

Master of Science Thesis

**Bryophyte diversity in semi-natural grasslands:
the effects of habitat quantity and quality**

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ABSTRACT

Agricultural practices in the previous centuries have created a set of unique semi-natural habitats, nowadays referred to as traditional rural biotopes (TRBs). Because of the transition to modern agriculture and other land-use changes, there is only a fraction left of these biologically, culturally and socially valuable habitats. High biological diversity of TRBs is often associated with openness, low nutrient levels and frequent disturbances. Several species have become threatened due to the decline and fragmentation of TRB-areas. As small microhabitat specialists, bryophytes are good indicators of habitat quality, which is especially reduced by insufficient management in the remaining TRBs. In this thesis, I studied the factors affecting bryophyte diversity in semi-natural grasslands. The effects of disturbance type (management by grazing or mowing), landscape structure (habitat amount) and local environmental variables (disturbance intensity, soil properties, competition) were studied. Data were collected from 24 semi-natural grasslands located in Central Finland and Päijänne Tavastia. At the time, 12 of the sites were mown and 12 grazed. The results suggest that management type does not affect the total species richness of bryophytes, although acrocarpous mosses are more common in grazed sites. Acrocarpous mosses benefited from the trampling of grazing animals, whereas pleurocarpous mosses responded negatively to grazing or mowing. Bryophyte diversity in studied grasslands reflects habitat quality, especially in terms of soil properties and substrate heterogeneity. No relationships with habitat quantity, i.e. landscape structure or grassland area, were observed. Vascular plants had no direct negative effects on species richness, but bryophyte cover was reduced by ground layer litter. Based on this study, the reducing quality of TRB-sites causes more changes in bryophyte communities than local or regional reductions in TRB area.

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Edeltäneiden vuosisatojen maatalouskäytännöt loivat elinympäristöjä, joihin tänä päivänä viitataan perinnebiotoopeina. Siirtymä moderniin maatalouteen on muiden maankäytön muutosten ohella vähentänyt näitä biologisesti, kulttuurisesti ja sosiaalisesti arvokkaita elinympäristöjä murto-osaan entisestä. Perinnebiotoopeille tyypillinen avoimuus, vähäravinteisuus ja säännölliset häiriöt tekevät niistä biologisesti monimuotoisia elinympäristöjä. Perinnebiotooppien pinta-alan pienenemisen ja pirstoutumisen seurauksena on ollut useiden lajien uhanalaistuminen. Jäljellä olevien perinnebiotooppien laatua uhkaa etenkin hoidon riittämättömyys. Sammalet ovat kooltaan pieniä ja ekologiaaltaan riippuvaisia sopivista mikrohabitaateista, mikä tekee niistä hyviä elinympäristön indikaattoreita. Tässä pro gradu -työssä tutkin sammalten monimuotoisuutta ja siihen vaikuttavia ekologisia tekijöitä perinnebiotooppiniityillä. Tarkastelin häiriötyypin (hoito laiduntamalla tai niittämällä), maisemarakenteen (elinympäristön määrä) ja paikallisten ympäristömuuttujien (häiriöintensiteetti, maaperän ominaisuudet, kilpailu) merkitystä. Aineisto kerättiin 24 niittykohteelta, jotka sijaitsivat pääasiassa Keski-Suomen alueella. Tutkimushetkellä 12 niittyä oli laitumena ja 12 niittyä hoidettiin niittämällä. Tulosten perusteella häiriötyyppi eli hoitomuoto ei vaikuta sammalten kokonaislajimäärään, mutta pesäkekärkisten (akrokarppisten) lehtisammalten määrä oli korkeampi laidunnetuilla kohteilla. Pesäkekärkiset sammalet hyötyivät laiduneläinten tallauksesta, kun taas pesäkekylkiset (pleurokarppiset) sammalet vähenivät laidunnuksen tai niiton seurauksena. Sammalten monimuotoisuus tutkituilla perinnebiotoopeilla riippui ensisijaisesti elinympäristön laadusta, etenkin maaperän ominaisuuksista ja kasvualustojen monipuolisuudesta. Elinympäristön määrällä eli maisemarakenteella tai niityn pinta-alalla ei ollut yhteyttä sammalten monimuotoisuuteen. Putkilokasvit eivät suoraan vaikuttaneet sammalten lajimäärään, mutta pohjakerroksen karike vähensi sammalten peittävyttä. Tämän tutkimuksen perusteella perinneympäristöjen laadun huonontumisella on suurempi merkitys sammalyhteisöille kuin perinnebiotooppien pinta-alan paikallisella tai alueellisella vähenemisellä.

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1. INTRODUCTION

The anthropogenic impact spans all terrestrial ecosystems (Barnosky *et al.* 2011). Actions of humans have resulted in high rates of species' extinctions (Chapin *et al.* 2000), especially when habitats have been artificially transformed. Sometimes, however, high biodiversity is associated with human presence. In traditional rural biotopes (TRBs) low-intensity farming and animal husbandry have favored species-rich communities (Vainio *et al.* 2001). Yet these communities also struggle keeping up with the changing environment.

Since the rapid development of agricultural practices from the end of 19th century, rural landscapes look quite different today. As a result, many TRB-dwelling species are suffering from the scarcity of habitat. Some species that were previously common in farms' surroundings have become ever rarer sights, some are even critically endangered (European Commission 1998, Rassi *et al.* 2010). These observations have led to the increase of TRB-related studies during the last decade or so (see for example Berlin *et al.* 2000, Löbel *et al.* 2006, Palo *et al.* 2013). The expansion of research effort signifies the need to find ways for sustainable modernization (Shackelford *et al.* 2014).

Mitigating the effects of land use change requires knowledge about the factors that make up the diversity: how did it originate and how is it maintained? Species diversity in TRBs is ultimately an outcome of natural selection, speciation, dispersal and ecological drift (Vellend 2010). These four processes, in turn, are affected by habitat quality and quantity. The habitat quantity is a combination of local patch area and habitat availability at landscape-level. In this sense, the spatial isolation typical to TRB-sites poses challenges for conservation (Luoto *et al.* 2003, Fischer and Lindenmayer 2007). The habitat quality is affected by multiple environmental variables – both biotic and abiotic ones. In TRBs, distinctive features are grazing and mowing disturbances that change the physical environment but also have an influence on biotic interactions (Jantunen 2003).

Different organismal groups have different responses to disturbance. Vascular plant surveys have dominated TRB-research, but recently more attention has been given to less well-known groups such as invertebrates and fungi (Ivask *et al.* 2012, Kivinen *et al.* 2006, Schnoor *et al.* 2011). Until now, bryophyte data have been relatively scarce. Bryophytes' potential to form diverse and functional assemblies has been recognized, however, and the number of publications is on the rise (see for example Klaus and Müller 2014). As expected, bryophytes have not been immune to the widespread decline TRB-habitats (in Europe: During and Willems 1986, Ejrnæs and Poulsen 2001, or in Finland: Rassi *et al.* 2010). In this thesis, I surveyed the bryophyte communities in mown and grazed semi-natural grasslands, which are representatives of Finnish TRBs. The aim was to get an overview of bryophyte diversity in these threatened habitats and to assess the importance of management type for conservation purposes. I was also interested to see if disturbance intensity, landscape structure or vascular plants (competition) significantly affected bryophyte communities.

2. TRADITIONAL RURAL BIOTOPES

Traditional rural biotopes (TRBs) are habitats characterized by anthropogenic disturbance, more specifically, disturbance associated with traditional agricultural practices (Vainio *et al.* 2001, Luoto *et al.* 2003). Unlike today's prevailing methods, traditional management did not include ploughing, drainage, reseeding or use of artificial fertilizers (Cousins and Eriksson 2008). Lack of heavy machinery used to restrict the farm size and thus agricultural landscapes consisted of a much finer-scale mosaic of yards, fields and pastures than they do nowadays. It has been proposed that TRBs substitute for naturally disturbed sites like flooded river banks, burnt forests and grasslands grazed by large herbivores (Pykälä 2000).

Accordingly, TRBs could provide secondary habitats for species that have lost their natural habitats due to human actions: preventing floods, extinguishing forest fires and hunting large mammals.

TRBs represent a continuum from open to semi-closed habitats – from meadows to wooded pastures (*hakamaa* in Finnish) and forest pastures (*metsälaidun sensu* Takala *et al.* 2014a). In this thesis, I use the term semi-natural grassland to refer to meadows and open pastures. Meadows are open areas traditionally managed by mowing, pastures by livestock grazing. Terms meadow, open pasture and semi-natural grassland are often used interchangeably in literature, but terminology is not consistent (Birge 2015, Takala 2015). Finnish TRB-classification is based on moisture level (dry, mesic and wet meadows) or the dominant tree type (conifers, deciduous trees or both equally represented) (Vainio *et al.* 2001, Schulman *et al.* 2008). Various subtypes exist, including special cases like flooded meadows, seashore meadows, pollarded meadows (*lehdesniitty*) and moorland. The common features of all TRBs are frequent disturbances that cause nutrient flow out of the system (Vainio *et al.* 2001, Birge 2015).

The most important disturbances in TRBs are caused by grazing and mowing, both of which result in regular removal of plant biomass. Thus, grazing and mowing halt or slow down secondary succession, making TRBs more open habitats than similar natural areas would be (Vainio *et al.* 2001). Grazing has additional effects related to the presence of grazing animals: the ground is trampled, feces and urine are produced and vegetation can be eaten selectively (Jantunen 2003, Stammel *et al.* 2003). Grazing and mowing also differ in temporal occurrence. Grazing can continue over the whole growing season, whereas mowing is usually done once at the end of the summer (Jantunen 2003). Mown vegetation is not left to decay but raked, collected and transferred somewhere else. Trampling and raking break the surface of the ground, which could enhance germination from the seed or spore banks (Grubb 1977, Kotanen 1997). Fine-grained clayey soils are more prone to these kinds of disturbances than sandy soils. Soils can also become compacted by the weight of large herbivores (Abdel-Magid *et al.* 1987). In addition, the effects of all disturbances mentioned above extend further to the soil chemistry, productivity (including plant-plant interactions) as well as the processes of nutrient cycling (Bloor and Pottier 2014).

The area of Finnish TRB's has decreased from 62% of total agricultural land in the 1880s to under 1% in the beginning of the 21st century (Luoto *et al.* 2003). This change is attributed to the intensification of land use beginning in the 1880s (Vainio *et al.* 2001, Eriksson *et al.* 2002, Luoto *et al.* 2003, Johansson *et al.* 2011). Since then, many houses and bigger farm units (cattle sheds, stables, silos *etc.*) have been built. Modern agriculture has also allowed the expansion of field area (Vainio *et al.* 2001). Where semi-natural rural habitats were not replaced by buildings and crop monocultures, they were sometimes forested (Vainio *et al.* 2001, Eriksson *et al.* 2002). Forestation could have taken place on economic purpose (forestry) or because of secondary succession after seized management (abandonment). Nowadays TRBs only exist as small habitat islands scattered across the country (average area 5 ha in Finland and 3.9 ha in Central Finland, Vainio *et al.* 2001). This geographic isolation and consequent suppression of gene flow is the main reason for the high estimates of extinction debt among TRB-dependent species (Cousins 2009, Kuussaari *et al.* 2009). However, the loss of TRB-area could be compensated by road verges and other regularly mown human-made habitats (*e.g.* railway verges) (Tikka *et al.* 2000, Jantunen *et al.* 2004). The conservation potential of these secondary habitats has been discovered in a few studies (Tikka *et al.* 2001, Cousins and Eriksson 2001, Jantunen *et al.* 2006), even though the chemical composition of the soil, disturbance regime and disturbance type are not equal to those in TRBs.

Also the remaining TRB-sites are threatened. For example eutrophication decreases the species richness of TRB-specialists adapted to nutrient-poor conditions (Schulman *et al.* 2008, Plassmann *et al.* 2009, Duprè *et al.* 2010, Stevens *et al.* 2010). Typical sources of nutrient release are atmospheric emissions, crop fertilization and supplementary feeding of animals with fodder (Vainio *et al.* 2001, Duprè *et al.* 2010). These should be compared with the natural and very local fertilizing effect caused by grazers' excrements (Gaujour *et al.* 2012). Invasive species can likewise reduce the habitat quality and they are a growing concern for conservationists (Eriksson *et al.* 2006). Abandonment and pressures towards other kinds of land use are still major threats as well, causing habitat loss for TRB-specialist species (Schulman *et al.* 2008).

The maintenance of the most valuable TRB-sites is financially supported by EU funds and governmental subsidies (The EU's Common Agricultural Policy 2013 and Finland's Rural Development Program 2014-2020). These financial incentives and projects focusing on sustainable agriculture have proven crucial for the preservation of TRBs (Schulman *et al.* 2008, Birge 2015). The objective is to guarantee the continuity of the management and sustain the associated biological diversity. Besides biodiversity, there are cultural, historical and social reasons for conserving these rare semi-natural biotopes (Vainio *et al.* 2001, Plieninger *et al.* 2006).

3. BRYOPHYTES

Bryophytes include mosses, liverworts and hornworts. The relatively high number of species proves that bryophytes are well suited for boreal conditions (892 bryophyte species in Finland, compared to 1197 vascular plants, Rassi *et al.* 2010). Bryophyte life strategy is roughly reflected in growth form (Müller *et al.* 2012). Mosses include both creeping species with abundant branching (pleurocarpous species) and erect species with little or no branching (acrocarpous species). The most common Finnish forest floor species such as *Pleurozium schreberi*, *Hylocomium splendens*, *Sciuro-hypnum spp.* and *Brachythecium spp.* are pleurocarpous. Acrocarpous species in turn encompass more fast-growing, light demanding ruderals (for example *Ceratodon purpureus*). Liverworts include both leafy and thalloid liverworts. The latter are more frequently found on recently disturbed soil (e.g. flower beds) (Klaus and Müller 2014), but liverworts in general thrive in moist and shady microhabitats. In Finland many of them are restricted to decaying logs in old-growth forests (Ulvinen *et al.* 2002). Only two hornwort species are known from Finland, and one of them has been found in Central Finland (Ulvinen & Juutinen 2014).

Bryophytes are involved in critical ecological processes such as nutrient cycling, moisture retention, photosynthesis and primary succession (Beringer *et al.* 2001, Turetsky 2003, Ryömä and Laaka-Lindberg 2005, Bortoluzzi *et al.* 2006). They also provide food and shelter for heterotrophic organisms (Lindo and Gonzalez 2010). Bryophyte traits such as lack of roots and drought tolerance (poikilohydry) make them ecologically flexible as a group (Glime 2013). There are species primarily growing on soil, rocks, decaying wood, trunks of living trees, animal dung or even carcasses. Root-like rhizoids help bryophytes to attach to the substrate. Many bryophyte species exist in places too sunny and dry for vascular plants, like some road verge patches. When vascular plants and bryophytes occupy the same space, they are likely to compete with one another (Virtanen *et al.* 2000, Aude and Ejrnæs 2005, Löbel *et al.* 2006).

So far, there seems to be no general consensus about the commonness of dispersal limitation among bryophytes (Hylander 2009, Shaw *et al.* 2011). Although sexually reproducing species are usually considered better disperses than exclusively asexual species (Kimmerer 1991, Söderström and During 2005), some studies have recorded the opposite

(Hedenås *et al.* 2003). Sexual spores are often relatively small and produced in large quantities, whereas asexual vegetative parts (ramets, fragments or gemmae) are typically heavier and thus less mobile (Glime 2014a, Klaus and Müller 2014, but see Pauliuk *et al.* 2011). Asexual reproduction is indeed considered more important for the establishment and persistence of populations (Söderström and During 2005). Eventually, dispersal potential is determined by a variety of factors: the size and weight of diaspores, height of diaspore release (i.e. length of seta and place of growth) as well as features of the surrounding landscape (Soons and Heil 2002).

Some bryophytes are generalists with near-global distributions, but most of the species are sensitive to both atmospheric and substrate quality (pH, nutrients, moisture, temperature, pollution) (Carroll *et al.* 2000, Hallinbäck and Hodgetts 2000). The indicator value of bryophytes is based on relatively short generation times, high microhabitat-specificity and small size (Vitt and Belland 1997, Hylander *et al.* 2002, Takala *et al.* 2012). Shorter generation times allow faster population- and community-level responses to changing environmental conditions. Indications exist that bryophytes better reflect the current soil conditions whereas vascular plants are lagging in their response (McGovern *et al.* 2011). To conclude, bryophytes should be treated as a separate group from vascular plants because of the notable ecological differences. Moreover, several studies have shown that the diversity of these two groups is poorly correlated (Pharo *et al.* 1999, Peintinger and Bergamini 2006, Chiarucci *et al.* 2007, but see Fensham and Streimann 1997, Ingerpuu *et al.* 1998, Müller *et al.* 2012).

4. BRYOPHYTE DIVERSITY IN TRADITIONAL RURAL BIOTOPES

4.1. Selection, speciation, dispersal and drift – the ultimate factors affecting species diversity

The species diversity of any particular area depends on four processes: natural selection, ecological drift, speciation and dispersal (Vellend 2010) (Fig. 1). The species richness of communities increases via speciation or dispersal. Species are lost via selection or drift, both of which can lead to extinction. The relative significances of these processes vary spatially and temporally along with changing environmental conditions (Vellend 2010). The resulting changes in species composition can be observed in ecological (roughly 10-100 years or tens of generations) or evolutionary time scale (Pianka 1966). The latter is not in the scope of this study so speciation will not be discussed further in the following chapters.

When studying the patterns of biodiversity, the contribution of any single process is difficult to trace in practice. Yet some processes proceed in more predictable manners than the others. Selection is deterministic and therefore directly related to the environmental context: resources, abiotic conditions and biotic interactions (Vellend 2010) (Fig. 1). Drift is a fully stochastic counterpart of selection, and it stems from the randomness of demographic events (births, deaths and reproduction) in populations (Rosindell *et al.* 2012) (Fig. 1). Even drift can be affected by the environment, but the association is always indirect and concerns merely the magnitude of drift (as stochastic process has no direction). For example, the impact of drift on population dynamics increases as the population size decreases (Orrock and Watling 2010). The size of a population, in turn, could be constrained by resource availability, predation pressure or some other ecological factor. Dispersal lies somewhere in between selection and drift, being partly deterministic and partly stochastic (Fig. 1). Interactions also exist between processes: an example would be selection for or against dispersal.

The next sections focus on connecting the distinctive characteristics of traditional rural biotopes, disturbances and spatial isolation, with processes of selection, dispersal and drift. Disturbance and competition mainly affect community dynamics locally via changes in habitat quality. The habitat quantity can be reduced by gradual degradation in habitat quality (e.g. eutrophication) or direct modifications (e.g. crop planting). The effects of such habitat loss are extended to regional level via changes in landscape structure.

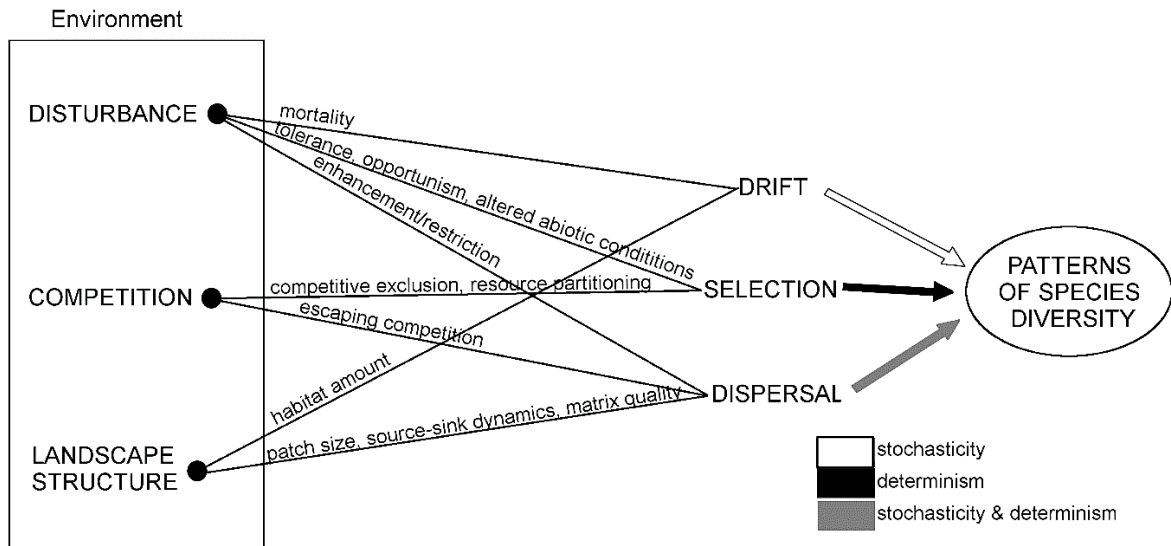


Fig. 1. The ecological impacts of disturbance, competition and landscape structure on the processes that ultimately affect patterns of species diversity. (The process of speciation is excluded from this illustration.) The predictability of these patterns depends on the relative contributions of stochasticity and determinism in underlying processes. Drift is always stochastic, selection is always deterministic and dispersal involves components of both kinds.

4.2 Habitat quality: disturbance and competition

Where abiotic conditions are favorable and stable enough, competition becomes one of the major determinants of species composition (Hardin 1960, Grime 1974, Grace 1999, Zamfir and Goldberg 2000). In TRBs, bryophytes and vascular plants compete over water and nutrients (scramble competition), but also over space and sunlight for photosynthesis (interference competition) (Klaus and Müller 2014). Water and nutrients are mainly acquired via different routes, however. Vascular plants primarily exploit resources stored in the soil, whereas bryophytes, having no vascular tissues or roots, absorb water and nutrients directly through cell walls (Økland 1995, but see Ayres *et al.* 2006). Hence, light and space availability are likely to be more critical for bryophyte survival under vascular plant cover (Virtanen *et al.* 2000). Especially the competition for light is dominated by vascular plants (Økland 2000). In competition over space, however, bryophytes stand a chance if they are the first to colonize bare soil (pre-emption). Established bryophytes could inhibit vascular plant seed germination (e.g. allelopathic compounds), but facilitation is also possible (favorable microclimate) (Keizer *et al.* 1985, Jeschke and Kiehl 2008).

External factors such as disturbances can prevent competitive exclusion (Turkington *et al.* 1993). Here, the definition of disturbance follows the one presented by Mackey and Currie (2001), disturbance being a “temporally discrete event that abruptly kills or displaces individuals or that directly results in the loss of biomass”. Disturbances in TRBs include grazing, trampling and animal droppings in open pastures, as well as mowing and raking in traditionally managed meadows (see Chapter 2). Grazing in this context is regarded as a series of frequent, discrete events experienced by plant individual, rather than a continuous

disturbance experienced by the grassland ecosystem (see discussion in White and Jentsch 2001).

Disturbance-diversity models explain diversity as a function of the level of disturbance (Svensson *et al.* 2012). The level of disturbance could refer to the spatial extent, temporal frequency or time since disturbance (Palmer 1994). The intermediate disturbance hypothesis (IDH, Connell 1978) predicts highest species richness at intermediate levels of disturbance. According to the dynamic equilibrium model (DEM, Huston 1979), species richness should peak at intermediate disturbance levels only when productivity is of intermediate level, too (Svensson *et al.* 2012). In contrast, for high and low levels of productivity DEM predicts different scenarios, in which highest species richness is achieved at high and low disturbance levels respectively. That is, larger disturbances are needed to prevent competitive exclusion at higher levels of productivity. If conditions are severe to begin with (low productivity), even low levels of disturbance may add to stress detrimentally and cause species extinction. Therefore factors that control productivity, such as soil properties, are important for understanding communities' responses to disturbance (Dickson and Foster 2008, Schultz *et al.* 2011).

What are the mechanisms that explain the significance of disturbance? Environmental conditions are often temporarily or permanently changed in a disturbed patch. Hence, the selection pressures are altered. When grazing or mowing reduces vascular plant biomass, soil-growing bryophytes may benefit from the increased light availability. In fact, the benefit is twofold: firstly, there is less shadowing by living vascular plants and secondly, bryophytes are less likely to get buried under leaf litter (Virtanen *et al.* 2000, Bergamini and Peintinger 2002, van der Wal and Brooker 2004, van Wijk *et al.* 2004). Bryophyte species could consequently increase in number, abundance, or both. On the other hand, associated changes in moisture and temperature may not be favorable for some bryophyte species.

When individuals are harmed but not killed by disturbance, selection favors tolerant species that are able to compensate the losses. Bryophytes are avoided by grazers because they have relatively low nutritional value and bitter taste, which is due to inhibitory compounds (Chollet *et al.* 2013, Glime 2014b). The adaptation of vascular plant communities could have various indirect effects on bryophytes, since they influence habitat quality. Plants with plastic phenotypes or adaptations allowing them to escape grazing (bitter taste, creeping growth form, spikes *etc.*) are likely to increase in abundance in grazed areas (Evju *et al.* 2009 and references therein). For example, the enrichment of leaf litter with anti-herbivory compounds could have long-term effects on bryophyte communities. Such effects on vascular plants have been recorded (Bonanomi *et al.* 2005, 2006; Ruprecht *et al.* 2010), but data on bryophytes are lacking (Peintinger and Bergamini 2006).

When random mortality is increased directly, disturbances reinforce ecological drift. Trampling and dung patches can create favorable microhabitats for plants and bryophytes, but they can also prove fatal for the interfered shoots (Abdel-Magid *et al.* 1987). In extreme cases these disturbances could destroy the only representatives of a species. Immediate stochastic extinctions are more likely to take place as a result of two or more additive factors, for example if competition restricts population sizes to a lower level. On the other hand, the elimination of vascular plant shoots can allow bryophytes to colonize new patches (Jonsson 1993, Kimmerer and Young 1996). This colonization could take the form of emergence from spore bank, vegetative spread or dispersal – in strict sense, only the latter has the potential to increase species richness (in broad sense, species that were formerly present only as spores could be considered “new”) (Connell and Slatyer 1977, Kotanen 1997). The alteration of habitat quality could also increase dispersal *per se*. For example the loss of surrounding plant biomass may be beneficial for wind-dispersed bryophyte spores. The process of dispersal

means that the effects of disturbance need not to be experienced directly in the disturbed patch but can be extended in the neighboring communities as well.

4.3 Habitat quantity: landscape structure

Landscapes are ecological entities ranging from few hectares to hundreds of thousands square kilometers. By landscape structure, I am referring to the spatial distributions of different land use classes. Using species-specific preferences as a basis, the landscape structure can be interpreted in an ecologically meaningful way: some patches are favorable enough for settling, some are merely visited (*e.g.* when foraging) and others are too hostile to be utilized at all (Fischer and Lindenmayer 2007). Landscape is often simplistically described as a combination of suitable and non-suitable habitat patches, later referred to as habitat and matrix respectively (Wiens 1997).

According to classical landscape ecology, important landscape features are patch area, connectivity and edge effect (Forman and Godron 1981, Fischer and Lindenmayer 2007). Habitat quantity is the combined area of all habitat patches in a landscape. Connectivity in strict structural sense means that these habitat patches should not be located too far from each other (physical connectivity, compare to functional connectivity, Kindlmann and Burel 2008). Due to the influence of neighbouring patches, abiotic conditions near habitat edges are not similar to those in habitat interior – this is called the edge effect (Forman and Godron 1981, non-fundamental use of the term also recognises biotic and social edge effects, see Fuentes-Montemayor *et al.* 2009). Most of the TRB-sites are isolated, but road verges and yards potentially improve connectivity by acting as ecological corridors and stepping stones between TRB-sites (Tikka *et al.* 2000, Zulka *et al.* 2014). The small size of many TRB-sites makes them prone to edge effect, which could reduce the habitat quality or even habitat quantity for strict specialist species (Fischer and Lindenmayer 2007).

According to classic species-area relationship (SAR), larger habitat patches support more species (Terborgh 1973, Connor and McCoy 1979, Lomolino 2000). But if high connectivity allows species to utilize several habitat patches, species richness could be a function of landscape-level habitat quantity rather than patch area (habitat amount hypothesis, Fahrig 2013). The positive effects of habitat area, be it landscape- or patch-level variable, is often attributed to the amount and variety (heterogeneity) of resources (Zanette *et al.* 2000, Krauss *et al.* 2004). Since resource-availability regulates population sizes by setting the carrying capacity of the environment, the link is formed between habitat area and the magnitude of drift. Dispersal can counteract drift, when habitat patches are well connected. This is demonstrated in source-sink dynamics (frequent local extinctions followed by recolonization) typical to metapopulations (Pulliam 1988, Hanski 1998, a bryophyte case study in Zartman *et al.* 2012). Similarly, dispersal allows species to exist in suboptimal habitat (rescue effect, Gotelli 1991): for example TRB-specialist plants are frequently found growing on road verges nearby TRB-sites (Cousins and Eriksson 2001, Jantunen *et al.* 2006). Sometimes dispersal and patch area interact to reduce drift. Everything else being equal, bigger habitat patches are more connected by definition (MacArthur and Wilson 1963). For example, the larger the patch the higher the probability that passive disperses such as bryophytes end up landing on it (*e.g.* Hutsemekers *et al.* 2008).

As agricultural landscapes keep fragmenting, the influence of edge effects on TRB-communities increases. These changes are likely to affect selection, favouring generalist species at the expense of specialists (Fischer and Lindenmayer 2007). Besides edge effect, classic landscape ecology rarely discriminates between habitat and matrix patches of different quality (Andr n 1994, Wiens 1997, Murphy and Lovett-Doust 2004, but see Prevedello and Vieira 2010). Using map-based landscape structures in the analysis requires considering these quality aspects when the results are interpreted.

5. STUDY QUESTIONS

The general aim was to find out what kind of bryophyte species are typical for TRBs, how many species there are and what factors affect species richness. More specifically, I was interested in factors that make TRBs distinctive habitats: type of disturbance, disturbance intensity and geographic isolation. The biomass-removing disturbance is likely to change competition dynamics between vascular plants and bryophytes, so I also wanted to see whether some variation in bryophyte species diversity could be directly linked to competition. Bryophyte cover and soil properties (grain size and pH) were also used as background variables to account for the interactions between bryophyte species and bryophytes' responses to substrate quality. My research questions concerning the bryophyte species diversity were the following:

1. Does species richness differ between grazed and mown grasslands, i.e. does management matter? I hypothesize that disturbances by grazing and mowing favor different kinds of bryophyte communities. Grazed sites could have higher species richness because of trampling that allows the colonization of ruderal species and dung-patches that provide an additional substrate for specialist bryophytes (During and Willems 1984).

2. How does disturbance intensity affect species richness? Based on Connell's (1978) IDH-theory, species richness is expected to be highest at intermediate disturbance intensities, regardless of disturbance type.

3. Is species richness positively affected by landscape-level habitat amount as Fahrig's (2013) theory suggests? If secondary habitats are important, adding them to habitat amount should improve the model.

4. Does competition with vascular plants restrict the species richness of bryophytes? High percentage cover of vascular plants should lead to very asymmetric competition for light, possible consequences being decreased species richness, total bryophyte cover, or both (Virtanen et al. 2000, Löbel *et al.* 2006).

6. MATERIALS AND METHODS

6.1 Study sites

All study sites are located in Central Finland, between N 6822429–6938141 and E 377204–456220 (ETRS89-TM35FIN). This geographic extent mainly consists of southern boreal vegetation, but two of the most northwestern sites belong to central boreal vegetation zone. A preliminary list of grassland study sites was selected from the database of the Centre for Economic Development, Transport and the Environment. The sites had to fulfill the following criteria: 1. The site was a representative of at least locally valuable traditional rural biotope according to the inventory carried out in the 1990s as a part of a national project (Kivelä 2000). 2. The site had a continuous management history (the objective was set at minimum of 10 years) and an ongoing current management status. 3. The site included a meadow patch or an open pasture area larger than 0.1 ha. 4. To reduce variation, meadows and pastures classified as moist, mesic or dry were selected while the rarer cases such as flooded meadows and shore meadows were excluded. This was done using the existing information about the TRB-types in each site (Kivelä 2000 and inventories conducted thereafter). All of the sites are representatives of critically endangered biotopes in Finland (CR, Schulman et al. 2008).

After the elimination phase, the final 24 sites were chosen from the remaining possibilities. The most important condition was that half of the study sites included mown grasslands (meadows) and the other half grazed grasslands (open pastures). Thus, a balanced

setting between the two management types was established. We also aimed at achieving similar geographic distributions of sites in both management type groups. Otherwise the decision was based on optimizing several practical issues such as travelling times and the land-owners' willingness to co-operate. The limited number of possible sites made it impossible to control for specific environmental variables.

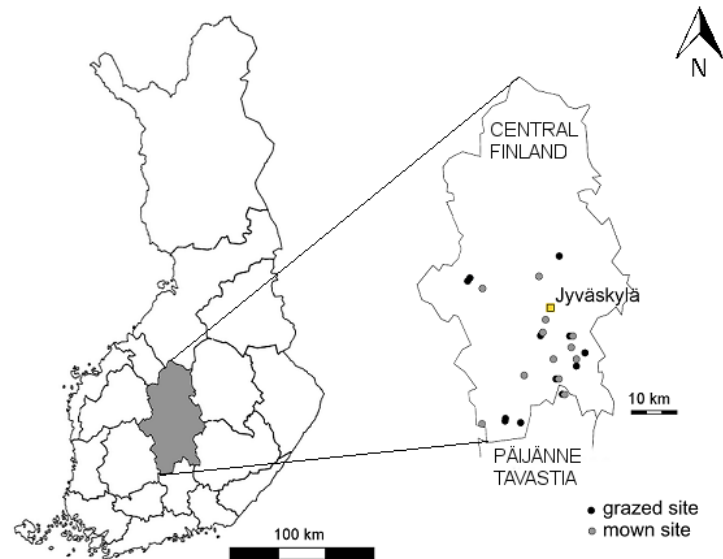


Fig. 2. The geographical extent of the study. Most of the study sites were located in the region of Central Finland, except for the two sites in northernmost of Päijänne Tavastia. Black dots represent grazed sites (N = 12) and gray dots represent mown sites (N = 12). Map ©Tilastokeskus.

6.2 Sampling

Five 2x2 m study plots on each site were arranged on a transect. The 44 m transect was placed using a randomized compass direction from the edge of the study area to the center of it. Five plots were placed on the right side of the transect, first plot was set at 2 m and the rest 10 meters apart from each other (at 12 m, 22 m, and so on) (Fig. 3). If one straight transect could not be fitted, the remaining part formed a second transect that crossed the first transect perpendicularly. The intersection of the two transects was set as close to the middle point of the first transect as possible without having to split the remaining transect further.

Only bryophytes growing on soil were recorded, as soil is the substrate most affected by the presence of animals, both physically (trampling) and chemically (nutrients transferred in feces and urine). In the study of Takala *et al.* (2014a), the highest number of bryophyte species was observed on soil. Due to our substrate-of-interest, the plots were relocated if more than 50% of the area would have consisted of some other substrate (rock *etc.*). Relocation could mean: 1. transferring the plot to the left side of the transect or, if the first option was not possible, 2. moving the plot forward along the transect until most of the substrate area consisted of soil.

Bryophyte flora was surveyed between late July and late August in 2014. All bryophyte species that were growing on soil or a layer of soil on some other substrate were identified and the covers of individual species were determined as a percentage area of each study plot. When a species could not be identified in the field, specimens were collected for microscopic identification. In addition, the percentage covers of substrates other than soil (rock, tree bases, deciduous or coniferous litter and dung) were recorded. Note that the bryophytes growing on these substrates are not included in the estimated total cover of bryophytes. In case of all variables, covers smaller than 1 % were recorded as 0.5 %.

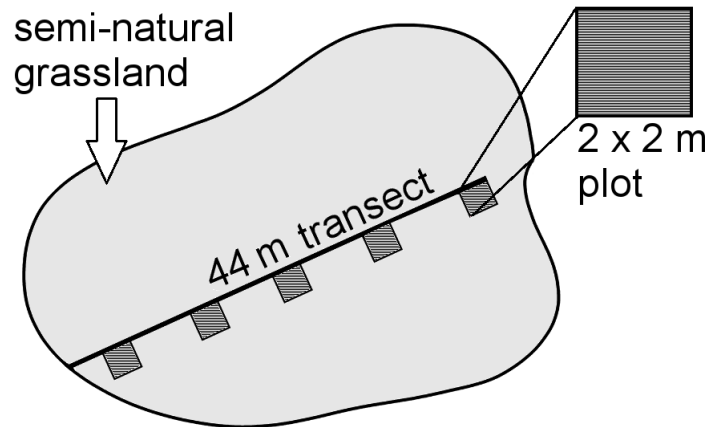


Fig. 3. The sampling design. Five study plots were placed on a transect, starting 2 meters from the edge of the semi-natural grassland patch. The next four plots were placed between every ten meters.

6.3 Assessing disturbance intensity and competition

The intensities of trampling and grazing were assessed for each plot during three repeated visits. The first visit was made between the end of June and early July, the second one in August and the third one between late September and early October. With these three surveys we were able to grasp temporal variation in disturbance intensity. Analyses were carried out using the average disturbance intensity.

Trampling intensity was calculated as the total percentage cover of soil that was markedly disturbed by grazing animals. Fresh hoof prints were easily distinguished, but older marks were less visible and observed as spots of exposed soil or bumpiness of the soil under bent vascular plant shoots. Grazing and mowing intensities were determined based on the amount of snapped vascular plant shoots. We included all shoots exceeding 5 cm in height and checked how large proportion (%) of them had been snapped. The minimum height was used to overcome bias that could arise because of plant adaptation. When grazing pressure is high, plants switch to growth forms that make them less reachable to the animals. Similarly, tall plants can become replaced by short-statured species at community level. Consequently, not excluding the shortest shoots would lead to an underestimation of the current grazing pressure.

The percentage cover of vascular plants was assessed for each plot between late June and early July, so the obtained values represent the maximum cover of the growing season. By then, no mowing had been done, but grazing had started in some sites. Vegetation was considered to be layered so that the overall cover could exceed 100%. The height of vascular plant vegetation was assessed like trampling and grazing/mowing, i.e. during repeated visits and for each plot separately. The recorded height represents the average height of all the vascular plant shoots observed in a plot.

6.4 Landscape variables

The landscape structure data were compiled by Kaisa Raatikainen as a part of her PhD studies. She had prepared two maps depicting present-day (2010) and historical (1960s) land use around our study sites. Using the location of each study site as a midpoint, circles with 2 km radius were drawn and the area within these circles was divided into land use classes. The six land use classes included the following: field, forest, mire or wetland, body of water, grassland and human residence. For bryophyte species inhabiting open and frequently disturbed environments, suitable habitat exists both in grasslands and yards. Thus, I

estimated habitat amount by combining the areas of grasslands and human residences within the 2 km radius. Fields were excluded, because the disturbance intensity was considered to be too high for most TRB-dwelling bryophytes (exceptions being for example *Dicranella spp.* and *Bryum spp.*). The estimates were drawn independently from the two maps, giving rise to variables “habitat amount 1960s” and “habitat amount 2010”.

For the present-day maps, the vector data of roads were also available. Using this information, I obtained the total length of trails, roads and railways to evaluate the area of possible secondary habitats (also within the 2 km radius). For trails, the trail length in meters was multiplied by width of 1 meter to estimate the amount of disturbed habitat. The road verge area was equal to the road length multiplied by total road verge width of 6 meters. The average of 3 meters per side was used in calculations, because the mowing of roadside vegetation extends 2–6 meters away from the road depending on the road’s management category (Liikennevirasto 2014). For railways, the estimated amount of suitable verge habitat was 15 meters per side. According to the management instructions given in Liikennevirasto (2012), trees are removed from a 60 meter strip around the railway. Only half of this strip was considered suitable for TRB-specialists, however, for the rest would probably include coppice forest or maintenance road, or be affected by forest edge. The third landscape variable “inclusive habitat amount 2010” was then created as a sum of “habitat amount 2010” and combined area of potential secondary habitats.

All of the landscape structure variables were extracted using ArcGIS (ESRI® ArcMAP™ 10.0). In addition, we used the site area information provided by the Centre for Economic Development, Transport and the Environment. Site areas in these data represented the area of a TRB, which sometimes encompassed multiple types of TRBs. For example many grazed sites were located as open grassland patches next to wooded pastures. In such cases the site area would refer to the total area of open *and* wooded TRB.

6.5 Soil variables

The soil samples were taken in May 2015. A soil corer of 3 cm diameter was used to take two samples from the opposite corners of every plot. Samples were taken from soil surface to the depth of 5 cm. All 10 samples from one site were mixed, homogenized with a 4 mm mesh sieve and preserved in the freezer. The soil types were classified as fine and medium silt (grain size 0.002–0.02 mm), coarse silt (0.02–0.06 mm), fine sand (0.06–0.2 mm) and medium sand (0.2–0.6 mm) (classification system SFS-EN ISO 14688-1 2007, Ronkainen 2012). No finer (clay) or larger grain sizes (gravel) were observed. These soil types were transformed into a numerical variable by replacing the grain size range with average grain size. Soil pH was measured from a suspension of 6 ml soil and 30 ml 0.01M CaCl₂. The median of three measurements was used in the analyses.

6.6 Statistical analysis

Separate models were built for the four dependent variables: species richness of acrocarpous mosses, species richness of pleurocarpous mosses, total bryophyte species richness (including liverworts) and bryophyte cover. Responses of liverworts species richness were not modelled, since liverwort observations were so rare. For the analyses, %-covers of bryophytes were transferred to relative %-covers. In other words, the proportion of soil substrate that was covered by bryophytes was calculated for every plot. Absolute covers could not be used, because the varying amounts of other substrates on plots would have caused bias (*i.e.* the maximum absolute cover for plots was not always 100 %). The analyses were performed for site-level and for plot-level explanatory variables separately. Bryophyte cover of a site was defined as the average relative cover of plots on that site. For species richness models, GLM (for sites) or GLMM (for plots) with a Poisson distribution and a log-

linear link function was applied. For bryophyte cover models, binary logistic regression was applied instead.

The effects of management type, TRB-area, soil properties and landscape structure were analyzed at site-level using a Generalized Linear Model (GLM, N=24). Variables entered into the model were management, area, pH, grain size and one of the three habitat amount variables (1960s, 2010 or inclusive, all tested in turn). In some cases non-linear responses were expected: therefore, squared terms of pH and grain size were added to the model. The interactions between management and soil properties (management*pH, management*grain size) were also included. This was done because the disturbance sensitivity of different soil types vary, but also because soil type can affect the responses of vascular plant community via regulation of productivity. All the explaining variables were standardized (mean 0 ± 1 SE) to account for scale differences.

An initial model included all the explanatory variables for a selected response variable (four GLM-models in total). Model simplification was performed for each of these models independently. The model simplification proceeded in a stepwise manner: the non-significant explanatory variables were removed in the order of highest p-value. No main effect was removed before the interaction. Variables with $p < 0.1$ were selected for the final model. During the simplification process, changes in Akaike Information Criteria (AIC) were monitored to verify that the models were improving (*i.e.* approaching the best fit with the smallest number of explaining variables).

The effects of disturbance, substrate heterogeneity and competition were analyzed at plot-level using a Generalized Linear Mixed Model (GLMM, n=120) with site as a random factor. Variables entered into the model were trampling intensity, grazing/mowing intensity, amount of bare rock, wood material and litter, cover of vascular plants, height of vascular plants, and the relative cover of bryophytes. When bryophyte cover was the response variable, it was removed from the model coefficients. Squared terms were included for vascular plant cover, vascular plant height and relative bryophyte cover. From now on, I will use a shorter version, grazing intensity, instead of grazing/mowing intensity. In the pursuit of parsimonious and interpretable solution, no interactions were included in the GLMM-models. Model simplification of the four GLMM-models proceeded as described above.

7. RESULTS

7.1 Bryophyte diversity and disturbance intensity: general observations

Overall, 52 bryophyte species were identified from the study sites, including 45 moss and 7 liverwort species (Appendix 1). 17 species were found to be unique to open pastures, whereas only 3 were unique to traditionally managed meadows. Out of observed moss species, 20 were acrocarpous and 25 pleurocarpous (Appendix 1).

The mean number of species was 17 in both mown and grazed sites, but there was more within-group variation among grazed sites (Fig. 4 A). On average, grazed sites had more acrocarpous species (6 species vs. 4 species in mown sites) but less pleurocarpous species (10 vs. 12 in mown sites), whereas liverwort observations were equally rare (mean 1 species per grazed or mown site). The average bryophyte cover was higher in mown plots (44.9%) than in grazed sites (38.2%), but again there was more variation among grazed plots (Fig. 4 B). Grazed plots were exposed to higher disturbance intensities regarding both grazing and trampling, yet the overall disturbance intensity in plots was relatively low (Table 1). On average, under 20% of the plots was trampled and under 50% of the vegetation grazed. Data were slightly biased towards larger site area and higher habitat amount in the landscape

for grazed sites (Table 1). Otherwise there were no considerable differences in the environmental variables between grazed and mown sites (Table 1)

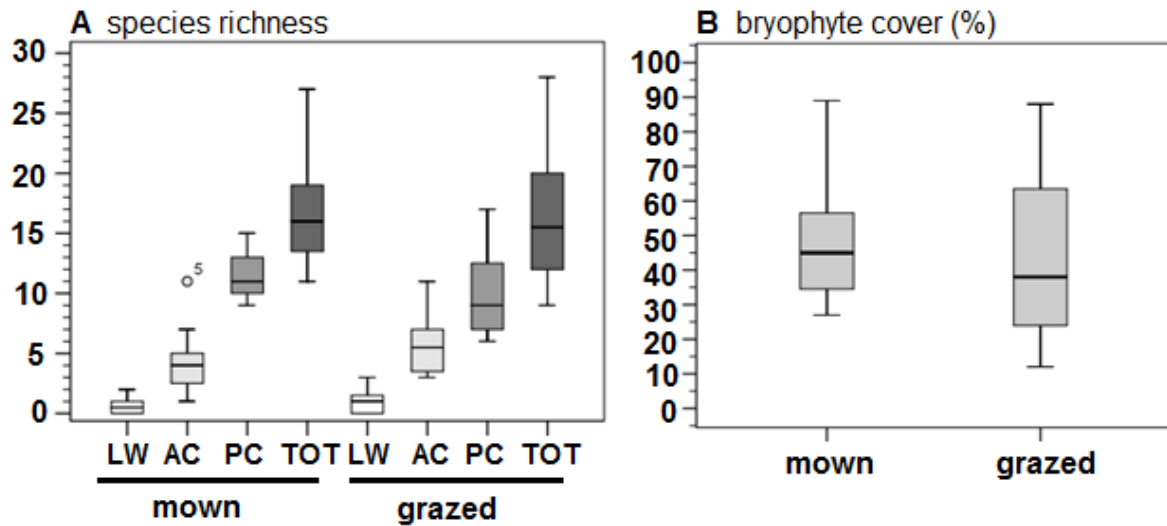


Fig. 4. Comparisons of observed species richness (A) and bryophyte cover (B) between mown (N = 12) and grazed (N = 12) sites. LW = liverworts, AC = acrocarpous mosses, PC = pleurocarpous mosses and TOT = total species richness. Bryophyte cover is shown for mown (n = 120) and grazed (n = 120) plots. Boxes represent the median values with 25th (bottom hinge) and 75th (top hinge) percentiles. In Fig. A, whiskers represent the maximum and minimum values observed. In Fig. B, they represent the 95% confidence intervals.

Table 1. The means and ranges of environmental variables in different management types. Instead of mean, median value was used for pH. For sites, N = 12 per management type and for plots, n = 60 per management type. None of the environmental variables correlated with management type ($p > 0.05$ in all Pearson correlations).

site-level variables	MOWN			GRAZED		
	mean	min	max	mean	min	max
site area (ha)	4.3	0.1	32.5	7.3	1.1	32.5
habitat amount 1960s (ha)	38.4	9.1	126.0	58.3	11.4	166.4
habitat amount 2010 (ha)	62.3	1.3	319.3	99.6	15.8	265.9
inclusive habitat amount (ha)	248.8	78.2	752.0	313.1	140.7	711.2
pH	*4.6	4.2	5.2	*4.3	3.7	5.2
grain size (mm)	0.17	0.01	0.4	0.14	0.01	0.4
plot-level variables	MOWN			GRAZED		
rock (%-cover)	1.5	0.0	22.0	1.9	0.0	17.0
wood (%-cover)	0.3	0.0	9.0	0.02	0.0	1.0
litter (%-cover)	59.9	1.0	98.0	53.8	5.0	100.0
vasc. plant cover (%-cover)	109.7	58.5	211	94.9	21.0	134.5
vasc. plant height (cm)	21.9	6.7	38.3	15.3	4.0	34.0
grazing (%)	18.8	0.0	55	45.2	5.6	91.7
trampling (%)	3.4	0.0	29.3	16.3	0.0	70.0

* median

The three habitat amount variables were not included in the models simultaneously, because high correlations between them were expected (Table 2 A). The correlations between plot-level explanatory variables proved statistically challenging. Grazing and trampling

intensities correlated in grazed ($r = 0.29$, Pearson correlation), mown ($r = 0.37$) and all sites ($r = 0.450$, $p < 0.01$, see Table 2 B). In addition, high negative correlation was observed between grazing intensity and height of vascular plants ($r = -0.71$ in grazed, $r = -0.51$ in mown and $r = -0.72$ in all sites, see Table 2 B). The tree vascular plant variables, i.e. vascular plant height, vascular plant cover and litter amount, were correlated as well (Table 2 B). All correlations between the environmental variables are shown in Table 2.

Table 2. Correlations between explanatory variables. Table A is for variables measured at site level and Table B is for variables measured at plot level. Statistically significant correlations are bolded. Abbreviations: *HA* = habitat amount, *vp.* = vascular plant, and *bryo* = bryophytes.

A	HA1960	HA2010	HA incl.	pH	grain size	management
area	-0.05	-0.06	-0.09	-0.23	-0.41*	0.17
HA1960	1	0.77**	0.77**	0.09	0.12	0.26
HA2010		1	0.98**	0.10	0.08	0.22
HA incl.			1	0.13	0.07	0.19
pH				1	0.00	-0.30
grain size					1	-0.09
management						1

Pearson correlations, significance * = $p < 0.05$, ** = $p < 0.01$ and *** = $p < 0.001$.

B	wood	litter	vp. cover	vp. height	bryo. cover	trampling	grazing
rock	-0.01	-0.13	-0.10	-0.136	-0.06	0.10	0.11
wood	1	-0.00	-0.06	-0.02	-0.093	-0.12	0.02
litter		1	0.24**	0.47**	-0.73**	-0.01	-0.27**
vp. cover			1	0.45**	-0.15	-0.17	-0.19*
vp. height				1	-0.35**	-0.40**	-0.72**
bryo. cover					1	-0.22*	0.09
trampling						1	0.50**
grazing							1

Pearson correlations, significance * = $p < 0.05$, ** = $p < 0.01$ and *** = $p < 0.001$.

7.2 Responses of bryophyte diversity on habitat quality and habitat quantity

7.2.1 Disturbance type, habitat amount and soil properties (site level)

Acrocarpous species richness was the only species richness variable that was dependent on disturbance type: more acrocarpous mosses were found on grazed sites (Table 3, Fig. 4 A). TRB-area and acrocarpous species richness were negatively associated (Table 3, Fig. 5 A). Less acrocarpous mosses were found on soils with the highest pH, which in this case was close to 5 (Table 3, Fig. 5 B). Acrocarpous species richness also showed a unimodal relationship with grain size (Table 3, Fig. 5 C) The total site-level species richness of bryophytes had a unimodal relationship with grain size (Table 3, Fig. 5 C), but was independent of all the other variables (Table 1). None of the site-level variables explained pleurocarpous species richness (Table 3).

Highest bryophyte covers were recorded from the largest TRB-areas (Table 3, Fig. 5 D). Bryophyte cover had a unimodal relationship with grain size as well (Table 3, Fig. 5 E). Higher soil pH was associated with higher bryophyte cover (Table 3, Fig. 5 F).

Landscape variables (habitat amount 1960s, habitat amount 2010 or inclusive habitat amount) had no significant effects in any model. The interactions between management type and soil properties were eliminated in the simplification process as well.

Table 3. The statistical overview of GLM and GLMM model results. Each column includes site and plot-level models for single response variable. Cells show the coefficients (B values) for statistically significant explaining variables.

		species richness			bryophyte cover (%)
		acro-carpous	pleuro-carpous	total	
model significance/AIC					
site-level variables (GLM)		**/108	ns.	*/142	***/376
	site area	-0.27*	–	–	-0.20***
	management type	-0.372	–	–	0.60***
<i>soil properties</i>	pH	3.50	–	–	-5.271**
	(pH) ²	-3.65	–	–	4.73***
	grain size	–	–	0.57*	-0.56*
	(grain size) ²	-0.35**	–	-0.62**	0.72**
model significance/AIC					
plot-level variables (GLMM)		*/109	**/118	**/129	***/1037
<i>substrate</i>	rock	0.11*	–	0.06	-0.15***
<i>heterogeneity</i>	wood	–	0.06	–	-0.23***
	litter	–	–	–	-0.92***
<i>competition</i>	bryophyte cover	0.93*	0.37	0.50**	–
	(bryophyte cover) ²	-0.99**	-0.39	-0.56**	–
	vasc.plant cover	–	–	–	0.19
	(vasc plant cover) ²	–	–	–	-0.20**
	vasc. plant height	–	–	–	-0.42***
<i>disturbance</i>	grazing	–	–	–	-0.10***
	(grazing) ²	–	-0.15**	–	1.03***
	trampling	–	–	-0.19	-0.92***
	(trampling) ²	0.13	–	0.190	0.50***

Asterisks refer to the level of significance: no asterisk for $p < 0.10$, * for $p < 0.05$, ** for $p < 0.01$ and *** for $p < 0.001$. Variables marked with (name)² are the quadratic terms included in the models.

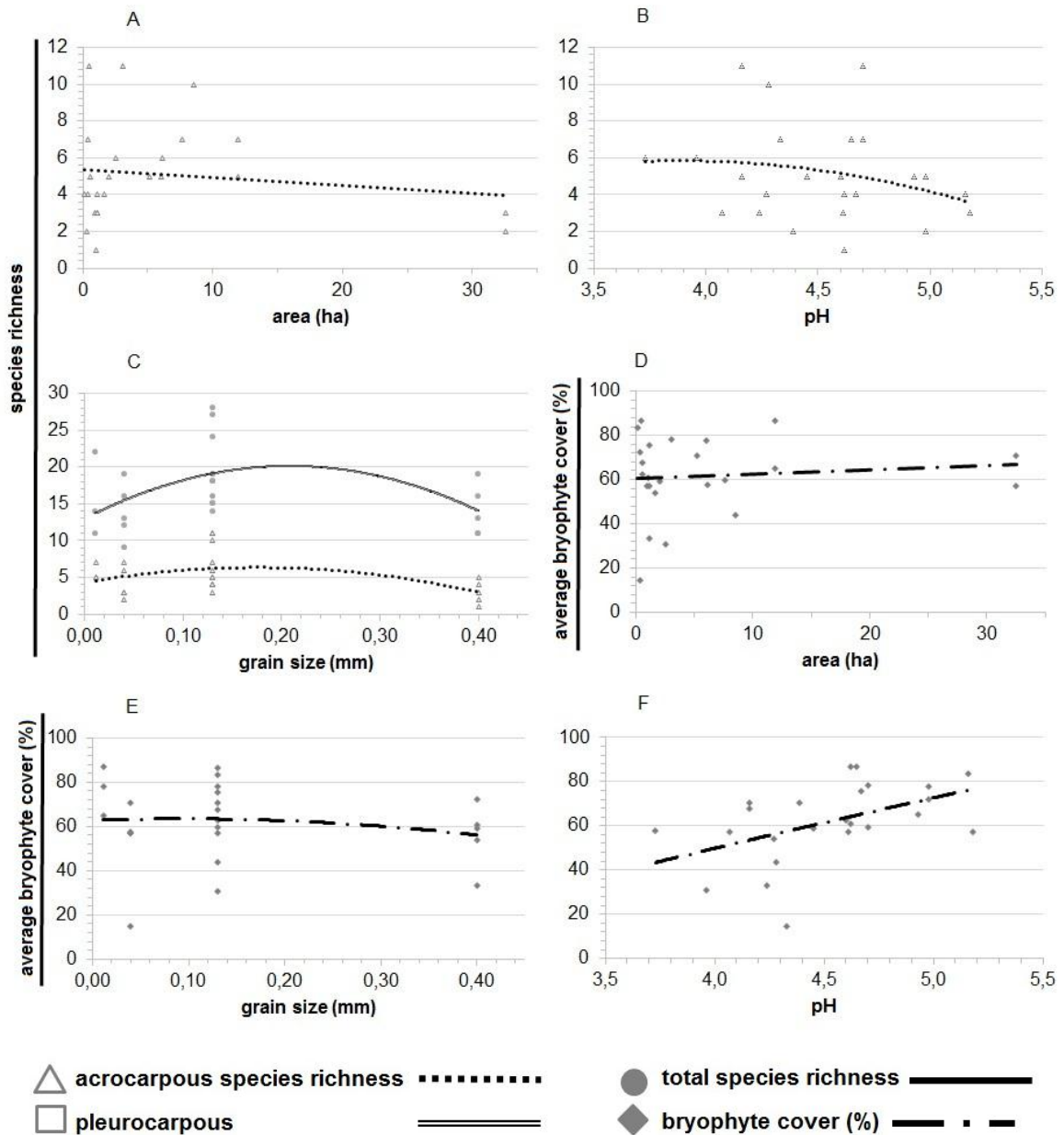
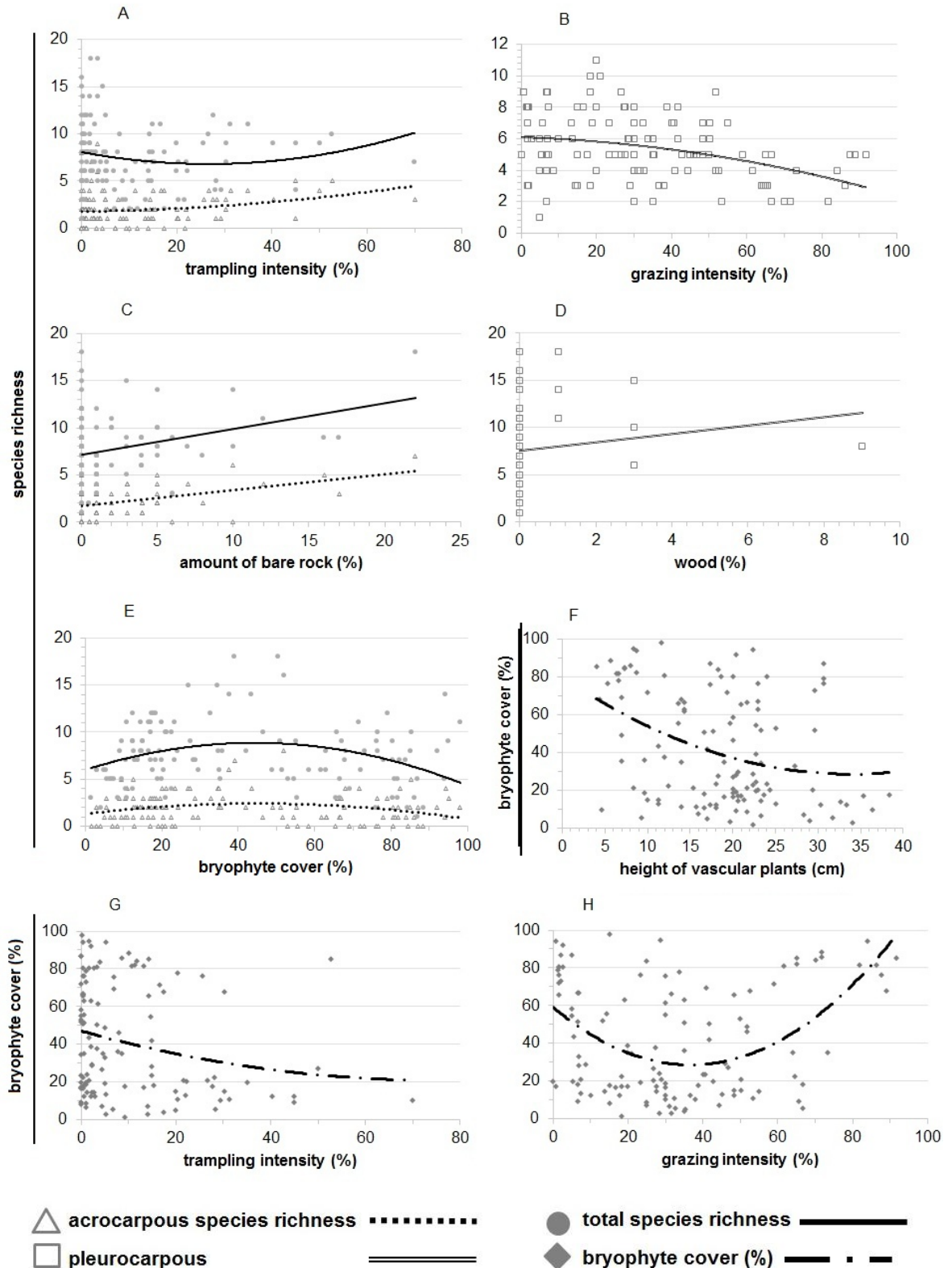


Fig. 5. Overview of the GLM model results for site data (N = 24). Figures are shown only for those variables that were included in the final model. Figures A–D show the responses of acrocarpous, pleurocarpous and total species richness, figures E–G of bryophyte cover (analyzed as average %-cover of all 5 plots on a site).

7.2.2. Disturbance intensity, substrate heterogeneity and vascular plants (plot level)

Higher trampling intensity was positively associated with the species richness of acrocarpous mosses (Table 3, Fig. 6 A). Acrocarpous species richness also had a unimodal relationship with bryophyte cover (Table 3, Fig. 6 E) and was higher on study plots including more bare rock surface (Table 3, Fig. 6 C). On contrast, the species richness of pleurocarpous mosses was highest on plots that included more woody material (Table 3, Fig. 6 D), but decreased on plots where trampling intensity was high (Table 3, Fig. 6 B). The species richness of pleurocarpous mosses had a unimodal relationship with bryophyte cover (Table 3, Fig. 6 E). The total species richness was positively associated with both trampling intensity and amount of bare rock (Table 3, Fig. 6 A and C), but unimodally related to bryophyte cover (Table 3, Fig. 6 E).

Amount of bare rock, woody material and litter negatively affected the bryophyte cover on plots (Table 3, Fig. 6 I, J and L). Higher trampling intensity and vascular plant height also reduced bryophyte cover on plots (Table 3, Fig. 6 F and G). In addition, bryophyte cover had a curvilinear relationship with grazing intensity and vascular plant cover (Table 3, Fig. 6 H and K). The inclusion of vascular plant variables was unique to this model and, because of the multitude of variables included, the AIC-value was high compared to the other models.



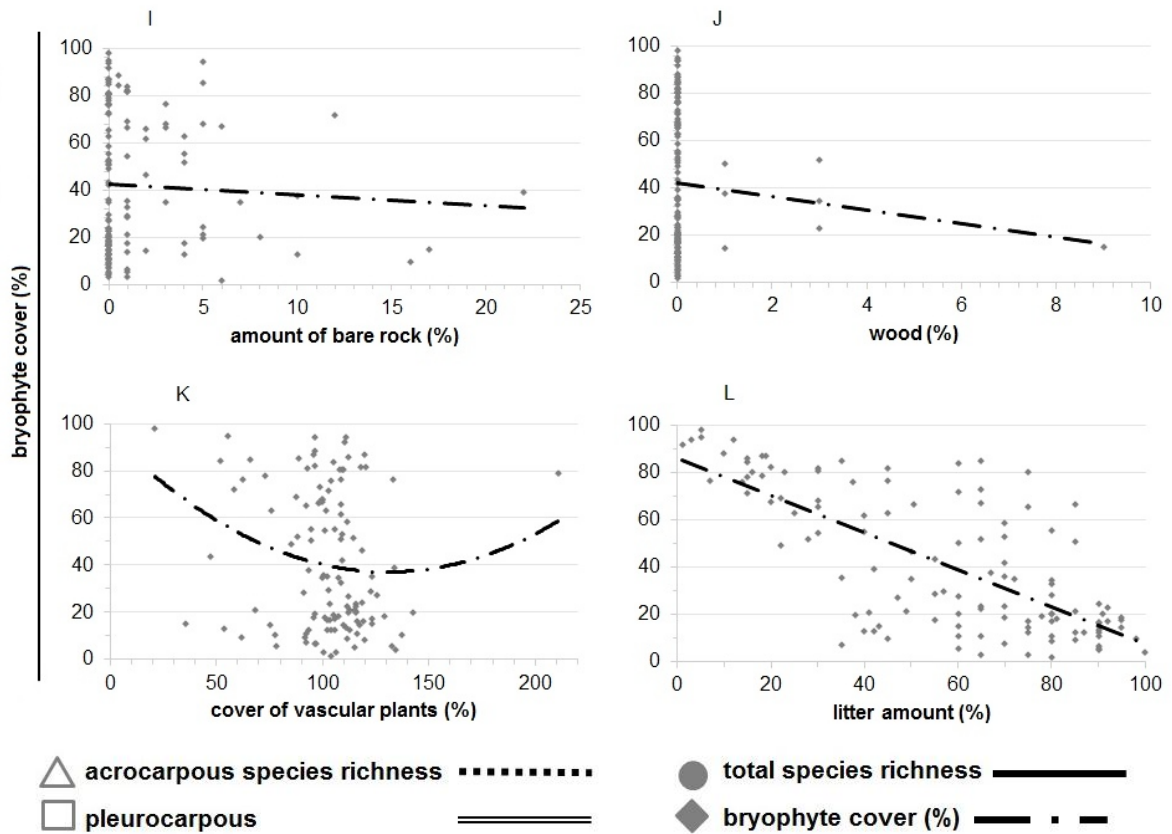


Fig. 6. Overview of the GLMM model results for plot data ($n = 120$). Figures are shown only for those variables that were included in the final model. Figures A–E show the responses of acrocarpous, pleurocarpous and total species richness, figures F–L of bryophyte cover.

8. DISCUSSION

8.1 Disturbance type

The average number of bryophyte species was equally high in mown and grazed sites, thus disturbance type had no effect on species richness at site level. Löbel *et al.* (2006) also found that in the dry grasslands of Öland, bryophyte species richness was independent of management type. Mown plots were clearly underrepresented in their data, however (341 grazed and 23 mown 4m^2 plots). In contrast, a previous study from Switzerland reported higher species richness in grazed calcareous fens than in mown ones (Bergamini *et al.* 2001).

My original hypothesis about higher species richness in grazed sites was based on substrate heterogeneity created by grazing animals. Dung patches and trampled ground were present in study plots, yet dung-growing specialist bryophytes were not recorded and the overall number of ruderal species growing on exposed soil was low. This could happen for three reasons: 1. Dispersal: species fail to colonize these substrates. Dispersal limitation is possible both in time and space. 2. Selection or drift: species fail to establish on these substrates. For example conditions can be too dry or disturbance intensity too high. 3. Species are not observed on these substrates. The detectability is lower for species specializing on ephemeral substrates, because they are smaller in size and have shorter life spans (Zartman *et al.* 2012). These traits affecting detectability have been favored by selection. In addition, the effect of additional substrates could be compensated by the stronger edge effects in mown grasslands, since they tend to be smaller in area (Łuczaj and

Sadowska 1997). Alternatively, source-sink dynamics or spatial autocorrelation could increase similarity where mown and grazed sites are located in the same landscape (Eriksson 1996, Koenig 1999).

The species composition was also quite similar in mown and grazed sites. Majority of the species (around 60%) were shared between mown and grazed grasslands. The most frequently observed species were the same regardless of the level of observation (sites or plots). In grazed sites, however, a slightly higher proportion of mosses were acrocarpous. This supports the findings of Bergamini *et al.* (2001), who observed only a modest impact of management type on the bryophyte community composition in calcareous fens. The grazed sites of my study were more different from each other (*i.e.* showing more between site variation) than mown sites, which is also reflected in the number of species unique to grazed grasslands (mainly single species observations). The study sites were grazed by horses, cattle and sheep, meaning that grazing actually refers to three different management regimes. Different grazers have different feeding preferences and patterns of movement (reviewed in Gaujour *et al.* 2012). In addition, the overall grazing intensity varied among sites: when there are less individuals feeding on larger pastures, grazing behavior has more prominent effects on the grazer-induced vegetation patterns (Demment and Soest 1985, Choquenot 1991, Mobæk *et al.* 2009). It is also possible that, by definition, grazed sites cover a wider range of environmental conditions. This could be true, if the placement of mown meadows has been more selective in the past than the placement of pasture areas.

In ecological comparisons, species richness often stays relatively constant despite high species turnover between communities (Berlin *et al.* 2000, Brown *et al.* 2001). The results of this study suggest that management by mowing is sufficient for maintaining viable bryophyte communities in grasslands. However, change of management is likely to alter habitat quality (selection) and thus modify species composition.

8.2 Disturbance intensity

Based on these data, there is no uniform pattern in the response of bryophyte communities to disturbance. Acrocarpous mosses responded to higher trampling intensity by increasing in number whereas pleurocarpous species responded to higher grazing intensity by decreasing in number.

The positive effect of trampling on acrocarpous species richness was expected, since many acrocarpous ruderals may not be able to establish in dense ground layer vegetation. In addition, trampling enhances the colonization from spore banks. Little is known about the relative contributions of different species in spore banks, but Ingerpuu and Sarv (2015) found that acrocarpous and pleurocarpous mosses were equally represented in the top soil layer of an Estonian coastal meadow. It is reasonable to assume that acrocarpous mosses with opportunistic life strategies are better adapted to take advantage of soil-breaking disturbances. Even in the absence of such adaptations (positive selection), acrocarpous species can benefit from the increased stochasticity in community establishment. In other words, acrocarpous species may become more common because they have better chances of succeeding in a random bet (which diaspores germinate and which do not) than in a competitive situation. An analogous hypothesis was tested, but not fully supported in the study of Fenton and Bergeron (2013). The effects of trampling are not confined to gap creation, however: when trampling compresses but does not break the soil, it can in fact hinder the germination process. Some bryophytes are known to disperse attached to grazing animals (endozoochory, Pauliuk *et al.* 2011, Klaus and Müller 2014), but whether this strategy bears any relation to growth form is not known. Finally, higher trampling intensity was also associated with less bryophyte cover. Thus, the relationships between acrocarpous species richness and trampling intensity could involve interactions with bryophyte cover.

Because the trampling intensity on plots was generally low, these results may not apply to grassland systems with higher trampling intensities.

Pleurocarpous species richness was negatively associated with grazing intensity. Since many pleurocarpous mosses are shade-tolerant, they could have suffered from excess light, increased temperatures or reduced humidity following the removal of plant biomass. The correlations between grazing and mowing mean that the response could be reinforced by sensitivity to trampling. Pleurocarpous mosses are mainly competitors that, according to the classic C-S-R theory, cannot regain the lost or damaged biomass as rapidly as more opportunistic species (Grime 1974, Glime 2013, but see Rydgren *et al.* 2001).

Observed disturbance intensities varied notably within some sites, but very little in others. Therefore, variation in disturbance intensity could be an important factor that was not included in the models of site-level species richness. More importantly, the observations made in the field question the traditional view of thinking mowing as a relatively uniform disturbance compared to grazing. The management of mown meadows often relies on bees, in which neither the number of participants nor the experience of mowers stays constant over the years. These factors cause interannual variation both in terms of mowing intensity and managed area. On the other hand, the generally expected patchiness of grazing intensity was not so strong in some sites. In fact, grazing is known to increase or decrease spatial heterogeneity depending on the grazing pattern and pre-existing distribution of vegetation (Adler *et al.* 2001, Alados *et al.* 2007, Bloor and Pottier 2014). Alterations in management intensity may sound undesirable from the view of TRB-conservation, but they could also be the foundations of the optimal management regime (Allan *et al.* 2014). The only condition is that the continuity of management is not disrupted.

To conclude, disturbance-diversity dynamics in bryophyte communities are a complex phenomenon involving disturbances, bryophyte species richness and bryophyte cover. The intermediate disturbance hypothesis (IDH, Connell 1978) fits poorly to these results, even though it has gained support in a previous study of bryophytes in agricultural landscapes (Zechmeister and Moser 2001). The dynamic equilibrium model (DEM, Huston 1979) seems more appropriate, since it has the effects of productivity included. In this data, the bryophyte cover could be interpreted as an indicator of bryophyte productivity. However, even DEM appears too simplistic to grasp the disturbance-diversity dynamics in bryophyte communities. By showing that bryophyte responses are better understood when the effects on acrocarpous and pleurocarpous growth forms are studied separately, this study highlights the importance of species-specific traits.

8.3 Landscape structure

Habitat amount did not affect bryophyte species richness at landscape- nor site-level. Several studies have found a positive effect of landscape structure on vascular plant diversity (Cousins and Eriksson 2001, Lindborg and Eriksson 2004, Gustavsson *et al.* 2007, Reitalu *et al.* 2012), but some have not (Pärtel and Zobel 1999, Pharo *et al.* 2004). Also, proportion of dry grassland area within 500 meters did not increase bryophyte richness in the study of Löbel *et al.* (2006). Differences arise because suitable habitat is defined using several alternative criteria and different landscape scales. Perhaps the definition of suitable habitat used in this study was too narrow and coarse-scaled. Even though the fields were excluded, for example the field margins could have supported bryophyte communities similar to TRB-sites. Above all, the irrelevance of habitat amount is attributed to the general absence of TRB-specialist bryophytes in these data. Considering the identities of observed species, it is likely that bryophyte diversity in grasslands would be better explained by the number of different habitat types in a landscape (landscape heterogeneity, Krauss *et al.* 2004, Fédoroff *et al.* 2005).

The negative effect of area on acrocarpous species richness was caused by an outlier: two sites (one mown and one grazed) were located within an exceptionally large entity of traditional farming. Yet these sites were among the most species poor-sites in my data. Leaving them out of the analysis did not change the final model substantially except for the removal of area from the explanatory variables. In case of sessile organisms like plants, failing to detect a relationship between species diversity and patch area is not uncommon (Debinski and Holt 2000). Nevertheless, Löbel *et al.* (2006) did discover a significant connection between the grassland area and species richness of bryophytes.

These results do not indicate a strong relationship between bryophyte species richness and landscape structure, be it present or historical. The observed species have wide ecological niches, which enable them to persist in a variety of habitats. This suggests that bryophyte species in semi-natural grasslands have no extinction debt like many of the specialized vascular plant species. In contrast, TRB-specialist bryophytes may have already disappeared from many sites, if they ever were present. For example *Brachythecium campestre* (NT), a pleurocarpous moss primarily known from the wooded pastures, seems to have disappeared from its old habitats in Southern Finland. It appears possible that *B. campestre* used to belong to the bryophyte flora of TRBs in Central Finland as well (S. Huttunen and T. Pitkämäki, unpublished; Rassi *et al.* 2010).

8.5 Soil properties

Soil properties explained acrocarpous species richness (pH and grain size), total species richness (grain size) and total bryophyte cover (pH and grain size). Especially the influence of pH has been observed in several other studies, although the shapes of response curves are varying (Virtanen *et al.* 2000, Bergamini *et al.* 2001, Löbel *et al.* 2006, Hydblom *et al.* 2012, A. Oldén *et al.* unpublished). Generally, higher species richness of bryophytes seems to be associated with higher pH (Löbel *et al.* 2006, A. Oldén *et al.* unpublished).

The acrocarpous species richness declined when pH increased, most likely because bryophyte cover increased with pH, indicating higher productivity and stronger competition. Pleurocarpous species richness was not affected by pH. Common pleurocarpous mosses grow on forest floors and on rocks in the forest, which can be very acidic substrates. Excluding the calcareous species, pleurocarpous mosses may be more indifferent to pH than acrocarpous mosses. Sites with pH values higher than the observed maximum (pH 5.18) would probably have a distinct species composition with more species typical to broad-leaved habitats. This kind of sites could also have higher species diversity. Thus, pH could increase bryophyte diversity in other kinds of habitats, but such effects are not visible in a pH range typical to semi-natural grasslands in Central Finland.

The results concerning grain size indicate that the highest number of bryophyte species fine sand and highest bryophyte cover on fine sand or silt. These are the soil types with intermediate and high moisture retention capacity, respectively. Interestingly, the observed patterns are quite opposite to what has been suggested before. Klaus and Müller (2014) hypothesize a U-shaped response curve of bryophyte abundance to soil moisture. According to them, there should be more specialized species at the both ends of the moisture gradient. While this may be the case when several different environments are considered, the results of this study only concern one habitat type, semi-natural grassland. Therefore, we could expect that highest species richness is found at the most frequently observed soil types. That soil type would be the optimum, to which most species in semi-natural grasslands have adapted to. Fine sand was the most commonly observed soil type in study sites (in 11 out of 24 sites).

8.6 Bryophyte interactions with other bryophytes and vascular plants

More bryophyte species were identified from plots with intermediate bryophyte cover, which supports the findings of Ingerpau *et al.* (2003) and Löbel *et al.* (2006). Thus, both facilitation (at low covers) and competition (at high covers) could be important in the studied bryophyte communities. Indeed, this kind of balanced situation has been proposed before (During and Lloret 2001). Bryophyte cover may generally reflect the suitability of environmental conditions for bryophyte growth, but there seems to be a point where the most competitive species exclude the others. In some plots, *Rhytidiadelphus squarrosus*, a strong competitor, had almost 100% cover.

Vascular plants (height and cover) had no direct effect on bryophyte species richness, but mixed effects on total bryophyte cover. There were slight trends towards decrease in bryophyte cover when the cover or height of vascular plants increased. Hence, if there is competition between bryophytes and vascular plants, the effects on species richness could be mediated via bryophyte cover. The dead vascular plant biomass seems to be a bigger threat for bryophytes, because the association between litter amount and bryophyte cover was clear and negative. Peintinger and Bergamini (2005) also observed that the bryophyte species density (species per unit area) was more reduced by litter than overall biomass of vascular plants. The importance of litter could be explained by the deciduous nature of grassland vegetation (Jägerbrand *et al.* 2012): bryophytes are able to exploit the less-shadowed conditions of early and late growing season (Karlsson 1985), if not hindered by the more permanent litter layer.

8.7. Substrate availability and structural heterogeneity

The between-plot differences in bryophyte species richness were partly caused by substrate heterogeneity (the number of available substrates on plots). Source-sink dynamics between preferred and secondary substrates could have increased bryophyte diversity in plots with higher substrate availability. The positive effects of bare rock on acrocarpous mosses and woody material on pleurocarpous mosses support this hypothesis, even though we have no information on substrate availability outside the plots. Rocks generally provide habitat for many acrocarpous mosses that are sometimes found to be growing on soil as well. The same is true for many pleurocarpous mosses preferring the roots and stumps of trees. The recognition of primary and secondary substrates is important for population viability and dispersal as well. Studies have shown that in some bryophyte species sexual reproduction can become suppressed on non-optimal substrates (Söderström 1993, Laaka-Lindberg 2000).

Substrate availability also reflects the structural heterogeneity of in plots. Trees, stumps and rocks act as sheltering formations in the middle of a disturbed habitat (Takala *et al.* 2014a). Especially rocks have a stabilizing effect on microclimatic conditions as they absorb heat, but stumps and tree roots could have similar functions. In a previous study, rocks but not woody material (coarse woody debris, tree bases or stumps) was considered important for the species richness of soil-growing bryophytes in forest pastures (Takala *et al.* 2014a). Also Löbel *et al.* (2006) found that bryophyte diversity on soil was higher where there was more bare rock. However, this sheltering effect discriminates between acrocarpous and pleurocarpous mosses only if the other group is generally more sensitive to physical disturbance and/or changes in microclimatic conditions. In addition, the observed connections of different growth forms to different substrates (wood or rock) are easier to interpret in the light of source-sink hypothesis.

8.9 Bryophyte communities in semi-natural grasslands

The total species richness (52) attained in this study is comparable with the observations of Takala *et al.* (2014b) who recorded 42 bryophyte species from Finnish mesic grasslands (21 grasslands, total sampled area 7.2 m³ in each). Surprisingly analogous results have been obtained from grasslands all over Europe (reviewed in Klaus and Müller 2014). At the time of this research, traditional rural biotopes were not considered hotspots of bryophyte diversity, nor were they designated as a conservation priority (Ulvinen *et al.* 2002) – my results do not contradict with these conclusions. Even though endangered bryophyte species are known to exist in TRBs (Ulvinen *et al.* 2002), none were observed in the studied semi-natural grasslands.

Most of the observed species were pleurocarpous and acrocarpous mosses. Best represented were the common pleurocarpous forest-floor species (*Brachythecium spp.*, *Sciuro-hypnum spp.*, *Pleurozium schreberi*, *Hylocomium splendens*) and widely appearing acrocarpous ruderals (*Bryum capillare*, *Pohlia nutans* and *Ceratodon purpureus*). Except for the occasional observations of species restricted to one single site, few species showed strong preferences to one management type over the other. *Climacium dendroides*, *Abietinella abietina* and *Syntrichia ruralis* were found primarily or exclusively on grazed grasslands. These species are potential indicators for continuously grazed grasslands, supporting the conclusions drawn in Takala *et al.* (2012). *Hylocomium splendens* and *Rhytidiadelphus triquetrus* were more frequently observed in mown sites, which suggests that the conditions in the understory of a mown grassland are more similar to forest floors. This makes sense, since bryophytes in mown grasslands experience more long-term shading and less trampling than in grazed grasslands.

There are 7 liverworts species in my data, whereas Takala *et al.* (2014b) found none. The low number of liverwort species could be explained by their preference on moister and shadier habitats (Ulvinen *et al.* 2002, Fenton *et al.* 2003). Liverworts are also often found on decaying wood – a substrate that is relatively uncommon in open grasslands. Dung-growing bryophytes were not observed at all, even though one such species (*Tayloria tenuis*) was recorded in 11 out of 24 sites in a related study of wooded pastures (A. Oldén *et al.* unpublished, but no observations in Takala *et al.* 2012). The dryness of open habitats can restrict the occurrence of these species also (Takala *et al.* 2014a). The weather conditions could have been extremely detrimental during the hot and dry summer when the field work was done (see Söderström and During 2005 for discussion). What's more, the detectability of dung-growing bryophytes and some liverworts is lowered due to small size and short life span.

8.5 Conclusions

This study shows that the present bryophyte diversity in semi-natural grasslands is not affected by habitat quantity, so the spatial isolation of TRBs is not likely to be an issue for bryophytes. Instead, bryophyte diversity responds more strongly to habitat quality. This means that the biggest threats for bryophyte diversity are caused by fertilization and insufficient management of semi-natural grasslands, which generally lead to an increase in vascular plant biomass. Schulman *et al.* (2006) have pointed out already, that the management of Finnish TRBs is often not intense enough to preserve TRB-communities in their current state. Disturbances also directly contribute to the diversity of bryophyte communities by allowing the colonization of competitively inferior bryophyte species. Acrocarpous and pleurocarpous mosses responded differently to disturbances, indicating that growth forms can be used as surrogates for ecological differences between species.

More research is still needed to evaluate the management of traditional rural biotopes on bryophyte perspective. Recent publications have already shown the importance of microsites (Takala *et al.* 2014a) and continuous grazing (e.g. Takala *et al.* 2014b, Ingerpuu and Sarv 2015, A. Oldén *et al.* unpublished) as well as promising responses to restoration (Huhta *et al.* 2001, Takala *et al.* 2012). Further analyses of these data include resolving the effects of management type on community composition and the impacts of temporal variation in disturbance intensity. Those will provide valuable information to complement the insights of this study. In addition, more attention needs to be given to the interactions between bryophytes and other endangered species in traditional rural biotopes (e.g. insects and fungi).

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Appendix 1. The frequency table of observed species. The observation frequency equals to the number of sites that a species was found to be present in. The species could have been present on multiple plots or just one. The percentages are calculated comparing the total number of sites to the number of sites where species was observed. For example *Aulacomnium palustre* grew on 1 out of 12 grazed sites and in none of the mown sites. The nomenclature follows (Juutinen and Ulvinen 2015).

acrocarpous	status	no. of obs. in grazed sites (N = 12)		no. of obs. in mown sites (N = 12)		total no. of obs. in all sites (N = 24)	
		f (g)	%	f (m)	%	f (t)	%
<i>Aulacomnium palustre</i>	LC	1	8.3	–	0.0	1	4.8
<i>Atrichum undulatum</i>	LC	2	16.7	2	16.7	4	19.0
<i>Bryum caespiticium</i>	LC	1	8.3	–	0.0	1	4.8
<i>Bryum capillare</i>	LC	4	33.3	7	58.3	11	52.4
<i>Bryum elegans</i>	LC	4	33.3	–	0.0	4	19.0
<i>Ceratodon purpureus</i>	LC	7	58.3	4	33.3	11	52.4
<i>Dicranum polysetum</i>	LC	2	16.7	4	33.3	6	28.6
<i>Dicranum scoparium</i>	LC	7	58.3	5	41.7	12	57.1
<i>Dicranella/Ditrichum sp</i>	LC	3	25.0	1	8.3	4	19.0
<i>Fissidens viridulus</i>	LC	–	0.0	1	8.3	1	4.8
<i>Polytrichum commune</i>	LC	1	8.3	2	16.7	3	14.3
<i>Plagiomnium cuspidatum</i>	LC	9	75.0	10	83.3	19	90.5
<i>Plagiomnium ellipticum</i>	LC	5	41.7	4	33.3	9	42.9
<i>Polytrichum juniperinum</i>	LC	6	50.0	4	33.3	10	47.6
<i>Plagiomnium medium</i>	LC	9	75.0	5	41.7	14	66.7
<i>Pohlia nutans</i>	LC	6	50.0	2	16.7	8	38.1
<i>Polytrichum piliferum</i>	LC	1	8.3	–	0.0	1	4.8
<i>Polytrichastrum longisetum</i>	LC	1	8.3	–	0.0	1	4.8
<i>Rhodobryum roseum</i>	LC	2	16.7	3	25.0	5	23.8
<i>Syntrichia ruralis</i>	LC	2	16.7	–	0.0	2	9.5
pleurocarpous		f (g)	%	f (m)	%	f (t)	%
<i>Abietinella abietina</i>	LC	1	8.3	–	0.0	1	4.8
<i>Amblystegium serpens</i>	LC	1	8.3	3	25.0	4	19.0
<i>Brachythecium albicans</i>	LC	11	91.7	12	100.0	23	109.5

<i>Brachythecium erythrorhizon</i>	LC	7	58.3	11	91.7	18	85.7
<i>Brachythecium mildeanum</i>	LC	4	33.3	–	0.0	4	19.0
<i>Brachythecium rutabulum</i>	LC	1	8.3	3	25.0	4	19.0
<i>Brachythecium salebrosum</i>	LC	8	66.7	11	91.7	19	90.5
<i>Brachytheciastrum velutinum</i>	LC	–	0.0	1	8.3	1	4.8
<i>Calliergonella cuspidata</i>	LC	1	8.3	–	0.0	1	4.8
<i>Climacium dendroides</i>	LC	8	66.7	3	25.0	11	52.4
<i>Cirriphyllum piliferum</i>	LC	8	66.7	9	75.0	17	81.0
<i>Hypnum cupressiforme</i>	LC	2	16.7	–	0.0	2	9.5
<i>Hylocomium splendens</i>	LC	2	16.7	10	83.3	12	57.1
<i>Oxyrrhynchium hians</i>	LC	5	41.7	7	58.3	12	57.1
<i>Plagiothecium denticulatum</i>	LC	1	8.3	1	8.3	2	9.5
<i>Pleurozium schreberi</i>	LC	11	91.7	11	91.7	22	104.8
<i>Rhytidiadelphus squarrosus</i>	LC	12	100.0	11	91.7	23	109.5
<i>Rhytidiadelphus triquetrus</i>	LC	1	8.3	6	50.0	7	33.3
<i>Sciuro-hypnum curtum</i>	LC	10	83.3	11	91.7	21	100.0
<i>Sciuro-hypnum plumosum</i>	LC	1	8.3	–	0.0	1	4.8
<i>Sciuro-hypnum populeum</i>	LC	1	8.3	3	25.0	4	19.0
<i>Sciuro-hypnum reflexum</i>	LC	10	83.3	11	91.7	21	100.0
<i>Sciuro-hypnum starkei</i>	LC	8	66.7	9	75.0	17	81.0
<i>Sanionia uncinata</i>	LC	1	8.3	2	16.7	3	14.3
<i>Thuidium recognitum</i>	LC	–	0.0	3	25.0	3	14.3
liverworts		f (g)	%	f (m)	%	f (t)	%
<i>Barbilophozia barbata</i>	LC	3	25.0	–	0.0	3	14.3
<i>Cephalozia bicuspidata</i>	LC	1	8.3	–	0.0	1	4.8
<i>Cephaloziella divaricata</i>	LC	1	8.3	–	0.0	1	4.8
<i>Fossombronia foveolatoata</i>	LC	1	8.3	–	0.0	1	4.8

<i>Lophocolea heterophylla</i>	LC	3	25.0	6	50.0	9	42.9
<i>Lophocolea minor</i>	LC	1	8.3	–	0.0	1	4.8
<i>Ptilidium ciliare</i>	LC	1	8.3	–	0.0	1	4.8
total no. of species observed		49		35		52	