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318

Anna Oldén

Plant Biodiversity in Boreal Wood-Pastures

Impacts of Grazing and Abandonment

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ABSTRACT

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Wood-pastures are traditional rural biotopes that host high biodiversity due to the small-scale heterogeneity of grazer activities and the structural diversity of trees. However, wood-pastures and their biodiversity are threatened by intensification of agricultural and forestry practices as well as by abandonment (cessation of grazing). Here I studied the biodiversity of vascular plants and bryophytes in 24 boreal wood-pastures that are still grazed and in 24 wood-pastures that have been abandoned during the past decades. The grazed sites had higher species richness of vascular plants, as well as of bryophytes that grew on soil or on rocks. The grazers increased the diversity of microhabitats via the small-scale variation in defoliation, trampling and defecating. These disturbances created suitable microhabitats for subordinate species that disappeared due to increased competition after abandonment. Bryophyte richness on trees and decaying wood was limited in both grazed and abandoned sites by the scarcity of large deciduous trees and large logs. Rare species were observed in both grazed and abandoned sites and they were mostly dependent on moist or naturally fertile soil conditions, decaying wood or dung. Grazing hampered the regeneration of deciduous trees, while abandonment resulted in a high density of small deciduous trees and spruces. In the long term, spruces can become dominant in all kinds of wood-pastures, which is generally unwanted from the conservation point of view. Based on my results maintaining grazing management in various kinds of wood-pastures is of primary importance in the conservation of plant biodiversity, but attention should also be paid on the diversity of trees and decaying wood. Some of the abandoned sites host high conservation values as well. Finally, there is a need to create new wood-pasture habitats within the landscape.

Keywords: Beta diversity; bryophytes; large herbivores; microhabitats; traditional rural biotopes; tree regeneration; vascular plants.

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LIST OF ORIGINAL PUBLICATIONS

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

I Oldén A., Raatikainen K.J., Tervonen K. & Halme P. 2016. Grazing and soil pH are biodiversity drivers of vascular plants and bryophytes in boreal wood-pastures. *Agriculture, Ecosystems and Environment* 222: 171-184.

II Oldén A. & Halme P. 2016. Grazers increase beta diversity of vascular plants and bryophytes in wood-pastures. *Journal of Vegetation Science*, in press.

III Oldén A. & Halme P. 2016. Microhabitat determines how grazing affects bryophytes in wood-pastures. *Biodiversity and Conservation* 25: 1151-1165.

IV Oldén A., Komonen A., Tervonen K., Halme P. 2016. Tree species composition of boreal wood-pastures changes under both grazing management and abandonment. Submitted manuscript.

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

	I	II	III	IV
Planning	AO, KJR, KT, PH	AO, PH	AO, PH	AO, KT, PH
Data	AO, KJR, KT	AO	AO	AO, KT
Analyses	AO, KJR	AO	AO	AO
Writing	AO, KJR, KT, PH	AO, PH	AO, PH	AO, AK, KT, PH

AO = Anna Oldén, KJR = Kaisa J. Raatikainen, KT = Kaisa Tervonen, PH = Panu Halme, AK = Atte Komonen

1 INTRODUCTION

1.1 Thesis background

Biodiversity is decreasing drastically on our planet. During the last millennia human actions have induced the sixth mass extinction of species on Earth, with extinction rates 100 to 1000 times their pre-human levels, and predicted to increase in the near future (Pimm *et al.* 1995). The most important reason for the loss of biodiversity, as well as the associated ecosystem services, is the loss and modification of natural ecosystems (Foley *et al.* 2005, Millennium Ecosystem Assessment 2005). In addition, the loss of biodiversity is driven at an exceeding pace by climate change, overexploitation, invasive alien species and pollution (Millennium Ecosystem Assessment 2005). The conservation of biodiversity has long focused on protecting natural habitats and individual threatened species, and more recently on the restoration of degraded habitats (Millennium Ecosystem Assessment 2005, Convention on Biological Diversity 2010).

However, some of the threatened habitats and species are dependent on human actions (Pärtel *et al.* 2005, Schulman *et al.* 2008a, Rassi *et al.* 2010). Many semi-natural habitats have been managed by livestock grazing, cutting vegetation or burning that influence the successional stage and the structure of the vegetation so that the changes benefit particular species or assemblages of species (Ausden 2007). Such management practices induce disturbances that can mimic natural disturbances (e.g. fires, storms, floods, grazing and browsing), and therefore they can provide habitats for the species typical to early successional stages (Ausden 2007). However, during recent decades the abandonment of traditional management methods, such as low-intensity livestock grazing in semi-natural areas, has become a threat to the survival of management-dependent species (Plieninger *et al.* 2006, Beilin *et al.* 2014). Nowadays attempts are being made to continue habitat management for conservation purposes (Pärtel *et al.* 2005, Ausden 2007).

In this thesis I study the effects of livestock grazing on plant biodiversity in wood-pastures, i.e. areas where livestock forages among trees. Currently grazed wood-pastures are compared to abandoned wood-pastures (where grazing has ceased) in order to reveal how continued grazing impacts the biodiversity of plants. The study focuses on the diversity of two distinct plant species groups: vascular plants and bryophytes (mosses and liverworts). Two aspects of diversity are studied: Species richness within a location (α-diversity), and the variation in species composition between localities (β-diversity). Together they determine the number of species within the whole landscape (γ-diversity).

1.2 Grazing affects biodiversity

Plants have coevolved with herbivores that have probably stimulated plant speciation (Coughenour 1985, Futuyma and Agrawal 2009), therefore increasing biodiversity on the planet. Large herbivores can also increase regional and local species richness by dispersing plant propagules in their fur (ectozoochory) or dung (endozoochory) (Fischer *et al.* 1996, Bakker and Olff 2003). On the other hand, large herbivores can kill or damage plant individuals, which can cause a random reduction or loss of some species (drift, *sensu* Vellend 2010). In addition, the presence of grazers creates selection that disfavors highly palatable species and those that cannot tolerate repeated defoliation or trampling (Augustine and McNaughton 1998, Olff *et al.* 1999). The abundances of other species can increase, especially of those that can avoid herbivory (e.g. are unpalatable, toxic, thorny or low-growing), or tolerate repeated damage (i.e. are able to regrow quickly) (Olff *et al.* 1999, Bakker and Olff 2003, Kohler *et al.* 2006a). Grazers can thus impact all of the processes that affect the occurrence of species in communities: speciation and dispersal that add species to the regional and local species pools, and selection and drift that forge the occurrence and abundance of each species (Vellend 2010).

Grazing can induce positive or negative changes in the local biodiversity of vascular plants, depending on grazing intensity and other site properties such as productivity. Livestock grazing can have negative impacts on plant diversity and ecosystem services if stocking levels are high (overgrazing) or if nutrient availability or drought restrict productivity (Milchunas *et al.* 1988, Fleischner 1994, Olff and Ritchie 1998, Proulx and Mazumder 1998). On the other hand, grazing by natural populations of large herbivores or by low to medium stocking levels of livestock usually increases plant diversity in mesic and nutrient-rich sites (Belsky 1992, VanWieren 1995, Proulx and Mazumder 1998, Pykälä 2003, 2005). If low productivity does not limit plant growth, plant species richness is usually maximized at moderate grazing intensity, i.e. there is a humped response curve of diversity to grazing intensity (Milchunas *et al.* 1988, Cingolani *et al.* 2005, Dengler *et al.* 2014).

The differential effects of grazing on plant diversity in areas with varying productivity are in accordance with the predictions of the Dynamic Equilibrium Model (Dengler *et al.* 2014, Huston 2014). In this model increasing plant mortality decreases species diversity if productivity is low, increases it if productivity is high, and produces a humped effect at intermediate productivity (Huston 1979, 1994). The humped pattern corresponds to the Intermediate Disturbance Hypothesis according to which the diversity of competing species is maximized at intermediate frequencies and/or intensities of disturbance, because rare or weak disturbances lead to competitive exclusion of subordinate species, while very frequent or intense disturbances eliminate disturbance-intolerant species (Grime 1973, Connell 1978).

The responses of bryophytes to grazing are less well known, but similarly to vascular plants their richness seems to be increased by low- or medium-intensity grazing in mesic areas (Bergamini *et al.* 2001, Aude and Ejrnæs 2005, Peintinger and Bergamini 2006, Takala *et al.* 2012). Other species groups show more variable responses to grazing (Pykälä 2001). For example, insect diversity can be maximized at much lower grazing intensities and intervals than the ones maximizing plant diversity (Völkl *et al.* 1993, Pykälä 2001, Pöyry *et al.* 2005).

1.3 Grazers induce disturbances

Large herbivores cause fine-scale disturbances by defoliating vascular plants, trampling and defecating (Figure 1). Defoliation (i.e. herbage removal or grazing *sensu stricto*) results in a loss of vascular plant biomass and nutrients, which cause further changes in microclimate, light availability and the competitive situation between plant species (Olff *et al.* 1999, Kohler *et al.* 2004a, Aude and Ejrnæs 2005). Defoliation is partly selective, i.e. the grazers prefer to feed on palatable plants that have high nutrient value (Hobbs and Swift 1988, Rook *et al.* 2004). Trampling damages, kills and detaches plants, creates empty gaps and compacts the soil (Abdel-Magid *et al.* 1987, Kohler *et al.* 2006a). Dung and urine create a fertilized patch, and dung also suffocates the original plants, reduces subsequent defoliation on nearby plants, and introduces a microhabitat for dung-dependent species (Afzal and Adams 1992, Gillet *et al.* 2010, Jaroszewicz *et al.* 2011).

Defoliation, trampling and dunging vary at several spatial scales, from small patches (few dm^2) to large parts of a pasture (Bokdam and Gleichman 2000, Kohler *et al.* 2004b, 2006b, Gillet *et al.* 2010). In addition, the occurrence of each disturbance type varies in time, especially at small spatial scales (Buttler *et al.* 2009, Gillet *et al.* 2010). Therefore, grazers may increase the heterogeneity of vegetation and plant resources at several scales.

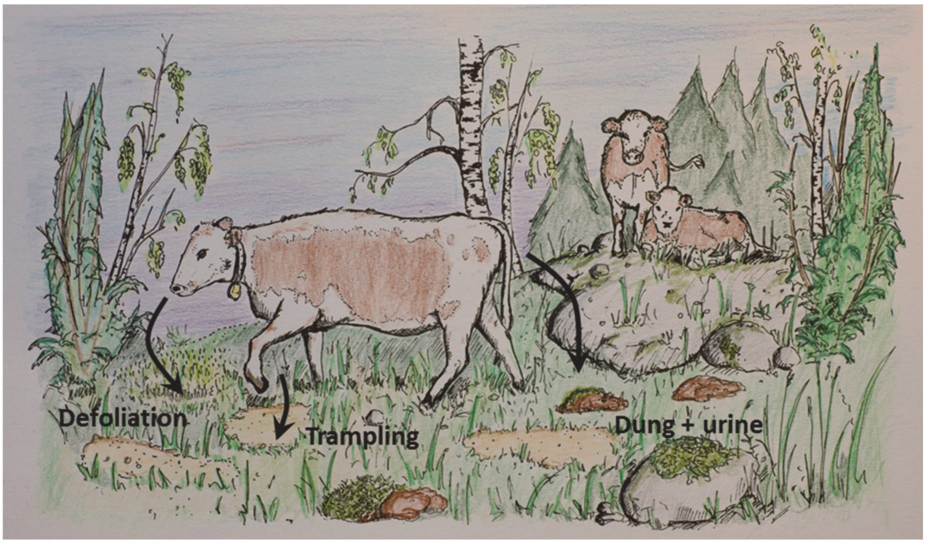

FIGURE 1 Large herbivores induce fine-scale disturbances through defoliation, trampling and defecating. Drawing: Markus Dernjatin.

Because the patches created by defoliation, trampling and defecating differ in their environmental conditions, they provide habitats for different species that can coexist in the pasture via spatial niche partitioning (Barot and Gignoux 2004, Bloor and Pottier 2014). In addition, the empty patches provide short-term habitats for competitively-inferior but quickly colonizing species (Tilman 1994, Bloor and Pottier 2014). These mechanisms increase the beta diversity of vascular plants, i.e. plant species composition varies more between patches, which in turn increases the species richness within a pasture (Adler *et al.* 2001, Bloor and Pottier 2014). However, similarly to the pasture-level species richness, beta diversity can also be decreased by grazers in unproductive areas or if stocking levels are too high (overgrazing) (Bloor and Pottier 2014).

1.4 Wood-pastures

Large herbivores were probably influential in forging pre-human ecosystems, although their role in maintaining open or semi-open areas is under debate (e.g. Vera 2000; Hodder et al. 2009). In Europe most plant species are dependent on open or semi-open conditions, which were probably created and maintained by large herbivores together with the effects of other natural disturbances such as fires, floods and storms (Ellenberg 1988, Rose 1992, Pykälä 2000, Vera 2000). After the extinction of megaherbivores and the suppression of other natural disturbances many of the species dependent on them have likely benefited from the effects of low-intensity livestock rearing (Olff *et al.* 1999, Pykälä 2000). During the past millennia animal husbandry created semi-natural habitats via livestock grazing, mowing, coppicing and other traditional agricultural methods (Ellenberg 1988, Pykälä 2001, Plieninger *et al.* 2006). The resulting traditional rural biotopes are among the most biodiverse habitats in Europe (Pykälä 2001, Plieninger *et al.* 2006).

Wood-pastures are traditional rural biotopes that have been formed by the long-term systematic use of wooded areas for livestock grazing, usually with cattle, horses or sheep (Bergmeier *et al.* 2010). Trees can be scattered, located in patches or as a closed canopy. Various types of wood-pastures occur throughout Europe and typically they have high values related to biodiversity, history, culture and the landscape (McAdam *et al.* 2009, Bergmeier *et al.* 2010).

During the last decades the economic and social conditions in rural areas have changed and traditional land-use practices have commonly been discarded (Plieninger *et al.* 2006, Beilin *et al.* 2014). Large areas of wood-pastures have become abandoned (Bergmeier *et al.* 2010). In addition to abandonment, wood-pastures are threatened by the intensification of livestock rearing, agricultural practices and forestry. Many wood-pasture ecosystems have been changed by overgrazing, eutrophication (nutrient accumulation), tree regeneration failure, the loss of old-growth trees, or even complete clearance (Bergmeier *et al.* 2010).

Several types of wood-pastures occur in Finland. Historically sparsely wooded areas around the farms were typically fenced in (*hakamaa* in Finnish), but livestock was also allowed to forage freely in the surrounding forest areas where tree density was typically higher (*metsälaidun*, i.e. forest pasture) (Jäntti 1945). Nowadays all wood-pastures are fenced but the density of trees and the resulting field layer vegetation are still used as classification criteria (Vainio *et al.* 2001, Schulman *et al.* 2008b). In addition, wood-pastures are classified to sub-types based on the dominant tree species. All of the types and subtypes are now endangered or critically endangered biotopes (Schulman *et al.* 2008b). Large areas have been abandoned since the 1800's or converted to arable fields or commercial forests. For example, the area of forest pastures has decreased by more than 99 % since the 1950's (Schulman *et al.* 2008b). The quality of the remaining wood-pastures has also decreased because the majority of them are not managed in a completely traditional manner. Many wood-pastures are eutrophicated, because additional fodder has been provided to the animals or they have been allowed to move between fertilized pastures and wood-pastures (Schulman *et al.* 2008b, Takala *et al.* 2015). In addition, old trees and decaying wood have been removed contrary to the traditions (Schulman *et al.* 2008b).

1.5 Biodiversity in wood-pastures

It has been argued that out of all present-day man-modified ecosystems, wood-pastures are closest resemblances to the past natural ecosystems, because they share the natural and varying tree cover as well as extensive grazing with large herbivores (VanWieren 1995, Vera 2000). The combination of trees and large grazers is what creates and maintains the high biodiversity values of present-day wood-pastures. The mosaic of trees, shrubs and open meadow-like areas create varying light availability and moisture conditions that favor different species (Gillet *et al.* 1999, Buttler *et al.* 2009). The grazers create patches with variable disturbances, successional stages and soil properties. The small-scale patchiness and the abundance of ecotones induce a fine mosaic of vegetation types and high plant species richness (Buttler *et al.* 2009, Luick 2009, Bergmeier *et al.* 2010). The plant communities of wood-pastures are mixtures of species that typically occur in different habitats, such as forests or ruderal areas (Schulman *et al.* 2008b, Bergmeier and Roellig 2014, Takala *et al.* 2015). There are no species that occur exclusively in wood-pastures, but some are nowadays regionally restricted to these habitats (Bergmeier and Roellig 2014). Grazing in wood-pastures favours vascular plant species that are unpalatable, small or seasonal and somewhat shade-tolerant (Kohler *et al.* 2004a, Bergmeier and Roellig 2014).

Traditionally managed wood-pastures have high structural diversity, which increases the biodiversity of species that are dependent on various microhabitats. Old trees have a high variety of microstructures (e.g. holes and old bark) that host diverse communities of bryophytes, lichens, beetles and birds, including several species that occur only on solitary trees in semi-open conditions (Mitchell and Kirby 1990, Pykälä 2001, Taboada *et al.* 2006, Paltto *et al.* 2011, Bergmeier and Roellig 2014). Dead and decaying wood is also important for e.g. bryophytes, lichens, beetles and wood-decaying fungi (Paltto *et al.* 2008, Bergmeier and Roellig 2014, Falk 2014). In addition, rocks increase biodiversity, at least for bryophytes (Takala *et al.* 2014). Due to their structural diversity and grazer-induced disturbances, wood-pastures may have provided compensatory habitats for species of old-growth forests as well as for species of frequently disturbed areas (Pykälä 2001, Paltto *et al.* 2008, Palo *et al.* 2013).

The decline of traditional wood-pasture management has been reported to reduce diversity at both local and landscape levels (Garbarino and Bergmeier 2014). Abandonment results in tree and shrub encroachment and the loss of open and semi-open areas and consequent declines in small-scale habitat diversity and ecotones (Bergmeier *et al.* 2010, Garbarino and Bergmeier 2014, VanUytvanck and Verheyen 2014). Following this, species typical to semi-open conditions decline (Paltto *et al.* 2011, Palo *et al.* 2013). Studies on the effects of abandonment on soil-dwelling plant communities are scarce in wood-pastures, but apparently the species typical to frequently disturbed microhabitats decline, while larger, dominant species increase. In grasslands abandonment leads to an increase in species that are tall, competitive or of high nutritive value, whereas declines have been observed for bryophytes and for species that are small, subdominant, stress-tolerant or of low nutritive value (Pykälä 2004, Mayer *et al.* 2009, Takala *et al.* 2012, Mariotte *et al.* 2013).

1.6 Aims of this thesis

In this thesis I explore the biodiversity of vascular plants and bryophytes in boreal wood-pastures. The broad aim is to shed light on the biodiversity values of wood-pastures that are still grazed, as well as of wood-pastures that have been abandoned in the past decades. I focus on the effects of grazing and abandonment on plant species richness and community composition. Special attention is paid to the within-site heterogeneity in grazer activities and their impacts on the variation in plant communities, measured as beta diversity and its two components, turnover (species replacement) and nestedness (species richness varies so that small assemblages are subsets of larger assemblages). In addition to vascular plants and soil-dwelling bryophytes, I study the impacts of grazers on bryophytes growing on other types of microhabitats, i.e. rocks, trees and decaying wood. Finally, I explore the effects of grazing and abandonment on tree regeneration because the future of wood-pastures and their biodiversity is dependent on the trees. More specifically, I focus on the following questions:

1. How do grazed and abandoned wood-pastures differ in the species richness of vascular plants and soil-dwelling bryophytes? How important is the effect of management by grazing compared to environmental conditions such as soil pH and moisture, tree density or historical land-use intensity? (I)
2. How do grazed and abandoned sites differ in the beta diversity, turnover and nestedness of vascular plants and soil-dwelling bryophytes at different spatial scales? How are the beta diversities within sites affected by defoliation, trampling and dunging? (II)
3. Do grazed and abandoned sites differ in the richness of bryophytes on rocks, trees and decaying wood? How important is the effect of grazing management relative to substrate area and diversity? (III)
4. How do the communities of vascular plants and bryophytes differ between grazed and abandoned sites? What kind of species benefit from grazing or abandonment? (I, III)
5. How does grazing or abandonment impact the regeneration of trees? What tree species are likely to dominate in the future? (IV)

2 MATERIAL AND METHODS

2.1 Study design

Forty-eight wood-pastures were chosen for the study. The study sites were located in Central Finland, with 44 of them on the southern boreal vegetation zone and the remaining 4 on the southern limits of the middle boreal zone. First, 24 currently grazed sites were chosen based on their tree species composition so that six of the sites were dominated by birches (*Betula pendula* Roth or *B. pubescens* Ehrh.), six by Norway spruce (*Picea abies* (L.) H. Karst.), six by Scots pine (*Pinus sylvestris* L.) and six by a mixture of coniferous species (spruce or pine) and deciduous species (mostly birches but sometimes mixed with European aspens *Populus tremula* L.). Photos of typical sites are in Figure 2. The sites were grazed during the summer season by cattle, horses, sheep or a mixture of these. One of the aims in choosing the sites was to include well-preserved wood-pastures where management was as close to traditional methods as possible (e.g. the animals are not provided with additional fodder or an access to fertilized pastures, the tree structure has not been strongly modified by logging, and decaying wood has not been removed). Nevertheless, based on field observations and landowner interviews, it turned out that one or more of such non-traditional practices have occurred during the past decades in most of the sites. Most commonly livestock was or had been allowed to move freely between fertilized pastures and the wood-pastures, potentially resulting in the eutrophication of the wood-pasture.

Second, 24 abandoned wood-pastures were chosen so that they were similar to the grazed sites in their regional location and the density and identity of the dominant trees (six sites of each of the four types based on the dominant trees, see Figure 2 for examples). In the abandoned sites grazing had ceased between 7 and 42 years earlier. Sites were included only if the year of abandonment was known at least approximately, thus excluding wood-pastures that had been abandoned several decades ago. Moreover, it was not possible to find such control sites where it would be known that no livestock grazing has taken place, because during past centuries cattle was allowed to forage freely in forests.

Three quadrate study plots of 100 m^2 (10 m * 10 m) were placed within each study site so that within each plot there were mature trees and they were of the species that was dominant in the site (birch, spruce, pine or mixed). The distance between two plots varied from 17 to 222 meters depending on the amount of variation in the tree structure within the site. Subplots of 4 m^2 (2 m * 2 m) were placed inside each corner of each plot, resulting in a total of 12 subplots within each site (Figure 3).

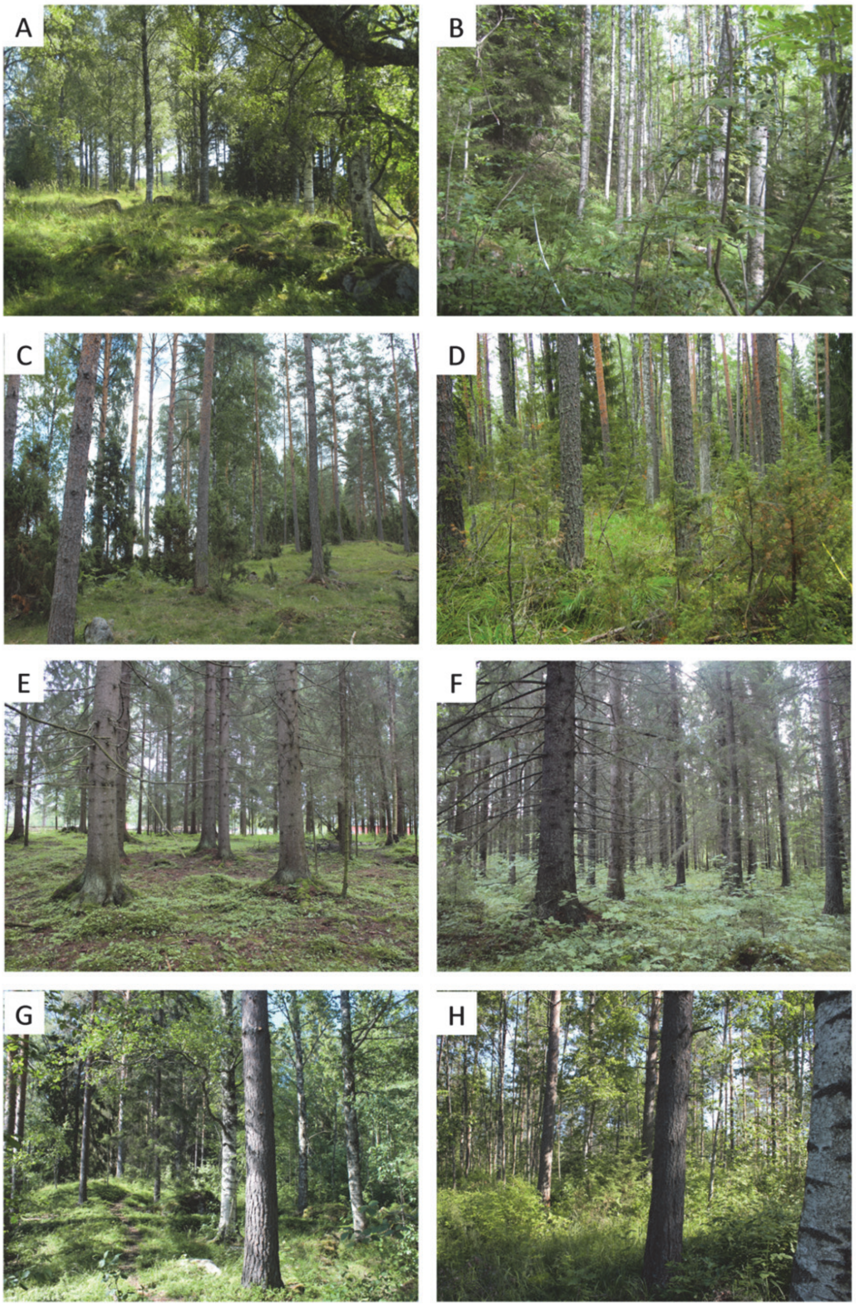

FIGURE 2 Typical wood-pastures in the study: a) grazed birch-dominated, b) abandoned birch-dominated, c) grazed pine-dominated, d) abandoned pine-dominated, e) grazed spruce-dominated, f) abandoned spruce-dominated, g) grazed with mixed deciduous and coniferous trees, and h) abandoned with mixed deciduous and coniferous trees. Each of these eight types was represented by six separate sites in the study. Photos: Kaisa Tervonen and the author. Reprinted from paper I.

2.2 Data collection

Vascular plant and bryophyte species were recorded from each subplot and the percentage cover of each species was estimated (I, II). Observations of bryophytes were recorded separately for the four microhabitat classes: soil, rocks, trees or decaying wood (III). The nomenclature of vascular plants is based on Hämet-Ahti *et al.* (1998) and that of bryophytes on Juutinen and Ulvinen (2015). Voucher specimens of rare bryophyte species are deposited in the natural history collection of the Jyväskylä University Museum (JYV).

Defoliation, trampling and dunging intensities were recorded for each subplot (II). Defoliation intensity was estimated as the proportion of clipped shoots out of all vascular plant shoots that had been over 5 cm high (excluding low-growing plants that are rarely eaten). Trampling intensity was estimated as the proportion of broken soil (i.e. hoofprints) out of total soil area within the subplot. Dunging intensity was estimated as the proportion of the subplot area covered by visible dung.

Microhabitats were also recorded within all subplots (III). The diameters of all rocks (at least 10 cm in diameter) were measured. For each tree (at least 130 cm high) the tree species and the diameter at the height of 130 cm were recorded and for large exposed roots the tree species and the diameters were recorded. For pieces of decaying wood (stumps, logs and fallen branches at least 1 cm in diameter) records were made of the length, average diameter and decay stage (1 to 5, see Renvall 1995).

Trees, soil properties and canopy openness were measured within the larger plots. For each tree within the plot the diameter at breast height (130 cm) was measured and the tree species identified (IV). Sixteen soil core samples were taken from each plot and mixed together. From them pH and moisture content were measured using standard methods (I). Canopy openness was measured as the proportion of visible sky in eight fisheye-photos taken towards different directions from the plot center (IV).

The owners of the currently grazed sites provided information on the possible gaps in grazing since 1990 and the owners of the abandoned sites told when the wood-pasture had been abandoned and whether spruces had been removed for conservation purposes since the abandonment. Finally, the historical land-use intensity was estimated as the number of farms surrounding the site within 1 km radius in the 1850–60’s, counted from cadastral maps (I).

2.3 Analyses

The species richness of vascular plants and soil-dwelling bryophytes was studied at four spatial scales: within subplots (α_1), within plots (α_2), within sites (α_3) and within the whole landscape (γ) (Figure 3). The effects of management (grazing or abandonment) and other environmental variables on the site-level species richness (α_3) were analysed with Negative Binomial Generalized Linear Models (GLM) (I). Three separate models were built for both species groups. First, the species richness on all sites was analysed with the effects of management, soil pH, soil moisture, basal area of trees and historical land-use intensity. Second, only grazed sites were included and management was excluded but grazing intensity (estimated as average defoliation intensity) was included. Third, only abandoned sites were chosen and time since abandonment was included instead of management or grazing intensity (I). In addition, the effects of the management situation on the species richness values at smaller spatial scales (within subplots, α_1, and within plots, α_2) were analysed with Generalized Linear Mixed-Effects Models (GLMM, with Poisson distribution) (II).

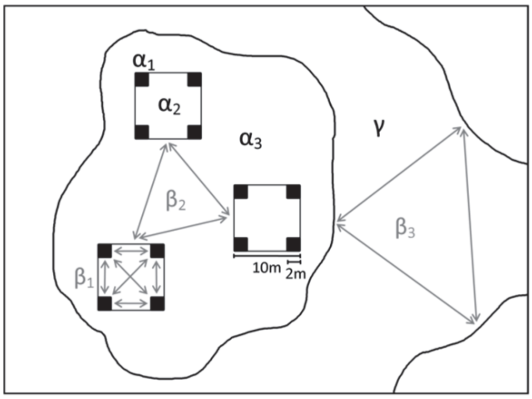

FIGURE 3 Illustration of the subplots (black squares), plots (empty squares) and sites (irregular shapes) and the corresponding alpha-, beta- and gamma-diversities used in the study. The grey arrows represent beta diversity between multiple subplots, plots or sites. In reality the plots and especially the sites are further away from each other. Reprinted from paper II.

The variation in the species composition of vascular plants and soil-dwelling bryophytes was calculated as the multiple-site additive beta diversity (β^+) (Ricotta and Pavoine 2015). It was calculated separately for three spatial scales: between subplots within plots (β^+_1), between plots within sites (β^+_2) and between sites within the landscape (β^+_3) (Figure 3). Linear Mixed Effects Models (LME) were used to analyse whether grazed and abandoned sites differ in the beta diversities within plots (β^+_1), as well as to analyse the effects of spatial variability (standard deviation) in defoliation, trampling and dunging within the plot. Similarly, Linear Models (LM) were used to analyse the effects of management and the effects of variation in defoliation, trampling and dunging on the beta diversities within sites (β^+_2). In addition, the two components of the multiple-site beta diversity, nestedness (β_N) and turnover (β_T) (Ricotta and Pavoine 2015) were calculated for each spatial scale.

The site-level species richness of bryophytes, the area of available microhabitats and the diversity (Shannon's entropy, Shannon 1948) of the microhabitats were calculated separately for rocks, trees and decaying wood (III). Wilcoxon Rank Sum Tests were used to analyse whether grazed and abandoned sites differ in their bryophyte richness, microhabitat area or microhabitat diversity, separately for each microhabitat type. Negative Binomial Generalized Linear Models (GLMs) were used to discern how bryophyte richness is affected by the management situation, microhabitat area or microhabitat diversity of the particular microhabitat type (rocks, trees or decaying wood).

Bioenv-analyses were performed to analyse the effects of the management situation and other environmental variables (soil pH, soil moisture, basal area of trees, historical land-use intensity, grazing intensity, time since abandonment) on the community composition of vascular plants and soil-dwelling bryophytes (I). Bioenv calculates the (Bray-Curtis) community dissimilarities and (Euclidean) distances of environmental variables for all pairs of sites and finds the best subset of environmental variables that has the highest (Spearman rank) correlation with the community dissimilarities (Clarke and Ainsworth 1993). In addition, the Indicator Species Analysis by Dufrêne and Legendre (1997) was used to find individual species that have high fidelity and high relative abundance in either grazed or abandoned sites. For bryophytes that grow on rocks, trees and decaying wood as well as soil, an extended version of the Indicator Species Analysis (DeCáceres *et al.* 2010) was performed to find species whose occurrence is associated with one of the microhabitat types (soil, rocks, trees or decaying wood) and with either grazed, abandoned or both kinds of sites (being indifferent to management) (III).

Factors affecting the regenerated numbers of small (diameter at breast height <20 cm) birch, spruce and pine trees were analysed with Generalized Linear Models (GLMs) (IV). First, the site-level numbers of small trees were compared between grazed and abandoned sites, while the number of conspecific large trees (diameter ≥20 cm) was included as an explanatory variable. Second, the numbers of small trees in grazed sites were analysed with the number of conspecific large trees, the occurrence of a gap in grazing, the number of junipers and canopy openness. Third, the numbers of small trees in abandoned sites were analysed with the number of conspecific large trees, spruce removal, time since abandonment and canopy openness. The analyses were done with Zero Hurdle Negative Binomial GLMs except for spruces in abandoned sites where Negative Binomial GLM was used.

All analyses were performed in R (version 3.1.1 by R Core Team 2014, or version 3.2.2 by R Core Team 2015). Functions were used from packages “MASS” (Venables and Ripley 2002), “lme4” (Bates *et al.* 2015), “nlme” (Pinheiro *et al.* 2014), “vegan” (Oksanen *et al.* 2013), “labdsv” (Roberts 2015), “indicspecies” (DeCáceres and Legendre 2009) and “pscl” (Jackman 2015).

3 RESULTS AND DISCUSSION

3.1 Grazing maintains high plant diversity by creating heterogeneity

Grazed sites had higher species richness of both vascular plants and soil-dwelling bryophytes than did abandoned sites (I, α_3 in Figure 4). There was a large difference in vascular plant species richness: grazed sites had on average 20 more species than abandoned sites (55 and 35, respectively). The difference in bryophyte species richness was smaller, with an average of 29 species on grazed sites and 23 in abandoned sites. The results are in accordance with those from semi-natural grasslands showing that grazing is of large importance in maintaining high plant diversity (Pykälä 2004, Takala *et al.* 2012, Mariotte *et al.* 2013). However, variation in other environmental properties has equal or even larger effects. Soil pH was the most important determinant for the species richness of both species groups, with vascular plant richness peaking at medium to high pH values (~4.5) and bryophyte richness at high pH values (4.5–5, which is still moderately acidic). In addition, high soil moisture and low tree density increased the species richness of especially bryophytes (I).

The positive impact of grazing management on plant species richness occurred already at the smaller spatial scales, i.e. in subplots (α_1) and in plots (α_2). (II, Figure 4). Previous work has shown that fine-scale alpha diversity can remain constant or even decrease in the presence of herbivores, while beta diversity between the patches can increase (Alados *et al.* 2007, Zhou *et al.* 2008, Bloor and Pottier 2014). Indeed, in our data the positive effects of grazing on plant species richness were high at the within-plot (β_1) and within-site (β_2) beta diversities, resulting in the notable differences in species richness at the site-level (α_3). The grazer-increased beta diversity was mostly composed of higher species turnover between subplots within plots (β_{T1}) and between plots within sites (β_{T2}) (II), indicating that the grazers cause high species replacement between different areas within a pasture by increasing the heterogeneity of habitats where different species can flourish.

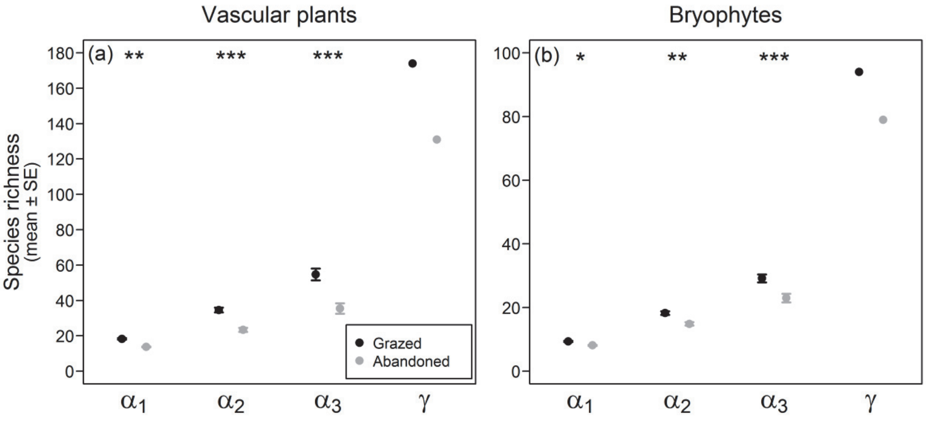

FIGURE 4 The species richness of vascular plants (a) and bryophytes (b) in grazed and abandoned wood-pastures at four spatial scales: within subplots (α_1), plots (α_2), sites (α_3) and the landscape (γ). The stars represent the significance of the difference (GLMM for α_1 and α_2; GLM for α_3): *** = $P \leq 0.001$, ** = $P \leq 0.01$ and * = $P \leq 0.05$. Reprinted from paper II.

The grazer-induced increases in the within-plot and within-site beta diversities were caused by the combined effects of defoliation, trampling and dunging (II). The within-plot beta diversity (β^{+}_{1}) of both vascular plants and bryophytes was influenced most strongly by variation in defoliation between subplots. Selective defoliation creates and maintains heterogeneity, because the same palatable plant individuals are likely to be eaten repeatedly (Hobbs and Swift 1988, Adler *et al.* 2001). As a result, defoliation is usually considered to be the most important grazer activity in structuring grassland vegetation (Olff *et al.* 1999, Adler *et al.* 2001). However, our results show that at larger scales plant beta diversity (β^{+}_{2}) is impacted more by trampling and even by dunging (II). At this scale trampling may be the factor that creates the most long-term heterogeneity: different areas within a wood-pasture are likely to receive continuous amounts of trampling from year to year because the animals tend to move along the same pathways (Kohler *et al.* 2006b). Finally, dunging was the second most important variable for increasing plant beta diversity at both of the studied spatial scales (β^{+}_{1} and β^{+}_{2}). Dung pats were sparse in the subplots, but when they do occur, they increase heterogeneity in several ways: they suffocate the original vegetation, introduce seeds, reduce the attractiveness of the surrounding vegetation, provide free regeneration patches for subordinate species, increase nutrient availability and provide a rare substrate for specialist species (Afzal and Adams 1992, Bakker and Olff 2003, Gillet *et al.* 2010, Jaroszewicz *et al.* 2011).

In paper I the average defoliation value of all the subplots was used as a general measure of grazing intensity on a site and it was found to be an important determinant for plant species richness in grazed sites. Vascular plant richness peaked at medium to high grazing intensities, while bryophyte richness peaked at high grazing intensities. It should be noted, though, that grazing intensity was low to moderate in most of our study sites and overgrazing was hardly an issue in any of the sites. The observed pattern is therefore similar to the one predicted by the Intermediate Disturbance Hypothesis (Grime 1973, Connell 1978). Plant species richness peaks at medium grazing intensities, because at low grazing intensities dominant species outcompete subordinate species while heavy grazing limits the regeneration or survival of sensitive species (Grime 1973, Milchunas *et al.* 1988, Mariotte *et al.* 2013). In addition, medium grazing intensity leads to high spatial heterogeneity in the grazing effects (Milchunas *et al.* 1988), which in turn increases the beta diversity of plants (see above).

Within the landscape more species were observed in grazed sites than in abandoned sites (γ), for both vascular plants (174 vs. 131 species) and soil-dwelling bryophytes (94 vs. 79 species). The grazed sites had higher turnover between them (β_{T3}), meaning that grazed sites host a higher variety of species between them than abandoned sites (II). Grazed sites vary in their management practices, which increases their differences in species composition. In addition, there is likely to be variation in the species composition of different sites due to e.g. soil fertility or historical events, and continuous grazing can maintain this variation. Abandonment results in fast biotic homogenization between sites when the same species start to dominate everywhere (see McCune and Vellend 2013). Nestedness was higher between the abandoned sites (β_{N3}, II), because all of them contain the same common species, but most sites are species-poor and only the most fertile or moist sites provide habitats for rare species (I). The grazed sites vary in their species composition, but all kinds of sites supported relatively high species numbers (I).

3.2 Grazers affect bryophytes on rocks but not on trees or decaying wood

Bryophytes grow on several substrates other than soil and the effects of grazers were studied also for species that grow on rocks, tree bases or decaying wood (III). While more species were observed on soil than on the other microhabitats, rocks hosted large numbers of bryophytes as well. In boreal wood-pastures epilithic species benefit from the abundance and diversity of rocks, boulders and cliffs, but the number of species is limited by the lack of calcareous formations (Ulvinen *et al.* 2002, Takala *et al.* 2014). Grazed sites had higher species richness of bryophytes on rocks than did abandoned sites (III). This was mostly due to the positive effects of grazing on the diversity of differently sized bare rock surfaces (III). Based on my observations, the grazers keep small, low-lying rocks and the flat parts of large boulders exposed by defoliating the surrounding vascular plants and by trampling the accumulating litter, soil and forest floor bryophytes, which provides free microhabitats for subordinate species.

Trees were the least bryophyte-rich microhabitat type (III), which is in accordance with previous studies from boreal forests (Mills and Macdonald 2004, Dynesius *et al.* 2009, Takala *et al.* 2014). Decaying wood, on the other hand, is usually abundant and very bryophyte-rich in old-growth boreal forests (Berg *et al.* 2002, Mills and Macdonald 2004, Dynesius *et al.* 2009), which contrasts with the scarce decaying wood and low diversity of epixylic bryophytes in wood-pastures (Takala *et al.* 2014, paper III). The diversity of epiphytic and epixylic bryophytes in wood-pastures is limited by the rarity of deciduous trees with favourable bark properties (e.g. aspen and goat willows, see Piippo 1982; Kuusinen 1996) and the removal of dead or dying trees and branches. In addition, browsing by grazers reduces tree regeneration, trampling destroys pieces of decaying wood, and the semi-open conditions may hamper species that require shade or moisture. Abandonment could improve habitat availability for epiphytic and epixylic species by increasing the numbers of young trees (IV), which improves microclimatic conditions for shade-requiring species, and in the long-term by increasing the amount of decaying wood and large deciduous trees (Nordén *et al.* 2004; Paltto *et al.* 2008, 2011). However, such positive effects were not clear in my data, although some abandoned sites did have slightly increased bryophyte richness, microhabitat area or microhabitat diversity on trees or decaying wood (III). These sites had been abandoned only 7–42 years earlier, and therefore the long-term positive effects were not detectable yet, and more studies are needed to confirm them.

3.3 Several species benefit from grazing

Grazed and abandoned sites differed in the species composition of vascular plants: their communities were best explained by the combined effects of soil pH and the management situation (I). The Indicator Species Analysis identified 40 vascular plant species that were significantly or nearly significantly ($p<0.1$) more common on grazed sites and 7 species that were more common on abandoned sites (Table 1). Therefore, 21 % of vascular plant species showed preference for grazed sites and 4 % for abandoned sites. Many types of species were more common in grazed sites, but a large proportion of them are forbs (Table 1). Many of the species are low-growing (*Cerastium fontanum*, *Festuca ovina*, *Fragaria vesca*, *Plantago major* and *Veronica* species), poisonous (e.g. *Ranunculus* species), or of low nutritive value (e.g. the grasses *Anthoxanthum odoratum* and *Festuca ovina*). Such species are typically subordinate, i.e. they lose in competition against larger dominant species if grazers do not create empty gaps (Mariotte *et al.* 2013). However, some of the species that were common in the grazed sites indicate eutrophication and may be common due to harmful management practices such as grazing in connection to fertilized pastures (*Poa pratensis*, *Rumex longifolius*, *Stellaria media* and *Urtica dioica*) (Pykälä 2001). The indicators of abandoned sites are common species on undisturbed forest soils, and while most of them occurred commonly in the grazed sites as well, their abundances have increased after abandonment. They include species that typically dominate boreal forest floors, e.g. *Calamagrostis arundinacea*, *Vaccinium myrtillus* and *V. vitis-idaea*. Thus, abandonment leads to the biotic homogenization of the wood-pasture habitat with the surrounding forest landscape, while continued grazing maintains hotspots of plant diversity where ruderal species co-occur with forest species (Schulman *et al.* 2008b).

TABLE 1 Vascular plant species with significant or nearly significant ($p<0.1$) indicator values in the Indicator Species Analysis comparing the occurrence and abundance of species on grazed vs. abandoned sites. The significance of the indicator value is given with symbols: *** = $P \leq 0.001$, ** = $P \leq 0.01$ and * = $P \leq 0.05$ and . = $P \leq 0.1$.

Indicators of grazed sites	**Type**	**Indicator value**
Achillea millefolium L.	forb	0.73 ***
Agrostis capillaris L.	grass	0.68 ***
Alchemilla spp.	forb	0.31 *
Anthoxanthum odoratum L.	grass	0.21 .
Anthriscus sylvestris (L.) Hoffm.	forb	0.45 **
Campanula persicifolia L.	forb	0.22 .
Carex pallescens L.	sedge	0.32 *
Cerastium fontanum Baumg.	forb	0.48 ***
Deschampsia cespitosa (L.) P. Beauv.	grass	0.65 **
Epilobium montanum L.	forb	0.21 .
Equisetum sylvaticum L.	horsetail	0.35 .
Festuca ovina L.	grass	0.24 .
Fragaria vesca L.	forb	0.59 *
Galium uliginosum L.	forb	0.33 **
Hieracium Sylvatica -group	forb	0.37 .
Leontodon autumnalis L.	forb	0.21 .
Leucanthemum vulgare Lam.	forb	0.38 **
Moehringia trinervia (L.) Clairv.	forb	0.30 *
Phleum pratense L.	grass	0.46 ***
Pilosella spp.	forb	0.46 ***
Plantago major L.	forb	0.58 ***
Poa annua L.	grass	0.25 *
Poa pratensis L.	grass	0.72 ***
Prunella vulgaris L.	forb	0.51 **
Ranunculus acris L.	forb	0.39 *
Ranunculus auricomus -group	forb	0.50 **
Ranunculus repens L.	forb	0.56 **
Rumex acetosa L.	forb	0.43 **

Rumex longifolius DC.	forb	0.21 *
Silene dioica (L.) Clairv.	forb	0.38 .
Stellaria graminea L.	forb	0.49 **
Stellaria media (L.) Vill.	forb	0.48 **
Taraxacum spp.	forb	0.75 ***
Trifolium pratense L.	forb	0.38 **
Trifolium repens L.	forb	0.67 ***
Urtica dioica L.	forb	0.44 **
Veronica chamaedrys L.	forb	0.60 *
Veronica officinalis L.	forb	0.63 **
Veronica serpyllifolia L.	forb	0.29 **
Vicia sepium L.	forb	0.41 .

Indicators of abandoned sites	**Type**	**Indicator value**
Calamagrostis arundinacea (L.) Roth	grass	0.62 *
Carex digitata L.	sedge	0.45 *
Melampyrum pratense L.	forb	0.51 .
Melica nutans L.	grass	0.34 .
Rubus saxatilis L.	forb	0.56 *
Vaccinium myrtillus L.	dwarf-shrub	0.65 **
Vaccinium vitis-idaea L.	dwarf-shrub	0.61 .

The community composition of soil-dwelling bryophytes was mostly determined by soil pH, and although the management situation was the most important variable after pH, it did not have a significant effect (I). 13 species showed significant or nearly significant indicator values for grazed sites and four species for abandoned sites (Table 2). These were 12 and 4 % of all bryophyte species found in the study. Many of the species that preferred grazed sites are light-demanding (e.g. *Brachythecium albicans*, *Climacium dendroides*, *Polytrichum juniperinum*, *Rhytidiadelphus squarrosus*) and therefore they benefit from the defoliation of field layer plants and the browsing of tree seedlings that maintain semi-open conditions (IV). Most of the grazing-indicating bryophytes are acrocarpous mosses (Table 2), many of which are typical pioneers of bare soil (e.g. *Bryum capillare*, *Ceratodon purpureus* and *Pohlia nutans*; Ulvinen et al. 2002) and thus they benefit from trampling. *Tayloria tenuis*, on the other hand, benefits from dunging as it grew exclusively on dung on our sites. *T. tenuis* is nearly threatened in Finland and regionally threatened in the southern boreal zone (Sammaltyöryhmä 2015), and it seems to be the only rare species that is rather strongly dependent on grazed wood-pastures, since it disappears soon after abandonment and does not occur on grazed open pastures (Takala *et al.* 2012, Pitkämäki 2015). The indicators of abandoned sites are very common forest floor mosses, including *Hylocomium splendens* and *Pleurozium schreberi* that dominate in Finnish forests.

TABLE 2 Bryophyte species with significant or nearly significant (p<0.1) indicator values in the Indicator Species Analysis comparing the occurrence and abundance of species on grazed vs. abandoned sites. The significance of the indicator value is given with symbols: *** = P≤0.001, ** = P≤0.01 and * = P≤0.05 and . = P≤0.1.

Indicators of grazed sites	Type	Indicator value
Atrichum undulatum (Hedw.) P.Beauv.	Acrocarpous moss	0.31 .
Brachythecium albicans (Hedw.) Schimp.	Pleurocarpous moss	0.33 **
Bryum capillare Hedw.	Acrocarpous moss	0.38 **
Ceratodon purpureus (Hedw.) Brid.	Acrocarpous moss	0.28 *
Climacium dendroides (Hedw.) F.Weber & D.Mohr	Pleurocarpous moss	0.46 *
Dicranum scoparium Hedw.	Acrocarpous moss	0.63 **
Oxyrrhynchium hians (Hedw.) Loeske	Pleurocarpous moss	0.32 *
Pellia spp.	Thalloid liverwort	0.17 .
Pohlia nutans (Hedw.) Lindb.	Acrocarpous moss	0.57 **
Polytrichastrum longisetum (Sw. ex Brid.) G.L.Sm.	Acrocarpous moss	0.34 **
Polytrichum juniperinum Hedw.	Acrocarpous moss	0.61 **
Rhytidiadelphus squarrosus (Hedw.) Warnst.	Pleurocarpous moss	0.59 **
Tayloria tenuis (Dicks.) Schimp.	Acrocarpous moss	0.46 **
Indicators of abandoned sites	**Type**	**Indicator value**
Dicranum polysetum Sw. ex anon.	Acrocarpous moss	0.58 *
Hylocomium splendens (Hedw.) Schimp.	Pleurocarpous moss	0.59 .
Pleurozium schreberi (Willd. ex Brid.) Mitt.	Pleurocarpous moss	0.59 .
Sciuro-hypnum curtum (Lindb.) Ignatov	Pleurocarpous moss	0.60 *

The occurrence of all bryophyte species on soil, rocks, trees or decaying wood and on either grazed or abandoned or both kinds of sites was tested with an extended Indicator Species Analysis (III). The majority of bryophyte species occurred more often on soil than on any of the other microhabitat types. In addition, several species were associated with rock microhabitats, with 13 species showing significant (p<0.05) indicator values (III). Four of these species occurred mostly on the rocks of grazed wood-pastures: the liverwort *Barbilophozia hatcheri* (A.Evans) Loeske and the mosses *Grimmia muehlenbeckii* Schimp., *Homomallium incurvatum* (Schrad. ex Brid.) Loeske and *Sciuro-hypnum* *populeum* (Hedw.) Ignatov & Huttunen. They are smaller in size than the common forest floor mosses that typically overgrow rocks in boreal forests (e.g. *Pleurozium schreberi*, *Hylocomium splendens* and *Plagiomnium cuspidatum* (Hedw.) T.J.Kop.) and as subordinate species they benefit from the occasional trampling of wood-pasture rocks that prevents the spread of the larger species. After wood-pasture abandonment much the rock surface becomes overgrown by the large forest floor species, resulting in the homogenization of the species composition with the surrounding forest floor as well as the surrounding forest landscape. The colonization of rock surfaces by large mosses was, however, beneficial to small liverworts that grow among their shoots, especially *Lophozia ventricosa* (Dicks.) Dumort. and *L. silvicola* (H.Buch) E.W.Jones ex R.M.Schust. (that were here analysed together because they are often unidentifiable). Compared to soil and rocks much fewer species were associated with microhabitats on trees or decaying wood. Both of these microhabitat types had only two significant indicator species and they were indifferent to the management situation (III). As discussed above, the lack of grazing impacts on the bryophytes of trees and decaying wood can result from the general scarcity of suitable substrates and the long time lag in the effects of abandonment.

Three of the vascular plant species found in this study are regionally threatened in the southern boreal zone (I, Ryttäri et al. 2012) and 11 of the bryophyte species are nationally or regionally red-listed (III, Juutinen and Ulvinen 2015). The dung-dwelling *Tayloria tenuis* is clearly dependent on grazers. For the other red-listed species my data are not sufficient to determine the effects of management, although some of them benefit from the grazing-induced openness and reduced competition, e.g. the regionally threatened forbs *Coeloglossum viride* (L.) Hartm. and *Vicia tetrasperma* (L.) Schreb. None of the red-listed species that were observed in the study occur exclusively on traditional rural biotopes, instead the majority of them are typical to herb-rich forests, such as the forb *Listera ovata* (L.) R. Br. and mosses *Campylium protensum* (Brid.) Kindb., *Eurhynchium angustirete* (Broth.) T.J.Kop., *Thuidium delicatulum* (Hedw.) Schimp. and *Thuidium tamariscinum* (Hedw.) Schimp. that are all regionally threatened (Hämet-Ahti *et al.* 1998, Ulvinen *et al.* 2002, Ryttäri et al. 2012). Thus, they are more dependent on naturally fertile soil conditions than on management. Several of the red-listed bryophytes are also dependent on decaying wood, for example the vulnerable moss *Herzogiella turfacea* (Lindb.) Z.Iwats. and the near-threatened and regionally threatened liverwort *Lophozia ciliata* Damsh. et al. (Ulvinen *et al.* 2002).

3.4 Grazing and abandonment lead to differences in tree regeneration

Wood-pastures are dependent on both their trees and their grazers, but based on my results grazing may cause unwanted changes in tree regeneration. In time all sites are likely to become spruce-dominated unless drastic actions are taken to prevent the changes (IV). Grazing alone is not sufficient to prevent sprucification (IV), because grazers avoid browsing spruces. In order to prevent the increase of spruces in the future dominant cohorts, young spruces need to be cut manually in all sites where the aim is to retain the dominance of other tree species (which is already recommended to Finnish wood-pasture owners, Jääskeläinen 2003). However, grazing threatens the regeneration of deciduous trees (IV), which is especially troublesome for birches that currently dominate in many sites, and for aspen that is usually scarce but hosts high biodiversity (Esseen *et al.* 1992, Kouki *et al.* 2004). In addition, the numbers of small pines varied strongly among grazed sites, and there seems to be regeneration failure in some of the pine-dominated sites (IV). The numbers of small birches and pines were higher in sites where junipers (*Juniperus communis* L.) were present in large numbers (IV). The spiky junipers may protect tree seedlings from browsing (Lampimäki 1939, Olff *et al.* 1999). Gaps in grazing have also been suggested as an option to aid tree regeneration (VanUytvanck *et al.* 2008, VanUytvanck and Verheyen 2014), but based on my results their success in increasing the numbers of young birches and pines is inconsistent (IV), and they may also threaten the survival of grazing-dependent species (I).

In abandoned sites deciduous trees had regenerated in large numbers. Rowans (*Sorbus aucuparia* L.) were especially abundant (IV) and usually they formed the majority of the abundant bush layer typical to recently abandoned wood-pastures. Birches increased as well, with the exception that they failed to regenerate in the shadow of spruce-dominated sites (IV). Spruces regenerated almost everywhere, while pines regenerated only in some pine-dominated or pine-mixed sites and only in small numbers (IV). The succession of most abandoned wood-pastures is likely to lead first to the dominance of birches and other deciduous trees and later to the dominance of spruce. The process of biotic homogenization is thus in progress in the tree layer as well as the ground and field layers (I, II). Attempts have been made to reduce sprucification by cutting spruces manually from some birch-dominated abandoned wood-pastures that host high biodiversity values (Laine and Heikkilä 2011). While this has been successful in reducing spruces, the regeneration of the aimed deciduous trees has not increased (IV, Mustonen and Saine 2013).

4 CONSERVATION APPLICATIONS

Based on my results the conservation values of boreal wood-pastures are related to their high species richness and the characteristic combination of species that typically live in different habitats (I). The conservation value of wood-pastures can be compared to that of species-rich semi-natural grasslands that are managed with the same pool of subsidies than wood-pastures. Table 3 shows a comparison of average and total species richness values at various scales on the 24 grazed wood-pastures against 24 grazed and mown grasslands in the same geographical area. Vascular plants were more species-rich on the grasslands at small spatial scales (4 m^2 subplots), but the difference evens out at the site-scale and within the landscape the total number of species is similar, considering that the number of subplots studied per site was higher for wood-pastures (Table 3, Hämynen and Toikkanen 2014). Only two red-listed species were observed on both of the two habitat types, partly because the subplots covered a very small proportion of the total area. Soil-dwelling bryophytes, on the other hand, were more numerous at all the spatial scales in grazed wood-pastures compared to grazed and mown grasslands (Table 3, Pitkämäki 2015). Five red-listed bryophyte species grew on the soil of grazed wood-pastures, while none were observed in the grasslands. In addition, the number of rare species and the total number of species were even higher for bryophytes if epilithic, epiphytic and epixylic species are included (III). Thus, the conservation value of wood-pastures is roughly similar to that of semi-natural grasslands for vascular plants, but higher for bryophytes.

The reasons for high species richness in wood-pastures are manifold. Within a representative wood-pasture the tree density varies so that there are open, semi-open and closed-canopy patches (Schulman *et al.* 2008b). The occurrence of many species is also dependent on the diversity of structural elements, such as rocks, trees and decaying wood (III). Thus, management practices should aim to increase the diversity and amount of structures, especially decaying wood. In addition, the variation in grazer activities results in differently disturbed patches, which provide microhabitats for various species. Variation in species composition between sites is further increased by differing soil conditions. Special attention should be paid to naturally fertile and/or moist sites that are likely to host several rare species (I).

TABLE 3 The average species richness on the subplots, plots and sites and the total number of all species and of rare species within the landscape: a comparison of the 24 grazed wood-pasture sites and 24 grazed and mown grassland sites. Only soil-dwelling bryophytes are included. Note that the plot-level was not included in the grassland study, but the number of subplots was comparable to their plot- and site-level numbers in the wood-pasture study. The numbers of vascular plant species on the grasslands is based on Hämynen and Toikkanen (2014) and that of bryophytes on Pitkämäki (2015).

Wood-pastures	Subplot ($4\ m^2$)	Plot (4 subplots)	Site (12 subplots)	Landscape (24 sites)	Red-listed (24 sites)
Vascular plants	18	35	55	174	2
Bryophytes	9	18	29	94	5

Grasslands	Subplot ($4\ m^2$)		Site (5 subplots)	Landscape (24 sites)	Red-listed (24 sites)
Vascular plants	22		44	164	2
Bryophytes	8		17	52	0

Identifying the biodiversity values in wood-pastures is complicated because they are dependent on so many factors. I suggest that three components should be taken into account:

1. Structural variation caused by grazer activities, such as paths and varying vegetation height;

2. Structural diversity caused by rocks (abundance and variation in size), trees (variation in density, tree size and tree species) and decaying wood (variation in size, tree species and decay stage, and the abundance of large logs, especially); and

3. Diversity of plant species. Vascular plant species richness and species composition respond strongly to continuous grazing and soil pH (I), so I suggest that they can be used to evaluate the general value of a wood-pasture. Indicator species are widely used in the surveys of open traditional rural biotopes (Pykälä 2001) and similar indicator species lists should be compiled for wood-pastures. Soil-dwelling bryophytes followed generally the same patterns of diversity than did vascular plants (I, II), so relatively quick surveys of indicator vascular plants can be sufficient to identify sites with highest plant diversity. However, because bryophytes and several other species groups are dependent on other microhabitats than those on soil (III), the use of indicator

species alone is not sufficient but has to be combined with the identification of structural diversity in the pasture.

Continuous grazing increased and maintained almost all aspects of plant biodiversity (I, II, III). Variation in plant species composition (beta diversity) was increased by the combined effects of defoliation, trampling and dunging (II), and thus the grazers create a unique set of disturbances that cannot be replaced by other disturbances or management actions. Grazing increased plant species richness in all kinds of sites, irrespective of their soil properties, tree density or historical land-use (I). In addition, there was high species turnover between the grazed wood-pastures (II). Based on these reasons, the primary aim should be to continue the grazing management in all kinds of wood-pastures. Secondary to this aim I recommend three management practices for boreal wood-pastures:

1. Grazing intensity should be kept at an intermediate level (neither low nor overgrazed) to maximize plant species richness (I) and beta diversity (II);
2. Eutrophication should be minimized by avoiding management practices such as providing additional fodder to the animals or fencing the wood-pasture together with a fertilized pasture or an old field (I); and
3. Junipers should not be removed, because they can improve the regeneration of browsing-prone tree species (IV).

Wood-pasture abandonment leads to decreased plant biodiversity and causes biotic homogenization of species assemblages of bryophytes, field layer vascular plants and trees (I, II, III, IV). Therefore, abandonment should be avoided, especially in sites with high biodiversity values related to grazer activities. The management of wood-pastures is expensive and labor-intensive and the landowners should be provided with counselling, information, encouragement, financial subsidies or contacts to cattle owners (Raatikainen 2016). However, the abandonment of some sites is inevitable. Biodiversity values should be surveyed also in abandoned wood-pastures, because they may host red-listed species typical to herb-rich forests, semi-open forests, or old-growth forests (I, III). The high plant species nestedness between abandoned wood-pasture sites (II) indicates that the permanent protection of the most species-rich sites can be a cost-effective way to conserve biodiversity. In some cases changes in ownership or the owner's interest in management may bring possibilities to restore the site back to a wood-pasture. Restoration includes expensive and labor-intensive work such as the removal of young trees (especially spruces, IV), fencing and resuming grazing. It should be encouraged and subsidized if the site still retains signs of past grazing activities (II), has diverse trees and abundant decaying wood (III), and hosts species typical to wood-pastures (I). Time since abandonment is less relevant (I, IV).

Grazers are able to halt succession in the ground- and field-layer vegetation (I), but the same is not true for trees: the proportion of spruces increases in time (IV). Other management practices, such as the removal of spruces can be used to slow down the changes, but are inefficient in the long-term. In my opinion the idea of a constant tree structure and the classification of wood-pastures based on the dominant trees should be discarded. Instead, there should be more flexibility for the landowners to allow the development of an individual site to either a more open pasture or to a wood-pasture dominated by a changing mixture of tree species, or for some to be abandoned and then proceed in natural succession. Meanwhile, the continuous provision of various types of wood-pastures should be ensured within landscapes, including the management of current wood-pastures, the restoration of abandoned ones and the creation of new wood-pastures. However, the large number of stakeholders and administrative authorities involved in the management of traditional rural biotopes makes this is a very complicated task. Promising approaches include increasing the collaboration between various stakeholders, coupling the management of traditional rural biotopes with modern cattle husbandry, and providing large-scale landscape-level management planning (Raatikainen 2016).

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During the past years I have spent hundreds of hours in the museum basement with thousands of bryophyte specimens from various research projects. Specimens collected from study plots or trunks are often not in a good shape or big enough, let alone fertile, which can cause quite a bit of desperation in the cold, dark basement. I felt a bit lonely with my specimens because I was the only bryophyte expert in our group (and sometimes I didn't even feel like an expert myself). Luckily there are saving angels outside the basement: I have a big group of bryophyte friends, with whom we formed our bryophyte club "Sammaltajat" a couple of years before I started working on this project. They have taught me so much and they have helped me with difficult specimens. We have spent countless hours on fieldtrips or microscopy evenings, we have studied together, and we have shared the pain of unidentifiable specimens. I would not have been able to make it with you guys. Thank you Riikka Juutinen, Emmi Lehkonen, Katriina Peltonen, Hilja Vuori, Timo Kypärä, Johanna Hallman and many others! Special thanks to Jukka Salmela for introducing me to bryophytes many years ago in a Latvian forest, and to Timo, Riikka and Riitta Ryömä for your help with the specimens from this project.

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YHTEENVETO (RÉSUMÉ IN FINNISH)

Laidunnuksen ja sen päättymisen vaikutukset kasvien biodiversiteettiin puustoisissa perinneympäristöissä

Biodiversiteetti eli luonnon monimuotoisuus on ihmistoiminnan vuoksi uhattuna maapallolla. Koska suurin syy lajien uhanalaistumiselle ja häviämiselle on luonnontilaisten elinympäristöjen muuttuminen ja häviäminen, on biodiversiteettiä pyritty turvaamaan ennen kaikkea perustamalla suojelualueita sekä ennallistamalla muuttuneita ekosysteemejä kohti luonnontilaa. Osa uhanalaisista lajeista on kuitenkin nykyisin ihmistoiminnasta riippuvaisia. Esimerkiksi perinneympäristöjen ja niiden lajiston säilyminen edellyttää elinympäristön jatkuvaa hoitoa, kuten karjan laidunnusta tai niittoa.

Puustoiset perinneympäristöt ovat syntyneet karjan laiduntaessa vuodesta toiseen samoilla puita kasvavilla alueilla. Laitumien kasvilajisto on sekoitus sellaisia lajeja, jotka ovat alun perin menestyneet hyvinkin erilaisissa elinympäristöissä, kuten vanhoissa luonnonmetsissä tai luonnonhäiriöiden (metsäpalojen, tulvien, myrskyjen tai suurten kasvinsyöjien) muovaamilla alueilla. Puustoisten perinneympäristöjen lajistollinen monimuotoisuus johtuu pienipiirteisestä vaihtelusta puuston rakenteessa ja laiduntajien toiminnassa. Suuret laiduntajat luovat keskenään erilaisia laikkuja syömällä putkilokasvien versoja, tallaamalla maata ja kasveja sekä virtsaamalla ja ulostamalla. Puusto puolestaan voi vaihdella sekä puulajien että puiden tiheyden ja koon osalta. Näin laitumelle muodostuu ympäristöoloiltaan vaihtelevia laikkuja, joilla voi esiintyä eri lajeja.

Puustoiset perinneympäristöt ovat nykyisin uhattuina, koska maatalouden rakennemuutoksen takia laidunnus on loppunut suurimmalla osalla niistä. Esimerkiksi Suomen yleisimpiä puustoisia perinneympäristöjä, metsälaitumia, on jäljellä alle 1 % 1950-luvun pinta-alasta, ja merkittävää vähenemistä tapahtui jo ennen 50-lukua. Laidunnuksen loppumisen lisäksi jäljellä olevia puustoisia laitumia heikentää ja uhkaa maa- ja metsätalouden voimaperäistyminen, jonka seurauksia ovat esimerkiksi maaperän rehevöityminen, liian suuri laidunnuspaine, puuston hakkuut ja lahopuun väheneminen.

Väitöskirjassani tutkin kasvien lajistollista monimuotoisuutta keskisuomalaisilla metsälaitumilla ja metsälaitumia hieman harvapuustoisemmilla hakamailla. Tutkimuksessa oli mukana 24 laiduntamalla hoidettavaa kohdetta, joilla laiduntajina oli joko lehmiä, hevosia, lampaita tai sekakarjaa. Kohteet luokiteltiin valtapuuston mukaan koivu-, kuusi- ja mäntyvaltaisiin sekä sekapuustoisiin, ja kustakin näistä neljästä luokasta valittiin kuusi laidunnettua kohdetta. Lisäksi mukana oli 24 vastaavaa kohdetta, joilla laidunnus oli loppunut 7–42 vuotta aiemmin. Myös nämä kohteet valittiin siten, että jokaista yllä mainittua neljää puustoluokkaa edusti kuusi kohdetta.

Putkilokasvien ja maalla kasvavien sammalten lajimääriä tarkastellessa havaittiin, että laidunnetuilla kohteilla oli suurempi lajimäärä kuin laidunnuksesta pois jääneillä kohteilla. Vastaavia tuloksia on aiemmin saatu tutkittaessa laidunnettujen niittyjen kasvien monimuotoisuutta, mutta vain sellaisissa tapauksissa, joissa laidunnuspaine ei ole ollut liian suuri niityn tuottokykyyn nähden. Lisäksi havaittiin, että laiduntajien läsnäolo kasvattaa lajimäärää jo pienellä mittakaavatasolla (4 m^2 suuruisilla tutkimusruuduilla) ja vielä lisää sitä suuremmilla alueilla. Laidunnettujen kohteiden suurempi lajimäärä johtui siitä, että kasvilajiston koostumus vaihteli eri alueiden välillä. Tämän puolestaan havaittiin olevan seurausta laiduntajien syömisen, tallauksen ja lannan määrän vaihtelusta. Laidunnuksesta hyötyivät monet pienikokoiset, myrkylliset tai ravintoarvoltaan heikot kasvilajit. Mikäli laiduntajat eivät luo niille vapaata kasvutilaa, ne yleensä häviävät paikalta, kun suurempikokoiset lajit valtaavat elintilan. Myös monet paljaalla maalla tai lannalla kasvavat tai runsaasti valoa vaativat sammallajit hyötyivät laidunnuksesta.

Maanpinnalla kasvavien sammalten lisäksi tutkin sammalia, jotka kasvavat kivillä, puilla ja lahopuilla. Kivillä esiintyi maanpinnan jälkeen toiseksi eniten sammallajeja. Kivipintojen lajimäärä oli laidunnetuilla kohteilla suurempi kuin kohteilla, joilla laiduntajia ei enää ole. Useat kivipintojen lajit olivat myös yleisempiä laidunnetuilla kohteilla. Tämä johtuu siitä, että laiduntajat pitävät esimerkiksi pieniä, matalia kiviä paljaina syömällä ympäröivää kasvillisuutta, tallaamalla suurikokoisia sammal- ja putkilokasveja, ja silloin tällöin myös virtsaamalla kivien päälle. Kun tällaisia häiriöitä osuu harvakseltaan kivelle, siinä pystyvät kasvamaan myös pienikokoiset sammallajit. Puiden ja lahopuiden sammallajisto oli melko niukkaa, koska tutkimuskohteilla oli vain vähän sammalten kasvulle suotuisia lehtipuulajeja ja suurikokoista lahopuuta. Lahopuulla kuitenkin esiintyi useita harvinaisia lajeja, erityisesti kostean maaperän omaavilla, rehevillä kohteilla. Puiden tai lahopuiden sammallajimäärä ei eronnut laidunnettujen ja laidunnuksesta pois jääneiden kohteiden välillä. On kuitenkin mahdollista, että puiden ja lahopuiden sammallajisto hyötyy laidunnuksen loppumisesta useiden vuosikymmenien jälkeen, koska silloin alueilla kasvaa runsaasti uusia, varjoa ja kosteutta lisääviä puita ja pidemmän ajan kuluessa suurten lehtipuiden sekä lahopuun määrä kasvaa.

Puustoisen perinneympäristön säilyminen edellyttää pitkällä tähtäimellä sekä laidunnuksen jatkumista että puuston uusiutumista. Laidunnus voi kuitenkin estää nuorten puiden kasvun, mikä on ongelmallista, sillä kuolevien puiden tilalle ei enää kasva uusia. Selvittääkseni tulevaisuuden uhkakuvia tutkin myös puuston uusiutumista. Keskityin erityisesti tarkastelemaan yleisimpien valtapuulajien eli koivujen, kuusen ja männyn uusiutumista. Havaitsin, että laidunnetuilla kohteilla kasvoi vanhaan valtapuustoon nähden liian paljon nuoria kuusia, minkä seurauksena kaikenlaiset puustoiset laitumet kuusettuvat pitkän ajan kuluessa, ellei kuusia poisteta. Toisaalta koivut ja muut lehtipuut uusiutuivat heikosti, koska laiduntajat syövät niiden taimia. Myös männyt ovat osalla kohteista vähenemässä. Tulosteni perusteella nuorten koivujen ja mäntyjen määrää voi kasvattaa katajien runsas esiintyminen, koska piikikkäät katajat voivat suojata taimia laiduntajilta. Laidunnuksesta pois jääneillä puustoisilla perinneympäristöillä lehtipuut, erityisesti pihlajat, ovat runsastuneet voimakkaasti laidunnuspaineen hävittyä. Koivu ja erityisesti kuusi näyttävät uusiutuvan runsaasti, kun taas valoa vaativa mänty uusiutuu heikommin muiden puiden varjossa. Pitkällä aikavälillä myös hylätyistä kohteista suuri osa muuttuu luultavasti kuusivaltaisiksi.

Tulosteni perusteella puustoisten perinneympäristöjen luonnonsuojelubiologinen arvo liittyy kohteiden suureen kasvilajimäärään ja erikoiseen yhdistelmään lajeja, jotka tyypillisesti elävät erilaisissa elinympäristöissä. Laidunnuksen jatkaminen on lajiston säilymisen kannalta ensiarvoisen tärkeää. Lajisto myös vaihtelee laidunnettujen kohteiden välillä ja olisikin hyvä, että hoidossa olisi mahdollisimman paljon erityyppisiä kohteita, siis esimerkiksi valtapuustoltaan ja maaperältään vaihtelevia metsälaitumia ja hakamaita. Lisäksi olisi syytä pyrkiä kasvattamaan laidunten sisäistä rakenteellista monimuotoisuutta, esimerkiksi suurten lehtipuiden ja suuriläpimittaisten lahopuiden määrää lisäämällä. Katajia ei tulisi poistaa, mutta nuoria kuusia sen sijaan voi olla tarpeen kaataa. Laidunnuksesta pois jääneillä kohteilla voi myös olla luontoarvoja, joten niiden lajistoa pitäisi selvittää. Osalla kohteista voi olla esimerkiksi kostean ja ravinteikkaan maaperän takia suuri lajimäärä tai useita harvinaisia lajeja, jolloin voidaan harkita esimerkiksi alueen suojelua. Toisaalta myös kohteen kunnostaminen takaisin laidunnetuksi metsälaitumeksi tai hakamaaksi voi olla suositeltavaa, erityisesti mikäli kohteella on vielä selviä laiduntajien muokkaamia rakennepiirteitä (esim. polkuja ja leveälatvuksisia vanhoja puita) sekä laidunnuksesta hyötyviä lajeja. Koska pitkällä aikavälillä on todennäköistä, että osa nykyisistä laitumista hylätään tai ne muuttuvat avoimemmiksi tai kuusivaltaisemmiksi, olisi syytä myös turvata uusien vastaavien puustoisten laidunympäristöjen syntyminen ja hoito.

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ORIGINAL PAPERS

I

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

by

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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).

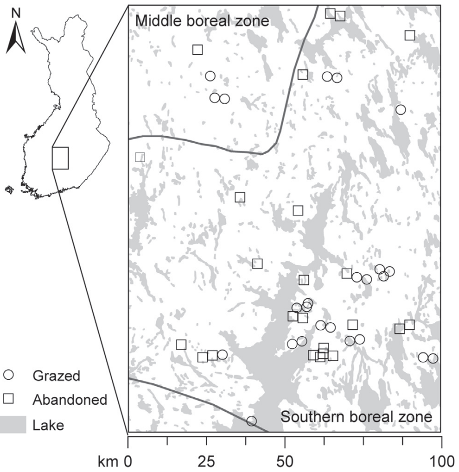

Fig. 1. The location of the study sites in Central Finland. © National Land Survey of Finland 2012.

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

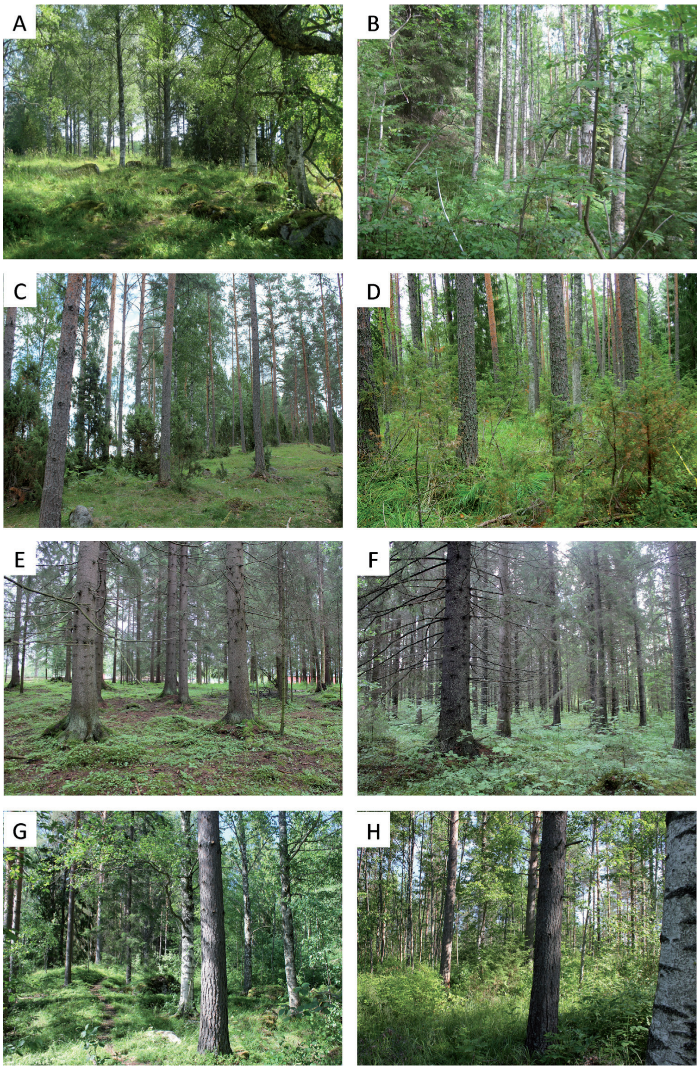

Fig. 2. Examples of study sites: (a) grazed dominated by birches, (b) abandoned dominated by birches, (c) grazed dominated by pines, (d) abandoned dominated by pines, (e) grazed dominated by spruces, (f) abandoned dominated by spruces, (g) grazed with mixed deciduous and coniferous trees, and (h) abandoned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

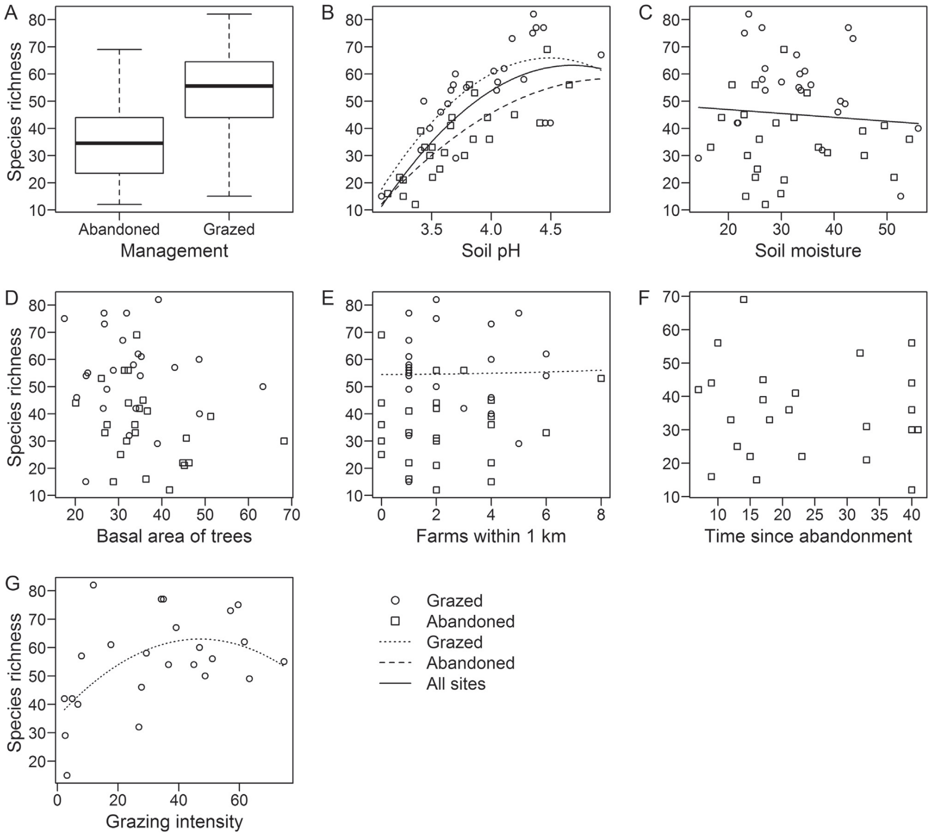

Fig. 3. Responses of species richness of all vascular plants to (a) management, (b) soil pH, (c) soil moisture content (%), (d) the basal area of all trees (m^2/ha), (e) the number of farms within 1 km from the site in the 1850s–1860s, (f) time since abandonment on abandoned sites (years), and (g) grazing 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

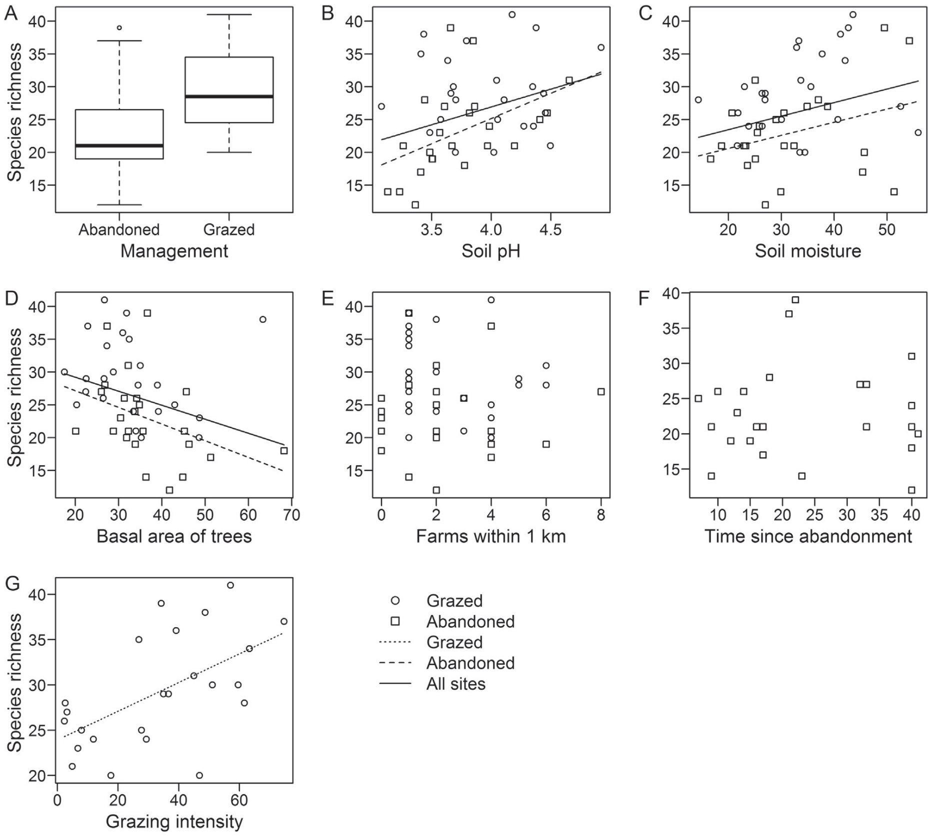

Fig. 4. Responses of species richness of all bryophytes to (a) management, (b) soil pH, (c) soil moisture content (%), (d) the basal are of all trees (m^2/ha), (e) the number of farms within 1 km from the site in the 1850s–1860s, (f) time since abandonment on abandoned sites (years), and (g) grazing 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).

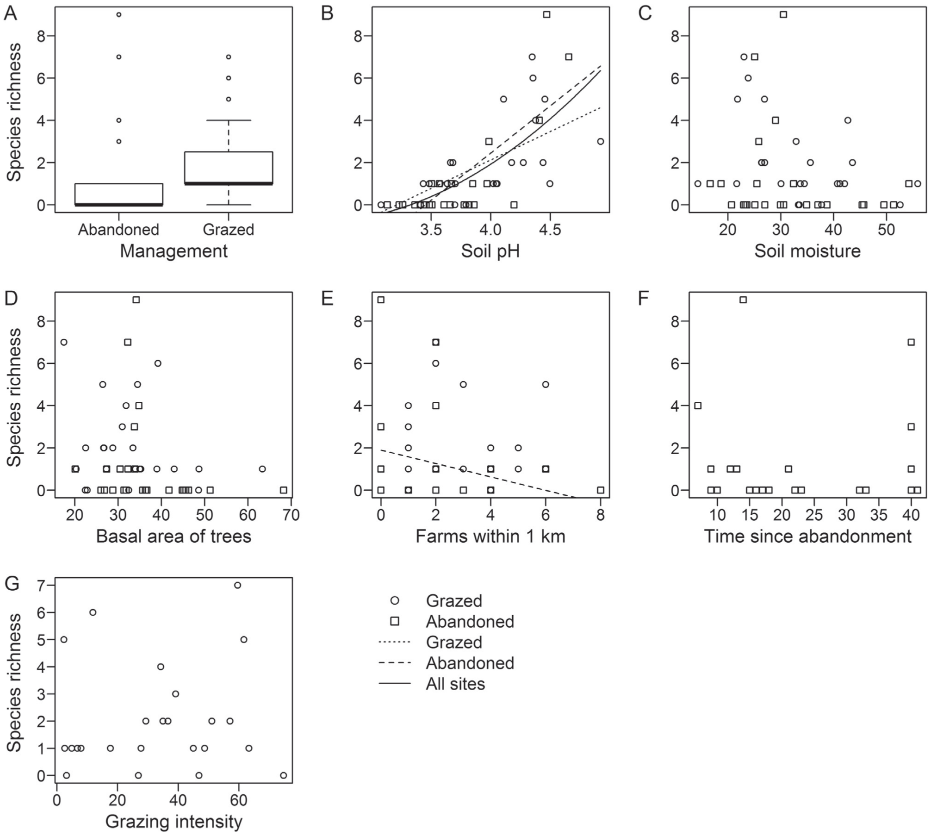

Fig. 5. Responses of species richness of rare vascular plants to (a) management, (b) soil pH, (c) soil moisture content (%), (d) the basal are of all trees (m^2/ha), (e) the number of farms within 1 km from the site in the 1850s–1860s, (f) time since abandonment on abandoned sites (years), and (g) grazing 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

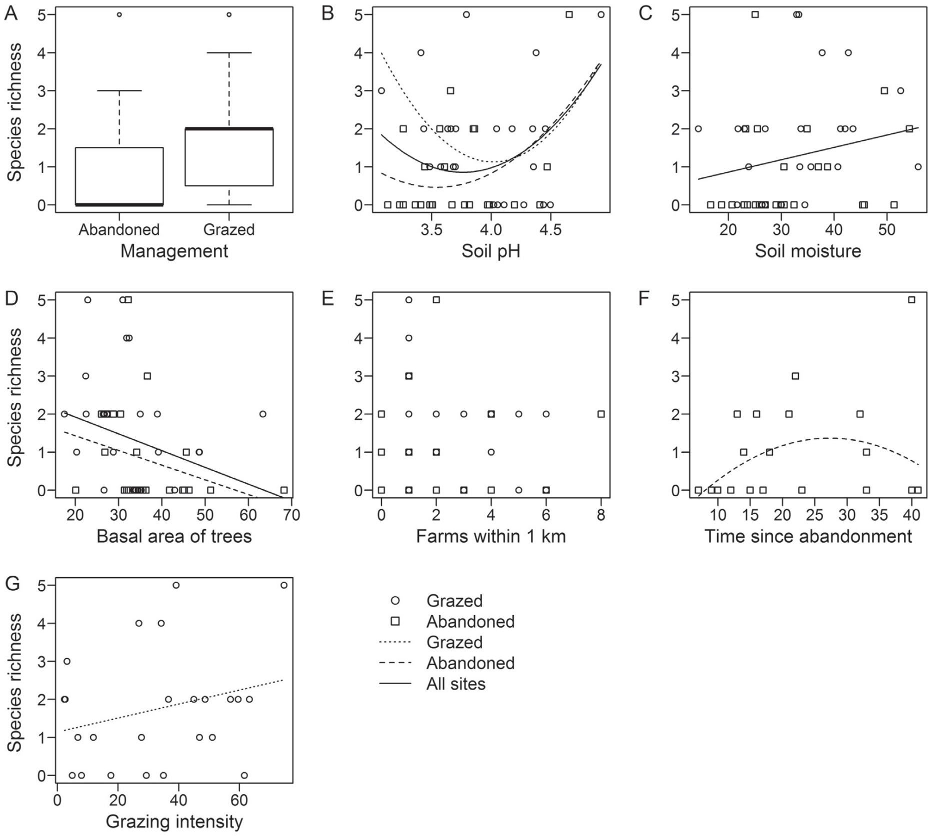

Fig. 6. Responses of species richness of rare bryophytes to (a) management, (b) soil pH, (c) soil moisture content (%), (d) the basal area of all trees (m^2/ha), (e) the number of farms within 1 km from the site in the 1850s–1860s, (f) time since abandonment on abandoned sites (years), and (g) grazing 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).

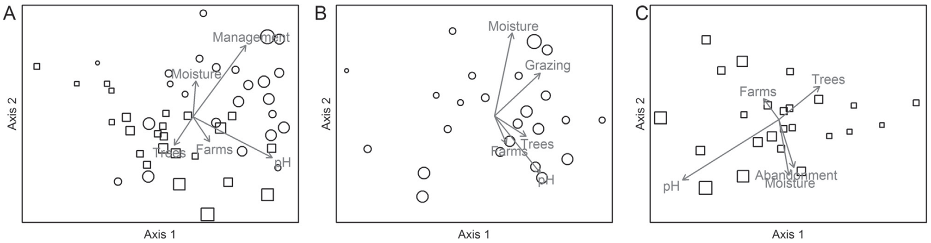

Fig. 7. Nonmetric Multidimensional Scaling (NMDS) for the community structure of vascular plants in (a) all sites, (b) grazed sites, and (c) abandoned sites. Grazed sites are depicted by circles and abandoned sites by squares, and the community composition of each site was derived from the average cover 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

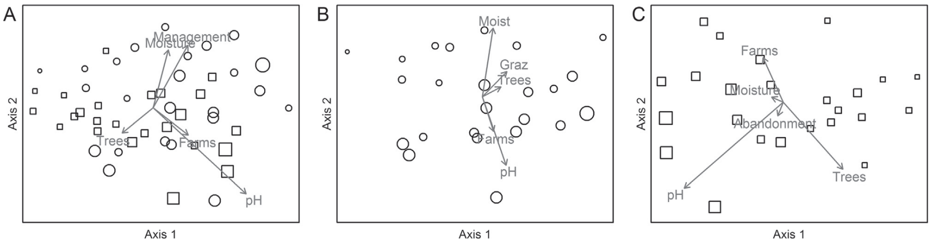

Fig. 8. Nonmetric Multidimensional Scaling (NMDS) for the community structure of bryophytes in (a) all sites, (b) grazed sites, and (c) abandoned sites. Grazed sites are depicted by circles and abandoned sites by squares, and the community composition of each site was derived from the average cover of 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

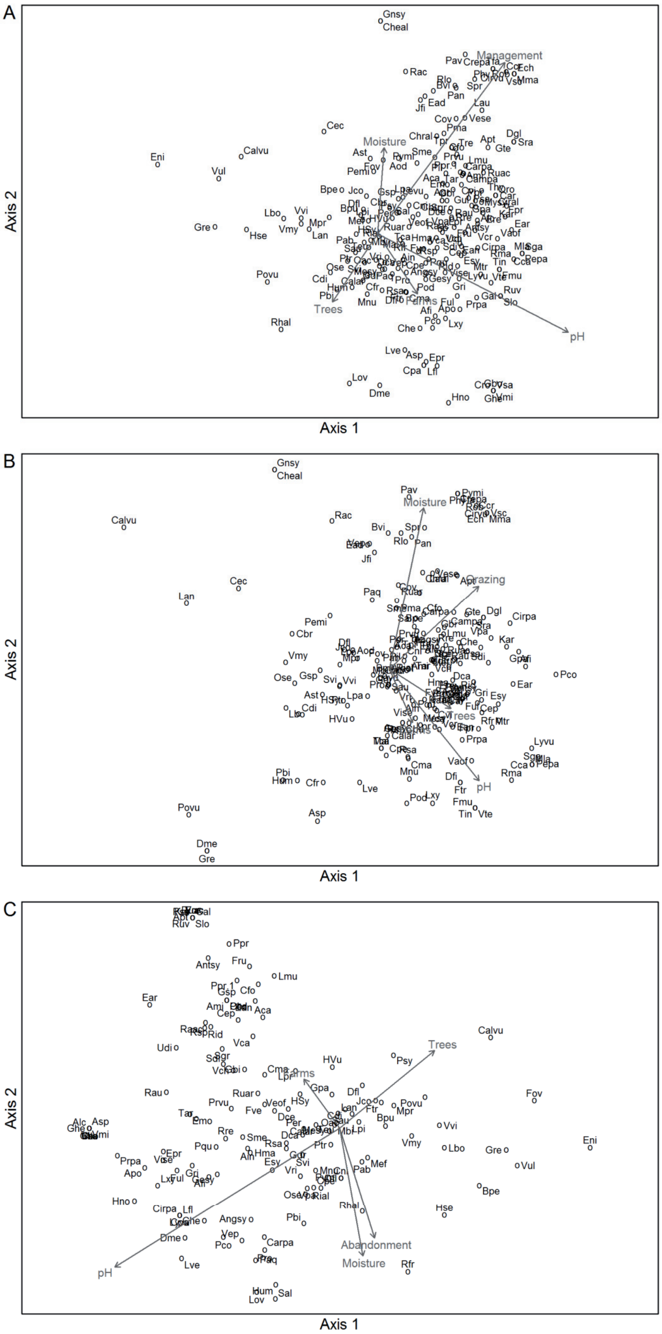

Figure 1. **Vascular plant species** centroids in the NMDS ordinations of a) all sites, b) currently grazed sites, and c) abandoned sites. The grey arrows represent the direction and strength of the effects of environmental variables. The species abbreviations include 1-3 letters from genus name and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

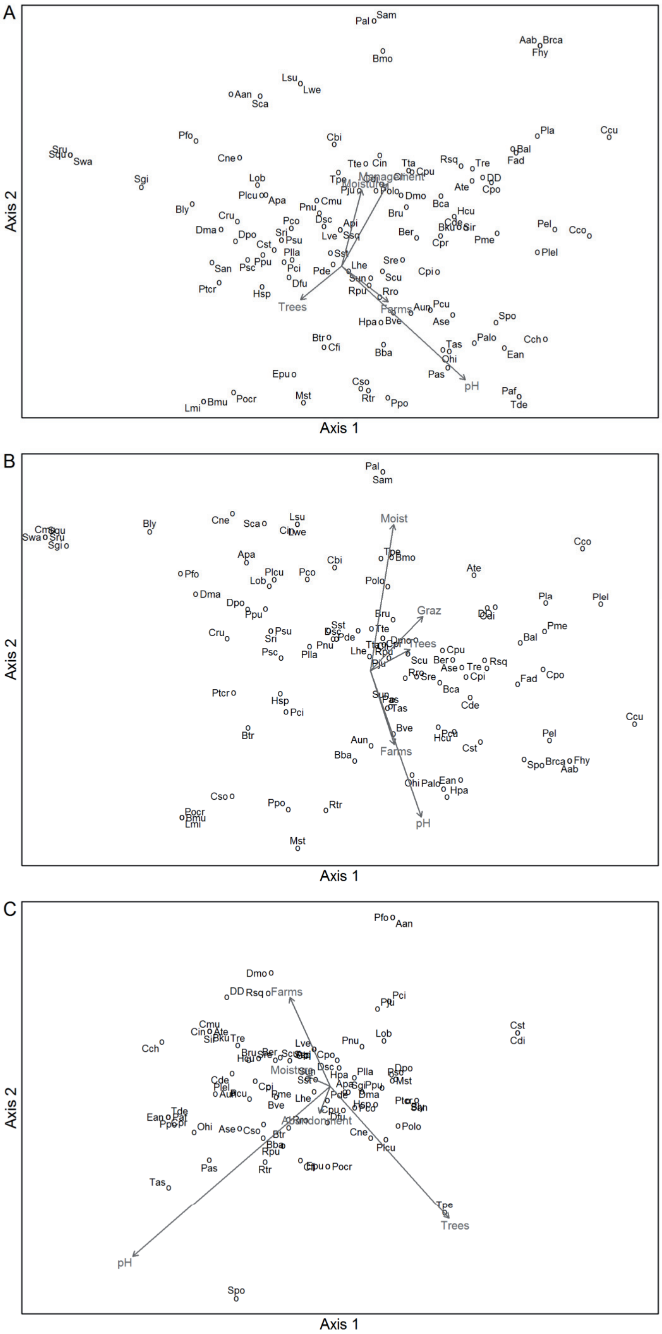

Figure 2. **Bryophyte species** centroids in NMDS ordinations of a) all sites, b) currently grazed sites, and c) abandoned sites. The grey arrows represent the direction and strength of the effects of environmental variables. The species abbreviations include 1-2 letters from genus name and 2 letters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

II

GRAZERS INCREASE BETA DIVERSITY OF VASCULAR PLANTS AND BRYOPHYTES IN WOOD-PASTURES

by

Anna Oldén & Panu Halme 2016

Journal of Vegetation Science, in press.

III

MICROHABITAT DETERMINES HOW GRAZING AFFECTS BRYOPHYTES IN WOOD-PASTURES

by

Anna Oldén & Panu Halme 2016

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IV

TREE SPECIES COMPOSITION OF BOREAL WOOD-PASTURES CHANGES UNDER BOTH GRAZING MANAGEMENT AND ABANDONMENT

by

Anna Oldén, Atte Komonen, Kaisa Tervonen & Panu Halme 2016

Submitted manuscript