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PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

Response of photosynthetic carbon gain to ecosystem retrogression of vascular plants and mosses in the boreal forest

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Abstract In the long-term absence of rejuvenating disturbances, forest succession frequently proceeds from a maximal biomass phase to a retrogressive phase characterized by reduced nutrient availability [notably nitrogen (N) and phosphorus (P)] and net primary productivity. Few studies have considered how retrogression induces changes in ecophysiological responses associated with photosynthetic carbon (C) gain, and only for trees. We tested the hypothesis that retrogression would negatively impact photosynthetic C gain of four contrasting species, and that this impact would be greater for vascular plants (i.e., trees and shrubs) than for non-vascular plants (i.e., mosses). We used a 5,000-year-old chronosequence of forested islands in Sweden, where retrogression occurs in the long-term absence of lightning-ignited wildfires. Despite fundamental differences in plant form and ecological niche among species, vascular plants and mosses showed similar ecophysiological responses to retrogression. The most common effects of retrogression were reductions in photosynthesis and respiration per unit foliar N, increases in foliar N, δ^{13}C and δ^{15}N, and decreases in specific leaf areas. In contrast, photosynthesis per unit mass or area generally did not change along the chronosequence, but did vary many-fold between vascular plants and mosses. The consistent increases in foliar N without corresponding increases in mass- or area-based photosynthesis suggest that other factor(s), such as P co-limitation, light conditions or water availability, may co-regulate C gain in retrogressive boreal forests. Against our predictions, traits of mosses associated with C and N were generally highly responsive to retrogression, which has implications for how mosses influence ecosystem processes in boreal forests.

Keywords *Betula pubescens* · Feather moss · Nitrogen · Respiration · *Vaccinium myrtillus*

Introduction

Successional changes in plant communities on the order of decades, centuries, and millennia have significant impacts on many ecosystem properties such as net primary productivity (NPP), nutrient cycling, and decomposition (Walker and del Moral 2003; Peltzer et al. 2010). The initial or progressive phases of succession that lead to a maximal biomass phase have been extensively studied (Walker and del Moral 2003). However, in the absence of major disturbances, the maximal biomass phase is often unsustainable, and, as soils age on the order of millennia, reductions in the availability of soil nitrogen (N) and phosphorus (P) can lead to 'ecosystem retrogression' (Walker and Syers 1976; Wardle et al. 2004; Peltzer et al. 2010). Ecosystem retrogression is characterized by a decline in rates of NPP, plant litter decomposition, and nutrient cycling, and has been observed in various ecosystems around the world (Vitousek 2004; Wardle et al. 2004). Concomitant with these ecosystem responses to retrogression are changes that occur in ecophysiological

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traits, which have been documented both among and within plant species in a growing number of studies (e.g., Walker et al. 1981; Joel et al. 1994; Wardle et al. 1997; Richardson et al. 2004). However, few studies in retrogressive systems have focused on traits that are directly linked to carbon (C) gain such as photosynthesis (A) and respiration (R), and these have all only focused on tree species in either Hawaii (Cordell et al. 2001) or in New Zealand (Turnbull et al. 2005; Whitehead et al. 2005).

There has been relatively little work performed on ecophysiological responses to long-term ecosystem decline and retrogression in boreal forest ecosystems, and none on photosynthetic C gain (Nilsson and Wardle 2005). This is despite boreal forests accounting for more global C sequestration and storage than any other terrestrial biome (Anderson 1991). The decrease in NPP and nutrient cycling during retrogression in boreal forests is attributable in part to long-term decreases in tree productivity with age (Bond and Franklin 2002; Winner et al. 2004), and also to changes in tree and shrub community composition, with a shift from species with resource acquisitive to resource conservative growth strategies (Hörnberg et al. 1998; Wardle et al. 2003). In addition, feather mosses are a major component of boreal forests because they comprise a significant fraction of total ecosystem NPP and play an important role in the N cycle through intercepting N deposition and hosting N-fixing cyanobacteria (DeLuca et al. 2002; Lagerström et al. 2007), especially as retrogression proceeds (Zackrisson et al. 2004; Gundale et al. 2010). Further, given the nearly continuous ground cover of feather mosses in many boreal forests, shifts in their A and R across environmental gradients could have major impacts on ecosystem C balance (Gorham 1991). However, few studies have explored A and R in mosses (Skre and Oechel 1981; Waite and Sack 2010), especially in boreal forests (Swanson and Flanagan 2001), and their responses to successional gradients remains relatively unexplored.

Photosynthetic C gain is often tightly related to soil N availability for vascular plants (Field and Mooney 1986; Poorter and Remkes 1990). However, C gain can also be influenced by extrinsic factors other than soil N availability, such as soil P, light conditions, and water availability (Oechel and Van Cleve 1986), or by intrinsic processes, such as nutrient and water use efficiency (Lambers et al. 2008), R (Turnbull et al. 2005), and specific leaf area (Cordell et al. 2001). Many of these extrinsic factors and intrinsic processes are known to change during retrogression (Peltzer et al. 2010), but very little is known about how plant traits specifically associated with C gain respond to these long-term changes associated with retrogression; to our knowledge, no study to date has considered boreal forest or plant functional groups other than trees. In the present study, we used a well-characterized chronosequence of 30 islands in northern Sweden that vary in historical fire regime, and undergo ecosystem retrogression as a result of reductions of available (mineral) forms of nutrients (notably N and P) in the long-term absence of fire over thousands of years (Wardle et al. 1997, 2003). We measured A, R, and several associated ecophysiological traits for each of four contrasting plant species that all commonly occur throughout the gradient: a deciduous tree (*Betula pubescens*), an understory dwarf shrub (*Vaccinium myrtillus*), and two species of feather moss (*Pleurozium schreberi* and *Hylocomium splendens*). We tested the hypothesis that, as retrogression proceeds, there would be declines in A for each of the four species, but that the magnitude of decline would differ among species due to differences in concomitant traits associated with C gain (e.g., specific leaf area, foliar N). We specifically predicted that the tree and shrub species that rely on nutrient inputs and water supply directly from the soil should be more affected by changes across the retrogressive gradient than mosses that can also obtain resources from the atmosphere (i.e., vascular plants are primarily minerotrophic while mosses are ombrotrophic) (Bates 1992). In testing this question, we aimed to learn how long-term shifts in growing conditions that occur during retrogression affect C gain in the boreal forest across contrasting plant life forms, thereby gaining a better understanding of the drivers of ecosystem C balance and sequestration in the boreal zone.

Materials and methods

Study site

The study site consists of 30 forested islands in lakes Hornavan and Uddjaure in the boreal forest zone of northern Sweden (65°55′–66°09′N, 17°43′–17°55′E). The tree species found on the islands are a mix of *Betula pubescens* (hereafter *Betula*), *Picea abies* and *Pinus sylvestris*. The understory vegetation consists primarily of the ericaceous shrubs *Vaccinium myrtillus* (hereafter *Vaccinium*), *V. vitis-idaea* and *Empetrum hermaphroditum*, and the feather mosses *Pleurozium schreberi* (hereafter *Pleurozium*) and *Hylocomium splendens* (hereafter *Hylocomium*). The relative abundances of these species change across the island size gradient, with a general shift from *Vaccinium* and *Pinus* dominance on larger islands towards *Empetrum* and *Picea* dominance and a small increase in moss biomass on smaller islands (Wardle et al. 2003; Lagerström et al. 2007). *Betula* occurs commonly across the gradient, but has its maximal biomass on medium-sized islands (Wardle et al. 2003). The islands range in size from 0.03 to 15 ha. Larger islands are struck by lightning more often than are smaller ones, and therefore burn more frequently, thus forming a retrogressive chronosequence with retrogression increasing as island size decreases (Wardle et al. 2004). It has previously been shown that island size effects on fire history drives soil fertility, with the long-term absence of fire leading to greater soil infertility and successional replacement of plant species, and the replacement of plant species in turn altering ecosystem-level processes (Wardle et al. 1997, 2003; Gundale et al. 2011). Further data on changes in ecosystem properties that occur during retrogression (e.g., humus depths, light conditions) across these islands are presented in Online Resource 1. The islands were divided into three size classes with 10 islands per class: small (<0.1 ha), medium (0.1–1.0 ha) and large (>1.0 ha), with a mean time since the last major fire of 3,250, 2,180, and 585 years, respectively (Wardle et al. 2003).

Sampling protocol and experimental approach

Field work was performed from 28 July to 9 August 2010. The order in which we visited the islands was random with respect to size class to avoid seasonal or diurnal effects from confounding the results, given that it was necessary to visit different islands at different times of the day if all islands were to be sampled during a comparable portion of the growing season. Consequently, any diurnal effects on photosynthesis likely increased the amount of variability in the dataset, but not in a biased manner with respect to island size. We also note that given the long day lengths during the growing season at 66°N, diurnal variation of both light and temperature during the day time would be less than at lower latitudes.

On each of the 30 islands, we measured gas exchange on six separate samples of each of the four study species, i.e., the vascular plants *Betula* and *Vaccinium*, and the mosses *Pleurozium* and *Hylocomium*. All plants were sampled within a plot area of approximately 20 × 20 m on each island, which was the same plot area that has been measured in previous studies on these islands; plots were always centered at similar distances from the shore (ca. 15 m) regardless of island size to prevent edge and microclimatic effects from confounding the results (Wardle et al. 1997, 2003). For the vascular plants, we selected six saplings of *Betula* and six adjacent *Vaccinium* shrubs. *Betula* leaves were sampled from understory saplings always at the same canopy position, approximately 1–2 m in height. Because of sampling position, the measured leaves for *Betula* are characteristic of sub-canopy shade leaves that are subjected to diffuse light and transient sun flecks, and as the mosses and *Vaccinium* measurements were performed in the same vicinity as the *Betula* saplings they were subjected to a comparable light environment; neither sampled moss nor *Vaccinium* shoots were shaded by any understory vegetation. We used one leaf near the end of a branch for each *Betula* sapling and the shoot tip (consisting of two or three leaves plus the stem) for each *Vaccinium* shrub for field measurements of gas exchange; leaves and stems remained attached to the plant during measurement.

For each of the two moss species, six patches (60 × 30 mm) of intact moss carpets (gametophytes) were collected in the plot area of each island that appeared healthy and/or representative of the island. Following protocols similar to Waite and Sack (2010), the humus and basal dead tissue were trimmed with scissors from the bottom of each moss patch, leaving only the photosynthetic (green) portion of moss (i.e., 2–3 cm depth). We placed two patches of the same species together into a 6 × 6 × 2 cm pot, being careful to preserve the natural canopy structure, thus giving us three pots of each species from each island. Moss carpets were generally well hydrated due to intermittent rain before and during the collection period. Each carpet was further sprayed liberally with water and gently covered by plastic wrap to reduce moisture loss. We kept the moss pots under ambient temperatures during the day and conducted gas exchange measurements indoors at the end of the same day. The majority of studies on moss photosynthesis have involved greenhouse measurements days or weeks after collection of mosses in the field, and have emphasized the importance of moisture status on gas exchange rates (Proctor et al. 2007). We conducted an extensive pilot investigation to confirm that waiting 2–3 h after re-wetting was sufficient time for these two moss species to regain photosynthetic competence comparable with in situ rates, and also that gas exchange rates declined sharply more than 24 h after collection. We also confirmed that the moisture status (wet dry^{-1} weight) of mosses at the time of measurements did not differ among island size classes (*Pleurozium*: $F_{2,27} = 0.54, P = 0.589$; *Hylocomium*: $F_{2,27} = 0.40, P = 0.674$), in line with what has been shown for gravimetric humus moisture content (Online Resource 1) across the gradient.

Ecophysiological measurements

We quantified the intrinsic rates of photosynthesis (A) and respiration (R) for each of the four species. We measured stomatal conductance to water vapor (g_s) for vascular plants only because water loss for mosses is mostly due to evaporation off the surface of the shoot, thus g_s is not relevant for mosses. To attain the gas exchange data, we measured CO_2 and H_2O flux using a portable gas exchange system (Li-Cor 6400XT; Li-Cor Biosciences, Lincoln, NE, USA) under saturating light levels, relative humidity of 60–80%, CO_2 concentrations of 400 μmol CO_2 mol^{-1}, and a constant temperature of 20°C. For all species, light intensities were set to saturating levels for A as determined prior to the study for each species using light-response curves. These light levels were 1,100, 500, 350, and 350 photosynthetic photon flux density (mmol m^{-2} s^{-1}) for *Betula*, *Vaccinium*, *Pleurozium*, and *Hylocomium*, respectively.

For the vascular plants, we inserted the intact leaf tissue into a 2 × 3 cm cuvette (model LI-6400-02b). For the mosses, we placed a single pot of moss carpet into a cuvette that we customized based on a model designed by M. Waite (Waite and Sack 2010). Our custom cuvette was acrylic material, cylindrical in shape with a 10 cm diameter, and attached to the photosynthesis machine using a mounting plate (model LI-6400-19). The air inlet holes for air flow in and out of the cuvette were positioned at 3 cm above the base of the cuvette. Therefore, when a pot of moss carpet was placed in the bottom of the chamber, air flowed across the surface of the moss carpet, as would occur under field conditions. Due to the high moisture content on the surface of moss, we added a small amount of silica gel desiccant in the base of the chamber to avoid excess relative humidity. Desiccant in the chamber did not affect A or calculations (as empirically tested and confirmed by Li-Cor technicians). The cuvette was illuminated by placing a full spectrum light source (model LI-6400-18) on top of the custom cuvette, and light intensity at the surface of the moss was determined using an external PAR sensor. We were primarily interested in obtaining measurements that would be representative of natural conditions, and for this reason we kept the moss carpets intact so that the lower shoots were self-shaded by the upper shoots as would occur in the field. Following measurements of A, the cuvettes were darkened (PAR = 0) until gas exchange rates had stabilized for measurements of R. Gross photosynthesis was estimated as the difference between chamber measurements made in the light and dark (Swanson and Flanagan 2001). This estimate of gross photosynthesis may be an overestimate because the magnitude of R in the dark is typically greater than in the light; however, our primary interest was in quantifying relative differences among islands and species rather than obtaining absolute measures of gross photosynthesis (e.g., Bansal and Germino 2008). Moreover, the values of net C flux from the moss carpets are largely dependent on the depth of the collection, with deeper samples having higher relative respiration (through containing a higher proportion of senescing tissue), potentially depressing rates of net C flux below zero for the entire carpet despite positive C gain occurring in the upper parts of the moss shoots. Therefore, all calculations and data reported on A are based on gross photosynthesis to justify comparisons among species.

Following gas exchange measurements of the vascular plants, we harvested the whole leaves of *Betula* and the leaves and stem of *Vaccinium* inside each cuvette. The fresh tissues were separated, laid flat with a reference scale (for calibration), and digitally photographed. Projected areas were later quantified using image processing software (Image J; Scion, Fredrick, MD, USA). These quantified areas, as well as the surface areas of the moss carpet in the pots (36 cm^2), were used to normalize gas exchange rates on an area basis (A_{area} and R_{area}). Previous studies have shown that a cluster of moss shoots that comprise the moss carpet can have relationships between A, N and SLA that are comparable to leaves of vascular plants; therefore, comparisons between moss carpets and leaves of vascular plants are more justified when each moss carpet is treated as a single leaf (Waite and Sack 2010, 2011). All tissues were then dried at 70°C for 48 h, weighed (± 0.1 mg) and gas exchange rates were re-calculated on a mass basis (A_{mass} and R_{mass}). Specific leaf areas were calculated by dividing leaf area by leaf mass. *Vaccinium* gas exchange rates were calculated with and without the photosynthetic stem, and there were no significant differences in trends across island gradients or among species, and therefore the results we report here include stem areas and masses.

We measured changes in foliar C and N concentrations and $\delta^{13}C$ and $\delta^{15}N$ values along the chronosequence to determine possible mechanisms for changes in traits associated with C gain. For each species on each island, leaf tissue was combined to form one bulked sample for analysis of foliar C, N, $\delta^{13}C$, and $\delta^{15}N$ concentrations. Following measurements of dry mass, each sample was ground using a ball mill, weighed, and placed in a folded tin capsule. Carbon and N concentrations for each sample were determined using a continuous-flow isotope ratio mass spectrometer after combustion in an elemental analyzer (Delta V Advantage Isotope Ratio Mass Spectrometer, Flash 2,000 Elemental Analyzer; Thermo Fisher Scientific, Bremen, Germany), which provided C, N, $\delta^{13}C$, and $\delta^{15}N$. Carbon and N concentrations were expressed as mg g^{-1} dry weight (C_{mass} and N_{mass} respectively), and divided by SLA for expression on an area basis (C_{area} and N_{area}). The natural abundances of ^{13}C and ^{15}N were expressed in per mil (‰) deviation from international standards (vPDB and atmospheric N for C and N, respectively); $\delta^{13}C$ or $\delta^{15}N$ was calculated as $(R_{sample}/R_{standard})/R_{standard} \times 1,000$, where $R = {}^{13}C/{}^{12}C$ or $^{15}N/^{14}N$, respectively. Photosynthesis and R were re-calculated per unit foliar N (A_N and R_N, respectively).

Data analysis

For individual response variables for each species, we used the average value of all measurements performed on each island as a single data point, so that individual islands served as the units of replication. Two-way split-plot analysis of variance (ANOVA) was used to test for effects of island size class (small, medium or large) as the main plot factor and species as the subplot factor on all response variables. When effects of ANOVA were significant at $P = 0.05$, the least significant difference test was used to compare means among size classes within species and among species across all size classes at $P = 0.05$. To examine the relationships across the 30 islands of each of the response variables with abiotic variables, Pearson's correlation coefficients were calculated by using each island as an independent data point. The abiotic variables that we used were humus depth, ammonium (NH_4), and phosphate (PO_4), total soil N, P, N:P, and amino N, and % light transmission (i.e., the relative fraction of light that penetrated through the forest canopy throughout the plot at a height of 20 cm above the ground layer) using data collected in the same plots area and presented elsewhere (Wardle et al. 1997, 2003; Lagerström et al. 2007, 2009; Gundale et al. 2011). Variables were transformed to meet the assumptions of homoscedasticity of error variance and normality.

Results

There were strong differences among species in both A_{area} and especially A_{mass} (Fig. 1a, b; Table 1). Values for A_{area} and A_{mass} for *Betula* were double those for *Vaccinium*, with *Hylocomium* and *Pleurozium* having lower values, particularly for A_{mass} (Fig. 1a, b). There were no overall effects of island size on either A_{area} or A_{mass} (Table 1), although for A_{mass} there was a significant species × island size interaction due to *Betula* (but not the other species) having significantly lower values on small than on medium and large islands (Fig. 1b). There were also differences among species for both R_{area} and R_{mass} (Table 1). Values of R_{area} were greater for the two moss species than for the two vascular species (Fig. 1c). Conversely, vascular plants had over three times greater R_{mass} than did the mosses, and *Vaccinium* had 10% overall greater R_{mass} than did *Betula* (Fig. 1d). There were no overall effects of island size or species × island size interaction on R_{area} or R_{mass} (Table 1), but R_{area} was 28 and 18% higher on small

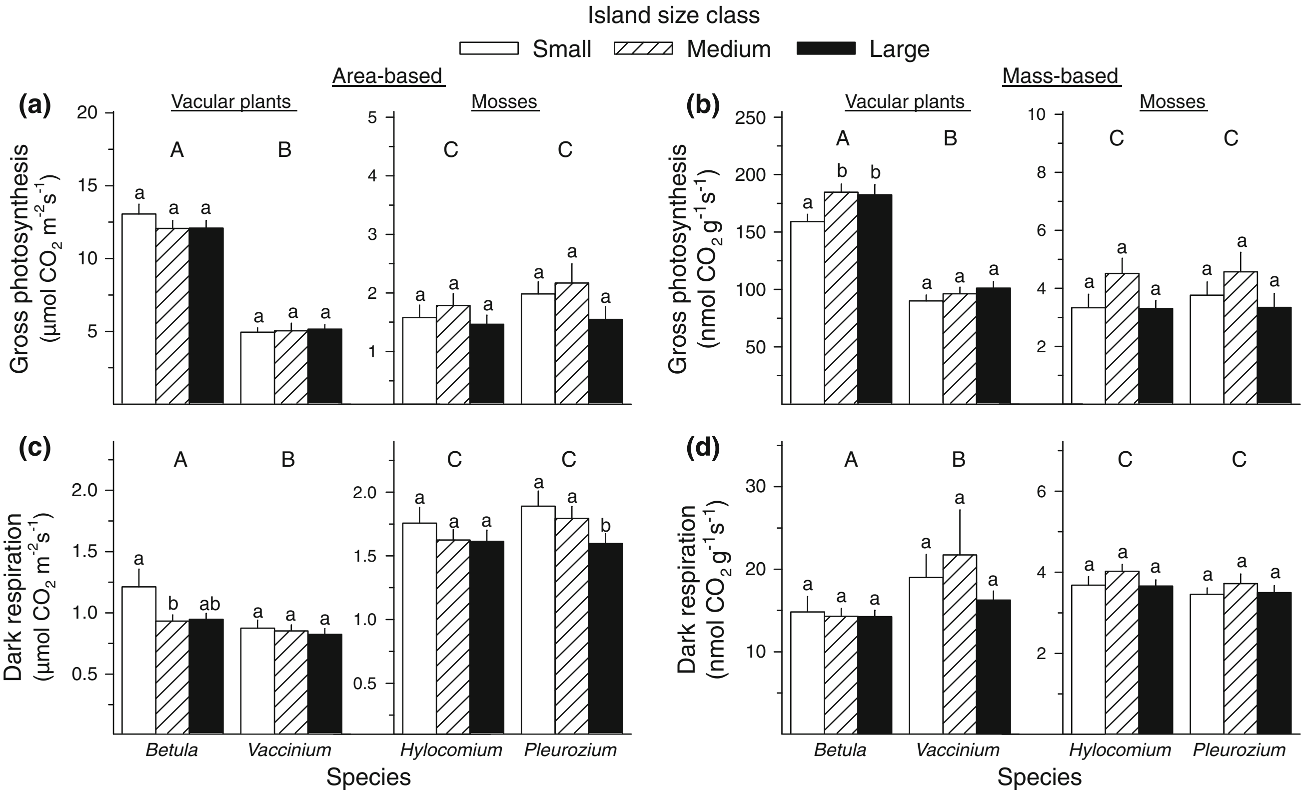

Fig. 1 The effect of island size (*white bars* for small, *hatched bars* for medium, and *black bars* for large islands) on leaf traits associated with photosynthesis (A) and respiration (R) (mean ± SE; $n = 10$) of two vascular plant species, *Betula* and *Vaccinium*, and two moss species, *Hylocomium* and *Pleurozium*. Traits include (**a**, **b**) gross photosynthesis and (**c**, **d**) dark respiration. **a** and **c** are normalized for leaf area and **b** and **d** are normalized for leaf mass. Leaf area and mass of mosses were based on intact carpets of moss. Scales are different for vascular plants and mosses because of the large differences between them. Within each group of three *bars*, different *lower case letters* indicate significant differences between island size classes, and within each *panel*, different *upper case letters* indicate significant overall differences between the four species following ANOVA (ANOVA results in Table 1)

Table 1 Results from a two-way split-plot ANOVA (*F* and *P* values) testing for the effects of island size class (small, medium and large) as the main plot factor, and species (*Betula, Vaccinium, Hylocomium*, and *Pleurozium*) as the sub-plot factor on leaf traits and trait ratios

Response variable	Units	Island size (IS)		Species (S)		IS × S	
		F	*P*	*F*	*P*	*F*	*P*
Gross photosynthesis	μmol CO_2 $m^{-2}s^{-1}$	0.92	0.412	**659.7**	**<0.001**	0.95	0.460
Gross photosynthesis	nmol CO_2 $g^{-1}s^{-1}$	2.31	0.120	**3,822.5**	**<0.001**	**2.18**	**0.049**
Dark respiration	μmol CO_2 $m^{-2}s^{-1}$	1.94	0.163	**196.5**	**<0.001**	0.61	0.721
Dark respiration	nmol CO_2 $g^{-1}s^{-1}$	0.20	0.825	**875.0**	**<0.001**	0.37	0.909
Leaf N concentration	g N m^{-2}	**11.93**	**<0.001**	**443.8**	**<0.001**	0.98	0.443
Leaf N concentration	mg N g^{-1}	3.02	0.066	**1,017.5**	**<0.001**	**3.00**	**0.009**
Carbon to N ratio	–	**5.86**	**0.008**	**357.71**	**<0.001**	**4.16**	**0.001**
Specific leaf area	cm^2 g^{-1}	**6.04**	**0.007**	**2,295.9**	**<0.001**	1.09	0.374
Conductance (vascular plants)	mol H_2O $m^{-2}s^{-1}$	2.24	0.136	**1,689.6**	**<0.001**	**2.51**	**0.031**

df IS = 2, 27, S = 3, 81, IS × S=6, 81, for all variables except *df* for conductance: IS = 2, 27, S = 1, 27, IS × S=2, 27

Significant effects ($P < 0.05$) are in bold

islands for *Betula* and *Pleurozium*, respectively, compared to medium and/or large islands (Fig. 1c).

Values of foliar N_{area} were affected by species and island sizes, but not their interaction (Table 1), and were greatest for the two moss species, followed by *Betula* and then *Vaccinium* (Fig. 2a). Values for foliar N_{mass} were affected by both species and the interaction with island size (Table 1), and were greatest for *Betula* and least for the two mosses (data not shown). For all species, N_{area} and N_{mass} were greatest on small and least on the large islands, except for *Betula* for which N_{mass} was independent of island size (Fig. 2a; data for N_{mass} not shown). The ratio of foliar C to N (C:N) was affected by species, island size, and their interaction (Table 1). *Pleurozium* had greater overall C:N than did *Hylocomium*, followed by *Vaccinium* and then *Betula* (Fig. 2b). Values of C:N were significantly lower on the smaller islands for the two mosses, but unresponsive to island size for the vascular species (Fig. 2b). Values of specific leaf area (SLA) were influenced by species and island sizes, but not their interaction (Table 1), and were lowest for *Hylocomium* and *Pleurozium*, followed by *Betula* and then *Vaccinium* (Fig. 2c). Values of SLA were generally least on the small islands and greatest on the large islands, although this was only statistically significant for *Betula* and *Pleurozium* (Fig. 2c; Table 1). Values of conductance (g_s), measured for the vascular plants, were 60% greater for *Betula* than for *Vaccinium* (overall means ± SE: 0.289 ± 0.01, 0.171 ± 0.01 mol H_2O m^{-2} s^{-1}, respectively). Conductance was not affected by island size or the species × island size interaction, although *Betula* had 20% greater g_s on the small compared to the medium and large islands, while g_s of *Vaccinium* was unresponsive to island size (data not shown).

There was a significant overall effect of species but not island size on the ratio of R to A (R:A) (Table 2), with R:A being highest for mosses and lowest for *Betula*, while *Vaccinium* was intermediate (Fig. 3a). Values for A and R per unit foliar N (A_N and R_N, respectively) were both affected by species and island size (Table 2). *Betula* had 45% greater A_N than did *Vaccinium*, and both vascular species had at least 8 times greater A_N than did the mosses (Fig. 3b). All species had their lowest A_N on the small islands, though this effect was statistically significant only for *Vaccinium* and *Hylocomium* (Fig. 3b). *Vaccinium* had the highest R_N, followed by *Betula* and the two mosses (Fig. 3c). The two moss species, but not the two vascular species, had significantly lower R_N on the small than on the medium and/or large islands (Fig. 3c). For vascular plants, values for water use efficiency (WUE, A g_s^{-1}) were responsive to effects of species, with *Betula* having greater WUE than *Vaccinium* (overall means ± SE: 43.30 ± 1.5, 25.93 ± 1.7 μmol CO_2 mol^{-1} H_20, respectively). Values of WUE were not affected by island size or the interaction of island size and species, although *Betula* had 11% lower WUE on the small compared to medium and large sized islands (data not shown).

Both foliar ^{15}N and ^{13}C values were affected by species and island size, but not their interactions (Table 2). *Vaccinium* was the most enriched and mosses were the most depleted in ^{15}N, while *Betula* was intermediate (Fig. 4a). In contrast, *Vaccinium* was the most and *Hylocomium* was the least depleted in ^{13}C (Fig. 4b). All species had relatively higher values in $\delta^{15}N$ and $\delta^{13}C$ on small compared to medium and/or large islands, and this effect was statistically significant except for $\delta^{13}C$ of *Hylocomium* (Fig. 4a, b).

Our correlation analyses showed that, across the 30 islands, the traits we measured were most commonly correlated with humus depth, total soil P, and the ratio of soil N to P (Table 3). Values for A_{area} and A_{mass} were not

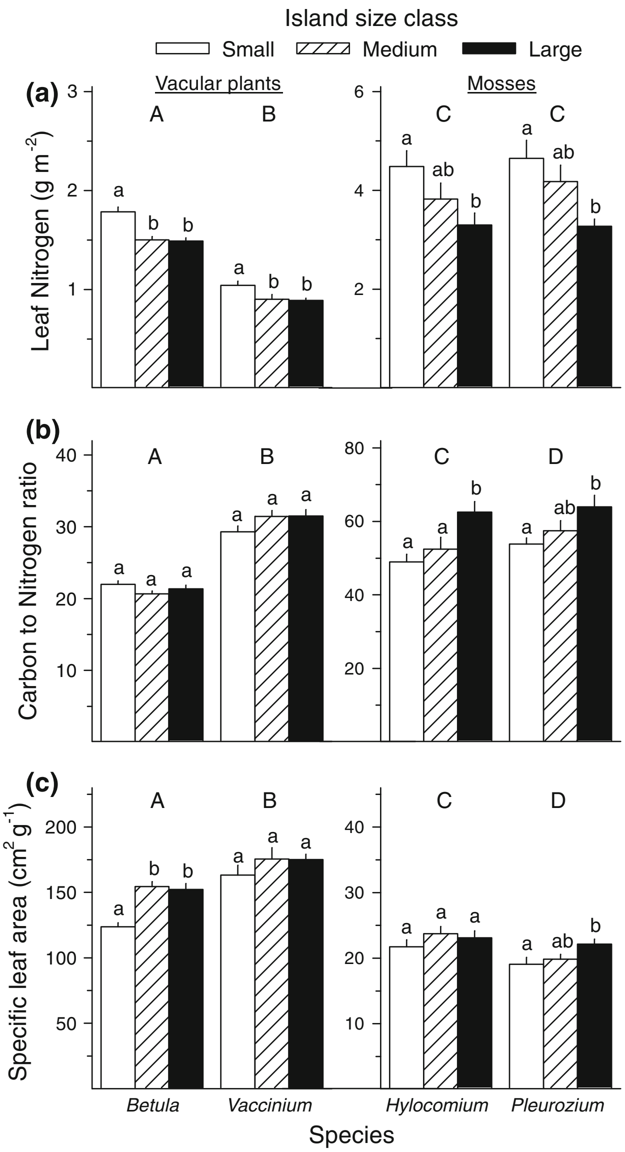

Fig. 2 The effect of island size (*white bars* for small, *hatched bars* for medium, and *black bars* for large islands) on leaf traits associated with nitrogen and carbon (mean ± SE; $n = 10$) of two vascular plant species, *Betula* and *Vaccinium*, and two moss species, *Hylocomium* and *Pleurozium*. Traits include (**a**) foliar N content per unit area, (**b**) the ratio of foliar C to N and (**c**) specific leaf area. Leaf area and specific leaf area of mosses were based on intact carpets of moss. *Scales* are different for vascular plants and mosses because of the large differences between them. Within each group of three *bars*, different *lower case letters* indicate significant differences between island size classes, and within each *panel*, different *upper case letters* indicate significant overall differences between the four species following ANOVA (ANOVA results in Table 1)

correlated with measures of soil fertility, and there was only a weak negative relationship of light transmission with A_{area} for *Hylocomium* and to A_{mass} for *Betula* (A_{mass} data not shown). Values of A_N were most strongly (negatively) correlated with humus depth for the two vascular species and with the ratio of N to P for the two mosses. Values of R_{area} and R_{mass} were not related to measures of soil fertility or light transmission (data not shown). Meanwhile, R_N was related to soil variables only for mosses, with the strongest (negative) relationships with humus depth. Values of N_{mass}, $\delta^{13}C$ and $\delta^{15}N$ were most commonly related (positively) with humus depth and soil P. *Betula* had positive relationships between foliar N_{mass} and total soil N ($r = 0.502$, $P = 0.005$), which was the only significant relationship with soil N in the entire data set (data not shown).

Discussion

Despite many fundamental differences in leaf structure, nutrient acquisition, and growth rates among vascular plants and mosses, there were several variables associated with C gain, resource use efficiency, and isotope discrimination for which all species responded similarly to island size. However, there were also some key traits associated with C and N allocation for which mosses and vascular plants responded quite differently to island size.

The most common effects of ecosystem retrogression on C gain across species were revealed through declining rates of photosynthesis (A) and respiration (R) per unit foliar N (A_N and R_N, respectively), which occurred in combination with increasing foliar N and decreasing specific leaf area (SLA). The decline in A_N during retrogression occurred because foliar N increased on smaller, retrogressive islands without corresponding changes in A, particularly for mosses. There are many possibilities for the decline in A_N and the disruption of a linear relationship between A and foliar N for mosses. First, the retrogressive phase of succession can also involve significant P co-limitation, as has been previously demonstrated for other biological processes on this study system (Lagerström et al. 2009), and for other retrogressive systems (Peltzer et al. 2010). As such, an increase in foliar N may be less effective in promoting A when P remains co-limiting (Warren and Adams 2002; Whitehead et al. 2005). Second, the mosses and *Betula* had greater R as retrogression proceeded, which could be attributable to an increase in allocation of foliar N to maintenance R instead of to A (Ryan 1995). Third, changes in light penetration to the forest floor could have driven changes in leaf traits such as A, foliar N, and SLA. However, the pattern of light penetration follows a parabolic curve (with the densest tree canopies on medium-sized islands) (Wardle et al. 2003), while many of the changes in leaf traits were unidirectional with respect to island size; as such, the traits showed few relationships with light transmission (Table 3). Finally, moisture status of plants, particularly mosses, prior to measurements could have legacy effects on A, but not foliar N (Proctor 2000).

Table 2 Results from a two-way split-plot ANOVA (*F* and *P* values) testing for the effects of island size class (small, medium and large) as the main plot factor and species (*Betula, Vaccinium, Hylocomium,* and *Pleurozium*) as the sub-plot factor on carbon, nitrogen and water use efficiencies and stable isotopes

Response variable	Units	Island size (IS)		Species (S)		IS × S	
		F	*P*	*F*	*P*	*F*	*P*
Respiration to photosynthesis ratio	–	1.11	0.353	**481.7**	**<0.001**	0.55	0.771
Photosynthesis per unit foliar N	µmol CO_2 g^{-1} N	**4.26**	**0.025**	**1,807.01**	**<0.001**	0.78	0.592
Respiration per unit foliar N	µmol CO_2 g^{-1}N	**4.71**	**0.018**	**126.89**	**<0.001**	0.39	0.884
Water use efficiency (vascular plants)	µmol CO_2 mol^{-1} H_2O	1.27	0.300	**352.13**	**<0.001**	0.13	0.879
$\delta^{15}N$	‰	**15.68**	**<0.001**	**152.52**	**<0.001**	1.44	0.213
$\delta^{13}C$	‰	**6.77**	**0.004**	**79.32**	**<0.001**	2.06	0.068

df IS = 2, 27, S = 3, 81, IS × S = 6, 81, for all variables except *df* for water use efficiency: IS = 2, 27, S = 1, 27, IS × S = 2, 27

Significant effects ($P < 0.05$) are in bold text

However, this is unlikely to be a confounding factor, because gravimetric humus moisture content (and thus availability of moisture in the uppermost portion of the humus) is independent of island size (Online Resource 1), and because our extensive pilot investigations indicated that the level of variation of moisture that the plants encountered was unlikely to be a primary driver of variation in A. In any case, regardless of the precise mechanism involved, our results point to important changes in several leaf traits as retrogression proceeds, which may occur either as a direct consequences of changes that occur in the soil environment over time or as an indirect consequence (i.e., through changes in the light environment).

Because of the multifaceted (albeit not linear) relationship of foliar N with A and R, factors affecting foliar N concentrations are of particular interest. There is often no clear relationship between total soil N and foliar N concentrations (Keeley 1980; He et al. 2010), and this can be the case during ecosystem retrogression because N is converted into increasingly unavailable forms (e.g., nitrogen–phenolic complexes) even when total N does not decline (Wardle et al. 1997). However, all functional groups had modest but greater foliar N concentrations during retrogression, consistent with what has been observed for *Metrosideros polymorpha* during retrogression in Hawaii (Vitousek et al. 1990). This may be due to a greater intensity of competition for plant-available N on the more productive earlier-successional islands (Wardle and Zackrisson 2005), and additionally for mosses, because of greater associative N-fixation by cyanobacteria as retrogression proceeds (Lagerström et al. 2007; Gundale et al. 2010). The discrepancies among soil N, foliar N, A, and R highlight the complex interplay among the suite of environmental properties, biotic interactions, and physiological traits that affect C gain during ecosystem retrogression.

The key drivers of variation in C gain among species were differences in mass-, area- and N-based A, which differed many-fold between mosses and vascular plants. The photosynthetic portion of moss shoots represents a continuous gradient from relatively high light exposure, N concentration, and photochemical performance near the upper tips (Tobias and Niinemets 2010) to lower light exposure and greater nutrient resorption and senescence towards the base (Eckstein 2000). This structure of live moss shoots helps explain the low values of A that we observed for them relative to vascular plants, and also the ratio of R to A of close to unity for the entire moss carpet as a whole. Given the delicate balance of R and A for mosses, even subtle changes in environmental conditions could influence the role of mosses on ecosystem C balance.

Foliar ^{15}N and ^{13}C values generally increased similarly for all species as retrogression proceeded, consistent with previous studies on these islands (Hyodo and Wardle 2009) and retrogressive chronosequences in Hawaii (Vitousek et al. 1989) and California (Brenner et al. 2001), but not New Zealand (Menge et al. 2011). The increasing $\delta^{15}N$ signature on smaller islands has been attributed to increased biological N-fixation and greater dependency of plants on organic N (Brenner et al. 2001). The increasing trend in $\delta^{13}C$ with ecosystem retrogression for both vascular plants and mosses has been observed along other stress gradients (Marshall and Zhang 1994; Lamont et al. 2002), including those that have undergone retrogression (Vitousek et al. 1990; Cordell et al. 1998), and may be related to lower SLA. These similarities in isotope concentrations among the four species occurred even with very large differences in their C, water, and N acquisition strategies and sources. These common trends suggest conservation of enzyme-level isotopic discrimination associated with intracellular photosynthetic activity (Whelan et al. 1973; Thornton et al. 2005) and N assimilation (Handley and Raven 1992) among both evolutionarily primitive (mosses) and recent (vascular) C3 plants (Shaw and Renzaglia 2004).

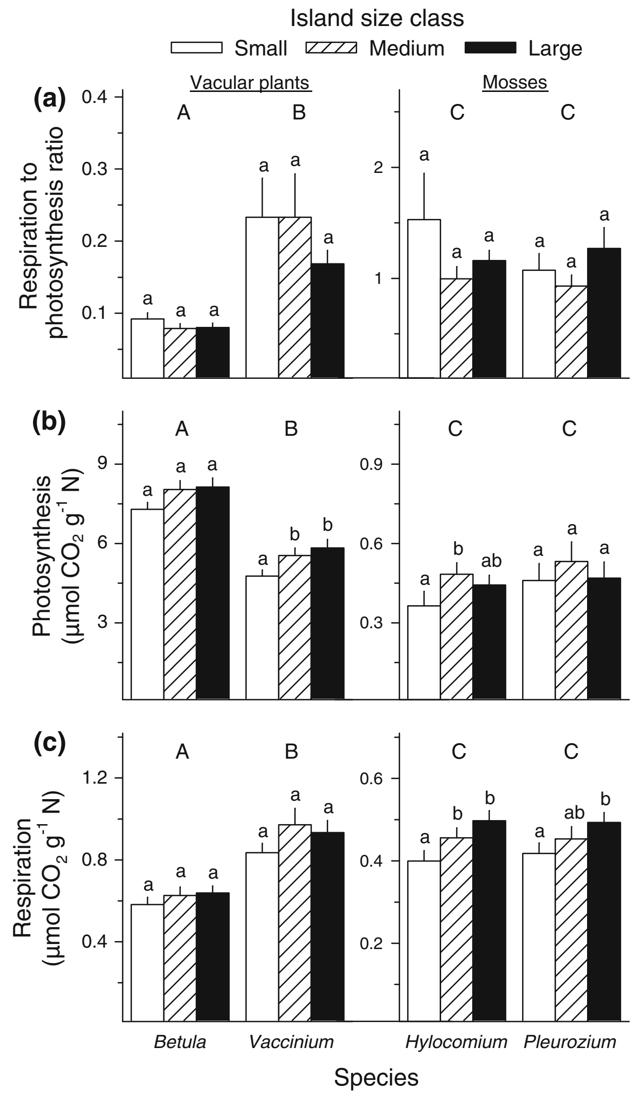

Fig. 3 The effect of island size (*white bars* for small, *hatched bars* for medium, and *black bars* for large islands) on leaf traits associated with carbon and nitrogen use efficiency (mean ± SE; $n = 10$) of two vascular plant species, *Betula* and *Vaccinium*, and two moss species, *Hylocomium* and *Pleurozium*. Traits include (**a**) the ratio of respiration to photosynthesis, (**b**) photosynthesis per unit foliar N, A_N and (**c**) respiration per unit foliar N, R_N. *Scales* are different for vascular plants and mosses because of the large differences between them. Within each group of three *bars*, different *lower case letters* indicate significant differences between island size classes, and within each *panel*, different *upper case letters* indicate significant overall differences between the four species following ANOVA (ANOVA results in Table 2)

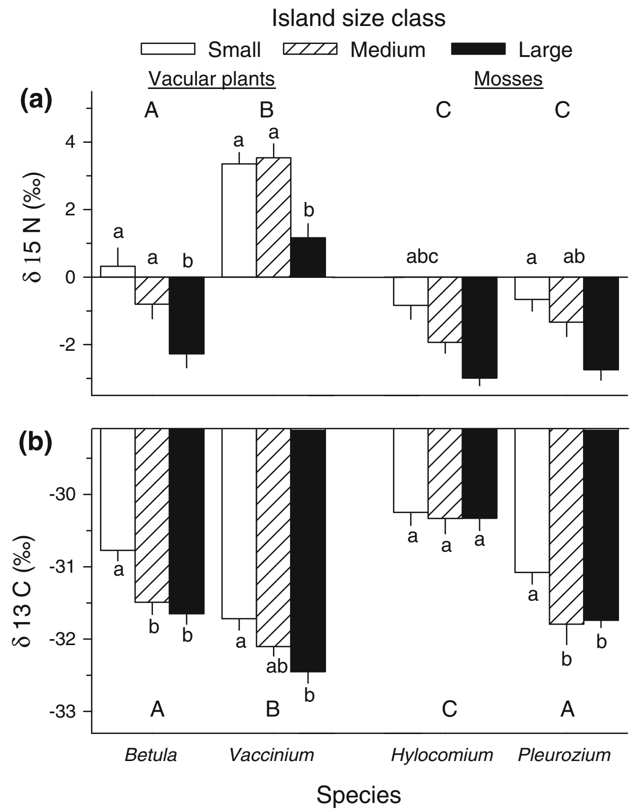

Fig. 4 The effect of island size (*white bars* for small, *hatched bars* for medium, and *black bars* for large islands) on **a** δ^{15}N and **b** δ^{13}C (mean ± SE; $n = 10$) of two vascular plant species, *Betula* and *Vaccinium*, and two moss species, *Hylocomium* and *Pleurozium*. Within each group of three *bars*, different *lower case letters* indicate significant differences between island size classes, and within each *panel*, different *upper case letters* indicate significant overall differences between the four species following ANOVA (ANOVA results in Table 2)

Despite occupying the same habitat, the four species that we considered represented a wide range of returns on investment of C and nutrients into leaves, from rapid (*Betula*) to very slow (*Hylocomium* and *Pleurozium*). As such, values for A of mosses were comparable with the lowest that were summarized by Wright et al. (2004) from >2,500 vascular plant species while values of *Betula* were within the upper 50%. This is consistent with recent suggestions that plant traits may show almost as much variation across species within a single plant community as they do globally (Richardson et al. 2008). Within individual species, changes in leaf traits in response to retrogression were much smaller compared to across species, indicating that inter-specific compared to intra-specific variation was a relatively more important driver of ecosystem properties.

Our findings can help us predict plant ecophysiological responses to the alteration of fire regimes in boreal ecosystems, which in turn may impact ecosystem C balance and sequestration. Boreal forests in northern Europe naturally burn every 50–100 years (Zackrisson 1977), but have been subjected to substantial fire suppression over the past two centuries, and therefore more often reach later stages of succession. There have been few studies on the effects of fire on photosynthetic C gain and only on the short-term responses to fire; these studies have primarily demonstrated positive responses to fire (Fleck et al. 1995; Kruger and

Table 3 Pearson's correlation coefficients between measures of soil fertility and light transmission of the islands and response variables for each species, for $n = 30$ islands

	Humus depth	Soil P (total)	Soil N:P	Light transmission
Betula				
A_{area}	0.115	0.057	−0.047	0.204
A_N	**−0.442***	−0.254	−0.147	−0.319
R_N	−0.254	−0.167	0.024	−0.190
N_{mass}	−0.079	0.323	0.223	**−0.377***
$\delta^{13}C$	**0.643*****	**0.573*****	0.161	**0.407***
$\delta^{15}N$	**0.651*****	**0.438***	0.234	0.172
Vaccinium				
A_{area}	−0.047	−0.088	0.143	0.046
A_N	**−0.450***	−0.305	0.034	−0.290
R_N	−0.052	−0.048	−0.241	−0.296
N_{mass}	**0.510****	**0.595*****	**0.457***	0.008
$\delta^{13}C$	0.343	**0.429***	0.090	0.126
$\delta^{15}N$	**0.518****	**0.472****	0.203	−0.158
Hylocomium				
A_{area}	−0.015	0.191	−0.253	**−0.387***
A_N	−0.355	−0.093	**−0.520****	−0.318
R_N	**−0.594*****	**−0.513****	**−0.488****	−0.092
N_{mass}	**0.532****	**0.545****	0.333	−0.167
$\delta^{13}C$	−0.005	0.054	0.072	0.142
$\delta^{15}N$	**0.728*****	**0.689*****	**0.421***	0.033
Pleurozium				
A_{area}	0.008	0.174	−0.211	−0.183
A_N	−0.122	0.003	**−0.359***	−0.072
R_N	**−0.402***	−0.284	−0.327	−0.033
N_{mass}	**0.477****	**0.453***	0.264	−0.089
$\delta^{13}C$	**0.565****	0.169	0.160	**0.411***
$\delta^{15}N$	**0.615*****	**0.592*****	**0.387***	0.003

Light transmission the % of light transmitted to the forest floor (data from Wardle et al. 2003); A_{area} gross photosynthesis per unit area, A_N photosynthesis per unit foliar nitrogen, R_N respiration per unit foliar nitrogen, N_{mass} foliar nitrogen per unit mass; N:P nitrogen to phosphorus ratio in soil.

Significance of correlation coefficients: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Reich 1997; Gilbert et al. 2003). Our study in contrast considers the long-term consequences of fire absence in boreal forests, and generally shows negative responses of several traits associated with C gain of the major functional groups (including mosses), which could contribute to the lower NPP observed on small islands (Wardle et al. 2003). Nevertheless, belowground microbial activity and decomposition rates decline sooner than does aboveground productivity during the long-term absence of fire, which is likely to lead to an increase in C sequestration (Wardle et al. 2003).

By performing direct comparisons of leaf-level gas exchange, we showed that the four species had relatively similar ecophysiological responses to retrogression. These included relative decreases in A_N, R_N, and SLA, and increases in foliar N, $\delta^{13}C$, and $\delta^{15}N$, across the gradient. These findings have several implications. First, although the effects of retrogression were relatively modest, the consistent responses of these four species to retrogression could have large influences when up-scaled, particularly because they are amongst the most abundant species within their functional groups both in this system and in the Fennoscandian boreal forest at large. Second, declines in A_N during retrogression suggest that increasing co-limitation by other factors, such as P availability (Vitousek 2004; Peltzer et al. 2010), may regulate photosynthetic C gain in late successional boreal forests. Consequently, even with increasing anthropogenic N deposition and fertilization occurring in many boreal forests, increases in photosynthetic C gain in retrogressive forests would be unlikely without additional changes in other ecosystem properties (e.g., a rejuvenation of soil P supply that occurs with fire). Third, as mosses are nearly ubiquitous in boreal regions, the relative increase in moss biomass and decrease in shrub and tree biomass during retrogression (Wardle et al. 2003; Lagerström et al. 2007) could potentially lead to substantial declines in photosynthetic C gain at the whole ecosystem level. Finally, traits of mosses in our study often responded equally or more strongly to the retrogressive gradient than did vascular plant traits, regardless of mosses being able to access N more easily from non-soil sources such as from atmospheric deposition and biological N fixation (Bates

1992; DeLuca et al. 2002). The ecological importance of mosses is attracting increasing recent recognition due to their interactions with vascular plants (Zackrisson et al. 1997) and their overall contribution to forest floor gas exchange (Kolari et al. 2006). We show through the simultaneous consideration of several moss traits that moss ecophysiology shows clear responses to environmental gradients, and anticipate that these responses may in turn regulate their contribution to community- and ecosystem-level processes in boreal forests.

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