

DISSERTATIONS IN
**FORESTRY AND
NATURAL SCIENCES**

TUOMO TAKALA

*Bryophytes in Semi-Natural
Rural Biotopes*



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EASTERN FINLAND

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No 175

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ABSTRACT

Traditional management of semi-natural rural biotopes have dramatically decreased during the last century. This development has been detrimental to the high biodiversity typical of these environments. In this thesis, I concentrate on two types of semi-natural rural biotopes – mesic grasslands and forest pastures – and study how the present management, notably cattle grazing, affects bryophytes in these biotopes. I found that bryophyte communities typical of semi-natural mesic grasslands are completely dependent on continuous grazing, whereas only individual bryophyte species depend on grazing in forest pastures. Frequent soil disturbances caused by grazing cattle were very important to bryophyte diversity in both biotopes. The continuously grazed mesic grasslands of this study sustained characteristic bryophyte communities including many species for which these unfertilized environments may be very essential, while individual species growing on bare mineral soil and dung were the most characteristic part of bryophyte communities in the forest pastures. Bryophyte species richness was, however, remarkably higher in the forest pastures in comparison to the mesic grasslands, apparently because of higher amount of available substrates. Thus, we can conclude that bryophytes form an integral part of biodiversity in both mesic grasslands and forest pastures. Seasonal grazing seems to be very sound management practice in the sustenance of bryophyte diversity in these biotopes, although additional measures, such as improvement of forest stand structure, may also be needed in forest pastures.

Universal Decimal Classification: 574.4, 582.32, 636.083.314, 636.084.22

CAB Thesaurus: Bryophyta; mosses; rural environment; rural areas; biotopes; grasslands; grassland management; pastures; forests; grazing; cattle; soil disturbance; species diversity; biodiversity; species richness

*Yleinen suomalainen asiasanasto: sammalet; maaseutu ympäristö;
maatalousalueet; biotooppi; laitumet; luonnonlaitumet; metsälaitumet;
laiduntaminen; karjanhoito; biodiversiteetti*

Preface and acknowledgements

This thesis is about bryophytes in semi-natural rural biotopes, which once formed a characteristic part of agricultural landscape in Finland. Nowadays, the vast majority of these biotopes are threatened like are many species dependent on them. However, we urgently need more knowledge of many insufficiently known species groups that live in these environments.

The decrease in semi-natural rural biotopes have manifold cultural, social and landscape effects but I concentrate on biodiversity aspect in this thesis. The main motivation for the study arises from the concern about the continuously accelerating global biodiversity loss by which we basically threaten our very own existence. While human being is especially skilled at destroying biodiversity, the main problem in semi-natural rural biotopes is that we have stopped doing what we have previously done. Unlike many other threatened biotopes, semi-natural rural biotopes are dependent on continuous management.

The aim of this thesis is to provide novel information on the basic bryophyte ecology in grazed environments and produce some practical recommendations for the management of semi-natural rural biotopes. This book is composed of a summary and four peer-reviewed articles (I-IV). In this summary part, I present the main results of the four articles but aim to view them in a wider context than possible in the concise articles.

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on data presented in the following articles, referred to by the Roman numerals I-IV.

- I** Takala T, Tahvanainen T and Kouki J. Can re-establishment of cattle grazing restore bryophyte diversity in abandoned mesic semi-natural grasslands? *Biodiversity and Conservation* 21: 981–992, 2012.
- II** Takala T, Tahvanainen T and Kouki J. Grazing promotes bryophyte species richness in semi-natural grasslands. *Annales Botanici Fennici* 51: 148–160, 2014.
- III** Takala T, Kouki J and Tahvanainen T. Bryophytes and their microhabitats in coniferous forest pastures: should they be considered in the pasture management? *Biodiversity and Conservation* 23: 3127–3142, 2014.
- IV** Takala T, Haverinen J, Kuusela E, Tahvanainen T and Kouki J. Does cattle movement between forest pastures and fertilized grasslands affect the bryophyte and vascular plant communities in vulnerable forest pasture biotopes? *Agriculture, Ecosystems and Environment* 201: 26–42, 2015.

The above publications have been included at the end of this thesis with their copyright holders' permission.

AUTHOR'S CONTRIBUTION

The table shows the contribution of the authors in each of the original articles. Abbreviations: A = Author (Tuomo Takala), EK = Eeva Kuusela, JH = Jasmiina Haverinen, JK = Jari Kouki, TT = Teemu Tahvanainen.

	I	II	III	IV
STUDY DESIGN	A,JK,TT	A,JK,TT	A,JK,TT	A,EK,JH,JK,TT
FIELDWORK	A	A	A	A,JH
SOIL ANALYSIS	-	-	-	A,JH
SPECIES IDENTIFICATION	A	A	A	A
STATISTICAL ANALYSIS	A,JK,TT	A,JK,TT	A,JK,TT	A,JK,TT
MANUSCRIPT PREPARATION	A,JK,TT	A,JK,TT	A,JK,TT	A,EK,JH,JK,TT

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1 Introduction

1.1 DECLINING BIODIVERSITY IN SEMI-NATURAL RURAL BIOTOPES

Intensification of agriculture has brought about various phenomena that adversely affect biodiversity and ecosystem services throughout Europe (Stoate et al. 2001, Geiger et al. 2010). One of the adverse effects has been the drastic decline of semi-natural rural biotopes. The decline was especially intensive in the latter half of the twentieth century (Luoto et al. 2003). In this period, fertilized grassland pastures on cultivated land effectively replaced semi-natural rural biotopes in the production of winter forage and in the provision of pastureland. As a result, all main types and the majority of subtypes of semi-natural rural biotopes are classified as either endangered (EN) or critically endangered (CR) in Finland (Schulman et al. 2008a). The decrease in these biotopes as well as the loss of their typically high biodiversity are recognized also at European level (Bignal & McCracken 1996, Poschold & WallisDeVries 2002; European Commission 2009, Habel et al. 2013). Semi-natural rural biotopes, notably grasslands, belong to the most species rich biotopes across Europe (Habel et al. 2013).

Not very surprisingly, numerous species dependent on semi-natural rural biotopes and traditional management have become threatened (Rassi et al. 2010). The quantitative decline and qualitative deterioration of semi-natural rural biotopes form a primary cause for the red-list status of ca 20 % of the Finnish threatened (CR, EN, VU) and near threatened (NT) species (Rassi et al. 2010). The majority of these species belong to vascular plants (Tracheophyta), fungi (Fungi) and certain insect orders (Coleoptera, Diptera, Homoptera, Hymenoptera, Lepidoptera) (Rassi et al. 2010). Vascular plants have traditionally received most attention in the planning of

biodiversity-sound management for semi-natural rural biotopes (WallisDeVries et al. 2002). However, effective biodiversity conservation requires that we also consider other species groups in the planning and management (WallisDeVries et al. 2002).

Dry grasslands stand out as the most important type of semi-natural rural biotopes for the threatened species and for threatened insects in particular (Rassi et al. 2010). Instead, less exposed and less dry semi-natural rural biotopes are more essential for many threatened vascular plants, fungi and lichens (Rassi et al. 2010). The overgrowth of formerly open biotopes is reported as the most important individual cause of biodiversity loss in agricultural environments (Rassi et al. 2010) and it obviously poses a threat to some bryophyte species also (Syrjänen et al. 2010). In total 23 threatened bryophyte species have been reported living primarily and 51 species secondarily in semi-natural rural biotopes and other cultural environments (Rassi et al. 2010).

1.2 MESIC SEMI-NATURAL GRASSLANDS AND FOREST PASTURES

This thesis concentrates on the bryophyte communities of two different semi-natural rural biotopes – mesic semi-natural grasslands (*tuore niitty* in Finnish) and forest pastures (*metsälaidun*). Both of these biotopes can be divided into several subtypes (Vainio et al. 2001, Schulman et al. 2008b) but I predominantly operate at the level of the main types in this thesis, aiming at the generalization of results at this level. The applied biotope classification follows the inventory of threatened biotope types in Finland in 2008 (Schulman et al. 2008a,b) with the distinction that what I call biotopes in this thesis (mesic grasslands and forest pastures) are two main categories composed of several biotopes in the classification. Mesic grasslands are further divided into low herb mesic grasslands (*tuore pienruohoniitty*), tall herb mesic grasslands (*tuore suurruohoniitty*) and graminoid mesic grasslands (*tuore*

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heinäniitty) in the classification. Forest pastures are categorized into forest pastures dominated by coniferous trees (*havumetsälaidun*), forest pastures with coniferous and deciduous trees (*sekametsälaidun*) and forest pastures dominated by deciduous trees (*lehtimetsälaidun*). The English term forest pasture is developed for the purposes of this thesis and may not be found in the earlier literature.

Common to all semi-natural rural biotopes is that they have been formed in and maintained by traditional animal husbandry, which aimed at winter forage production and the provision of pastureland in these environments (Salminen & Kekäläinen 2000). Importantly, traditional management included no tilling, fertilizing or sowing (Salminen & Kekäläinen 2000), leaving a stronger natural imprint on the landscape in comparison to other agricultural environments. The existence and characteristics of semi-natural rural biotopes are thus dependent on both natural processes and active traditional-type management (Poschold & WallisDeVries 2002, European Commission 2009).

Mesic semi-natural grasslands are treeless or nearly treeless biotopes that sustain the most species-rich vascular plant communities among all semi-natural rural biotopes in Finland (Vainio et al. 2001). Traditional use of this biotope included mowing or grazing or both – a common practice was to use grasslands as pastures after each haymaking (Salminen & Kekäläinen 2000). Removal of rocks and shrubs also belonged to the management of this open biotope, whereas controlled burning was apparently occasional (Salminen & Kekäläinen 2000). Pure traditional-type management is, however, virtually extinct in Finland and the remaining mesic grasslands are typically utilized as pastures (Vainio et al. 2001).

The majority of Finnish mesic semi-natural grasslands were converted to fields already in the turn of the 19th and the 20th century (Soininen 1974). Nevertheless, the areal decrease continued and was over 95 % from the 1950's to the beginning of the present century (Vainio et al. 2001, Schulman et al. 2008a,b). Abandonment and conversion to forests have been the main

causes for the decline after the 1960's. The present area of mesic semi-natural grasslands in Finland is approximately 3000-5000 ha and all subtypes of this biotope category are classified as either critically endangered (CR) or endangered (EN) (Schulman et al. 2008a,b).

Forest pastures are seldom separated from other wooded pastures in European literature (e.g. Bergmeier 2010, European Council Directive 92/43/EEC Annex I). In the Finnish context, however, it is rational to make difference between forest pastures (*metsälaidun*) and more open wooded pastures (*hakamaa*). The term wooded meadow is sometimes used to refer to sparsely wooded semi-natural rural biotopes that are exclusively or predominantly managed by mowing (e.g. Ingerpuu et al. 1998). At present extremely rare pollarding and coppicing were practised in some of the wooded meadows (*lehdetniityt, vesaniityt*) (Salminen & Kekäläinen 2000).

In forest pastures (*metsälaidun*), field layer vegetation is dominated by forest species but grassland species are also present (Salminen & Kekäläinen 2000, Schulman et al. 2008b). Canopy cover is generally over 35 % but small openings are typical of this biotope (Salminen & Kekäläinen 2000, Schulman et al. 2008b). In wooded pastures (*hakamaa*), field layer vegetation is dominated by grassland species and canopy cover is typically between 10-35 %. If low-intensity grazing has not changed the characteristics of field layer vegetation, the site is not regarded as a semi-natural rural biotope (Schulman et al. 2008b). I concentrate on the forest pastures on the boreal vegetation zone in this study.

Forest pasture, as defined above, has always been the most common type of semi-natural rural biotope in Finland (Vainio et al. 2001, Schulman et al. 2008b). This biotope was mainly used as pastureland in the traditional animal husbandry (Salminen & Kekäläinen 2000). Other management was apparently occasional and of low intensity, including selective felling of trees for domestic use and removal of spruce (*Picea abies*) (Salminen & Kekäläinen 2000). These practices resulted in small openings in tree canopy that enhanced the growth of field layer vegetation.

Some of the forest pastures were established in former slash-and-burn areas that can be seen in their tree species composition even today (Vainio et al. 2001).

The area of forest pastures decreased by over 99 % from the 1950's to the present, and there is now 5000-9000 ha of this biotope in Finland (Schulman et al. 2008b). The decrease started already before the 1950's, but was less dramatic than for mesic semi-natural grasslands (Schulman et al. 2008b). All subtypes of forest pastures are either critically endangered (CR) or endangered (EN) at present (Schulman et al. 2008a). The remaining sites are threatened by abandonment, eutrophication and intensive forestry (Schulman et al. 2008a). Agri-environmental subsidies for the management of semi-natural rural biotopes have relieved the areal decrease of forest pastures during the last two decades to some extent (Schulman et al. 2008b).

1.3 BRYOPHYTES IN SEMI-NATURAL RURAL BIOTOPES

Very few endotherm species feed on bryophytes and, thus, their presence in semi-natural rural biotopes was mainly seen as a nuisance in the past (Vainio et al. 2001). The elimination of bryophytes by drying, inundating or covering was an essential part of grassland management (Soininen 1974, Vainio et al. 2001). Indeed, a rich bryophyte layer can hamper the emergence of vascular plant seedlings in grasslands (Van Tooren 1990) and some individual bryophyte species can compete with vascular plants also vegetatively, even posing a threat to grassland biodiversity in some occasions (Essl et al. 2014). *Brachythecium* spp. and *Rhytidiadelphus squarrosus* may be the most effective competitors among the bryophytes of Finnish mesic semi-natural grasslands.

However, the impact of bryophyte layer on vascular plants apparently depends on various abiotic and biotic factors. The effects on vascular plant seedling emergence and mortality, for example, are very species-specific and positive relationships

have also been reported (Keizer et al. 1985). It has even been hypothesized that spatial and seasonal variation in bryophyte cover can enhance vascular plant diversity by increasing the differentiation of regeneration niche for vascular plants in calcareous grasslands (Keizer et al. 1985). This hypothesis emphasizes the role of bryophytes as an integral component of ecosystem function, the viewpoint that is easily overlooked when studying bryophytes in productive grassland environments. Soil conditions, for example, are different under bryophyte layer and on bare soil (Concostrina-Zubiri 2013) and some heteropteran species live predominantly on bryophytes (Rintala & Rinne 2011).

More commonly, the subordinate role of bryophytes in the competition for light and space with vascular plants have been highlighted (Chapman & Rose 1991, Virtanen et al. 2000, Bergamini et al. 2001, Aude & Ejrnaes 2005, Löbel et al. 2006, Rydin 2008, Mayer et al. 2009). Both living and dead vascular plant biomass can hamper the growth of bryophytes (Noy-Meir 1989, Chapman & Rose 1991, Mayer et al. 2009). In fact, bryophyte community characteristics most often depend on the structure of vascular plant vegetation, while the characteristics of vascular plant vegetation are typically explained by soil properties (Hejcman et al., 2001; Kull et al., 2005). This pattern may be especially pronounced in productive open grasslands where the competition for light and space is probably strong in the ground layer.

Considering the subordinate role of bryophytes in many grassland biotopes, the abandonment of traditional management and the consequent overgrowth may pose a threat for bryophytes in particular. In Finland, the decrease and deterioration of semi-natural rural biotopes threaten a few bryophyte species, the majority of which grow on bare mineral soil and on old deciduous trees (Laaka-Lindberg et al. 2009, Syrjänen et al. 2010). Many of the species dependent on bare soil are calcicolous and old deciduous trees with basic bark provide the most favourable microhabitats for the epiphytic species (Laaka-Lindberg et al. 2009, Syrjänen et al. 2010). This means

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that probability to encounter red-listed bryophytes is highest in calcareous grasslands and wooded pastures in southeastern Finland among all Finnish semi-natural rural biotopes. The value of these biotopes for Finnish bryophyte diversity is also recognized while the value of mesic grasslands and boreal forest pastures is still largely unknown.

In fact, we know very little about the bryophyte species assemblages of any of the semi-natural rural biotopes in Finland and still less about the effects of management on bryophytes. Lampimäki (1936) reported a decrease in bryophyte cover in forest pastures in comparison to forests, particularly in the open parts of the pastures. Häeggström (1983) documented bryophyte taxa in wooded pastures in the island of Nåtö in Åland while Huhta et al. (2001) recorded the effects of mowing on bryophytes in a mesic semi-natural grassland (meadow) in northern Finland. However, none of these studies concentrated on bryophytes, specifically, and bryophyte communities or community responses were neither analysed nor depicted in more detail.

The effects of management on bryophytes have been studied more in other parts of Europe. The essential role of asymmetric competition with vascular plants is apparent in several works, especially in the most productive biotopes. The abandonment of annual mowing in calcareous fen meadows (semi-natural rich fens) in Switzerland led to an increase in vascular plant biomass and litter and, consequently, to a decrease in bryophyte biomass and species richness (Peintinger & Bergamini 2006). Rapid changes in bryophyte species composition were also documented. The negative impact of abandonment and consequent overgrowth by vascular plants on bryophyte diversity was also evident in a previously grazed semi-natural rich fen in central Sweden (Sundberg 2012). The negative relationship between bryophyte and vascular plant biomass has also been shown in a modern lawn plant community (Virtanen et al. 2000).

The positive relationship between continuous management and bryophyte diversity is not so consistently found in less

productive biotopes. Löbel et al. (2006) found that management (mowing and grazing) had no effect on bryophyte richness or cover in dry calcareous grasslands in the Baltic island of Öland. Instead, grazing increased bryophyte species richness, as well as the species richness of small subordinate vascular plants, in dry British dune grasslands (Plassmann et al. 2010).

Grazing may be generally more favourable management practice for bryophytes than mowing, as very slight changes in bryophyte cover and species richness have been recorded in mowing experiments (Huhta et al. 2001, Vanderpoorten et al. 2004). Small annual ruderal species, in particular, may suffer from the shortage of exposed mineral soil in mown meadows (Van Tooren et al. 1990, Vanderpoorten et al. 2004).

More universally, understanding the availability of different substrates or microhabitats may be the key to understand bryophyte diversity patterns in semi-natural rural biotopes, as many bryophytes are strict substrate specialists. Variation in microhabitat conditions, indeed, increases bryophyte richness in open dry grasslands (Löbel et al. 2006). High microhabitat heterogeneity is related to high bryophyte diversity in many forest biotopes (Mills & Macdonald 2004, Weibull & Rydin 2005, Lõhmus et al. 2007, Marialigeti et al. 2009) and this is expected also in the forest pastures. However, we do not know which microhabitats are important for bryophyte diversity in the wooded environments subjected to grazing.

Given that semi-natural rural biotopes are partly man-made and rather new from the perspective of evolution and speciation, one may ask where did the rich flora and fauna of these biotopes come from. Surprisingly many indigenous European species appear to depend on traditional animal husbandry (Pykälä 2000). Reflecting a more general idea that the present species distribution patterns do not necessarily coincide with the present conditions (e.g. Pärtel 2002), Pykälä (2000) hypothesized that traditional animal husbandry has compensated the human-induced loss of many natural processes, such as floods, fires and megaherbivore grazing. Thus, many European species may have evolved in conditions that almost exclusively can be found in

semi-natural rural biotopes nowadays. The abundance or merely presence of some bryophyte species in mesic grasslands and forest pastures may hence reflect natural processes that are rare in the surrounding landscape at present. Processes important for bryophytes in these semi-natural biotopes may then imitate the suppressed natural processes.

1.4 MITIGATING BIODIVERSITY LOSS

1.4.1 Increasing the area of semi-natural rural biotopes

Considering the unfavourable conservation status of numerous species dependent on semi-natural rural biotopes (Rassi et al. 2010), the prevailing area and quality of these biotopes appear to be insufficient for sustaining their originally high biodiversity in Finland. Restoration of formerly abandoned pastures and meadows by the re-establishment of traditional-type management is one promising way to counteract this trend (Bobbink & Willems 1993, Willems & Bik 1998, Pykälä 2003). The effects of resumed grazing or mowing, sometimes combined with the initial removal of shrubs or trees, on vascular plants have been studied a lot in different semi-natural rural biotopes and in various time-scales (e.g. Bobbink & Willems 1993, Kotiluoto 1998, Huhta et al. 2001, Bakker et al. 2002, Wahlman & Milberg 2002, Hellström et al. 2003, Pykälä 2003, Plassmann et al. 2010, Bakker et al. 2012, Metsoja et al. 2012). However, vascular plant diversity cannot be used as a surrogate measure for bryophyte diversity (Pharo et al. 1999, Virtanen et al. 2000, Vellak et al. 2003, Virtanen & Crawley 2010).

Re-establishment of grazing and mowing are promising measures in the restoration of bryophyte communities in abandoned semi-natural rich fens (Peintinger & Bergamini 2006, Sundberg 2012) and resumed grazing is an effective measure in dry dune grasslands (Plassmann et al. 2010). Instead, mere mowing may be an ineffective way to restore bryophyte communities in dry calcareous (Vanderpoorten et al. 2004) and mesic (Huhta et al. 2001) grasslands. In this thesis, I present an

example of restoration of bryophyte communities in mesic semi-natural grasslands.

The recovery of vascular plant vegetation in a restored site is often very slow in the long term (Bakker et al. 2002, Hellström et al. 2006) although immediate floristic changes during the first few years can be rapid (Bobbink & Willems 1993, Pykälä 2003). Even with an optimal grazing pressure, changes in community structure and species assemblage may continue for decades (Güsewell et al. 1998) and complete recovery is apparently rare still (Bakker et al. 2002). Similarly, Plassmann et al. (2010) found that changes in bryophyte species richness and community structure were especially rapid in the first seven years after the onset of grazing in a 16-year study period in dry dune grasslands. Sundberg (2012) recorded a considerable increase in bryophyte cover and target species abundance in a six-year restoration trial in a semi-natural rich fen. Contrasting these results, Vanderpoorten et al. (2004) documented few changes in bryophyte species richness after 15 years of restorative mowing in a dry calcareous grassland. Fieldwork for the restoration example in this thesis was carried out on average 15 years after the onset of restorative grazing; thus, also relatively long-term effects of restoration can be inferred from this example.

1.4.2 Enhancing the quality of management

Apart from the decline in area, semi-natural rural biotopes are also threatened by suboptimal management (Pykälä 2001, Schulman 2008a). Practices potentially causing eutrophication, such as feeding cattle by additional forage or allowing cattle free access to fertilized areas, are of special concern (Pykälä 2001, Vainio et al. 2001). Airborne nitrogen pollution threatens semi-natural rural biotopes even without such practises throughout Europe (Sala et al. 2000, Bobbink et al. 2010, Stevens et al. 2010). Furthermore, the adverse effects of phosphorous on the biodiversity of semi-natural rural biotopes have been highlighted (Merunkova & Chytry 2012, Ceulemans et al. 2013).

Among vascular plants, competitively subordinate species are especially vulnerable to the increased production, the

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increase of a few competitive species and competitive exclusion caused by eutrophication (Grime 2001). Thus, bryophytes may be especially sensitive to eutrophication due to their minute size (Aude & Ejrnaes 2005). They can also be very slow in recovery if eutrophication has once taken place (Virtanen et al. 2000, Cunha et al. 2002, Edmondson et al. 2013). Furthermore, direct toxic effects of nutrient deposition may particularly threaten poikilohydric bryophytes (Aude & Ejrnaes 2005).

In this thesis, I examine whether the common management practice of fencing forest pastures within the same enclosures as fertilized grassland pastures leads to eutrophication and consequent decline in bryophyte diversity in Finnish forest pastures. It is hypothesized that when cattle can freely roam between the fertilized grassland pastures and unfertilized forest pastures, nutrients are transported to the forest pastures in the faeces and urine of grazing animals (*see* Pykälä 2001). Besides eutrophication, this kind of grassland connection may also change the intensity and spatial patterns of grazing in forest pastures. Vainio et al. (2001) assessed that approximately every second forest pasture was connected to grasslands at the end of the 20th century in Finland.

Intensive forestry is yet another problem that has decreased the ecological value of wooded semi-natural rural biotopes in Finland (Vainio et al. 2001, Schulman et al. 2008b). Forest stand structures in Finnish forest pastures have become increasingly homogenous in their age-class distribution, tree species composition and spatial distribution. This issue is closely linked to the availability of microhabitats in forest pastures, and even if the effects of forest stand structure did not belong to the specific study issues in articles III-IV, I briefly address the theme at the end of this summary part. Similarly, I briefly discuss the risk of excessively high grazing intensities in mesic semi-natural grasslands and forest pastures.

1.5 AIMS OF THE THESIS

This thesis is based on four articles (I-VI) of which the two first concern mesic semi-natural grasslands and the two last forest pastures. The aim of the thesis is to present the most important results of the articles, but in a larger context than they are treated in the articles. The original study questions in the articles are not precisely followed in this summary part. The study design, statistical analyses and results are all presented briefly in the following text and in more detail in the articles. The discussion part is emphasized here, instead.

I first assess the importance of mesic semi-natural grasslands and forest pastures to bryophyte diversity in Finland and next the effects of pasture management on bryophytes in these two biotopes. Finally, I present examples of how to sustain bryophyte diversity in mesic grasslands and forest pastures by restoration and by improving the management practices. The specific study questions are presented below.

Main questions:

1. What is the conservation value and which are the characteristics of bryophyte communities in mesic semi-natural grasslands and forest pastures?
2. How is pasture management related to bryophyte diversity in mesic semi-natural grasslands and forest pastures?
3. Can bryophyte communities be restored by the re-establishment of grazing in abandoned mesic semi-natural grasslands in a decadal time scale?
4. Is the common practice of fencing forest pastures within the same enclosures as fertilized grassland pastures a threat to bryophyte diversity in forest pastures?

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Minor questions:

5. What is the ecological quality of forest stand structures in forest pastures?
6. May high grazing intensities threaten bryophyte diversity in mesic semi-natural grasslands and forest pastures?

2 *Material and methods*

2.1 STUDY AREAS AND MEASUREMENTS

The mesic grasslands of this study (articles I-II) are located on the steep (15°–25°) river valley slopes of the river Rekijoki and its tributaries in the rural municipality of Somero, SW Finland. The mesic grasslands of the region form the largest still remaining entity of this biotope type in Finland (Vainio et al. 2001, Kontula et al. 2000). The area belongs to the ancient seabed of various Baltic Sea stages and is characterized by thick and homogenous layers of deposited clay (Aartolahti 1975). Up to 30 m deep ravines in the study region form a conspicuous feature in this otherwise very flat lowland landscape (Aartolahti 1975). The area is situated in the southernmost fringe of the south-boreal vegetation zone (Kalliola 1973).

Three classes of mesic grassland were included in the study on the basis of their past use for cattle grazing: i) grasslands that had been continuously grazed for at least 50 years (n=7, Fig 1), ii) previously abandoned grasslands where grazing had been re-established 15-20 years ago (n=7) and iii) grasslands abandoned at least 30-50 years ago (n=7, Fig 2). All of the grazed sites were seasonally (in the summer) grazed by cattle. Twenty study plots (60x60 cm) were randomly placed on each of the 21 grasslands. At each plot, the cover of each bryophyte species was estimated in the full percentage scale. The cover of vascular plant litter, the cover of bare soil and the height of vascular plant vegetation were also measured at every study plot, like were the covers of graminoid and herbaceous vascular plant species. The fieldwork was carried out in July 2009.



Figure 1. A continuously grazed mesic grassland in Häntälä village in Somero.



Figure 2. Abandoned mesic grasslands are typically dominated by few competitive graminoid species. Häntälä, Somero.

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As regards the biotope classification in the inventory of threatened biotope types in Finland in 2008 (Schulman et al. 2008a,b), the mesic grasslands of this study belong to the subclasses of low herb mesic grasslands (*tuore pienruohoniitty*) and graminoid mesic grasslands (*tuore heinäniitty*). The continuously grazed and re-established (restored) grasslands were mosaics of these two subclasses, while the abandoned grasslands were predominantly graminoid mesic grasslands. Low herb mesic grasslands typically change into graminoid mesic grasslands after abandonment (Schulman et al. 2008b).

A total of 42 boreal forest pastures on non-calcareous soil in North-Karelia were included in this study (articles III-IV). The study region is situated in the northern fringe of the south-boreal vegetation zone (Kalliola 1973).

The effect of microhabitat heterogeneity (microsite entropy in article III) and microhabitat availability (microsite availability in article III) on bryophyte species richness was studied in 17 traditionally managed pine-dominated (*Pinus sylvestris*) forest pastures (III). All of these pastures hence belonged to the subclass of forest pastures dominated by coniferous trees (*havumetsälaidun*). Four study plots (5x5 m) were set on each forest pastures. At each plot, bryophyte species growing on five different microhabitat types were separately recorded: rocks, coarse woody debris (CWD), tree bases, mineral soil patches and closed vegetation on ground. A species growing on a boundary between closed vegetation and another microhabitat type (rocks, CWD, tree bases, mineral soil patches) was included in the latter if it was not found elsewhere in the surrounding closed vegetation within the radius of one meter. This was because the occurrence of a species on a boundary between closed vegetation and another microhabitat type apparently resulted from specific microenvironmental conditions created by the latter. The surface area (cm²) of each microhabitat type at every plot was also estimated. The measurements were accomplished in July 2011.

The other 25 forest pastures belonged to the study of the effects of grassland connection on forest pasture vegetation (IV).

In these sites, Silver birch (*Betula pendula*), Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and Grey alder (*Alnus incana*) were the dominant tree species. All of the three subclasses of forest pastures presented in the inventory of threatened biotope types in Finland in 2008 (Schulman et al. 2008a,b) were thus included in this study. In 18 of the 25 forest pastures, cattle could freely roam between the semi-natural forest pastures and fertilized grassland pastures (Fig 3). Cattle had no access to fertilized grasslands in the remaining seven, traditionally managed, forest pastures. In addition to the 25 forest pastures, 18 forests and 18 fertilized grassland pastures on cultivated land were also included in this study (Fig 4).



Figure 3. An example of the controversial management practice of fencing forest pastures within the same enclosures as fertilized grassland pastures. Kitee.



Figure 4. Forests included in the study (at right) were selected so that they resembled nearby forest pastures (at left) as much as possible. Tohmajärvi.

The study area of 50 x 50 m was established on each of the 25 forest pastures and 18 forests so that each of these areas bordered a fertilized grassland on one side (see Fig 2 in article IV). The study areas were further divided to an inner and an outer sector in order to study whether the grassland connection has different effects near the grassland border and in the inner parts of the forest pastures. Five study plots of 50 x 50 cm were randomly placed in each sector, and the cover of bryophyte and vascular plant species was estimated in the full percentage scale (Fig 5). The cover of vascular plant litter, the cover of bare soil and the height of vascular plant vegetation were also measured at every study plot.

Soil electrical conductivity, pH and nutrient levels (Ca, K, P, Mg, S) were measured from the soil samples collected in the forest pastures with grassland connection (n=18), in the forests (n=18) and, furthermore, in the adjacent fertilized grassland pastures (n=18). These measurements were not carried out in the forest pastures without grassland connection (n=7). The

fieldwork was carried out in July 2012 in the forest pastures with grassland connection, in the forests and in the fertilized grasslands. The forest pastures without grassland connection were sampled in July 2010.

Bryophyte specimens for microscopic identification were collected during the fieldwork when identification in field conditions was not possible. The collected species are stored either as voucher specimens in the Botanical Museum of Oulu or as mixed (plot-level) samples in the personal collection of the author.



Figure 5. Vegetation sampling at a study plot.

Figure: Päivi Jokinen

2.2 SELECTION OF DIVERSITY VARIABLES

Several dependent variables depicting bryophyte species richness and diversity are used in this thesis and some variables have different names in different articles (Table 1). This inconsistency indicates how difficult it was to find completely satisfying variable names for bryophyte species richness, in

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particular, and my personal opinion of the best alternatives has evolved through the thesis project. It has often been crucial to clearly separate the species richness at the plot and pasture scales. For this purpose, the terms alpha and gamma richness are useful, leading a reader to think just the scale of measurement. However, the terms total and average species richness possibly tell a reader more about the calculation of these variables. In this thesis, I use the terms alpha and gamma richness to refer to species richness at the plot and pasture scales, respectively, instead of the terms in the original articles.

Table 1. *The variables depicting the species richness, diversity and abundance of bryophytes in articles I-IV. Shannon's diversity in article IV is also included although it was only calculated for vascular plants.*

	Article I	Article II	Article III	Article IV
1	Species richness	Gamma richness	Gamma richness	Total species richness
2	Species density	Alpha richness	Alpha richness	Average species richness
3	-	Beta richness (alpha/gamma)		-
4	Species diversity	-		Diversity (Shannon's index)
5	Bryophyte cover	Bryophyte cover		Bryophyte cover

1 The number of species in a grassland /pasture.

2 Average number of species at the study plots in a grassland/pasture.

3 Species "turnover", average number of species at the study plots in a grassland/pasture per the number of species in the same grassland/pasture.

4 Species diversity (mathematical), average diversity at the study plots in a grassland/pasture; ${}^qD = (\sum p_i^q)^{1/(1-q)}$ (Tuomisto 2010) in article I; $H' = -\sum (p_i * \ln p_i)$ (Shannon 1948) in article IV.

5 Average cover of bryophytes at the study plots in a grassland/pasture.

Similarly, the selection of diversity measures has been rather complicated. Different mathematical measures and indexes for diversity mean strictly speaking different things, and the

selection should depend on the case in question (Tuomisto 2010). However, selection on mathematical grounds is not always easy and factors like journal traditions and referee opinions have also affected the final selections in the articles. In the following text, references to mathematically defined diversity measures are highlighted while the term diversity is mainly used as its general meaning.

2.3 DATA ANALYSIS

The three grassland categories (n=7) were compared using nonparametric Kruskal-Wallis test in order to reveal the effects of abandonment and restoration on bryophyte diversity in the mesic grasslands (I). The response variables were bryophyte species richness (alpha and gamma), bryophyte species diversity and bryophyte cover (Table 1). Non-metric multidimensional scaling (NMS), multiresponse permutation procedure (MRPP) and the indicator species analysis of Dufrêne and Legendre (1997) were applied in the comparison of community structures and species assemblages between the three grassland categories.

Before a closer examination of the relationship between bryophytes and environmental variables (II), the bryophyte species found in the mesic grasslands were classified to the life-strategy groups of During (1992). The strongly correlated environmental variables were next converted to a smaller set of orthogonal principal components using principal component analysis (PCA). The species richness (alpha and gamma) and cover of all bryophytes and of life-strategy groups (perennial stayers and colonists) were then explained by these components in a linear regression analysis. Finally, distribution patterns of individual bryophyte species along the gradients of the exposure of bare soil, the height of vascular plant vegetation and the cover of vascular plant litter were explored. Differences in the distribution patterns between the life-strategy groups were tested with *t*-test.

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In the study of the effects of microhabitat heterogeneity and availability in the forest pastures, differences in bryophyte richness (alpha and gamma) between the microhabitat types were tested using permutative ANOVA (III). Linear regression was used to explain bryophyte species richness (alpha and gamma) by the availability of microhabitats and, separately, by the diversity (Shannon's index) of microhabitats. The indicator species analysis of Dufrêne and Legendre (1997) was applied in the examination of the distribution patterns of bryophyte species between the microhabitat types.

In order to reveal the impacts of grassland connection in the forest pastures, Wilcoxon matched-pairs signed rank test was first used to examine differences in soil chemistry (pH, electrical conductivity, Ca, K, P, Mg, S) between the forest pastures with grassland connection, the adjacent grassland pastures and the nearby forests (IV). The species richness (alpha and gamma) and the cover of bryophytes between i) the forest pastures with and without grassland connection and the forests and ii) between the front and the inner sectors were next compared with a mixed model ANOVA, including the front and inner sector division as a within-subject factor. The same analyses were done for vascular plant species richness (alpha and gamma) and diversity (Shannon's index).

The species richness (alpha and gamma) of bryophytes and vascular plants and the cover of bryophytes were then explained by the pre-selected environmental variables in linear regression analyses. The analyses were performed separately for the forest pastures with grassland connection and for the forests. The forest pastures without grassland connection were not included in the regression analyses. Finally, differences in the community structures and species assemblages of both bryophytes and vascular plants between the forest pastures with and without grassland connection and the forests were analysed using detrended correspondence analysis (DCA), MRPP and the indicator species analysis of Dufrêne and Legendre (1997).

The Kruskal-Wallis test, PCA, *t*-test and the parametric analyses of variance were performed using SPSS 17.0 (SPSS Inc.

2008, Chicago). The program PC-ORD 5 (McCune and Mefford 1999) was applied while doing the NMS, MRPP, permutative ANOVA and the indicator species analyses. The Wilcoxon matched-pairs signed rank test was conducted with Excel 2013 for Windows.

3 Results and discussion

3.1 BRYOPHYTE COMMUNITIES

3.1.1 Mesic semi-natural grasslands sustain characteristic bryophyte communities

A total of 42 moss and none liverwort species were found in the mesic grasslands of this study (I, II). Of these, 34 species grew in the continuously grazed, 27 in the restored and 25 in the abandoned grasslands (I). Altogether 19 species were exclusively found in the grazed grasslands and five species only in the abandoned sites (I). Keizer et al. (1985) reported 47 bryophyte species in a mown six ha calcareous grassland in the Netherlands, including many calcicole species which do not grow in the mesic grasslands of Rekijoki region. Only 13 species were shared with this study. Ingerpuu et al. (1998) reported 63 epigeic bryophyte species in a 100 ha calcareous wooded meadow in Estonia, of which 19 species were the same as in the mesic grasslands of this study. The average bryophyte species richness in the continuously grazed mesic grasslands, four species per 0.36 m² (I), was also roughly similar or little lower than in a mown calcareous grassland in Belgium (seven species per m²) (Vanderpoorten et al. 2004) or in the wooded meadow in Estonia (4–10 species per m²) (Ingerpuu et al. 1998). Hence, considering that the mesic semi-natural grasslands of this study are on non-calcareous soil, the bryophyte species richness of this biotope is relatively high.

However, the bryophyte species richness in the mesic grasslands (42 species) does not stand out in comparison to many other species groups. Pykälä (2003) found 252 vascular plant species in 30 mesic grasslands in the same area, 209 species in continuously grazed, 173 species in restored and 156 species in abandoned sites. Pöyry et al. (2004) recorded altogether 96 species of moths and butterflies in 33 mesic grasslands in

Rekijoki region in two separate sampling years. This study also covered the same three grassland categories than the present study. The mesic grasslands of the region are also very important for Finnish dung beetle diversity (Roslin & Heliövaara 2009).

Perennials (perennial stayers) and colonists comprised the most species-rich life-strategy groups (During 1992) among bryophytes in the mesic grasslands (II). In addition, a few shuttle species were recorded. Shuttle species are characterized by short or medium lifespan and production of few large (>20 µm) spores (During 1992). Perennials formed 85 % of the total bryophyte cover and 48 % of the total number of species (II). Corresponding values for colonists were 14 % of the total bryophyte cover and 40 % of the total number of species. The remaining 1 % of the total cover and 2 % of the total species richness consisted of annual, short-lived and long-lived shuttle species. The scarcity of annual shuttle species in the data may be caused, at least in part, by the transient vegetative shoots of these species that makes them easily overlooked in a non-recurrent inventory. Annual shuttle species have been documented in very low frequencies in grassland vegetation also earlier (Van Tooren et al. 1990).

Despite their low cover in the mesic grasslands, colonists and annual shuttle species evidently formed the most remarkable species groups in terms of biodiversity conservation (II). Grazed unfertilized semi-natural rural biotopes on clay soil can be important habitats for many of these species, e.g. *Barbula unguiculata*, *Bryum rubens*, *Bryum violaceum*, *Fissidens* spp., *Phascum cuspidatum* and *Weissia controversa*. Small ruderal bryophytes of this kind may be especially sensitive to eutrophication in agricultural environments (During & Willems 1986, During 1992, Aude & Ejrnaes 2005).

Unfertilized mesic grasslands may also be important for perennial *Brachythecium campestre* (NT), the only red-listed species found in the mesic grasslands of this study (I). *Plagiomnium affine*, *Syntrichia ruralis* and *Thuidium* spp. are other

perennial species that appear to be typical of traditionally managed mesic semi-natural grasslands.

The mesic grasslands of this study sustained especially few substrates for bryophytes. In addition to the lack of woody substrates, rocks and rock outcrops were also absent. These grasslands are, in this sense, rather atypical of most grasslands in Finland. Rock substrate in particular would increase bryophyte diversity in the grasslands, but very few rare or threatened species could be found on exposed rocks in this non-calcareous area.

The results presented in articles I-II suggest that even if bryophytes should not be prioritized over many other species groups in the biodiversity conservation of mesic semi-natural grasslands, they evidently form an integral and characteristic part of biodiversity in this biotope. Hence, bryophyte communities should also be considered in the planning of management in mesic grasslands.

3.1.2 Individual species separate the bryophyte communities of boreal forest pastures and non-grazed boreal forests

Altogether 65 mosses and 18 liverworts were found on different microhabitats (rocks, coarse woody debris, tree bases, mineral soil patches and closed vegetation) in 17 forest pastures (III). This was roughly similar to species richness documented in comparable studies of non-grazed boreal forests: e.g. 73 mosses and 32 liverworts in four stands (2 ha each) of unmanaged boreal mixed forest in Canada (Cole et al. 2008), 52 mosses and 22 liverworts in three unmanaged boreo-nemoral forest stands (1.1–1.2 ha each) in Estonia (Vellak & Paal 1999) and 85 mosses and 25 liverworts in 26 stands (<2 ha each) belonging to three types of managed boreal forests in Canada (Ross-Davis & Frego 2002). Furthermore, on average 22.6 species of mosses and 4.5 species of liverworts were found in the forest pastures of this study (0.1 ha per site) (III), while Dynesius et al. (2009) found on average 20 moss and 10 liverwort species at 18 plots (0.1 ha each) in 30–50 years ago clear-cut non-grazed north-boreal pine forests in Sweden.

In addition to the similarities in bryophyte species richness, the similarities in bryophyte communities between the forest pastures and non-grazed boreal forests were substantial (III, IV). One clear difference between these two biotopes was, however, that small ruderal bryophytes, such as *Bryum* spp., *Dicranella* spp., *Ditrichum* spp., *Tortula truncata* and *Ceratodon purpureus*, were more abundant in the forest pastures (IV). Furthermore, the only red-listed species found in the forest pastures, *Tayloria tenuis* (NT), was only found in the grazed sites. This species grows on manure that is evidently much more frequently available in forest pastures in comparison to non-grazed forests. *Tayloria tenuis* is worth highlighting, given that it was rather common in the forest pastures, signalling the positive effects of grazing on biodiversity. Instead, not any dung-dwelling bryophyte species were found in the mesic grasslands of Rekijoki region, probably because of too dry microenvironmental conditions in summer (I, III).

Still another difference between the forest pastures and forests was that individual pleurocarpous perennial species, such as *Abietinella abietina*, *Brachythecium albicans*, *Climacium dendroides* and *Rhytidiadelphus squarrosus*, were exclusively found in the forest pastures (IV). *Climacium dendroides* is common in various mesic and moist biotopes but the other three species grow in exposed and dry environments, possibly indicating the general openness of the forest pastures. Furthermore, all of these species can be defined as ruderals (Ulvinen et al. 2002). As forest pasture vegetation is defined as a mixture of vascular plant species from forests and grassland biotopes (Sculman et al. 2008b), we can add that it is also a mixture of bryophyte species from forests and grassland biotopes.

The forest pastures sustained more bryophyte species than the open mesic grasslands (I, III, IV). Bryophytes also seem to form a more substantial part of total plant diversity in boreal forest pastures in comparison to mesic grasslands. This is indicated by 43 epigeic bryophyte species against 120 vascular plant species in the seven traditionally managed forest pastures (IV), while the 42 mosses in the mesic grasslands clearly lags

behind 252 vascular plants found by Pykälä (2003) in the same grasslands. Noteworthy, only epigeic bryophyte species are considered in this comparison.

Ingerpuu et al. (1998) emphasized the importance of traditionally managed wooded meadows (on calcareous soil in the temperate vegetation zone) to Estonian bryophyte diversity. A similar emphasis cannot be put on non-calcareous forest pastures in eastern Finland. Individual bryophyte species on ephemeral microhabitats (bare soil and dung) in this biotope are still important for bryophyte diversity in a larger context: even the slight differences in bryophyte communities between the forest pastures and forests denote that forest pastures have potential to increase biodiversity at landscape level.

3.2 EFFECTS OF PASTURE MANAGEMENT AND MICROHABITAT AVAILABILITY

3.2.1 Grazing is vital for bryophytes in mesic semi-natural grasslands

The cessation of grazing had led to nearly complete exclusion of bryophytes from the abandoned mesic semi-natural grasslands within 40-50 years (I). This was probably due to an increase in vascular plant biomass and litter and to a decrease in soil disturbances after the abandonment that resulted in a substantial intensification of competition for space and light in the ground layer (II, Miller et al. 2010). Other vegetation changes, such as an increase in the cover of graminoid species after the abandonment, may also have had influence on competition regime and on bryophyte communities (II, Miller et al. 2010). It seems that bryophytes are well comparable to other small and subordinate plant groups that suffer from an increased interspecific competition in abandoned or eutrophicated grasslands (*for vascular plants see Pykälä 2003, 2004*).

The height of vascular plant vegetation and the cover of vascular plant litter were the best surrogate measures for aboveground vascular plant biomass in this study and

covariation in these two variables revealed the main grazing intensity gradient in the mesic grasslands (II). High vascular plant vegetation and abundant vascular plant litter were related to low bryophyte species richness and cover (II). This observation supports the view of the predominantly negative relationship between vascular plant biomass and the species richness and biomass of bryophytes in productive grassland biotopes (Virtanen et al. 2000, Bergamini et al. 2001, Aude & Ejrnaes 2005, Hejcman et al. 2010, Müller et al. 2012). Competition with vascular plants is even considered as the main determinant of bryophyte occurrence in some grassland environments (Virtanen et al. 2000, Bergamini et al. 2001, Aude & Ejrnæs 2005).

No signs of competitively strong bryophyte growths covering large continuous areas were found in the study sites (I,II). So, even if some pleurocarpous bryophyte species may have potential to vegetatively compete with vascular plants in certain conditions, this seems unlikely or at least rare in productive mesic grasslands. Instead, bryophytes probably compete with vascular plants by pre-emptying the space also in Finnish mesic grasslands, but this issue is beyond the reach of this study.

The positive effects of soil disturbances on bryophyte diversity in the mesic grasslands are worth emphasizing. The availability of bare soil was strongly related to high bryophyte species richness (II). In addition to relieving competition in the ground layer, the patches of bare soil probably act as sites for establishment, the function that can be very essential to bryophyte diversity in this biotope. The importance of soil disturbances also supports the impression that grazing may be generally more beneficial management practice for bryophytes in comparison to mowing (Huhta et al. 2001, Vanderpoorten et al. 2004).

The distribution of colonist species, in particular, was centred in those grasslands where soil disturbances were most frequent (II). This species group obviously evades competition by utilizing the ephemeral patches of mineral soil (II, During 1992, Van Tooren et al. 1990). Indeed, the availability of suitable

substrate is often a more important determinant of survival for colonists than dispersal limitation (Miller & McDaniel 2004).

Shuttle species were too scarce to be included in the analyses but the distribution of especially annual shuttle species was also strongly inclined to the intensively grazed grasslands (II). The annual shuttle species of this study, *Tortula truncata* and *Phascum cuspidatum*, are common in Finnish agricultural environments but this species group includes many rare and threatened species for which the frequent and continuous soil disturbances in grazed semi-natural rural biotopes may be very important (Ulvinen et al. 2002, Laaka-Lindberg et al. 2009). Unlike colonists, shuttle species are not capable of an effective airborne spore dispersal (During 1992) that may make them especially vulnerable to the areal decrease and fragmentation of semi-natural rural biotopes.

3.2.2 Exposed mineral soil and dung are key microhabitats in North-Karelian forest pastures

The availability of different microhabitats was naturally higher in the North-Karelian forest pastures in comparison to the open mesic grasslands in Rekijoki region (II, III). However, the patches of bare mineral soil were of high importance to bryophyte diversity also in the forest pastures (III). Bryophyte species richness (in total 42 species, gamma richness 6.3, alpha richness 2.2) was not especially high on this microhabitat type (III) and, in contrast to the mesic grasslands, the cover of bare soil did not explain bryophyte species richness in the forest pastures (III, IV). Instead, the characteristic species found on bare mineral soil give reason to emphasize the importance of soil disturbances. The forest floor (closed) vegetation mainly hosted common forest and grassland species in the forest pastures (III, IV). In total 38 species (gamma richness 11.2, alpha richness 5.5) were found on this microhabitat.

The recurrent nature of soil disturbances, specifically, is important in forest pastures (III, IV). The number of bryophyte species growing on exposed mineral soil also increases after forest cuttings in forest biotopes but decreases again in forest

succession (Dynesius & Hylander 2007). Jonsson & Esseen (1998) hypothesized that bryophyte communities in boreal forests may be generally more dependent on soil disturbances than vascular plants are. Continuity of soil disturbances is, however, dependent on sporadic treefalls in non-grazed forests (Jonsson & Esseen 1990).

Grazing cattle also creates microhabitats for *Tayloria tenuis* that grows on dung patches, another microhabitat that is worth emphasizing in the non-calcareous forest pastures (III). Obviously, the positive effects of grazing on bryophyte diversity are largely mediated through ephemeral microhabitats in forest pastures. Bare soil and cattle dung were probably the most unique microhabitat types in the forest pastures while the other included microhabitats were apparently common in surrounding biotopes.

Of the other microhabitat types in the forest pastures, rocks proved to be the most species rich (III). Altogether 63 species (gamma richness 19.0, alpha richness 9.5) were found on this microhabitat. Non-calcareous rocks and boulders are, however, common elsewhere in Finnish nature, like are the species growing on them. One ecologically interesting detail is still worth noting: many common forest floor bryophytes were most frequently found on or around rocks in the forest pastures, apparently because rocks offered shelter from trampling in this grazed environment (III). Similarly, rocks provide refugia for bryophytes during a forest fire and after a clearcutting in forests (Hylander & Johnson 2010, Schmalholz & Hylander 2011).

Bryophyte species richness on coarse woody debris (CWD, comprising branches, logs and stumps with the mean diameter over 5 cm) was the second highest of the microhabitat types included in this study (in total 46 species, gamma richness 12.2, alpha richness 5.2). However, the species list consisted of very common epixylic and generalist species (III). In unmanaged boreal forests, large logs often sustain high bryophyte diversity (Jonsson & Esseen 1990, Berg et al. 2002, Dynesius et al. 2009, Mills & Macdonald 2004, Rajandu et al. 2009, Madzule et al. 2012) and many red-listed liverworts are dependent on dead

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wood (Laaka-Lindberg et al. 2009). Large stumps cannot compensate the loss of large logs (Rajandu et al. 2009). In fact, large logs were practically absent in the forest pastures (III). This probably indicates the effectiveness of modern forestry in these sites (Vainio et al. 2001, Schulman et al. 2008b).

Actually, the 17 forest pastures of this study (III) could be too exposed and dry for many epixylic liverwort and moss species even if there was dead wood. These species are generally more diverse in humid and cool conditions (Söderström 1988, Berg et al. 2002, Hylander 2005, Odor et al. 2006, Dynesius & Hylander 2007, Shelley et al. 2012). In oak-rich forests in southern Sweden, bryophyte species richness on dead wood decreased after the removal of 25 % of tree basal area (Paltto et al. 2008). Grazing cattle may also trample and rearrange twigs and logs disturbing the survival of epixylic species. It is still recommended to leave large logs in forest pastures, as many other species groups (e.g. lichens, polypores and hymenopterans) may benefit from dead wood also in very exposed environments. For bryophytes, dead wood may be more significant substrate in moist and shady forest pastures. The importance of dead wood should also be studied in forest pastures dominated by deciduous trees. The 17 forest pastures in the study of microhabitat availability (III) were dominated by coniferous trees; thus, occasional dead wood was also predominantly coniferous.

Bryophytes on tree bases (on bark or on ground near the trunk) were also recorded in this study. Altogether 39 species (gamma richness 11.4, alpha richness 5.5) were found, almost all of which were common forest floor species (III). Bryophytes growing on higher trunk parts were practically lacking and it seems that epiphytic species are generally rare in North-Karelian forest pastures. However, epiphytic bryophyte species may be somewhat more abundant in forest pastures where aspen (*Populus tremula*), goat willow (*Salix caprea*) and rowan (*Sorbus aucuparia*) are more common. These species were only occasionally documented in the 17 forest pastures of this study (III). Southern deciduous trees, such as oaks (*Quercus*) and ashes (*Fraxinus*), are practically absent from natural habitats in these

latitudes. These tree species provide basic substrates for some rare and threatened epiphytic bryophyte species in grazed biotopes of the southern hemiboreal vegetation zone (Ulvinen et al. 2002, Laaka-Lindberg et al. 2009). Especially important they are when pollarded (Moe & Botnen 2000, Berg et al. 2002).

Grazing evidently moulds the characteristics of bryophyte communities in North-Karelian forest pastures on non-calcareous soil, but unlike in the mesic grasslands, only individual bryophyte species appear to be dependent on it. Furthermore, whereas grazing is practically the only applied management practice in mesic grasslands nowadays, forestry practices have potentially strong biodiversity effects in forest pastures. The effects of forestry and forest-stand structure on the ecological quality of forest pastures are further discussed in chapter 3.3.4.

3.3 SUSTAINING BRYOPHYTE DIVERSITY IN SEMI-NATURAL RURAL BIOTOPES – EXAMPLES AND RECOMMENDATIONS

3.3.1 Re-establishment of grazing is an effective way to restore bryophyte communities in mesic grasslands

Re-establishment of grazing is a promising way to restore vascular plant communities in abandoned mesic semi-natural grasslands (Pykälä 2003) and the same conclusion can be made concerning the restoration of bryophyte communities in this biotope (I). Pykälä (2003, 2005) found that the restored grasslands in the very same study region more often resembled the abandoned than the continuously grazed sites in their vascular plant communities five years from the restart of grazing. In this study, the majority of the restored grasslands were similar to the continuously grazed sites in their bryophyte communities after 10-15 years of restorative grazing (I). However, the recovery pace of bryophytes and vascular plants cannot be compared in this instance, as we do not know how much the vascular plant communities had recovered in the ten years which separates these two studies.

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Despite the predominantly promising results of restoration, high variability in the species richness (alpha and gamma) and cover of bryophytes in the restored grasslands indicates that the recovery of bryophyte communities had not been equally successful at every site (I). Some individual restored grasslands were even similar with the abandoned ones in their bryophyte species richness and cover (I). This was probably due to an insufficient grazing intensity in these sites, maintaining intensive competition in the ground layer and preventing frequent soil disturbances typical of traditionally managed grasslands (I). Pykälä (2003) also assessed that low grazing pressure in some of the restored grasslands hampered the recovery of vascular plant communities. Grazing intensity can be regarded as a key factor in the conservation of grassland biotopes (Stewart & Pullin 2008) and comparatively high intensity seems to be essential for the recovery and maintenance of valuable bryophyte communities in mesic grasslands.

Because of the importance of soil disturbances for bryophytes, grazing may be a generally more suitable tool for the restoration of bryophyte communities than mowing (I, Vanderpoorten et al. 2004). Cattle may be the most suitable grazer in the restoration of both bryophyte and vascular plant communities in mesic grasslands, as it consumes graminoids more effectively than sheep (Haeggström 1990). The abundance of a few competitive graminoid species tends to increase in this biotope after abandonment (Pykälä 2005) and these species may restrict the recovery of bryophyte communities via dense turfs and effective litter production (II). The importance of soil disturbances and dung (in moist and shady biotopes) to bryophyte diversity in semi-natural rural biotopes also indicates that mown substitutive environments, such as road verges, may not compensate the loss of grazed biotopes for bryophytes, while they may be more effective in the sustenance of vascular plant diversity (Auestad et al. 2011).

It has been hypothesized that traditional combination of mowing and grazing could be the most effective management practice in the restoration of vascular plant communities in

abandoned mesic grasslands (Hellström et al. 2003). Mowing is usually a more effective way to remove nutrients from grasslands in comparison to grazing (Pykälä 2001) but mowing alone may be ineffective if the lack of soil disturbances limit plant recruitment (Huhta et al. 2001). Undoubtedly, the combination of mowing and grazing would also restore and sustain characteristic bryophyte communities in mesic grasslands. Including also mowing and hay removal in the management may benefit bryophyte communities by decreasing the production of vascular plant biomass in the long term.

In this study, at least one continuously grazed grassland was always found in an immediate vicinity of each restored grassland and the promising results of restoration may reflect a rich regional species pool in the study region. The limited dispersal capacity of species from neighbouring biotopes and from soil seed bank is often posed as an explanation for the incomplete success of restoration of vascular plant communities in grassland biotopes (Stampfli & Zeiter 1999, Mitlacher et al. 2002, Bakker et al. 2002, Aavik et al. 2008, Hellström et al. 2009, Aavik et al. 2013) and bryophytes may also suffer from dispersal limitation. Many pleurocarpous bryophytes, in particular, are slow in dispersal, even when source populations are found in an immediate vicinity (Van Tooren et al. 1990). Shuttle species may also be slow to colonize new grasslands (During 1992), at least when there is no epizoochorous dispersal by grazing animals (Pauliuk et al. 2011). Instead, colonists are adapted to an effective spreading by their light spores (During 1992, Hutsemekers et al. 2008). The role of soil propagule bank in the establishment of bryophytes is insufficiently known although the high investment of some short-lived acrocarpous species (shuttle species) in large spores implies its importance (During & Willems 1986, During 1992). However, this issue was not tackled in more detail in this study.

The findings of this study are potentially applicable to the restoration of other open or sparsely wooded mesic semi-natural rural biotopes. Of course, grazing intensity has to be adjusted separately in each biotope and site, keeping in mind that

insufficient grazing intensity can hamper the recovery of both bryophyte (I) and vascular plant communities (Kotiluoto 1998, Pykälä 2003). However, many other species groups demand lower grazing or mowing intensities (Söderström et al. 2001, Kruess & Tschardtke 2002, Vessby et al. 2002, Hoste-Danyłow et al. 2010). Hence, management has to be both continuous in time and variable in space (Vessby et al. 2002, Pöyry et al. 2004, 2006). With the aid of the field inventories of different taxonomic groups, management efforts and different management practices can ideally be directed to the sites where their effects are optimal (WallisDeWries et al. 2002). The results of this thesis may be less useful in the restoration and management of the moistest and driest ends of semi-natural rural biotopes, as the relationship between bryophyte diversity and management may deviate from what found in this study (e.g. Löbel et al. 2006).

3.3.2 Grassland connection may be more serious threat to vascular plants than for bryophytes in forest pastures

Grassland connection had led to changes in soil chemistry in the forest pastures when compared with the background levels in the adjacent forests (IV). Soil electrical conductivity and K concentration were significantly higher in the forest pastures while pH and Ca, P and Mg levels only tended to be elevated in this biotope (IV). K in particular appears to move effectively from fertilized grasslands to forest pastures, as there was no statistical difference in K levels between these two biotopes (IV). The effects of high K concentrations on plant diversity are not as well known as they are regarding N and P (Janssens et al. 1998, Austrheim et al. 1999, Crawley et al. 2005). If K is a limiting factor in a forest pasture, as it is in some grassland biotopes (Olf & Pegtel 1994), high K input apparently leads to a higher vascular plant biomass and decreased diversity. High K concentration can also strengthen the harmful effects of P (Crawley et al. 2005). However, many aspects of nutrient dynamics, such as possible differences in mineralization processes between the forest pastures and forests, remained unstudied in

this thesis. Thus, the vegetation patterns are emphasized here instead of the difference in soil chemistry.

Bryophyte species richness (alpha and gamma) did not differ between the forest pastures with or without grassland connection and the forests (IV). Bryophyte cover was higher in the forests than in the two forest pasture types while there was no difference in bryophyte cover between the forest pastures with or without grassland connection (IV). Furthermore, when neither bryophyte species richness nor cover could be explained by the soil variables in the forest pastures with grassland connection (IV), not any direct and easily interpreted effects of grassland connection on bryophyte diversity were revealed in this study.

The cover of vascular plant litter was the strongest explanatory variable for bryophyte species richness and cover in both the forest pastures and forests (IV). This finding supports the view that the diversity and abundance of bryophytes generally depend more on the characteristics of vascular plant vegetation than on abiotic factors in productive environments (Hejman et al. 2001, Kull et al. 2005, Müller et al. 2012). Ingerpuu et al. (1998) found that fertilization led to a decrease in bryophyte cover in a wooded meadow and concluded, as well, that this was apparently due to intensified competition with vascular plants. Direct toxic effects of fertilizers may also affect bryophytes in the experiments of this kind (Aude & Ejrnaes 2005). The negative relationship between the cover of vascular plant litter and the species richness of bryophytes in this study is worrying against the background that there was significantly more vascular plant litter in the forest pastures with grassland connection in comparison to the unconnected ones (IV). Grassland connection may lead to lower consumption of vascular plant biomass by cattle and, consequently, to increased cover of vascular plant litter in forest pastures, as cattle has access to more attractive vegetation in fertilized grasslands.

The forest pastures with and without grassland connection were clearly separated in the DCA by their bryophyte communities (IV). A few common forest floor species, such as

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Pleurozium schreberi and *Hylocomium splendens*, were more abundant in the forest pastures with grassland connection, while some individual species benefitting from soil disturbances, such as *Oxyrrhynchium hians* and *Atrichum undulatum*, were more frequently found in the forest pastures without grassland connection (IV). Hence, bryophyte communities in the forest pastures with grassland connection were to some extent closer to the communities in the forests. This may signal differences in grazing intensity between these two forest pasture biotopes. Instead, no differences were found in the abundance of short-lived acrocarpous bryophytes between the forest pasture types (IV) although it has been hypothesized that these species, in particular, may be sensitive to eutrophication in agricultural landscapes (During & Willems 1986, During 1992, Aude & Ejrnaes 2005).

Unlike in the case of bryophyte diversity, detrimental effects of grassland connection on vascular plant diversity were evident in this study (IV). Remarkable (in terms of biodiversity conservation) and rare grassland species were less abundant in the forest pastures that were connected to fertilized grasslands (IV). Furthermore, several species with high Ellenberg scores for nitrogen (Ellenberg et al. 1991) were more abundant in these sites (IV). Vascular plant species richness (alpha and gamma) and diversity (Shannon's index) were also significantly lower in the forest pastures with grassland connection when compared with the traditionally managed forest pastures without grassland connection (IV). Nutrient accumulation and eutrophication are potential explanations for these worrying results while other factors, such as differences in grazing intensity between the forest pasture types, may also have had effect.

Bryophyte species richness (alpha and gamma) did not correlate with vascular plant species richness (alpha and gamma) in the forest pastures or in the forests (IV). The same observation has been made in various biotopes (Pharo et al. 1999, Virtanen et al. 2000, Vellak et al. 2003, Virtanen & Crawley 2010) and it implies that we cannot predict bryophyte species richness by

estimating vascular plant species richness or vice versa in forest pastures.

In sum, forest pastures should not be connected with fertilized grassland pastures. As eutrophication is a threat to the majority of Finnish semi-natural rural biotopes (Pykälä 2001, Vainio et al. 2001), this recommendation can readily be followed in the other Finnish semi-natural rural biotopes as well. Of course, the intensity of nutrient accumulation and other impacts caused by grassland connection depends on the proportional area of grasslands and semi-natural rural biotopes in an enclosure and on the daily movements of cattle (Uytvanck et al. 2010). Sensitivity to the harmful effects of grassland connection may also vary between the biotopes. There can even be differences between the three subclasses of forest pastures, something we could not reveal with the applied study design. Further studies are, thus, needed before we have a detailed picture of this controversial but most likely harmful management practice.

3.3.3 Bryophytes can be used as indicators of valuable pasture biotopes in mesic grasslands

The sensitivity of bryophytes to grassland abandonment and to the consequent overgrowing by vascular plants (Aude & Ejrnæs 2005, Peintinger & Bergamini 2006) means that bryophytes may be especially useful as the indicators of grassland quality. The continuously grazed mesic semi-natural grasslands sustained more diverse bryophyte communities than the abandoned and the most of the restored sites in this study (I). The most valuable vascular plant communities are also found in the continuously grazed grasslands (Pykälä 2003). As bryophyte cover was also highest in these sites, the cover may potentially be used in the identification of those mesic semi-natural grasslands that host the most valuable bryophyte and vascular plant communities (I). Instead, the diversity of many insect orders apparently peaks at the lower grazing intensities (e.g. Pöyry et al. 2004).

Species *Abietinella abietina*, *Climacium dendroides* and *Syntrichia ruralis* are potential species-level indicators for diverse

grassland plant communities on Finnish non-calcareous clay soils as their abundance was strongly inclined to the continuously grazed sites (I). These species are also easy to identify already in the field. During & Willems (2003) mention *A. abietina* as a species that suffer from overgrowth and eutrophication in Dutch chalk grasslands. Among other species abundant in the continuously grazed sites, *Rhytidiadelphus squarrosus* is also known to thrive in very eutrophicated growing conditions (Ingerpuu et al. 1998) and it is thus less useful as an indicator.

The use of bryophytes as the indicators of valuable forest pasture biotopes is questionable. There were very few species characteristic of the traditionally managed forest pastures (III, IV). Furthermore, neither bryophyte richness nor cover correlated with the species richness of vascular plants in this study (IV). Near threatened (NT) *Tayloria tenuis* seems to be typical of at least North-Karelian forest pastures and its presence in a pasture may indicate a long continuity of grazing in that particular site. However, we do not know if its abundance correlates with any other factors except the continuous supply of dung patches. Beyond species level indicators, the abundance of acrocarpous bryophytes on bare mineral soil may indicate high ecological quality in this biotope. Before further studies, however, the ecological quality only refers to the conditions for bryophytes.

3.3.4 Intensive forestry homogenize forest stand structures in forest pastures

Vainio et al. (2001) reported that the most of the Finnish forest pastures have considerably lost their ecological value because of intensive forestry. Forestry practices have decreased the variation in tree species composition, forest stand density and age-class structure typical of representative forest pastures (Vainio et al. 2001). The lack of dead wood is also a common problem (Vainio et al. 2001). As a consequence, intensive forestry is regarded as a major threat to wooded semi-natural rural biotopes in Finland (Schulman et al. 2008a,b). The

biodiversity effects of forest stand structure were not studied in more detail in this study, but the results and field observations indicate that this issue should receive more attention in the future.

High microhabitat heterogeneity or diversity (Shannon's index) was related to high bryophyte species richness in the forest pastures (III), and forest stand structure is one factor that fundamentally affects the variation in microhabitat conditions. Vascular plant vegetation, for example, differs between open and wooded parts of wooded meadows (Haeggström 1983). In general, vascular plant diversity increases with light availability in hemiboreal wooded meadows (Einarsson & Milberg 1999, Aavik et al. 2008) although contrasting results have locally been obtained (Skornik et al. 2008). In this study, bryophyte cover was lower near the edge of the grassland pastures than in the inner parts of the forest pastures (IV). Many bryophyte species prefer shaded and moist microhabitats (Moen & Jonsson 2003, Hylander 2005). These results indicate that high variation in forest stand structure may result in high overall plant diversity in forest pastures.

The internal heterogeneity of forest stand was, however, generally low in the forest pastures of this study. The number of tree species was practically the same in the forest pastures connected to grasslands (on average 2.8 species per site) and in the adjacent forests (on average 2.9 species per site). The age-class structures and stand densities also appeared very homogenous. In fact, the forest stand structures in the forest pastures resembled the ones in the forests managed for commercial purposes. Furthermore, large logs were very occasional (III). There were also a few sites with spruce as the dominant tree species and it is questionable whether these sites provide any forage for cattle or if their only function is to offer shelter and resting sites (Fig 6). An increase in the abundance of spruce is one of the ecological problems associated with the decrease in traditional-type management in Finnish forest pastures (Vainio 2001).



Figure 6. Homogenous forest stand structure and the dominance of spruce are two ecological problems in forest pastures. Kitee.

Even without and before further studies, it can be stated that more attention should be paid on forest stand structure in the management of forest pastures. The goal should be a structurally diverse forest stand consisting of both living and dead trees of various tree species (Fig 7). This would also result in a spatially more heterogeneous grazing pattern. It is unlikely that the increase in structural heterogeneity in forest pastures would harm any species group. Instead, positive effects on biodiversity are evident. The amount of structural heterogeneity and the availability of microhabitats (mineral soil patches, CWD and old deciduous trees in particular) may also be useful measures when evaluating the ecological value of forest pastures.



Figure 7. An example of a representative forest stand structure in a forest pasture. The lack of dead wood is still a problem also in this site. Kitee.

3.3.5 Forest pastures may be more vulnerable to high grazing intensities than mesic grasslands

The risk of too high grazing intensity is another issue worth addressing in this thesis, even if it was only briefly touched in articles I-IV. By too high I mean intensities that decrease biodiversity to a remarkable degree. The risk of too low grazing intensity in mesic grasslands has been discussed in chapter 3.3.1.

The effects of cattle grazing on vascular plant diversity are usually positive in productive biotopes in northwestern Europe (Olf & Ritchie 1998, Proulx & Mazumder 1998). The positive effects are potentially attributable to the survival of many subordinate life-forms that are absent or scarce in an overgrown

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vegetation (Pykälä 2004, Johansson et al. 2010) and the results of this study illustrate that bryophytes form one of these subordinate species groups benefitting from grazing (I, II).

The impacts of grazing on biodiversity are often scale-dependent (Bello et al. 2007, Giladi et al. 2011). In this study, species richness at gamma level presumably is the most suitable response variable when exploring the effects of grazing intensity on bryophyte and vascular plant diversity. This variable depicts species richness at the level of grassland/pasture and it was used in all of the articles I-IV.

In the mesic semi-natural grasslands, the positive relationship between bryophyte species richness (gamma) and grazing intensity was evident even in the highest intensities (II). Pykälä (2003) did not record any adverse effects of high grazing intensities on vascular plant diversity in this biotope, either. The cover of bare soil was selected to measure grazing intensity (trampling effect to be precise) in the forest pastures (IV). It turned out that the species richness of neither bryophytes nor vascular plants decreased even in very high covers of bare soil. This was somewhat surprising as the cover of bare soil was very high in a few sites (the range of mean 0–49.5 %) and generally much higher than in the mesic grasslands (the range of mean 0.01–0.02 %). Müller et. al (2014) found that the cover of bare soil exceeding 12 % decreased bryophyte diversity in a grassland environment in Germany.

In conclusion, grazing intensities that threaten plant diversity are apparently rare in mesic grasslands on clay soils. Instead, forest pastures may be more vulnerable to high intensities and this issue should be kept in mind in the management of this biotope.

4 *Concluding remarks*

This study demonstrates that bryophytes form an integral part of biodiversity in mesic semi-natural grasslands and forest pastures. Undoubtedly, this is the case in the other semi-natural rural biotopes as well, but there is a lot of work before we have a comprehensive picture of bryophyte communities in all of these environments. Wet coastal grasslands, currently very rare grazed fens, wooded pastures in the hemiboreal vegetation zone and dry grasslands on mesotrophic and calcareous soils would be good scenes for future studies.

Based on the results, bryophytes should be taken into account in the management of mesic semi-natural grasslands and forest pastures. One relevant reason to enhance bryophyte diversity in these two biotopes by restoration and proper management is that the measures beneficial to bryophytes seem to benefit many other species groups as well. The most severe conflict is expected between the high grazing intensity required by bryophytes and the low intensity required by some insect groups. This highlights the need for spatially varying grazing intensities and management practises at landscape level. We also need more studies that genuinely compare the effects of management and restoration on different species groups.

The major importance of soil disturbances to bryophyte diversity in the mesic semi-natural grasslands and forest pastures was evidently one of the main results of this thesis. It would be interesting to examine the role of soil disturbances also in a larger scale, beyond the borders of semi-natural rural biotopes. Bryophytes on bare mineral soil should also be studied at different times of the year, as midsummer is not necessarily the most favourable moment to find many short-lived species.

This study was concentrated on cattle grazing. Although cow seems to be very suitable species for the management of semi-natural rural biotopes, further studies should also focus on the

effects of other potential grazers. This is important not only because of the divergent effects of different grazer species but also because “recreational” species, such as horse and pony, and even exotic species in Finnish context, such as bison and alpaca, may have potential to counteract the decrease in traditional animal husbandry in Finland.

In this thesis, I have presented various ideas and recommendations of the management practices that would benefit bryophytes and increase biodiversity in the semi-natural rural biotopes. However, the real challenge is how to keep the management of these biotopes alive in the modern world, where economic reasoning rules the decision making of both individuals and societies. The management of semi-natural rural biotopes is rarely profitable in free markets nowadays. While the management is of low intensity in terms of chemical inputs, it usually demands lots of expensive labour (Bignal & McCracken 1996). Natural sciences can only point out the ecological importance of these biotopes. At present, subsidies form the main mechanism by which the management is tried to keep alive in Finland. Subsidies are, however, prone to ever changing political climate and we urgently need other ways to make the management of semi-natural rural biotopes a real alternative (economically, socially and culturally) for different landowners, even for those who do not have a former experience of the management.

5 References

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TUOMO TAKALA
*Bryophytes in Semi-Natural
Rural Biotopes*

Modernization of agriculture has led to a dramatic decrease of semi-natural rural biotopes in many European regions, and many species dependent on these environments have become threatened. However, we still know little about many species groups living in these biotopes. This thesis concentrates on two types of semi-natural rural biotopes – mesic grasslands and forest pastures – and illustrates how the present management, notably cattle grazing, affects bryophytes in these environments.



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