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ECOSYSTEMS

Direct and Indirect Drivers of Moss Community Structure, Function, and Associated Microfauna Across a Successional Gradient

Micael Jonsson,[1]* Paul Kardol,[2] Michael J. Gundale,[2] Sheel Bansal,[2,3]
Marie-Charlotte Nilsson,[2] Daniel B. Metcalfe,[2,4] and David A. Wardle[2]

[1]Department of Ecology and Environmental Science, Umeå University, 90187 Umeå, Sweden; [2]Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, 90183 Umeå, Sweden; [3]USDA Forest Service, Pacific Northwest Research Station, Olympia Forestry Sciences Laboratory, 3625 93rd Avenue SW, Olympia, Washington 98512, USA; [4]Department of Physical Geography and Ecosystem Science, Lund University, 22362 Lund, Sweden

ABSTRACT

Relative to vascular plants, little is known about what factors control bryophyte communities or how they respond to successional and environmental changes. Bryophytes are abundant in boreal forests, thus changes in moss community composition and functional traits (for example, moisture and nutrient content; rates of photosynthesis and respiration) may have important consequences for ecosystem processes and microfaunal communities. Through synthesis of previous work and new analyses integrating new and published data from a long-term successional gradient in the boreal forest of northern Sweden, we provide a comprehensive view of the biotic factors (for example, vascular plant productivity, species composition, and diversity) and abiotic factors (for example, soil fertility and light transmission) that impact the moss community. Our results show that different aspects of the moss community (that is, composition, functional traits, moss-driven processes, and associated invertebrate fauna) respond to different sets of environmental variables, and that these are not always the same variables as those that influence the vascular plant community. Measures of moss community composition and functional traits were primarily influenced by vascular plant community composition and productivity. This suggests that successional shifts in abiotic variables, such as soil nutrient levels, indirectly affect the moss community via their influence on vascular plant community characteristics, whereas direct abiotic effects are less important. Among the moss-driven processes, moss litter decomposition and moss productivity were mainly influenced by biotic variables (notably the community characteristics of both vascular plants and mosses), whereas moss functional traits (primarily specific leaf area and tissue nutrient concentrations) also were important in explaining moss di-nitrogen-fixation rates. In contrast, both abiotic and biotic variables were important drivers of moss microfaunal community structure. Taken together, our results show which abiotic and biotic factors impact mosses and their associated organisms, and thus highlight that multiple interacting factors need to be considered

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Author contributions All authors conceived and designed the study. Each author collected one part, or several parts, of the data, of which moss decomposition (Micael Jonsson) and microfauna (Paul Kardol) were not previously published. Micael Jonsson performed all statistical analyses and led the writing of the manuscript. All authors took part in the writing.

Corresponding author; e-mail: micael.jonsson@emg.umu.se

to understand how moss communities, associated food webs, and the ecosystem processes they influence will respond to environmental change.

Key words: boreal forest; bryophytes; feather mosses; island ecosystems; nematodes; nitrogen fixing cyanobacteria.

INTRODUCTION

Boreal forests comprise approximately 27% of the world's forests (Hansen and others 2010), provide habitats for a wide range of organisms, and deliver ecosystem services of global importance (Hayes and others 2011; Pan and others 2011; Elbert and others 2012). In these forests, mosses are often a dominant component of the ground layer, forming an important transitional zone that mediates interactions between below- and aboveground ecosystem components (that is, 'the bryosphere', Lindo and Gonzalez 2010). For example, mosses contribute substantially to the production of total aboveground biomass (Cornelissen and others 2007; Wardle and others 2012), regulate abiotic conditions such as soil temperature and moisture (Gornall and others 2007; Blok and others 2011), and are important drivers of ecosystem biogeochemical cycles (DeLuca and others 2002a; Lagerström and others 2007; Turetsky and others 2010; Bansal and others 2012; Street and others 2013). Further, many moss species, including feather mosses, host di-nitrogen-(N_2)-fixing cyanobacteria that provide large nitrogen (N) inputs to boreal forests (DeLuca and others 2002b; Lagerström and others 2007; Lindo and Gonzalez 2010; Lindo and others 2013). Mosses also provide microhabitats for a wide diversity of microorganisms and invertebrates (Gerson 1982; Boeckner and others 2006; Lindo and Gonzalez 2010). In turn, these moss-associated organisms form complex food webs that regulate organic matter decomposition, carbon (C) sequestration and nutrient cycling, reinforcing the link between above- and belowground ecosystem components (Wardle and others 2004).

Mosses differ greatly from vascular plants in functional traits such as relative growth rate, secondary chemistry, herbivore resistance, litter decomposability, water relations, and N_2-fixation and photosynthetic capacity (Cornelissen and others 2007; Bansal and others 2012; Turetsky and others 2012). These moss traits may influence their sensitivity to environmental change (Bates and Farmer 1992; Turetsky 2003; Callaghan and others 2004; Cornelissen and others 2007; Lindo and Gonzalez 2010; Lindo and others 2013). For example, the distinctive morphology of mosses makes them particularly sensitive to abiotic conditions such as light levels, atmospheric and soil moisture, and soil fertility (Stewart and others 2011; Gundale and others 2012a, 2012b). Mosses are also sensitive to changes in biotic conditions, and their abundance is linked to the composition and structure of their associated vascular plant communities (Sonesson and others 1992; Lange and others 1996; Renhorn and others 1997; Gundale and others 2013). Although significant conceptual advances have been made in our understanding of how vascular plant communities respond to environmental changes associated with ecosystem succession, the responses of mosses to succession, and the associated ecosystem changes in biogeochemical cycling and moss-associated fauna, remain less well understood.

Here, we synthesize data from a well-characterized retrogressive fire-driven ecosystem chronosequence spanning over 5000 years in the boreal forest of northern Sweden, to provide a holistic picture of the patterns of changes in moss structure and function that occur with ecosystem development. The chronosequence consists of lake islands that differ in time since the last major wildfire and, hence, in ecosystem age and several biotic (for example, plant productivity, species composition and diversity) and abiotic properties (for example, soil fertility, light transmission) (Wardle and others 1997, 2003, 2012). We compiled a large dataset consisting of both newly collected and previously published data and used it to conduct new analyses to investigate which sets of biotic and abiotic environmental factors best explain variation in moss community composition and functional traits (that is, specific leaf area, moisture and nutrient content, $\delta^{13}C$ and $\delta^{15}N$ enrichment, and rates of photosynthesis and respiration), moss-driven ecosystem processes (that is, moss production, decomposition and N_2 fixation, and contribution to total ground carbon dioxide (CO_2) efflux), and moss-associated microfaunal communities (that is, nematodes and tardigrades). We test the general hypothesis that the changes in environmental conditions that occur during forest succession and ecosystem development affect moss community composition and functional traits, which in turn impact on moss-driven processes and communities of associated organisms. Specifically, we address the following questions:

1. Are moss community composition and functional traits most strongly predicted by abiotic environmental conditions or by characteristics of the vascular plant community?
2. Can rates of moss production, decomposition, and N_2-fixation be predicted by moss community composition and/or moss functional traits? Or are shifts in other environmental variables, such as abiotic factors and characteristics of the vascular plant community, more important as predictors of these processes?
3. Does the community structure of moss microfauna vary predictably with moss community composition, and with the abiotic and vascular plant community characteristics that may drive moss community structure?

METHODS

Study System

The study system consists of 30 forested islands in the freshwater lakes Hornavan and Uddjaure in the boreal region of northern Sweden (65°55′N to 66°09′N, 17°43′E to 17°55′E). Wildfire is the main abiotic disturbance agent on these islands. The islands differ in size (from 0.02 to 15.0 ha), with size determining fire history, because smaller islands are struck by lightning less frequently (Wardle and others 1997). These islands fall into three size classes with 10 islands per class: large ($>$1.0 ha), medium (0.1–1.0 ha), and small ($<$0.1 ha), with a mean time since last major fire disturbance of 585, 2180, and 3250 years, respectively (Wardle and others 2003). The differences in disturbance history across the island size classes have resulted in a successional gradient or chronosequence. As such, as island size decreases and time since fire increases there is a decline in vascular plant productivity, decomposition rates, available soil nutrients, and microbial biomass, and an increase in vascular plant species richness and humus depth (Wardle and others 1997, 2003, 2004, 2012; Peltzer and others 2010). Further, vascular plant community composition changes as succession proceeds (Jonsson and Wardle 2010): *Pinus sylvestris* and *Vaccinium myrtillus* dominate on the large islands, *Betula pubescens* and *Vaccinium vitis-idaea* dominate on the medium-sized islands, and *Picea abies* and *Empetrum hermaphroditum* dominate on the small islands. Hence, the islands represent gradients in both biotic and abiotic environmental conditions associated with ecosystem succession.

In this study, we consider the relationships of moss community composition, moss functional traits, moss-driven processes, and moss-associated microfauna with several biotic variables, as well as island area and ecosystem age (that is, time since fire) that serves as proxies for a number of abiotic variables (that is, disturbance frequency, light conditions, soil nutrient availability, and humus depth) (Wardle and others 1997, 2003, 2012). Of the study islands, none have burned in the past 60 years and some have not burned for over 5000 years (Wardle and others 2003). All data used in this study were collected on the same islands, but for different variables in different years spread across a seven-year period (2005–2012). However, this 7-year window is very short relative to the length of the chronosequence, and so we assume that this is not a significant source of bias. Below, we present the methods used to obtain data on moss community composition, moss functional traits, moss-driven processes, and moss-associated microfauna. For data previously published, we provide only a brief summary of key methodologies and refer instead to the original publications for more detailed descriptions. For newly collected data we provide complete, detailed descriptions of the methods used.

Moss Community Composition

To determine moss species abundance and community composition, we established a 9.5 × 9.5 m plot on each island (see Gundale and others 2011), directly adjacent to a set of pre-existing experimental plots used for previous studies (Wardle and others 2003; Wardle and Zackrisson 2005). Within each plot, 49 subplots (19.6 cm^2) were established, where moss community data (that is, percentage ground cover of each species) were recorded in 2008. These already published data were combined with other data to perform new analyses.

Moss Functional Traits

To obtain specific leaf area (SLA; that is, fresh leaf area/dry leaf mass), the green parts of 30 gametophytes of each of the three dominant feather moss species (constituting more than 96% of total moss biomass; Wardle and others 2012) were collected from each island, in 2010 (*Pleurozium schreberi* and *Hylocomium splendens*) and 2011 (*Ptilium crista-castrensis*), hereafter referred to as *Pleurozium*, *Hylocomium*, and *Ptilium*, respectively. On the day of collection, these gametophytes were photocopied. Later, the photocopies were scanned onto a computer, and the images were used to determine gametophyte area using image analysis software (JPEGView), and then dried and weighed for measurement of biomass. Leaf-level photosynthesis, respiration, N, C, $\delta^{13}C$, and $\delta^{15}N$ data were obtained from Bansal and others (2012). Briefly, gas exchange measurements were made for *Pleurozium* and *Hylocomium* on excavated, intact moss carpets (with humus and basal dead tissue removed) that were collected from each island. Moss carpets were kept intact and measured *ex situ* under laboratory conditions using a modified CO_2 gas exchange system (Li-Cor 6400XT, Li-Cor Biosciences, Inc., Lincoln, NE, USA) with an attached infrared gas analyzer. The mosses were then used for analysis of tissue N, C, $\delta^{13}C$, and $\delta^{15}N$. Gas exchange and tissue nutrient concentrations were normalized for mass and area. Photosynthesis and respiration rates were additionally normalized for leaf N.

Moss-Driven Ecosystem Processes

Moss net primary productivity (NPP) was measured, through randomized sampling of 30 gametophytes for each of *Hylocomium* and *Pleurozium*, on each island in August 2010 (data presented in Wardle and others 2012). Briefly, moss NPP was obtained by first separating and weighing the current year's biomass from living biomass that had been produced in previous years. For *Hylocomium*, annual production was easily assessed because a new stem emerges each year. For *Pleurozium*, a slight deviation in the stem angle and a change in color distinguished the current year's growth from that of previous years. Then, the proportion of new biomass grown annually was multiplied by measures of total moss biomass for each island to estimate moss NPP (Wardle and others 2012).

In August 2009, gametophytes (that is, the full length of live moss and senesced parts) of each of *Pleurozium* and *Hylocomium* were collected from each island and kept alive in outdoor conditions for 10 months. From these collections, senesced moss material was separated and placed in litterbags (0.5 g dry matter per bag; mesh size = 0.1 × 1.0 mm). For each island, three litterbags were prepared for each of the two species, and in August 2010 the moss litterbags were returned to the same islands that the litter had been collected from in the previous year. The litterbags were placed individually in the upper soil layer (5–10 cm below the soil surface). In August 2012, the litterbags were retrieved, their contents were sorted (with roots and fungal hyphae removed), and the moss litter was oven-dried at 70°C for 24 h and weighed, to calculate mass loss.

Moss N_2-fixation rates were assessed by collecting 90 and 30 shoots of the moss species *Pleurozium* and *Hylocomium*, respectively, from a 20 × 20 m sampling area on each island, at three occasions both in 2005 and 2006 (data presented in Lagerström and others 2007). Briefly, N_2-fixation was estimated using the acetylene reduction method (Schöllhorn and Burris 1967), whereby the conversion of acetylene to ethylene by the nitrogenase enzyme was used as a proxy for N_2-fixation. For further details on this method, see DeLuca and others (2002b) and Gundale and others (2010).

In addition, in 2010, total ground CO_2 efflux per unit ground area was recorded *in situ* within control plots of the experiment described in Wardle and Zackrisson (2005) on intact areas of understory vegetation (that is, shrubs and mosses) (data presented in Wardle and others 2012). Briefly, on each island, a 40 × 40 cm opaque plastic chamber was sealed to the ground with plastic skirts, and the rate of CO_2 accumulation was measured within the chamber over two minutes with a portable infrared gas analyzer (EGM-4, PP Systems, PP Systems, Hitchin, UK). The contribution of *Pleurozium* and *Hylocomium* to total CO_2 efflux was then calculated by dividing moss respiration per unit ground area by total (that is, shrub, mosses, soil, and tree roots) ground CO_2 efflux per unit ground area (Wardle and others 2012).

Moss-Associated Microfauna

In August 2010, the upper 4 cm of 20–30 green moss gametophytes were collected from each of the three feather moss species, that is, *Hylocomium*, *Pleurozium*, and *Ptilium*, for each island. For each species, the gametophytes were then bulked to provide one sample per island. For each sample of each moss species, a subsample was used to determine moisture content after drying for at least 48 h at 70°C. Another subsample was ground in a ball mill and analyzed for N and phosphorus (P) content using standard colorimetric methods.

Nematodes and tardigrades were extracted from a subsample (on average about 1.3 g dry weight) of each sample for each moss species using Baermann funnels. Subsamples were cleaned of organic debris before being placed in the funnels. Nematodes and tardigrades were harvested from the funnels after 24, 48, and 72 h, and immediately stored at 4°C. For each subsample, extracted animals were bulked into one composite sample, heat-killed, and fixed using 35% formaldehyde diluted to 4%. For nematodes, individuals were counted, and about 200 randomly selected individuals in each sample were identified to family or genus level and allocated to feeding groups (that is, plant feeders, bacterial feeders, fungal feeders, omnivores, and predators) according to Yeates and others (1993). If less than 200 individuals were present, all nematodes were identified. For each subsample, tardigrades were counted but not identified. Nematode and tardigrade densities were normalized per g oven-dried moss biomass.

Statistical Analyses

Principal component analyses (PCA) were used to obtain measures of moss, vascular plant, and microfauna community composition across the 30 islands that were used as continuous variables in multiple regression analyses. For these three taxonomic groups, we used scores from the first axis of PCA (PC1) as a measure of community composition. For mosses, high PC1 values are related to greater abundance of *Hylocomium*, and low values are related to a greater abundance of *Dicranum* sp. For vascular plants, high PC1 values are related to late-successional vascular plant species (for example, *P. abies* and *E. hermaphroditum*) and low values to early-successional vascular plant species (for example, *P. sylvestris* and *V. myrtillus*) (Jonsson and Wardle 2010).

For each of the three dominant feather moss species, we analyzed changes in moss functional traits (described above) and associated microfauna in response to factors that vary with island size. Besides these species-specific variables, we also calculated a community-weighted average (CWA) value for each island, for moss traits, moss litter decomposition, and moss-associated microfauna community variables, as described by Garnier and others (2007), that is,

$$\text{trait}_{\text{agg}} = \sum_{i=1}^{n} p_i \times \text{trait}_i,$$

where p_i is the biomass of each of the three dominant moss species i as a proportion of the total moss biomass on the island, and trait_i is the trait value of moss species i.

For previously published data that had been analyzed using one-way analysis of variance (ANOVA) with island size as a factor (that is, moss ground cover, standing biomass, moisture content, SLA, and NPP), and for new data (that is, moss decomposition and microfauna), split-plot ANOVA tests were performed with island size as a main plot categorical factor (small, medium, and large islands; see Wardle and others 2003, 2012), and moss species as the subplot factor. For whole-community measures (that is, CWAs), one-way ANOVAs were used to test for effects of island size. Means were then compared using Tukey's HSD posthoc pairwise tests whenever ANOVAs indicated that significant differences were present.

Further, for all data (that is, previously published and new data) we used best subsets multiple regressions, with Akaike Information Criterion (AICc) values to determine the best-fitting model. The multiple regressions were performed to simultaneously test several potential drivers (both biotic and abiotic) of moss community composition for both the entire moss community and separately for the three feather moss species. Drivers of moss functional traits, processes, and microfauna for the three feather moss species were also investigated, using the same statistical approach. As such, compared to previous analyses (mostly one-way ANOVA based) in which usually only one (and occasionally up to three) predictor variables were used, the multiple regression analyses provided a more powerful and comprehensive test of the underlying drivers of moss properties and processes across the gradient. In particular, a key advance of the regression approach on previous analyses was the determination of which set of this expanded range of potential predictor variables served as the strongest predictor of the dependent variables, and if these sets of predictor variables differed depending on the type of dependent variable. Different sets of predictor variables were used for different questions addressed. Island area and age (that is, proxies for variation in abiotic conditions; Wardle and others 1997) and biotic vascular plant variables (that is, species diversity, NPP, standing biomass, and PC1 scores) were used as predictors of both moss community composition and moss functional traits; for the latter, measures of moss community composition were also included as predictor variables. For moss-driven ecosystem processes and moss microfauna, island area and age, vascular plant variables, measures of moss community composition, moss functional traits, and (for the microfauna data) moss NPP were included. If applicable, analyses were run both for individual moss species and for CWAs. Data on moss standing biomass, SLA, percentage ground cover, moisture content, N and P content, and microfauna were available for *Hylocomium*, *Pleurozium*, and *Ptilium*, whereas the other variables only had data for *Hylocomium* and *Pleurozium*. In all analyses, the variance inflation factor with a cut-off value of 5 was used to determine if collinearity was present, and collinear variables were removed from subsequent analyses. If necessary, data were log-transformed to meet the requirements of parametric statistical analyses.

RESULTS

Moss Community Composition

Among island size classes, moss species composition (PC1, explaining 80.5% of the variance) and total percentage ground cover did not differ (Figure 1A) ($F_{2,30} = 1.923$, $P = 0.166$ and $F_{2,30} = 1.446$, $P = 0.253$, respectively). However, total moss standing biomass was significantly lower on medium-sized islands than on small islands (Figure 1B). Further, there were significant differences among moss species, across all island size classes, in both percentage ground cover and standing biomass ($F_{2,81} = 34.148$, $P < 0.001$ and $F_{2,81} = 37.506$, $P < 0.001$, respectively), with generally higher cover and biomass for *Hylocomium* and *Pleurozium* than for *Ptilium* (Figure 1A, B).

Multiple regression analyses revealed that vascular plant community characteristics were important for explaining both total and species-specific feather moss standing biomass. These moss biomass variables all showed not only positive relationships with vascular plant PC1 scores (indicative of higher moss biomass in late-successional stands), but also—with the exception of *Pleurozium*—positive relationships with vascular plant NPP (Table 1). However, island area was also an important explanatory variable; moss species richness was negatively related to island area, and both total and *Pleurozium* standing biomass were positively related to island area (Table 1).

Moss Functional Traits

Physicochemical Traits

Feather moss moisture content differed both among island size classes and among species ($F_{2,81} = 6.542$, $P = 0.002$ and $F_{2,81} = 4.872$, $P = 0.010$, respectively). Moisture content was higher on large islands than on small and medium islands, with the highest and lowest species-specific values in *Ptilium* on large islands and *Pleurozium* on mid-sized islands, respectively (Figure 1C). Values of CWAs for moisture, and N and P content showed no significant differences among island size classes (Appendix 1).

Multiple regression analyses revealed that both *Pleurozium* (Table 2) and CWA (Appendix 2) tissue moisture content decreased with ecosystem age, whereas *Hylocomium* and *Ptilium* tissue moisture contents were negatively related to vascular plant PC1 (that is, the lowest moisture content in late-successional stands). *Ptilium* moisture content also showed a positive relationship with total moss biomass. For moss N concentration, the CWA decreased with island area and increased with vascular plant standing biomass (Appendix 2), whereas for moss P concentration, the CWA was positively related to *Hylocomium* abundance, and negatively related to total moss biomass (Appendix 2). In addition, *Pleurozium* N concentration was positively related to *Hylocomium* abundance and vascular plant NPP (Table 2). Moss δ^{15}N decreased with island area for *Pleurozium*, and increased with ecosystem age for *Hylocomium* (Table 2). *Pleurozium* δ^{13}C was higher in late-successional vascular plant stands and in moss communities dominated by *Hylocomium*. For both *Pleurozium* and *Hylocomium*, the C:N ratio decreased with ecosystem age. Further, for *Pleurozium*, a high C:N ratio was associated with high abundance of *Dicranum* sp. and high total moss biomass (Table 2). The CWA for moss P content was associated with *Hylocomium* dominance and decreased with total moss biomass (Appendix 2).

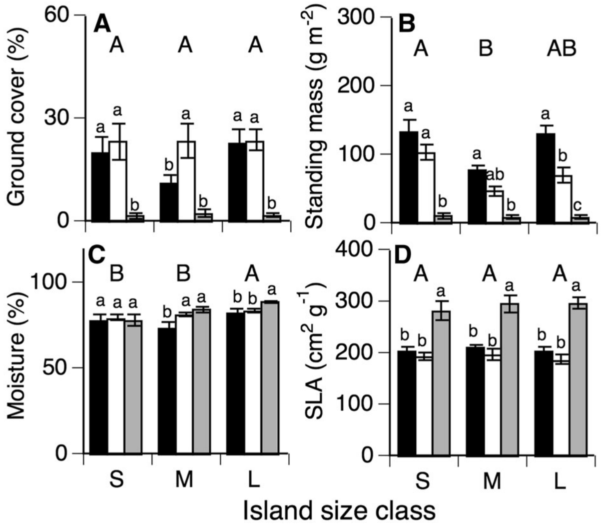

Figure 1. Effects of island size (S = small, M = medium, L = large) on **A** moss ground cover, **B** standing biomass, **C** moisture content, and **D** specific leaf area (SLA), for the three moss species *Pleurozium* (*black*), *Hylocomium* (*white*), and *Ptilium* (*gray*). *Different letters* denote significant differences ($P < 0.05$) using Tukey's posthoc tests; *capital letters* for between groups and *lower case letters* for within groups. *Error bars* represent ± 1 S.E.

Physiological Traits

Specific leaf area (SLA) was significantly different among species ($F_{2,81} = 66.590$, $P < 0.001$), with

Table 1. Results from Best Subsets Multiple Regression Analyses of Measures of Moss Community Composition (Dependent Variables) with the Following Abiotic and Biotic Predictor Variables: Island Area (AR), Ecosystem Age (AGE), and Vascular Plant (V) Productivity (NPP), Standing Biomass (M), Shannon Diversity (H), and Community Composition (C)

Moss community composition	Abiotic variables		Vascular plant variables				R^2	P
	AR	AGE	H	vNPP	vM	vC		
Total								
Species richness	−		−				0.403	0.001
Standing biomass	+			+	−	+	0.501	0.001
Pleurozium								
Standing biomass	+					+	0.274	0.013
Percentage cover	+	+	−		−	+	0.628	<0.001
Hylocomium								
Standing biomass				+		+	0.370	0.002
Ptilium								
Standing biomass				+		+	0.379	0.002

The direction of the relationships is shown by '+' and '−'. Only significant models (P < 0.05) are presented.

Table 2. Results from Best Subsets Multiple Regression Analyses of Moss Functional Traits (Dependent Variables) with the Following Abiotic and Biotic Predictor Variables: Island Area (AR), Ecosystem Age (AGE), Vascular Plant (V) Productivity (NPP), Vascular Plant (V) and Moss (M) Standing Biomass (M), and Vascular Plant (V) and Moss (M) Community Composition (C), and Vascular Plant Shannon Diversity (H) and Moss Species Richness (S)

Moss functional traits		Abiotic variables		Vascular plant variables				Moss composition			R^2	P
		AR	AGE	H	vNPP	vM	vC	S	mM	mC		
Physicochemical	*Pleurozium*											
	Moisture content		−								0.141	0.041
	N content				+					+	0.201	0.048
	C:N		−						+	−	0.483	0.001
	$\delta^{15}N$	−									0.359	<0.001
	$\delta^{13}C$						+			+	0.433	<0.001
	Hylocomium											
	Moisture content						−				0.221	0.009
	C:N		−								0.414	<0.001
	$\delta^{15}N$		+								0.385	<0.001
	Ptilium											
	Moisture content						−		+		0.511	<0.001
Physiological	*Pleurozium*											
	Dark respiration (area)	−		−					−	+	0.527	0.001
	Respiration per unit N		+								0.350	0.001
	Hylocomium											
	SLA									−	0.174	0.022
	Gross photosynthesis (area)	−		−		+		−			0.446	0.005
	Gross photosynthesis (mass)	−				+		−			0.337	0.015
	Dark respiration (area)			−	+		+		−	+	0.407	0.021
	Photosynthesis per unit N					+		−			0.336	0.006
	Respiration per unit *N*		−					−			0.397	0.002

The direction of the relationships is shown by '+' and '−'. Only significant models (P < 0.05) are presented.

greater SLA for *Ptilium* than for *Hylocomium* and *Pleurozium*, but not among island size classes ($F_{2,81} = 0.328$, $P = 0.721$; Figure 1D; Appendix 1). Multiple regression analyses showed that island area or age, vascular plant diversity, and vascular plant standing biomass were most important for predicting moss physiological traits (Table 2). Further, when present in the final model, vascular plant diversity was always negatively related, and vascular plant biomass was always positively related, with moss physiological traits. However, the most parsimonious models also included moss community-level variables, that is, moss species richness, moss PC1 scores, and total moss biomass. In these models, moss species richness always showed negative relationships, and moss PC1 scores mostly positive relationships (that is, positively associated with *Hylocomium* dominance), with moss physiological traits.

Moss-Driven Ecosystem Processes

Feather moss NPP differed significantly among island size classes ($F_{2,81} = 4.996$, $P = 0.010$), with significantly higher values on small than on medium-sized islands, and higher values for *Pleurozium* than for *Hylocomium* ($F_{2,81} = 17.605$, $P < 0.001$; Figure 2A). Moss decomposition ranged from 25 to 35% of initial moss mass over two years, and differed among island size classes and between species ($F_{2,81} = 3.942$, $P = 0.025$ and $F_{2,81} = 20.619$, $P < 0.001$, respectively), with significantly lower decomposition rates on small than on large islands and higher decomposition rates for *Pleurozium* than for *Hylocomium* (Figure 2B). The contribution by mosses to the total ground CO_2 efflux did not differ significantly among island size classes or between moss species ($P > 0.2$, in both cases).

Multiple regression analyses showed that moss NPP and decomposition rates were, in general, mostly influenced by a combination of vascular plant and moss community variables (Table 3). Both total and species-specific moss NPP increased with total moss biomass; total and *Pleurozium* NPP were also associated with high *Dicranum* sp. abundance. For *Pleurozium* decomposition, the best-fitting model included moss community composition and moss and vascular plant standing biomass, whereas for *Hylocomium* decomposition only functional traits (that is, *Hylocomium* moisture, N, and P content) were important (Table 3). However, for community-weighted moss litter decomposition, ecosystem age was important, with lower decomposition in late-successional stands (that is, a negative relationship with vascular plant PC1 and island age) (Appendix 2). Moss contribution to the total ground CO_2 efflux was influenced by a combination of vascular plant and moss variables both for *Pleurozium* and *Hylocomium*, but for *Pleurozium* abiotic variables were also important (Table 3). Measures of moss community composition and moss functional traits were the main predictors of *Pleurozium* N_2 fixation. For *Hylocomium* N_2 fixation, the vascular plant variables biomass (negatively associated) and community composition (positively associated with PC1, that is, promoted in late-successional stands) also served as predictors (Appendix 2).

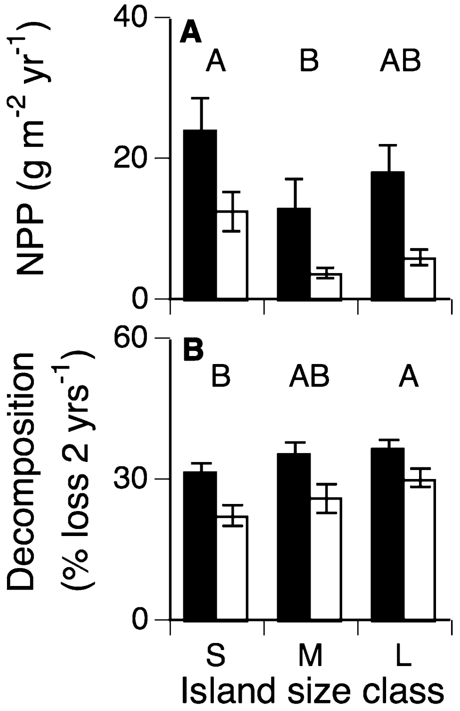

Figure 2. Effects of island size (S = small, M = medium, L = large) on **A** moss NPP and **B** moss tissue decomposition rate, for the moss species *Pleurozium* (*black*) and *Hylocomium* (*white*). *Different capital letters* denote significant differences ($P < 0.05$) using Tukey's posthoc tests between groups. *Error bars* represent ± 1 S.E.

Moss-Associated Microfauna

Total densities of tardigrades and nematodes, and the densities of most nematode taxa, did not differ among island size classes (Figure 3; Table 4; Appendix 3; Appendix 4). However, total densities of tardigrades and nematodes, the densities of some nematode taxa, and most nematode community variables differed significantly among the three feather moss species (Table 4). Specifically, total nematode densities were higher for *Hylocomium* and *Ptilium* than for *Pleurozium*

Table 3. Results from Best Subsets Multiple Regression Analyses of Moss-Driven Ecosystem Processes (Dependent Variables) with the Following Abiotic and Biotic Predictor Variables: Island Area (AR), Ecosystem Age (AGE), Vascular Plant (V) and Moss (M) Productivity (NPP), Standing Biomass (M), and Community Composition (C), and Vascular Plant Shannon Diversity (H) and Moss Species Richness (S), and the Moss Functional Traits Specific Leaf Area (SLA), Moisture Content (MOI), N Content (N), and P Content (P)

Moss-driven process	Abiotic variables		Vascular plant variables				Moss composition			Moss functional traits				R^2	P
	AR	AGE	H	vNPP	vM	vC	S	mM	mC	SLA	MOI	N	P		
Total															
Moss NPP				−				+	−					0.808	<0.001
Moss decomposition						−								0.381	<0.001
Pleurozium															
NPP							+	+	−					0.647	<0.001
Decomposition	+				−			−	+					0.310	0.050
CO_2 efflux	+	+	−	−							+			0.540	0.001
Hylocomium															
NPP		−	+			+	−	+						0.733	<0.001
Decomposition											+	−	+	0.401	0.004
CO_2 efflux				−			−					+	−	0.360	0.021

The direction of the relationships is shown by '+' and '−'. Only significant models (P < 0.05) are presented.

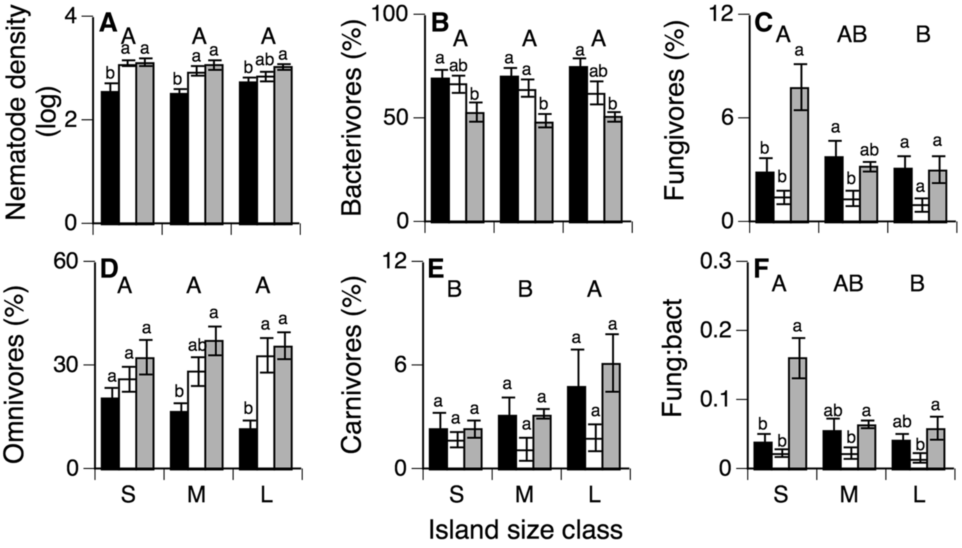

Figure 3. Effects of island size (S = small, M = medium, L = large) on **A** total nematode density (individuals g moss DW^{-1}), percentage **B** bacterial feeders, **C** fungal feeders, **D** omnivores, and **E** percentage carnivores, and **F** ratio between fungal feeders and bacterial feeders, for the moss species *Pleurozium* (*black*), *Hylocomium* (*white*), and *Ptilium* (*gray*). Different letters denote significant differences ($P < 0.05$) using Tukey's posthoc tests; *capital letters* for between groups and *lower case letters* for within groups. *Error bars* represent ± 1 S.E.

(Figure 3A), whereas the density of tardigrades was much higher for *Hylocomium* than for *Pleurozium* and *Ptilium* (Table 4, Appendix 3). As for taxon-specific densities, nematode feeding group densities were significantly different among moss species (except for plant-associates) (Table 4), with higher densities of bacterial feeders and carnivores in *Hylocomium* and *Ptilium* than in *Pleurozium* (Appendix 3). Feeding group densities did not differ among island size classes. Nematode feeding group percentages strongly differed among moss species. Moreover, for percentage fungal feeders and the fungal feeder:bacterial

Table 4. Results from Split-Plot ANOVA on Effects of Island Size (IS), Moss Species Identity (ID), and the Interaction Between IS and ID on Tardigrade and Nematode Density, and Nematode Community Variables

Variable	IS		ID		IS × ID	
	$F_{2,78}$	P	$F_{2,78}$	P	$F_{4,78}$	P
Taxa						
Tardigrades	0.539	0.586	47.353	<**0.001**	1.148	0.340
Total nematodes (density)	2.568	0.083	3.803	**0.026**	1.738	0.150
Tylenchidae	0.689	0.504	2.467	0.091	1.399	0.242
Cephalobidae	1.854	0.164	1.811	0.170	0.714	0.585
Plectidae	1.823	0.168	12.331	<**0.001**	1.605	0.181
Bunonematidae	2.950	0.058	1.974	0.146	0.676	0.610
Alaimidae	1.662	0.196	1.629	0.203	2.653	**0.039**
Teratocephalidae	0.001	0.999	6.187	**0.003**	2.853	**0.029**
Aphelenchoididae	1.231	0.298	4.351	**0.016**	1.599	0.183
Aphelenchidae	0.721	0.490	0.190	0.827	1.181	0.326
Anguinidae	10.622	<**0.001**	16.105	<**0.001**	3.863	**0.006**
Dorylaimoidea	0.153	0.858	1.979	0.145	1.671	0.165
Prismatolamidae	1.117	0.332	1.725	0.185	1.386	0.247
Tripylidae	0.076	0.927	20.568	<**0.001**	0.529	0.715
Mononchidae	0.399	0.672	2.144	0.124	0.221	0.926
Monhysteridae	0.014	0.986	7.645	**0.001**	1.290	0.281
Nematode community variables						
Plant-associated (density)	0.689	0.505	2.467	0.091	1.399	0.242
Plant-associated (%)	0.554	0.577	0.842	0.435	0.274	0.894
Bacterial feeders (density)	0.929	0.399	13.593	<**0.001**	2.396	0.057
Bacterial feeders (%)	0.183	0.833	19.256	<**0.001**	0.432	0.785
Fungal feeders (density)	1.985	0.144	11.908	<**0.001**	2.120	0.086
Fungal feeders (%)	4.194	**0.019**	15.911	<**0.001**	4.626	**0.002**
Omnivores (density)	0.497	0.611	34.909	<**0.001**	0.127	0.972
Omnivores (%)	0.074	0.929	18.424	<**0.001**	1.269	0.289
Carnivores (density)	0.779	0.463	13.711	<**0.001**	1.225	0.307
Carnivores (%)	3.286	**0.043**	3.670	**0.030**	0.736	0.570
Fung:bact	5.291	**0.007**	21.747	<**0.001**	5.748	<**0.001**
Nematode PC1	0.791	0.457	2.691	0.074	0.865	0.486

Significant P-values are highlighted in bold. Fung:bact = ratio between fungal-feeding and bacterial-feeding nematodes.

feeder ratio there was also a significant interaction effect of species with island size (Table 4; Figure 3C, F), with particularly high relative density of fungal feeders in *Ptilium* on small islands. Generally, *Ptilium* showed the lowest percentage of bacterial feeders (Figure 3B), *Hylocomium* the lowest percentage of fungal feeders (Figure 3C), and *Pleurozium* the lowest percentage of omnivores (Figure 3D). Likewise, for three nematode families (*Alaimidae*, *Teratocephalidae*, and *Anguinidae*), there was a significant interaction effect between moss species and island size, indicating that the importance of feather moss species identity for microfauna varied with island size class. Nematode community composition (that is, PC1, explaining 78.4, 76.3, and 70.8% of the variance for *Pleurozium*, *Hylocomium*, and *Ptilium*, respectively) did not, however, differ with island size or moss species (Table 4).

Multiple regression analyses showed that moss functional traits partially explained patterns in tardigrade and nematode densities (Table 5). For example, tardigrade density increased with *Pleurozium* and *Ptilium* moisture content, and fungal-feeding nematode density increased with *Pleurozium* moisture content. Also, tardigrade density decreased with *Hylocomium* and *Ptilium* SLA, and bacterial-feeding, fungal-feeding, and omnivorous nematode densities decreased with *Ptilium* SLA. However, abiotic and other biotic variables were also important; with ecosystem age there were increases in plant-associated and omnivorous nematode densities in *Pleurozium* and of fungal feeders in *Ptilium*. Further, in *Pleurozium*, densities of tardigrades and plant- and bacterial-feeding nematodes were negatively related to vascular plant NPP, whereas densities of total nematodes in both *Pleu-*

Table 5. Results from Best Subsets Multiple Regression Analyses of Nematode Community (and Tardigrade) Density and Proportional Density (%) for Each Moss Species (Dependent Variables), with the Following Abiotic and Biotic Predictor Variables: Island Area (AR), Ecosystem Age (AGE), Vascular Plant (V) and Moss (M) Productivity (NPP), Standing Biomass (M), and Community Composition (C), and Vascular Plant Shannon Diversity (H) and Moss Species Richness (S), and Species-Specific Moss Standing Biomass (M), the Moss Functional Traits Specific Leaf Area (SLA), Moisture Content (MOI), N Content (N), and P Content (P), and the Moss-Driven Process Moss NPP

Variable	Abiotic variables		Vascular plant variables				Moss composition				Moss functional traits				Moss processes	R^2	P
	AR	AGE	H	vNPP	vM	vC	S	mM	M	mC	SLA	MOI	N	P	mNPP		
Pleurozium																	
Tardigrades			+	–	+			+		–		+			–	0.505	0.017
Nematodes						–								–	+	0.306	0.021
Plant-associated		+		–									+	–		0.428	0.006
Plant-associated (%)								–			–				+	0.312	0.019
Bacterial feeders				–					–							0.258	0.018
Bacterial feeders (%)	–	–	+	–	+			+		–					–	0.609	0.005
Fungal feeders							+	–		+		+	–		+	0.441	0.025
Omnivores		+														0.138	0.043
Omnivores (%)	+	+	–		–			–		+						0.461	0.018
Carnivores			+							+						0.337	0.004
PC1		–							+		+			+	–	0.456	0.009
Hylocomium																	
Tardigrades						+				–	–					0.262	0.045
Nematodes									–					+	+	0.441	0.002
Bacterial feeders (%)		–														0.190	0.016
Fungal feeders (%)		+			+											0.252	0.020
Omnivores (%)		+								+	+					0.358	0.008
Carnivore (%)											–					0.169	0.024
Fung:bact		+			+							–				0.398	0.004
Ptilium																	
Tardigrades						+		–	+	+	–	+		+	+	0.591	0.018
Nematodes			–		–			–						+		0.414	0.015
Plant-associated (%)	–	–		–	+			–				+			+	0.709	<0.001
Bacterial feeders											–					0.194	0.021
Bacterial feeders (%)								–		+	–	+			+	0.484	0.011
Fungal feeders	+	+			–			–		+	–		–			0.782	<0.001
Fungal feeders (%)				–									–			0.598	<0.001
Omnivores											–					0.157	0.041
Omnivores (%)	+					+		–								0.366	0.013
Carnivore (%)	+	+	–		–					+			–			0.530	0.011
Fung:bact	+				–	+	+	–		+			–			0.775	<0.001
PC1						–		+				–			–	0.439	0.010

The direction of the relationships is shown by '+' and '–'. Only significant models (P < 0.05) are presented. Fung:bact = ratio between fungal-feeding and bacterial-feeding nematodes.

rozium and *Hylocomium*, fungal feeders in *Pleurozium*, and tardigrades in *Ptilium* were positively related to moss NPP.

DISCUSSION

We present a comprehensive synthesis of patterns of change in moss community composition, moss functional traits, moss-driven processes, and moss-associated microfauna along a successional gradient in boreal Sweden, and we provide general insights into which biotic and abiotic factors underpin these successional shifts (Figure 4). Below, we discuss the results in relation to our overall hypothesis and the research questions.

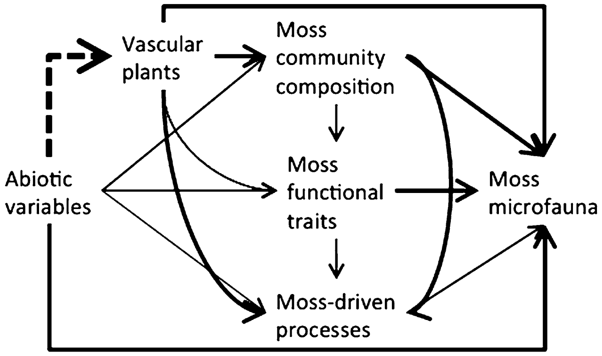

Figure 4. Conceptualization of the relationships between abiotic variables (represented by island area and age), and biotic vascular plant variables, moss community composition, moss functional traits, moss-driven ecosystem processes, and moss microfauna. Line thickness indicates the strength of the relationship based on the number of significant predictor variables contained in each predictor-variable category in the best-fitting multiple regression models. A *dashed line* indicates a relationship that was not tested in this study.

Moss Community Composition

Vascular plant community characteristics vary strongly with island size: there is higher species diversity and lower standing biomass per unit area on small islands compared to large islands (Wardle and others 1997). In contrast, mosses do not differ in species richness or community composition among island size classes (Gundale and others 2011; Wardle and others 2012); instead, biotic factors, and in particular vascular plant characteristics, were most important for explaining variation in measures of moss community composition (Figure 4). Nevertheless, as vascular plant communities on these islands are ultimately shaped by abiotic factors associated with time since wildfire (Wardle and others 1997), these factors have strong indirect influences on the moss community. The contrasting responses of vascular plants and mosses could reflect their differing sensitivities to abiotic (for example, soil nutrient and light levels) and biotic factors. Alternatively, contrasting moss responses to a range of co-occurring biotic and abiotic conditions that vary across the successional gradient (Wardle and others 1997) may result in non-linear trends in moss variables. For example, the U-shaped patterns of percentage moss ground cover (Figure 1A), moss standing biomass (Figure 1B), and moss NPP (Figure 2A), which were found for some of the three dominant feather moss species among the island size classes, could be explained by the simultaneous influence of two or more predictor variables that are negatively related to each other across the chronosequence (that is, ecosystem age and island area or vascular plant NPP).

Moss Functional Traits

Several feather moss functional traits are known to differ significantly among the island size classes (Bansal and others 2012), and our multiple regression analyses showed that both biotic and abiotic factors influenced these traits. The higher moss moisture content and moss biomass in early-successional communities could in part be caused by greater shade (Skre and Oechel 1981) associated with the higher tree canopy density in these systems (Bansal and others 2012). In the younger ecosystems, mosses have been shown to contain higher tissue N concentrations (Wardle and others 1997; DeLuca and others 2008), which could be a consequence of higher soil nutrient availability in early-successional systems. However, we have also shown that mosses are more reliant on associated N_2 fixation as a source of N in late-successional systems (Lagerström and others 2007; Hyodo and Wardle 2009; Gundale and others 2010), as shown by increased cyanobacterial N_2-fixation rates, and $\delta^{15}N$ values increasing toward zero, with increasing ecosystem age. Further, as indicated by the increasing moss $\delta^{13}C$ signatures with increasing ecosystem age (Bansal and others 2012), mosses are less limited by light in late-successional stands (Dawson and others 2002). Moss respiration rates were also sensitive to changes in environmental conditions along the successional gradient. Most notably, gas exchange rates for mosses tended to be higher on younger islands and respiration was positively related to early-successional factors (that is, young ecosystem age, low vascular plant diversity, and high vascular plant NPP). Hence, our new analyses show how both biotic and abiotic properties that change with succession are important drivers of moss functional traits (Figure 4). As such, abiotic factors determine both directly and indirectly (that is, via their effect on vascular plant and moss community characteristics) how moss functional traits are expressed.

Moss-Driven Ecosystem Processes

Measures of moss community composition and feather moss functional traits—not abiotic factors—explained the majority of the variance in moss-driven ecosystem processes, which indicates that the rates of these processes vary at relatively small scales where patches of different moss species dominate. However, shifts in vascular plant composition across the island gradient were also influential, with slower moss decomposition in late-successional stands (that is, on small islands), which is consistent with previous work showing slower decomposition rates for vascular plant litter in these older ecosystems (Jonsson and Wardle 2008). Lower moss decomposition rates in late-successional stands may have been caused by drier surface conditions associated with a more sparse vascular plant cover, or by lower soil nutrient availability, both of which are known to retard decomposition rates (Cisneros-Dozal and others 2007; Jonsson and Wardle 2008). Because moss NPP peaks in late-successional systems where decomposition is the slowest, our results suggest that mosses make a substantial contribution to accumulation of soil C in older ecosystems (Benscoter and Vitt 2007; Lindo and others 2013), a process that has often been assumed to be attributable mainly to inputs from late-successional vascular plant species (Jonsson and Wardle 2010), their roots, and their root-associated fungi (Clemmensen and others 2013).

Di-nitrogen fixation was best explained by a combination of biotic variables, in particular vascular plant biomass, moss biomass, moss community composition, and moss SLA and N content. The fact that island area and ecosystem age—both representing shifts in abiotic variables—were only included in four of the 24 models on moss N_2 fixation (Appendix 2) suggest that moss N_2-fixation rates are predominantly regulated by biotic factors (Gundale and others 2010; Lindo and others 2013), such as composition and functional traits of the moss community. Taken together, our findings indicate that moss-driven ecosystem processes were directly influenced by vascular plant characteristics and moss community composition and to a lesser extent by moss functional traits, whereas direct effects of abiotic factors were of minor importance (Figure 4).

Moss Microfauna

To our knowledge, no studies to date have addressed changes in moss-associated microfauna along successional gradients. Here, we show that the functional traits of feather mosses explain a significant portion of the variation in density patterns of associated invertebrate communities. Tardigrades and nematodes live in the water film surrounding the moss tissue; hence we expected moisture to be an important controlling factor of invertebrate densities (for example, Kinchin 1989). However, we found limited positive correlations between invertebrate densities and moss moisture content. Possible explanations are that the measured moisture content did not capture longer term desiccation cycles that may be more important in controlling moss-associated invertebrate communities (Hengherr and others 2008; Glime 2013), or that the moss-associated invertebrates are well adapted to survive periods of drought (Overgaard-Nielsen 1948; McSorley 2003; Wharton 2004). Negative correlations between SLA and the densities of tardigrades and some nematode feeding groups support the idea that the observed patterns reflect longer term population dynamics; low SLA (that is, thick leaves) may moderate adverse effects of desiccation. Similarly, high moss and vascular plant standing biomass may buffer against desiccation of mosses. Taken together, our results suggest that moss-associated invertebrate communities are controlled by a combination of moss functional traits that vary both within and across species, and a range of environmental factors that are either directly or indirectly controlled by ecosystem succession (Figure 4).

Nematodes may also respond to host type (that is, moss species identity) and moss tissue quality (Spaull 1973). Although only few nematodes directly feed on the moss tissue (Gadea 1964), inter- and intra-specific variation in moss microclimate and nutrient concentration may influence moss-associated microbial communities, and therefore food sources for the nematodes. We found that total nematode density and the densities of individual feeding groups, and their relationship with moss tissue nutrient concentrations, differed among moss species. For example, *Ptilium* appeared to provide a more favorable habitat for nematodes, in particular for fungal feeders and omnivores, than did *Hylocomium* or *Pleurozium*. The dense morphological structure of *Ptilium* promotes water retention, which may stimulate fungal growth and, hence, fungal-feeding nematodes. Although we lack data on moss-associated microbial communities in our study, previous studies have shown strong host-specificity of communities of moss-associated fungi (Kauserud and others 2008; Davey and others 2012) and cyanobacteria (Ininbergs and others 2011). Hence, bottom-up control may have played an important role in host-specific patterns of nematode density. We can, however, not rule out that predation on nematodes by microarthropods or tardigrades also played a role. Notably, for *Hylocomium,* there was a particularly high density of tardigrades that could potentially have suppressed nematode populations (for example, Doncaster and Hooper 1961; Sánchez-Moreno and others 2008).

Synthesis

The boreal region is relatively species poor, at least in terms of plants, and our study system hosts comparatively few species. However, we found considerable within- and between-species variation in feather moss functional traits across the successional gradient. Importantly, we showed that variation in moss community composition across the gradient, together with other biotic and/or abiotic variables, influenced the expression of these functional traits and the rates of key moss-driven ecosystem processes. As such, we show that mosses respond differently to ecosystem succession than do vascular plants. For example, although vascular plant NPP and nutrient uptake decrease with succession, moss NPP and N_2-fixation rates tend to increase, as mosses are less limited by soil nutrients and more regulated by vascular plant community characteristics. In addition to such differences between vascular plants and mosses, different moss variables were best explained by distinct sets of environmental variables (Figure 4). Extrinsic biotic and abiotic factors were often of relatively high importance, but for moss N_2 fixation and moss-associated microfauna, moss functional traits were at least as important as extrinsic biotic and abiotic factors. Despite the importance of several biotic factors, many of these factors, notably the characteristics of the vascular plant community, are regulated by abiotic conditions. In a natural succession such as our study system, this means that the influence of vascular plants on mosses is ultimately determined by abiotic conditions. However, the strong direct effect of vascular plants on moss community composition, moss-driven ecosystem processes, and moss microfauna suggests that anthropogenic changes in vascular plant community characteristics (through, for example, forestry) may also impact moss communities despite no immediate changes in abiotic conditions. Hence, our results are important for understanding how the different components of the boreal moss community respond to changes in environmental conditions that may occur naturally or through anthropogenic activities, with these changes having important consequences for key community and ecosystem properties.

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