light by young adults and why. This is especially important as Finnish farmers are ageing, and finding successors is often difficult (Ministry of Agriculture and Forestry 2014).

The process of landscape change was examined in more detail in terms of meadow loss with respect to 24 study landscapes (I). Here data from mid-19th century (time step 1) were included, and it is clear that land cover conversions between time steps 1 and 2 were even more substantial than those between time steps 2 and 3. This is in accordance with the historical records that show the meadow coverage was most extensive during the latter half of 19th century (Soininen 1974, Salminen and Kekäläinen 2000) (see also Fig. 3A).

A notable decline was observed in both functional connectivity and total amount of meadows (Fig. 6A–C; I). At the same time, the distances to nearest-neighbouring meadows increased, indicating that the study sites became increasingly isolated (Fig. 6D; I). The changes were similar on both studied spatial levels (1 and 2 km), for which reason only results for landscapes with one kilometre radius are presented.

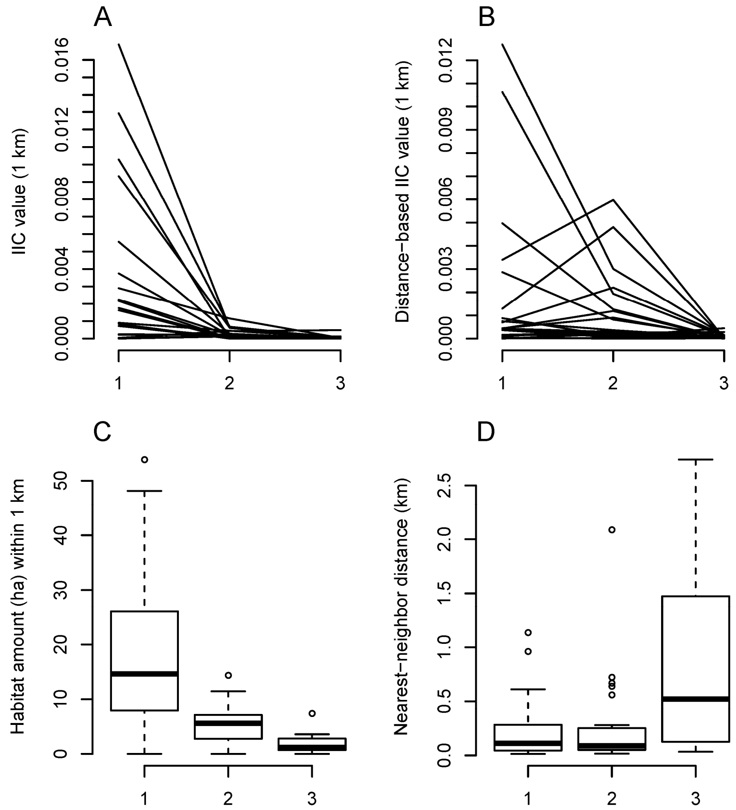

FIGURE 6 Values for meadow coverage variables for three time steps (1: 1841–1855, 2: 1958–1973, and 3: year 2010). In panels A and B, lines connect values of a given study site (n=24). IIC refers to Integral Index of Connectivity. Panel C depicts the distribution of total amount of meadows within a 1 km buffer zone. Panel D gives distances from each study site to its nearest-neighbouring meadow patch. Reprinted from chapter I.

Albeit the loss of meadow habitat between time steps 1 and 2 was pronounced, this initial decline in meadow coverage did not increase nearest-neighbour distances (I). Thus, the isolation effect became observable only after time step 2. Within some landscapes a fragmentation effect was observed: the habitat was divided into more patches with shorter inter-patch distances (I). This is reflected in peaks of distance-based connectivity values on time step 2 (Fig. 6B). For a given amount of habitat, fragmentation *per se* may have positive ecological effects. It is suggested to benefit species richness, population sizes, and dispersal as it increases the functional connectivity of the landscape by making habitat patches more accessible (Fahrig 2003, 2017).

However, there were landscape-specific differences in the way meadow habitat was lost and the fragmentation effect was not always observed. Within several studied landscapes habitat loss occurred together with declining number of patches and increasing inter-patch distances (I). In these landscapes, adverse ecological consequences are possible. These include declines in population sizes and increases in extinction probabilities which have been demonstrated in cases where there is little habitat left across large areas (Hanski 2011, Rybicki and Hanski 2013).

Differences in local landscape dynamism were observed also when the total amount of meadows within the study landscapes were compared between time steps 1 and 3. The median of remaining coverage was 7.7 %, but the range was wide and on three specific occasions the amount of meadows increased during the time interval (I). This indicates that the process of meadow loss has followed landscape-specific trajectories in Central Finland.

The general distribution of meadows was sparse and isolated throughout the time frame of the study (I). On time step 1, the proportional meadow coverages surrounding the study sites ranged from zero to 17.2 %, whereas the current meadow coverage was 2.3 % in maximum, and in twenty cases less than one percent (I). This leads to a question whether meadows have ever been widespread in Central Finland.

3.1.2 No extinction debt in meadow plant species communities

No evidence was found for an extinction debt in plant species assemblages on the 24 study meadows (I). Despite the overall loss of meadows, the species richness or the community composition did not respond to historical habitat amount or connectivity (I).

A total of 74 meadow plant species were recorded from the study plots, but only four of them were meadow specialists according to Pykälä's (2001) categorisation (I). This may be one reason that contributes to the observed lack of connection between current species assemblages and historical habitat amount and configuration. Extinction debt is most pronounced among habitat specialists (Cousins 2009, Kuussaari *et al.* 2009, Krauss *et al.* 2010, Cousins and Vanhoenacker 2011). Generalist species can utilise the landscape in a more flexible manner (Andrén *et al.* 1997), and therefore their populations are not as prone to decline after the loss of primary habitat. There is evidence that grassland plant communities are influenced by spill-over of species from adjacent habitats, indicating that species diversity in specific habitat types cannot be considered in isolation from the surrounding landscape matrix (Schmucki *et al.* 2012). This mixing of communities may further complicate the detection of extinction debt, as it affects the occurrence and abundance of habitat specialists.

There are two plausible explanations for the observed situation: either the meadow specialists are already extinct, or extinction debt never developed. Cousins (2009) noted that extinction debt was evident only in landscapes where over ten percent of the original grassland habitat was left; the debt is paid off faster if habitat is scarce and strongly fragmented (Kuussaari *et al.* 2009). Of our study landscapes, 58.3 % were below the ten percent threshold. It is usual to conclude that extinction debt is already paid if observed species richness follows from contemporary factors (Öster *et al.* 2007, Cousins 2009, Kolk and Naaf 2015). This may be the situation also on meadows in Central Finland, as the habitat patches are small and isolated (I), and contemporary environment factors are the main drivers of biodiversity on traditional rural biotopes (I, II).

However, the second explanation may be more plausible considering the regional context. If current meadows are relatively young and have a history as arable fields, they may lack meadow specialists because of limitations in the species' dispersal abilities. It is important to note that the concept of extinction debt is inherently based on an assumption of an equilibrium state where the number of species is not changing because the rate of local extinctions equals the rate of local colonisations (Kuussaari *et al.* 2009). The observed dynamism in meadow coverage and their land-use history indicates that the species communities may have been under constant change (I). If this is the case, it is logical that the numbers of meadow specialists are low; they probably were so to start with. If there never was equilibrium in species composition, no extinction debt may have formed in the first place.

3.2 The present

3.2.1 Contemporary factors drive plant biodiversity

Factors that significantly explained species richness on the study meadows were contemporary (I). Of meadow coverage variables, current habitat amount and distance-based connectivity had a positive relationship with species richness, whereas distance to nearest-neighbouring meadow decreased richness (Fig. 7A–C; I). The effects of these variables were tested through different GLMs, and the overall conclusion is that the amount and spatial configuration of habitat within the local landscape are important determinants of meadow plant richness (I). Nearest-neighbour distance equals the availability of habitat in the immediate landscape surrounding the focal patch and thus is an indirect and inverse measure of habitat amount (Fahrig 2003). Distance-based connectivity, on the other hand, reflects the number and reachability of habitat patches within a one kilometre dispersal threshold.

The best fit based on Akaike Information Criterion was for the model that included total amount of meadow habitat within one kilometre radius from the study sites (I). Current habitat amount positively impacted species richness (Fig. 7A). The positive relationship between species number and area is a well-known pattern that has its roots in island biogeography (MacArthur and Wilson 1967), and several grassland studies have confirmed this connection either on landscape or patch level. For example, Öster *et al.* (2007) demonstrated in Sweden that meadow size and plant diversity were positively connected through increased habitat heterogeneity. A Danish study showed that local species pool was determined by the number of meadow patches, which in turn was strongly correlated with the total habitat area (Bruun *et al.* 2009). Although there is no consensus whether the size of the focal habitat patch or the total amount of habitat in the landscape is more important (Öster *et al.* 2007), on general, availability of habitat seems to be an important driver of biodiversity on meadows. This is in concordance also with the present study.

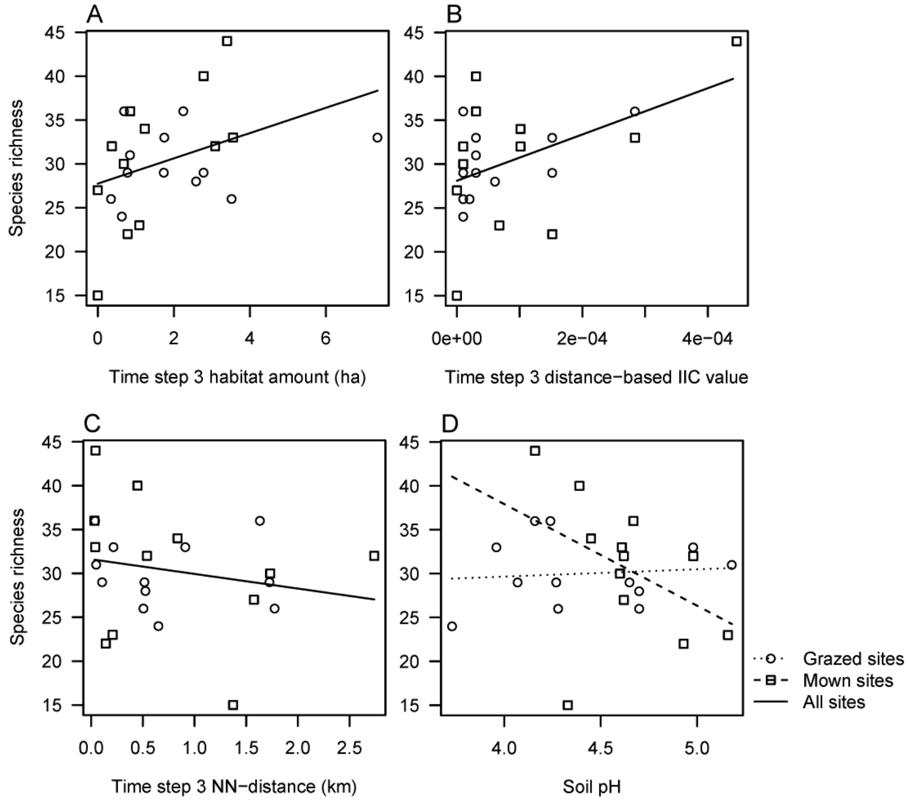

FIGURE 7 Results from the Generalised Linear Model on vascular plant species richness on 24 study meadows. Grazed sites are open circles and mown sites squares. Lines denote significant effects (dotted line: grazed sites, dashed line: mown sites, solid line: all sites). Time step 3 refers to year 2010, and IIC to integral index of connectivity. Reprinted from chapter I.

In addition to the spatial extent of habitat, also other environmental factors promote species richness on traditional rural biotopes. Small-scale diversity and number of grassland specialists on wood-pastures has been shown to increase with grazing intensity and the spacing and proportion of open land in the surrounding landscape within a 500 metre radius (Schmucki *et al.* 2012). The diversity and composition of plant species assemblages are structured by a combination of local conditions and landscape context (Schmucki *et al.* 2012).

This seems to be the case also on meadows of Central Finland. When the GLM with habitat amount explaining meadow species richness was simplified by stepwise removal of terms, the model included also an interaction between soil pH and management type (grazing or mowing) as a significant explanatory variable for species richness (I). Soil pH impacted species richness differently on mown and grazed sites (Fig. 7D). On meadows, the effect of soil pH was tied to the effect of management, and on grazed sites, no increase in species richness was observed (I; Fig. 7D). Species richness of mown meadows decreased with increasing soil pH (I; Fig. 7D).

Same factors — management and soil pH — impacted plant biodiversity also on wood-pastures (II), but the patterns were not similar to meadows (I). Grazing benefited diversity of vascular plants and bryophytes on wood-pastures, as grazed sites had higher species richness of both species groups when compared to abandoned sites (Fig. 8A, C; II). Abandonment of grazing management seemed to lead to the biotic homogenisation of the wood-pasture habitat with the surrounding forest landscape (II). Also grazing intensity impacted species richness of both vascular plants and bryophytes (II).

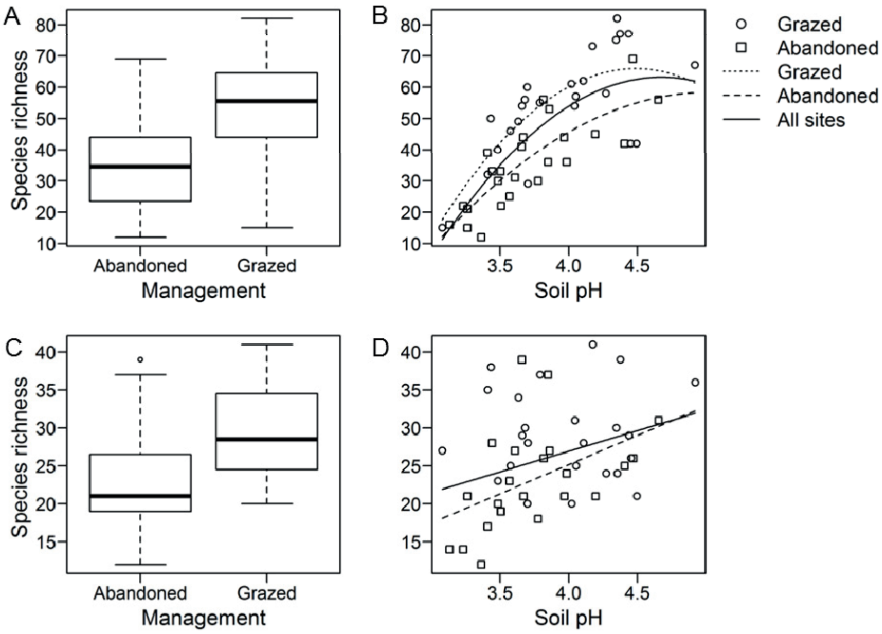

FIGURE 8 The effect of grazing vs. abandonment and soil pH on vascular plant species richness (panels A and B) and bryophyte species richness (panels C and D) according to Generalised Linear Models on 48 wood-pastures. Grazed sites are depicted as open circles and abandoned sites as squares. Lines denote significant effects (dashed lines: grazed sites, dotted lines: abandoned sites, solid lines: all sites). Reprinted from chapter II.

In addition to current management, soil pH increased richness of observed species on wood-pastures (Fig. 8B, D; II). The impact of soil pH on plant diversity is usually positive (Dupré and Ehrlén 2002, Pärtel *et al.* 2004). It is interesting that in Central Finland the positive effect was observed on wood-pastures but not on meadows (I, II). The observed negative impact of pH on species richness of mown meadows was surprising (I).

The contrasting results may be explained by the fact that the pH values of wood-pastures ranged from 3.1 to 4.9 and on meadows the range was from 3.7 to 5.2. It is possible that in boreal traditional rural biotopes the relationship between plant species richness and soil pH is humped, and peaks somewhere between values 4.0 and 4.5 (I; see Fig. 8B).

An alternative explanation for the observed negative relationship is that on mown sites higher soil pH possibly indicates increased competition, which reduces species richness (I). Soil pH was strongly correlated with average height of the vegetation, indicating higher productivity and possible presence of rapidly growing strong competitors. This may lead to the competitive exclusion of subordinate species and dominance of fewer species (Grime 1973, Hautier *et al.* 2009, Ceulemans *et al.* 2013).

On wood-pastures, species richness was the highest on sites with high soil pH, moisture, and grazing intensity, but low tree cover (II). Although management and soil fertility (which is affected by both soil pH and moisture) were the most important factors, also other environmental variables impacted plant biodiversity. The amount of shading limits the occurrence of light-demanding species on wood-pastures, and the biodiversity of herbaceous plants is likely to be maximised at medium to low tree densities (Einarsson and Milberg 1999, Gillet *et al.* 1999). This means that increasing tree cover does not linearly decrease species richness, although our results point to this way (II). It should be noted that the tree cover on the study wood-pastures was generally quite dense (II). Out of all traditional rural biotopes, sparsely wooded meadows may have the highest overall species richness because trees provide habitat for certain species and add to the heterogeneity of the habitat (Kull and Zobel 1991, Einarsson and Milberg 1999, Gillet *et al.* 1999). As soil fertility and moisture are slowly changing ecosystem variables (Chapin *et al.* 2009), the practical implication of this finding is that wood-pasture management should aim for sparse or patchy tree coverage and relatively high grazing intensity, at least on sites that resemble the study sites (II).

It is important to note also that through forest succession some of the abandoned wood-pastures, especially the fertile ones, had developed complementary conservational values (II). Many of the rare bryophyte species observed on the study sites were typical to moist mesotrophic forest habitats rather than wood-pastures (II). Moist herb-rich forests are rare in Central Finland, and given suitable environmental conditions, fertile wood-pastures develop into such without grazing (Oldén *et al.* 2016). Thus on certain sites land abandonment may be beneficial to biodiversity. This relates to the emerging wilderness and rewilding conservation in Europe (Linnell *et al.* 2015). However, based on red-list statuses of habitats (Raunio *et al.* 2008), wood-pastures hold higher conservation priority when compared to herb-rich forests. Therefore the overall conclusion is that grazing is the preferred land management option (II).

The importance of environmental factors was clear also in the NMDS ordination, where the vascular plant community composition of wood-pastures was affected most strongly by the combination of soil pH, soil moisture, and the current management situation (II). The bryophyte community, on the other hand, was strongly driven by soil pH (II). Thus, grazing impacted the community composition of vascular plants more than that of bryophytes (II). This is in line with earlier results from boreal wood-pastures (Takala *et al.* 2015).

The effects of soil pH and management on species community were observed also on meadows (I). The composition and abundances of species differed between meadows according to their soil pH and management type (I). The effect of soil pH is likely related to the occurrence of tall-growing species and possibly to eutrophication (Hautier *et al.* 2009, Ceulemans *et al.* 2013). This may explain why mown meadows with high soil pH had relatively low species richness; they may have been poorly managed in comparison to grazed meadows (Fig. 7D). In addition, grazed and mown meadows hosted different species (I). The management regime clearly affects species composition, but the mechanisms involved in the difference in effect of grazing and mowing are unclear (Tälle *et al.* 2015, 2016). Inadequate management quality in terms of intensity and nutrient enrichment was observed both on studied meadows and wood-pastures (I, II), and their ecological impacts would be an important subject for future research. Low-quality management has been shown to deteriorate the conservational quality and diversity of species communities on traditional rural biotopes, especially in case of vascular plants (Takala *et al.* 2015).

In sum, the overall effect of grazing management and soil fertility on plant species richness was positive on wood-pastures, although there were differences in the ways vascular plants and bryophytes responded to grazing and soil pH (II). On meadows, on the other hand, the impact of soil pH on vascular plant species richness depended on the management (I). The total amount and configuration of meadow habitat within the local landscape was also an important driver of species richness on meadows (I). None of the meadow coverage variables, historical or present, had an effect on species richness or community structure (I). No land-use legacy effects were found on wood-pastures, either (II). Large differences in the species assemblages between grazed and abandoned wood-pastures suggest that most grazing-dependent species had already declined during the first ten years after abandonment (II).

It is clear that current factors, rather than historical land uses, drive biodiversity related to traditional rural biotopes in Central Finland. Yet the causal relationships are not straightforward but depend on focal species group, habitat type, and management regime. It is important to manage different kinds of traditional rural biotope habitats in order to support a wider range of biodiversity. An emphasis on present, not past, patterns and interactions better supports conservation of traditional rural biotopes.

3.2.2 Management actions need spatial targeting

Based on the results of the national level GIS analysis, the total amount of managed traditional rural biotopes continues to decline in Finland (III). The overall cover of sites under management contracts was less than 20,000 hectares in year 2014 (III). During years 2005–2007 the corresponding coverage was ca. 24,500 hectares (Kemppainen and Lehtomaa 2009). This recent decline in the management effort, together with the overall habitat loss (Fig. 3A, Fig. 6; Raunio *et al.* 2008), implies that it will be difficult to reverse the trend in endangerment of species inhabiting traditional rural biotopes. A goal of 60,000 managed hectares has been repeatedly set to mark a minimum coverage that would safeguard the biodiversity dependent on traditional rural biotopes (Salminen and Kekäläinen 2000, Kemppainen and Lehtomaa 2009, Kotiaho *et al.* 2015). This goal will continue to escape unless management effort is increased (III).

Furthermore, we also found out that a majority (79.1 %; 23,923.2 ha) of surveyed traditional rural biotopes with high conservation value are unmanaged (Fig. 9A, E, III). At the same time over 40 % of agri-environmental payment contracts are made for sites without documented biological value (covering 12,890.4 ha; III). Less than 4 % of the occurrences of red-listed specialist vascular plant species included in the study were managed through payment contracts (III). This indicates that management funding has not been successfully targeted to ecologically most valuable traditional rural biotopes. The same conclusion was presented also in an study that focussed on a smaller region within South-Western Finland (Arponen *et al.* 2013). This implies that agri-environmental policies have compensated for management costs without accounting for biodiversity outcomes (Arponen *et al.* 2013).

Maps for optimised management scenarios provided insight into how future conservation efforts could be spatially targeted according to the red-listed specialist species' occurrences and different traditional rural biotope habitats (Fig. 9). In all scenarios, South-West–West coastal region received most of the prioritised management effort (Fig. 9A–D, III). Additional small clusters of inland sites with species specialised in traditional rural biotopes should be managed in a network-like manner (III). Also on coastal region specialist species' occurrences are important signals to where management should be first targeted (Fig. 9G, III).

According to the spatial prioritisation analysis, targeting management only to surveyed traditional rural biotopes (scenario A; Fig. 9A) would not suffice to safeguard management-dependent species and habitats (III). Allocating additional management according to scenarios B and C would substantially improve the conservational status of red-listed vascular plants specialised in traditional rural biotopes (III). At the same time, the representativeness of different habitat types within the management network would increase on protected areas (Fig. 9F, III). The spatial distribution of all scenarios was clustered, indicating a high level of connectedness among habitat patches (III).

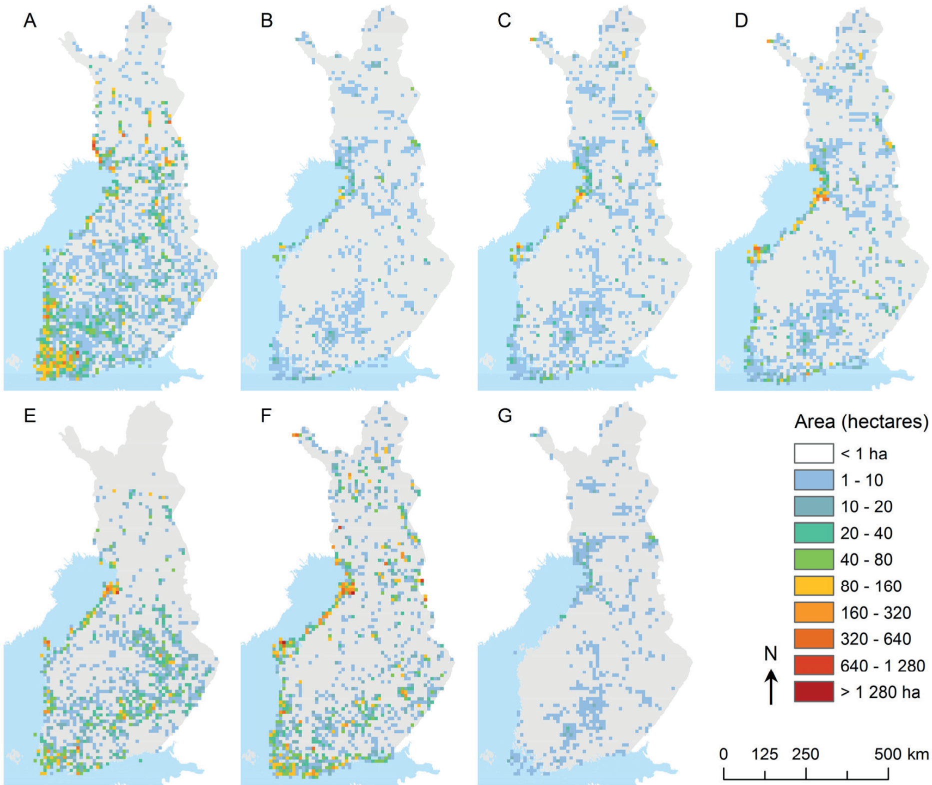

FIGURE 9 Distribution of surveyed traditional rural biotopes (management scenario A; panel A) and allocation of cumulative management network expansion according to subsequent scenarios B, C, and D (panels B–D, respectively). For comparison, the distributions of currently managed sites (according to agri-environmental payment contracts; panel E), protected sites (surveyed and unsurveyed; panel F) and specialist vascular plant species occurrences (panel G) are also shown. Note that the Åland islands were excluded from the analyses. Reprinted from chapter III.

Realisation of targeted management according to the scenarios would promote the ecological resilience of traditional rural biotopes within the management network. Systematic spatial coordination of management actions has great potential to promote habitat connectivity and the associated ecological functions, such as population densities, dispersal, and outbreeding (Hanski 2011, Arponen *et al.* 2013). Availability of heterogeneous habitat patches would provide stepping stones and support areas for mobile specialist species (Nyström and Folke 2001). Targeted habitat restoration may relax remnant population's extinction thresholds and revive the patterns and processes that carry on the ecological memory of traditional rural biotope ecosystems (Bengtsson *et al.* 2003, Rybicki and Hanski 2013). The current management effort (Fig. 9E) does not seem to achieve these ecological benefits (III). This is especially concerning if management is allocated to sites that have a short history as traditional rural biotopes (I), if there is potential for restoration of more species-rich but abandoned sites (III, Pitkänen *et al.* 2014).

As a conclusion, the conservation status of traditional rural biotopes remains ecologically inadequate in Finland. The current network of managed traditional rural biotopes appears to be spatially dislocated and too restricted in order to sustain habitat specialist species' populations in the long term (I, III). In order to improve the situation, management actions need to be systematically targeted to ecologically most valuable sites (III). To advance effectiveness of conservation, the cover of managed traditional rural biotopes should be rapidly doubled in order to form ecologically functional networks (III). This may demand for reallocation of management payments in a more cost-effective manner (III).

3.2.3 Social-ecological complexity challenges current policies

Interviews with landowners of traditional rural biotope sites demonstrated that besides biodiversity, traditional rural biotope management fosters a variety of cultural, aesthetic, and utilitarian values (IV). Precise understanding of the complexity of assigning such values is shown to be important for decision-making on the conservation and development of cultural landscapes and the biodiverse habitats within them (Lindborg *et al.* 2008, Plieninger *et al.* 2015). Landowners expressed these values through conservationist's, profit-oriented farmer's, landscape manager's, and landscape admirer's discourses on management of traditional rural biotopes (IV).

The conservationist's discourse addressed both communal and subjective values of traditional rural biotopes. Landowners justified management with personal joy, experienced place-bound uniqueness of their sites, biodiversity, cultural heritage, and aesthetic scenery (IV). Taking these subjective perceptions into account would benefit future conservation policies, management actions, and ecological outcomes (Bennett 2016). Conservationist's discourse had a critical tone towards the effectiveness of the agri-environment scheme in securing the continuity of management actions (IV). This suspicion is in line with earlier studies demonstrating that agri-environmental policies to enhance biodiversity and landscape quality are unsustainable when social-ecological interactions are unnoticed, simplified, or disregarded (Pelosi *et al.* 2010, de Snoo *et al.* 2013).

The profit-oriented farmer's discourse focussed on the effects of agri-industrial practices and possible drawbacks for management of traditional rural biotopes (IV). This discourse reasoned that traditional rural biotopes generate little profit because agricultural modernisation has diminished their role in contemporary farming (IV). Here the motivation for traditional rural biotope management is utilitarian: these landowners considered farms' livestock production rather than intrinsic or communal value driving management (IV). The discourse also described how rural livelihoods are controlled by international and domestic markets and politics; they drive abandonment of management actions indirectly through impeding integration of traditional rural biotopes with farming practices, or inducing giving up farming (IV). Such abatement of management of traditional rural biotopes initiates a process of deterioration in ecological, cultural, social, and economic values of rural landscapes (Lindborg *et al.* 2008).

Despite the current circumstances, some landowners were able to use the agri-environment scheme in order to establish diversified rural livelihood strategies that build on management of biodiversity and landscape (IV). These "traditional rural biotope entrepreneurs" (*sensu* Birge and Herzon 2014) based their farming strategy on grazing traditional rural biotopes. They contributed to landscape manager's discourse, which emphasised the opportunities of farmers to foster rural landscapes (IV). This discourse was strongly connected to the conservationist's one, but it was more practice-oriented and utilitarian (IV). Landscape manager's discourse pointed out that management of traditional rural biotopes is dependent on modern agricultural practices, especially livestock rearing, and that management actions are inseparable from other farming practices (IV). These landowners aimed to farm in a multifunctional, small-scale manner in order to oppose the trend of agricultural intensification and to avoid the vulnerability to economic volatility of large farms (IV).

Landscape admirer's discourse pointed out that contemporary farming practices do not self-evidently promote traditional rural biotopes (IV). Contributors to this discourse expressed a general admiration of open rural sceneries (IV). Desire to maintain open and aesthetic landscape is often mentioned as an important motivator for management of traditional rural biotopes (Kumm 2003, Stenseke 2006, Lindborg *et al.* 2008, Birge and Herzon 2014), and this was present also in other discourses (IV). However, those portrayed farmers as stewards of the desired landscapes. Landscape admirer's discourse questioned this. It was concerned with the negative impacts of modern agriculture (IV). The discourse took a position outside of agricultural production and criticised modern cattle farming practices, pointing out that industrialised farming has contributed to the deterioration of the rural environment through overgrowing of landscapes, pollution, and nutrient enrichment (IV).

Based on the interviews, site-level management actions foster biodiversity, landscape aesthetics, cultural heritage, and human-nature relationship alike (IV). Understanding of this social-ecological complexity is crucial in promoting management actions among landowners. Current policies, however, seem to fail to do this. Agri-environment schemes incentivise farmers to change their behaviour using money as the main motivator (Kaljonen 2008, de Snoo *et al.* 2013). Landowners pointed out that because the focus of current governance is overly on monetary compensation of management costs, the multiple values tied to traditional rural biotopes are bypassed (IV). Target-wise, agri-environment schemes tend to focus on single outcomes instead of aspiring for a broader variety of landscape values (Lindborg *et al.* 2008). This was reflected in the way the administration gave excessive attention on ecological determinants of traditional rural biotopes when compared to social values (IV). Landowners, too, held ecological qualities important but emphasised that these were tied to social aspects through management action (IV). Development of new policies that could be more attendant to the social-ecological complexity inherent in traditional rural biotope management calls for adoption of a more participatory governance approach (IV).

3.2.4 To manage or not to manage?

The structural analysis of the social-ecological system revealed 16 key features that contributed to landowners' decision-making on management continuation on traditional rural biotopes (Fig. 10, IV). Based on both managers' and non-managers' accounts, grazing animals were the most important resource in contemporary management, whereas fodder and agri-environmental payments were of secondary importance (IV). Non-farming managers arranged grazers on their traditional rural biotopes through collaboration with cattle farmers who lent grazing animals for summer pasturage (IV). Similar practice that includes renting of grazers for pasturage has been documented in Sweden, where the conservation goals concerning traditional rural biotopes are unlikely met with continuing grazing solely on existing farms with the farmers' own animals (Kumm 2003).

Although historical management practices were valued, contemporary management of traditional rural biotopes utilises modern farming practices; e.g. the continuance of grazing often was secured by changing the type of grazers on the basis of what animals were available (IV). This means that there is flexibility in the way management is practiced; similar observations were made also in Sweden (Kumm 2003).

Non-managers saw that the regional administrative organisation (ELY Centre) discouraged management and restoration actions through top-down control (Fig. 10, IV). Based on their accounts, giving up grazing cattle and perceived bureaucracy of national agri-environment scheme both contribute to abandonment of management action (IV). Earlier studies demonstrate that agri-environmental schemes appeal primarily to farmers already aware of environmental issues (Kleijn and Sutherland 2003, Matzdorf and Lorenz 2010, Batáry *et al.* 2015), and fail to catalyse new environmentally-friendly motivation and behaviour (de Snoo *et al.* 2013). As non-managers are averse to engage in current policies, they fall short of encouraging restoration of traditional rural biotopes (IV).

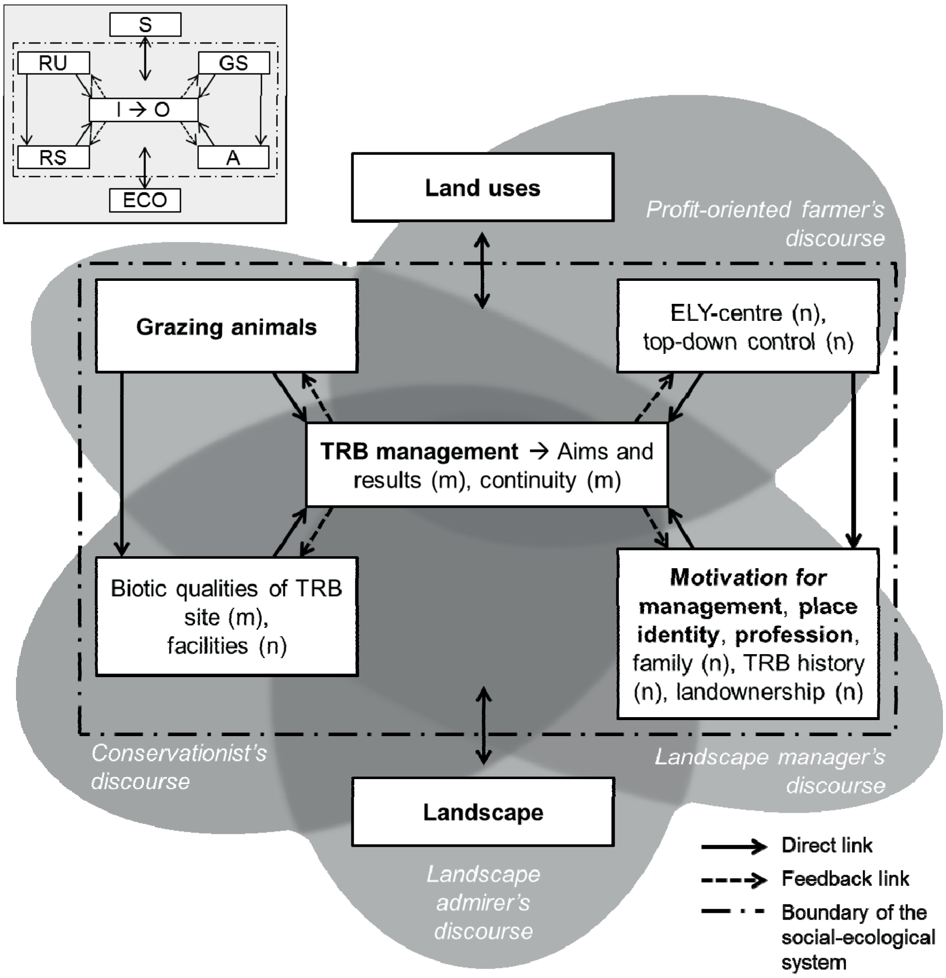

FIGURE 10 Incorporation of landowner interview results into social-ecological system framework (adapted from McGinnis and Ostrom 2014). Main system components are shown in the top-left panel as abbreviations: S=social, economic, and political settings, RU=resource units, RS=resource system, A=actors, GS=governance system, I=interactions, O=outcomes, ECO=related ecosystems. Large panel represents respective key social-ecological features in relation to decision-making on management or abandonment, derived from the landowner interviews. Features perceived important by both managers and non-managers are in bold face. Additional important features mentioned by either managers or non-managers are indicated with (m) and (n), respectively. Grey ellipses correspond to four discourses, which reflect the values contributing to management decision-making and practices. Their location and extent is approximate; they represent how different points of view put more emphasis on different social-ecological features. "TRB" is an abbreviation of traditional rural biotope and "ELY Centre" refers to the regional administrative organisation governing implementation of agri-environmental measures in Central Finland. Reprinted from chapter IV.

An important finding was also that the current policies do not reach all landowners, because they are targeted towards active farmers (IV). In addition to farmers, also civic associations are eligible for agri-environmental payments (Ministry of Agriculture and Forestry 2013, 2014), but landowners generally refused the opportunity to apply for management funding through an outside party due to its unpracticality. The restrictedness of the agri-environment scheme hinders both the utilisation of management funding and spread of information on traditional rural biotopes (IV). Sufficient demonstration and advisory work are essential to practising conservation on farmland (Herzon and Mikk 2007), but the current policies apparently lack these (IV). Together with the unprofitability of small-scale agriculture, overall failure to raise awareness of traditional rural biotopes and their value seem to have contributed to landowner decisions that lead to abandonment (IV).

Managers were generally accustomed to the agri-environmental policies and said these had only minor effects on their decisions on how to conduct management (IV). Yet, managers pointed out that the agri-environment scheme authoritatively detaches management of traditional rural biotopes from what is defined as “regular agriculture”, and marginalises their management into a highly regulated, site-specific special measure (IV). This loss of agricultural function causes traditional rural biotopes to lose resilience. If management becomes dependent on the amount and continuation of agri-environmental payments, direct links between farmers and their environments erode, and traditional rural biotopes become susceptible to abandonment (Kumm 2003, Sutcliffe *et al.* 2013).

In general, landowners felt that they had a responsibility to protect their land for future generations (IV). They connected landownership and continuation of management actions to a sense of belonging to the place — the farm — and to the chain of generations. Such appreciation of the rural landscape and the values tied to it promote management of traditional rural biotopes (Kumm 2003, Stenseke 2006, Lindborg *et al.* 2008, Kaljonen 2008, Birge and Herzon 2014).

Thus, resilience of traditional rural biotope systems relies on the local connections between landowners and landscapes that foster the sense of place and landscape identity (IV). These can be supported by knowledge sharing and collaborative grazing efforts (IV). Current agri-environmental policies do not self-evidently encourage these connections or efforts. New adaptive governance policies that encourage networking and social learning among different actors are needed, because hierarchical top-down control hinders conservation of traditional rural biotopes (IV).

3.2.5 The virtuous cycle of traditional rural biotope management

Managing traditional rural biotopes, as any other social-ecological system, sustainably requires enhancing their resilience to future changes (Berkes *et al.* 2003, Plieninger and Bieling 2013, Chapin *et al.* 2015). My results show that on local level, the resilience of traditional rural biotopes is tied to continuance of low-intensity grazing and accompanying land-use practices that are based on a mutual human–nature relationship. The species community and vegetation dynamics of the traditional rural biotope site forms a basis for its value, and provides an ecological feedback system through which managers were able to adjust their management practices (Fig. 10, IV).

Overall, landowners considered grazing management and its social-ecological outcomes motivating and rewarding (IV). Managers described how grazers brought them joy and maintained desired features of vegetation such as openness and species richness, and created habitats for rare species (Fig. 10, II, IV).

Management included also other practices, e.g. clearing of bushes. Such hands-on work strengthened the managers' relationship with nature and the surrounding landscape (IV). This led to a mutual interaction where positive experience, emotion, and ecological knowledge together supported management and improved its environmental outcomes and vice versa (Fig. 10, IV). Landowners expressed this affinity to the surrounding landscape, and management actions further reinforced their experienced place attachment (IV). Management contributed to landowners' way of life, relationship to nature, appreciation of cultural landscape, and perceptions of landownership and continuity (Fig. 10, IV).

Reinforcing such positive feedback loops is of particular importance in building social-ecological resilience (Berkes *et al.* 2003). These connections are the core material for reconstruction of the virtuous cycle (*sensu* Selman and Knight 2006) that created and maintained the traditional rural biotope systems in the first place. Here reconstruction does not mean reproduction of the vernacular landscape, but re-connecting social and economic entrepreneurship with environmental processes and patterns within contemporary contexts (Selman and Knight 2006, Plieninger and Bieling 2013).

Currently, management is tied to a perception of traditional rural biotopes as nexuses of values related to biodiversity, landscape, and living cultural heritage (IV). Positive experiences and observed ecological impacts of management actions together strengthen the linkage between landowners and the land owned (IV). These reciprocal connections with the landscape motivate further management (IV, Selman and Knight 2006). On a wider level, management of traditional rural biotopes provides beneficial outcomes also for the general public, and positive feedback from the community acts as a further motivator for management (Stenseke 2006, Herzon and Mikk 2007). In this cyclical process biodiversity, cultural heritage, and landscape aesthetics are simultaneuosly the results and the motivators of management actions.

The social-ecological system that underlies traditional rural biotopes has diverged from traditional agriculture. Grazers are no longer kept solely because they provide manure, milk, or meat, but increasingly for conservational and cultural purposes. Through this social-ecological reorganisation, traditional rural biotopes are adapting to their new role as conservation endeavours.

3.3 The future(s)

3.3.1 Landscape scenarios as social-ecological domains of attraction

The change of rural landscape has been a central feature of my research throughout its course. At the centre of the observed landscape change is the loss of traditional rural biotopes following from abandonment of management due to land-use conversions (land cover change analysis, I, II, IV). This social-ecological change was affected by following factors: the dependence of biodiversity on traditional rural biotope management (I, II, III), the availability of grazing animals for management (I, II, IV), the dependence of management on rural livelihoods (IV), the intensification and industrialisation of agriculture and forestry (land cover change analysis, I, II), the observed constraints in agri-environmental measures (IV), the ineffective governance of traditional rural biotope conservation (III, IV), urbanisation and depopulation of rural areas (IV), rewilding of rural landscapes (II, IV), and a tension between globalisation and localisation (IV).

From this list, the two main factors that notably affect the resilience of traditional rural biotope systems are the availability of grazing animals and the level of intensity of rural land use (land cover change analysis, I, II, IV). These factors contribute to management effort and underline the continuity of traditional rural biotopes (IV). As a result, I built the descriptions of plausible future scenarios around them (Figs. 11–15).

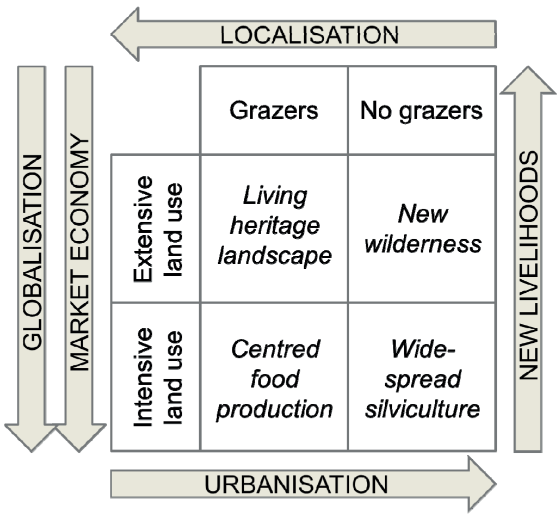

FIGURE 11 Illustration of four future scenarios for traditional rural biotope management (in italics). The double dichotomy was built on two main factors (availability of grazing animals and land-use intensity). Drivers of change are depicted as arrows; changes in human values are excluded because the effect is not unimodal.

In the case of Finnish traditional rural biotopes, important drivers of social-ecological system reorganisation appear to be changes in human values, emergence of new livelihoods, market economy, urbanisation, and the friction between globalisation and localisation. These feed into local traditional rural biotope systems through the two main factors — availability of grazers and land use intensity — and their interactions (Fig. 11).

Depending on the influence of drivers on the main factors and adaptive capacity of the social-ecological system, the system will either maintain its current state or change. Drivers of landscape change can be interpreted as social-ecological disturbance agents. Change occurs when disturbance drives the system to a trajectory that leads to a new domain of attraction (Holling 1973). The future scenarios represent such domains of attraction as different landscape characterisations. Landscapes have unique social-ecological system properties, including stable states and adaptive capacity that maintains the current state. Every landscape has its own resilient property, which is based on self-reinforcing feedbacks among its structures and functions. This means landscapes can be paralleled to social-ecological systems in order to develop resilience-oriented strategies for biodiversity conservation (Plieninger and Bieling 2013, Hanspach *et al.* 2016). From the resilience perspective, landscapes are capable of coping with disturbances, e.g., demographic or economic changes, without changing their structure or functions, until they cross certain thresholds (Plieninger and Bieling 2013).

The scenarios visualise what happens when those thresholds are crossed. The crossings significantly impact biodiversity within the landscape. It is challenging to develop an understanding on the overall effect of landscape changes on biodiversity, but this kind of interdisciplinary insight is a prerequisite for advancing conservation and management of traditional rural biotopes (Lindborg *et al.* 2008). The scenarios can be seen as alternative landscape states for a certain location, as presented here, but they can also co-occur. In future, all four scenarios are most likely present in some form but in different locations and with uneven frequencies.

3.3.2 Living heritage landscape

FIGURE 12 First scenario: grazing animals, extensive land use.

This landscape is in many ways an objection to current megatrends of globalisation and urbanisation. It is strongly driven by localisation, which grows from the opposition to harmful consequences of globalisation. It also contrasts the idea that life is better in cities and claims that people are happier and healthier when they are part of nature. Intrinsic value of nature is widely acknowledged and it motivates people to conservation action. Agri-environmental funding is used to support rural entrepreneurs that are specialised in maintaining biodiversity and flow of ecosystem services. Different types of meadows and wood-pastures are restored and managed for their ecological, social, cultural, and utilitarian value. Their prevalence in the landscape increases the appeal of rural areas. The increased management effort is also seen in the recovery of populations of red-listed species. In addition to the intangible benefits, traditional rural biotopes are managed in order to produce a variety of different products and ecosystem services. Agriculture aims for self-sustenance.

The first scenario builds on the virtuous cycle of traditional rural biotope management and the conservationist's and landscape manager's discourses (IV). It also draws on the need to manage and restore all kinds of traditional rural biotope habitats (I, II, III). When sites are managed in a network like manner, habitat loss can be counteracted and functional connectivity of species' populations can be supported (I, III). Ecologically, management helps to maintain dynamics in populations and communities, and socially, it enhances the vitality of the countryside and the fulfilment of the environmental goals concerning cultural landscape management (Lindborg *et al.* 2008). It also increases the value of common goods and ecosystem services provided by the rural landscape (Lindborg *et al.* 2008, Birge and Herzon 2014).

The view on nature presented by the first scenario is the "people and nature" view that emphasises the importance of cultural structures and institutions for developing sustainable and resilient interactions between human societies and the natural environment (Mace 2014). This approach has deep roots in European nature conservation tradition, where nature and culture are intertwined in a complex way (Linnell *et al.* 2015). The rural community of the scenario is supported by appreciation of natural and cultural values and cohesiveness and farming identity among locals (Beilin *et al.* 2014). To many rural people, traditional landscapes and the agricultural activities with which they are associated are important elements of place-bound identity, leading to a widespread support for conservation of traditional rural landscapes (Linnell *et al.* 2015). However, the social and aesthetic qualities of landscapes are often neglected in contemporary conservation policies, probably because they are not easy to measure or assess (Lindborg *et al.* 2008).

3.3.3 Centred food production

FIGURE 13 Second scenario: grazing animals, intensive land use.

In order to keep farming profitable, agriculture has become strongly market-oriented and dependent on national and international market prices. Competition with cheaper products from other countries has increased the importance of production subsidies. Farming is heavily centred on certain regions where production chains have become efficient. Due to this, agri-environmental policies focus on minimising the environmental detriments caused by intensive farming. Water protection is of primary importance, whereas biodiversity issues are secondary. Traditional rural biotopes are managed if they bring added value to regular cattle farming; usually they are grazed together with fertilised pastures. Management of rural landscapes is mainly practiced through cattle grazing on improved pastures. This mimics the image of a traditional rural landscape. Land use is driven by utilitarianism and a friction between globalisation and localisation. Urbanisation is to some extent controlled by politics that aim to keep the countryside populated.

The second scenario describes modern agricultural landscape as profit-oriented farmer's and landscape admirer's discourses portray it (IV). Here agriculture is intensive according to the demands of global market economy. In Finland, industrial farming is challenging because of climatic conditions (Ministry of Agriculture and Forestry 2014). Unfavourable physical conditions for cultivation and livestock keeping drive abandonment of agricultural practices, but these can be counteracted to some extent by official funding and subsidies for land management (Beilin *et al.* 2014). As a likely result, agriculture eventually centres in most favourable locations. Within those regions, land scarcity drives up the intensity of pasturage and cultivation and shifts production toward the market and to higher value products (Lambin *et al.* 2001).

In landscapes where areas of cultivated grasslands and arable fields are increased, habitat isolation may be counteracted and species' dispersal opportunities can be increased (Lindborg *et al.* 2008). These positive ecological outcomes, however, depend on whether the species can adapt to practices of intensified agriculture (e.g. usage of heavy machinery, chemical fertilisation and herbicides). Furthermore, if the livestock grazes on improved grasslands instead of more diverse traditional rural biotopes, biodiversity is negatively affected (Lindborg *et al.* 2008). A combination of pasturage on improved grasslands and traditional rural biotopes can also have negative ecological impacts, if the animals are allowed to move freely between different pastures (Takala *et al.* 2015). This practice was often observed on study wood-pastures (II). Many landowners seem to consider that division of pasture into smaller rotational blocks is inconvenient (IV).

According to this scenario, management of biodiversity is of secondary importance in agri-environmental policies. Here agri-environment schemes continue to focus on mitigation of negative environmental impacts of industrial agriculture rather than promoting biodiversity (Kleijn and Sutherland 2003, Batáry *et al.* 2015). In Finland, the eutrophication of the Baltic Sea has for long been recognised as the most severe environmental problem caused by intensified agriculture (Kaljonen 2006). Conservation issues on farmland therefore continue to be dominated by water protection, which has been the major focus also in earlier national agri-environmental programmes (Kuussaari *et al.* 2004, Aakkula and Leppänen 2014). Their general focus has been on human threats to nature, and on strategies to reverse or reduce these threats ("nature despite people" view according to Mace 2014). Because biodiversity of traditional rural biotopes needs active management for maintenance, its conservation does not fit into this view and is largely neglected.

3.3.4 Widespread silviculture

FIGURE 14 Third scenario: no grazers, intensive land use.

In order to produce bioenergy and other wood-based products, rural areas are covered with commercial forests in different growth phases. Spruce forest is the ecosystem that provides the society with the raw material for life. Agriculture is practiced only on few most favourable regions; elsewhere fields are afforested. Cattle husbandry has largely ceased due to its low profit-to-cost ratio. Land use is intensive and monotonous because resources need to be derived cost-efficiently. The homogeneous and intensively used landscape benefits some generalist species. Remnant old-growth forests, traditional rural biotopes, and other biodiverse habitats are restricted to protected areas. Most of the people live in cities. Those who want to spend time in nature have summer cottages in countryside. Rural properties are kept for timber production. Land-use is driven by globalisation, urbanisation, and opportunism.

Third scenario assumes that the land-use conversion of traditional rural biotopes to afforested land continues (land cover change analysis). This land-use change trajectory has been observed also elsewhere in Europe (Kumm 2004, Lindborg *et al.* 2008, Beilin *et al.* 2014). Silvicultural practices were evident on some of the abandoned wood-pastures, although stands taken into forestry were excluded from the study (II). Opportunities and constraints for new land uses are created by local and national markets and policies (Lambin *et al.* 2001); in this scenario the economy and politics build strongly on silviculture. When social pressures reduce diversity of land uses, the result is a homogeneous, biodiversity-poor landscape (Beilin *et al.* 2014). As the number of grazing animals decreases, biodiversity declines both at the local and landscape levels (Lindborg *et al.* 2008). Lack of grazers may also negatively affect the attractiveness of rural areas as living environments for people (Stenseke 2006, Lindborg *et al.* 2008).

Urbanisation affects landscape change on rural areas through the increasing ecological footprint of city dwellers (Lambin *et al.* 2001). In this scenario nature is managed in an integrated fashion with the goal of providing benefits for the society in the form of ecosystem goods and services (Mace 2014). This “nature for people” thinking has a clear utilitarian orientation (Mace 2014). In general, large-scale exploitation disfavours cultural values in the landscape (Lindborg *et al.* 2008).

3.3.5 New wilderness

FIGURE 15 Fourth scenario: no grazers, extensive land use.

Rural depopulation has led to widespread agricultural land abandonment. Urban livelihoods have drawn people to cities. Land use is driven by urbanisation and globalisation. As a result, farming and other primary production sectors have lost their central role in the Finnish society. Economies related to immaterial goods such as education, services, and information dominate. This leads to a relaxation of rural land-use pressure. Forest succession proceeds freely, facilitating spontaneous rewilding that benefits biodiversity related to boreal taiga ecosystems. Most of the infrastructure located on rural areas is related to travelling and accommodation. Traditional rural biotopes are managed only on few locations where they attract visitors. Some of their species survive in low numbers in this restored wilderness because the human-suppressed disturbances such as natural fires, floods, and grazer populations are again proliferated.

The fourth scenario combines findings from abandoned wood-pastures (II) and landowners' descriptions of the landscape effects of rural depopulation and management abandonment (IV). As grazing ends, forest succession begins to change the landscape (Kumm 2004, Oldén *et al.* 2016). Currently, traditional rural landscapes all over Europe suffer from abandonment, leading to encroachment by a few species of trees and shrubs as an alternative for planned reforestation (Lindborg *et al.* 2008). In addition, remote and economically unproductive farm areas can also be purposefully rewilded for natural values (Beilin *et al.* 2014, Linnell *et al.* 2015). Although through overgrowing the wood-pasture biodiversity is eventually lost, values related to boreal forest ecosystems may to some degree regenerate unless the site is taken into forestry (II, IV).

Conservation thinking in this scenario relies on the "nature for itself" type of human–environment relationship, which prioritises wilderness and intact natural habitats (Mace 2014). This has been the dominant ideology in conservation since the 19th century, and continues to be so (Cronon 1996, Mace 2014). It sees that protecting wilderness is the solution to our culture's problematic relationship with the nonhuman world (Cronon 1996). As conservation approaches, wilderness and rewilding highlight the integrity of ecological patterns and processes without human intervention (Mace 2014, Linnell *et al.* 2015). Management of traditional rural biotopes is difficult to fit into this paradigm, as it challenges the basic assumption on the supreme value of pristine nature that is the core of "nature for itself" thinking. Some supporters of this ideology are willing to embrace the loss of early successional habitats (Linnell *et al.* 2015), including traditional rural biotopes.

4 CONCLUSIONS: IS IT POSSIBLE TO MANAGE FOR RESILIENCE?

Based on my results, I conclude that one major reason behind the inefficiency in conservation of traditional rural biotopes is a scale mismatch between the extent and location of management actions and the desired ecological response. It is suggested that the loss of traditional rural biotope habitats should be compensated for until the endangerment of their species is reversed (Ministry of the Environment 1992, Salminen and Kekäläinen 2000, Heikkinen 2007). My work indicates that this goal will be extremely difficult to meet unless conservation policies concerning traditional rural biotope management are profoundly improved.

The observed mismatch occurs between spatial and managerial scales (Fig. 4). The national strategies on traditional rural biotope conservation do not meet the local decision-making on management or abandonment of individual sites (III, IV). This has resulted in a situation where the management effort continues to decline (III), ecologically valuable sites are left without management (III), and a considerable amount of landowners is left outside of the governance system (IV). Although local management effort has important social-ecological benefits (I, II, IV), its combined volume is not enough to promote the conservation status of traditional rural biotope habitats and species on the national level (III).

In the end of the introductory part of this thesis I argued that governance plays a key role in conservation successes or failures. My results confirm this and indicate that the current conservation governance of traditional rural biotopes has several weak points that contribute to the observed scale mismatch (III, IV). In order to achieve the desired ecological outcomes of traditional rural biotope management, I would recommend that the following critical factors and challenges are considered in forthcoming agri-environmental and conservation policies.

It is clear that current management effort and funding are too restricted in order to safeguard the biodiversity and cultural values tied to traditional rural biotopes (III, IV). It is concerning that these manifold values are dismissed by both agri-environmental and conservational policies (III, IV). The scarce management payments have not been targeted according to ecological value of the sites (III). Although the network of traditional rural biotopes has become extremely fragmented and sparse, the current policies fail to encourage initiating additional management (I, III, IV). On the contrary, the policies may threaten the continuity of management through oversimplification of social-ecological interactions (IV). The quality of management may deteriorate on site-level as the ecological impacts of management actions are not effectively communicated and reasoned to the managers (I, II, IV). Overall, there is a general lack of communication on issues related to traditional rural biotopes and their management (IV).

Development of more effective policy tools through adoption of a new type of governance may provide solutions to above challenges. A more participatory approach could be able to create a connection between guiding conservation action on national level and supporting self-organising local efforts (III, IV). My results indicate that establishment of a conservationally sound network of managed traditional rural biotopes is possible only through better incorporation of local actors (III, IV). To be successful, governance should be able to integrate and communicate ecological and cultural values of traditional rural biotopes within the contemporary social-ecological context (IV). This calls for building and sharing knowledge on traditional rural biotope systems and their best management practices in collaboration with national, regional, and local actors (IV). Further case studies are needed to investigate the possibilities of adaptive governance and co-management approaches in conservation of rural landscapes. Practical applications of these rather theoretical concepts could exemplify how to design policy measures to promote multiple values in landscapes where a range of land-cover types and regional characteristics are considered (Lindborg *et al.* 2008).

Another challenge in improving conservation of traditional rural biotopes is that the drivers of their decline operate on temporal and spatial scales beyond the reach of current policies. Land use changes, habitat loss, and endangerment of species result from changes in local rural livelihoods. These, in turn, are impacted by global megatrends such as urbanisation, market economy, and globalisation, as exemplified in the future scenarios. Based on my results, I propose that these large-scale drivers can be counteracted by systematically supporting local management efforts. The key to improve the conservation status of traditional rural biotopes lies in promoting their social-ecological resilience through local livelihoods and farming systems that are based on management of biodiversity and foster the related social and cultural values (IV).

Participatory governance and local focus can be mediated through resilience-oriented measures that can be incorporated into traditional rural biotope conservation agendas (Kemppainen and Lehtomaa 2009, Raatikainen 2017), national biodiversity strategy (Heikkinen 2007, Council of State 2012), and agri-environmental programme (Ministry of Agriculture and Forestry 2014). Certain practical suggestions for resilience-based actions can be derived from my results. To support traditional rural biotope habitats and species, management effort and funding should be targeted to ecologically most valuable sites (III). This spatial targeting could aim for a site network where local clusters of wood-pasture and meadow habitats are able to maintain high species richness and host different kinds of species communities (I, II, III). To ensure ecological continuance, currently managed sites need to be kept under continuous management (II, IV), and the quality of management should be monitored more carefully (I, II, IV). Temporal continuity and quality of management can be fostered through supporting the self-reinforcing social-ecological interactions that include monitoring by managers (IV). To enable self-monitoring, managers need training and feedback regarding management quality from the administration (IV), and this would benefit from site-specific information on species assemblages, soil properties, and land-use history (I, II). In addition to current management effort, planned restoration of abandoned traditional rural biotopes is needed (III). In regions where land-use legacies are weak, additional management can be targeted according to occurrences of traditional rural biotope specialist species (I, III). Their populations on managed sites can act as sources for dispersal given that the sites are located near to each other (I, III). Locally targeted increase in the availability of habitat can promote both species richness and populations of red-listed species (I, III). Increasing the cover of managed traditional rural biotopes requires that also those sites that are located outside of active farms are managed (III, IV). This can be realised by transferring grazing animals from cattle farms to management sites (IV). Building and maintaining management networks in this manner calls for true collaboration and sharing of information between authorities and local actors (IV). Communication on manifold values that are tied to traditional rural biotopes is needed in order to motivate their management and restoration and to raise public awareness on their disappearance (IV).

This list of recommended actions exemplifies that it is possible to manage traditional rural biotopes for resilience. This, however, does not mean that the traditional rural biotope systems are resilient in their current state. Although my thesis has focussed on traditional rural biotopes, only the first future scenario represented a landscape where their management was continued. Three of the four scenarios represented landscapes that provided only little space for traditional rural biotopes. This exploratory expedition out of the scope of my research was done for a reason: traditional rural biotopes have become extremely rare in Finland. It is important to know what the alternatives for traditional rural biotope systems are in order to understand how vulnerable they are. How much change is too much? What magnitude of disturbance, in a social-ecological sense, leads to a loss of remnant traditional rural biotopes? Or, as Folke (2006) has put it: what is the amount of disturbance a system can take before its controls shift to another set of variables and relationships that dominate another stability region?

Most of that change is ongoing. The scenarios are already set up out there, and the first one is by far the rarest. The continuous transformation of rural social-ecological systems has evident ecological and cultural consequences. In this process a major concern is the time frame of change (Lindborg *et al.* 2008);

are traditional landscapes able to keep up with the pace of social transformation of the Anthropocene?

Species that live on traditional rural biotopes have evolved in dynamic ecosystems with frequent disturbances. They will survive the loss of traditional rural biotopes if there are other habitats for them, and if the amplitude and frequency of change do not cross the limits they are adapted to. It is true that 122 traditional rural biotope specialists are already extinct in Finland, and more are on the verge of extinction, but there are still meadow generalist species that can populate road verges, power line clearings, and other ruderates (Rassi *et al.* 2010, Lampinen *et al.* 2017). There is an alternative to manage and conserve at least some of their populations on these complementary habitats instead of traditional rural biotopes.

However, the cultural value of traditional rural biotopes cannot be transferred to other environments. Therefore, the social dimension of management of traditional rural biotopes is much more vulnerable than the ecological, as long as it is dependent on diminishing rural livelihoods. The cultural heritage that is tied to traditional rural biotopes is irreplaceable and seems to be much less resilient than their biodiversity.

We have already lost much of biodiversity and cultural heritage, which both are ingredients of social-ecological resilience (Berkes *et al.* 2003). They are also definitive for traditional rural biotopes. Yet the ecological determinants, especially those related to semi-naturalness, have thus far dominated the semantic discussion on what these habitats actually are (III, IV). I suggest that there is a need to redefine traditional rural biotopes in order to better acknowledge their social value. One perception that I have outlined from my results is that traditional rural biotopes embody a mutual human–nature interaction that is based on ecologically adaptive animal husbandry, which fosters multiple values, including biodiversity, living cultural and ecological legacies, landscape aesthetics, and place-bound identity (I, II, IV). Here I do not categorise traditional rural biotopes according to observable ecological patterns but emphasise the versatile positive outcomes of their management, including intangible and dynamic ones. This social-ecological approach is not tied to Finnish context. It aims to capture the mutual linkages between people, farming systems, and the surrounding landscape that can be observed also elsewhere. Globally, it relates to land management questions of the Anthropocene, as solving of current environmental problems require approaches that integrate biodiversity conservation, food production, and livelihoods at landscape level (Plieninger and Bieling 2013). I suggest that studying traditional rural biotopes as archetypes of coupled social-ecological systems has the potential to advance our understanding of the dynamism, resilience, and collapse of farming systems.

Despite the decline of traditional rural biotopes, all is not lost, and as long as the species prevail in the landscape they represent the ecological memory of the past traditional rural biotope systems. As long as people remember what traditional rural biotopes are and how they are managed, the cultural heritage remains. If management is reintroduced to an abandoned site, the meadow or the wood-pasture can renew itself; the social-ecological system reorganises.

In the beginning of my thesis I asked how much disturbance is needed to surpass the limits of ecosystem recovery. Now, based on my work, I can say this much: For traditional rural biotopes, we are almost there. If we do nothing, if we continue with business as usual, we will eventually lose them. This is a matter of both too little and too much disturbance. Therefore the correct question has two parts; how much "good" disturbance caused by management is needed, and how the "bad" disturbance following from land-use conversion and social transformation could be avoided in order to safeguard traditional rural biotopes. I believe that the answer lies in understanding how the disturbance by management helps traditional rural biotopes to resist both land-use conversion and social change. Their dynamism and ability to affect people maintains their resilience.

This means that there is still time left. This is the point where we can take the necessary action and start to recover traditional rural biotope systems. And as nature is full of wonders, the renewed traditional rural biotopes may end up being something totally novel.

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Conducting this research and writing of this thesis is a result of an itch to know more about traditional rural biotopes. The questions that did not leave me alone were, for example: *Why is it so hard to conserve traditional rural biotopes? Why some people manage them and others do not? Despite careful management, why some sites lack specialist species?* The questions grew from places I visited and people I talked to. Surrounded by those beautiful landscapes we chatted with each other about the importance of managing traditional rural biotopes and your personal struggles and triumphs in conserving biodiversity and cultural heritage. You are the anonymous landowners, farmers, civil servants, and management advisors who inspired me to do this work. I am indebted to all of you for sharing your thoughts and experiences with me. We all wanted to have more scientific knowledge on how to better manage traditional rural biotopes. So there was the itch that I decided to start scratching.

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Making of this thesis was surprisingly creative and enjoyable from beginning to the end; researching is by far not easy, but I found it to be intriguingly challenging. Often I followed my intuition, asking questions that I originally did not have in my mind. *What if traditional rural biotopes function differently when compared to other ecosystems, such as forests? What if nature and people become intertwined in them? If these aspects are correct and specific to traditional rural biotopes, do our policies and practices take them into account?* For the freedom of thinking and working independently I thank my supervisors: Panu, Mikko, and Za. You have been immensely patient and broad-minded in guiding me. I know I can be a bit hard-headed, and that combined with the will to follow my hunches has resulted in a few unpredictable turns of events during these years. Still you had the courage to let me work in my own way, do mistakes, make independent decisions, and when I got stuck you nudged me forward. I am grateful to you for all that.

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YHTEENVETO (RÉSUMÉ IN FINNISH)

Sosioekologinen näkökulma perinnebiotooppien suojeluun Suomessa

Perinnebiotoopit ovat suomalaisista luontotyypeistä monimuotoisimpia ja uhanalaisimpia. Niihin kuuluvat elinympäristöt ovat perinteisen karjatalouskäytön myötä muovautuneet erilaisiksi nummiksi, kedoiksi, niityiksi, hakamaiksi ja metsälaitumiksi. Näiden myös luonnonlaitumiksi ja -niityiksi kutsuttujen alueiden raivaus, niitto ja laidunnus olivat 1800-luvun loppuun saakka keskeinen osa suomalaista ruoantuotantoa, ja perinnebiotoopit olivat tuolloin varsin yleisiä.

Niiton ja laidunnuksen aiheuttama kevyt häiriö ylläpitää perinnebiotooppien lajistollista ja maisemallista monimuotoisuutta. Hoitotoimet estävät alueiden umpeenkasvua ja mahdollistavat usean lajin esiintymisen samalla paikalla. Niiton tai laidunnuksen loppuessa perinnebiotoopit pensoittuvat ja metsittyvät, ja niille ominainen lajisto katoaa. Tämän vuoksi maankäytön pysyvyys on perinnebiotooppien säilymisen kannalta tärkein yksittäinen tekijä. Perinnebiotooppien ja niiden monimuotoisuuden olemassaolo on siis riippuvaista ihmistoiminnasta.

Maailma muuttuu jatkuvasti, ja tämä koskee myös perinnebiotooppeja sekä niitä maisemia, joissa yksittäiset perinnebiotooppikohteet sijaitsevat. Maatalouden tehostuessa 1900-luvun aikana perinteinen karjatalous väistyi ja perinnebiotoopit harvinaistuivat. Elinympäristöjen määrän romahtaessa myös niiden lajisto alkoi uhanalaistua. Nykyään luonnonlaidunnus ja -niitto ovatkin ensisijaisesti luonnonhoitoa, jolla tähdätään perinnebiotooppien luontotyyppien ja lajiston säilyttämiseen suomalaisessa maisemassa. Perinnebiotooppien hoito on parhaimmillaan tehokas luonnonsuojeluteko, mutta hoidossa olevan pinta-alan kasvattaminen on käytännössä vaikeaa.

Vaikka ruoantuotanto ei enää perustu luonnonlaitumien ja -niittyjen hyötykäyttöön, perinnebiotooppien hoidossa kiteytyy yhä ihmisen ja luonnon välinen vuorovaikutussuhde. Tutkimukseni ydinteema oli juuri tämän, maatalouden arkisesta työstä luonnonsuojelun toimeksi muuntuneen sosioekologisen yhteyden tarkastelu. Tutkimukseni sai vaikutteita systeemianalyysistä, jonka avulla pyritään ymmärtämään paremmin ihmisten ja ekosysteemien keskinäistä riippuvuutta kaikessa jakamattomuudessaan, moniulotteisuudessaan, dynaamisuudessaan ja yllätyksellisyydessään. Koska perinnebiotoopit ovat häiriövaikutteisia ja alati muuttuvia elinympäristöjä, pohjasin työni teoreettisen taustan myös ekosysteemien palautuvuutta käsittelevään resilienssiteoriaan. Sen keskeinen tavoite on selittää, miksi ja miten ekosysteemit säilyttävät omaleimaiset piirteensä, vaikka niihin kohdistuu jatkuvasti muutosta aiheuttavia tekijöitä. Näitä ovat esimerkiksi maankäyttöön kohdistuvat yhteiskunnalliset tarpeet ja ilmastonmuutos.

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ratkaisukeinoja havaitsemiini ongelmiin. Tarkastelin perinnebiotooppeihin liittyviä muutoksia käyttäen ekologiaa ja maantiedettä yhdistelevää tutkimusotetta ja erilaisia ongelmalähtöisiä menetelmiä. Arvioin havaittuja muutoksia suhteessa aikaan, tilaan ja tekoihin. Tarkastelin perinnebiotooppien sijoittumista, määrän vähentymistä ja vähenemiseen johtaneita tekijöitä sekä kansallisella tasolla että käyttäen Keski-Suomen maakuntaa esimerkkialueena. Keskisuomalaisilla niityillä ja metsälaitumilla tutkin kasvillisuuden monimuotoisuutta lisääviä ympäristömuuttujia. Lopulta selvitin, millaiset tekijät vaikuttavat yksittäisten maanomistajien päätöksiin perinnebiotooppinsa hoidon jatkamisesta tai lopettamisesta.

Tulokseni osoittavat, että hoidettujen perinnebiotooppien määrä on jatkuvasti vähentynyt. Nykyiset hoitotoimet eivät myöskään ylläpidä luontoarvoja parhaalla mahdollisella tavalla. Lukuisia arvokkaita perinnebiotooppeja ja uhanalaisten lajien esiintymiä on hoidotta. Olemassa olevat suojelukeinot eivät näin ollen riitä parantamaan perinnebiotooppien heikkoa tilaa. Tilanteen korjaamiseksi tarvittaisiin laajamittaista luontoarvojen perusteella suunnattua perinnebiotooppien ennallistamista. Hoito- ja ennallistamistoimia tulisi kohdentaa erityisesti maamme lounais- ja länsirannikolle, mutta koska perinnebiotooppien luontotyypeissä ja lajistossa on alueellista vaihtelua, niitä olisi hoidettava myös muualla Suomessa.

Ennallistamis- ja hoitokohteita voidaan tunnistaa esimerkiksi uhanalaisten kasvilajien esiintymien perusteella. Tämä perustuu sukupuuttovelan käsitteeseen. Sukupuuttovelka tarkoittaa sitä, että vaikka elinympäristön määrä vähenee tai laatu heikkenee, lajistossa muutos näkyy viiveellä. Hoidon lakattua perinnebiotooppien lajit yhä sinnittelevät kasvupaikoillaan, ja yksilömäärien väheneminen on hidasta. Ajan kuluessa lajit kuitenkin katoavat kasvupaikalta. Kuitenkin yksilö- ja lajimäärät voivat palautua vähitellen ennalleen, mikäli hoitotoimet aloitetaan uudelleen ennen lopullista paikallista sukupuuttoa. Sama pätee myös perinnebiotooppeihin, jotka ovat olleet jatkuvasti hoidossa, mutta hoidon laatu on heikentynyt eikä enää ylläpidä kohteen lajiston ja luontotyyppien vaihtelevuutta.

Kaikilla perinnebiotoopeilla sukupuuttovelkaa ei kuitenkaan esiinny. Havaitsin tämänkaltaisen tilanteen tutkiessani eteläisen Keski-Suomen niitto- ja laidunniittyjen kasviyhteisöjä. Vaikka niittyjen määrässä ja sijainnissa on tapahtunut suuria muutoksia viimeisen 150 vuoden aikana, tätä ei voinut havaita lajistossa. Niittykasvien lajimäärä ja lajiyhteisön rakenne näyttivät riippuvan ensisijaisesti hoitotavasta ja maaperän happamuudesta. Lajimäärää kasvatti lisäksi nykyisten niittyjen kokonaisala yhden kilometrin säteellä tutkimusniitystä. Mikäli lajistossa olisi ollut sukupuuttovelkaa, historiallinen niittyjen määrä olisi vaikuttanut lajimäärään.

Sukupuuttovelan puute johtuu mitä todennäköisimmin siitä, että Keski-Suomessa niittyjen maankäyttöhistoria on ollut erittäin dynaaminen. 1800-luvun puolivälistä vuoteen 2010 niittyjen kokonaisala väheni voimakkaasti, ja samalla yksittäisten niittyjen koot pienenivät ja niiden välimatkat kasvoivat. Niittyjen ajallinen pysyvyys oli heikkoa, sillä vain alle kolme prosenttia 1960-luvun niityistä säilyi vuoteen 2010. Nykyään jäljellä olevista niityistä puolestaan yli 70 %

oli 1900-luvun puolivälissä peltoina. Koska maankäyttöhistoria on näin vaihteleva, Keski-Suomen niittyjen lajisto on ollut alituisen ympäristömuutoksen kohteena. Tämän seurauksena lajiesiintymät ovat jatkuvasti mukautuneet kulloinkin vallitseviin oloihin, ja vaateliaimmat lajit puuttuvat niityiltä.

Nykyisten ympäristötekijöiden vaikutus kasvien lajimäärään näkyi myös keskisuomalaisilla metsälaitumilla. Tämä koski erityisesti metsälaidunnusta ja kasvupaikan tuottavuutta, joka on käänteisesti yhteydessä maaperän happamuuteen. Sekä metsälaidunnus että alueen tuottavuus lisäsivät putkilokasvien ja sammalten lajimäärää, kun vertasin laidunnettuja ja hylättyjä metsälaitumia keskenään. Niittyjen kohdalla ilmiö ei ollut yhtä yksiselitteinen, vaan siellä hoitotavan vaikutus oli sidoksissa maaperän happamuuteen. Laidunniityillä putkilokasvien lajimäärä pysyi vakiona, mutta niitetyillä niityillä lajimäärä kasvoi maaperän happamoituessa. On selvää, että tutkituilla kohteilla nykyiset ympäristötekijät vaikuttavat voimakkaasti lajistoon, ja perinnebiotooppien hoito ylläpitää kasvien monimuotoisuutta.

Tähänastiset tutkimustulokseni korostavat perinnebiotooppikohtaiset ominaisuudet huomioon ottavien hoitotoimien luonnonsuojelullista tärkeyttä. Mutta miksi hoidettujen perinnebiotooppien määrä jatkaa edelleen vähenemistään? Miten hoitotoimia saataisiin lisättyä? Ratkaistakseni nämä toisiinsa liittyvät ongelmat perehdyin perinnebiotooppien hoidon jatkuvuuteen vaikuttaviin tekijöihin kohdetasolla. Havaitsin, että perinnebiotooppien hoidon lakkaaminen on yhteydessä maankäytön tehostumiseen. Tämä ilmenee useimmiten kohteiden raivaamisena pelloksi, metsittämisenä tai rakentamisena. Maankäytön muutokset puolestaan ovat seurausta laajoista yhteiskunnallisista ilmiöistä kuten globalisaatiosta, kaupungistumisesta ja markkinatalouden lisääntyvästä vaikutuksesta maatalouteen. Perinteisen maankäytön korvaamiseen nykyaikaisilla maankäyttömuodoilla vaikuttavat myös maaseudun elinkeinot sekä ihmisten arvomaailma, joka konkretisoituu elintapojen kautta. Muutos voi myös kääntyä päälaelleen: esimerkiksi vapaisiin kysynnän sääntelemiin markkinoihin perustuvaa globalisaatiota vastustava lokalisaatio on ilmiö, joka tukee perinnebiotooppien hoitoa. Lokalisaatio edustaa tuottajilta kuluttajille virtaavaa maataloustuotannon mallia, jossa paikallinen tarjonta on tärkeässä roolissa.

Paikallisella tasolla perinnebiotooppien hoitoa koskeviin päätöksiin vaikuttivat tekemieni maanomistajahaastatteluiden perusteella erityisesti laidunneläinten saatavuus ja maankäyttöpaineet. Perinnebiotoopin hoidon lopettamisen taustalla oli useimmiten luopuminen karjataloudesta. Laiduneläimet nähtiin keskeisenä osana perinnebiotooppien hoitoa: ne olivat paitsi hoitotoimien edellytys, myös tärkeä elementti maaseutumaisemassa. Monille perinnebiotooppejaan hoitaville maanomistajille eläintenpito oli paitsi osa elinkeinoa, myös elämäntapa ja ilon lähde. Jotkut karjatilalliset toimittivat kesälaiduntajia tiloille, joilla omia eläimiä ei enää ollut. Verkostoitumalla maanomistajat turvasivat perinnebiotooppiensa hoidon jatkuvuutta.

Maanomistajat kannattivat yleisesti perinnebiotooppien hoitoa. Haastatteluissa nousi esiin perinnebiotooppien merkitys moninaisten arvojen keskittyminä. Luonnon monimuotoisuuden lisäksi perinnebiotooppien hoito ylläpitää kansallista, alueellista ja paikallista kulttuurihistoriaa sekä maaseutumaiseman estetiikkaa. Moni maanomistajista koki omaan perinnebiotooppiinsa sitoutuneen myös henkilökohtaisia merkityksiä. Hoitotoimien avulla he ylläpitivät suvun tai tilan perintöä ja omaa luontosuhdettaan.

Perinnebiotooppien hoito vahvisti maanomistajien ja luonnon välistä yhteyttä. Hoito vaikutti perinnebiotooppien lajistoon ja maisemakuvaan, ja hoitajat kokivat tuloksekkaan työn motivoivan heitä jatkamaan ja laajentamaan hoitotoimia. Näin maaseutumaisema toimii sosioekologisten vuorovaikutusten näyttämönä; se muovautuu ihmistoiminnan ja luonnon yhteisvaikutuksessa. Perinnebiotooppien kohdalla hoidon koettu tuloksellisuus ylläpitää hoidon jatkuvuutta myös tulevaisuudessa. Tämä on tärkeä osa perinnebiotooppien resilienssiä.

Haastattelut nostivat esiin perinnebiotooppien itseisarvon, mutta kohteilla oli karjanomistajille myös välineellistä arvoa laidunalueina. Luonnonlaiduntaminen toteutettiin kiinteänä osana tilan muuta toimintaa. Osa haastatelluista oli rakentanut elinkeinonsa maiseman- ja luonnonhoitoon painottuvan yrittäjyyden ympärille. Maatalouden ympäristökorvausjärjestelmä, jonka avulla perinnebiotooppien hoitoa rahoitetaan, oli tärkeä osa heidän elinkeinoaan.

Vaikka perinnebiotooppien hoitajien suhtautuminen ympäristökorvaukseen oli pääsääntöisesti positiivista, kohteitaan hoitamattomat maanomistajat nostivat esiin epäkohtia, jotka heikentävät korvausjärjestelmän toimivuutta. Useimmiten he olivat joko epätietoisia hoitokorvausten olemassaolosta tai pitivät järjestelmää turhan byrokraattisena. Tämä on ongelmallista, sillä Suomessa perinnebiotooppeihin ja niiden hoitoon liittyvät resurssit, viestintä, koulutus ja hallinnointi keskittyvät tavalla tai toisella ympäristökorvausjärjestelmään. Nykyisin huomattava osa perinnebiotooppien omistajista jää kokonaan järjestelmän ulkopuolelle, koska he eivät ole enää tekemisissä maatalouden kanssa. Tämän vuoksi korvausjärjestelmän keinot kannustaa ja rahoittaa perinnebiotooppien ennallistamista ja hoitoalan lisäämistä eivät vastaa luonnonsuojelullista tarvetta.

Tulosteni perusteella päättelin, että perinnebiotooppien nykyiset hoitotoimet eivät mahdollista niiden suojelutilanteen parantamista. Lajiston ja luontotyyppien uhanalaistumisen pysäyttäminen edellyttää hallinnollisten ohjauskeinojen ja hoitoon käytettävien resurssien lisäämistä, monipuolistamista ja tehokkaampaa kohdentamista. Perinnebiotooppien suojelun edistäminen on hallinnollinen haaste, johon tarttuminen vaatii uskallusta yhdistää aktiivinen luonnonsuojelu maatalouteen, maisemanhoitoon ja ylipäätään maaseudun elinkeinoihin.

Tutkimukseni pohjalta tunnistin useita käytännön toimia, joilla perinnebiotooppien suojelua voitaisiin uudistaa. Ensinnäkin hoitotoimia ja niiden rahoitusta voitaisiin suunnata tehokkaammin luontoarvoiltaan parhaille kohteille. Tavoitteena olisi luoda sellainen kohdeverkosto, jossa paikalliset perinnebiotooppien keskittymät ylläpitäisivät korkeita lajimääriä ja rakenteeltaan vaihtelevia lajiyhteisöjä. Jatkuvuuden turvaamiseksi nykyisin hoidetut kohteet tulisi pitää hoidettuina, mutta hoitotoimien vaikuttavuutta pitäisi seurata nykyistä tarkemmin. Sekä hoidon ajallista jatkuvuutta että laatua voidaan tukea toimilla, jotka vahvistavat hoitoon liittyviä sosioekologisia vuorovaikutuksia. Esimerkki tästä on perinnebiotooppien omistajien harjoittama hoitoseuranta. Jotta seuranta olisi toimivaa, hoitajat ja maanomistajat tarvitsevat opastusta ja palautetta hoidon laadusta. Hoitotoimien tulisi olla tavoitteellisia ja perustua kohdekohtaiseen tietoon perinnebiotoopin lajistosta, maaperän laadusta ja maankäytön historiasta.

Hoitotoimien alueellinen kohdentaminen edellyttää, että nykyisellään hoidettujen perinnebiotooppien lisäksi ennallistettaisiin hylättyjä kohteita. Alueilla, joilla maankäytön jatkumot ovat heikkoja, ennallistamis- ja hoitotoimia voidaan suunnata olemassa olevien perinnebiotooppilajien esiintymien perusteella. Hoidetuilta kohteilta lajit voivat levittäytyä ennallistetuille perinnebiotoopeille, mikäli kohteet vain ovat riittävän lähellä toisiaan. Paikallinen lisäys elinympäristön määrässä voi tukea paitsi lajimäärää myös uhanalaisten lajien esiintymien elinvoimaisuutta.

Hoidettavan pinta-alan lisääminen on kuitenkin mahdotonta, ellei perinnebiotooppeja hoideta myös maatilojen ulkopuolella. Tämä voidaan toteuttaa siirtämällä laiduneläimiä laidunkauden aikana eläintilojen ja perinnebiotooppikohteiden välillä. Tällaisten hoitoverkostojen rakentaminen edellyttää yhteistyötä ja tiedonjakoa hallinnon ja paikallistoimijoiden välillä. Perinnebiotoopeista riippuvaisten moninaisten arvojen esilletuonti on tässä työssä erittäin tärkeää. Arvojen tiedostaminen motivoi perinnebiotooppien hoitoon ja ennallistamiseen.

Viimeisenä johtopäätöksenäni esitän, että perinnebiotooppien katoaminen ja sen seuraukset olisi nostettava julkiseen tietoisuuteen. Tähän asti muutos on tapahtunut kaikessa hiljaisuudessa, lähestulkoon huomaamatta. Perinnebiotooppeihin keskittyvä viestintä on tarpeen, mikäli halutaan turvata niihin sidoksissa oleva luonnon monimuotoisuus, kulttuuriperintö ja myönteinen ihmisen ja luonnon välinen suhde.

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ORIGINAL PAPERS

I

CONTEMPORARY SPATIAL AND ENVIRONMENTAL FACTORS DETERMINE VASCULAR PLANT SPECIES RICHNESS ON HIGHLY FRAGMENTED MEADOWS IN CENTRAL FINLAND

by

Kaisa J. Raatikainen, Anna Oldén, Niina Käyhkö, Mikko Mönkkönen &
Panu Halme 2018

Submitted manuscript.

II

GRAZING AND SOIL PH ARE BIODIVERSITY DRIVERS OF VASCULAR PLANTS AND BRYOPHYTES IN BOREAL WOOD-PASTURES

by

Anna Oldén, Kaisa J. Raatikainen, Kaisa Tervonen & Panu Halme 2016

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Grazing and soil pH are biodiversity drivers of vascular plants and bryophytes in boreal wood-pastures

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ABSTRACT

Wood-pastures have been formed by traditional low-intensity livestock grazing in wooded areas. They host high biodiversity values that are now threatened by both management abandonment (ceased grazing) and agricultural intensification, and therefore these habitats are of conservation interest in Europe. In order to explore the effects of grazing on the biodiversity of boreal wood-pastures, we studied the communities of vascular plants and bryophytes in 24 currently grazed and 24 abandoned sites. In addition to the current management situation, we studied the effects of soil pH and moisture, tree density, historical land-use intensity, time since abandonment (in abandoned sites) and grazing intensity (in grazed sites). Grazed sites had higher species richness of both species groups and rare species were also slightly more numerous. Grazing impacted the community composition of vascular plants more than that of bryophytes. For both species groups soil pH (which ranged from 3 to 5) was the most important variable in determining species richness, the number of rare species and the composition of communities. The responses of the two species groups varied somewhat, but generally species richness was maximized on sites with higher soil pH, moisture and grazing intensity, but lower tree cover. We conclude that more effort should be paid on maintaining currently grazed sites under management. If a site has been abandoned, it could be restored into a wood-pasture if it still retains some structural features such as openness and typical species of a wood-pasture. Highest biological conservation values for both management and protection can be found among those sites that are naturally most fertile, but attention should also be paid on the landscape-scale versatility of managed sites.

1. Introduction

Wood-pastures are traditional rural biotopes characterized by long-term systematic grazing of livestock and a varying cover of trees, which can be scattered, located in patches or as a closed canopy. Throughout Europe, different types of wood-pastures have been formed and maintained by traditional low-intensity farming practices (Bergmeier et al., 2010). Wood-pastures host high biodiversity values that are induced by the small-scale heterogeneity of both livestock activities and structural diversity of trees, resulting in small-scale variation in light conditions, microclimate, soil properties, disturbances and various successional stages (Bergmeier et al., 2010; Buttler et al., 2009; Luick, 2009; Olff et al., 1999). Wood-pastures and their biodiversity are threatened by both management abandonment (ceased grazing) and intensification (eutrophication by nutrient accumulation, overgrazing, clearance, regeneration failure, loss of old-growth trees) (Bergmeier et al., 2010). Both abandonment and intensification can result in the decrease of patchiness within a pasture, but also in habitat fragmentation and segregation at landscape-level (Peringer et al., 2013). The abandonment of wood-pastures leads to encroachment of young trees and loss of species that are adapted to semi-open habitats and frequent disturbances (Mariotte et al., 2013; Palo et al., 2013; Paltto et al., 2011; Van Uytvanck and Verheyen, 2014). On the other hand, the climax communities of long-ago abandoned wood-pastures may themselves have high conservation value as they harbor structures (such as old trees and large decaying wood) that are similar to those in old-growth forests (Palo et al., 2013; Paltto et al., 2008).

Large herbivores, including domestic animals, induce fine scale disturbances by removing herbage, trampling and depositing dung and urine (Gillet et al., 2010; Kohler et al., 2004). At the pasture scale these frequent fine scale disturbances create heterogeneity and impact the local processes of species colonization and competitive exclusion (Dufour et al., 2006; Gillet et al., 2010; Kohler et al., 2006a,b; Olff and Ritchie, 1998; Olff et al., 1999). The

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effects of grazing on biodiversity can be positive or negative depending on grazing intensity and other site properties. Grazing by natural populations of large mammals or by domesticated animals at low grazing intensity usually increases the diversity of vascular plants, whereas high stocking rates of grazers may have negative impacts on diversity (Belsky, 1992; Milchunas et al., 1988; Pykälä, 2005; Van Wieren, 1995). In addition, other environmental factors such as soil pH, nutrient levels, moisture and light impact the competitive situation between plants and therefore they can have interactions with the impact of grazing intensity. For example, grazers can increase diversity in environments where moisture and nutrients are readily available, but they can decrease diversity if drought or low nutrient levels restrict plant growth (Olff and Ritchie, 1998; Proulx and Mazumder, 1998). Grazers also tend to cause larger changes in species composition in more productive environments (Milchunas and Lauenroth, 1993). Trees improve soil and moisture conditions but also decrease light availability and increase litter accumulation, and as a result, the species richness of field layer plants may be maximized at low to medium tree densities (Gillet et al., 1999). The composition of a plant community, and therefore its response to grazing, is also affected by the site's management history and current and historical habitat connectivity (Bruun et al., 2001; Cousins et al., 2009; Johansson et al., 2008).

The impacts of grazers on bryophytes (mosses and liverworts) are less well known, but grazing has been found to increase bryophyte diversity in several habitat types (Bergamini et al., 2001b; Peintinger and Bergamini, 2006; Takala et al., 2012). However, this is not always the case, especially overgrazing may harm bryophytes as well as vascular plants (Bergamini et al., 2001b). Unlike vascular plants, bryophytes are not grazed by large mammals, but they can be affected by the direct impacts of trampling and dung deposition and by the indirect impacts of herbage removal through decreased competition with vascular plants (Aude and Ejrnæs, 2005; Bergamini et al., 2001b). Many studies have found that a smaller biomass or cover of vascular plants results in higher biomass and diversity of bryophytes, most likely due to decreased competition for light and space and decreased amounts of plant litter (Aude and Ejrnæs, 2005; Bergamini et al., 2001a; Löbel et al., 2006; Takala et al., 2015). On the other hand, the biomass of bryophytes themselves may correlate negatively with their species richness (Ingerpuu et al., 1998). In many cases bryophytes respond to grazing and soil fertility differently than vascular plants and therefore they provide complementary data in the study of grazed habitats (Bergamini et al., 2001b; Takala et al., 2012; Zechmeister et al., 2003). Understanding the effects of grazing on bryophytes is of great importance in habitats such as boreal forests where bryophytes have a large impact on biodiversity and ecosystem functioning (Lindo and Gonzalez, 2010).

The vegetation and biodiversity of boreal wood-pastures have received less research attention than temperate ones. The communities of both vascular plants and bryophytes are a combination of species of forests and open habitats (Schulman et al., 2008; Takala et al., 2015). In Finland a large proportion of forests have historically been grazed by free-ranging domestic cattle during the summers, while a small proportion have been used as fenced semi-open pastures (Jäntti, 1945; Schulman et al., 2008). The currently remaining wood-pastures are all fenced and the tree structure ranges from scattered trees to a closed canopy. Most wood-pastures in the area are densely wooded and they can be called forest pastures (sensu Takala et al., 2015, 2014). In Finland, all types of wood-pastures are threatened habitats due to large declines in their area (more than 99% lost since the 1950s) and quality (eutrophication and intensive forestry practices) (Schulman et al., 2008). Other types of traditional rural biotopes have experienced similar declines and in 2009 only half of the currently remaining Finnish traditional rural biotopes were managed; of these 80% (20,000 ha) were subsidized via the national agri-environment scheme (Kemppainen and Lehtomaa, 2009). Tree encroachment after abandonment of open and semi-open cultural biotopes is the primary threat to 26% of all threatened species in the country (Rassi et al., 2010). In addition to the biodiversity values, multifold social and cultural values are related to these traditional land-use systems (Plieninger et al., 2006).

In order to deepen the understanding of the patterns of biodiversity in boreal wood-pastures, we studied the combined effects of grazing and environmental variables on vascular plant and bryophyte communities by comparing a large number of grazed and abandoned sites with varying environmental properties. The objectives of the study were (1) to determine the effects of current management (grazing vs. abandonment) on the species richness and community composition of vascular plants and bryophytes, (2) to assess how trees, soil properties and historical factors affect the communities relative to the management situation, and (3) to provide recommendations for the management and conservation of different kinds of boreal wood-pasture sites. Based on earlier studies in temperate grasslands and wood-pastures we hypothesized that current grazing increases species richness and changes community composition of both species groups, and more so in sites with high soil moisture and high soil pH. We also expect that the biodiversity of both groups is maximized at low to medium tree densities, medium grazing intensities, high historical land-use intensities, and (in the case of abandoned sites) soon after the abandonment.

2. Materials & methods

2.1. Study sites

Our study sites were located in Central Finland (62°14′N 25°44′E) where the mean annual air temperature is 3–4 °C and precipitation is 600–700 mm year^{-1} (average from 1981 to 2010, Finnish Meteorological Institution, 2015). Out of the 48 study sites, 44 were located on the southern boreal vegetation zone and four close to the border on the middle boreal zone (Fig. 1).

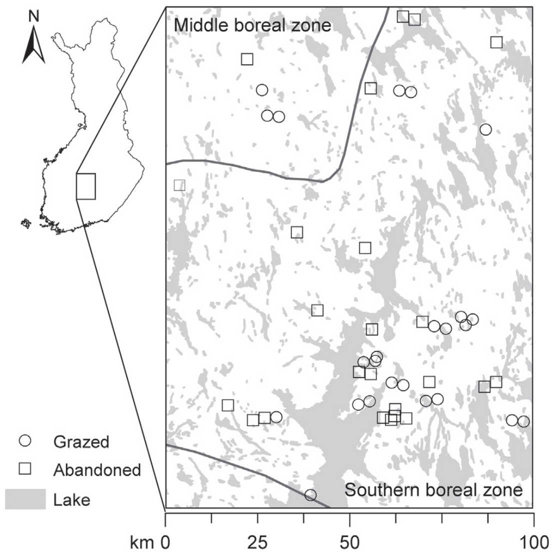

Fig. 1. The location of the study sites in Central Finland. © National Land Survey of Finland 2012.

The selection of the 48 study sites was based on available records on the current management status and tree structure of wood-pastures. This information was provided by the Centre for Economic Development, Transport, and the Environment for Central Finland. We searched for both currently grazed sites where the grazing had continued for decades (some had experienced short breaks in grazing) and sites that had been abandoned at least 7 years ago. Our aim was that the currently grazed sites would be comparable to the abandoned sites in terms of dominant tree species and tree density. For this balanced sampling setup we chose six grazed and six abandoned sites from each of the four groups based on dominant trees: birch (*Betula* spp.), spruce (*Picea abies*), pine (*Pinus sylvestris*) and mixed deciduous and coniferous. We wanted to study sites with relatively similar mature tree densities and therefore excluded some very open sites that were structurally close to grazed meadows (thus, we included sites with semi-open or closed canopies). In practice, we selected first the sites that were still grazed (because there was

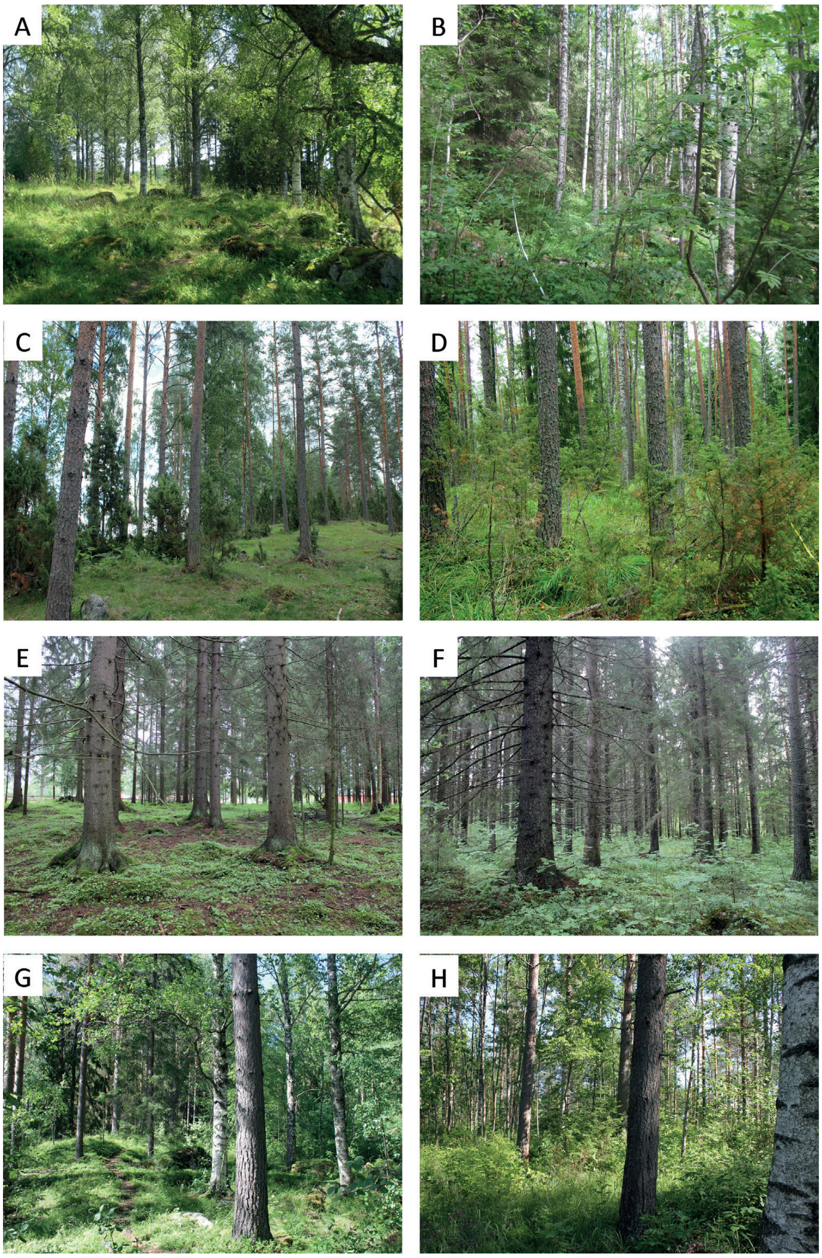

Fig. 2. Examples of study sites: (a) grazed dominated by birches, (b) abandoned dominated by birches, (c) grazed dominated by pines, (d) abandoned dominated by pines, (e) grazed dominated by spruces, (f) abandoned dominated by spruces, (g) grazed with mixed deciduous and coniferous trees, and (h) abandoned with mixed trees.

a shortage of these sites) and then selected the abandoned sites so that they were spread in the region in a similar way than the grazed sites. Because of the scarcity of the potential study sites, it was not possible to control for other factors, such as the type of grazing animals (cattle, horses, sheep or a mixture of these), or conduct a random selection of study sites. For the same reason, we studied two or three separate wood-pastures in 13 farms (while the other 20 farms included only one site). The wood-pastures were considered separate if they had different dominant trees and they were separated in the farm's pasture rotation by a fence. In abandoned, unfenced sites a road or a distance of at least 175 m was used as a separation criterion. Photographs of typical sites are provided in Fig. 2 and information on the study sites is provided in Table 1 in the Appendix.

2.2. Sampling design and measurements

To create a surrogate for the intensity of historical land-use, we derived information from old cadastral maps drawn during the 1850s and 1860s. We calculated the number of farms within one kilometer buffer zone around each study site. This was used as an estimate of the land-use intensity in the mid-1800s and before that. In the 1800s farming in Finland was based on small-scaled but extensive cattle husbandry and in summertime cattle mostly grazed freely in the surrounding forests (Jäntti, 1945) and therefore the number of surrounding farms should also correlate with historical grazing intensity. For the abandoned sites, we obtained the year of abandonment by interviewing the landowners.

Within each study site we placed three permanent, quadrate plots of 100 m^2 (ten by ten meters). The plots were placed so that within them there were mature trees and the tree species corresponded to the dominant trees of the pasture. This was necessary because many of the wood-pastures are very heterogeneous in their tree structure, including patches without trees or with a different dominant tree species. The distance between two plots within a study site varied from 17 to 222 m and the average distance was 58 m in grazed and 53 m in abandoned sites.

Within each of the plots we measured all trees that were at least 130 cm high. The diameter of each tree was measured and used to calculate the basal area, i.e., the area of the circular cross-section of the tree. For each plot, the basal areas of the trees were then summed into groups of deciduous trees, *Picea abies*,*Pinus sylvestris* and all trees combined. Deciduous trees were summed together because only Birch was common and other species (*Populus tremula*, *Alnus incana*, *Sorbus aucuparia*, *Salix caprea*) were too low in their numbers to be analyzed separately. In the analyses we used the site-level averages of the basal areas.

Soil samples were collected from each plot between 3rd and 13th June 2013. Within each plot we took sixteen randomly placed core samples with a soil corer of 3 cm diameter. The litter layer was excluded and the sample was taken to the depth of 5 cm (after which large stones and tree roots made sampling impossible in many sites). The sixteen samples from each plot were mixed together and then sieved through a sieve (4 mm mesh size) and frozen before measurements. To measure the soil moisture content, a subsample was placed in a crucible, weighed, dried in an oven (at 105 °C for 12 h), and weighed again. Soil pH was measured three times from a calcium chloride suspension of 1:5 soil–$CaCl_2$ ratio (w/v) after one hour of shaking, and the median value of the three was used for the plot. For each site we used average moisture and pH values in the analyses.

To record the vascular plants and bryophytes we used four subplots of 2 × 2 m placed inside the corners of each plot. A total of twelve subplots or 48 m^2 were therefore studied in each study site. Vascular plant species were recorded from each subplot during the summer (between late June and late July in 2012 or 2013) and bryophytes after that (between mid-July and early October). We recorded all bryophytes growing on all substrates, but for this study we used the data on species that grew either directly on soil or on soil that covered other substrates such as boulders, or among other bryophytes growing on soil. The percentage cover of each plant species was estimated within each subplot. When necessary, specimens were collected for later identification with a microscope (mostly bryophytes). Within some genera several specimens were not identifiable to the species level and in these cases all specimens of the genus were combined and they were analyzed as one "species". A complete list of genera and species found in the study is available in Tables 2 and 3 in the Appendix. The nomenclature of bryophytes follows Juutinen and Ulvinen (2015) and vascular plants Hämet-Ahti et al. (1998).

We also divided a subset of rare species from both species groups. For vascular plants we included threatened or nearly threatened species (Kalliovirta et al., 2010), regionally threatened species on the southern boreal zone (Ryttäri et al., 2012) and indigenous or archaeophytic species that are rare in the biogeographical provinces of the study area (Tavastia australis, Tavastia borealis and/or Savonia australis, Hämet-Ahti et al., 1998). For bryophytes we included species that are threatened or nearly threatened, regionally threatened, rare or indicating habitats of high nature value on the southern boreal zone (Sammaltyöryhmä, 2015).

Grazing and trampling intensities were measured on the subplots once at the end of the grazing season (September or

Table 1
Results from GLM analyses for the richness of all vascular plant species on all sites, on grazed sites and on abandoned sites. Management is current grazing/abandonment. ^2 refers to the quadratic effects of the continuous variables (soil pH, soil moisture content, the basal area of trees, the number of farms within 1 km from the site in the 1850s–1860s, grazing intensity and time since abandonment).

	Estimate	Std. error	*z* value	*P*
All sites				
(Intercept)	3.75	0.05	69.48	<0.001
Management	0.25	0.06	3.82	<0.001
pH	0.38	0.04	9.48	<0.001
pH^2	−0.14	0.03	−4.71	<0.001
Moisture	0.08	0.03	2.26	0.024
Moisture^2				
Trees				
Trees^2				
Farms				
Farms^2				
Grazed sites				
(Intercept)	4.17	0.06	70.36	<0.001
pH	0.31	0.04	7.60	<0.001
pH^2	−0.13	0.03	−4.31	<0.001
Moisture				
Moisture^2				
Trees				
Trees^2				
Farms				
Farms^2	−0.07	0.03	−2.32	0.021
Grazing	0.15	0.03	4.82	<0.001
Grazing^2	−0.12	0.03	−3.56	<0.001
Abandoned sites				
(Intercept)	3.74	0.07	55.46	<0.001
pH	0.37	0.05	6.96	<0.001
pH^2	−0.13	0.05	−2.43	0.015
Moisture				
Moisture^2				
Trees				
Trees^2				
Farms				
Farms^2				
Abandonment				
Abandonment^2				

early October) following the surveys of plant species. Grazing (i.e. herbage removal or defoliation) intensity was estimated as the proportion of clipped shoots out of all vascular plant shoots that had been over 5 cm high. Shoots and leaves under the height of 5 cm are rarely eaten and under long grazing history the plant community develops more short-statured shoots and therefore grazing intensity would have been underestimated if also the lower shoots were counted. Trampling intensity was estimated as the proportion of broken soil out of total soil surface on the subplot (thus excluding the area occupied by rocks, tree bases or decaying wood). Our measure of trampling intensity is thus dependent on both the hoof action of the herbivores and on the sensitivity of the soil (e.g. soil particle size and moisture). For the analyses we used site-level averages of the grazing and trampling intensities.

2.3. Statistical analyses

We used R version 3.1.1 (R Core Team, 2014) to perform all statistical analyses. All analyses were performed at the site-level. In order to reduce the collinearity among the variables used in the statistical models, we first tested for correlations between the continuous explanatory variables, including the historical number of farms surrounding the site, soil moisture, soil pH, basal areas of *Picea*, *Pinus* and deciduous trees as well as all trees together, grazing and trampling intensities on grazed sites, and time since abandonment on abandoned sites. As expected, the basal areas of *Picea*, *Pinus* and deciduous trees correlated with each other and with soil pH (Table 4 in the Appendix) and therefore we excluded them from the analyses to reduce their effects in the statistical models. In addition, trampling intensity showed a positive correlation with grazing intensity and it was excluded. Thus, we included in the subsequent statistical models variables that correlated weakly with each other: soil pH, soil moisture, basal area of all trees, the historical number of farms, grazing intensity in grazed sites and time since abandonment in abandoned sites.

Possible spatial autocorrelation within the variables used in the analysis was examined with Moran's test (separately for two- and four-nearest-neighbor structures based on the distances between

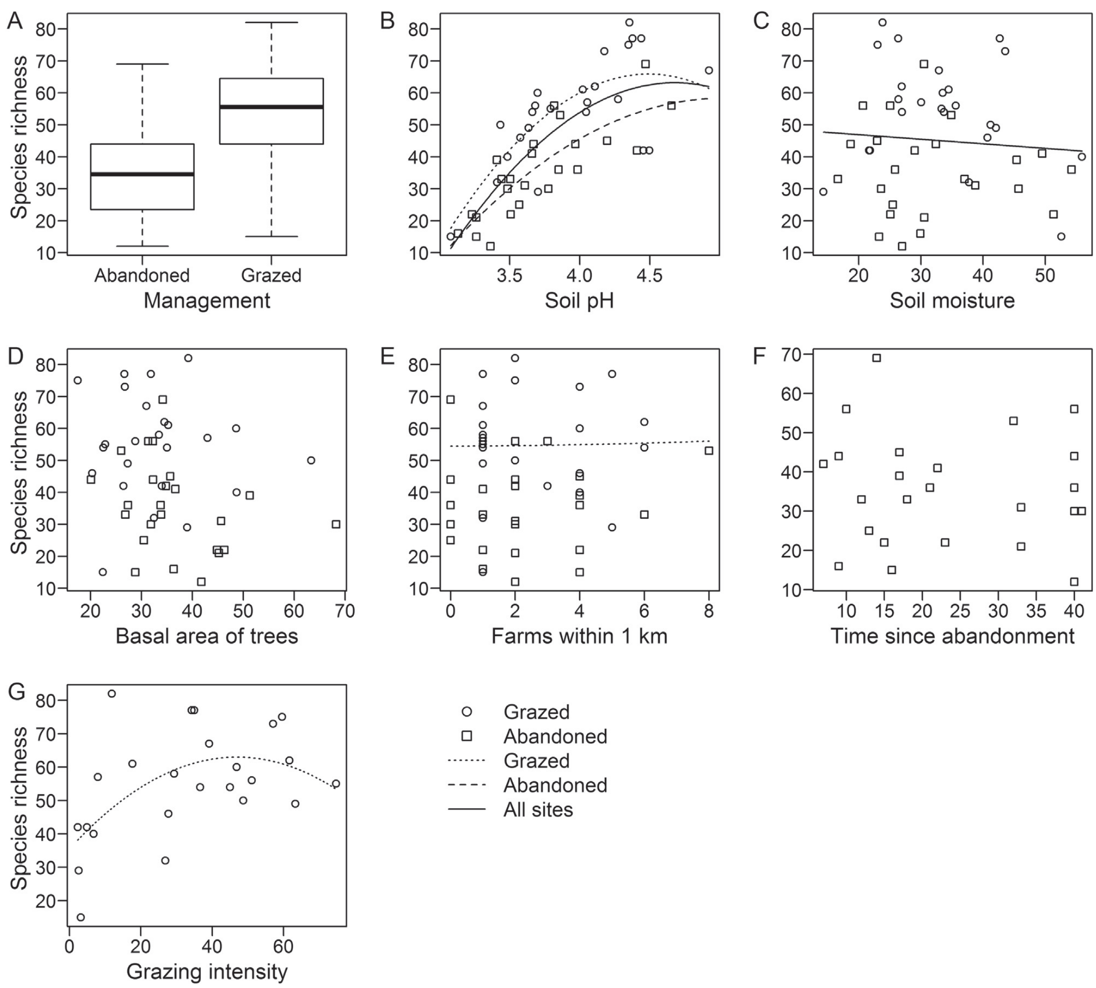

Fig. 3. Responses of species richness of all vascular plants to (a) management, (b) soil pH, (c) soil moisture content (%), (d) the basal area of all trees (m^2/ha), (e) the number of farms within 1 km from the site in the 1850s–1860s, (f) time since abandonment on abandoned sites (years), and (g) grazing intensity (% of clipped shoots out of >5 cm high vascular plants). The fitted linear and quadrate lines depict significant effects from the GLM analyses (see Table 1).

the study sites). The factors significantly explaining species richness or community composition (pH, moisture, basal area of trees and grazing intensity; see Section 3) did not show spatial autocorrelation and therefore the location of sites was excluded from the final models. Spatial autocorrelation was, however, observed for the historical number of farms and for the time since abandonment and the results for these variables should therefore be interpreted with caution. These observed autocorrelations most likely result from our sampling setup in which some study sites were located on the same farm, and therefore these farm-specific factors are shared among them.

Finally, prior to analyses the values of all the continuous explanatory variables were standardized to zero mean and unit variance to make the effect sizes of different variables comparable. In addition, the abundance values of the species (average percentage cover on the site) were square root transformed to reduce the large effect of very abundant occurrences in the analysis of community composition.

To analyze the effects of management and other environmental variables on species richness we used Negative Binomial Generalized Linear Models (GLM) with log link. Separate models were built for species richness of all vascular plants, all bryophytes, rare vascular plants and rare bryophytes. For each species group we built one model for all study sites, including the management situation (grazed or abandoned), soil pH, soil moisture, basal area of trees and historical number of surrounding farms. A second, similar model was built for currently grazed sites (excluding management situation but including grazing intensity) and a third for abandoned sites (excluding management situation but including time since abandonment). In each case we started with a maximal model that included all the variables and both linear and quadratic terms for the continuous variables. This maximal model was simplified by a stepwise removal of the least significant explanatory variables until only significant ($P < 0.05$) variables remained. The analysis was performed with the function "glm.nb" from package "MASS" (Venables and Ripley, 2002).

The effects of the above-mentioned variables on the community compositions of vascular plants and bryophytes were also analyzed separately for all sites, grazed sites and abandoned sites. For each site, we used the average cover of each species on the 12 subplots within the site. First we calculated Bray–Curtis dissimilarities for pairs of sites from square-root transformed abundances of species on sites. Then we used Bioenv-analysis to find the best subset of environmental variables (Euclidean distance) that have the highest Spearman rank correlation with the community dissimilarities (function "bioenv" from "vegan" package by Oksanen et al., 2013). To visualize the effects of the environmental variables on the species compositions, we performed Nonmetric Multidimensional Scaling (NMDS) with the Bray-Curtis dissimilarities and chose the best two-dimensional solutions (function "metaMDS" in "vegan"). Each ordination result was then overlaid with environmental vectors that describe the maximal correlations of the environmental variables with the locations of sites in the ordination result (function "envfit" in "vegan").

3. Results

We found 190 species of vascular plants out of which 174 were observed in at least one grazed site and 131 in at least one abandoned site. Three of the vascular plant species are regionally threatened (RT) in the southern boreal zone of Finland: *Coeloglossum viride* (found in two grazed sites), *Listera ovata* (two abandoned sites) and *Vicia tetrasperma* (one grazed site).

We observed 107 species of bryophytes, including 84 mosses and 23 liverworts. 94 of the bryophyte species occurred in at least one grazed site and 79 in at least one abandoned site. Eight of the bryophyte species are classified as regionally threatened: *Calypogeia fissa* (also nearly threatened [NT] in Finland, found in one abandoned site), *Campylium protensum* (one grazed and one abandoned site), *Eurhynchium angustirete* (one grazed and one abandoned site), *Plagiomnium affine* (one abandoned site), *Plagiothecium latebricola* (also NT, three grazed sites), *Tayloria tenuis* (also NT, 11 grazed sites), *Thuidium delicatulum* (one abandoned site) and *Thuidium tamariscinum* (one grazed site).

The levels of the continuous variables did not differ between grazed and abandoned sites except that grazed sites had higher soil pH than abandoned sites (Wilcoxon rank-sum test: $W = 189$, $P = 0.041$).

3.1. Species richness of all species

The richness of all vascular plant species was mostly explained by the current management situation (more species in currently grazed than in abandoned sites, on average 55 and 35 species, respectively) and soil pH (positive linear and humped effect) (Table 1 and Fig. 3a and b). In the GLM analysis combining all study sites there appeared to be a slight positive effect of increasing soil moisture, but this is not observed in the graph drawn from the raw data, and the effect disappeared when grazed and abandoned sites were analyzed separately (Table 1 and Fig. 3c). Among the grazed sites increasing grazing intensity had a positive and humped effect on vascular plant richness (Table 1 and Fig. 3g). The GLM analysis of

Table 2
Results from GLM analyses for the richness of all bryophyte species on all sites, on grazed sites and on abandoned sites. Management is current grazing/abandonment. ^2 refers to the quadratic effects of the continuous variables (soil pH, soil moisture content, the basal area of trees, the number of farms within 1 km from the site in the 1850s–1860s, grazing intensity and time since abandonment).

	Estimate	Std. error	*z* value	*P*
All sites				
(Intercept)	3.17	0.04	72.08	<0.001
Management	0.15	0.06	2.42	0.016
pH	0.09	0.03	2.89	0.004
pH^2				
Moisture	0.11	0.03	3.60	<0.001
Moisture^2				
Trees	−0.06	0.03	−2.01	0.045
Trees^2				
Farms				
Farms^2				
Grazed sites				
(Intercept)	3.37	0.04	88.44	<0.001
pH				
pH^2				
Moisture				
Moisture^2				
Trees				
Trees^2				
Farms				
Farms^2				
Grazing	0.12	0.04	3.12	0.002
Grazing^2				
Abandoned sites				
(Intercept)	3.18	0.04	73.46	<0.001
pH	0.15	0.05	3.15	0.002
pH^2				
Moisture	0.12	0.04	2.92	0.003
Moisture^2				
Trees	−0.10	0.05	−2.09	0.037
Trees^2				
Farms				
Farms^2				
Abandonment				
Abandonment^2				

grazed sites also suggested a humped effect by the historical number of farms surrounding the site; however, this was not observable in the raw data (Table 1 and Fig. 3e).

The species richness of all bryophytes was also positively affected by current grazing management (Table 2 and Fig. 4a): there was an average of 29 species on grazed sites and 23 on abandoned sites. The species richness on abandoned sites was positively affected by increasing soil pH and increasing soil moisture and negatively by increasing basal area of trees, and these effects were clear also in the results for all study sites (Table 2 and Fig. 4b–d). On grazed sites the species richness was explained only by the positive effect of increasing grazing intensity (Table 2 and Fig. 4g).

3.2. Species richness of rare species

Rare vascular plant species were slightly more numerous on grazed sites (mean 2.0 species) than on abandoned sites (mean 1.2 species) (Fig. 5a), but the effect of management was not statistically significant in the GLM model (Table 3). The richness of rare vascular plant species was strongly explained by the positive linear effect of soil pH (Table 3 and Fig. 5b). The GLM analysis for all sites also suggested a slightly humped effect of soil pH (Table 3), but this is not apparent in the raw data (Fig. 5b). The increasing number of historical farms around the site had a small negative impact on the number of rare species in abandoned sites (Table 3 and Fig. 5e).

The species richness of rare bryophyte species was higher on grazed (mean 1.8 species) than on abandoned sites (mean 0.8 species), but this effect was not significant in the GLM model (Table 4 and Fig. 6a). Instead, the U-shaped effect of soil pH dominated on the number of rare bryophytes, with highest numbers in the extremes of soil fertility (Table 4 and Fig. 6b). Among grazed sites the infertile extreme appeared to have slightly more rare species than the fertile extreme (Table 4 and Fig. 6b). When all sites were analyzed together, a positive effect of increasing soil moisture was found, but this was not observed when grazed and abandoned sites were analyzed separately

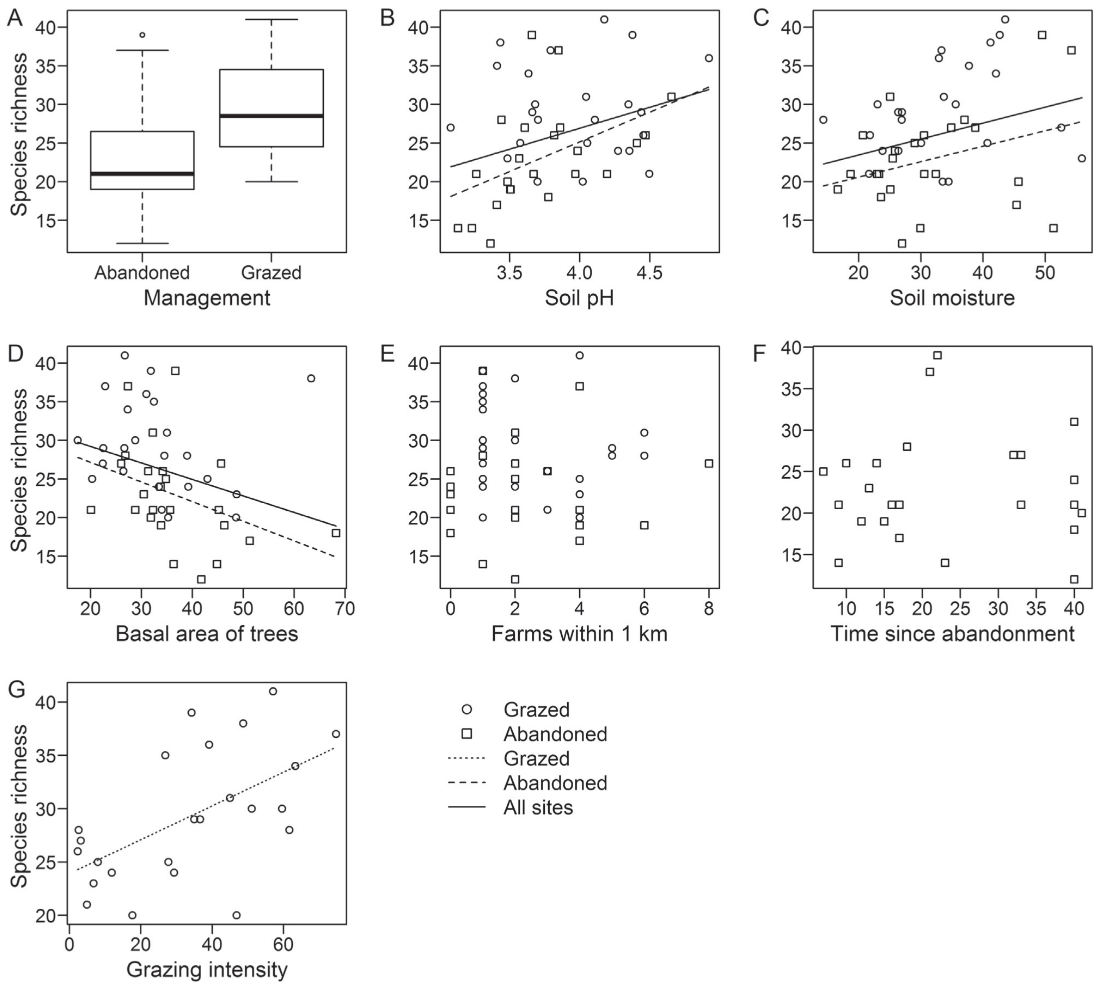

Fig. 4. Responses of species richness of all bryophytes to (a) management, (b) soil pH, (c) soil moisture content (%), (d) the basal are of all trees (m^2/ha), (e) the number of farms within 1 km from the site in the 1850s–1860s, (f) time since abandonment on abandoned sites (years), and (g) grazing intensity (% of clipped shoots out of >5 cm high vascular plants). The fitted linear and quadrate lines depict significant effects from the GLM analyses (see Table 2).

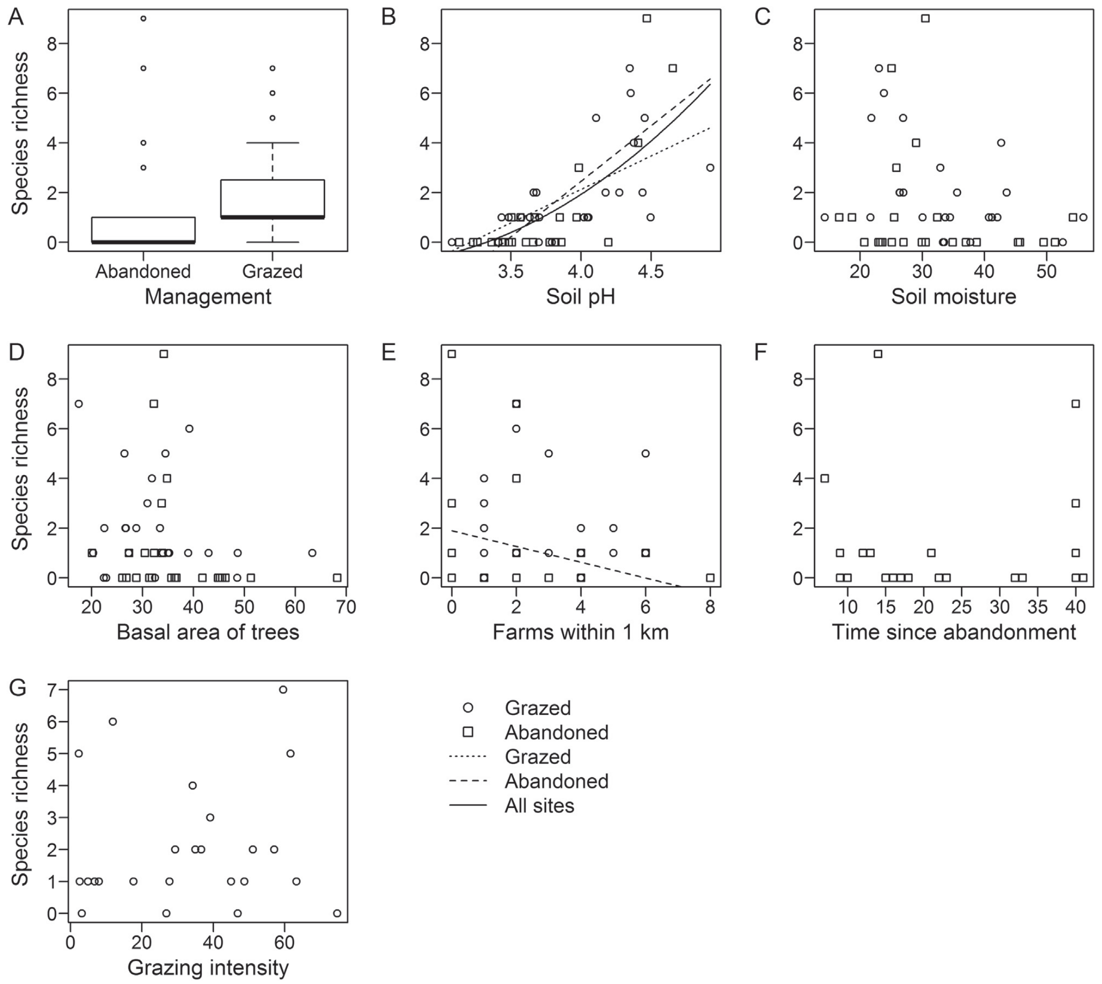

Fig. 5. Responses of species richness of rare vascular plants to (a) management, (b) soil pH, (c) soil moisture content (%), (d) the basal are of all trees (m^2/ha), (e) the number of farms within 1 km from the site in the 1850s–1860s, (f) time since abandonment on abandoned sites (years), and (g) grazing intensity (% of clipped shoots out of >5 cm high vascular plants). The fitted linear and quadrate lines depict significant effects from the GLM analyses (see Table 3).

(Table 4 and Fig. 6c). A negative effect of increasing tree density was found in the analyses of all sites and of abandoned sites, but not among grazed sites (Table 4 and Fig. 6d). Among abandoned sites the increasing time since abandonment had positive and humped effects (Table 4 and Fig. 6f). In grazed sites the number of rare species responded positively to increasing grazing intensity (Table 4 and Fig. 6g).

3.3. Community composition

Based on our data, the community composition of vascular plants is mostly the result of the combination of soil pH, soil moisture and the current management situation (Table 5 in the Appendix, Fig. 7). When all sites were analyzed together, the combined effect of soil pH and management explained the community compositions best (Table 5 in the Appendix, Fig. 7a). Soil moisture was the next variable with most explanatory value, but it did not improve the correlation between the community dissimilarities and environmental distances (Table 5 in the Appendix). However, among grazed sites soil moisture and pH together explained most variation in the community matrix, while grazing intensity was the next fitted variable that did not increase the correlation anymore (Table 5 in the Appendix, Fig. 7b). The community composition of abandoned sites could be best explained by the sole effect of soil pH (Table 5 in the Appendix, Fig. 7c). Adding the time since abandonment decreased the correlation (Table 5 in the Appendix). The final stress values for the two-dimensional NMDS ordination results shown in Fig. 7 were 0.175 for all sites, 0.187 for grazed sites and 0.138 for abandoned sites. The species centroids in the ordination space are available in Fig. 1 in the Appendix.

The bryophyte community composition was strongly affected by soil pH (Table 6 in the Appendix, Fig. 8). When all sites were analyzed together, pH alone explained the community compositions better than pH and management combined (Table 6 in the Appendix, Fig. 8a). On grazed sites, pH and moisture together

Table 3
Results from GLM analyses for the richness of rare vascular plant species on all sites, on grazed sites and on abandoned sites. Management is current grazing/abandonment. ^2 refers to the quadratic effects of the continuous variables (soil pH, soil moisture content, the basal area of trees, the number of farms within 1 km from the site in the 1850s–1860s, grazing intensity and time since abandonment).

	Estimate	Std. error	*z* value	*P*
All sites				
(Intercept)	0.12	0.19	0.65	0.514
Management				
pH	1.41	0.26	5.36	<0.001
pH^2	−0.33	0.15	−2.24	0.025
Moisture				
Moisture^2				
Trees				
Trees^2				
Farms				
Farms^2				
Grazed sites				
(Intercept)	0.35	0.21	1.67	0.096
pH	0.63	0.17	3.71	<0.001
pH^2				
Moisture				
Moisture^2				
Trees				
Trees^2				
Farms				
Farms^2				
Grazing				
Grazing^2				
Abandoned sites				
(Intercept)	−0.69	0.37	−1.87	0.061
pH	1.42	0.23	6.13	<0.001
pH^2				
Moisture				
Moisture^2				
Trees				
Trees^2				
Farms	−0.59	0.28	−2.08	0.038
Farms^2				
Abandonment				
Abandonment^2				

formed the best combination of explanatory variables and adding grazing intensity did not improve the correlation between the environmental distances and community dissimilarities (Table 6 in the Appendix, Fig. 8b). On abandoned sites pH alone explained the community matrix most efficiently, while tree density was the next fitted variable that did not increase the correlation (Table 6 in the Appendix, Fig. 8c). The final stress values for the two-dimensional NMDS ordination results shown in Fig. 8 were 0.152 for all sites, 0.138 for grazed sites and 0.117 for abandoned sites. The species centroids in the ordination space are available in Fig. 2 in the Appendix.

4. Discussion

4.1. Management by grazing induces and maintains high species richness and characteristic communities

According to our findings, both vascular plants and bryophytes showed higher species richness on grazed sites and the grazed sites also differed largely from abandoned sites in their community composition. Rare species were also slightly more numerous on grazed than on abandoned sites, but this difference was not statistically significant for either species group. Thus, the activities of the grazers (herbage removal, trampling, and dunging) have either increased the chances of gap-colonization for a variety of species or they have decreased the risk of local extinctions of species. This can occur, for example, by increasing the spatial and temporal heterogeneity in plant biomass removal, availability of regeneration niches or availability of nutrients (Dufour et al., 2006; Olff and Ritchie, 1998).

The responses of bryophyte species to the current management status were generally weaker than those of vascular plants: the effect on the species richness was slightly smaller and the effect on community composition was not significant. Such weaker responses by bryophytes have been observed earlier in boreal wood-pastures (Takala et al., 2015) and could result from bryophytes not being consumed like vascular plants. The positive effects of the grazers on bryophyte diversity result from the reduced amount of living and dead vascular plant foliage, patches of bare soil created by trampling and the specific microhabitats resulting from dung and urine deposition (Aude and Ejrnæs, 2005; Mayer et al., 2009; Peintinger and Bergamini, 2006; Takala et al., 2014). Dung patches are especially important for *Tayloria tenuis* (NT/RT) that was observed on cow dung in almost half of the currently grazed sites.

The majority of individual species in both species groups were more often observed on the currently grazed sites than on the abandoned ones. The species preferring grazed sites have a wide variety of life-forms and habitat requirements. Most of them require either more light or more bare soil than what is available in typical boreal forests (Hämet-Ahti et al., 1998; Ulvinen et al., 2002). Many of the vascular plants are adapted to herbivory by defensive mechanisms, such as bitter taste. The species typical to the abandoned sites are mostly common species of undisturbed forest soil surfaces. Most of them occurred commonly in the grazed sites as well, but with lower abundances. Thus, abandonment seems to lead to the biotic homogenization of the wood-pasture habitat with the surrounding forest landscape. Continued grazing, on the other hand, creates and maintains hotspots of plant diversity where ruderal species co-occur with forest species in semi-open, intermediately disturbed conditions (Schulman et al., 2008; Takala et al., 2015).

Among the currently grazed sites, the intensity of grazing was also of importance for the species richness of both species groups, although less so for the community compositions. The community compositions are likely to be more dependent on long-term grazing and trampling intensities than on the current year from which we had data. The species richness of all vascular plant species showed a positive but humped response to increasing grazing intensity. At lower grazing intensities the competition from dominant species is likely to limit the number of subordinate species (Mariotte et al., 2013) while at the highest intensities the excess consumption of the vascular plants limits the regeneration of the most sensitive species (Intermediate disturbance hypothesis, sensu Connell, 1978). On the other hand, bryophytes responded to increased grazing intensity only in a positive linear manner. As they are not consumed, they may benefit from the highest grazing intensities through reduced competition with vascular plants. Since individual bryophyte shoots are also smaller than those of vascular plants, they may also have a higher chance of surviving and regrowing after trampling events.

4.2. Soil pH has large implications for species richness and community composition

Soil pH was the most important variable in explaining the community composition and species richness of both vascular plants and bryophytes. It strongly determines the possibilities of individual plant species to grow on the soil and affects the competitive situation between the species (Dupré and Ehrlén, 2002; Löbel et al., 2006). In the Circumboreal floristic region soil pH correlates positively with local plant species richness because

Table 4
Results from GLM analyses for the richness of rare bryophyte species on all sites, on grazed sites and on abandoned sites. Management is current grazing/abandonment. ^2 refers to the quadratic effects of the continuous variables (soil pH, soil moisture content, the basal area of trees, the number of farms within 1 km from the site in the 1850s–1860s, grazing intensity and time since abandonment).

	Estimate	Std. error	*z* value	*P*
All sites				
(Intercept)	−0.15	0.21	−0.74	0.459
Management				
pH				
pH^2	0.23	0.10	2.19	0.028
Moisture	0.31	0.14	2.12	0.034
Moisture^2				
Trees	−0.45	0.18	−2.48	0.013
Trees^2				
Farms				
Farms^2				
Grazed sites				
(Intercept)	0.15	0.22	0.68	0.496
pH	−0.34	0.17	−2.05	0.040
pH^2	0.36	0.11	3.21	0.001
Moisture				
Moisture^2				
Trees				
Trees^2				
Farms				
Farms^2				
Grazing	0.41	0.18	2.27	0.023
Grazing^2				
Abandoned sites				
(Intercept)	−0.06	0.41	−0.15	0.878
pH				
pH^2	0.74	0.25	2.90	0.004
Moisture				
Moisture^2				
Trees	−1.30	0.42	−3.09	0.002
Trees^2				
Farms				
Farms^2				
Abandonment	0.97	0.40	2.41	0.016
Abandonment^2	−1.51	0.56	−2.69	0.007

the evolutionary center was located on high pH soils and thus there are more species adapted to high pH than to low pH (Pärtel, 2002). Indeed, we found positive effects of increasing soil pH on the species richness of all vascular plant species, all bryophyte species and rare vascular plant species. In the most acidic sites there were almost exclusively common species typical to heath forests, but increasing soil pH increases the number of species and reduces the dominance of the heath species.

Rare bryophyte species showed a pattern that contrasts with the others: species richness was maximized at the extreme values of soil pH and therefore the response curve was U-shaped. In the most fertile sites occurred several rare moss species that are typical to moist herb-rich forests which themselves are rare habitats in the study region. On the other hand, the most acidic sites harbored rare liverwort species that typically occurred in the trampled soil of infertile but grazed sites. The disturbances caused by grazing are vital in creating microhabitats free of the common, dominating heath species. Among the currently grazed sites the richness of all bryophyte species was evenly high at varying pH levels, indicating that for bryophytes grazing increases the conservation value relatively more in the least fertile sites. This contrasts with our hypothesis (based on Olff and Ritchie, 1998; Proulx and Mazumder, 1998) according to which grazing should have caused an increase in species richness in fertile sites and possibly even a decrease in infertile sites.

Currently grazed sites had higher soil pH than unmanaged sites, which could result from the grazing itself or from eutrophication related to the management. The effects of grazers can increase or decrease soil pH in some environments, but Milchunas and Lauenroth (1993) found no consistent effects in their extensive review of various environments. In addition, the long grazing history should have increased pH in the abandoned sites as well, and the effect would probably remain now, only 7–42 years after abandonment. Therefore it is likely that in some sites the increased pH has resulted from management-related calcification during the last decades. Soil pH may become increased by the provision of additional fodder to the animals (Eghball, 1999), by allowing the animals to move freely between calcified pastures and the wood-pastures (Takala et al., 2015), or by including old, historically calcified fields in the pasture. We observed at least one of these effects in 23 out of the 24 currently grazed sites in our study. These actions are not permitted if the site is subsidized via the agri-environmental scheme, but in practice they are often allowed because otherwise there is a risk that the wood-pasture becomes abandoned. They increase the risk of eutrophication, which causes increased plant production and the increase of a few competitive species, resulting in the competitive exclusion of subordinate species (Ceulemans et al., 2013; Hautier et al., 2009; Mariotte et al., 2013). The eutrophication of wood-pastures is considered to be especially harmful to the occurrence of rare vascular plant species and less so to bryophytes (Takala et al., 2015). Based on our results an increase in soil pH may cause similar effects: the species richness of vascular plants showed a positive but somewhat humped response where the peak occurred already at approximately pH 4.5, although earlier studies in forests suggest that species richness levels off at around pH 7.0 (Chytrý et al., 2007). This may indicate that unnaturally high pH levels have increased the extinctions of some species. However, we cannot differentiate between natural pH and management-related increases in it. In addition, we measured pH only at the depth of 0–5 cm and different results could have been obtained from other soil stratums: rootless bryophytes can respond more to litter quality while vascular plants may respond to deeper layers. The extent and effects of wood-pasture calcification and eutrophication should be studied further.

Soil pH correlated positively with the basal area of deciduous trees and negatively with the basal area of spruce trees. It is possible that the observed effects of soil pH on the plant communities are partly caused by the differences in litter quality or shading properties of different tree species. In addition, the litter of different tree species may cause differences in soil pH (Hansson et al., 2011) and pH has probably partly determined the dominating tree species. While it is not possible to discern between these mechanisms, it is possible to use the dominating tree species as an indicator of soil fertility, especially in the case of spruce and birch.

4.3. Soil moisture had weak but mostly positive effects on species richness

Soil moisture had positive linear effects on the richness of all bryophyte species and that of rare bryophyte species. Indeed, many of the rare bryophyte species in the data were species typical to moist mesotrophic forest habitats. Their conservation values are highest in wet, occasionally flooded sites. In contrast, the richness of vascular plants showed almost no response to soil moisture, but the highest numbers of rare vascular plants were observed in rather dry sites. Many rare vascular plant species typical to traditional rural biotopes are poor competitors and they are expected to flourish in drier grazed habitats. Moisture also had a small effect on the community composition of both species groups, indicating that there were partially different species in sites of

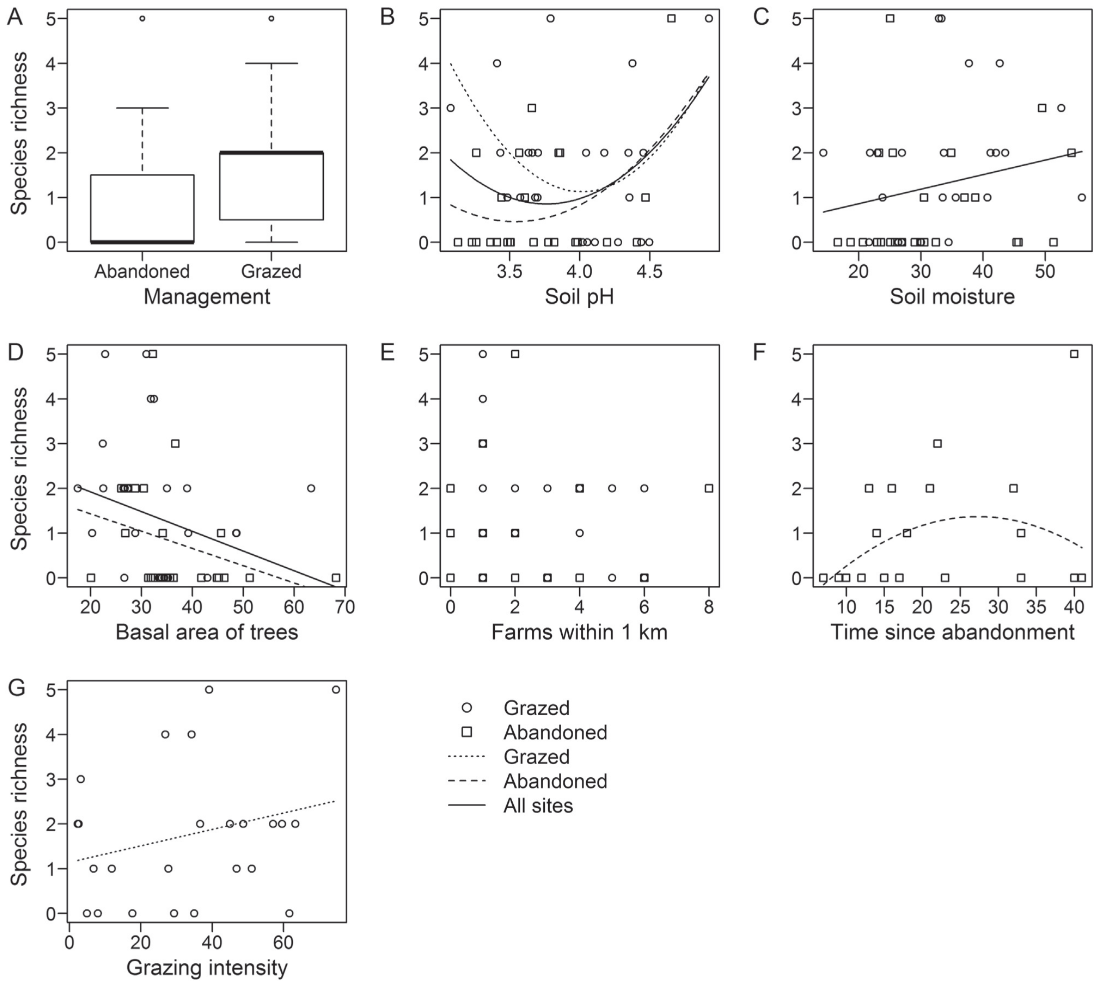

Fig. 6. Responses of species richness of rare bryophytes to (a) management, (b) soil pH, (c) soil moisture content (%), (d) the basal area of all trees (m^2/ha), (e) the number of farms within 1 km from the site in the 1850s–1860s, (f) time since abandonment on abandoned sites (years), and (g) grazing intensity (% of clipped shoots out of >5 cm high vascular plants). The fitted linear and quadrate lines depict significant effects from the GLM analyses (see Table 4).

different moisture qualities. Thus, soil moisture is of importance for the biodiversity of boreal wood-pastures, but since the responses of the two species groups as well as that of individual species differed from each other, it is best to manage sites with varying moisture conditions.

We found no significant effects of soil moisture among currently grazed sites, indicating that grazing maintains equally high species richness at all moisture levels. This is in contrast with earlier observations from grasslands where large herbivores may have positive effects on plant diversity in wet sites but negative effects in dry sites (Olff and Ritchie, 1998). A possible explanation is that the one-time measurement of soil moisture content may not be accurate enough to observe exact interactions. The measured moisture contents did, however, correlate well with our field observations of site wetness.

4.4. Low tree densities enhance biodiversity

The increasing basal areas of trees resulted in declining species richness, especially for bryophytes. This negative impact is likely to arise through the amount of litter that falls from the trees and suffocates subordinate species (especially bryophytes), and from the amount of shading that limits the occurrence of light-demanding species (especially vascular plants) (Einarsson and Milberg, 1999; Gillet et al., 1999). The tree cover on our study sites was generally quite dense because sparsely wooded meadows were excluded from the study. Thus, our finding of negative impacts of increasing tree density refers only to medium to high tree densities. More generally, the biodiversity of herbaceous plants in wood-pastures is likely to be maximized at medium to low tree densities (Einarsson and Milberg, 1999; Gillet et al., 1999).

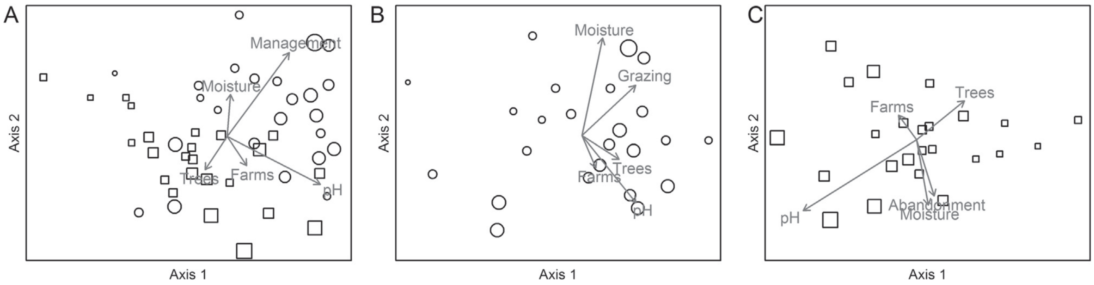

Fig. 7. Nonmetric Multidimensional Scaling (NMDS) for the community structure of vascular plants in (a) all sites, (b) grazed sites, and (c) abandoned sites. Grazed sites are depicted by circles and abandoned sites by squares, and the community composition of each site was derived from the average cover of each species on 12 subplots. Symbol size represents soil pH. The grey arrows represent the direction and strength of the a posteriori correlations between the site locations and the environmental variables: management (currently grazed/abandoned), soil pH, soil moisture content, the basal area of trees, the number of farms within 1 km from the site in the 1850s–1860s, grazing intensity, and the time since abandonment.

Interestingly, the negative effect of increasing tree density was not significant for either the richness of all vascular plants or that of rare vascular plants, although especially rare vascular plants have been considered to benefit greatly from semi-open conditions (Kalliovirta et al., 2010). However, the richness values did peak at fairly low tree densities, which could mean that semi-openness is a prerequisite for vascular plant diversity, but other factors such as soil pH determine the occurrence of many species.

Tree density had practically no effects on the community compositions of either species groups. This is likely to be partly the result of the differential effects of different tree species. Here we did not analyze their effects separately, but it is likely that some of their effects correlate with the very large effects of soil pH (see Section 4.2).

4.5. Historical factors are not the most important ones

Time since abandonment on the abandoned sites did not have almost any effects on the community composition or species richness of either vascular plants or bryophytes. Most of the changes after abandonment seem to happen already within the first ten years and are therefore weakly represented in our data where time since abandonment varied from seven to 42 years. In addition, some species may be showing a longer extinction debt and are still present in several abandoned sites but will go extinct later. Nevertheless, the large differences in the community composition and species richness between grazed and abandoned sites suggest that most species typical to grazed wood-pastures become rare or disappear soon after abandonment. The only exception was the positive and humped effect of increasing time since abandonment on the number of rare bryophyte species. However, the effect was weak, and was probably caused by few exceptional sites with fertile soil. Such long-ago abandoned wood-pastures with fertile soils may have higher values as ungrazed protected areas than as restored wood-pastures.

Historical land-use intensity (measured as the number of farms in the 1850s–1860s within 1 km radius from the site) had no effects on community composition of either group. It had no effects on bryophyte species richness and mostly no effects on vascular plant species richness either. However, the GLM analysis of all vascular plant species on grazed sites found a significant humped effect, which was, though, very weak and not apparent in the raw data at all. The only clearer effect of historical land-use intensity was the negative effect on the number of rare vascular plants in abandoned sites. This rather weak effect might be caused by some rare plant species that are sensitive to human disturbance and therefore prefer abandoned sites with a weak history of human impacts. On the contrary, there is strong evidence that the biodiversity of vascular plants in semi-natural grasslands is positively affected by extensive historical land-use (Cousins and Eriksson, 2002; Cousins

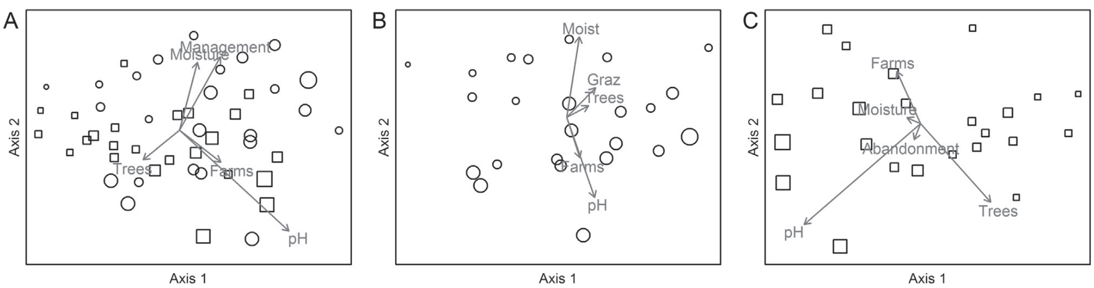

Fig. 8. Nonmetric Multidimensional Scaling (NMDS) for the community structure of bryophytes in (a) all sites, (b) grazed sites, and (c) abandoned sites. Grazed sites are depicted by circles and abandoned sites by squares, and the community composition of each site was derived from the average cover of each species on 12 subplots. Symbol size represents soil pH. The grey arrows represent the direction and strength of the a posteriori correlations between the site locations and the environmental variables: management (currently grazed/abandoned), soil pH, soil moisture content, the basal area of trees, the number of farms within 1 km from the site in the 1850s–1860s, grazing intensity, and the time since abandonment.

and Vanhoenacker, 2011; Cousins et al., 2009; Helm et al., 2006; Kuussaari et al., 2009). In our study the historical effect may be masked by the low number of rare species that could respond to landscape connectivity, or by the combination of ruderal species and forest species that respond differently to human impacts.

Our conclusions on the effects of these historical factors are limited by the way we measured them: time since abandonment varied from seven to 42 years and the historical number of farms was a snapshot from one time (from 1850s or 1860s depending on the site) and was measured with only one radius (1 km). The duration of grazing history (in years) or historical habitat extent and connectivity might also be of importance to the plant communities, but unfortunately it proved impossible to estimate them in this area due to a lack of historical records. Finally, historical land uses could have large impacts on shorter or longer timespans or on smaller or larger spatial scales than the site-level. We hope that other studies will shed more light on the effects of historical factors on the biodiversity of boreal wood-pastures.

5. Conclusions

Based on our results of vascular plants and ground-dwelling bryophytes, the conservation values of boreal wood-pastures are related to high site-level species richness and characteristic community compositions, which are created and maintained by management, namely grazing. More resources should be directed toward maintaining management practices in currently grazed wood-pastures. Grazing increases the conservation value of all kinds of sites and attention should be paid on targeting management to sites with different soil fertility and moisture conditions. The conservation value of a site is increased by a fertile soil, sparsely growing trees and a relatively high grazing intensity. The number of threatened species dependent on boreal wood-pastures is rather low, and the occurrence of rare species is largely dependent on high soil pH.

If a wood-pasture has been abandoned, the future land-use decisions should be informed by the site's structure, species and soil fertility (as well as cultural, social, historical and landscape-related values). Reintroduction of grazing should be encouraged if the site retains characteristics of a wood-pasture in its tree structure and plant species composition. In cases where many of the wood-pasture qualities have been lost, the site is likely to have high value as an ungrazed protected area if the soil is fertile, but otherwise its conservation value is relatively low.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2016.02.018.

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Appendix for Oldén et al.: Grazing and soil pH are biodiversity drivers of vascular plants and bryophytes in boreal wood-pastures

Table 1. Site information: Farm ID (same letter for those sites that are located on the same farm), the area of traditional rural biotopes on the farm, the dominant tree species on the site, current management situation, current grazing animal, the year of abandonment and the municipality where the site is located. The area of traditional rural biotopes on each farm was obtained from the inventory records of the Centre for Economic Development, Transport and the Environment of Central Finland and they include wood-pastures as well as meadows.

Site	Farm ID	Area (ha)	Dominant trees	Management	Grazer	Abandoned	Municipality
1	A	7.22	birch	grazed	sheep		Luhanka
2	B	unknown	birch	abandoned		~1972	Luhanka
3	C	6.12	birch	grazed	horse & cattle		Äänekoski
4	D	7.62	birch	grazed	cattle		Joutsa
5	E	3.26	birch	abandoned		2005	Jyväskylä
6	F	unknown	birch	abandoned		~1972	Luhanka
7	G	6.79	birch	abandoned		~1971	Luhanka
8	H	11.82	birch	grazed	cattle		Joutsa
9	I	2.51	birch	grazed	cattle		Multia
10	J	5.59	birch	abandoned		1991	Joutsa
11	K	2.63	birch	grazed	cattle		Jyväskylä
12	L	3.45	birch	abandoned		~1980	Joutsa
13	K	2.63	spruce	grazed	cattle		Jyväskylä
14	I	2.51	spruce	grazed	cattle		Multia
15	D	7.62	spruce	grazed	cattle		Joutsa
16	M	8.41	spruce	abandoned		1994	Konnevesi
17	N	6.11	spruce	grazed	cattle		Jyväskylä
18	O	3.91	spruce	abandoned		1999	Luhanka
19	P	2.26	spruce	grazed	cattle		Multia
20	Q	6.48	spruce	abandoned		1995	Äänekoski
21	R	5.94	spruce	grazed	cattle		Hankasalmi
22	S	0.35	spruce	abandoned		~1997	Petäjävesi
23	T	3.67	spruce	abandoned		~2000	Jyväskylä
24	U	2.02	spruce	abandoned		~1990	Muurame
25	D	7.62	mixed	grazed	cattle		Joutsa
26	B	unknown	mixed	abandoned		~1972	Luhanka
27	C	6.12	mixed	grazed	horse & cattle		Äänekoski
28	V	15.36	mixed	grazed	cattle		Joutsa
29	X	3.20	mixed	abandoned		1996	Saarijärvi
30	Y	1.60	mixed	grazed	cattle		Jyväskylä
31	Z	3.85	mixed	abandoned		2003	Keuruu
32	Å	12.90	mixed	grazed	horse		Luhanka
33	Ä	2.60	mixed	abandoned		1998	Jämsä
34	Ö	unknown	mixed	abandoned		~1979	Kuhmoinen
35	Q	6.48	mixed	abandoned		1995	Äänekoski
36	AA	2.19	mixed	grazed	cattle		Jämsä
37	A	7.22	pine	grazed	sheep		Luhanka
38	AB	16.87	pine	abandoned		~1989	Joutsa
39	Å	12.90	pine	grazed	horse		Luhanka
40	H	11.82	pine	grazed	cattle		Joutsa

41	V	15.36	pine	grazed	cattle		Joutsa
42	AC	5.17	pine	grazed	cattle		Kuhmoinen
43	N	6.11	pine	grazed	cattle		Jyväskylä
44	B	unknown	pine	abandoned		~1972	Luhanka
45	F	unknown	pine	abandoned		~1972	Luhanka
46	AD	6.48	pine	abandoned		2003	Äänekoski
47	AF	1.83	pine	abandoned		2002	Joutsa
48	Ö	unknown	pine	abandoned		~1979	Kuhmoinen

Table 2. **Vascular plant species** found in the study. The nomenclature follows Hämet-Ahti et al. (1998). The abbreviations ("Short") are used in Figure 1 in this Appendix. The status follows Kalliovirta et al. (2010) for the national IUCN classification, Ryttäri et al. (2012) for regionally threatened species (RT) on the southern boreal zone and Hämet-Ahti et al. (1998) for rare species (indigenous or archaeophytic species that are rare in the biogeographical provinces of the study area: Tavastia australis, Tavastia borealis and/or Savonia australis). The number of occurrences on grazed (total 24), abandoned (total 24) and all sites (total 48) are also given.

Species	**Short**	**Status**	**Grazed**	**Aband.**	**All**
Achillea millefolium	Ami	LC	18	1	19
Achillea ptarmica	Apt	LC	5	1	6
Actaea spicata	Asp	LC / rare	2	1	3
Aegopodium podagraria	Apo	LC	5	6	11
Agrostis capillaris	Aca	LC	21	12	33
Agrostis stolonifera	Ast	LC / rare	2	0	2
Alchemilla sp.	Alc	LC	10	1	11
Alnus incana	Ain	LC	14	10	24
Alopecurus pratensis	Apr	LC	1	0	1
Angelica sylvestris	Angsy	LC	7	6	13
Anthoxanthum odoratum	Aod	LC	5	0	5
Anthriscus sylvestris	Antsy	LC	13	3	16
Athyrium filix-femina	Afi	LC	8	8	16
Betula pendula	Bpe	LC	6	3	9
Betula pubescens	Bpu	LC	13	13	26
Bistorta vivipara	Bvi	LC	2	0	2
Calamagrostis arundinacea	Calar	LC	21	22	43
Calamagrostis canescens	Cca	LC	1	0	1
Calamagrostis epigejos	Cep	LC	5	6	11
Caltha palustris	Cpa	LC	0	1	1
Calluna vulgaris	Calvu	LC	2	2	4
Campanula patula	Campa	LC	2	0	2
Campanula persicifolia	Cpe	LC / rare	7	3	10
Campanula rotundifolia	Cro	LC	0	1	1
Capsella bursa-pastoris	Cbu	LC	1	0	1
Carduus crispus	Ccr	LC / rare	1	0	1
Carex brunnescens	Cbr	LC	1	1	2
Carex digitata	Cdi	LC	10	16	26
Carex echinata	Cec	LC	3	0	3
Carex nigra	Cni	LC	2	1	3
Carex ovalis	Cov	LC	4	0	4
Carex pallescens	Carpa	LC	9	3	12
Cerastium fontanum	Cfo	LC	13	2	15
Chenopodium album	Cheal	LC	1	0	1
Chrysosplenium alternifolium	Chral	LC / rare	1	0	1
Circaea alpina	Ciral	LC / rare	1	0	1
Cirsium arvense	Car	LC	1	0	1
Cirsium helenioides	Che	LC	4	6	10
Cirsium palustre	Cirpa	LC	4	1	5
Cirsium vulgare	Cirvu	LC / rare	2	0	2
Coeloglossum viride	Cvi	LC / RT	2	0	2
Convallaria majalis	Cma	LC	10	15	25

Species	Short	Status	Grazed	Aband.	All
Crepis paludosa	Crepa	LC	1	0	1
Cystopteris fragilis	Cfr	LC	2	0	2
Dactylis glomerata	Dgl	LC	1	0	1
Daphne mezereum	Dme	LC / rare	1	3	4
Deschampsia cespitosa	Dce	LC	20	14	34
Deschampsia flexuosa	Dfl	LC	24	21	45
Dryopteris carthusiana	Dca	LC	16	20	36
Dryopteris filix-mas	Dfi	LC / rare	1	1	2
Elymus repens	Ere	LC	4	1	5
Empetrum nigrum	Eni	LC	0	1	1
Epilobium adenocaulon	Ead	LC	2	0	2
Epilobium angustifolium	Ean	LC	6	3	9
Epilobium montanum	Emo	LC	6	2	8
Equisetum arvense	Ear	LC	3	2	5
Equisetum pratense	Epr	LC / rare	1	3	4
Equisetum sylvaticum	Esy	LC	11	6	17
Erysimum cheiranthoides	Ech	LC	1	0	1
Festuca ovina	Fov	LC	7	3	10
Festuca pratensis	Fpr	LC	2	0	2
Festuca rubra	Fru	LC	8	4	12
Festuca trachyphylla	Ftr	LC	1	1	2
Filipendula ulmaria	Ful	LC	8	5	13
Fragaria muricata	Fmu	LC	1	0	1
Fragaria vesca	Fve	LC	23	16	39
Galeopsis bifida	Gbi	LC	8	5	13
Galeopsis tetrahit	Gte	LC	1	0	1
Galium album	Gal	LC	0	1	1
Galium boreale	Gbo	LC	0	1	1
Galium palustre	Gpa	LC	4	1	5
Galium spurium	Gsp	LC	2	1	3
Galium uliginosum	Gul	LC	8	0	8
Geranium sylvaticum	Gesy	LC	15	11	26
Geum rivale	Gri	LC	12	7	19
Glechoma hederacea	Ghe	LC	0	1	1
Gnaphalium sylvaticum	Gnsy	LC	1	0	1
Goodyera repens	Gre	LC	1	4	5
Gymnocarpium dryopteris	Gdr	LC	13	16	29
Hepatica nobilis	Hno	LC / rare	0	3	3
Hieracium Sylvatica	HSy	LC	13	8	21
Hieracium umbellatum	Hum	LC	4	1	5
Hieracium Vulgata	HVu	LC	6	3	9
Huperzia selago	Hse	LC	0	3	3
Hypericum maculatum	Hma	LC	9	6	15
Juncus filiformis	Jfi	LC	2	0	2
Juniperus communis	Jco	LC	13	11	24
Knautia arvensis	Kar	LC	2	1	3
Lathyrus pratensis	Lpr	LC	9	6	15
Lathyrus vernus	Lve	LC / rare	6	3	9
Leontodon autumnalis	Lau	LC	5	0	5
Leucanthemum vulgare	Levu	LC	9	0	9

Species	Short	Status	Grazed	Aband.	All
Linnaea borealis	Lbo	LC	6	7	13
Listera ovata	Lov	LC / RT	0	2	2
Lonicera xylosteum	Lxy	LC	3	2	5
Luzula multiflora	Lmu	LC	4	1	5
Luzula pallidula	Lpa	LC	2	0	2
Luzula pilosa	Lpi	LC	24	24	48
Lychnis flos-cuculi	Lfl	LC	0	1	1
Lycopodium annotinum	Lan	LC	2	2	4
Lysimachia vulgaris	Lyvu	LC	2	1	3
Maianthemum bifolium	Mbi	LC	23	24	47
Malus sp.	Mal	LC	1	0	1
Matricaria matricarioides	Mma	LC	1	0	1
Melampyrum pratense	Mpr	LC	15	19	34
Melampyrum sylvaticum	Mesy	LC	14	20	34
Melica nutans	Mnu	LC	7	13	20
Milium effusum	Mef	LC	1	1	2
Moehringia trinervia	Mtr	LC / rare	8	1	9
Myosotis laxa	Mla	LC / rare	1	0	1
Myosotis sylvatica	Mysy	LC	1	0	1
Orthilia secunda	Ose	LC	6	6	12
Oxalis acetosella	Oac	LC	21	22	43
Paris quadrifolia	Pqu	LC	14	9	23
Persicaria hydropiper	Phy	LC / rare	1	0	1
Persicaria minor	Pemi	LC / rare	2	0	2
Peucedanum palustre	Pepa	LC	1	0	1
Phegopteris connectilis	Pco	LC	2	3	5
Phleum pratense	Ppr	LC	12	2	14
Picea abies	Pab	LC	15	18	33
Pilosella sp.	Pil	LC	11	0	11
Pimpinella saxifraga	Psa	LC	5	1	6
Pinus sylvestris	Psy	LC	8	5	13
Plantago major	Pma	LC	14	0	14
Platanthera bifolia	Pbi	LC	5	4	9
Poa annua	Pan	LC	6	0	6
Poa pratensis	Ppr	LC	19	3	22
Polygonatum odoratum	Pod	LC / rare	3	1	4
Polypodium vulgare	Povu	LC	3	2	5
Polygonum aviculare	Pav	LC	2	0	2
Populus tremula	Ptr	LC	10	10	20
Potentilla erecta	Per	LC	13	10	23
Prunella vulgaris	Prvu	LC	13	2	15
Prunus padus	Prpa	LC	5	2	7
Pteridium aquilinum	Paq	LC	6	5	11
Pyrola minor	Pymi	LC	1	1	2
Pyrola rotundifolia	Pro	LC	4	5	9
Quercus robur	Qro	LC	1	0	1
Ranunculus acris	Raac	LC	12	5	17
Ranunculus auricomus	Rau	LC	14	4	18
Ranunculus repens	Rre	LC	19	7	26
Rhamnus frangula	Rfr	LC	5	1	6

Species	Short	Status	Grazed	Aband.	All
Rhynchospora alba	Rhal	LC	0	1	1
Ribes alpinum	Rial	LC / rare	2	2	4
Ribes spicatum	Rsp	LC	7	4	11
Ribes uva-crispa	Ruv	LC	0	1	1
Rosa majalis	Rma	LC	2	0	2
Rubus arcticus	Ruar	LC	8	10	18
Rubus idaeus	Rid	LC	17	9	26
Rubus saxatilis	Rsa	LC	13	19	32
Rumex acetosa	Ruac	LC	11	1	12
Rumex acetosella	Rac	LC	3	0	3
Rumex longifolius	Rlo	LC	5	0	5
Rumex obtusifolius	Rob	LC	1	0	1
Sagina procumbens	Spr	LC	4	0	4
Salix sp.	Sal	LC	7	2	9
Sambucus racemosa	Sra	LC	1	0	1
Scutellaria galericulata	Sga	LC	1	0	1
Silene dioica	Sdi	LC	12	6	18
Solidago virgaurea	Svi	LC	17	18	35
Sorbus aucuparia	Sau	LC	24	23	47
Stellaria graminea	Sgr	LC	15	5	20
Stellaria longifolia	Slo	LC	0	1	1
Stellaria media	Sme	LC	13	4	17
Taraxacum sp.	Tar	LC	19	2	21
Thlaspi caerulescens	Tca	LC	1	0	1
Trientalis europaea	Teu	LC	24	23	47
Trifolium hybridum	Thy	LC	1	0	1
Trifolium pratense	Tpr	LC	9	0	9
Trifolium repens	Tre	LC	16	0	16
Tripleurospermum inodorum	Tin	LC	1	0	1
Tussilago farfara	Tfa	LC	1	0	1
Urtica dioica	Udi	LC	14	4	18
Vaccinium myrtillus	Vmy	LC	23	24	47
Vaccinium uliginosum	Vul	LC	0	1	1
Vaccinium vitis-idaea	Vvi	LC	24	22	46
Valeriana officinalis	Vaof	LC / rare	2	0	2
Valeriana sambucifolia	Vsa	LC / rare	0	1	1
Veronica chamaedrys	Vch	LC	22	17	39
Veronica officinalis	Veof	LC	21	15	36
Veronica scutellata	Vsc	LC	1	0	1
Veronica serpyllifolia	Vese	LC	7	0	7
Vicia cracca	Vcr	LC	5	1	6
Vicia sepium	Vise	LC	15	6	21
Vicia tetrasperma	Vte	LC / RT	1	0	1
Viola canina	Vca	LC	15	9	24
Viola epipsila	Vep	LC / rare	2	3	5
Viola mirabilis	Vmi	LC / rare	0	1	1
Viola palustris	Vpa	LC	9	8	17
Viola riviniana	Vri	LC	16	18	34

Table 3. **Bryophyte species** found in the study. The nomenclature follows Juutinen and Ulvinen (2015). The abbreviations ("Short") are used in Figure 2 in this Appendix. The status follows Sammaltyöryhmä (2015) for species that are nationally threatened or nearly threatened (NT), regionally threatened (RT), rare on the southern boreal zone or indicating habitats of high nature value (IND) on the southern boreal zone. The number of occurrences on grazed (total 24), abandoned (total 24) and all sites (total 48) are also given.

Species	Short	Status	Grazed	Aband.	Total
Abietinella abietina	Aab	LC	1	0	1
Amblystegium serpens	Ase	LC	3	6	9
Aneura pinguis	Api	LC / IND	0	1	1
Atrichum tenellum	Ate	LC	2	1	3
Atrichum undulatum	Aun	LC	11	6	17
Aulacomnium androgynum	Aan	LC / IND	0	1	1
Aulacomnium palustre	Apa	LC	7	6	13
Barbilophozia barbata	Bba	LC	8	3	11
Barbilophozia kunzeana	Bku	LC	0	1	1
Barbilophozia lycopodioides	Bly	LC	2	1	3
Blepharostoma trichophyllum	Btr	LC	2	6	8
Brachytheciastrum velutinum	Bve	LC	13	14	27
Brachythecium albicans	Bal	LC	8	0	8
Brachythecium erythrorrhizon/salebrosum	Ber	LC	23	21	44
Brachythecium rutabulum	Bru	LC / IND	9	5	14
Bryum caespiticium	Brca	LC	1	0	1
Bryum capillare	Bca	LC	9	0	9
Bryum moravicum	Bmo	LC	3	0	3
Bryum muehlenbeckii	Bmu	LC / rare	1	0	1
Calliergon cordifolium	Cco	LC	3	0	3
Calliergonella cuspidata	Ccu	LC	1	0	1
Calliergonella lindbergii	Cli	LC	1	0	1
Calypogeia fissa	Cfi	NT / RT	0	1	1
Calypogeia integristipula	Cin	LC	1	1	2
Calypogeia muelleriana	Cmu	LC / IND	1	1	2
Calypogeia neesiana	Cne	LC	3	2	5
Campyliadelphus chrysophyllus	Cch	LC / IND	0	1	1
Campylium protensum	Cpr	LC / RT	1	1	2
Campylophyllum sommerfeltii	Cso	LC	1	3	4
Cephalozia bicuspidata	Cbi	LC	3	1	4
Cephaloziella divaricata	Cdi	LC	3	1	4
Cephaloziella rubella	Cru	LC / rare	4	0	4
Ceratodon purpureus	Cpu	LC	8	2	10
Chiloscyphus polyanthos	Cpo	LC	3	1	4
Cirriphyllum piliferum	Cpi	LC	19	16	35
Climacium dendroides	Cde	LC	15	9	24
Cynodontium strumiferum	Cst	LC	1	1	2
Dicranella / Ditrichum spp.	DD	NA	8	3	11
Dicranum fuscescens	Dfu	LC	0	2	2
Dicranum majus	Dma	LC	9	12	21
Dicranum montanum	Dmo	LC	2	2	4
Dicranum polysetum	Dpo	LC	18	23	41

Species	Short	Status	Grazed	Aband.	Total
Dicranum scoparium	Dsc	LC	24	24	48
Eurhynchiastrum pulchellum	Epu	LC	0	1	1
Eurhynchium angustirete	Ean	LC / RT	1	1	2
Fissidens adianthoides	Fad	LC / IND	2	0	2
Funaria hygrometrica	Fhy	LC	1	0	1
Hylocomium splendens	Hsp	LC	24	24	48
Hypnum cupressiforme	Hcu	LC	5	1	6
Hypnum pallescens	Hpa	LC	3	4	7
Lophocolea heterophylla	Lhe	LC	24	23	47
Lophocolea minor	Lmi	LC	1	0	1
Lophozia obtusa	Lob	LC / rare	5	4	9
Lophozia sudetica	Lsu	LC	1	0	1
Lophozia ventricosa / silvicola	Lve	LC	0	1	1
Lophozia wenzelii	Lwe	LC / rare	1	0	1
Mnium stellare	Mst	LC	4	1	5
Oxyrrhynchium hians	Ohi	LC	10	5	15
Paraleucobryum longifolium	Palo	LC	4	0	4
Pellia spp.	Pel	NA	4	0	4
Plagiochila asplenioides	Pas	LC	6	6	12
Plagiochila porelloides	Ppo	LC	3	1	4
Plagiomnium affine	Paf	LC / RT	0	1	1
Plagiomnium cuspidatum	Pcu	LC	18	18	36
Plagiomnium ellipticum	Plel	LC	7	5	12
Plagiomnium medium	Pme	LC	13	10	23
Plagiothecium curvifolium	Plcu	LC	6	2	8
Plagiothecium denticulatum	Pde	LC	19	20	39
Plagiothecium laetum	Plla	LC	17	19	36
Plagiothecium latebricola	Pla	NT / RT	3	0	3
Plagiothecium succulentum	Psu	LC	1	0	1
Pleurozium schreberi	Psc	LC	24	24	48
Pohlia cruda	Pocr	LC	1	1	2
Pohlia nutans	Pnu	LC	20	13	33
Polytrichastrum alpinum	Pal	LC	1	0	1
Polytrichastrum formosum	Pfo	LC	2	1	3
Polytrichastrum longisetum	Polo	LC	9	1	10
Polytrichum commune	Pco	LC	13	15	28
Polytrichum juniperinum	Pju	LC	19	8	27
Ptilidium ciliare	Pci	LC	6	3	9
Ptilidium pulcherrimum	Ppu	LC	8	9	17
Ptilium crista-castrensis	Ptcr	LC	8	9	17
Rhizomnium punctatum	Rpu	LC	6	8	14
Rhodobryum roseum	Rro	LC	19	16	35
Rhytidiadelphus squarrosus	Rsq	LC	18	7	25
Rhytidiadelphus triquetrus	Rtr	LC	16	16	32
Sanionia uncinata	Sun	LC	17	18	35
Scapania irrigua	Sir	LC	0	1	1
Sciuro-hypnum curtum	Scu	LC	24	23	47
Sciuro-hypnum populeum	Spo	LC	2	1	3
Sciuro-hypnum reflexum	Sre	LC	24	21	45
Sciuro-hypnum starkei	Sst	LC	18	21	39

Species	Short	Status	Grazed	Aband.	Total
Sphagnum angustifolium	San	LC	0	1	1
Sphagnum capillifolium	Sca	LC	2	0	2
Sphagnum girgensohnii	Sgi	LC	2	2	4
Sphagnum quinquefarium	Squ	LC	1	0	1
Sphagnum riparium	Sri	LC	1	0	1
Sphagnum russowii	Sru	LC	1	0	1
Sphagnum squarrosum	Ssq	LC	0	1	1
Sphagnum warnstorfii	Swa	LC / IND	1	0	1
Splachnum ampullaceum	Sam	LC	1	0	1
Tayloria tenuis	Tte	NT / RT	11	0	11
Tetraphis pellucida	Tpe	LC	4	1	5
Thuidium assimile	Tas	LC / IND	1	1	2
Thuidium delicatulum	Tde	LC / RT	0	1	1
Thuidium recognitum	Tre	LC	4	2	6
Thuidium tamariscinum	Tta	LC / RT	1	0	1

Table 4. Correlations between the environmental variables.

All sites

	Farms	Moisture	pH	Picea	Pinus	Deciduous
Moisture	-0.14					
pH	0.04	-0.35 *				
Picea	-0.11	0.10	-0.39 **			
Pinus	0.02	-0.19	-0.01	-0.31 *		
Deciduous	0.06	0.03	0.54 ***	-0.48 ***	-0.22	
Trees	0.03	0.06	-0.20	0.30 *	0.35 *	-0.09

Grazed sites

	Farms	Moisture	pH	Picea	Pinus	Deciduous	Trees	Grazing
Moisture	-0.23							
pH	0.14	-0.61 **						
Picea	-0.13	0.17	-0.40 .					
Pinus	0.31	-0.18	0.12	-0.33				
Deciduous	0.1	-0.07	0.53 **	-0.39 .	-0.23			
Trees	0.21	0.01	-0.07	0.27	0.32	0.09		
Grazing	-0.03	0.21	-0.05	-0.05	-0.21	0.13	-0.21	
Trampling	-0.14	0.04	0.21	-0.12	-0.11	0.16	0.13	0.57 **

Abandoned sites

	Abandonment	Farms	Moisture	pH	Picea	Pinus	Deciduous
Farms1	-0.22						
Moisture	0.38 .	-0.16					
pH	0.04	-0.09	-0.20				
Picea	-0.35 .	-0.03	0.03	-0.27			
Pinus	0.05	-0.25	-0.22	-0.29	-0.25		
Deciduous	0.40 .	0.03	0.12	0.68 ***	-0.62 **	-0.23	
Trees	0.18	-0.12	0.13	-0.26	0.26	0.37	-0.31

***=p<0.001, **=p<0.01, *=p<0.05

Table 5. Results from the Bioenv analyses of factors affecting **vascular plant** community structure, with the Spearman rank correlation between the community and environmental matrices.

All sites		
Size	Variables	Correlation
1	pH	0.354
2	ph, Management	0.439
3	ph, Management, Moisture	0.401
4	ph, Management, Moisture, Trees	0.339
5	ph, Management, Moisture, Trees, Farms	0.280
Grazed sites		
Size	Variables	Correlation
1	Moisture	0.442
2	Moisture, pH	0.513
3	Moisture, pH, Grazing	0.479
4	Moisture, pH, Grazing, Trees	0.453
5	Moisture, pH, Grazing, Trees, Farms	0.357
Abandoned sites		
Size	Variables	Correlation
1	pH	0.436
2	pH, Abandonment	0.326
3	pH, Abandonment, Farms	0.279
4	pH, Abandonment, Farms, Moisture	0.244
5	pH, Abandonment, Farms, Moisture, Trees	0.185

Table 6. Results from the Bioenv analyses of factors affecting **bryophyte** community structure, with the Spearman rank correlation between the community and environmental matrices.

All sites		
Size	Variables	Correlation
1	pH	0.381
2	pH, Management	0.344
3	pH, Management, Moisture	0.307
4	pH, Management, Moisture, Farms	0.275
5	pH, Management, Moisture, Farms, Trees	0.223
Grazed sites		
Size	Variables	Correlation
1	pH	0.325
2	pH, Moisture	0.414
3	pH, Moisture, Grazing	0.379
4	pH, Moisture, Grazing, Farms	0.360
5	pH, Moisture, Grazing, Farms, Trees	0.308
Abandoned sites		
Size	Variables	Correlation
1	pH	0.467
2	pH, Trees	0.408
3	pH, Trees, Abandonment	0.316
4	pH, Trees, Abandonment, Farms	0.264
5	pH, Trees, Abandonment, Farms, Moisture	0.226

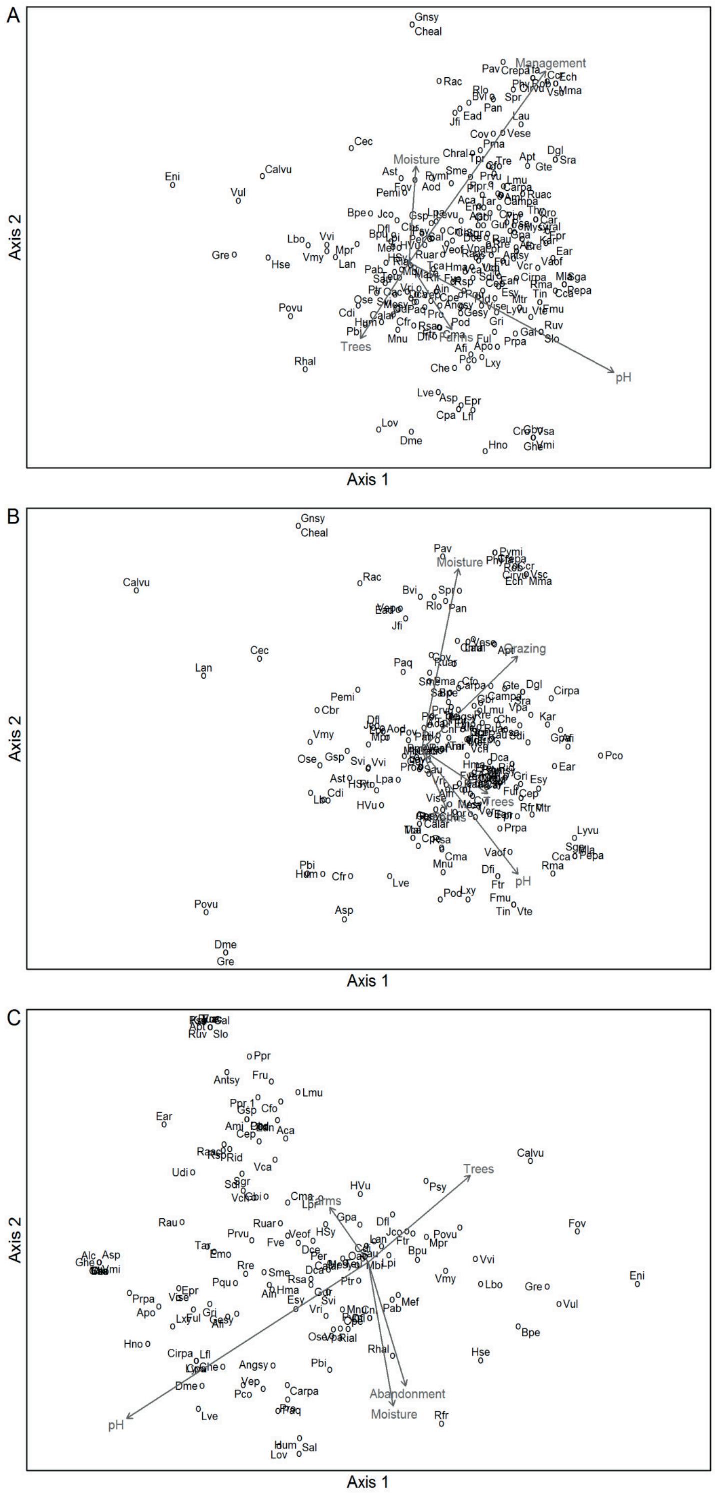

Figure 1. **Vascular plant species** centroids in the NMDS ordinations of a) all sites, b) currently grazed sites, and c) abandoned sites. The grey arrows represent the direction and strength of the effects of environmental variables. The species abbreviations include 1-3 letters from genus name and 2 letters from species name and the long names can be found in Table 2 in this Appendix.

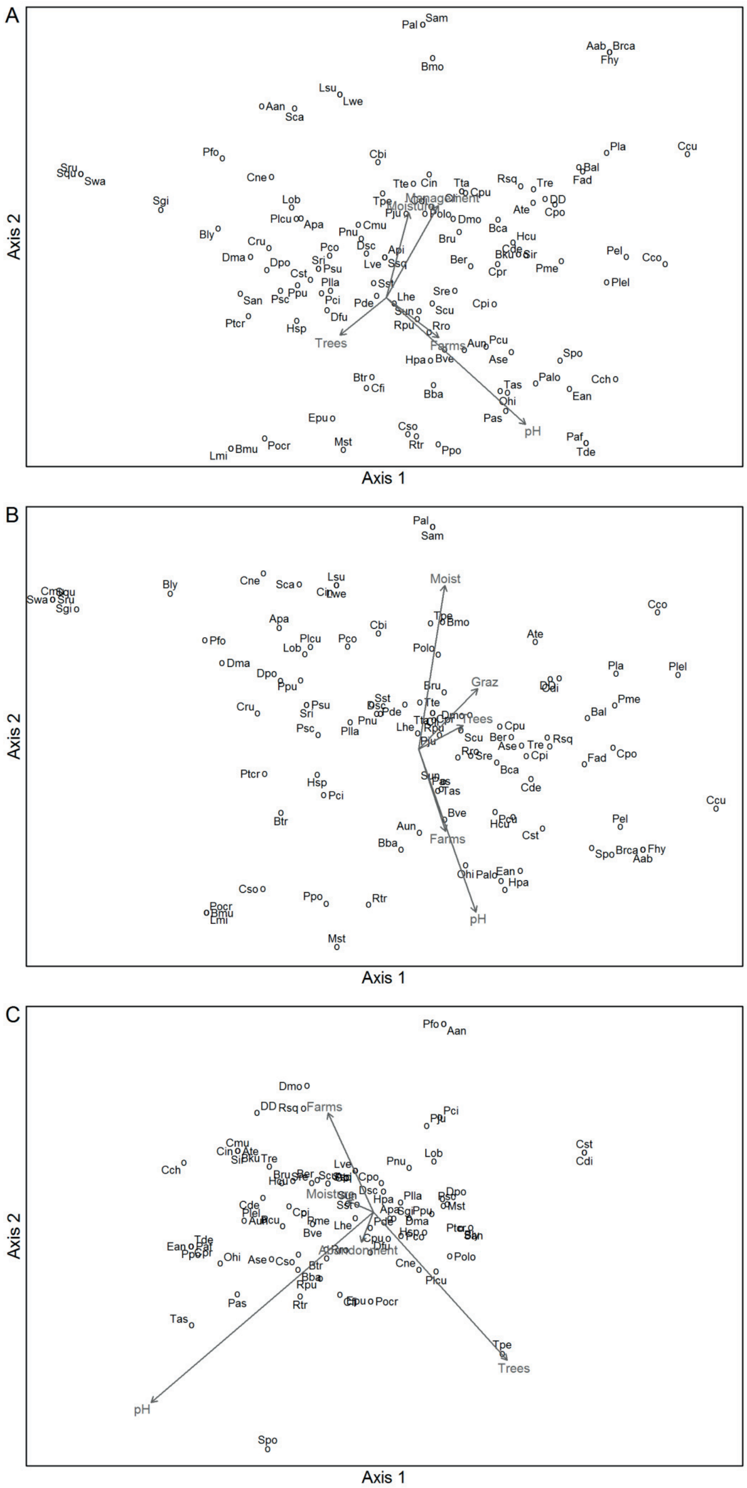

Figure 2. **Bryophyte species** centroids in NMDS ordinations of a) all sites, b) currently grazed sites, and c) abandoned sites. The grey arrows represent the direction and strength of the effects of environmental variables. The species abbreviations include 1-2 letters from genus name and 2 letters from species name and the long names can be found in Table 3 in this Appendix.

III

SYSTEMATIC TARGETING OF MANAGEMENT ACTIONS AS A TOOL TO ENHANCE CONSERVATION OF TRADITIONAL RURAL BIOTOPES

by

Kaisa J. Raatikainen, Maija Mussaari, Katja M. Raatikainen & Panu Halme 2017

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Systematic targeting of management actions as a tool to enhance conservation of traditional rural biotopes

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ABSTRACT

Traditional rural biotopes (TRBs), which are biologically and culturally valuable habitats maintained by low-intensity grazing and mowing, are a core element of biodiversity in Europe. During the last decades, TRBs have faced severe habitat loss and fragmentation due to agricultural modernization. Despite their well-known critical state, their conservation remains inadequate, thus raising a need to advance TRB conservation via spatial land-use planning. In this study we analyze a national GIS database on TRBs in order to examine how the current TRB network can be complemented in terms of conservation value based on known ecological characteristics. Given different target scenarios for the amount of managed TRBs, we demonstrate where management should be directed to both on protected and unprotected areas. We conclude that in current state, biodiversity depending on TRB management is not efficiently sustained in Finland. Substantial amount of TRB habitats and populations of threatened TRB species are left unmanaged. Based on our results, we suggest that to advance TRB conservation in Finland, the cover of managed TRBs should be rapidly extended to form ecologically functional networks. The expansion would prioritize additional management to the Baltic Sea coast and smaller clusters within inland Finland, double the cover of managed TRBs, and direct management subsidies in a more cost-effective way.

1. Introduction

Although protection of biodiversity has been a fundamental tenet of conservation biology since its early beginning (Soulé, 1985), tight coupling of social and natural systems escaped conservation scientists' attention for a long time in many regions (Kareiva and Marvier, 2012). Recently, temporal changes in how conservation is perceived have raised global attention to a social-ecological approach in conservation (Corlett, 2014; Mace, 2014). In Europe, a significant proportion of biodiversity is situated in landscapes formed through a sequential overlay of traditional rural land-use systems (Plieninger et al., 2006). This process has continued for thousands of years, resulting in a rich diversity of cultural landscapes and associated species which are sustained by human land use (Batáry et al., 2015; Plieninger et al., 2006; Pullin et al., 2009).

Since low-intensity land use is important for existence of a lot of European biodiversity (Halada et al., 2011; Pullin et al., 2009), much of nature conservation aims to halt the loss of farmland biodiversity, and many protected areas are managed in ways that reflect traditional agricultural practices (Batáry et al., 2015; Linnell et al., 2015). Challenges, however, are substantial. Agricultural industrialization has caused a widespread decline in farmland heterogeneity and biodiversity (Benton et al., 2003; Strijker, 2005). Modern socioeconomy drives rural landscapes towards land abandonment and agricultural land-use intensification, centralization, and specialization (Beilin et al., 2014; Fjellstad and Dramstad, 1999; Knickel, 1990; Lambin et al., 2001). Therefore some of the most critical conservation issues today relate to the abandonment of traditional farming practices and the disappearance of biodiverse habitats dependent on them (Halada et al., 2011; Henle et al., 2008).

Traditional rural biotopes (TRBs) are heterogeneous disturbance-dependent grasslands and wood-pastures maintained through long-term grazing and mowing. The term “traditional rural biotope” refers to culturally influenced natural habitat complexes that are part of a traditional landscape formed through archaic rural livelihoods (Ministry of the Environment, 1992), and although its usage is specific to Finland, similar habitats are found throughout Europe (e.g. Bergmeier et al., 2010). Typical TRB habitats in Finland are grazed woodlands, sparsely wooded pastures, and mesic to moist meadows (Raunio et al., 2008). Management of TRBs is based on low-intensity raising of livestock on unfertilized vegetation growing on non-tilled soils, a practice that is especially valuable

Abbreviations: AES, agri-environment scheme; TRB, traditional rural biotope.

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for biodiversity conservation across Europe (Beaufoy and Cooper, 2013). TRBs are among the most diverse and species-rich habitats of rural landscapes (Cousins and Eriksson, 2002; Fjellstad and Dramstad, 1999; Luoto et al., 2003), and they are mentioned as central elements of high-nature-value farmland (Heliölä et al., 2009; Plieninger et al., 2015). As ecosystems, TRBs are highly variable and dynamic. Their species assemblages depend on the interplay between active management, vegetation succession, and metapopulation dynamics (Allan et al., 2014; Halada et al., 2011; Hanski, 2011).

Ongoing TRB loss and fragmentation has serious ecological effects. TRB species' metapopulations lose their viability, because unoccupied habitat patches are not colonized at the same rate as extant populations disappear, i.e. they reach their extinction threshold (Hanski, 2011). Yet, some species – especially vascular plants – react slowly to land-use changes and persist on abandoned TRBs for long time periods (Cousins, 2009; Eriksson et al., 2002; Lindborg and Eriksson, 2004). Unless targeted habitat restoration and proper management actions are secured, species specialized in TRBs continue to decline and their populations face inevitable local extinctions (Cousins, 2009; Krauss et al., 2010; Kuussaari et al., 2009).

Loss of farmland biodiversity has created a need for agri-environment measures, which are incentives designed to encourage farmers to protect and enhance the environment on their farmland (Anonymous, 2005). Countries within European Union are increasingly funding habitat management and restoration actions through voluntary, contract-based subsidies within national agri-environment schemes (AESs) (Batáry et al., 2015; Kleijn and Sutherland, 2003). The AES contracts are the main tool for encouraging management of TRBs. However, the effectiveness of AESs has been questioned in TRB management and biodiversity conservation in general (Arponen et al., 2013; Batáry et al., 2015; Kleijn and Sutherland, 2003). In Finland, during the 20th century, over 99% of TRB cover disappeared as a consequence of agricultural modernization (Raunio et al., 2008; Salminen and Kekäläinen, 2000). Currently, TRBs are the most threatened of all Finnish habitat types (Raunio et al., 2008) and provide habitat for a total of 1807 red-listed species (Rassi et al., 2010). Despite this, current conservation measures have been insufficient to tackle the situation.

Several reasons contribute to inefficient conservation of TRBs in Finland. These include capacity, knowledge, institutional, and ideological obstacles (cf. Bennett et al., 2016). Firstly, besides the AES, other funding sources for TRB management are scarce (Ministry of Agriculture and Forestry, 2013). Secondly, management actions have not been efficiently directed to biologically valuable sites (Arponen et al., 2013; Kemppainen and Lehtomaa, 2009), and thirdly, the dynamic and management-dependent character of TRBs challenges Finnish environmental authorities, who have mostly relied on establishing permanent set-asides to conserve natural habitats, aiming to exclude most or all human influence from them (Vuorisalo and Laihonen, 2000). In this sense, Finnish nature conservation has not followed the European tradition where nature and culture are intertwined, but rather a wilderness-oriented approach that separates people from nature (Linnell et al., 2015). In this context, the biological value of TRBs is deemed “semi-natural”, and the motivation for conserving these “unnatural” habitats is undermined (Cronon, 1996; Mace, 2014).

As a result, TRBs are weakly represented in Finnish nature conservation policies. They have often been excluded from conservation networks such as Natura 2000 (Ministry of the Environment, 2015; Council of State, 1996; Vuorisalo and Laihonen, 2000). Although sole establishment of protected areas is insufficient for TRB conservation (Arponen et al., 2013; Bengtsson et al., 2003), there are valuable TRB sites on protected areas. However, the majority of them are unmanaged, and protection status is regularly based on conservation of other habitats (Pakkanen et al., 2015; Raatikainen and Raatikainen, 2015).

Several means to enhance the conservation of TRBs have been proposed. These include establishing complementary management funding sources (Keränen et al., 2012), increasing AES uptake (Grönroos et al., 2007), and targeting funding to manage locations with high biodiversity (Arponen et al., 2013). Achieving a favorable TRB conservation status needs increasing their cover under protection, restoration, and active management alike. Because human influence essentially drives TRB ecology, TRB restoration requires reviving traditional social-ecological interactions. Therefore we refer to it as bio-cultural restoration (Egan et al., 2011).

In this paper we explore if and how conservation of TRBs could be improved by directing restoration and management actions spatially on a national scale. We began by evaluating the current management status of TRBs (Fig. 1). Then we explored how the current surveyed network of valuable TRBs can be complemented, assuming that the most important aim of network expansion is to secure the maintenance of threatened habitats and species dependent on TRB management. We answered the questions via a spatial prioritization analysis, where several layers of information contribute to the conservation value of a given habitat patch, and yield an optimized management network solution.

The purpose of the analysis was to inform management allocation on large scale instead of suggesting whether a specific site should be managed or not, and we did not aim to exclusively point out the most valuable individual TRB sites in whole Finland. Rather, we synthesized currently available spatial information. The quantified results provide a starting point for developing a national implementation strategy for further conservation action (Knight et al., 2006).

Given the national goal of securing management of all valuable surveyed TRBs and increasing the total cover of managed TRBs to 60,000 ha (Kemppainen and Lehtomaa, 2009; Kotiaho et al., 2015; Salminen and Kekäläinen, 2000), we formulated a spatial prioritization solution for four nested management scenarios (A: surveyed TRBs, B–D: surveyed TRBs with a progressive addition of managed area). In each consecutive scenario, ca. 4000 managed hectares were added, thus forming a realistic step-wise plan for expansion of the management network. The most extensive scenario (D) yielded a spatial allocation of nearly 45,000 ha of managed TRBs.

2. Materials and methods

2.1. Data sets

We used existing GIS data derived from five different sources: (1) a national network of surveyed TRBs, covering ca. 30,300 ha; (2) AES subsidy contracts on TRB management in year 2014, ca. 19,200 ha; (3) habitat type inventories on protected and state-owned areas, ca. 4,620,200 ha; (4) database on protected private and state-owned TRBs, ca. 32,200 ha; and (5) 16077 point occurrences of 133 TRB-specialized red-listed vascular plant species. The data sets are further described in Supplementary Appendix A. The Åland islands were excluded because of their self-governmental status. Without the Åland islands, the land area of Finland is 30,234,700 ha (National Land Survey of Finland, 2016).

We incorporated data on surveyed and protected TRBs in the analyses without modifications. AES contract sites outside surveyed TRBs or protected areas were omitted from spatial prioritization, as their biological value as TRBs has not been surveyed in the field, and according to our personal experience their quality varies from good to very poor. Habitat type inventory data is built on a nested structure, which was used to form GIS layers of different TRB habitats on two levels. Firstly, we derived an upper-level TRB habitat classification comparable to the assessed threatened habitat types (Raunio et al., 2008). Secondly, we categorized more strictly defined Natura 2000 -habitats (listed in the Habitats Directive Annex I: Council of Europe, 1992) as separate layers (Table 1). This allowed us to give increased weight on sites having high conservation value at the European level. However, the inventory did not cover all TRB sites. For these sites, a layer of undefined TRB habitat was formed, as there were no data on specific habitat types available.

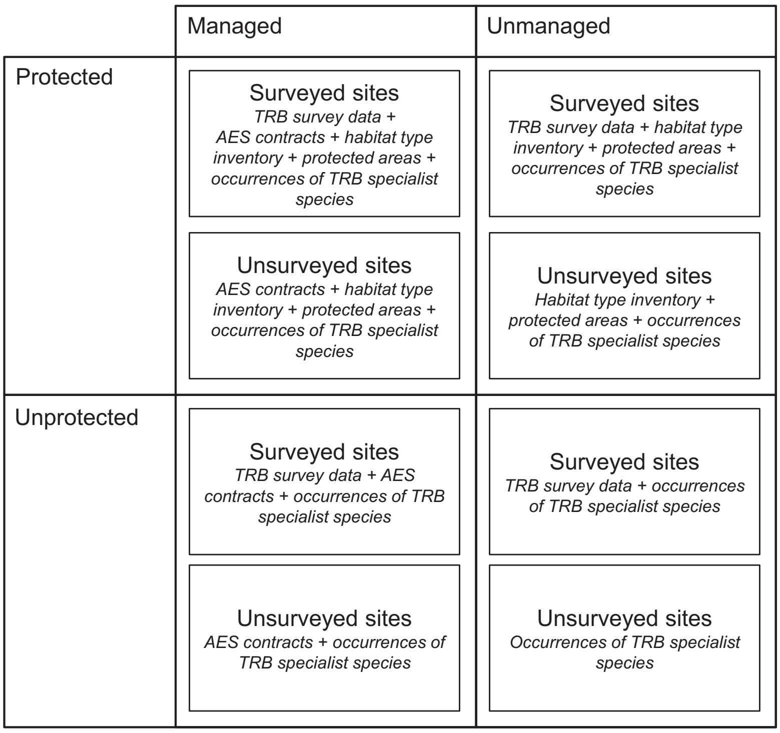

Fig. 1. A framework for categorizing traditional rural biotopes from a governance perspective. Key determinants are management, protection, and survey statuses. Information on management status is mainly available through AES contracts. Protected TRBs are located both on private and state-owned land. A recognized network of valuable sites is based on nationally and regionally conducted surveys on TRBs. The management and protection statuses of surveyed TRBs are variable. Ecologically, TRBs are detected via distinct structural features such as the occurrence of TRB habitat specialist species, whether the site is managed or not. On national level, the data on TRBs vary in quality. The level of knowledge positively correlates with the ability of Finnish environmental authorities to influence management of TRBs belonging to different categories. Data sets utilized in detecting sites belonging to each category are listed in italic (for detailed descriptions of data, see Supplementary Appendix A).

We included certain complementary habitat layers because they contribute to TRB connectivity by sharing similar species communities. These were old traditional yards, reindeer gathering grounds, Sami camp sites, managed esker habitats, and dry, sandy sunlit dunes. In addition, occurrences of TRB specialist vascular plants may indicate undetected TRBs and act as source populations for nearby known TRB sites.

In order to control for biogeographical bias in species richness, we pooled existing red-listed species occurrences together according to their threat status. All species occurrences categorized as potentially or certainly disappeared were merged to form one data layer that reflected the historical range of TRB specialists.

2.2. Current management status

To estimate the amount of currently managed TRBs, we performed an overlay analysis by unioning the data on AES subsidy contracts, surveyed TRBs, and protected TRBs. The latter were divided according to landownership (either private or state-owned). Circa 2500 ha of managed TRBs are not subsidized (Kemppainen and Lehtomaa, 2009), but as there are no inclusive GIS data available on these sites, we were forced to exclude them. All GIS data handling were done with ArcGIS (ESRI® ArcMAP™ version 10.3.1).

2.3. Management scenarios

We used conservation prioritization software Zonation (version 4; C-BIG Conservation Biology Informatics Group, 2014) to produce spatial management scenarios. Starting from a full landscape, Zonation iteratively removes locations (cells or planning units) of least contribution to remaining biodiversity while minimizing marginal loss of overall conservation value following from the removal (Moilanen et al., 2005). Zonation accounts for connectivity measures and weights given for different biodiversity features, which are entered into the analysis as separate raster data layers. During prioritization, Zonation aims to retain a complementary-based balance across all features (Moilanen et al., 2011), and for each step, it calculates conservation performance as the average proportion remaining over all features within the analysis (Arponen et al., 2013).

Data layers and feature-specific weights used in the prioritization are listed in Table 1. Original data were rasterized with a cell size of 25 m × 25 m, as TRB sites and habitat patterns are small and highly fragmented. For computational reasons, initial cells were aggregated to binary 50 m × 50 m resolution. Total number of grid cells within the analysis was 307,072. We weighted habitat and species layers based on their red-list status (Rassi et al., 2010; Raunio et al., 2008), by giving a higher weight to a more threatened type. Critically endangered (CR), endangered (EN), vulnerable (VU), and near-threatened (NT) classes were given weights of 4, 3, 2, and 1, respectively. Additively, Natura 2000 habitats were weighted in respect to their importance according to the Habitats Directive (Council of Europe, 1992); priority habitats within the European Union were given a weight of 3 whereas other Natura 2000 habitats received a weight of 2. There were few exceptions based on national emphases on TRB management (Ministry of the Environment, 2013; Salminen and Kekäläinen, 2000): the weights of slash-and-burn areas and semi-natural dry grasslands and scrubland facies on calcareous substrates were raised by one unit; and the weight of boreal Baltic coastal meadows was lowered by one unit.

Table 1
Analysis layers. "No." refers to continuous numbering of data layers. For each layer, also name, weight value, and distribution are listed. Base layers (1–3) included site-level information on survey and management status. Habitat type inventory data was used to form layers 4–14 and 16–28. TRB habitat layers 4–11 are comparable with the Finnish assessment on threatened habitats (CR: critically endangered, EN: endangered, NE: not evaluated; according to Raunio et al., 2008). Natura 2000-layers are listed according to the TRB habitats in directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora (Council of Europe, 1992). Habitats marked with an asterisk (*) are classified as priority habitats within the European Union. Undefined TRB habitat (layer 15) includes all area that is not covered by habitat type inventory. Species layers include information on the occurrence of red-listed vascular plant species specialized in TRB habitats. Transformed layers (34 and 35) were included only in the analyses with landscape connectivity measures. Weight sums were balanced between layers 1–28 and 29–33. Cell size in the analysis was 0.25 ha (50 m × 50 m).

	No.	Layer name	Weight	Distribution (cells)
Base layers	1	Nationally and regionally surveyed traditional rural biotopes on private and state-owned land (corresponds to scenario A)	2	160,830
	2	Protected TRBs on private and state-owned land: extended network	1	166,457
	3	AES management contract areas (on layers 1 and 2)	2	65,745
Habitat layers	4	Heaths (CR)	4	5950
	5	Dry meadows (CR)	4	2834
	6	Mesic meadows (CR)	4	7625
	7	Moist meadows (CR)	4	35,640
	8	Wooded meadows (CR)	4	215
	9	Wooded pastures (CR)	4	3630
	10	Grazed woodlands (EN)	3	7364
	11	Slash-and-burn areas (NE)	4	188
	12	Old traditional reindeer gathering grounds	1	163
	13	Old traditional yards and Sami camp sites	1	1204
	14	Dry sandy sunlit dunes and eskers	1	3302
	15	Undefined TRB habitat	2	242,034
Natura 2000 layers	16	Boreal Baltic coastal meadows (1630)*	2	19,502
	17	European dry heaths (4030)	2	4207
	18	Semi-natural dry grasslands and scrubland facies on calcareous substrates (6210)	3	24
	19	Species-rich *Nardus* grasslands on siliceous substrates (6230)*	3	7
	20	Fennoscandian lowland species-rich dry to mesic grasslands (6270)*	3	1792
	21	Nordic alvar and precambrian calcareous flatrock (6280)*	3	60
	22	*Molinia* meadows on calcareous, peaty or clayey-silt-laden soils (6410)	2	1
	23	Hydrophilous tall herb fringe communities (6430)	2	1227
	24	Northern boreal alluvial meadows (6450)	2	3905
	25	Lowland hay meadows (6510)	2	190
	26	Mountain hay meadows (6520)	2	93
	27	Fennoscandian wooded meadows (6530)*	3	146
	28	Fennoscandian wooded pastures (9070)	2	3979
Species layers	29	Critically endangered (CR) plant species inhabiting TRBs	32.4	34
	30	Endangered (EN) plant species inhabiting TRBs	21.6	1816
	31	Vulnerable (VU) plant species inhabiting TRBs	10.8	5213
	32	Near threatened (NT) plant species inhabiting TRBs	3.6	5213
	33	NT, VU, EN, or CR plant species historically inhabiting TRBs; disappeared or potentially disappeared locations	3.6	2936
Transformed layers	34	Contribution of protected TRBs (layer 2) to connectivity of surveyed TRB network (layer 1)	5	166,457
	35	Contribution of dry sandy sunlit dunes and eskers (layer 17) to connectivity of surveyed TRB network (layer 1)	2	3299

Since species layers were fewer, we balanced the sum of their weights against the sum of weights of habitats (Lehtomäki and Moilanen, 2013). The final weights for species layers were: 32.4 for CR species, 21.6 for EN species, 10.8 for VU species, and 3.6 for NT species. We weighted remaining layers with the aim of producing weights that were as balanced as possible with the previously determined weights.

We chose the additive benefit function as the location removal rule. It is suitable for cases in which different co-occurring data layers are considered to provide additional value to each other, and the data is interpreted as indicating general conservation value rather than specific features (Moilanen, 2007). We assumed that TRBs with high heterogeneity (various TRB habitats), several species occurrences, and possibly an AES subsidy contract are the most important ones in conservational sense. Also, as we pooled the species data, it no longer represented specific species occurrences but reflected a general distribution of red-listed species dependent on TRBs.

Surveyed TRBs, protected unsurveyed TRBs, complementary habitat sites, and species occurrence sites were used as distinct planning units, because it was more purposeful to remove spatially separate sites rather than single cells from the landscape. We used a hierarchical removal mask to force all surveyed TRBs to the top fraction of the prioritization, thus forming management scenario A in our analysis. To determine subsequent management scenarios we utilized Zonation's hierarchical landscape zoning in which the order of site removal implies the conservational importance of different areas (Moilanen et al., 2011). We identified top-ranked residual unsurveyed TRBs corresponding to area targets within scenarios B–D to produce nested management networks.

We conducted separate analyses with and without landscape connectivity measures. While other feature-specific parameters were kept the same, we added interaction connectivity (Rayfield et al., 2009) by including a positive contribution of protected TRBs and complementary habitats for surveyed TRBs. We ran two connectivity analyses utilizing distribution smoothing with 2 km (according to Arponen et al., 2013) and 5 km mean dispersal distances. To determine whether including connectivity significantly affected the prioritization, we analyzed the rank orders of sites from the prioritizations with Wilcoxon signed rank test in R3.3.0 (R Core Team, 2016).

In ArcGIS, we extracted management scenarios from the prioritization rank map, and further examined their spatial patterns with average nearest-neighbor analyses. As our main interest was to locate the most optimal solution for the expansion of surveyed TRB network regionally, we created generalized prioritization maps, in which each scenario was combined and mapped with a resolution of 10 km × 10 km.

2.4. Assumptions and limitations

There are several assumptions related to our data and the analyses, which affect the interpretation of the results:

1) Surveyed TRB sites are more valuable than unsurveyed ones.

2) Sites within habitat type inventory are more valuable than sites without habitat information.
3) Sites with many TRB habitats are more valuable than sites with only one TRB habitat type.
4) Unmanaged sites retain some value as TRBs despite the level of vegetational changes after abandonment.

We acknowledge that the national data on surveyed TRBs are not up-to-date for each individual site. Also, the AES subsidy contract data do not include all managed TRBs. The database on protected TRBs was formed by merging several different data sets into a collection of all sites with some value as TRBs (Pakkanen et al., 2015; Raatikainen and Raatikainen, 2015). It includes sites where lack of management has launched successional substitution of a TRB habitat by another habitat type, as disturbance-dependent vegetation changes rapidly after management ceases. The database includes also fjell and shore grasslands, where natural disturbances maintain populations of TRB specialists. As a result, all sites within the prioritization may not be in need of active management. Species occurrence data are dependent on sampling effort, and the habitat data are similarly spatially restricted, as only protected TRB sites are covered by habitat type inventory. For the sake of our research questions these assumptions and limitations are not major problems.

3. Results

3.1. Current management status

Subsidized TRB management spread over different TRB categories (Table 2). Altogether 19,225 ha received AES subsidy for TRB management. Of the total subsidized area, 42.8% comprised of unprotected and unsurveyed sites located on private land.

Protected TRBs covered 38.0% of the subsidized area. Among them, surveyed sites were more often managed than unsurveyed sites. Also, there were more managed private than state-owned TRBs.

Despite their substantial total area, unprotected privately-owned surveyed TRBs were rarely managed. They covered 19.2% of the total subsidized area.

3.2. Spatial allocation of TRB management

Accounting for connectivity changed site ranking (Wilcoxon signed rank test, $n = 25.136$, $p < 0.001$ for both 2 km and 5 km scales). Also the connectivity analyses differed from each other ($p = 0.04$). However, conservation performances of prioritization analyses were quite similar (Table 3). We derived management scenarios from the analysis with 2 km connectivity, which had the highest average performance. In each scenario, a fifth of the total area was under AES-funded management. Site pattern in all scenarios was spatially significantly clustered.

Table 2
Management status of traditional rural biotopes in Finland (in hectares and percents) in year 2014. Note that managed TRBs include only sites where management is funded through national agri-environment scheme. For unmanaged sites, private unprotected and unsurveyed sites are excluded, as there is no existing data on them. Original vector data were used in the analysis.

		Managed (ha)	Unmanaged (ha)	Managed (%)
Protected	State-owned surveyed	1122.0	2946.6	27.6
	State-owned unsurveyed	1460.7	14,555.2	9.1
	Private surveyed	1531.2	1739.4	46.8
	Private unsurveyed	3199.9	6468.3	33.1
Unprotected	Private surveyed	3681.8	19,237.2	16.1
	Private unsurveyed	8229.8	N.A.	N.A.
Total (protection status)	Protected	7313.8	25,709.4	22.1
	Unprotected	11,911.5	N.A.	N.A.
Total (survey status)	Surveyed	6335.0	23,923.2	20.9
	Unsurveyed	12,890.4	N.A.	N.A.
Grand total		19,225.4	N.A.	N.A.

Scenario A, which consisted of surveyed TRBs, encompassed 52.4% of the analysis landscape and 0.1% of the total land area of Finland. Areawise the scenario centered on SW Finland and the large river valley close to Swedish border (Fig. 2, A). There were surveyed sites throughout the country, but in Lapland and near the Russian border the spatial distribution was sparse. Protected sites comprised 24.0% of scenario A (Table 3).

The prioritization analysis targeted TRB management especially to Baltic Sea coast, but also other distinct clusters in parts of Southern, Central, and Northern Finland emerged in the results (Fig. 2, B–D). When compared to the current extent of TRB management (Fig. 2, E), the core areas along the western coast were strengthened, and management allocation within Lapland and inland was increased. Along the western coastline the prioritized unsurveyed TRBs were mostly located on protected areas (Fig. 2, F). Inland areas expressed a more fragmented pattern where management was largely targeted according to TRB specialist species occurrences (Fig. 2, G).

3.3. Red-listed vascular plant species specialized in TRBs

Most of the existing occurrences of TRB specialists within the analysis were located on unprotected and unsurveyed sites. Only 3.8% (501 out of 13,038 occurrences) were managed through an AES contract (Table B.1). Surveyed TRBs (scenario A) hosted 1123 occurrences of 58 threatened and 33 near-threatened species. This included 68.4% of all species in the data, but only 8.6% of their occurrences (Fig. 3). Targeting management actions according to scenario B included a total of 122 red-listed species (with 8422 existing occurrences), with a focus on threatened species. Half of scenario B′s additional management effort was allocated to unprotected sites indicated by occurring specialist species (Table 3). Extending management according to scenario C incorporated 127 species (11,668 occurrences). It especially increased management of populations of near-threatened species. Scenario D did not cover any additional species, and the rise in the amount of species occurrences was small (168 additional occurrences).

3.4. TRB habitats on protected areas

The majority of scenario A consisted of sites without specific habitat information, including all unprotected surveyed sites (Table C.1). On protected areas, different TRB habitats were unevenly represented when compared to their total coverages (Fig. 4, A). The pattern was somewhat similar when Natura 2000-habitats were explored (Fig. 4, B). Areal summaries (Tables C.1 and C.2) showed that the most frequent habitats on protected TRBs in scenario A were moist to mesic meadows, wooded pastures, or grazed woodlands, whereas other TRB types were rare.

Scenarios B–D hosted increasing proportions of different TRB habitats (Fig. 4, A and B). Scenario B emphasized habitat rarity and it included the scarcest TRB habitats, except for heaths. Scenario C especially increased the total area of mesic and moist meadows, heaths, and grazed woodlands. Considering Natura 2000 -habitats, scenario C included over 90% of all types other than wooded pastures, coastal meadows, and dry heaths. Scenario D covered nearly all TRB habitats on protected areas. Only moist meadows were left to 68.8% representation. Similarly, coastal meadows were the only Natura 2000 -habitat left under 90% representation within scenario D (exact coverage 87.8%).

4. Discussion

Our results show that the conservational status of TRBs remains ecologically inadequate in Finland. We demonstrated that the overall cover of TRBs managed through an AES contract has decreased to <20.000 ha in ten years (from ca. 24,500 ha in 2005–2007 according to Kemppainen

Table 3
A summary of spatial prioritization from Zonation analysis. Rows 1–3 give conservation performances of different prioritization analyses in terms of average proportion of conservation value remaining within the prioritized landscape of given size. Nested management scenarios were further investigated only for connectivity analysis with 2 km dispersal distance (rows 4–12). Original vector data were used in the calculations instead of raster data from the analysis. However, the coverage of species point occurrences outside of surveyed traditional rural biotopes or protected areas was estimated from rasterized data (cell size 0.25 ha). Currently managed area is derived from agri-environment scheme contracts on TRB management in year 2014. ANN refers to Average Nearest-Neighbor analysis conducted for each scenario.

	Scenario A (surveyed TRBs)	Scenario B (A + 5000 ha)	Scenario C (A + B + 5000 ha)	Scenario D (A + B + C + 5000 ha)
Conservation performance (without connectivity)	0.333	0.719	0.865	0.940
Conservation performance (with 5 km dispersal distance)	0.335	0.722	0.864	0.937
Conservation performance (with 2 km dispersal distance)	0.345	0.727	0.866	0.939
Additional area (ha)	0.0	4362.6	8256.5	12,133.1
Total area within scenario (ha)	30,258.1	34,620.7	38,514.6	42,391.2
Coverage on protected areas (ha)	7258.8	9194.4	12,280.6	16,150.1
Coverage on unprotected areas (ha)	22,999.3	25,426.4	26,234.0	26,241.1
Currently managed area (ha)	6335.0	6740.2	7752.5	8851.7
ANN: observed mean distance (m)	1254.7	926.0	833.8	801.1
ANN: expected mean distance (m)	4311.5	2950.4	2650.0	2587.9
ANN: z-score	−122.2	−175.7	−196.6	−202.8
ANN: *p*-value	<0.001	<0.001	<0.001	<0.001

and Lehtomaa, 2009). In 1950s, TRB cover was over 2.1 million hectares (Raunio et al., 2008). Thus we conclude that after the collapse during late 20th century, the total cover of managed TRBs is further declining. Although our data on the general management status of TRBs were deficient, the change is clear and we doubt that more accurate data would change the interpretation. With such prevalent habitat loss, both the low amount of remaining habitat and the high degree of fragmentation will strongly reduce remaining species richness (Rybicki and

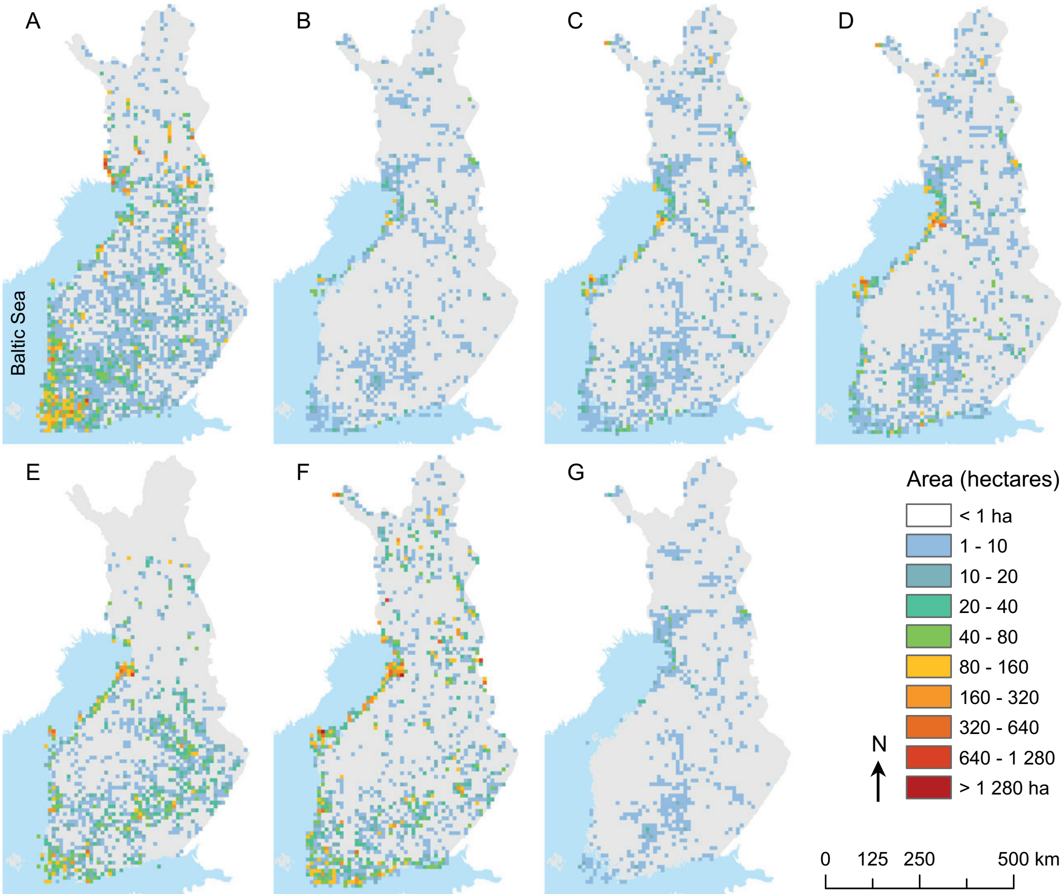

Fig. 2. Distribution of surveyed traditional rural biotopes (management scenario A; panel A) and allocation of cumulative TRB network expansion according to management scenarios B, C, and D (panels B–D, respectively). For comparison, the distributions of currently managed TRBs (according to AES contracts; panel E), protected TRBs (surveyed and unsurveyed; panel F) and TRB-specialist vascular plant species occurrences (panel G) are also shown. Note that the Åland islands were excluded from the analyses.

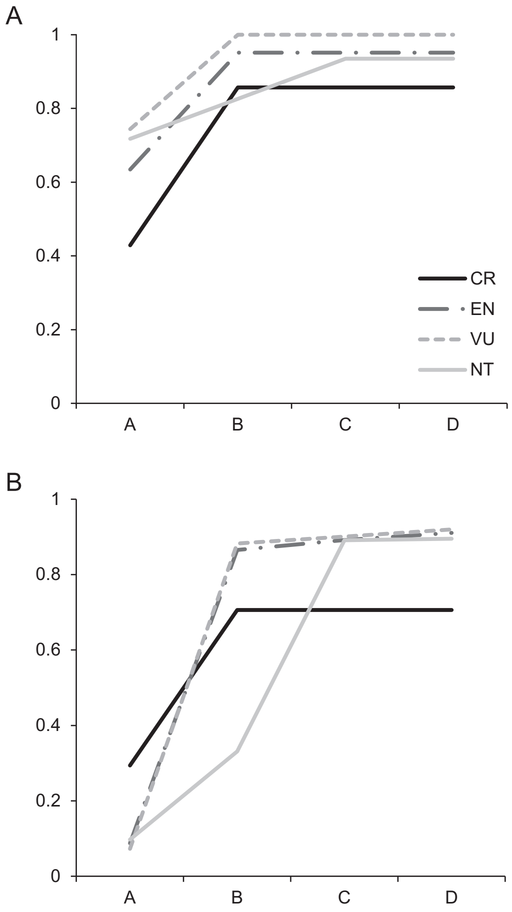

Fig. 3. The proportional increase in the number of specialist vascular plant species (A) and their occurrences (B) according to nested management scenarios (A–D, on x-axis). Curves are drawn according to red-list status: CR: critically endangered; EN: endangered; VU: vulnerable, and NT: near-threatened. The numbers of occurrences per species are summarized in Table B.1.

Hanski, 2013). In the long term, habitat loss and fragmentation also lead to genetic and evolutionary changes in remnant populations of specialized species, often reducing their viability (Hanski, 2011).

We prove that while a majority of remaining conservationally valuable TRBs is unmanaged, over 40% of area under AES management consists of sites whose biological value is not documented. This finding confirms the earlier notion that Finnish authorities have been unsuccessful in targeting TRB management according to the conservational value and connectedness of the sites (Arponen et al., 2013; Kemppainen and Lehtomaa, 2009). AES policies have compensated for management costs without accounting for effects on biodiversity (Arponen et al., 2013). We suggest that these unsurveyed and unprotected sites should be inspected by authorities in order to determine their value as TRBs.

Building a management network that best benefits biodiversity is challenging with limited resources (Kotiaho et al., 2015). If appropriate, reallocation of management funding should be considered. It is essential that future subsidies are systematically directed to sites that either are biologically representative or will develop into such. Targeting management funding spatially in a more optimal manner would increase the effectiveness of TRB management both economically and ecologically (Arponen et al., 2013).

Our spatial prioritization produced management scenarios that reflect the distribution of TRB-related conservation value. In all scenarios, the South–West–West coastal region receives most of the prioritized management effort. Spatial coordination of management actions promotes habitat connectivity and the associated ecological functions, such as population densities, dispersal, and outbreeding (Arponen et al., 2013; Hanski, 2011). Targeting additional TRB management and restoration primarily to the Baltic Sea coast would promote the extent and connectedness of TRB habitats and support species populations' viability. Within this core area, a 30% cover of TRB habitat should be locally pursued in order to maintain a large fraction of specialist species (Hanski, 2011). This target, however, calls for large-scale bio-cultural restoration of abandoned TRBs. The success of TRB restoration, in turn, is dependent on the successional vegetation changes following management abandonment. Remnant species, interactions, and TRB structures compose an ecological memory that makes ecosystem reorganization possible (Bengtsson et al., 2003). Occurrence of TRB specialists makes it possible to discriminate restorable TRBs from sites that are difficult to restore.

According to the prioritization, small clusters of inland sites with red-listed TRB specialist species should be managed in a network-like manner. The observed spatial clustering of prioritized TRBs serves as a good platform for strengthening species' metapopulations. It counteracts the fragmentation effect and enables creation of new high-quality habitat patches via restoration and management reinitiation, therefore relaxing populations' extinction threshold (Eriksson and Kiviniemi, 1998; Rybicki and Hanski, 2013).

Management scenarios B and C would substantially improve the conservational status of TRB-dependent species. Our analysis took into account 133 vascular plants, but it should be noted that there are a vast number of TRB specialists also in other red-listed taxa (Rassi et al., 2010). Majority of these are insects living on dry meadows, especially butterflies and beetles, but unfortunately records on their populations are scattered (Rassi et al., 2010). In addition, bird species breeding on coastal and alluvial meadows have faced population declines due to habitat degradation, and many of them are categorized as threatened (Rassi et al., 2010).

Because of spatial segregation between species occurrences and TRB habitat sites and higher weights given to species data, the prioritization process emphasized species over habitats. However, different TRB habitats became well represented within the largest management scenario (D). Scenario D encompasses nearly all protected sites with TRB habitats of European level conservation interest (Halada et al., 2011). We conclude that the order of scenarios A–D serves as an initiative and a guideline for prioritization of additional TRB management in Finland. Realization of the national target of 60,000 managed hectares of TRBs needs further increase in available resources and their purposeful allocation. Without systematic targeting of field surveys, management planning, and restoration it is impossible to achieve a two- to threefold increase in the total amount of managed area when compared to the current situation.

Our work is the first nation-wide attempt to advance TRB conservation on the basis of ecological functionality instead of administrative categorizations (see Fig. 1 and Table 2). Although surveyed TRBs (scenario A) provided a basis for management network building, we demonstrated the conservational potential of TRB management on unsurveyed sites. Protected and unprotected TRBs, in turn, complement each other by forming habitat networks within the landscape (Bengtsson et al., 2003).

Our suggestions for future work concern effective ways to advance TRB conservation. The systematic assessment presented here is only one part of conservation planning, and its results should be critically evaluated (Knight et al., 2006). Because conservation of TRBs is dependent on collaboration between authorities, landowners, and managers,

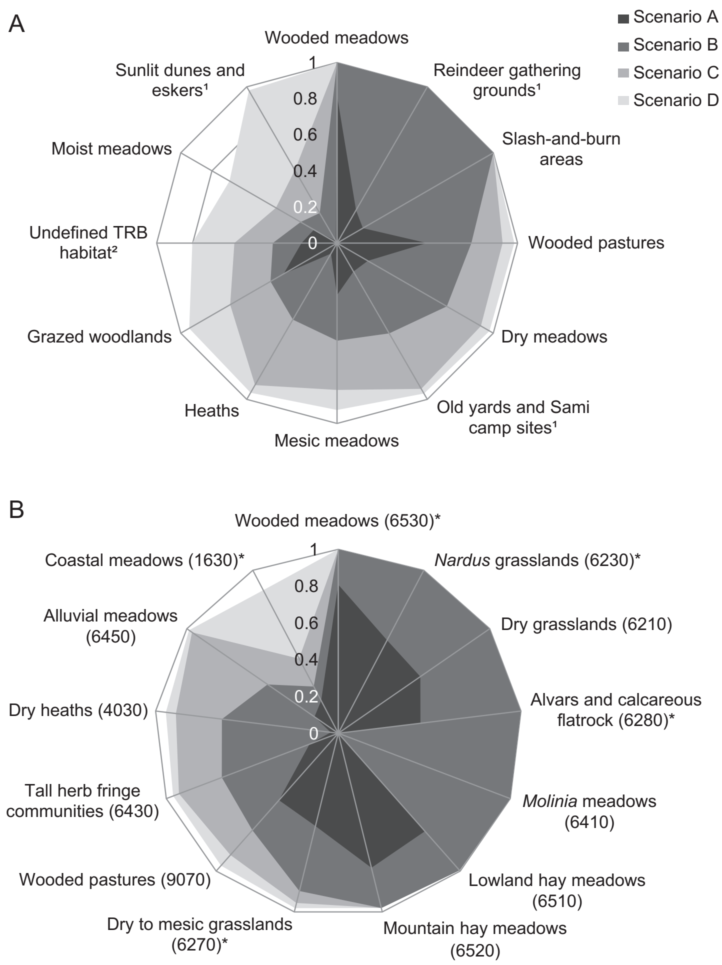

Fig. 4. The increase in the proportion of different habitat types included in the nested management scenarios (A–D; represented in grayscale). Panel A shows upper-level habitat type inventory classes. In panel B more specific Natura 2000 -habitats are depicted (codes in brackets). The numeric data are provided in Tables C.1 and C.2. Only sites located on protected areas are included. [1]: complementary habitats; [2]: sites without habitat information, including all unprotected TRBs; *: priority habitats within the European Union.

we propose adoption of and research on modern systematic conservation strategies, which are based on promoting resilience and cooperation. These include multi-use conservation landscapes (Hanski, 2011), dynamic reserves (Bengtsson et al., 2003), contract-based temporary conservation (Moilanen et al., 2014), and adaptive co-management (Berkes, 2007).

As a final note, we argue that current incoherent governance of TRB conservation hinders promotion of TRB management and more efficient utilization of management funding. This finding is based on an observation we gained through our data collection process. There are several Finnish authorities involved in TRB-related decision-making, none of which carries a clear responsibility on coordinating TRB conservation (Ministry of the Environment, Ministry of Agriculture and Forestry, Finnish Environment Institute, Metsähallitus Parks & Wildlife Finland, Agency for Rural Affairs, and 15 regional ELY centres). Also elsewhere in Europe disintegration to static, isolated, and monosectoral conservation strategies has proven to be inefficient in tackling the biodiversity loss in rural landscapes (Plieninger and Bieling, 2013). Individual organizations and structural institutions shape how the environment is governed, and often impede integrative conservation practice (Bennett et al., 2016). This should be taken into account while our results are implemented.

5. Conclusions

Throughout Europe, traditional rural biotopes and their species are declining. This has caused substantial biodiversity loss. We noticed two main challenges in TRB conservation. On the one hand, the total area under management is too small to safeguard TRB-dependent biodiversity. On the other, management actions are not targeted to sites that are conservationally most important. As a solution, we present a nationwide and spatially explicit management network optimization. It introduces ecological functionality into systematic promotion of TRB management and targeting of management funding, and can be implemented in a step-wise manner.

Allocating additional management and large-scale restoration actions to Baltic Sea coastal region emerges as a strategic starting point. This would create a large, well-connected core area for a Finnish TRB habitat network. In addition, reviving populations of red-listed TRB species requires that smaller inland clusters of TRB sites are managed in order to promote habitat connectivity. However, as current policies are failing in sustaining biodiversity dependent on TRBs, we stress that implementation of targeted TRB management calls for adopting new perspectives on their conservation and governance.

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Supplementary material

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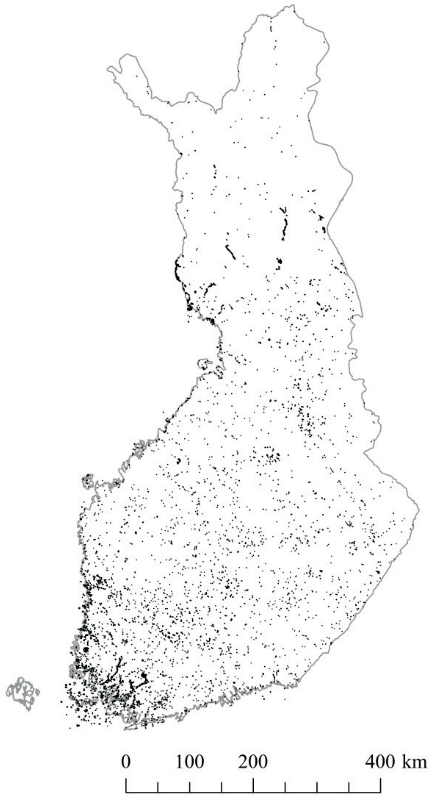
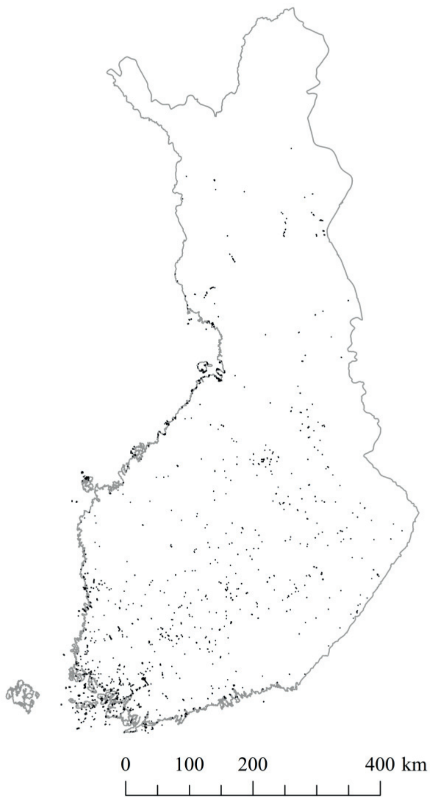
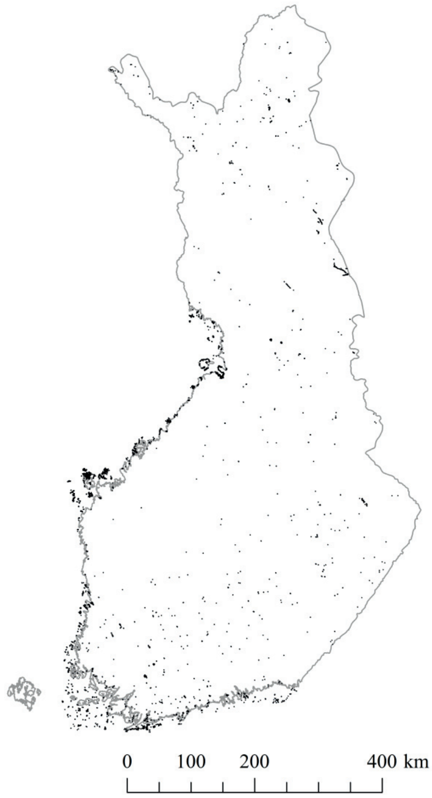
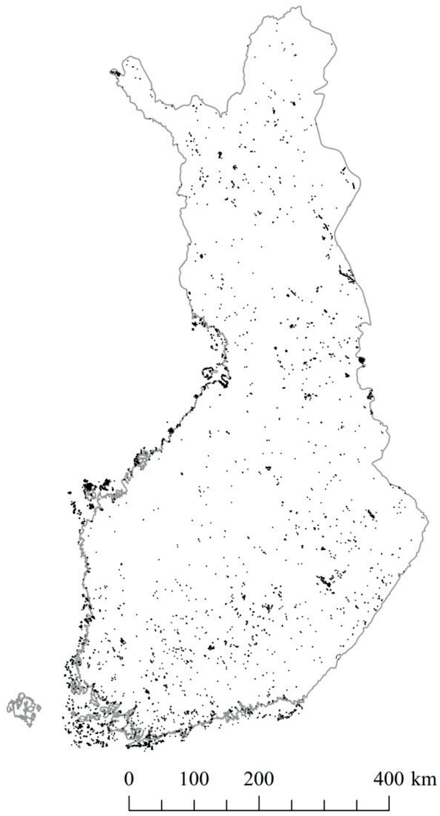
Appendix A.

Original vector data sets used in the analysis:	Snapshot:
1. Surveyed traditional rural biotopes *Type*: Polygon *Description*: Includes site-level geometries and attributes of TRBs detected in field surveys by environmental authorities (regional ELY Centres). Sites are classified as nationally, regionally, and locally valuable (with sub-classes). Also sites classified as restorable are included. Database is compiled and updated by the Finnish Environment Institute. Originally, the national survey on Finnish TRBs was conducted during 1992–1998. It covered 18 640 hectares of TRBs classified as biologically valuable. After that, additional surveys and follow-ups have been done regionally, and the database has been updated accordingly (latest update in summer 2014). The coverage of the data is 30 258 ha. Because the data is combined from several sources, it is heterogeneous and its accuracy varies spatially and temporally. *Extent*: Nationwide data *Date of acquisition*: November 4th 2014. Field data are collected during a time period 1992–2014. *Source*: Finnish Environment Institute *References*: (Kemppainen and Lehtomaa, 2009; Raatikainen, 2009; Vainio et al., 2001)	
2. Agri-environment scheme contract areas *Type*: Polygon *Description*: Plot-level geometries of five-year AES subsidy contracts on TRB management. Only contracts valid on year 2014 were included. The combined coverage of the data is 19 225 ha. *Extent*: Nationwide data *Date of acquisition*: June 19th 2014. Continuously updated. *Source*: Ministry of Agriculture and Forestry	

3. Habitat type inventory
Type: Polygon
Description: Includes plot-level geometries and attributes on habitats located on private protected areas and all state-owned land. Geometries are formed with a high level of accuracy and habitat information is categorized within a multi-level database structure, where general habitat classes are further divided into more detailed Natura 2000 -habitat classes and/or vegetation classes. In total, the inventory covers 4 620 235 ha (including water bodies). For Zonation analysis, geometries without TRB-related attributes were discarded, leaving a data set covering 11 143 ha (depicted in the right-hand map).
Extent: Protected and state-owned areas
Date of acquisition: December 4th 2012 (privately-owned protected areas) and June 11th 2014 (state-owned areas). Inventories started in year 2001, and most of the field work was conducted during 2003–2006. The database is continuously updated.
Source: Metsähallitus, Parks & Wildlife Finland
References: Airaksinen and Karttunen, 2001; Metsähallitus, 2010; Pakkanen et al., 2015; Raatikainen and Raatikainen, 2015



4. Protected traditional rural biotopes
Type: Polygon
Description: Geometries and attributes of surveyed and unsurveyed TRB sites located on protected areas (either private or state-owned) and unprotected state-owned land. Database was compiled from the national survey on TRBs, existing and expired AES contracts on TRB, landscape, and biodiversity management, NTI data, and additional GIS data on managed and unmanaged TRBs on protected areas available during years 2012–2014. The information level of the database varies according to the original data source, and it includes sites whose value as TRBs is unsure. Total coverage of the data is 32 229 ha.
Extent: Protected private and all state-owned areas
Date of acquisition: September 17th 2014.
Source: Metsähallitus, Parks & Wildlife Finland
References: Pakkanen et al., 2015; Raatikainen and Raatikainen, 2015



5. Occurrences of vascular plant species specialized in traditional rural biotopes

Type: Point

Description: Includes existing and historical occurrences of red-listed TRB-dependent vascular plants derived from national Hertta database. Species are listed in table B.1. Species were selected according to their specialization in TRB habitats, and this information was based on the national survey guide for TRBs (Raatikainen, 2009) and the 2010 Red List of Finnish Species (Kalliovirta et al., 2010). Compilation of the data set is described in Pakkanen et al. (2015) and Raatikainen and Raatikainen (2015). Oldest observations of the data are from 19th century herbariums, and in recent years environmental authorities have recorded their red-listed vascular plant observations routinely to the database. Only occurrences with at least 100 meter accuracy were included. Number of currently existing occurrences within the data is 13 038. In addition, there are 3 039 historical occurrences that are categorized as potentially or certainly disappeared.

Extent: Nationwide data

Date of acquisition: June 2nd 2014. Continuously updated.

Source: Finnish Environment Institute

References: Kalliovirta et al., 2010; Ryttäri et al., 2012

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Appendix B.

Table B.1. Red-listed vascular plant species specialized in traditional rural biotopes and a summary of their occurrence data. The red-list statuses are according to Kalliovirta et al. (2010) and the nomenclature follows Hämet-Ahti et al. (1998). Columns 3–5 present the number of existing occurrences of the species on different TRB sites, column 6 lists all occurrences within the data, and column 7 summarizes the number of occurrences located on TRB management subsidy contract areas. Note that surveyed TRBs are equivalent to scenario A in the prioritization analysis. Scenarios B–D, however, allocate additional management to unsurveyed TRB sites without accounting for protection status.

Red List status	Species	Occurrences on surveyed TRBs	on protected, unsurveyed TRBs	on unprotected, unsurveyed TRB habitats	Total n:o of existing occurrences	Managed through AES subsidy
CR	*Anthyllis vulneraria* subsp. *polyphylla*			9	9	
CR	*Armeria maritima* subsp. *intermedia*			7	7	
CR	*Asperula tinctoria*	2			2	
CR	*Botrychium simplex*	4		2	6	2
CR	*Pimpinella major*	4		3	7	
CR	*Thalictrum lucidum*			1	1	
CR	*Veratrum album* subsp. *lobelianum*			2	2	
EN	*Agrimonia pilosa*	12		27	39	
EN	*Anagallis minima*	1		4	5	
EN	*Androsace septentrionalis*			19	19	
EN	*Arctium nemorosum*	14	1	8	23	12
EN	*Armeria maritima* subsp. *elongata*	5	4	6	15	
EN	*Asplenium ruta-muraria*	1	3	88	92	
EN	*Botrychium matricariifolium*	12		18	30	2
EN	*Carex hartmanii*			1	1	
EN	*Carex hostiana*			1	1	
EN	*Carex vulpina*			2	2	
EN	*Carlina biebersteinii*	3	3	28	34	
EN	*Crepis praemorsa*			8	8	
EN	*Epilobium lamyi*	1		5	6	
EN	*Epipactis palustris*			18	18	
EN	*Euphrasia micrantha*			1	1	
EN	*Euphrasia rostkoviana* subsp. *fennica*	4		36	40	
EN	*Galium saxatile*	7		6	13	
EN	*Gentianella amarella*	12	2	149	163	9
EN	*Gentianella campestris*	28	2	56	86	9
EN	*Gentianella uliginosa*	4			4	3
EN	*Hippuris tetraphylla*	11	103	88	202	35
EN	*Lithospermum arvense*	7	1	26	34	
EN	*Lonicera caerulea*	1	19	38	58	
EN	*Malaxis monophyllos*	1	5	75	81	
EN	*Ophrys insectifera*			3	3	
EN	*Orchis militaris*			3	3	
EN	*Persicaria foliosa*	13	6	266	285	3
EN	*Potentilla anglica*	11	2	10	23	9
EN	*Potentilla tabernaemontani*			1	1	
EN	*Primula stricta*	1		189	190	
EN	*Pulsatilla patens*		2	262	264	
EN	*Rosa sherardii*	4			4	2
EN	*Sagina maritima*	4	1	6	11	1
EN	*Salicornia europaea*	3	18	6	27	18
EN	*Samolus valerandi*			27	27	
EN	*Saxifraga adscendens*	5	3	39	47	
EN	*Scleranthus perennis*			5	5	

Red List status	Species	Occurrences on surveyed TRBs	on protected, unsurveyed TRBs	on unprotected, unsurveyed TRB habitats	Total n:o of existing occurrences	Managed through AES subsidy
EN	*Stellaria crassifolia* var. *minor*	1		3	4	1
EN	*Vicia cassubica*			6	6	
EN	*Viola persicifolia*	2		29	31	1
EN	*Viola uliginosa*			5	5	
VU	*Alchemilla hirsuticaulis*	1		5	6	
VU	*Antennaria nordhageniana*			15	15	
VU	*Antennaria porsildii*		1	32	33	
VU	*Botrychium boreale*	29	21	200	250	12
VU	*Botrychium lanceolatum*	27	10	168	205	7
VU	*Campanula cervicaria*	14	17	487	518	3
VU	*Carex caryophyllea*	8		22	30	
VU	*Carex pulicaris*			1	1	
VU	*Carex viridula* var. *bergrothii*	1	1	108	110	
VU	*Carlina vulgaris*		1	1	2	
VU	*Cirsium oleraceum*			2	2	
VU	*Crassula aquatica*	5	9	144	158	4
VU	*Crataegus monogyna*	7	3	4	14	6
VU	*Crataegus rhipidophylla*	6	7	10	23	
VU	*Dactylorhiza incarnata* subsp. *cruenta*	13	30	318	361	11
VU	*Dactylorhiza incarnata* subsp. *incarnata*	5	17	1 241	1 263	3
VU	*Dactylorhiza traunsteineri*	1	4	395	400	
VU	*Drosera intermedia*			67	67	
VU	*Elymus fibrosus*	7	10	77	94	3
VU	*Epipactis atrorubens*		1	82	83	
VU	*Erigeron acris* subsp. *decoloratus*	3	6	32	41	
VU	*Eriophorum brachyantherum*	1		105	106	
VU	*Fragaria viridis*	6		1	7	6
VU	*Galium verum*	28	2	77	107	9
VU	*Gymnadenia conopsea* var. *conopsea*	43	4	136	183	12
VU	*Gypsophila muralis*			32	32	
VU	*Leersia oryzoides*	2		78	80	
VU	*Lythrum portula*			23	23	
VU	*Malus sylvestris*	34	12	65	111	19
VU	*Melampyrum arvense*	2	1	5	8	1
VU	*Melampyrum cristatum*	19		10	29	12
VU	*Ononis arvensis*		2	13	15	
VU	*Polygala amarella*	11		8	19	10
VU	*Polygala vulgaris*	7		10	17	1
VU	*Potentilla neumanniana*	26		2	28	23
VU	*Primula nutans* subsp. *finmarchica*	67	165	530	762	84
VU	*Sorbus intermedia*	3		2	5	2
VU	*Thalictrum simplex* subsp. *simplex*	26		39	65	8
VU	*Ulmus laevis*	5	2	292	299	1
NT	*Ajuga pyramidalis*	2		8	10	1
NT	*Alchemilla samuelssonii*			3	3	
NT	*Allium schoenoprasum* subsp. *alpinum*	3	1	5	9	
NT	*Allium ursinum*	1	4	7	12	
NT	*Anchusa officinalis*	3		7	10	
NT	*Antennaria dioica*	18	21	260	299	1
NT	*Antennaria villifera*			11	11	
NT	*Anthyllis vulneraria* subsp. *lapponica*			62	62	
NT	*Blysmus rufus*	7			7	2
NT	*Botrychium lunaria*	169	74	585	828	50
NT	*Botrychium multifidum*	103	26	485	614	26
NT	*Carex acutiformis*			15	15	

Red List status	Species	Occurrences on surveyed TRBs	on protected, unsurveyed TRBs	on unprotected, unsurveyed TRB habitats	Total n:o of existing occurrences	Managed through AES subsidy
NT	*Carex atherodes*	8	1	66	75	2
NT	*Carex glareosa*	5			5	2
NT	*Carex paleacea*		1	1	2	
NT	*Carex rhynchophysa*			14	14	
NT	*Carex riparia*		1	45	46	1
NT	*Catabrosa aquatica*	11	5	133	149	8
NT	*Cerastium glutinosum*	5		1	6	3
NT	*Cynoglossum officinale*			10	10	
NT	*Cypripedium calceolus*	1	17	1 565	1 583	1
NT	*Dactylorhiza fuchsii*	2	1	63	66	
NT	*Dactylorhiza sambucina*	14	4	25	43	3
NT	*Dianthus deltoides*	64	13	339	416	21
NT	*Draba muralis*	13		3	16	8
NT	*Euphrasia bottnica*	3	2	6	11	2
NT	*Geranium bohemicum*	2		19	21	
NT	*Helianthemum nummularium*	2		2	4	1
NT	*Leontodon hispidus*	3	1	17	21	
NT	*Melica picta*	1		1	2	
NT	*Mentha aquatica* var. *litoralis*	1		1	2	
NT	*Myosotis nemorosa*	26		55	81	3
NT	*Nardus stricta*	18	5	106	129	4
NT	*Orchis mascula*			2	2	
NT	*Phleum phleoides*			1	1	
NT	*Phleum pratense* subsp. *serotinum*	2		1	3	
NT	*Prunus spinosa*			3	3	
NT	*Sesleria caerulea*	5			5	5
NT	*Stellaria fennica*	4	1	118	123	
NT	*Thalictrum minus* subsp. *kemense*	6		24	30	
NT	*Thymus serpyllum* subsp. *serpyllum*		1	332	333	
NT	*Trifolium aureum*	5	3	118	126	1
NT	*Trifolium fragiferum*	4		1	5	4
NT	*Trifolium montanum*	2		1	3	
NT	*Trifolium spadiceum*	25		279	304	8
NT	*Valerianella locusta*			1	1	
	Total:	**1 123**	**683**	**11 232**	**13 038**	**501**

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Appendix C.

Table C.1. Cumulative cover of different habitat types located on prioritized sites included in the nested management scenarios (A–D). In addition, total coverage of each habitat type within the analysis is given. Note that areas are derived from rasterized data, which somewhat overestimates total coverages. Due to generalization into 50 × 50 m cell size, the covers of different habitat classes overlap. The data are represented proportionally in Fig. 4A. Habitat data were available only from protected sites covered by habitat type inventory. All sites without habitat information, including all unprotected sites, are classified as undefined TRB habitat.

	Scenario A (surveyed TRBs)	Scenario B (incl. A)	Scenario C (incl. A and B)	Scenario D (incl. A, B, and C)	Total coverage (ha)
Heaths	101.2	728.9	1 352.1	1 425.0	1 487.5
Dry meadows	139.6	497.4	651.8	690.8	708.5
Mesic meadows	549.0	1 031.3	1 551.7	1 763.3	1 906.3
Moist meadows	1 318.7	2 076.0	3 483.8	6 130.1	8 910.0
Wooded meadows	43.8	53.8	53.8	53.8	53.8
Wooded pastures	451.0	675.2	832.2	891.2	907.5
Grazed woodlands	629.6	784.3	1 259.2	1 741.6	1 841.0
Slash-and-burn areas	7.8	47.0	47.0	47.0	47.0
Old traditional reindeer gathering grounds	8.6	40.8	40.8	40.8	40.8
Old traditional yards and Sami camp sites	54.8	174.0	280.8	289.9	301.0
Dry sandy sunlit dunes and eskers	11.6	158.5	385.5	806.5	825.5
Undefined TRB habitat	11 920.2	21 541.0	34 429.3	48 527.8	60 508.5

Table C.2. Cumulative cover of Natura 2000 -habitats located on prioritized sites included in the nested management scenarios (A–D), and total coverage of each habitat type within the data. Note that areas are derived from rasterized data, which somewhat overestimates total coverages. Due to generalization into 50 × 50 m cell size, the covers of different habitat classes overlap. Habitats marked with an asterisk (*) are classified as priority habitats within the European Union. The data are represented in Fig. 4B. Only sites located on protected areas are included.

	Scenario A (surveyed TRBs)	Scenario B (incl. A)	Scenario C (incl. A and B)	Scenario D (incl. A, B, and C)	Total coverage (ha)
Boreal Baltic coastal meadows (1630) *	975.1	1 399.3	2 233.0	4 280.7	4 875.5
European dry heaths (4030)	43.1	670.0	935.0	992.9	1 051.8
Semi-natural dry grasslands and scrubland facies on calcareous substrates (6210)	3.3	6.0	6.0	6.0	6.0
Species-rich *Nardus* grasslands on siliceous substrates (6230)*	1.0	1.8	1.8	1.8	1.8
Fennoscandian lowland species-rich dry to mesic grasslands (6270)*	232.5	395.6	425.6	438.6	448.0
Nordic alvar and precambrian calcareous flatrock (6280)*	6.8	15.0	15.0	15.0	15.0
Molinia meadows on calcareous, peaty or clayey-silt-laden soils (6410)	0.0	0.3	0.3	0.3	0.3
Hydrophilous tall herb fringe communities (6430)	51.2	207.7	284.1	294.5	306.8
Northern boreal alluvial meadows (6450)	153.3	455.9	943.1	962.6	976.3
Lowland hay meadows (6510)	33.8	47.3	47.3	47.3	47.5
Mountain hay meadows (6520)	17.5	22.7	22.7	22.7	23.3
Fennoscandian wooded meadows (6530)*	29.5	36.5	36.5	36.5	36.5
Fennoscandian wooded pastures (9070)	483.4	700.3	879.4	956.0	994.8

IV

CURRENT AGRI-ENVIRONMENTAL POLICIES DISMISS VARIED PERCEPTIONS AND DISCOURSES ON MANAGEMENT OF TRADITIONAL RURAL BIOTOPES

by

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Current agri-environmental policies dismiss varied perceptions and discourses on management of traditional rural biotopes

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ABSTRACT

Traditional rural biotopes (TRBs) are threatened habitats that host significant biodiversity and several ecosystem services, and depend on active management such as low-intensity grazing. The current study explores private landowners' decision-making on TRB management and abandonment within a social-ecological system framework. We provide insight into supporting resilience of TRB systems in the face of agricultural modernization. Using a mixed methods approach with content analysis and Q analysis, we demonstrate that TRB management fosters cultural, biological, aesthetic, and utilitarian values. These are reflected in different ways through conservationist's, profit-oriented farmer's, landscape manager's, and landscape admirer's discourses on TRB management. Overall, management reinforces landowners' place attachment, and reflects an approach to landscapes as spatial representations of cultural heritage and identity over multiple generations. Landowners consider TRB pasturage and its social-ecological outcomes motivating and rewarding. Giving up grazing cattle and perceived bureaucracy of national agri-environment scheme contribute to TRB abandonment. Landowners point out that current policies detach TRB management from what is seen as "regular agriculture", and the focus on monetary compensation bypasses the multiple values tied to TRB management. Based on our results, we suggest that promoting TRBs requires reconfiguring the current arrangement of remedial management payments and adopting a more participatory governance approach. Locally, resilience of TRB systems relies on the connections between landowners and landscapes that foster sense of place and landscape identity, which can be supported by knowledge sharing and collaborative grazing efforts among landowners.

1. Introduction

Agricultural intensification threatens maintenance of traditional farming systems, which have historically shaped a variety of rural landscapes and fostered a significant amount of biodiversity and cultural heritage in Europe (Benton et al., 2003; Plieninger et al., 2014, 2006). Consequently, there is increasing public expenditure and scientific interest in conservation of farmland biodiversity (Batáry et al., 2015; de Snoo et al., 2013; Kleijn and Sutherland, 2003). Of special conservation concern are semi-natural habitats managed by low-intensity grazing or mowing, such as different types of meadows and wood-pastures, which support several threatened species (Halada et al., 2011).

In Finland, semi-natural grasslands and wood-pastures are collectively referred to as traditional rural biotopes (TRBs). TRBs are defined as culturally influenced natural habitat complexes that are part of a traditional landscape formed through archaic rural livelihoods (Ministry of the Environment, 1992). This official definition acknowledges how ecological and social factors are intertwined in the concept of TRBs, depicting them as social-ecological systems. Yet, in practice, TRBs are detected and evaluated mainly based on ecological qualities, particularly specific vascular plant species assemblages surveyed in the field (Pykälä et al., 1994). As a result, TRBs are generally perceived through ecological patterns and processes as species-rich semi-natural habitats maintained by human-induced intermediate disturbances (e.g., Raunio et al., 2008). Ecocentric perspectives such as this permeate the scientific research concerning European agri-environmental policies targeting biodiversity conservation (de Snoo et al., 2013). Agri-environmental policies to enhance biodiversity and landscape quality are unsustainable when social-ecological interactions are unnoticed, simplified, or disregarded (de Snoo et al., 2013; Pelosi et al., 2010). Thus, a more pluralistic offset that takes social aspects into account would benefit conservation policies, management actions, and ecological outcomes (Bennett, 2016).

Despite its importance, incorporating social science into farmland biodiversity conservation efforts is challenging. The multiplicity and

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complexity of agricultural social-ecological systems makes their management an elusive task (Berkes et al., 2003; Cash et al., 2006; Pelosi et al., 2010). Since 1980s, member states of European Union started to launch agri-environmental schemes (AESs) with the principle of paying farmers for undertaking desirable conservation-oriented actions. Although the AESs aim for supporting environmentally-friendly and less intensive farming as a livelihood (Clark et al., 1997; Robinson, 2005), their benefit for biodiversity has been questioned on several occasions (Batáry et al., 2015; Kleijn and Sutherland, 2003; Robinson, 1991). Several studies have noted that if the causes of agri-environmental problems are not well understood and AESs are therefore not appropriately designed, their implementation can be ineffective or have unintended effects (Uthes and Matzdorf, 2013).

Despite their "patchy" effectiveness, AESs have become the main tool to conserve farmland biodiversity throughout Europe (Batáry et al., 2015; Kleijn and Sutherland, 2003; Uthes and Matzdorf, 2013). Due to the voluntariness of AESs, a number of studies have explored farmers' motivations to adopt the schemes. Such information is usually derived from interviews or surveys targeted to farmers either participating in AESs or not (Uthes and Matzdorf, 2013). Factors explaining AES uptake include age, likelihood of having a successor, and sufficiency of financial incentives (Prager et al., 2012; Uthes and Matzdorf, 2013); also ease of management (Morris, 2006), interest in wildlife (Herzon and Mikk, 2007; Matzdorf and Lorenz, 2010), and a will to maintain landscape aesthetics (Birge and Herzon, 2014) are important motivators. Additionally, these findings could benefit from a holistic approach that aims to synthesize a range of issues affecting farm-level decision-making. Furthermore, as studies specifically target farmers, they rarely include other landowners whose land-use decisions are undeniably important in conserving biodiversity.

One approach to better understand issues on conservation of farmland biodiversity is to study the renewal of rural social-ecological systems such as TRBs. Social-ecological systems are dynamic and deal with change; they sustain themselves as a function of the system's adaptive capacity (Berkes et al., 2003). A key property of this process is resilience: the capacity of a social-ecological system to remain within the same regime, essentially maintaining its structure and functions, despite the external perturbations or other stressors disturbing the system (Holling, 1973; Resilience Alliance, 2017). Given that the evolution of European Union's Common Agricultural Policy (CAP) has been guided by the principles of ensuring rural stability by guaranteeing occupancy of agricultural land and emphasizing the importance of small-scale and family farming (Clark et al., 1997), a resilience-oriented farm-level approach to AESs seems justified. Here a farm is seen as a social-ecological system; stressors are externally imposed ecological, social, or economic changes affecting farming, such as climate change or fluctuations in market prices; the ability of the farm enterprise to react to these changes through modifying but not giving up farm production reflects the adaptive capacity; and regimes are relatively stable combinations of farming practices that form the basis of the farmer's livelihood through alternative land uses. The role of AESs in this context is to build social-ecological resilience by supporting environmentally and socially sustainable farming practices.

Social-ecological resilience is particularly important for social groups that are dependent on ecological and environmental resources for their livelihoods (Adger, 2000). These include farmers and landowners managing TRBs. Their decisions on whether to continue TRB management or to abandon it have a direct connection to TRB conservation. Given the urgent need to increase the number of managed TRBs in order to safeguard the biodiversity dependent on them (Heikkinen, 2007; Raatikainen et al., 2017), knowledge on the resilience of TRB systems within contemporary agricultural context needs to be gathered.

In this paper, we apply a social-ecological approach to TRBs by focusing on two phenomena that reflect decision-making on TRB management on different levels: subjective perceptions and communal discourses. Bennett (2016) defines "perception" as "the way an individual observes, understands, interprets, and evaluates a referent object, action, experience, individual, policy, or outcome", and states that studying perceptions provide insight and indispensable evidence for monitoring, evaluating, and adapting conservation programs and policies. Although perceptions are subjective, they are to some extent socially influenced and thus share commonality, and are further reflected in socially shared discourses (Barry and Proops, 1999). Discourses are "structured ways of representation that evoke particular understandings and may subsequently enable particular types of actions to be envisaged" (Hugé et al., 2013). They guide practices and reflect underlying values (Benitez-Capistros et al., 2016; Hugé et al., 2013). Understanding and contextualization of discourses is a prerequisite for evaluating the social acceptability and sustainability of environmental policies (Barry and Proops, 1999; Benitez-Capistros et al., 2016; Hugé et al., 2013). Long-term effectiveness of conservation actions is ultimately enabled through local support (Bennett, 2016; de Snoo et al., 2013), and together perceptions and discourses affect the design, implementation, and outcomes of different environmental policies.

The paper is structured as follows. First, based on literature, we present how TRBs can be incorporated into a social-ecological system framework. Second, we empirically explore the resilience of TRB systems through landowners' perceptions and discourses on TRB management. Here we aim to understand the landowners' motivations for TRB management or abandonment, and investigate the role of the national AES in TRB conservation. Our driving research question is: What kinds of social-ecological factors underlie maintenance of TRBs in the context of current Finnish agriculture? We hypothesize that landowners' personal values, feeling of place attachment, and knowledge of land-use history are more important to TRB conservation than agri-environmental policies. Based on our findings, we interpret emerging new meanings related to TRBs and discuss how these fit into current governance practices. Ultimately we argue TRB management will benefit from resilience-oriented policies targeting key variables that are attendant to landowners' decision-making strategies for successful TRB management.

2. Conceptualizing management of traditional rural biotopes as a social-ecological system

Contemporary TRB management has its roots in practices of traditional 19th century subsistence farming, where cattle husbandry was based on natural resources derived from the landscape surrounding the farm (Soininen, 1974). Although social-ecological systems such as this are inherently complex, their composite parts can be identified for structural analyses (Ostrom, 2007). This conceptual partitioning is important for achieving a better understanding of the systems and developing effective policies to improve their performance (Ostrom, 2007). In the following, factors relating to contemporary TRB management are categorized into four social-ecological subsystems: resource system, resource units, governance system, and actors (Ostrom, 2009, 2007). Because of conceptual and historical similarities, we parallel TRBs with Pan-European semi-natural grasslands and wood-pastures, but specify aspects particular to Finland within the text.

TRBs are special types of agricultural resource systems that are tied to long-term, low-intensity cattle husbandry. They share four key unifying characteristics: 1) dependence on mowing or low-intensity grazing (Mládková et al., 2015; Pykälä, 2000), often accompanied by other multifunctional actions such as coppicing, pollarding, and pruning (Hartel and Plieninger, 2014); 2) long-term usage as unfertilized pastures or meadows, resulting in nutrient impoverishment (Kumm, 2003; Mládková et al., 2015; Pykälä, 2000); 3) exceptional biodiversity (Halada et al., 2011; Pykälä, 2000); and 4) decline in contiguous coverage due to agricultural modernization (Plieninger et al., 2006; Raunio et al., 2008).

The resource units derived from TRBs are various. In Finland, TRBs have traditionally been used to collect fodder for livestock; dung from pastures to fertilize fields; and wood from wood-pastures (Ministry of the Environment, 1992). Many of these old land-use practices have nearly vanished. Still, grazed TRBs provide pasture, and the importance of quality meat production on TRBs is growing (Birge and Herzon, 2014). Across Europe, TRBs also provide a multitude of non-agricultural ecosystem services such as cultural heritage and scenic beauty (Birge and Fred, 2011; Birge and Herzon, 2014; Plieninger et al., 2015a; Stenseke, 2006; Sutcliffe et al., 2013). Yet, the most material benefit to Finnish TRB managers is the monetary compensation of management costs paid for via national AES (hereafter "payment"). The AES promotes voluntary environmentally-friendly agriculture by incentivizing farmers for providing desired environmental benefits, which are regularly inspected (Armsworth et al., 2012; Kaljonen, 2006). In year 2012, Finnish farmers received a total of 8.4 million euros of payments for covering costs of TRB management, comprising 2.4% of the total AES expenditure (Aakkula and Leppänen, 2014).

In Finland, management of TRBs is the single most effective AES measure in terms of promoting biodiversity (Aakkula and Leppänen, 2014; Grönroos et al., 2007; Kuussaari et al., 2004). As a consequence, the governance, funding, and advisory services on TRB management are arranged around the implementation of the national AES.

The emergence of an AES-based governance system on TRB management has introduced a range of new actors that are involved in TRB-related decision-making. As agricultural issues are central for national politics, politicians play an important role in development and implementation of agri-environmental policies. Tasks of targeting and channeling management funding to TRB managers is decentralized to several officers working in Finnish authorities, which include two ministries, three national agencies, and 15 regional administrative organizations (Raatikainen et al., 2017). A number of NGO employees and volunteers provide assistance for managers in AES-related issues, e.g. by giving advice on payment application process and supervising farmers' interests; or they may themselves conduct TRB management. In addition, there are a variety of actors with other connections to TRB management, such as academic researchers, consumers, and local community members.

Yet key actors in TRB management are farmers and landowners who may or may not actively manage their land. Increasing costs in agricultural inputs, volatile markets, and ageing of farmers drive collapses of traditional farming systems, leading to TRB abandonment (Beilin et al., 2014). However, individual-level idealism, tradition, and landscape aesthetics counteract abandonment (Birge and Herzon, 2014; Kumm, 2003; Stenseke, 2006). Finnish farmers appreciate agricultural heritage and cultural landscapes, and reflect these values through childhood memories related to TRBs (Kaljonen, 2008).

As centres of value, TRBs foster and reflect specific identities. For managers, TRB management often invokes a strong sense of place, defined as a feeling of belonging that results from an experienced reciprocal linkage between places and people, mediated by personal active sensory participation with a place (Howard et al., 2013). For communities and their members, TRBs contribute to landscape identity, i.e. the perceived uniqueness of a place, where "perceiving" is both a personal and social matter, and "uniqueness" is based on the interaction between spatial and social factors (Stobbelaar and Pedroli, 2011). Nationally, because of the importance of agrarian history for Finnish national identity, TRBs are an essential part of Finnish cultural heritage (Ministry of the Environment, 1992). Thus TRB management contributes to the evolution of place-related identity, which includes an affective bond to the place and cognitive representations giving the place a special character or entity (Loupa Ramos et al., 2016). Sense of place, landscape identity, and cultural heritage develop from the interaction between people and their environment, and we argue they have an important role in maintenance of TRBs. The focus of our study is the analysis of the practical aspect of these interactions.

Although deriving key social-ecological components offers valuable information for policy-making, Ostrom's framework's approach to social-ecological systems is structural, not interpretive. Therefore complementing it with discourse analysis gives insight into how people themselves view the system in question. Discourse analysis is able to reveal underlying patterns or meanings in people's beliefs and opinions with a focus on verbal interaction, dialogue, and practices in which these shared meanings are embedded (Creswell, 2009; Hugé et al., 2013; Webler et al., 2009). Thus it provides policy-makers a better understanding on how to apply the refined social-ecological knowledge.

3. Material and methods

3.1. Overview on methodology

This paper uses a social constructivist framing to explore discourses and perceptions, rather than ascribing to fixed categories or ideas (Creswell, 2009). A mixed methods approach was used to gather complementary qualitative and quantitative data sets. We chose a case study approach to collect data, and interviewed TRB landowners to study the relationship between policy and practice. We limited the study to a selection of TRB sites within the province of Central Finland, but the landowners of the sites did not have to live in the region. In both Central Finland and Finland in general, urbanization has created a situation where non-farming urban residents increasingly own rural family estates and TRB sites located on them, and this group was of special interest for us. Including both farmers, and non-farmers detached from farming livelihoods and everyday living environments, allowed us to examine a broader diversity of cultural and social meaning related to TRBs and TRB management.

We analyzed interview transcripts qualitatively in two phases: firstly in inductive and secondly in a deductive manner (Elo and Kyngäs, 2008). Specific perceptions that emerged from the interviews were analyzed first, giving initial insight for different social-ecological aspects of TRB management. In order to attain a more coherent interpretation, we next utilized Elinor Ostrom's social-ecological system framework (McGinnis and Ostrom, 2014; Ostrom, 2009, 2007). In this deductive part of our analysis we related the initial perceptions to Ostrom's holistic framework, and studied their connections. We chose this framework because it was developed for analyzing social-ecological systems from a sustainability perspective, meant to directly inform policy development (Ostrom, 2009). The framework functions as a diagnostic tool for analyses on how attributes of social-ecological systems jointly affect and are indirectly affected by interactions and outcomes achieved at a particular time and place (Ostrom, 2009, 2007). The framework also relates social-ecological systems to larger socio-economic, political, and ecological settings, thus enabling matching governance arrangements to specific problems embedded in a social-ecological context (Ostrom, 2007).

To better contextualize our qualitative findings, we derived shared discourses, interpreted as different ways of explaining, reasoning, and valuing TRB management. We gathered data on how landowners agreed on general statements related to TRB management, and analyzed the data using Q methodology, a quantitative method to assess subjectivity (Stephenson, 1935).

Finally, we interrelated the emergent perceptions, social-ecological system properties, and discourses to each other in order to examine how landowners consider and process their decision-making on TRB management or abandonment in relation to current agri-environmental policies.

3.2. Data collection

The interviews were conducted in January and February 2015 by first author. Variation was incorporated in initial purposive sampling of TRB sites by 1) dispersing the sites spatially within Central Finland, 2) choosing sites surrounded by variable coverage of agricultural

Table 1
Characteristics of the participating landowners. For those not living on the TRB farm, "residence" refers to whether they live in a rural or urban location, or both. "Highest education" level ranges from 1 = primary school to high school, 2 = professional training, 3 = lower degree in polytechnic or university, 4 = higher degree in polytechnic or university. "Subsidy familiarity" refers specifically to TRB management subsidies. "TRB status" is defined according to TRB management practices (grazing or mowing); abandoned sites are typically used for silviculture. Note that some TRB sites are not managed by their landowners.

ID	Gender	Age	Residence	Highest Education	Active farmer	TRB manager	Subsidy familiarity	TRB status
1	female	62	Farm	4	yes	yes	received	managed
2	female	58	Farm	2	yes	yes	knows	managed
3	male	67	Farm	1	yes	yes	received	managed
4	female	23	Farm	3	yes	yes	knows	managed
5	male	24	Farm	2	yes	yes	knows	managed
6	female	62	Farm	2	yes	yes	knows	managed
7	male	80	Farm	1	no	no	unfamiliar	abandoned
8	female	53	Urban	2	no	yes	unfamiliar	managed
9	female	52	Rural & urban	1	no	no	received	abandoned
10	male	55	Rural & urban	1	no	no	received	abandoned
11	male	69	Farm	1	yes	yes	received	managed
12	male	35	Farm	2	yes	no	knows	abandoned
13	female	60	Farm	2	no	yes	received	managed
14	female	56	Farm	3	yes	yes	received	managed
15	male	46	Farm	4	no	yes	received	managed
16	male	46	Farm	2	yes	no	received	abandoned
17	female	42	Urban	4	yes	no	knows	managed
18	female	38	Urban	3	yes	no	knows	managed
19	male	44	Urban	4	yes	yes	knows	managed
20	male	75	Farm	2	yes	yes	received	managed

landscape, and 3) contacting landowners with a range of backgrounds. A total of 26 landowners were contacted, and from them, 20 landowners of 14 TRB sites volunteered to participate in the study. Four landowners refused to participate referring to their old age; the other two did not provide any specific reason for their refusal. Six participants had met the interviewer at least once on an earlier occasion. Participants were grouped into "managers" or "non-managers" based on whether they actively managed their TRB site themselves (Table 1). This categorization reflects decisions on whether to continue or to abandon TRB management. Site locations and surrounding landscape structure are shown in Fig. 1.

The landowners chose the location for the interview, which was usually in their home. If the farm had more than one landowner that was responsible for land-use decisions, all landowners were interviewed together. Note that here and henceforth we refer to landowner's property generally as "farm", even though farming may have ended, or the landowner may have rented the fields out and would not farm him/herself. The interviews were audiorecorded with landowners' permission.

The first part of the interview included a semi-structured discussion around three themes relating to the owned TRB property: Farm and its history, change in surrounding landscape, and the TRB site itself. The second part of the interview included Q-sorting, where landowners individually ranked a curated selection of TRB-related statements according to their level of agreement or disagreement with each statement. Details of this procedure are given in section 3.4 (Q analysis).

Thirty seven hours 45 min of interview data (resulting in 526 pages of transcripts) were transcribed verbatim using WAVPedal 7 (Programmers' Consortium, Vienna, VA).

3.3. Content analysis

Content analysis of interviews explored landowners' personal perceptions on TRB management or abandonment. Data handling, coding, and documentation of the analysis were done in ATLAS.ti (version 7.5.7). Ostrom's social-ecological system framework (*sensu* McGinnis and Ostrom, 2014) was used in structuring the coding scheme used in the analysis, thus directly connecting the interview data to the social-ecological system theory.

In initial stages of the analysis, transcribed data were read through and emerging, repetitive meanings within it were detected. These meanings provided the foundation for 40 codes, which were then used to code all data accordingly (this is intended to be a somewhat circular process to draw out the underlying meaning and discourses in textual data). The codes were then grouped into five code families: management decision-making and practices, knowledge on land-use history, agri-environment scheme, sense of place, and landowner subjectivities.

Code- and code family − based queries were run in order to identify specific sections of relevant text. When purposeful, these queries were run separately for managers and non-managers in order to detect differences in the perceptions of these two groups. After each query, resulting quotations were read through and notes written to a memo.

In order to detect key social-ecological variables, we paralleled our coding scheme with Ostrom's social-ecological system framework, which was outlined in section 2 (Conceptualizing management of traditional rural biotopes as a social-ecological system). In addition to the framework's subsystems (actors, resource system, resource units, governance system), its main components include action situations and outcomes, related ecosystems, and social, economic, and political settings (Ostrom, 2009, 2007). All of these include second-tier variables that affect the patterns of social-ecological interactions and outcomes (McGinnis and Ostrom, 2014). In our analysis, each code was defined as relating to one social-ecological component and a corresponding second-tier variable was sought for. For managers and non-managers separately, we detected ten most often co-occurring codes within the code families "landowner subjectivities" and "management decision-making and practices". For the social-ecological system variables that corresponded to these codes, detailed insights were derived from the interview transcripts.

3.4. Q analysis

Q-analysis focused on discourses on TRBs and TRB management, reflecting the values and priorities related to TRBs on a general level (Barry and Proops, 1999; Robbins and Krueger, 2000; Stephenson, 1935). The procedure started with identification of the body of information about the research topic, following Webler et al. (2009). The main source materials were published TRB manager interviews (Raatikainen, 2012) and meeting documents of the Biodiversity and Landscape working group that was called together upon the preparation the AES 2014–2020 (Ministry of Agriculture and Forestry, 2014). The source materials were read through and TRB-related assertative quotes were systematically collected. From this set of 135 initial

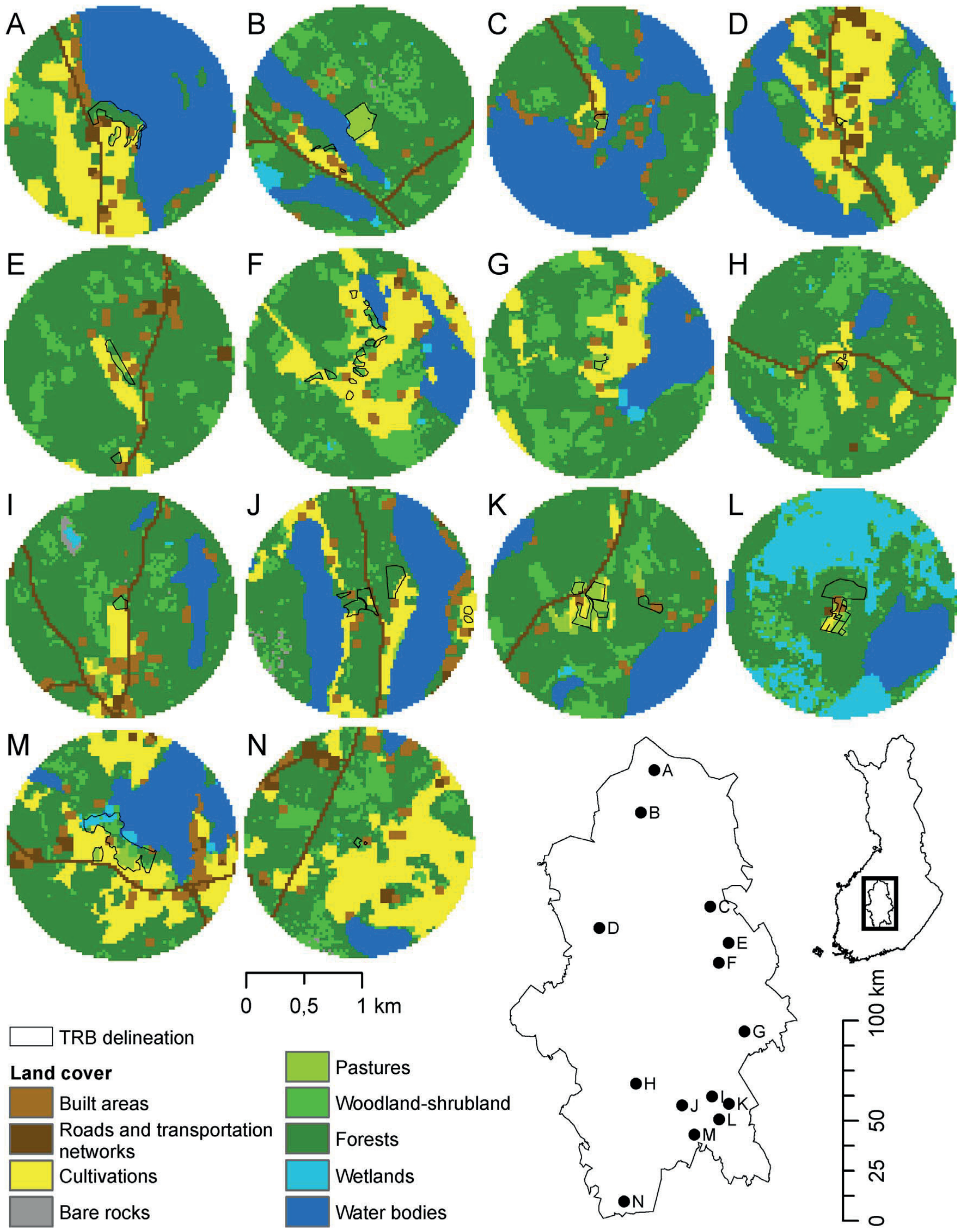

Fig. 1. Location of study sites (A–N) and their surrounding landscape structure. Letters refer to individual traditional rural biotope sites. Circular maps show physical landscape features around sites within a 1 km radius. TRB delineations made by authorities are drawn with black line (data from Centre for Economic Development, Transport and the Environment for Central Finland, abbreviated as ELY Centre for Central Finland). Land cover classes are derived from national CORINE Land Cover 2006 database (© Finnish Environment Institute, under CC BY 4.0 license). For full-color version, the reader is referred to the electronic version of the article.

statements we extracted 60 final statements that reflected the diversity of opinions around TRB management.

During interviews, landowners ranked the statements according to their agreement. The scale ranged from “least how I think” to “most how I think”, with a neutral position in the middle. The sorting was laid out in a normal distribution that guided the landowners to make distictions among their priorities (how they related the statements to each other). During and after sorting, landowners were encouraged to ask questions, give comments, and clarify ranking of specific statements. The sorts were recorded by writing down the ranks of individual statements.

Latent patterns in sorting of the statements were analyzed with factor analysis using PQMethod (release 2.35). Factor analysis reduced redundancy and drew attention to inter-subjective ordering of the statements. The information was further condensed by exploring correlations between variables, i.e. Q sorts done by landowners ($n = 19$). Using principal components analysis with Varimax rotation, we clustered the sorts into four factors for further analysis. Together the factors

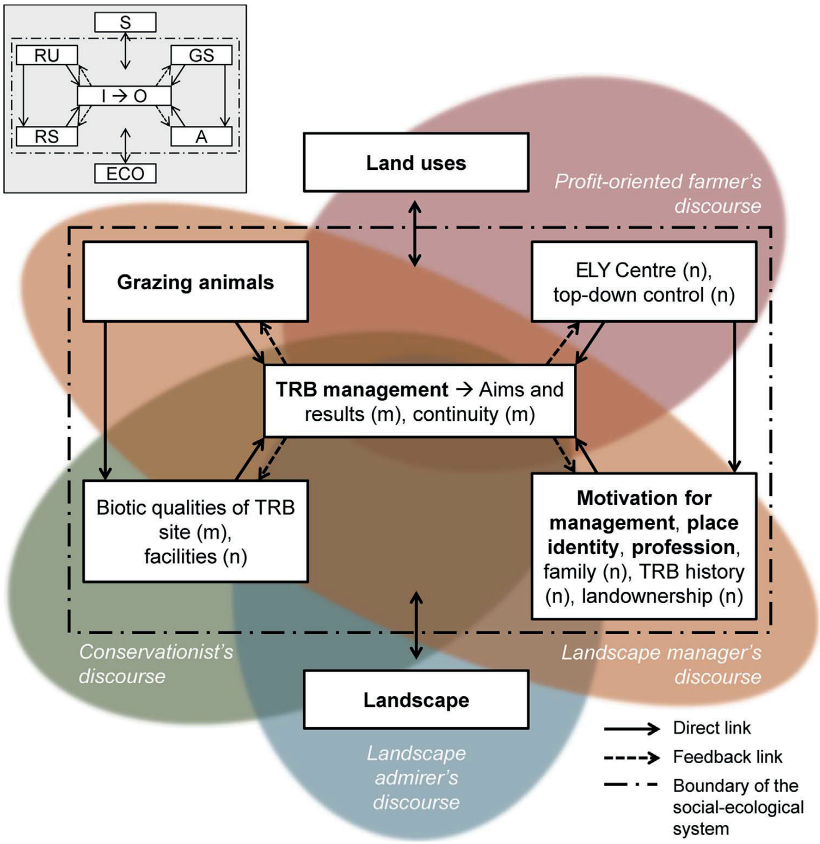

Fig. 2. Incorporation of interview results into social-ecological system framework (adapted from McGinnis and Ostrom, 2014). Main system components are shown in the top-left panel as abbreviations: S = social, economic, and political settings, RU = resource units, RS = resource system, A = actors, GS = governance system, I = interactions, O = outcomes, ECO = related ecosystems. Large panel represents respective key social-ecological features in relation to decision-making on TRB management or abandonment, derived from the landowner interviews. Features perceived important by both managers and non-managers are in bold face. Additional important features mentioned by either managers or non-managers are indicated with (m) and (n), respectively. Detailed insights of the features are provided in the text. Colored circles (depicted in grey in printed version) correspond to four discourses identified through Q-analysis, which reflect the values contributing to TRB management decision-making and practices. The location and extent of the circles is approximate, but they represent how different points of view put more emphasis on different social-ecological features. "ELY Centre" refers to the regional administrative organization governing implementation of agri-environmental measures in Central Finland.

explained 63% of the variance within the data. In this solution, every Q sort loaded to (i.e. correlated with) at least one of the factors. Thus, all landowners were connected to one or more factors.

Factor scores and arrays, distinguishing statements, salient statements, and landowners' comments were used for the development of descriptive narratives (Electronic appendix). These were interpreted into general discourses on TRB management.

4. Results

4.1. Key social-ecological factors affecting landowners' motivations for TRB management

We identified 16 key variables that contributed to TRB management continuation. Here we connect them to Ostrom's social-ecological system framework in order to structure the complexity of TRB systems (Fig. 2).

Based on both managers' and non-managers' accounts, grazing animals are the most important resource in contemporary TRB management (Fig. 2: RU). Fodder and AES payments were of secondary importance. For some managers grazers provided primarily income or meat, while several others enjoyed the sight of grazers in the landscape and connected with the animals (Table 2). Non-farming managers arranged grazers on their TRBs by collaborating with cattle farmers who lent their animals for summer pasturage. Eight landowners were involved in this purposeful co-operation between farms that resulted in self-organizing grazer networks. Transferring animals within these networks was important in securing the continuation of management, since all non-managers mentioned that a key factor contributing to TRB abandonment was giving up grazing cattle.

Historical management practices, especially grazing, were seen as the best ones by both managers and non-managers (Fig. 2: I). Yet the knowledge on historic land-use and livelihood was guiding rather than restrictive, as contemporary TRB management utilizes modern farming practices; e.g. the continuance of grazing often was secured by changing the type of grazers on the basis of what animals were available. When compared to mowing, all landowners agreed that grazing is the most viable way to manage TRBs, facilitating and motivating TRB management (Table 2).

Managers and non-managers had differing ideas regarding their TRB as a resource system, which was likely a result of different levels of involvement with the land itself (Fig. 2: RS). Managers focused on the site-specific biotic qualities; they described how species community and vegetation dynamics of the TRB form a basis for its value, providing an ecological feedback system through which TRB management practices are adjusted. Non-managers, on the other hand, adopted a landscape perspective. They saw the TRB as part of the overall scenery, with high value on human-constructed facilities such as buildings, fences, and yards.

Managers highlighted the importance of management outcomes tied to the ecological characteristics of the TRB site (Fig. 2: O). They felt that the correspondence between the aims and observed results of the management was rewarding. Through management − usually grazing − they maintained desired features of vegetation such as openness and species richness, and provided habitat for rare species. Clearly, overall continuity of TRB management and persistence of the biotic qualities of

Table 2
Emergent perceptions on TRBs, TRB management, and AES subsidies. The number (N) and ID codes of landowners contributing to a given perception are presented separately for managers and non-managers.

	Managers:		Non-managers:	
Landowners' perceptions	N	Landowner IDs	N	Landowner IDs
Managed TRBs are intrinsically valuable.	13	All	7	All
TRBs hold utilitarian value, and contemporary land-use practices link TRB management to every-day farming.	7	1, 2, 3, 4, 5, 13, 15	1	16
TRB site is an undistinguishable part of nature and farm's domains.	11	1, 2, 3, 4, 5, 8, 11, 13, 14, 15, 20	2	7, 16
The surrounding local landscape, including the TRB, facilitates a sense of belonging.	11	1, 2, 3, 4, 5, 6, 13, 14, 15, 19, 20	3	9, 10, 12
TRB management fosters temporal continuity of multiple values within the landscape.	9	1, 2, 3, 4, 8, 11, 13, 15, 19	2	9, 10
Land-use history created by a long chain of generations is alive on managed TRBs.	8	3, 4, 8, 11, 13, 14, 19, 20	2	17, 18
Grazing is crucial for TRB management.	13	All	7	All
Having grazing animals is a way of life and enjoyable.	8	1, 2, 3, 4, 5, 11, 13, 14	0	n/a
TRBs, their management, and TRB subsidies are positive things.	13	All	7	All
TRB management is not driven by money.	13	All	7	All
AES and inspections by ELY Centre bring excess bureaucracy into TRB management.	8	1, 2, 3, 4, 5, 11, 14, 20	5	9, 10, 12, 16, 19
Voluntariness of TRB management is important.	5	4, 6, 13, 14, 15	2	7, 16
All landowners should share same opportunities and possibilities of TRB subsidies.	5	3, 8, 13, 14, 15	5	7, 9, 10, 12, 16

Table 3
Factor characteristics. Factor 1 corresponds to conservationist's discourse, factor 2 to profit-oriented farmer's discourse, factor 3 to landscape manager's discourse, and factor 4 to landscape admirer's discourse. Initial eigenvalue represents the variance accounted for by a specific factor before rotation. The proportion of total variance explained by each factor is given both before and after Varimax rotation. Number of defining Q sorts corresponds to the number of participants whose sorts were utilized in factor rotation. Composite reliability indicates the level to which each factor is explained by its observed variables. Factor scores are created for each observation for each factor and standardized according to a z-score, and their standard error is shown in the last row.

	Factor 1	Factor 2	Factor 3	Factor 4
Initial eigenvalue	8.1448	1.6248	1.1486	1.0641
Total variance explained (%) before rotation	43	9	6	6
Total variance explained (%) after rotation	23	9	18	12
Number of defining Q sorts	11	2	8	4
Composite reliability	0.978	0.889	0.970	0.941
Standard error of factor scores	0.149	0.333	0.174	0.243

the TRB site are important motivators for management.

Non-managers relayed some negative comments related to governance of TRB management (Fig. 2: GS). They saw that the regional administrative organization (ELY Centre) discouraged TRB management through top-down control. Landowners experienced the AES as bureaucractic and burdensome, but they related this to the entire programme rather than to TRB payments, which all landowners considered as advantageous (Table 2). They agreed that payments are needed because TRB management, especially fencing, is expensive. Managers were more accustomed to the AES and said it had only minor effects on their decisions on TRB management. They claimed that entering the AES did not directly change their management practices.

Both managers and non-managers discussed their role in TRB management (Fig. 2: A). On the one hand, landowners wanted to treasure TRBs as special places having intrinsic value. On the other hand, manager's profession was important. Incorporating TRB management to active farming or connecting it to alternative livelihoods as a side-business or a hobby were mentioned as viable options in securing continuity of management.

Non-managers raised additional features that contributed to continuation of TRB management (Fig. 2: A). Owners of family farms saw the work of ancestors as a motivator for TRB management, and they wished that future generations would continue farming. Landowners felt that they had a responsibility to protect the land for future generations, since each generation holds possession of it only temporarily. They connected landownership to a sense of belonging to the place − the farm − and to the chain of generations. Landowners' knowledge on TRB history and ability to detect patterns of past land uses from the landscape motivated and inspired management.

Both managers and non-managers explained how socioeconomic drivers behind TRB loss have become visible through land-use changes (Fig. 2: S). For example, they described how urbanization has resulted in depopulation of rural areas and abandonment of TRBs. Land uses are the main sculptor of landscape, and landowners structured functions of their farm spatially based on different forms of land use, which were dynamic and related to prevailing livelihoods: older landowners described how meadows were transformed into fields through intensification of agricultural production, and fields re-forested when farming seized.

In relation to other ecosystems, landowners perceived TRBs nested within the surrounding landscape (Table 2, Fig. 2: ECO). They acknowledged how TRB management essentially transforms landscapes, building landscape identity over multiple generations. Thus the relationship between landscape and TRB management is reciprocal and dynamic, making landscape of material and conceptual significance in TRB management.

4.2. Discourses reflecting emergent meanings tied to TRB management

Four underlying discourses were interpreted from the factor analysis (Table 3; see also Electronic appendix). They represent different holistic ways of translating, structuring, and understanding the social-ecological complexity of TRB management (Fig. 2). All discourses emphasized three main points: continuing TRB management and other agricultural practices significantly maintain biodiversity in Finland; because of this overall importance, the responsibility for TRB management should not be left to farmers alone; and the role of authorities in promoting TRBs is minor. Although participants agreed that AES payments covered management costs sufficiently, they generally did not rank scheme-related statements high. This implies that the AES was not considered driving TRB management.

Excluding these similarities, each discourse represents different points of view that were agreed upon by slightly differing groups of landowners. Following paragraphs present the discourse descriptions together with selected excerpts from the interviews that exemplify each discourse. These include data from both the content and Q analyses, which are synthesized and interpreted together.

4.2.1. Conservationist's discourse

According to the first discourse, TRB management creates concrete clusters of manifold values which need active sustaining. This discourse accounted for the greatest amount of variation in the data (Table 3) and several perceptions related to it emerged from the interviews (Table 2);

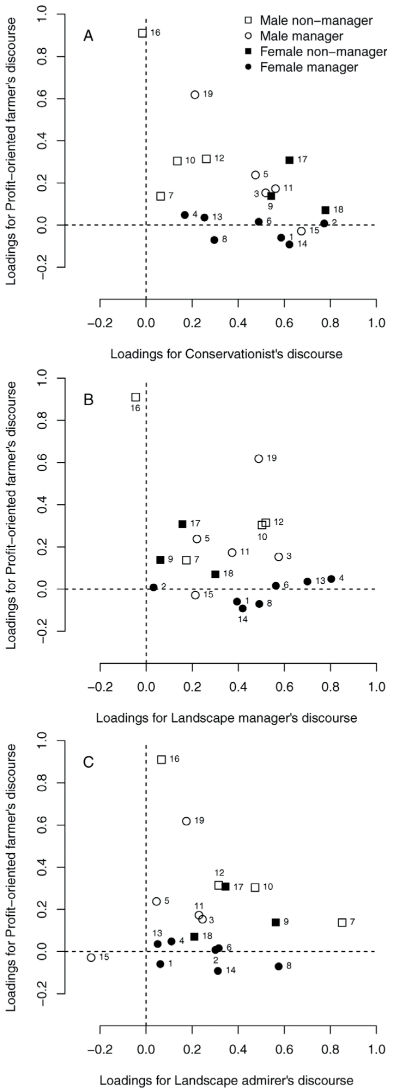

Fig. 3. Paired comparisons of discourse loadings (i.e. the level of agreement) of landowners according to Q analysis. Profit-oriented farmer's discourse was chosen as a reference, because it was the least correlated with other discourses (correlation coefficients were 0.152, 0.240, and 0.231 for conservationist's, landscape manager's, and landscape admirer's discourse, respectively). Dashed lines mark zero values. Symbols correspond to landowner groups: circles are managers, squares are non-managers, open symbols are males and filled symbols females. Numbers refer to landowners' ID codes (see Table 1).

among them was a predominant view of TRBs as places or specific sites having intrinsic value. During interviews, landowners addressed the value of TRBs in several ways. They justified management with place-bound uniqueness of TRBs, or emphasized specific values, such as biodiversity, cultural heritage, and aesthetic scenery. To protect these values, managers highlighted the importance of continuity, which they defined across temporal, social, and ecological dimensions:

TRB management is [about] maintaining culture, old practices and past ways of life, for future generations. It is good for them to see where we came from, how rural areas have developed. Of course the plants and other biodiversity are passed on at the same time. I am sure that people will highly value this work in the future, as long as we can keep the little that is left. (Participant 3, male manager)

In addition to communal value, managers also personally felt that managing their site invoked joy, pride, and enthusiasm. This is evident in the following quotation from a landowner, whose Q sort was strongly associated with the discourse (Fig. 3A):

When I look out, I feel greatly satisfied. I see how the TRB site is getting more and more beautiful. It is so concrete how the work bears fruit. My understanding of TRBs and biodiversity has increased, and as my knowledge has gotten deeper I have learned to see what TRB management means to nature. The scenery makes me feel good about the work I have done. I am touched by it. (Participant 2, female manager)

Her description exemplifies how hands-on work strenghtens the manager's relationship with nature and the surrounding landscape. This leads to a mutual interaction where positive experience, emotion, and ecological knowledge together support management and improve its environmental outcomes and vice versa. Landowners expressed this affinity to the surrounding landscape, and management actions further reinforced their experienced sense of place:

I sit on that rock and just enjoy being there, in that moment, feeling at home. Maybe I manage the TRB in order to thrive in it, and when I do, I just look at the landscape. It is my territory. Because I know every rock, every spot… it is mine, my home. And by home I really mean the surrounding environment, not only the house. (Participant 15, male manager)

Following from the strong feeling of landownership, managers saw themselves as links in the chain of generations fostering this valued landscape. The idea of intrinsic value of TRBs was so strong that all landowners rejected the idea of payments as a primary motive for TRB management. The contributors to the first discourse further stated that conserving nature was more important to them than receiving money to compensate for management actions; for this reason, the discourse was named as a conservationist's discourse. According to it, monetary compensation through AES was seen as potentially diverting TRB management from its actual value basis:

Maybe, if we were offered more information on TRBs, rather than always told to apply for AES payments, we could see the versatile opportunities in TRB management. (Participant 8, female manager)

Landowners emphasized how TRB management contributes to biodiversity as a whole, and they were worried about the decline of TRBs as a result of agricultural modernization. One of the managers wished that the AES could be modified to better promote TRB management:

The AES should move towards paying for provision of ecosystem services. It would bring TRB management to the same line with other production sectors, and farms could specialize in it, in producing biodiversity. (Participant 1, female manager)

As the two previous quotes show, managers were aware of possible indirect negative consequences of agri-environmental policies on TRB management. They pointed out that although the AES seeks to remedy environmental issues caused by agriculture, it simultaneously is part of a system that holds industrialized production as a norm, thus promoting further degradation of the environment. Managers claimed that this conflicts with overall aims of biodiversity conservation. In terms of TRB management, they feared that short-term payment contracts threaten the continuity of management and leave ecological targets unattained. In the AES, TRB management is described as a voluntary special measure that is conceptually separated from other farming practices. Managers criticized this delineation between "regular" agriculture and TRB management; they saw that the AES marginalizes TRB management and detaches TRBs from everyday farming.

4.2.2. Profit-oriented farmer's discourse

The second discourse focused on the effects of agri-industrial practices and possible drawbacks for TRB management. Whereas the conservationist's discourse presented TRBs as sites or patches holding specific value, the second discourse approached them at the farm level. Generally, TRB management is seen as a low priority generating little profit, because agricultural modernization has diminished the role of

TRBs in contemporary farming. What motivation there is for TRB management is utilitarian: the incorporation into farms' livestock production drives management, rather than intrinsic or communal value. Because of the content, this discourse was named as a profit-oriented farmer's discourse. Participant 16 strongly exemplifies this discourse (Fig. 3A-C), and as the following quotation shows, he saw TRBs as expendable:

TRB management may work for others. Personally, I don't have motivation for it. It is, in my opinion, a waste of time. I do not see our TRB as valuable anymore, because it has transformed into a forest. During time [ten years] *it has changed completely. (Participant 16, male non-manager)*

His comment describes how land use and corresponding vegetation dynamics determine the identity of the TRB site. When management ceases, the process of overgrowing starts, and eventually the TRB site loses its original function and is taken into commercial forestry. Because land-use functions form the basis of farm production, profit-oriented farmer's discourse sees the farm landscape as dynamic: it adapts to the prevailing livelihood. Later during the interview participant 16 described the process of TRB abandonment in more detail, exemplifying how ecological and social processes are tied to each other:

Our TRB had been a pasture for decades, and when the cattle grazed there, it looked fine. The vegetation was neatly eaten: no willows, no bushes, nothing. My parents got excited about the payment, but then came the restrictions on pasturing… In practice, it was impossible to prevent cows from moving between the TRB and fertilized pastures, or regulate their numbers. Then we gave up dairy production, and grazing ended. During the rest of the contract period we cleared the bushes by hand, but it was hard work, and the payment was low. (Participant 16, male non-manager)

The discourse further highlighted several obstacles to promoting TRB management. Lack of grazing animals and presumed low quality of TRB fodder were mentioned as practical reasons, but also increasing bureaucracy involved in AES payments and farmers' fear of AES inspection were seen as contributing to TRB abandonment. These factors and the above account reveal how TRB management has become separated from farming practices, a process which cannot be reverted by current − often unappealing − AES measures. Functional separation between TRB management and contemporary farming, in turn, resulted from agricultural modernization, which essentially works against TRB management:

TRBs are the losers in this game. Agriculture centres in more productive regions and aims for higher yields and TRBs are not competitive in that sense. (Participant 19, male manager)

In essence, this landowner is identifying what many feel: TRBs cannot compete, financially, with newer intensive farming and commercial forestry practices that dominate the landscape. Thus, if it is a matter of maintaining livelihoods, the AES payments are not enough to support the continuation of TRB management.

4.2.3. Landscape manager's discourse

The third discourse reflects an alternative farm-level approach to TRBs: it focused on the opportunities of farmers to foster traditional rural landscapes. This discourse connected to the conservationist discourse (correlation coefficient between these two factors was 0.737) but was more practice-oriented. Statements related to landscape management were ranked higher and those related to biodiversity or cultural heritage were seen less important (Table A.1). With its hands-on approach, the aptly named "landscape manager's discourse" adopted another utilitarian perspective towards TRBs.

Within farms, TRBs were seen as parts of pasture rotation together with fertilized pastures. Wood-pastures also contributed to farms' forest cover even if they were excluded from silvicultural purposes; they needed to be cleared of bushes, and provided wood from selective logging. Because of this upscaling through management practices, TRBs were not perceived as separate sites but as parts of a larger functional entity: the farm or surrounding landscape.

Landscape manager's discourse emphasized that TRB management is dependent on modern agricultural practices, especially livestock rearing. It highlighted the importance of grazers, pasture rotation, and transferring grazing animals between farms (i.e. situations where livestock farms pastured grazing animals on another landowner's TRB site). Although landscape manager's discourse shares the interest in cattle farming with the profit-oriented farmer's discourse, it contrasts the latter by criticizing agricultural intensification:

Finnish farmers are idealizing intensive production and big units; they say that small-scale production is not profitable. But it is more complex than that. In reality small farms often get on better than large ones. (Participant 3, male manager)

Things are going far worse because farms specialize in their production. We try to be more self-sufficient. Nowadays, because farms get larger, farmers can keep only few kinds of domestic animals, if any. We are going to an opposite direction. (Participant 4, female manager)

The above comments refer to vulnerability of large farms to economic volatility. Both landowners state that by farming in a multi-functional, small-scale manner they are able to control for this unsecurity. Participant 4 contributed strongly to the landscape manager's discourse (Fig. 3B). She and five other managers said they had incorporated TRB management efficiently into an environmentally sustainable livelihood. For them, AES payments were encouraging taking larger areas into TRB management:

With payments I am able to manage several TRBs, not only the one near my house. The payment is not a motive, but it makes things possible. The payment motivates me to expand TRB management, but it is not the reason why I manage TRBs. (Participant 15, male manager)

His passage exemplifies how conservationist's and landscape manager's discourses can be integrated; the former may provide the underlying motivation for TRB management and the latter reflects the practical context enabling the management actions. In contrast with the profit-oriented farmer's discourse, which criticized the bureaucracy involved in the AES, landscape manager's discourse adopted a positive attitude towards AES contracts.

4.2.4. Landscape admirer's discourse

Contributors to the fourth discourse expressed a general admiration of rural landscapes with a detachment from modern cattle husbandry. Landscape admirer's discourse did not focus on management of TRBs *per se*, but rather on maintaining the aesthetics of open sceneries, thus reflecting a broader landscape level approach. This is exemplified in a quote from participant 7, who contributed notably to the discourse (Fig. 3C):

Open landscape is beautiful. […] If management ceases, it doesn't take long before bushes and trees start to grow. Landscape needs to be managed. (Participant 7, male non-manager)

The will to maintain open scenery was expressed also in other discourses, but whereas those underlined the importance of agricultural management, the fourth discourse questioned its environmental benefits. It especially criticized modern animal husbandry, which became clear when discussing whether grazing on lake and river shores should be permitted. This issue aroused strong opinions among some landowners. If they had experienced that shore grazing deteriorated water quality, they deemed it a generally poor practice:

They have a large cattle farm, and the animals are allowed to graze along the shore [on a fertilized pasture]. And the cows defecate into the lake. I think it doesn't improve the shore. I would say it's the same for TRB pastures. (Participant 14, female manager)

Participant 7 gave a very similar account from his neighborhood. Importantly, the shore grazing dispute exemplifies how landscape admirer's discourse positions itself outside of agricultural production. This is in contrast with the other three discourses, which underlined the positive outcomes of farming for TRB management. Those landowners who agreed most with the landscape admirer's discourse did not have cattle or sheep. Their removal from cattle farming may explain why the discourse adopted a critical approach towards it.

When compared to other discourses, the focus of landscape admirer's discourse is in the past, not in the future. It appreciates traditional sceneries and reproves modern agriculture that reshapes rural landscape. It expresses a concern for the diminishing traditional landscape and points out that industrialized farming has contributed to the deterioration of the rural environment. Although the discourse emphasizes management of rural landscape, it questions the role of farmers as stewards of that landscape, and criticizes the effectiveness of modern practices in maintaining its values. It presents negative outcomes of contemporary farming practices such as grazing, and expresses a need for state intervention and regulations to control farmers' behaviors. Despite this demand for more rigorous governance, landscape admirer's discourse was the least familiar with the AES, and its contributors expressed a lack of knowledge on the scheme's structure, aims, and measures.

5. Discussion

5.1. The effect of current agri-environmental policies on TRB management

Our main finding is that TRB management fosters a diversity of cultural values and meanings. Although the Finnish AES provides important resources for TRB management, it fails to recognize this multifacetedness of TRB management. This is concerning, because if agri-environmental policies overlook the social context in which management actions actually occur, their regulations may fail to achieve their objectives, or worse, lead to negative side effects (Kaljonen, 2006; Uthes and Matzdorf, 2013). Our study indicates that the current agri-environmental policies do not meet large-scale needs in advancing TRB conservation in Finland. In the following paragraphs we discuss the ineffectivess of current TRB policies in more detail.

The participants of our study pointed out that the Finnish AES marginalizes TRB management into a highly regulated, site-specific special measure, and conceptually detaches it from regular agricultural practices. The main focus of AESs is on mitigation of environmental detriments of industrial agriculture (Batáry et al., 2015; Kleijn and Sutherland, 2003), but at the same time the CAP system as a whole supports economic efficiency, profit maximization, and maximum use of technological inputs (Robinson, 1991). We argue that this situation dismisses social complexities and a multitude of values that are distinctive for landscape management actions such as TRB management. Precise understanding of the complexity of assigning values to landscapes is shown to be important for decision-making on the protection and development of cultural landscapes (Plieninger et al., 2015b), but the AES overlooks this need. It isolates the actions that maintain these valued landscapes from the socioeconomic context that is the basis of their existence; in a sense, it separates the "cultural" from the "agricultural".

The loss of agricultural function makes TRBs vulnerable to abandonment. Our results indicate that this process operates on more than one spatial level. On the farm level TRBs are dependent on land-use decisions of the landowners, and TRB abandonment largely follows from changes in landowners' livelihoods. Such functional characteristics of the TRB system were revealed through discourse analysis. We found out that in social-ecological systems context, discourses provide useful lenses into different ways in which the system's actors perceive and explain the system's structure and behavior. They are able to reveal causal interactions that control the system's outcomes, and thus are potentially responsive for policy interventions. For example, the profit-oriented farmer's discourse speaks on the fact that rural livelihoods are controlled by international and domestic markets and politics; they drive TRB abandonment indirectly through impeding integration of TRB management with farming, or inducing giving up farming. The migration of young people from rural to urban areas due to diminishing livelihood opportunities also contributes to the process. This transformation is seen not only in the landscapes of Central Finland but throughout the country, as landowners point out. Also throughout Europe, changes in economic conditions for farming drive agricultural land abandonment and land-use intensification (Beilin et al., 2014; Plieninger et al., 2006). Because of the large-scale nature of these drivers, it is not surprising that the AES lacks the means to confront them; instead, it tries to adapt to the current economic conditions, which drive the decline of TRBs.

Despite the socioeconomic pressures, some TRBs persist, because landowners have a will to manage them. Yet what people actually value about TRBs is not supported nor acknowledged by monetary payments. Although the AES covers the site-specific costs of management, landowners rejected the idea that monetary benefits drive TRB management. This supports earlier results in which TRB managers' motivations were largely intrinsic and related to an affection to open landscapes (Birge and Herzon, 2014; Kumm, 2003; Stenseke, 2006). Under the AES, farmers are incentivised to change their behavior for a fixed number of years using money as the main motivator (de Snoo et al., 2013; Kaljonen, 2008), based on the assumption that all people are equally motivated by money to behave in specific ways. We found that TRBs hold a variety of additional values: conservation, utilitarian, aesthetic, and nostalgic. Many of these are tied to rural livelihoods, especially small-scale cattle farming. We argue that these are the factors counteracting TRB loss, rather than the AES contracts.

Certain landowners announced TRB management as their primary livelihood and said that they could handle the bureaucracy of the AES payments as long as TRB management was possible. These managers represent an emerging group of farmers that are able to use the AES in order to establish diversified rural livelihood strategies that build on management of biodiversity and landscape. Birge and Herzon (2014) identified these "TRB entrepreneurs", whose farming strategy is based on TRB grazing; in our study, their chosen livelihood resonates with the landscape manager's discourse. Although TRB entrepreneurs take advantage of the AES, they have to be cautious to not rely completely on the payments. Agri-environmental policies are constantly changing (Batáry et al., 2015), and if TRB management becomes dependent on the amount and continuation of payments, direct links between farmers and their environments erode, leaving TRBs susceptible to abandonment (Kumm, 2003; Sutcliffe et al., 2013). In fact, TRB entrepreneurs said they feel rebellious because their way of life opposes current agri-environmental policies. They have a will to conserve TRBs, but they feel the AES contracts both enable and confine their means to do so. These concerns were reflected in conservationist's discourse, which criticized the effectiveness of the AES in TRB conservation.

Furthermore, the AES falls short in encouraging TRB restoration. Non-managers were generally set against its bureaucracy and the payments did not motivate them to initiate restoration. This finding contributes to earlier studies demonstrating that AESs appeal primarily to farmers already aware of environmental issues (Batáry et al., 2015; Kleijn and Sutherland, 2003; Matzdorf and Lorenz, 2010), and fail to catalyze environmentally-friendly motivation and behavior (de Snoo et al., 2013). Landscape admirer's discourse points out that on the large-scale, contemporary farming practices do not self-evidently promote TRBs. AES payments may slow the abandonment of traditional grazing farms but be incapable of stopping it (Kumm, 2003). In Finland this most likely relates to the fact that the payments are utilized by a small proportion of all TRB landowners.

We observed that the Finnish AES does not reach all TRB landowners because it is targeted towards active farmers. This results in biased and ineffective governance of TRB conservation on a national level. This deficiency hinders both the utilization of management funding and spread of information on TRBs. As Herzon and Mikk (2007) point out, sufficient demonstration and advisory work are essential to practicing conservation on farmland. Based on our study, the AES currently lacks these. Together with the unprofitability of small-scale cattle farming, overall failure to raise awareness of TRBs and their value seem to contribute to landowner decisions that lead to TRB abandonment.

In sum, the AES oversimplifies TRB management by defining it as an external practice to what is seen as regular farming. The management payments provide resuscitation but are unable to cure the ultimate cause behind TRB loss: detachment from agricultural practices. Conflictually, this implies that the AES strengthens the very phenomenon that drives TRB abandonment. Finnish AES also fails in educating general public on values related to TRBs, encouraging TRB restoration, and providing support for non-farming TRB landowners. Given these shortcomings, we conclude that the Finnish environmental administration should take precautions to account for the risks involved in its reliance on the AES in implementing TRB conservation.

5.2. Insight for developing new effective policies: a resilience approach

Maintaining TRBs for future generations requires managing them in order to enhance their resilience to future changes (Chapin et al., 2009; Olsson et al., 2004; Plieninger and Bieling, 2013). In the previous section we described several factors that reduce the resilience of TRB systems and make them vulnerable for abandonment. In this section, we outline main findings that give insight into developing new resilience-promoting policies.

Advancing TRB management needs new policies that build on the relation between people and landscape (Bürgi et al., 2004; Stenseke, 2006; Stobbelaar and Pedroli, 2011) and reconstruct the "virtuous cycle" (*sensu* Selman and Knight, 2006) that created and maintained the social-ecological system of which TRBs were a part. In practice, this does not mean reproduction of the vernacular landscape, but re-connecting social and economic entrepreneurship with environmental processes and patterns within contemporary contexts (Plieninger and Bieling, 2013; Selman and Knight, 2006).

What is the contemporary virtuous cycle of TRB management? Our results demonstrate that TRB management is tied to a perception of TRBs as nexuses of values related to biodiversity, landscape, and living cultural heritage. Landowners express the positive interactions between TRB management and their way of life, relationship to nature, appreciation of cultural landscape, and perceptions of landownership and continuity. Positive experiences and ecological effects of management actions strengthen the linkage between landowners and the land owned, thus building landowners' sense of place and landscape identity. These reciprocal connections with the landscape motivate further management. On a wider level, TRB management provides beneficial outcomes also for the general public, and positive feedback from the community acts as a further motivator for management (Herzon and Mikk, 2007; Stenseke, 2006). Reinforcing these positive feedback loops is of particular importance in building social-ecological resilience, as these interrelations are responsible for the stability of the system (Berkes et al., 2003).

Effective policies would support these self-regulating interactions through spreading information on values tied to TRBs, rather than concentrating on monetary incentives, as one of the landowners noted. Here we do not propose discontinuation of AES payments, but their development into a less bureaucratic and more open system. One possibility would be to utilize result-oriented payments, which are directly linked to achieving specific environmental goals (Birge et al., 2017; Matzdorf and Lorenz, 2010). Result-oriented payments facilitate manager motivation, continuity of participation, and flexibility and innovation in management (Matzdorf and Lorenz, 2010). They support better understanding of the environmental goals through managers' self-control (e.g. detecting indicator species; Matzdorf and Lorenz, 2010). The practice of coupling observed biodiversity outcomes to payment level would strengthen the ecological feedback link reflecting effectiveness of TRB management, and would especially correspond to TRB entrepreneurs' way of life. A case study that tested a hypothetical result-oriented payment scheme for environmental grasslands found out that Finnish farmers were generally positive about the approach, but administrative officials were critical towards it, arguing that it could not fit into the current institutionalised programme (Birge et al., 2017). This, however, is not the case for TRB payments. In the current AES 2014–2020, nationally and regionally valuable TRBs are provided with a higher management payment (600 €/ha/year) when compared to sites surveyed as locally valuable (450 €/ha/year) (Ministry of Agriculture and Forestry, 2014). This means that the idea of payment-by-results is already introduced to Finnish AES, although its implementation remains authority-driven.

One of the main criticisms for result-oriented payments is that they may be unsuitable for risk-averse farmers (Matzdorf and Lorenz, 2010). They, and those non-managers who wish to avoid the bureaucracy involved in the AES, might better benefit from a coupled support promoting TRB management. Although the trend has been to cut down such direct payments, European Union member states can allocate a limited share of CAP pillar I funding for securing the continuity of potentially vulnerable production sectors. For example, the current Finnish Rural Development Programme has such a measure for helping young farmers to set up their farm enterprise (Ministry of Agriculture and Forestry, 2014). It could be possible to tailor a respective measure for small-holder farmers with diversified production − a group where TRB managers identify themselves, according to our study. This payment would not be tied to AES, which is paid from CAP pillar II budget. Its main benefit lies in its potential to encourage TRB maintenance and restoration indirectly by supporting farming livelihoods compatible with TRB management.

The two options presented above build on existing policies, for which reason they target only farmers. Increasing land tenure of non-farmers is challenging current TRB conservation (Ministry of Agriculture and Forestry, 2014). This calls for innovation of new governance practices that reach beyond farmers, and support landowners' self-organizing efforts to TRB management. Such opportunities could be mediated through and funded by general rural development measures under CAP pillar II, but they yet need to be planned and tested in practice. This work, and development of possible result-oriented or direct payments, should follow the principles of social learning and flexible governance that contribute to the adaptive capacity of the social-ecological system (Berkes et al., 2003).

Thus knowledge on TRB systems and their best management practices needs to be built, shared, and applied, and this is essentially a collaborative process. We agree with Kaljonen (2008) that the current agri-environmental policies would benefit from increased discussion and co-operation between authorities and different stakeholders. Overall, there is an increasing recognition of the necessity to include the values and priorities of people in any activity of natural or cultural resources conservation (Plieninger et al., 2006). As a mutual will to safeguard TRBs and traditional landscapes emerged from the interviews, we argue that funding and advice for TRB management should be available more widely, easily, and transparently. Landowners need to be enabled to implement their own strategies to maintain TRBs. Such a linkage between people and their environment helps navigate transitions through periods of socioeconomic uncertainty (Berkes et al., 2003).

Concentrating on sources of innovation and renewal is important in enhancing social-ecological resilience (Berkes et al., 2003). We documented a practical example of emerging novel TRB management: through co-operative grazer networks TRB and cattle owners spread grazing animals on TRB sites that would otherwise have been abandoned. Grazer networking enhances TRB resilience in the face of changes in the non-farming landowners' livelihoods as long as cattle husbandry continues within the surrounding landscape. From a policy perspective, grazer networking and similar innovations should be supported more in order to promote TRB pasturage through collaborative efforts. Corresponding measures have also been proposed in Sweden (Kumm, 2003).

Most importantly, the connection between TRB management and rural living needs to be revived through the development of opportunities to support TRB-based livelihoods. As a livelihood, agriculture is connected to markets; as a land-use practice, TRB management has become at least partially about environmental conservation. Thus, the current context has created a mismatch between the historical context in which TRBs formed and how they are currently valued. Contemporary TRB management must adapt to current circumstances in order to persist. In the end, new markets for TRB-based products are needed in order to affect the large-scale socioeconomic drivers of TRB abandonment. These may include organic or regional specialty products, high-quality food, and ecotourism (Plieninger and Bieling, 2013). Creation of such production chains could be based on collaboration between cattle farms, nature conservancy entrepreneurs, and meat-producing enterprises (Kumm, 2003).

A word of caution is required at this point. If social-ecological linkages maintaining land-use systems break apart, landscape functionality and distinctivess are lost (Selman and Knight, 2006). We have shown that TRB management is tied to cattle farming, and rural livelihoods are under constant pressure. At the same time, TRBs are ecologically dynamic, and as managers point out, their biotic qualities respond rapidly to changes in management regimes (realized as alternative land uses). Ecological succession, visible as invasive shrubland or woodland, is the most obvious sign of TRB disappearance. Shortly after abandonment, landowners experienced rapid overgrowth notably for the worse. As one non-manager said, sometimes TRBs do not get noticed until they are abandoned, and after that their value is recognized. This corresponds to Lindborg et al. (2008) conclusion that abatement of management actions initiates a process of deterioration in ecological, cultural, social, and economic values alike. However, we noted that the situation changes when the process surpasses a certain threshold. At this phase the site loses its appearance as a TRB and becomes susceptible to alternative land-uses. Crossing such a threshold significantly reduces resilience of the social-ecological system, making it vulnerable for disturbances (Berkes et al., 2003; Plieninger and Bieling, 2013). Finally, if the process continues until the adaptive capacity of the TRB system is lost, the system shifts into an alternative regime.

Our results indicate that this social-ecological conversion is mentally difficult to overcome: e.g., when the site turns into a forest, landowners become increasingly reluctant to restore it as a TRB. Thus social value and the very identity of a TRB site are bound to its biotic qualities and the remnants of past land-use. Therefore landowners' motivation to reinitiate TRB management depends on time since abandonment and rate of vegetational change. Often the process is slow and may go unnoticed (Bürgi et al., 2004), but non-managers' descriptions on TRB abandonment indicate how abrupt changes may result in a loss of sense of place and a decline in landowners' identification with the landscape. This is an example on how the formerly virtuous cycle becomes a vicious cycle, and there appears to be no spontaneous mechanism whereby this process can be reversed; thus, a public intervention appears necessary if TRBs are indeed a national priority (Selman and Knight, 2006).

Based on these findings, we propose that promoting existing TRB management and advancing TRB restoration are of utmost importance and need rapid proactive and reactive actions. The Finnish environmental and agricultural administrations need to join their forces and take a leading role in developing more flexible and collaborative governance for TRB conservation.

6. Conclusion

6.1. Counteracting the loss of farmland biodiversity and cultural heritage

Thus far TRB conservation as a governance practice has focused excessively either on the AES payments or the ecological qualities of TRB sites, leaving the diversity of social-ecological interactions underrated. Because current policies do not take the social-ecological complexity of the whole TRB system into account, they are unable to sustain TRBs in the long term. Strong reliance on authority-driven payments makes TRB management vulnerable for changes in agri-environmental policies. The current system conceptually detaches TRB management from regular farming practices, further reducing the resilience of TRB systems.

We suggest that it is time to make a transition from top-down control to promoting actor-oriented approaches to TRB management. We derived discourses on TRB management that can guide and facilitate development of more effective policies, and the key social-ecological features presented suggest starting points for this work. According to our results, landowners perceive TRBs as nexuses of biodiversity and several ecosystem services, a view that could form the basis for new policies. It is essential that the AES is complemented with more resilient and participatory governance. Building such governance requires a shift of focus to the versatile benefits of TRB management and its ability to adapt to modern cattle farming practices. It also calls for increasing collaboration between authorities, local actors, and rural communities. To encourage sustainable TRB management, spreading information on experienced value of TRBs and advice on management is important. New funding opportunities are needed for non-farmers, who manage TRBs for recreation. Supporting TRB entrepreneurship, promoting grazer networks, facilitating collaborative management, and sharing knowledge should be the main foci of effective TRB governance.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.landusepol.2017.10.004.

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Appendix

Table A.1. List of Q statements with factor-wise Z-scores and factor arrays emergent from the Q analysis. Ranks vary between -6…6 with respect to transition from strong disagreement to strong agreement with the statement. For each factor, distinguishing statements – i.e. statements that were ranked significantly differently when compared to other factors – are indicated by their statistical significance (* for P<0.05 and ** for P<0.01). Factor 1 corresponds to conservationist's discourse, factor 2 to profit-oriented farmer's discourse, factor 3 to landscape manager's discourse, and factor 4 to landscape admirer's discourse. "AES" refers to agri-environment scheme.

		Factor 1		Factor 2		Factor 3		Factor 4	
Statement		Z-score	Rank	Z-score	Rank	Z-score	Rank	Z-score	Rank
S1	Traditional rural biotopes are a significant addition to biodiversity.	1.57*	5*	0.12	0	0.80	2	0.95	2
S2	Agriculture significantly contributes to maintaining biodiversity in Finland.	1.04	2	1.59	5	1.04	3	1.46	4
S3	Biodiversity has declined because of changes in agriculture and the intensification of land use.	1.33**	4**	0.30	1	0.62	1	0.44	1
S4	The simplification of agricultural landscape is a bad thing.	1.69	6	0.44	1	1.26	4	0.81	2
S5	Traditional rural biotopes are beautiful.	1.08	3	0.06**	0**	1.29	4	1.50	4
S6	Traditional rural biotopes have special plant species that hard to find elsewhere.	0.95	2	0.26	1	0.96	2	0.66	2
S7	There is a growing appreciation for rural landscapes, which is expected to continue.	0.38	1	0.32	1	0.42	1	1.27*	3*
S8	Every grazed traditional rural biotope is valuable for the rural landscape.	0.64*	2*	-1.93**	-6**	1.14	3	1.31	3
S9	Management of traditional rural biotopes is a separate or useless part of the farm's production.	-2.37	-6	-0.82*	-2*	-2.47	-6	-1.69*	-5*
S10	Management of nature and landscape can support the livelihoods of a farm in many ways.	0.17	0	0.20	0	1.50**	5**	-0.08	0
S11	More of the available money should be directed to finding abandoned traditional rural biotope sites and getting them into management.	-0.96	-4	1.22	4	-0.74	-2	1.15	3
S12	It is difficult to recognize the potential sites for AES payments on a farm.	-0.32	-1	-0.38	-1	-0.93	-3	-0.44	-1
S13	Overgrown vegetation that threatens the openness of landscapes needs to be curtailed.	0.44	1	-0.96	-2	0.49	1	-0.21	0
S14	Decrease in the amount of uncultivated open and semi-open habitats is a major problem.	0.82**	2**	-1.09	-3	-0.39	-1	-0.97	-3
S15	Practice of agriculture is a prerequisite for maintenance of open and managed rural landscape.	0.50**	1**	-1.56	-5	1.49**	5**	-0.86	-2
S16	Transferring animals from other farms to the managed traditional rural biotope for AES payments is artificial.	-1.49	-4	-1.53	-4	-2.17	-5	-0.92	-3
S17	A traditional rural landscape is best maintained by grazing animals.	0.66	2	2.17	6	1.99	6	0.14	0
S18	Management of traditional rural biotopes is important to landscape and overall environment management.	1.30	3	0.12**	0**	1.10	3	1.59	5
S19	A managed area is always better than an unmanaged one.	-0.29**	-1*	1.01	3	0.39	1	1.66	6
S20	Grazing traditional rural biotopes located on shores improve ecological quality of adjacent lakes.	-0.19	0	1.02**	3**	-0.58	-1	-1.88**	-6**
S21	Grazing always increases the species diversity of traditional rural biotopes.	0.30	1	1.02	3	0.44	1	-1.57**	-4**
S22	Fodder from traditional rural biotopes is of lower quality when compared to cultivated pastures.	-0.96	-3	1.53**	4**	-0.61	-1	-0.29	-1
S23	Grazing on traditional rural biotopes is important for animal well-being.	0.38	1	-1.85	-6	0.50	1	-1.81	-6
S24	Management of traditional rural biotopes is getting harder because there are not enough grazing animals.	-0.53	-2	2.11**	6**	-0.57	-1	-0.20	0
S25	Big farms do not graze their animals on traditional rural biotopes.	-0.23	0	-0.06	0	-1.13**	-4**	-0.30	-1
S26	Large predators restrict the opportunities to graze domesticated animals on traditional rural biotopes.	-1.60**	-5**	0.82	2	0.86	2	0.59	1
S27	Management of traditional rural biotopes has not improved enough in Finland.	-0.36	-1	-0.76	-2	-0.39	-1	-0.18	0
S28	European Union's support for industrial agriculture works against management of traditional rural biotopes.	0.45**	1**	-0.62	-1	-1.25	-5	-1.65	-4
S29	Giving grazers extra fodder and access to cultivated pastures negatively affects biodiversity of traditional rural biotopes.	-0.23	0	-0.70	-2	-1.24	-4	-0.66	-2
S30	There are too few traditional rural biotopes and they must all be managed better.	-0.22	0	-0.82	-2	-0.34	0	0.57**	1**
S31	Bureaucracy of the AES payments is increasingly complex.	-0.22	0	1.67**	5**	-0.14	0	0.39	1
S32	Making applications for traditional rural biotope management payments is hard.	-0.74	-2	-0.44	-1	-0.88	-2	-0.95	-3
S33	It takes a long time to get decisions on traditional rural biotope management payments.	-0.42	-1	-0.64	-2	-0.75	-2	-0.62	-1

	Statement	Factor 1 Z-score	Rank	Factor 2 Z-score	Rank	Factor 3 Z-score	Rank	Factor 4 Z-score	Rank
S34	Simplifying the regulations of traditional rural biotope management payments would make them more appealing.	0.26	0	0.38	1	0.68	2	-0.12	0
S35	Traditional rural biotopes are maintained only because of the AES payments.	-2.51	-6	-1.01	-3	-2.39	-6	-1.69	-5
S36	National funding for non-farmers is needed to encourage management of traditional rural biotopes.	0.71	2	1.49*	4*	-0.37*	-1*	0.34	1
S37	Farmers need new incentives in order to maintain traditional rural biotopes and diverse landscapes.	-0.24	-1	1.21	3	0.67	2	-0.17	0
S38	Farmers are afraid to apply for traditional rural biotope management payments because it increases the chance of inspection.	-0.80	-3	0.64**	2**	-0.43	-1	-1.05	-3
S39	Traditional rural biotope management payments should allow for more flexible management.	-0.04	0	0.64	2	0.07	0	-0.20	0
S40	Many farmers are unwilling to pay for counseling on environmental management.	-0.25	-1	0.64*	2*	-0.21	0	-0.22	0
S41	Counseling visits and support are of utmost importance in improving the management of traditional rural biotopes.	0.61	1	-0.00	0	-0.12	0	0.65	2
S42	Many farmers would benefit from counseling on AES payments.	-0.21	0	0.38	1	0.33	0	0.39	1
S43	Farmers cannot manage traditional rural biotopes properly without counseling.	-1.49	-4	-1.02	-3	-0.23	0	0.25	1
S44	Grazing a large traditional rural biotope is profitable for the farm.	-0.21	0	0.32	1	-0.99*	-3*	-0.35	-1
S45	The commodification of landscape and traditional rural biotopes is part of modern agriculture.	-0.49	-1	0.06	0	0.36	0	-0.44	-1
S46	Management of traditional rural biotopes is not profitable even with the AES payment.	-0.70	-2	0.38	1	-0.17	0	-0.61	-1
S47	Money is the main reason farmers engage in environmental protection.	-2.20*	-5*	-1.33	-4	-0.62	-2	-0.22	-1
S48	It is almost impossible to make a durable fence with the traditional rural biotope management payment.	-0.78	-3	-0.50	-1	-0.99	-3	-0.81	-2
S49	Traditional rural biotope management payments do not meet the management and labor costs.	-0.54	-2	-0.44	-1	-0.42	-1	-0.72	-2
S50	Traditional rural biotopes that have national or regional value deserve management payments higher than the current maximum.	0.36	1	-0.20	-1	0.29	0	0.13	0
S51	Through traditional rural biotopes Finns remember their history.	1.32	4	-1.29**	-3**	0.99	3	1.45	4
S52	Cultural landscape created and shaped by agricultural livelihoods is a central part of Finland.	1.35*	4*	0.18	0	0.63	1	2.06*	6*
S53	Besides agricultural production, cultivated landscapes produce intangible benefits.	1.45**	5**	0.12	0	0.82	2	0.61	2
S54	Farmers have to take the responsibility for management of traditional rural biotopes.	-0.88	-3	-1.53	-4	-0.69	-2	-1.36	-4
S55	Quality of traditional rural biotopes is getting worse because authorities do not have resources for working with them.	-0.72	-2	-0.30	-1	-0.96	-3	-0.69	-2
S56	Quality of traditional rural biotope and landscape management should be coordinated nationally.	-0.29	-1	-1.79**	-5**	-0.64	-2	0.38*	1*
S57	Farmers feel that managing for landscape is more important than managing for biodiversity.	-0.60	-2	0.90**	2**	-1.13	-4	-0.79	-2
S58	Managed traditional rural biotopes speak to people. There is something special about them.	1.17	3	-0.38**	-1**	0.62*	1*	1.65	5
S59	Children benefit from traditional rural biotopes, because they bring animals and nature close.	1.32	3	-0.20**	-1**	1.32	4	0.89	2
S60	It is important that traditional rural biotopes are maintained for future generations.	1.80	6	0.82	2	1.86	6	1.40	3

Discourse narratives derived from compiling the sorting statements.

Factor 1. Conservationist's discourse

It is important that future generations get to know TRBs (S60). Children benefit from visiting TRBs, as it brings them closer to animals and nature (S59). TRBs add significantly to biodiversity in Finland (S1), but because of agricultural intensification and alarming simplification of rural landscape this biodiversity has become threatened (S3, S4). This is realized in the decrease of TRBs and other uncultivated open and semi-open habitats (S14). Open and managed rural landscape is central for Finland, and it needs agriculture (S15, S52), which provides not only food, but also intangible benefits related to nature and culture (S53). Grazed TRBs often are valuable for rural landscape (S8), but there should also be sites without management (S19), if they contribute to biodiversity. Predatory animals do not pose a threat for grazing on TRBs (S26); they also belong to nature. Farmers can easily incorporate TRB management into farms' production (S9, S43), but economic purposes are not driving TRB management or agri-environmental protection (S35, S47). Instead, inner conflicts of the AES payment system are possibly working against TRB management, as the AES promotes also industrial agriculture (S28).

Factor 2. Profit-oriented farmer's discourse

Although agriculture contributes significantly to biodiversity (S2), features of rural landscape can be maintained without it (S15). Yet, management of traditional rural landscape is dependent on grazing and livestock production (S17). TRB management is only one part of landscape management and environmental protection (S18), just as animal welfare is not solely tied to grazing on TRBs (S23). All TRBs are not special, beautiful, or otherwise valuable for the rural landscape (S5, S8, S58). There are several reasons why promoting TRB management is hard: lack of grazing animals (S24), increasing bureaucracy involved in AES payments (S31), the fear of AES inspection (S38), and the low quality of TRB fodder (S22). Motivation for TRB management comes from utility value; its incorporation into farm production and landscape management (S9, S57), rather than from national history or environmental education (S51, S59). For example, TRB grazing should be encouraged because it improves the water quality of lakes adjacent to TRB pastures (S20). Advisory services or national coordination for TRB management are of secondary importance (S40, S56). Also non-farming TRB landowners should be able to conduct management and receive funding for it (S36).

Factor 3. Landscape manager's discourse

Continuing practice of agriculture is a prerequisite for maintenance of rural landscape (S15). Management of biodiversity and landscape can support a farm's livelihoods in many ways (S10), and TRB management is tied to farming (S9). Maintaining TRBs for future generations is important (S60), and this work is best done through livestock grazing (S17). Contemporary farming practices and financial support for agricultural intensification are not compromising the biodiversity related to TRBs (S28). Also large farms utilize TRBs as pastures (S25), although grazing on TRBs is rarely profitable for the farm (S44). Lending and borrowing grazing animals for TRB management is a good practice that should be encouraged (S16). AES payments are not the basis for TRB management (S35), and funding for non-farmers is not crucial in encouraging TRB management (S36). Managed TRBs hold some intrinsic value (S58).

Factor 4. Landscape admirer's discourse

Rural landscape created and shaped by agricultural livelihoods is a central part of Finland (S52), and the appreciation for it is growing (S7). Landscape management should be promoted so that the number of abandoned, overgrowing areas would decrease (S19). In general, TRB management is important work for the rural landscape and the environment (S18), and it is not driven by the AES payments (S35). Managed TRBs are something special; they speak to people (S58). TRBs often are a useful part of a farm's production (S9). In reality TRBs are scarce and they need better management (S30); for this reason the quality of TRB and landscape management might benefit from national coordination (S56). Grazing has potential harmful consequences that need to be considered: grazing near lakes or streams should not be encouraged, as it deteriorates the quality of water (S20); and sometimes grazing decreases the species diversity of TRB sites (S21). Furthermore, grazing animals need to be tended well also outside of TRBs (S23).