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Patterns of bryophyte succession in a 160-year chronosequence in deciduous and coniferous forests of boreal Alaska

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Abstract: Bryophytes are dominant components of boreal forest understories and play a large role in regulating soil microclimate and nutrient cycling. Therefore, shifts in bryophyte communities have the potential to affect boreal forests' ecosystem processes. We investigated how bryophyte communities varied in 83 forest stands in interior Alaska that ranged in age (since fire) from 8 to 163 years and had canopies dominated by deciduous broadleaf (*Populus tremuloides* Michx. or *Betula neoalaskana* Sarg.) or coniferous trees (*Picea mariana* Mill B.S.P.). In each stand, we measured bryophyte community composition, along with environmental variables (e.g., organic layer depth, leaf litter cover, moisture). Bryophyte communities were initially similar in deciduous vs. coniferous forests but diverged in older stands in association with changes in organic layer depth and leaf litter cover. Our data suggest two tipping points in bryophyte succession: one at the disappearance of early colonizing taxa 20 years after fire and another at 40 years after fire, which corresponds to canopy closure and differential leaf litter inputs in mature deciduous and coniferous canopies. Our results enhance understanding of the processes that shape compositional patterns and ecosystem services of bryophytes in relation to stand age, canopy composition, and changing disturbances such as fire that may trigger changes in canopy composition.

Key words: boreal forest, succession, moss, chronosequence, leaf litter, canopy effects, fire, bryophyte.

Résumé : Les bryophytes sont des éléments dominants du sous-bois de la forêt boréale et jouent un grand rôle dans la régulation du recyclage des nutriments et du microclimat dans le sol. Par conséquent, les changements dans les communautés de bryophytes peuvent avoir un impact sur les processus de l'écosystème de la forêt boréale. Nous avons étudié de quelle façon les communautés de bryophytes variaient dans 83 peuplements forestiers de l'intérieur de l'Alaska, dont l'âge (depuis un feu) allait de 8 à 163 ans et dont le couvert était dominé par des feuillus (*Populus tremuloides* Michx. ou *Betula neoalaskana* Sarg.) ou des conifères (*Picea mariana* Mill B.S.P.). Dans chaque peuplement, nous avons mesuré la composition des communautés de bryophytes, ainsi que des variables environnementales (p. ex., la profondeur de l'horizon organique, la couverture de la litière de feuilles, l'humidité). Les communautés de bryophytes étaient initialement semblables dans les forêts de feuillus et de conifères mais divergeaient dans les peuplements plus vieux en lien avec la profondeur de l'horizon organique et la couverture de litière de feuilles. Nos données indiquent qu'il y a deux points de bascule dans la succession des bryophytes : un lors de la disparition des taxons pionniers 20 ans après un feu et l'autre 40 ans après un feu, moment qui correspond à la fermeture du couvert forestier et à l'apport différent de litière de feuilles dans les couverts matures de feuillus et de conifères. Nos résultats améliorent la compréhension des processus qui déterminent les patrons de composition et les services de l'écosystème des bryophytes en relation avec l'âge du peuplement, la composition du couvert forestier et les différentes perturbations, telles que le feu, qui peuvent déclencher des changements dans la composition du couvert forestier. [Traduit par la Rédaction]

Mots-clés : forêt boréale, succession, mousse, chronoséquence, litière de feuilles, effets du couvert forestier, feu, bryophyte.

Introduction

In high-latitude ecosystems such as boreal forests, bryophytes (mosses, liverworts, and hornworts) are dominant and ubiquitous components of the understory and account for a significant proportion of plant diversity (Turetsky et al. 2012). Boreal ecosystems are also characterized by large stand-replacing fires, which trigger successional changes in bryophyte communities. General patterns of postfire bryophyte regeneration have been investigated in coniferous stands (Foster 1985; Turetsky et al. 2010; Fenton and Bergeron 2013) in which colonization, competition (Rydin 1997), and facilitation (Fenton and Bergeron 2006) are known to be important in shaping bryophyte succession. However, the boreal forest is a mosaic also composed of mixedwood and deciduous stands in which bryophytes are less abundant and bryophyte succession is poorly documented (Hart and Chen 2006). Bryophyte roles have often been overlooked in ecosystem studies, even though they can account for a surprisingly large portion of net aboveground primary production and influence regulation of soil microclimate, permafrost stability, nutrient cycling, and ground fuel loads (Turetsky et al. 2012). Knowledge of where, when, and why bryophyte communities change throughout succession is an important gap in our understanding of boreal ecosystem functioning.

Canopy composition in boreal forests is one of the major factors influencing understory communities, including bryophytes (De Grandpré et al. 1993; Hart and Chen 2006). Thus, factors that drive changes in canopy composition will likely cause concomitant changes in

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bryophyte communities. Changes in the fire regime associated with recent climate warming in Alaska and northwestern Canada are predicted to have dramatic impacts on succession, composition, and structure of boreal forest ecosystems (Johnstone et al. 2010*a*, 2010*b*). For example, increases in fire severity that more fully combust bryophyte and organic soil layers have caused recruitment of canopy species to shift from dominant conifer species such as black spruce (*Picea mariana* Mill B.S.P.) to alternate deciduous species such as Alaska paper birch (*Betula neoalaskana* Sarg.) and trembling aspen (*Populus tremuloides* Michx.) (Johnstone et al. 2010*b*). Shifts from conifer to deciduous dominance may affect bryophyte communities because the high inputs of leaf litter and warm, dry soils characteristic of deciduous forests are hypothesized to reduce bryophyte abundance (Van Cleve and Viereck 1981; Hart and Chen 2006). Changing bryophyte communities as a consequence of shifting forest dominance could affect key processes such as nutrient cycling, soil temperature, and vascular plant recruitment (Hart and Chen 2006).

In this context, understanding bryophyte succession under alternate pathways of canopy succession in boreal forests will provide insight into possible driving mechanisms of the different patterns of composition and ecosystem function found in mature deciduous and coniferous forests (Van Cleve and Viereck 1981; Johnstone et al. 2010*a*). Currently, it remains unclear whether contrasting bryophyte communities in mature stands develop from diverging or completely distinct successional trajectories in deciduous and coniferous stand types. Distinct successional trajectories could be caused by initial differences that persist through time such as legacies from fire severity, colonization, or site-specific characteristics (Foster 1985; Hart and Chen 2006; Turetsky et al. 2012). Diverging successional trajectories of bryophytes in which community composition is similar early in succession but forms distinct bryophyte associations as stand age may be caused by canopy-driven changes in processes such as light transmission, evapotranspiration, throughfall, or litter production (Van Cleve and Viereck 1981).

The purpose of this study was to examine patterns of postfire bryophyte succession in boreal forests dominated by coniferous or deciduous trees. We explicitly tested competing hypotheses of distinct or diverging trajectories of succession by testing for differences in bryophyte abundance and species assemblages among forest canopy types in different successional stages. We gathered data on bryophyte communities from stands in interior Alaska that shared similar environmental conditions and prefire history but ranged in postfire age from 8 to 163 years. We predicted that bryophyte cover and species assemblages would vary with stand age and forest canopy type, but if bryophyte succession followed "distinct" patterns among canopy types, these differences would appear early in succession, whereas "divergent" succession processes would lead to differences in bryophyte cover and composition appearing among canopy types only later in succession. By investigating how patterns of bryophyte abundance change at different time points during succession and looking for overlap or differences both in cover and species composition, we can differentiate between the two types of succession. We used information on stand ages to identify time periods when divergence occurs, if present, and investigated associations of environmental covariates with changes in bryophyte communities to develop hypotheses of important factors shaping patterns of bryophyte succession in deciduous and coniferous forest stands. Results of this study provide insights into the processes that drive bryophyte community assembly in boreal forests, which is critical in understanding the role of bryophytes in boreal forests in the context of global change.

Methods

Study area

Bordered to the north by the Brooks Range (~67°N) and to the south by the Alaska Range (~63°N), interior Alaska is characterized by isolated mountain ranges, gently sloping uplands, flat lowlands, and large floodplains around the Yukon, Tanana, and Kuskokwim rivers. Interior Alaska has an extreme temperature range, with temperatures ranging between −70 °C and 35 °C, a mean annual air temperature of −2.5 °C, and a growing season that lasts about 135 days. Approximately 35% of the annual 286 mm of precipitation falls as snow (Hinzman et al. 2005). Interior Alaska is within the discontinuous permafrost zone, and about 75%–80% of the ground is underlaid by permafrost (Osterkamp and Romanovsky 1999).

Forests in the uplands of interior Alaska are typically dominated by one of three tree species: black spruce, trembling aspen, and Alaska paper birch. Black spruce stands are the most common forest type in interior Alaska, accounting for an estimated 39% of the forested landscape (Calef et al. 2005), and are mostly found on wet and cold north-facing slopes with permafrost (Van Cleve et al. 1983*a*; Yarie and Billings 2002). In black spruce stands, the forest floor is usually covered by extensive bryophyte carpets composed of pleurocarpous (feather) mosses such as *Hylocomium splendens* (Hewd) Schimp., *Pleurozium schreberi* (Brid.) Mitt., and *Ptilium crista-castrensis* (Hewd.) De Not or by *Sphagnum* spp. (Van Cleve et al. 1983*a*). Deciduous-dominated stands are estimated to occupy about 24% of interior Alaska, while the remainder of the landscape is principally tundra (27%) or forested by white spruce (*Picea glauca* (Moench) Voss; 10%) (Calef et al. 2005). Aspen stands occupy well-drained south-facing slopes with deep active layers, while birch stands, also found in deep active layer sites, are more common on colder and wetter east- and west-facing slopes (Chapin et al. 2006*b*). Only about 6% of interior Alaska's boreal forest is composed of mixed stands with both coniferous and deciduous species sharing canopy dominance (Yarie and Billings 2002). While these different forest types vary in their preferred habitat, there is a considerable amount of overlap in their ecological tolerances (Chapin et al. 2006*b*), allowing for changes canopy composition triggered by disturbance such as fire or dispersal events (Johnstone et al. 2010*a*, 2010*b*).

Differences in fire severity in black spruce stands can lead to the establishment of black spruce, trembling aspen, or Alaska paper birch postfire stands (Johnstone et al. 2010*a*, 2010*b*), thus creating three distinct successional pathways based on canopy dominance. In the boreal forests of western North American, most seedlings establish within a few years after fire and they are strong predictors of the mature canopy composition of the forest (Johnstone et al. 2004); thus canopy dominance appears to be principally determined by initial patterns of direct regeneration (e.g., Ilisson and Chen 2009). Moreover, with a fire interval of about 100 years, succession from a deciduous stand to a coniferous stand via relay dominance is rarely completed (Yarie 1981). We checked our assumption of direct regeneration vs. relay dominance by surveying woody debris in all stands and found no evidence of deciduous trees being replaced by later establishment of conifers. We therefore assume that stand age and forest composition do not co-vary within the range of ages that we surveyed.

We used a chronosequence or space-for-time substitution approach to examine postfire bryophyte succession. This type of study assumes that climate, regional pool of organisms, topography, and parent material are held constant across sites and only time after disturbance varies (Walker et al. 2010). All of the stands sampled here had originated from a fire in stands that formerly contained at least some black spruce, confirmed by evidence of dead and charred black spruce trees (Alexander et al. 2012). At the time of sampling, these stands were dominated by black spruce, Alaska paper birch, or trembling aspen. To limit other confounding

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Table 1. Number of sites sampled and average site characteristics (with standard errors) according to estimated time since fire (years) and forest canopy type.

	Early succession (8–19 years)			Mid-succession (20–59 years)			Late succession (60–163 years)		
	Black spruce	Alaska paper birch	Trembling aspen	Black spruce	Alaska paper birch	Trembling aspen	Black spruce	Alaska paper birch	Trembling aspen
Number of sites	7	9	13	21	7	14	5	4	3
Bryophyte cover (%)[a]	69.5be (12.2)	71.3de (16.1)	66.3be (15.1)	52.7bcd (19.6)	33.9ac (26.3)	23.5a (15.5)	87.7e (15.3)	8.6a (10.4)	31.7ab (13.6)
Leaf litter cover (%)	68.3 (4.2)	62.6 (11.3)	74.8 (8.5)	50.9 (17.7)	73.6 (20.3)	75.1 (19.8)	33.8 (13.2)	94.8 (2.5)	88.0 (3.7)
Organic layer (cm)	9.7 (3.5)	9.9 (2.0)	7.6 (3.8)	10.1 (5.1)	8.0 (4.1)	4.9 (2.2)	24.7 (4.3)	8.9 (4.4)	3.8 (1.2)
Spruce basal area ($cm^2 \cdot m^{-2}$)	1.5 (2.0)	0.4 (0.3)	1.1 (1.2)	6.5 (4.5)	2.6 (3.7)	1.4 (1.1)	15.0 (8.2)	2.3 (3.2)	0.2 (0.1)
Birch basal area ($cm^2 \cdot m^{-2}$)	0.2 (0.2)	3.7 (4.1)	0.3 (0.6)	1.0 (1.8)	14.0 (12.6)	0.3 (0.7)	0.4 (0.5)	26.9 (11.5)	2.4 (4.1)
Aspen basal area ($cm^2 \cdot m^{-2}$)	0.1 (0.1)	0.4 (0.8)	1.9 (2.4)	0.7 (1.5)	0.1 (0.1)	8.8 (5.2)	0.0 (0.0)	1.3 (2.7)	31.0 (3.1)
Shrubs basal area ($cm^2 \cdot m^{-2}$)[b]	2.9 (2.4)	1.9 (1.7)	3.7 (3.4)	3.0 (3.4)	1.8 (2.2)	1.8 (2.6)	0.5 (0.5)	3.4 (3.0)	0.9 (1.0)

[a] Averages that do not share a letter are significantly different based on a Tukey HSD post-hoc test ($p < 0.05$).

[b] Shrubs includes large deciduous shrubs, i.e. *Alnus* spp., *Salix* spp., and *Betula* spp.

factors, we focused our sampling on north-, east-, and west-facing (or relatively flat) mesic black spruce, Alaska paper birch, and aspen stands and measured a number of environmental covariates, including a soil description. Southeast-facing slopes and poorly drained black spruce stands were avoided as they are usually not dominated by black spruce or have a longer fire cycle, respectively.

Sampling design

We surveyed a total of 83 stands ranging in age from 8 to 163 years in upland boreal forests in interior Alaska between 2008 and 2015. The stands were stratified by time since fire and forest type; stands burned within the fire history record (>1945) were located within 32 different areas burned by a single fire event and mature forests were sampled in surrounding areas that had not burned since 1945 (Table 1; Supplementary Table S1[1]). Burned areas were mapped by the Alaska Fire Service, and their locations were acquired from the Alaska Geospatial Data Clearinghouse (U.S. Department of the Interior Bureau of Land Management 2012). Where possible, we selected at least one pure black spruce stand and one pure deciduous stand in each burned area (Supplementary Table S1[1]). To minimize travel time between sites, all sites were located >100 and <600 m from a road. We conducted extensive sampling within a successional stage for each forest type to enable robust inferences from our chronosequence design (Walker et al. 2010). Our study included 29 stands from early successional forests (8–19 years since fire), 45 stands in mid-successional forests (20–59 years since fire, as per Alexander et al. (2012)), and nine stands in late successional forests (60–163 years since fire). Early successional forests were sampled in 2013–2014 using the same design as that used in the sampling of mid- to late successional forests in 2008–2009 (Alexander et al. 2012).

Environmental variables and bryophyte identification

In each stand, we positioned a 100 m long transect perpendicular to the slope or used a random compass bearing if the ground was flat. The methods used to measure stand structure are presented in more detail in Alexander et al. (2012). Basal diameter (BD) and diameter at breast height (DBH) of all living and dead trees and large shrubs were recorded within 1 m on each side of the transect over a 10 m section for every 20 m subsection. In some instances, this area was reduced to allow measurements of very dense early successional stands. In stands >20 years old, we collected a core or a basal disk from 10 trees of the dominant canopy species to confirm the stand age obtained from fire history maps. Allometric equations from Alexander et al. (2012) and Berner et al. (2015) were used to estimate aboveground biomass of individual trees and tall shrubs (*Salix* spp., *Betula* spp., and *Alnus* spp.). All stands were attributed to a forest type (black spruce, Alaska paper birch, or aspen) based on the tree species with the largest contribution to total woody biomass (Table 1; Supplementary Table S1[1]). A deciduous importance value (DecIV) index was calculated based on the contribution of deciduous trees to total stand aboveground biomass (for calculations, see Alexander et al. 2012). Organic layer thickness (fibric and humic layers), mineral soil texture (only in stands sampled in 2013–2014), and pH were measured every 10 m along the transect. Soil moisture was measured using a ECH2O EC-TM soil moisture probe read by an Em50 data logger (Decagon Devices Inc., Pullman, Washington, U.S.A.) next to the soil sampling core in all the stands sampled by Alexander et al. (2012). Soil moisture was not measured in the early successional stands in 2013 and 2014, but a general drainage class was recorded for each stand (Johnstone et al. 2008). A drainage class was estimated for older stands using topography and soil moisture data. Finally, we recorded slope, aspect, and GPS coordinates of each transect and calculated a heat load index (McCune and Keon 2002).

We used a 50 × 50 cm grid with 25 equally spaced sampling points to survey the understory plant species composition by point-intercept sampling. All vascular and nonvascular species, as well as bare ground and dead organic material (wood and leaf litter), that touched a pin inserted at each sampling point were recorded. The grid was placed perpendicular to, and 1 m from, the transect every 20 m (five replicates). Cover (%) of bare ground, coarse woody debris, leaf litter, total vascular plants, and lichen were calculated and used as environmental covariates.

We did not sample bryophytes that grew on live or dead wood and focused instead on the dominant forest floor taxa. The point-intercept sampling method presents accurate estimation of the abundance of common species but may not allow for the recording of uncommon or rare species (Mamet et al. 2016; Vanderpoorten et al. 2010). Given that our main interest was linked to understanding how bryophytes affect ecosystem processes, the most important information from community composition would come from common species, and we felt confident that missing rare bryophyte species was not a problem in that regard. Samples of all encountered unknown species were collected for identification in the lab. Bryophyte nomenclature followed Anderson et al. (1990). We identified a total of 106 species in our samples: 67 vascular plants, 10 lichens, and 29 bryophytes (Table 2). Within the bryophytes, we recorded taxa from 10 families of true mosses, three families of liverworts, and one *Sphagnum* family. We could identify 20 true mosses to the species level and six species could only be identified to the genus level. Some unknown bryophytes could not be identified because of the small size or poor quality of the samples. Because of the limited taxonomic resolution, we use the

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[1] Supplementary Tables S1–S4 are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2017-0013.

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Table 2. Bryophyte taxa list, taxa code for the ordinations, functional type, and average percent cover in the forest types and successional stages.

				Successional stage								
				Early (0–20 years)			Mid- (20–62 years)			Late (63 years+)		
Order	Family	Taxa name	Functional type	PM	BN	PT	PM	BN	PT	PM	BN	PT
Bryales	Aulacomniaceae	*Aulacomnium palustre* (Hedw.) Schwägr.	Acrocarpous mosses	10.3	3.1	1.7	10.8	0.9	0.5	10.6	0.0	0.0
		Aulacomnium turgidum (Wahlenb.) Schwägr.		1.7	0.1	0.4	0.0	0.0	0.0	0.0	0.0	0.0
	Bryaceae	*Bryum* spp.	Colonizer	3.2	2.7	0.1	0.0	0.0	0.1	0.0	0.0	0.0
		Leptobryum pyriforme (Hedw.) Wilson		2.6	2.4	0.1	0.0	0.0	0.0	0.3	0.0	0.0
		Pohlia sp.		0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0
		Ceratodon purpureus (Hedw.) Brid.		34.7	32.5	41.2	0.7	0.0	2.3	0.0	0.0	0.0
Dicranales	Dicranaceae	*Dicranum* spp.	Acrocarpous mosses	0.5	0.1	0.0	0.3	1.4	0.3	0.2	3.5	0.3
		Dicranum sp.		0.0	0.0	0.0	1.4	0.3	0.3	3.5	0.2	0.3
		Dicranum undulatum Schrad. ex Brid.		7.0	9.0	13.0	21.0	7.0	14.0	5.0	4.0	3.0
Hypnales	Amblystegiaceae	*Sanionia uncinata* (Hedw.) Loeske	Pleurocarpous mosses	0.2	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
	Brachytheciaceae	*Tomentypnum nitens* (Hedw.) Loeske		0.0	0.0	0.0	1.1	0.0	0.0	1.0	0.0	0.0
	Hylocomiaceae	*Hylocomium splendens* (Hedw.) Schimp.		0.0	0.0	0.1	5.7	6.3	1.6	42.7	4.6	24.3
		Pleurozium schreberi (Brid.) Mitt.		2.2	1.6	0.2	14.2	18.6	1.8	24.5	0.2	1.1
	Hypnaceae	*Hypnum* spp.		0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
		Hypnum cupressiforme Hedw.		0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		Hypnum plicatulum (Lindb.) A. Jaeger		0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
		Hypnum revolutum (Mitt.) Lindb.		0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
	Rhytidiaceae	*Rhytidium rugosum* (Hedw.) Kindb.		0.0	0.0	0.1	0.2	0.0	2.1	0.0	0.0	0.0
	—	Hypnales		0.3	0.1	0.1	0.04	0.3	0.0	0.0	0.0	0.0
	Amblystegiaceae	*Amblystegium* sp.		0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		Drepanocladus sp.		0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Brachytheciaceae	*Brachythecium* sp.		0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
	Thuidiaceae	*Thuidium abietinum* (Hedw.) Schimp.		0.0	0.0	0.0	0.04	0.0	0.0	0.0	0.0	0.0
	Hypnaceae	*Ptilium crista-castrensis* (Hedw.) De Not.		0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
Polytrichales	Polytrichaceae	*Polytrichum commune* Hedw.	Colonizer	14.3	19.5	6.1	16.1	12.1	14.3	7.0	0.0	0.0
		Polytrichum juniperinum Hedw.		13.7	10.9	29.8	0.00	0.0	0.0	0.0	0.0	0.0
		Polytrichum piliferum Hedw.		0.0	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		Polytrichum strictum Menzies ex Brid.		0.2	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Jungermanniales	—	Jungermaniales	Liverwort	1.3	0.5	0.2	0.0	0.0	0.0	2.4	0.0	0.0
	Myliaceae	*Mylia* sp.		0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0
	Jungermanniaceae	*Lophozia ventricosa* (Dicks.) Dumort. cf.		1.3	0.5	0.2	0.0	0.0	0.0	1.0	0.0	0.0
	—	Unknown liverworts		0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Marchantiales	Marchantiaceae	*Marchantia polymorpha* L.		3.9	9.5	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Sphagnales	Sphagnaceae	*Sphagnum* spp.	*Sphagnum*	1.4	0.6	1.4	6.6	1.5	0.0	29.4	0.0	1.4
—	—	Unknown moss 1	Unknown mosses	0.0	0.0	0.0	0.1	0.2	0.1	0.0	0.0	0.0
—	—	Unknown moss 2		0.0	0.0	0.0	0.0	0.0	1.2	1.2	1.3	3.2
—	—	Unknown moss 3		0.0	0.0	0.0	3.1	4.0	0.8	3.0	0.6	4.8
—	—	Unknown moss 4		0.0	0.0	0.0	0.8	3.1	0.0	0.0	0.0	0.0

Note: Stands types: PM, *Picea mariana*; BN, *Betula neoalaskana*; PT; *Populus tremuloides*.

term "bryophyte taxa" here rather than species. Bryophyte taxa were further classified in functional groups of colonizers, pleurocarpous mosses (feather mosses), acrocarpous mosses, liverworts, and *Sphagnum* spp. (Table 2). Bryophyte cover was summarized in three forms: total bryophyte cover, cover by functional types, and cover of individual taxa. We resampled understory taxa composition in five stands of varied canopy dominance surveyed by Alexander et al. (2012) in 2015 to make sure that there was no significant observer bias in taxa identification and detection.

Analyses of bryophyte abundance

All of our analyses were conducted in R 3.1.2 (R Core Team 2016) using the package vegan (Oksanen et al. 2016). We were interested in testing whether patterns of bryophyte succession in different forest successional trajectories were similar when considering (*i*) total bryophyte cover, (*ii*) functional group cover, and (*iii*) taxa composition. Using different levels of precision allowed us to make stronger inferences about the successional patterns observed (Walker et al. 2010). We did not include burn area or spatial region as a random effect in our analyses because spatial arrangement was partially confounded with age (sampling within discrete burned areas) and we expected age effects to supersede spatial effects on bryophyte communities. Patterns of total bryophyte, functional group, and individual taxa cover were compared among forest types (black spruce, birch, and aspen) and successional stages (early, mid-, and late succession).

Total bryophyte cover, as well as the three main functional types (colonizers, pleurocarpous mosses, and acrocarpous mosses) were analyzed using a two-way ANOVA (stand type and successional stage) with a type III sum of squares for unbalanced data and followed by a Tukey honest significance difference (HSD) post-hoc test. We assessed differences in bryophyte cover among the three canopy types within each successional stage based on whether 95% confidence intervals were overlapping. Data for functional groups and taxa cover did not meet ANOVA assump-

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tions because of the large number of zero values, so permutation ANOVAs were used (4999 permutations; Anderson and Legendre 1999).

We used a PerMANOVA (multivariate analysis of variance (ANOVA) by permutations using a distance-based RDA) adapted for an unbalanced design with 4999 permutations to compare taxa assemblages among forest types and successional stages to patterns observed under random sorting (Anderson and Legendre 1999). The Bray–Curtis distance was used on taxa composition data as it is an ecologically appropriate distance measure (Anderson and Legendre 1999). Multivariate dispersion differed between the different successional stages but not among forest types. This is a well-recognized issue with multivariate analyses, which can lead to confusion between within-group variation (dispersion) and mean values of the groups. PerMANOVA is thought to be less sensitive to this issue than some of its alternatives (ANOSIM or MRPP) (Anderson 2001). When a significant interaction was found, we conducted a series of one-way PerMANOVAs within each age category, followed by a Tukey HSD post-hoc test.

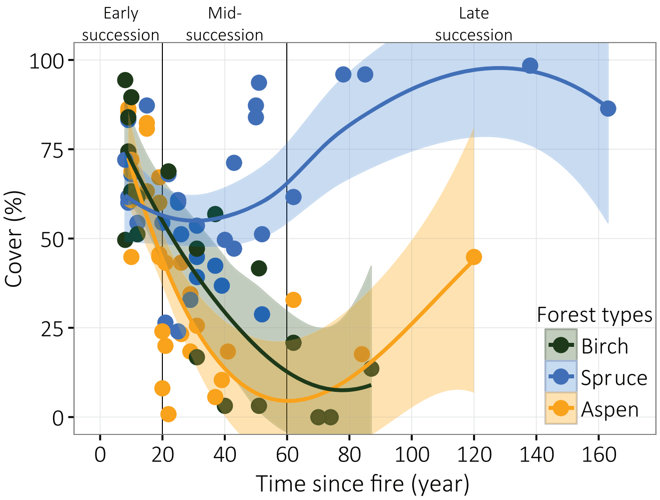
To support the PerMANOVAs conducted on taxa composition data, we conducted a visual analysis of taxa composition using a nonmetric multidimensional scaling (NMDS) ordination that was conducted on taxa data from the 83 stands using the Bray–Curtis distance (McCune et al. 2002). The best solution was selected from 20 independent runs with 200 iterations per run. The number of ordination axes was determined by comparing stress and dimensionality against randomized outcomes (McCune et al. 2002). This analysis was used to detect the main patterns in taxa composition among different forest types and different successional stages.

Analyses of environmental covariates

We used two different approaches to investigate how patterns of bryophyte cover were related to measured environmental covariates: univariate and multivariate regression trees and vector overlay on the NMDS ordination. Analyses were conducted in R (R Core Team 2016) using the packages vegan (Oksanen et al. 2016) and mvpart (Therneau and Atkinson 2013). Ecologically relevant environmental variables (cover of bare ground cover, coarse woody debris, leaf litter, vascular plant, and lichen; DecIV index; basal area of black spruce, birch, aspen, and large shrubs; elevation; heat load index; and moisture class) were selected to minimize collinearity.

Univariate and multivariate regression (MRT) trees were the main tools used to investigate the relationship between bryophyte cover or composition and environmental covariates. Regression trees are nonparametric methods that are robust to issues associated with ecological data such as non-normality and heteroscedasticity and make no assumptions with regards to the form of the relationship between response variables and explanatory covariates (De'ath and Fabricius 2000). MRTs partition the dataset recursively into subsets to minimize within-group heterogeneity, providing a clustering-like result and a dichotomous classification key (McCune et al. 2002). Multivariate responses of functional groups (six groups) and taxa cover (25 taxa) were transformed using the Bray–Curtis distance (83 stands) prior to analysis. No transformations were applied to environmental covariates. We excluded stand age and categories of forest type from these analyses to focus on how changes over time in environmental covariates and continuous variables of forest composition were related to bryophytes. This approach allowed us to include information about the co-occurring tree species in the stands and interpret the potential effects of gradients in canopy composition rather than simple canopy dominance. MRT results are described both by their fit, or percent variation explained, which is calculated as the inverse of the relative error (RE), and their predictive accuracy estimated by the cross-validated error (CVRE). This number estimates the probability of misclassifying a new sample and varies from 0 (good predictor) to 1 (poor predictor) (De'ath and Fabricius 2000). To compare variations in leaf litter cover according to forest types and successional stage, we conducted a two-way ANOVA followed by a Tukey HSD post-hoc test.

Fig. 1. Variations in total bryophyte cover (%) versus time after fire in forest stands dominated by black spruce, Alaska paper birch, or trembling aspen. Points represent percent cover for each of the 83 sampled stands, fitted with LOESS (locally weighted scatterplot smoothing) curves with a smoothing parameter of 1 for each series of points. Shadings represent the 95% confidence interval. [Colour online.]



We used vector overlays on the NMDS ordination to determine how all covariates were related to bryophyte taxa composition. Pearson correlation coefficients between environmental variables and NMDS scores defined the strength of correlations with ordination axes. Significance of the correlation was determined using 999 permutations.

Results

Part I: temporal changes in bryophyte communities

Total bryophyte cover

Bryophyte cover varied according to forest type and the three postfire successional stages (interaction $F_{[4,74]} = 8.524$, $p < 0.0001$; Fig. 1; Table 1). Bryophyte cover was high in all early successional forest types ($\bar{x} = 69\%$; Fig. 1; Table 1). While total bryophyte cover was reduced to an average of 40% during the mid-successional stage, it was higher in stands dominated by spruce ($\bar{x} = 53\%$) compared with birch or aspen ($\bar{x}$ = 34% and $\bar{x}$ = 23%, respectively; Table 1). Bryophyte cover increased in late succession to an average of 88% in spruce stands, much higher than the cover observed in aspen ($\bar{x} = 32\%$) or birch ($\bar{x} = 9\%$) during late succession (Fig. 1; Table 1). However, it is important to note that the time series for birch was not as long as for the other tree species. Differences in total bryophyte cover among forest types indicate a divergence in bryophyte cover between coniferous (spruce) and deciduous (birch and aspen) forest types between 20 and 40 years after fire (Fig. 1).

Functional groups

Colonizer taxa declined quickly from 8 to 40 years, demonstrating a strong effect of successional stage ($F_{[2,74]} = 91.435$, $p = 0.0002$; Supplementary Table S3a[1]), and followed very similar trends in all forest types (Table 3; Fig. 2). Bryophyte communities in all forest types were dominated by *Ceratodon purpureus* and *Marchantia polymorpha* from 10–20 years after fire and were then dominated by larger acrocarpous taxa such as *Polytrichum commune* and *Polytrichum juniperinum* from 20–40 years after fire (Table 2). Pleurocarpous mosses remained low in deciduous stands throughout

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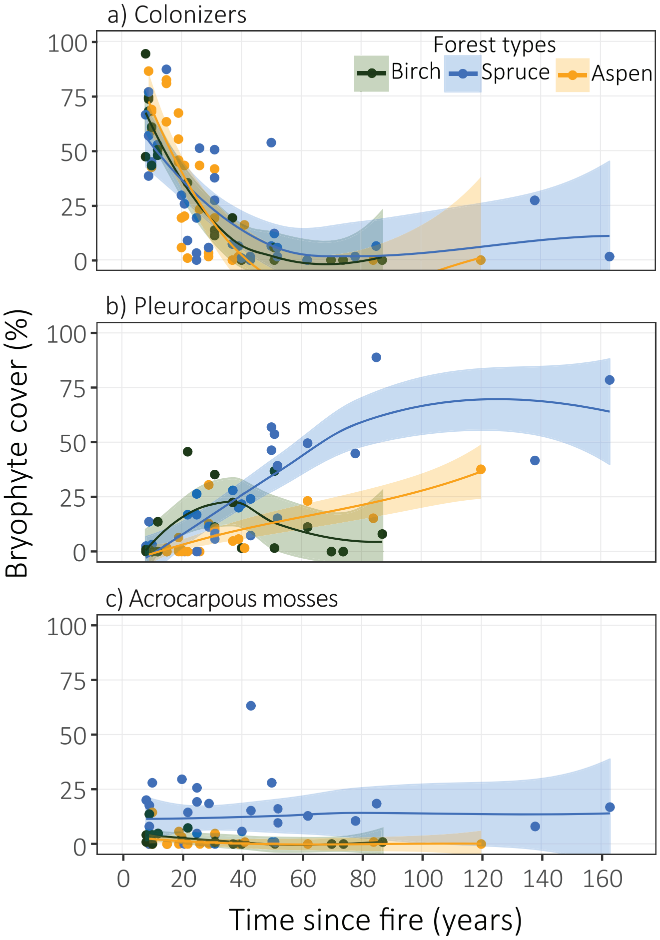
Table 3. Abundance of bryophytes grouped by functional types and compared according to forest type and successional stage.

Functional group	Successional stage	Forest type	*n*	Average cover (%)	Standard error	Tukey results[a]
Colonizer	Early	Spruce	7	60.5	6.6	a
		Birch	9	62.2	5.6	
		Aspen	13	64.7	4.1	
	Mid-	Spruce	21	16.8	4.0	b
		Birch	7	12.1	4.7	
		Aspen	14	17.0	4.3	
	Late	Spruce	5	7.4	5.1	b
		Birch	4	0.0	0.0	
		Aspen	3	0.0	0.0	
Pleurocarpous moss	Early	Spruce	7	2.9	1.9	a
		Birch	9	1.7	1.5	a
		Aspen	13	0.7	0.5	a
	Mid-	Spruce	21	19.4	3.8	a
		Birch	7	22.1	6.7	a
		Aspen	14	5.4	2.3	a
	Late	Spruce	5	60.6	9.6	b
		Birch	4	4.8	2.8	a
		Aspen	3	25.3	6.6	a
Acrocarpous mosses	Early	Spruce	7	11.2	4.1	a
		Birch	9	3.7	1.4	b
		Aspen	13	1.8	1.1	b
	Mid-	Spruce	21	12.2	3.4	a
		Birch	7	1.3	1.0	b
		Aspen	14	0.8	0.4	b
	Late	Spruce	5	13.3	1.9	a
		Birch	4	0.2	0.2	b
		Aspen	3	0.3	0.3	b
Sphagnum	Early	Spruce	7	1.4	0.9	NA
		Birch	9	0.6	0.6	NA
		Aspen	13	1.4	1.2	NA
	Mid-	Spruce	21	6.6	3.4	NA
		Birch	7	1.5	1.4	NA
		Aspen	14	0.0	0.0	NA
	Late	Spruce	5	29.4	16.3	NA
		Birch	4	0.0	0.0	NA
		Aspen	3	0.0	0.0	NA
Liverworts	Early	Spruce	7	5.6	2.8	NA
		Birch	9	10.0	7.1	NA
		Aspen	13	0.2	0.2	NA
	Mid-	Spruce	21	0.0	0.0	NA
		Birch	7	0.0	0.0	NA
		Aspen	14	0.1	0.1	NA
	Late	Spruce	5	2.4	1.5	NA
		Birch	4	0.0	0.0	NA
		Aspen	3	0.0	0.0	NA

[a]Tukey HSD post-hoc tests were conducted after two-way ANOVA by permutation. Relevant ANOVA results are presented in Supplementary Table S3. Different letters indicate a significant difference among forest cover types or successional stages for that functional type ($\alpha = 0.05$). NA, not available.

Fig. 2. Variations in bryophyte cover grouped into functional types of (*a*) colonizers, (*b*) pleurocarpous (feather) mosses, and (*c*) other true mosses, plotted against time since fire (years) in spruce, birch, and aspen stands ($n = 83$). LOESS curves were fit to each series of points with a smoothing parameter of 1. Shadings represent the 95% confidence interval. [Colour online.]



succession but increased in spruce stands to an average of 63% cover in late succession ($F_{[4,74]} = 10.111$, $p < 0.0001$; Table 3; Fig. 2; Supplementary Table S3*b*[1]). Pleurocarpous mosses represented about two-thirds of the total bryophyte cover in mature spruce stands. The feather mosses *Pleurozium schreberi* and *Hylocomium splendens* shared the dominance of the pleurocarpous moss cover in all stands (Table 2). *Pleurozium schreberi* seemed to be slightly more abundant than *H. splendens* until about 100 years since fire in spruce stands (Table 2). The cover of acrocarpous mosses (e.g., *Aulacomnium* spp., *Dicranum* spp.) was higher in spruce stands (about 18%) than in deciduous stands (<7%) ($F_{[2,74]} = 10.460$, $p = 0.0014$; Supplementary Table S3*c*[1]) and remained relatively low in all forest types regardless of stand age (Table 3; Fig. 2*b*). *Sphagnum* spp. cover increased steadily in older spruce stands and was absent from deciduous stands, while liverworts were rare in all forest types at every stage of succession (Table 3).

Taxa composition

Ordination of the bryophyte taxa for all forest types and all ages resulted in a two- dimensional NMDS solution that captured 38% of the variation in the original ranked distance matrix (Fig. 3, stress 0.18). This level of stress indicates that the ordination is able to capture meaningful patterns in the data, with small distortions in the representation (McCune et al. 2002). The two axes from the NMDS represent two main ecological gradients: changes associated with stand age (NMDS 1) and leaf litter cover (NMDS 2; Table 4). There was a significant interaction between forest type and successional stage (interaction $F_{[4,74]} = 2.19$, $p = 0.003$; Supplementary Table S2*a*[1]).

During early succession (5–19 years since fire), taxa composition did not significantly differ among the three forest types ($F_{[2,26]} = 1.89$, $p = 0.057$; Supplementary Table S2*b*[1]). Stands of different types occupied a similar area of the multivariate space in the NMDS ordination (Fig. 3*a*). Composition of nonvascular understory taxa in all forest types was dominated by colonizers such as *M. polymorpha*, *P. juniperinum*, *C. purpureus*, and taxa of the Bryaceae family (including taxa such as *Leptobryum pyriforme*, *Bryum* spp., and *Pohlia* spp.) (Fig. 3*a*).

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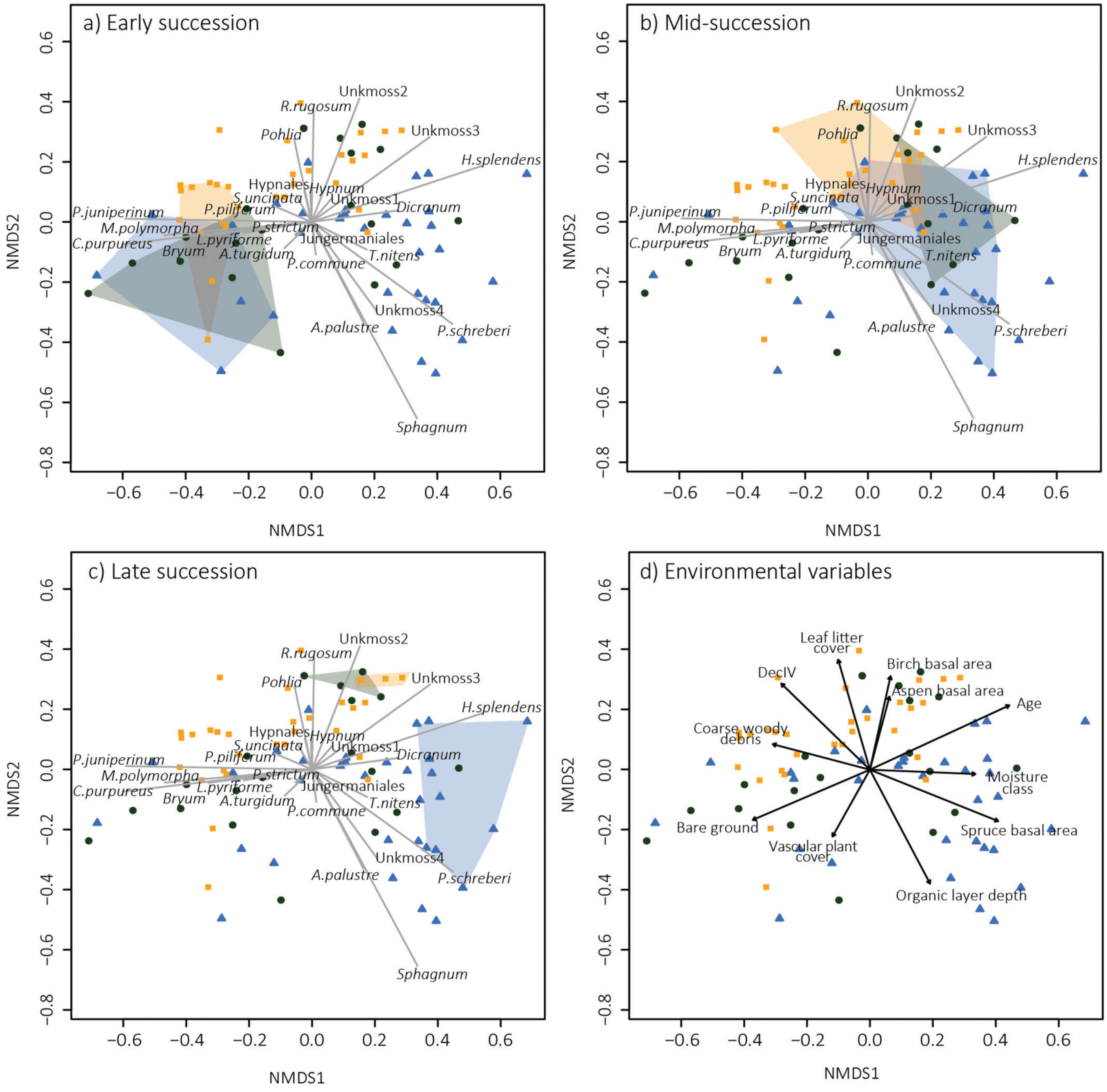
Fig. 3. Distribution of the stands in a two-dimensional NMDS ordination (stress of 0.18, 100 iterations, Bray–Curtis distance) based on bryophyte community composition (83 stands and 25 taxa). The two axes capture 38% of the variation in the original ranked matrix, with axes 1 and 2 capturing 33.1% and 6.5% of the variation, respectively. Individual points represent sample units (stands) grouped by forest type: spruce (blue, triangles), birch (green, circles), and aspen (yellow, squares). All stands are represented on each of the four panels, irrespective of age. Polygons in each panel are drawn to encompass stands representing (*a*) early succession (8–20 years since fire), (*b*) mid-succession (20–60 years since fire), and (*c*) late succession (more than 60 years since fire) (color code same as stands); (*d*) black vectors show correlations with environmental and stand covariates.



During mid-succession (20–60 years since fire), taxa composition started to diverge among forest types ($F_{[2,39]} = 2.848$, $p > 0.001$; Supplementary Table S2*c*[1]). Bryophyte communities in birch and aspen stands only partly overlapped the multivariate space occupied by communities in coniferous spruce stands (Fig. 3*b*). Taxa composition in spruce stands differed from that of aspen stands but was similar to that of birch stands, and there was no difference in taxa composition among the two deciduous forest types (*p* values in Supplementary Table S4*c*[1]). Rare taxa from the Hypnales order such as *Amblystegium* spp., *Drepanocladus* spp., *Brachythecium* spp., and *Ptilium crista-castrensis* dominated the bryophyte layer in deciduous stands (Fig. 3*b*). In spruce stands, feather mosses (*P. schreberi*, *H. splendens*) became dominant, along with *Dicranum* spp. and *Aulacomnium palustre*. Taxa composition in the earliest years of the mid-successional stage overlapped among all forest types.

Bryophyte communities in late succession (≥60 years since fire) were significantly different in taxa composition among forest types

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Table 4. Axis loadings of environmental and stand covariates on the two NMDS axes.

	NMDS 1	NMDS 2	r^2	Pr(>r)[d]
Age (years)[a]	0.9085	0.4180	0.529	0.001*
Bare ground cover (%)	−0.9195	−0.3930	0.364	0.001*
Coarse woody debris cover (%)	−0.9674	0.2533	0.227	0.001*
Leaf litter cover (%)	−0.2781	0.9606	0.293	0.001*
DecIV index[b]	−0.7182	0.6959	0.342	0.001*
Black spruce basal area[c]	0.9286	−0.3711	0.428	0.001*
Aspen basal area[c]	0.2162	0.9763	0.205	0.001*
Organic layer depth (cm)	0.4683	−0.8836	0.371	0.001*
Moisture class (six classes)	0.9992	−0.0407	0.251	0.001*
Vascular plant cover (%)	−0.4895	−0.8720	0.131	0.005*
Birch basal area[c]	0.2595	0.9657	0.128	0.009*
pH	−0.9967	−0.0812	0.054	0.101
Elevation (m)	−0.7995	0.6007	0.032	0.283
Lichen cover (%)	−0.1675	−0.9859	0.024	0.374
Heat load	−0.9970	0.0781	0.017	0.497
Shrub basal area[c]	−0.9999	−0.0125	0.010	0.623

[a] Years since fire (age) based on sampling year minus year burned.

[b] Deciduous importance value (DecIV) index; see Alexander et al. (2012) for calculation.

[c] Total basal area calculated for each taxa group (m² basal area per m² sample area). Tall shrubs included *Betula* spp., *Alnus* spp., and *Salix* spp.

[d] The r^2 values are Pearson correlation coefficients, and significance of the correlations was obtained from 999 permutations. An asterisk (*) indicates significant correlations at $\alpha = 0.05$.

($F_{[2,9]} = 4.429$, $p > 0.001$; Supplementary Table S2*d*[1]). Some bryophyte taxa found in older stands could not be identified, often because the specimens were too small to lead to a conclusive identification, but likely comprised *Brachythecium* spp. and *Hypnum* spp., among others. Bryophyte taxa composition of aspen and birch stands was similar ($p = 0.417$; Supplementary Table S4*d*[1]) but differed from spruce stands ($p = 0.048$ and $p = 0.001$, respectively; Supplementary Table S2*d*[1]). In spruce stands, the feather mosses *H. splendens* and *P. schreberi* remained dominant components of the bryophyte carpet, and *Sphagnum* spp. cover increased.

Part II: environmental covariates related to bryophyte divergence

Total bryophyte cover

In the regression tree analysis, leaf litter was the best predictor of total bryophyte cover, with 76% cover identified as a threshold value (Fig. 4). This threshold value was reached at about 20 years in aspen stands and at 40 years in birch stands, and only a few very young spruce stands presented such a high leaf litter cover, probably derived from the high cover of deciduous shrubs in those stands. When leaf litter cover was high, stands with more than 4% cover of bare ground had higher bryophyte cover (younger stands), while stands having less than 4% bare ground cover had lower bryophyte cover and corresponded to older stands (Fig. 4). When leaf litter cover was low, depth of the organic layer was the next important variable associated with total bryophyte cover (Fig. 4). Stands with an organic layer <8 cm deep had a lower bryophyte cover and were slightly younger, and canopy composition was split evenly between spruce and deciduous stands. Stands with a deeper organic layer were mostly spruce stands and had the highest bryophyte cover of all groups (72%; Fig. 4).

Fig. 4. Univariate regression tree partitioning variation in total bryophyte cover (%). Thresholds associated with environmental variables for each split are shown next to each node of the tree, along with the percentage of total variation explained by each split. The percentage of the variation explained by the tree is 61.2% and the cross-validated error to estimate prediction error on new samples is 74.6%. Each terminal group is shown with its average bryophyte cover (%), age (years since fire), and number of stands; pie charts show the relative abundance of forest types in each group. [Colour online.]

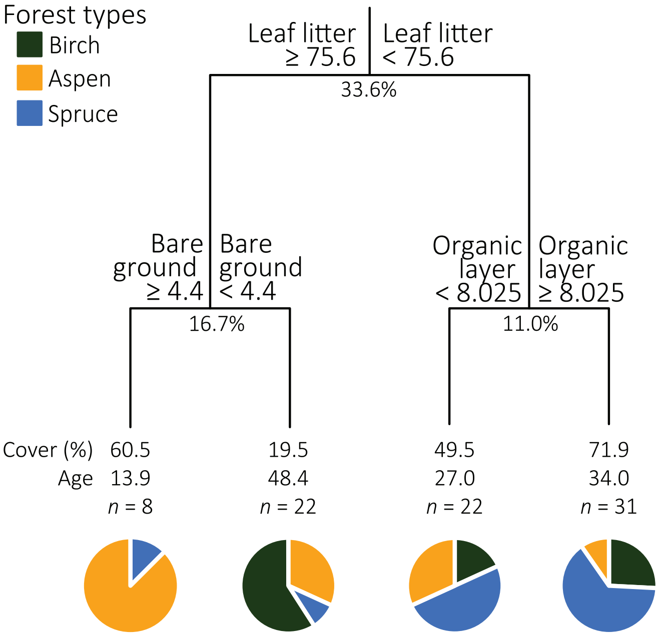
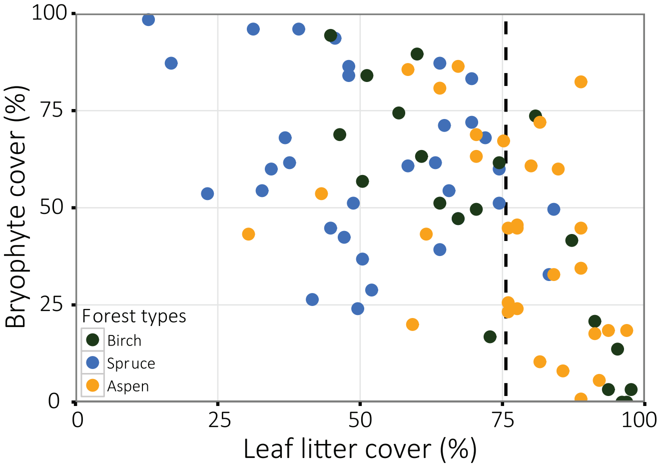


Fig. 5. Variations in total bryophyte cover (%) versus leaf litter cover (%) in stands ($n = 83$) dominated by spruce, birch, or aspen. The dashed vertical line identifies the 75.6% threshold in leaf litter cover identified by the regression tree analysis. [Colour online.]

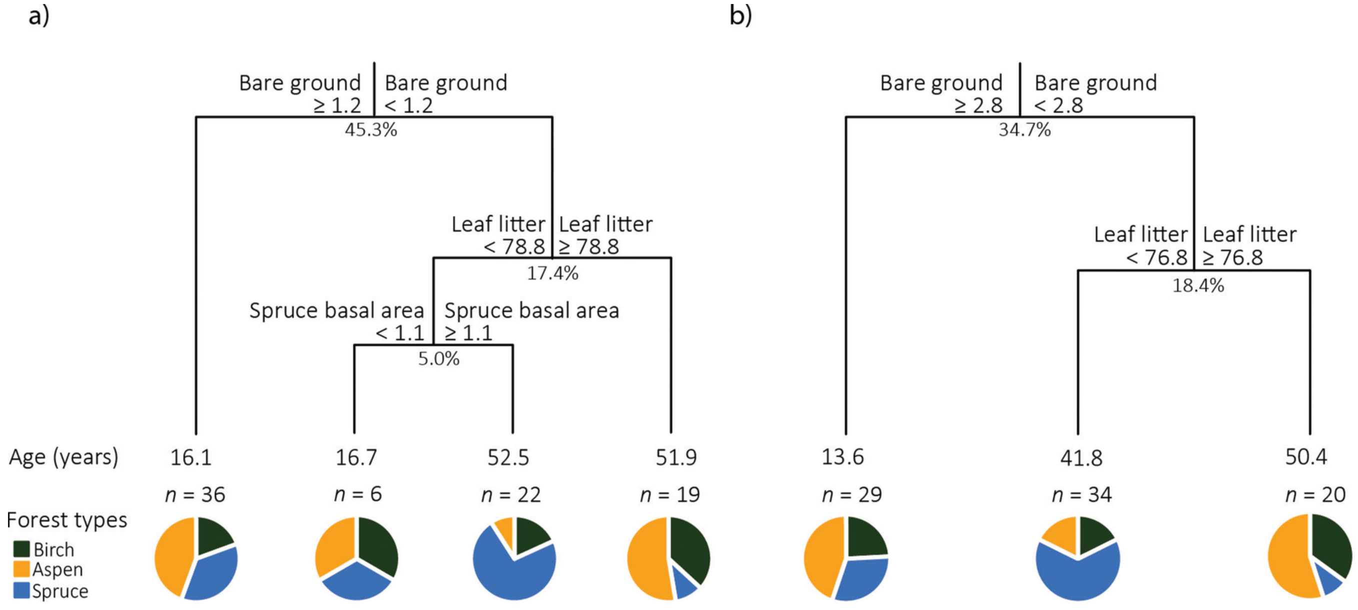


Leaf litter cover varied according to forest type and postfire successional stage ($F_{[4,74]} = 6.938$, $p < 0.0001$; Fig. 5). During early succession, leaf litter cover was similar among forest types ($\bar{x} = 69\%$). Differences in leaf litter cover occurred during mid-succession when litter cover decreased to 50% in spruce stands and increased to about 76% (threshold identified by the regression tree) in both deciduous forest types. The difference in litter cover among stand types increased during the late successional stage, with litter cover reduced to a mean of 33% in spruce stands, and increased to 94% in birch and aspen stands. The divergence in leaf litter cover among the forest types occurred at 20–40 years after fire.

Functional groups and taxa composition

Multivariate regression trees predicting functional group cover or bryophyte taxa composition were very similar (Fig. 6). In both cases, bare ground was the most prominent covariate associated with bryophyte communities, as it captured a threshold between younger (high bare ground cover) and older (low bare ground

Fig. 6. Multivariate regression trees partitioning the Bray–Curtis distances among stands ($n = 83$) calculated from (*a*) functional group cover ($n = 5$) and (*b*) bryophyte taxa composition ($n = 25$). Thresholds associated with environmental variables for each split are shown next to each node of the tree, along with the percentage of total variation explained by each split. In (*a*), the percentage of variation explained is 64.8% and the cross-validated error is 52.5%; in (*b*), the percentage of variation explained is 43.5%, the error is 56.5%, and the cross-validated error is 67.1%. Each terminal group is shown with its average bryophyte cover (%), age (years since fire), and number of stands; pie charts show the relative abundance of forest types in each group. [Colour online.]



cover) stands. Leaf litter cover was the next most important variable, with thresholds of 78.8% for functional groups and 76.8% for taxa composition (Fig. 6). A lower leaf litter cover was associated with either younger stands or mature spruce stands for functional groups (Fig. 6*a*) or with mature spruce stands for the taxa composition data (Fig. 6*b*). In both regression trees, stands with a high leaf litter cover were associated with distinct bryophyte communities mostly in mature deciduous stands (Fig. 6).

Results from the environmental vector fitting on the NMDS indicated that bare ground cover and age, which were inversely correlated to each other, were the main variables associated with the distribution of the stands along axis 1 in the multidimensional space of the ordination (Table 4). Leaf litter cover was the main variable associated with the distribution of stands along axis 2 (Fig. 3*d*; Table 4). Spruce stands in mid- and late succession were associated with a thick organic layer, higher spruce basal area, and higher soil moisture. Birch and aspen stands in mid- and late succession were associated with higher basal areas of birch and aspen and higher leaf litter cover (Fig. 3*d*; Table 4). We found a significant interaction of forest type and successional stage ($F_{[4,74]} = 2.194$, $p = 0.0030$; Supplementary Table S4*a*[1]) in explaining taxa composition, which supported the visual interpretation of the NMDS plot in Figs. 3*a*–3*c*.

Discussion

We identified a clear time scale of changes in bryophyte abundance and taxa composition driven by canopy composition in boreal forests of interior Alaska. Our results are based on a unique empirical dataset documenting patterns of bryophyte cover and community composition across an 8- to 163-year chronosequence of contrasting boreal forest canopy types. To our knowledge, few studies have focused on boreal understory communities in different forest types of similar ages (Hart and Chen 2006) or included different successional stages in such a comparison. Our findings support the interpretation of bryophyte communities diverging in response to changing canopy composition (De Grandpré et al. 1993; Hart and Chen 2006). Bryophyte cover and community composition were similar among forest types in early succession but then diverged between coniferous (black spruce) and deciduous (Alaska paper birch and trembling aspen) forest types between 20 and 40 years after fire. These changes in the bryophyte understory appear to be driven by differences in litter cover caused by higher annual production of litter in deciduous stands (Melvin et al. 2015), consistent with the hypothesis that chemical and physical aspects of leaf litter affect the growth and survival of understory taxa (Barbier et al. 2008). A threshold of about 75% leaf litter cover was associated with a large reduction in bryophyte cover and a change in taxa composition among the 83 stands in our study. Our results identify unique successional patterns strongly related to canopy types and highlight the important role of leaf litter in regulating bryophyte communities.

Bryophyte communities in postfire aspen, birch, and spruce forests were similar in the early successional stages during the first 6–20 years after fire. Thus, we must reject the hypothesis that differences in bryophyte composition among mature coniferous vs. deciduous stands are attributable to distinct successional trajectories that arise immediately after fire. Instead, our data suggest that bryophyte communities in early succession are strongly influenced by common dynamics of colonization that are similar regardless of the composition of the young forest canopy. Young stands of all forest types had a high bryophyte cover (~75%) dominated by colonizing and pyrophilic taxa such as *Ceratodon purpureus*, *Leptobryum pyriforme*, *Marchantia polymorpha*, and *Polytrichum* spp. (Hart and Chen 2006; Turetsky et al. 2010). Early successional stands had more exposed bare ground than older stands, which is representative of the time necessary to recruit bryophytes from diaspores. The youngest stands were dominated by *C. purpureus* (6–20 years), a pioneer taxa intolerant of competition, which was likely overgrown by the larger and more competitive *P. juniperinum* and *P. commune* that dominated stands 20–40 years after fire (Gloaguen 1990). Extensive carpets of *Polytrichum* spp. are common following disturbances in multiple ecosystems (Foster 1985; Gloaguen 1990).

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The similarity among bryophyte communities that we observed in early succession contrasts with existing research showing impacts of fire severity on bryophyte abundance and richness two years after fire (Bernhardt et al. 2011; Hollingsworth et al. 2013). We hypothesize that the short-term responses of bryophyte communities to fire severity are likely masked within a few years by the opposing impacts of fire severity on survival versus colonization. Immediately after fire, incomplete combustion of the organic layer in low severity fires promotes bryophyte abundance because of remnant live bryophytes and fragments (Thomas et al. 1994; Bernhardt et al. 2011; Fenton and Bergeron 2013). However, high-severity fires provide seedbeds of mineral soil and ashes that are good substrates for subsequent bryophyte colonization (Thomas et al. 1994; Bernhardt et al. 2011; Fenton and Bergeron 2013). Thus, bryophyte regeneration after fire is supported by opposite mechanisms of recruitment depending on the fire behaviour and leads to a similar trajectory of bryophyte development in early successional stands.

At the transition between early and mid-successional stages, the cover of colonizing taxa declined abruptly and at a similar pace in all forest types. We suspect that different processes led to the change in bryophyte communities in coniferous vs. deciduous forest types. In spruce stands, the decrease in abundance of colonizers between 20 and 40 years since fire is synchronous with an increase in abundance of pleurocarpous feather mosses, suggesting that competition between colonizing taxa and feather mosses may be an important process (autogenic succession) (Rydin 1997). In deciduous stands, this decline in colonizers corresponded to a significant increase in leaf litter cover, meaning that in deciduous stands, external factors such as leaf litter and canopy closure may be more important (allogenic succession). More detailed studies, e.g., manipulative experiments with reciprocal bryophyte transplants, would help to clarify the role of competition and environmental variables in bryophyte succession.

By 40 years after fire, bryophyte cover and community composition differed among forest cover types, indicating a divergence in successional pathways related to canopy cover in mid-succession. This time period corresponds with the timing of canopy closure in spruce-dominated stands (Chapin et al. 2006*a*), which comes with a decrease in light availability and, as we observed, a decrease in deciduous tree and shrub litter in spruce stands (Turetsky et al. 2010). Bryophyte cover was high in mid- and late successional spruce stands (close to 100% in older stands) and was dominated by the feather mosses *Pleurozium schreberi* and *Hylocomium splendens*. *Pleurozium schreberi* remained the dominant taxa throughout most of this period, always covering between 5% and 15% more than *H. splendens* until about 100 years after fire. In some of our oldest black spruce stands, *Sphagnum* spp. was present. The few stands older than 90 years limit the conclusions that we can draw for this successional stage. The patterns that we observed are consistent with other studies of black spruce forests that document establishment of *Sphagnum* after about 100 years after fire, following changes in soil temperature and moisture initiated by extensive development of feather mosses (Fenton and Bergeron 2006; Turetsky et al. 2010). Bryophyte succession in spruce stands seems first to be triggered by the decrease in deciduous leaf litter associated with spruce canopy closure and afterwards to be driven by autogenic processes influenced by feather mosses.

Canopy composition and associated variations in leaf litter production are recognized as major factors influencing understory communities in boreal forests (De Grandpré et al. 1993; Hart and Chen 2006). Broadleaf litter may form a physical barrier to bryophyte growth (Van Cleve et al. 1983*b*; Startsev et al. 2008), increase nutrient availability in ways that reduce the competitive ability of bryophytes, and have allelopathic effects (Startsev et al. 2008). Strong (2011) found a decline in the abundance of *Hylocomium splendens* in northwestern Canada in stands with aspen canopy cover over 40%, consistent with our observations of a significant decline in bryophyte abundance above a threshold of 75% leaf litter cover, or roughly 50% deciduous canopy cover (estimated from basal area). Bryophytes in deciduous stands were rare throughout mid- and late succession and often restricted to decomposing logs or mounds where leaf litter was blown away. Increases in canopy gaps and decomposing logs that shed leaf litter with aging deciduous stands may allow feather mosses to increase in abundance late in succession (Jonsson and Esseen 1990). This pattern was reported for aspen stands >75 years old by Strong (2009) and was apparent in one of our old aspen stands (Fig. 1); however, our inference is constrained by a low sample size of deciduous-dominated forest stands older than 100 years. Nevertheless, the change in bryophyte communities in deciduous stands seems to be mostly driven by allogenic factors linked to canopy development.

The dominance of pleurocarpous feather mosses in spruce stands (Turetsky et al. 2012) and their low abundance in aspen and birch stands are critical from an ecosystem functioning perspective. Feather mosses are long-lived perennials, relatively large and fast growing, and are good competitors that can quickly take advantage of newly opened substrates by shoot encroachment (Frego 1996). Feather mosses build organic layers that enhance soil insulation and maintain shallow active layers (Turetsky et al. 2012), as well as retain soil moisture (Turetsky et al. 2010). We found a positive association between bryophyte abundance and organic layer depth, which can be linked to re-establishment of permafrost 20–30 years after fire (Viereck et al. 2008). Associations between feather mosses and cyanobacteria are also involved in biological nitrogen (N) fixation (DeLuca et al. 2002). If deciduous seedlings take advantage of exposed mineral soil following severe fires and replace black spruce as the dominant forest canopy (Johnstone et al. 2004, 2010*b*), increased production of leaf litter may prevent the subsequent recovery of feather mosses during succession. Low bryophyte cover in deciduous stands in mid-succession promotes the stability of this alternate forest type by supporting warm and dry soil conditions with high nutrient availability (Johnstone et al. 2010*a*). Colonizing bryophyte taxa such as *Polytrichum* spp. do not have the same impacts on the ecosystem in terms of insulation (Soudzilovskaia et al. 2011), water retention (Elumeeva et al. 2011), and hosting N fixers (Gavazov et al. 2010).

Divergence of bryophyte communities among canopy types at about 40 years after fire, i.e., during mid-succession, indicated that divergence in succession is arising due to increasing canopy effects as stands mature, rather than differences being caused by direct initial effects of fire severity. Black spruce forests are the most widespread forest type in interior Alaska (Calef et al. 2005), and bryophyte functional traits promote the resilience of black spruce forests through their effects on soil moisture, soil temperature, nutrient cycling, and flammability, among others (Johnstone et al. 2010*a*; Turetsky et al. 2012). Feedbacks between canopy, leaf litter production, and understory bryophytes throughout postfire forest regeneration are keys to our understanding of ecosystem resilience in interior Alaska in a context of climate change (Johnstone et al. 2010*a*). Changes in canopy dominance towards more mixed and deciduous stands will therefore have major impacts on boreal ecosystem functioning through the negative impacts of deciduous trees and leaf litter on feather mosses.

Conclusion

Bryophyte communities in interior Alaska followed divergent successional trajectories associated with vascular canopy cover (deciduous vs. coniferous) despite similar patterns during the first 40 years after fire. Autogenic processes such as competition within the bryophyte layer in spruce stands and allogenic processes such as changes in leaf litter cover in deciduous stands were associated with divergence in bryophyte communities among forest types, with a transition to feather moss in spruce stands and

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low bryophyte abundance in birch and aspen stands. Black spruce stands in mid- and late succession are characterized by an understory of feather mosses and *Sphagnum* spp. with thick organic layers, conditions that support further dominance of black spruce. However, in deciduous stands, reduction in bryophyte cover at a threshold of ~75% leaf litter cover supports conditions favorable to maintenance of deciduous dominance such as warm soils and high nutrient availability. Feather mosses also affect important ecosystem processes in boreal ecosystems such as carbon storage, soil microclimate regulation, and nitrogen fixation. Changes in fire regime that lead to an increase in deciduousness in interior Alaska (Mann et al. 2012) will likely also alter bryophyte communities and have cascading impacts on boreal ecosystem functioning. Temporal changes in bryophyte communities induced by leaf litter cover is a key aspect to our understanding of the processes that stabilize compositional patterns of boreal forests and is critical for predicting ecosystem responses to environmental change.

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