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Recovery of forest-floor vegetation after a wildfire in a *Picea mariana* forest

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Abstract We aimed to detect the trajectories of forest-floor vegetation recovery in a *Picea mariana* forest after a wildfire. Since fire severity in boreal forests is expected to increase because of climate changes, we investigated the effects of ground-surface burn severity, a surrogate for overall fire severity, on the revegetation. We annually monitored vegetation <1.3 m high in 80 1 m × 1 m quadrats at Poker Flat Research Range (65°12′N, 147°46′W, 650 m a.s.l.) near Fairbanks, interior Alaska, where a large wildfire occurred in the summer of 2004, from 2005 to 2009. *Sphagnum* mosses were predominant on the unburned ground surface. In total, 66 % of the ground surface was burned completely by the wildfire. Total plant cover increased from 48 % in 2005 to 83 % in 2009. The increase was derived mostly by the vegetative reproduction of shrubs on the unburned surface and by the immigration of non-*Sphagnum* mosses and deciduous trees on the burned surface. Deciduous trees, which had not been established before the wildfire, colonized only on the burned surface and grew faster than *P. mariana*. Although species richness decreased with increasing slope gradient, these deciduous trees became established even on steep slopes. The wildfire that completely burned the ground surface distorted the revegetation, particularly on steep slopes. The restoration of the *Sphagnum* surface was a prerequisite after the severe wildfire occurred, although the *Sphagnum* cover had difficulty returning to predominance in the short term.

Keywords Burned ground surface · Deciduous trees · Mosses · Revegetation · Slope gradient

Introduction

Lightning-caused wildfire is a key to maintaining the regeneration of taiga dominated by *Picea mariana* (P. Mill.) B.S.P. (black spruce) in boreal regions including interior Alaska (Engelmark 1999). Lightning has led to crown fires, which moderately burn the forest floor, providing safe sites for *P. mariana* seedlings (Greene et al. 2004; Jayen et al. 2006). *P. mariana* produces a semi-serotinous cone that releases most of its seeds after wildfires, and the seedlings establish themselves steadily on incompletely burned ground surfaces (Ilisson and Chen 2009). In recent years, however, wildfires have been increasing fuel consumption above and below the ground surface in the boreal forest zones of the Northern Hemisphere because of dry lightning (Kashischke and Turetsky 2006; Johnstone et al. 2011). Climate projections suggest that these extreme disturbances will increase during this century (Flannigan et al. 2000; Anisimov et al. 2007).

Species recovering after wildfires are often divided into two types: seeders that recover by sexual reproduction and sprouters that recover by vegetative reproduction. Revegetation patterns after wildfires differ with fire severity because of changes in the contributions of seeders and sprouters (Santana et al. 2012). When fire severity is low, i.e., the ground surface is incompletely burned, sprouters contribute more to revegetation, and vice versa (Schimmel and Granstrom 1996; Gurvich et al. 2005). Consequently, vegetation recovery is delayed or altered when disturbance exceeds the threshold

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of the resilience of sprouters (Dale et al. 2001; Johnstone and Chapin 2006). Delayed recovery induces an increase in active layer depth in permafrost zones (Burn 1998; Tsuyuzaki et al. 2009) and accelerates positive feedback on global warming (Kaplan and New 2006). Severe wildfire burning of ground surfaces may accelerate establishment of species that did not exist pre-fire and reorganize the flora.

Physical site characteristics, such as aspect, elevation and slope gradient, affect regeneration patterns after disturbances (Chapin et al. 2006). Permafrost distribution is related to the presence of *P. mariana*-dominated forests in discontinuous permafrost zones (Davis 2001; Hollingworth et al. 2006) and is decreased in post-fire vegetation because of decreasing albedo and increasing soil temperature until the vegetation recovers well (Chambers et al. 2005; Tsuyuzaki et al. 2009). Therefore, the paces and patterns of revegetation are a key to sustaining permafrost and to conserve the ecosystems. Since large-scale disturbances, including burn-out wildfires, delay or alter the revegetation more than small-scale ones such as crown fires (Dale et al. 2001; Rydgren et al. 2004), we hypothesized that burned-out wildfires were associated with shifts in species composition by removing the ground-surface plant cover and by species immigration from the external environments. We had a chance to obtain revegetation patterns after various-scale wildfires, including both crown and burn-out fires, coded as ‘‘Boundary Fire,’’ that occurred in interior Alaska in the summer of 2004. We report the first 5 years of monitoring of forest-floor vegetation after the wildfire.

Materials and methods

Study area

The study site is located at Poker Flat Research Range, approximately 50 km north of Fairbanks, Alaska. It is a scientific rocket-launching facility owned by the University of Alaska Fairbanks. The region is located in the discontinuous permafrost zone. Annual precipitation averaged 297.4 mm in Fairbanks from 1971 to 2000, the maximum monthly mean air temperature was 23.0 °C in June, and the minimum was −25.0 °C in January (ACRC 2007). The Boundary Fire occurred in the region including Poker Flat from mid-June to late August in 2004, and it burned ca. 217,000 ha of forests with various severities (Betts and Jones 2009; Johnstone et al. 2011). Before the wildfire, the tree layer was dominated by *P. mariana* (Tsuyuzaki et al. 2009), and the ground surface was covered with thick mosses dominated by *Sphagnum* spp. [*S. capillifolium* (Ehrh.) Hedw., *S. subsecundum* Nees and others] and *Hylocomium splendens* (Hedw.) Schimp. Since *Sphagnum* spp. often establishes on wetter sites than *Hylocomium* in pre-burned forests (Heijmans et al. 2004; Nicole and Yves 2006), *Sphagnum* was likely to remain more abundant than *Hylocomium* on the unburned surface after the wildfire.

Sampling

Sixteen 10 m × 10 m plots were established on a north slope of different fire severities, ranging from 0 to 100 %, before leaf flushing began in the spring of 2005, to detect relationships between burned areas and revegetation (Tsuyuzaki et al. 2009). Five 1 m × 1-m quadrats were randomly set up in each plot, and the percentage of burned area was estimated visually in each quadrat. Burned ground surface was divided into two types in each quadrat: complete burning that removed the organic layer and exposed soil, and incomplete burning that left blackened organic matter such as peat. Measurements of burned areas were conducted over the whole burned area, including complete and incomplete burning as well as completely burned area. Monitoring continued annually from 2005 to 2009.

Percent cover was recorded for each plant taxa in a layer less than 1.3 m high on each quadrat every summer. The vascular plant species were identified by the first author and the vouchers stored in SAPS. The mosses were sampled, identified by M. Higuchi, NMNS, and the vouchers kept in TNS. The lichens were sampled and the vouchers kept in GSES, HU. The layers more than 1.3 m high had few vascular plants except *P. mariana*, the density of which averaged 24 stems per plot.

Photos were taken toward the canopy on each quadrat at 1.3 m above the ground surface by a fish-eye lens in the summers of 2005 and 2008. The photos were used to evaluate canopy openness, using a freeware Gap Light Analyzer ver. 2.0 (Frazer et al. 1999). Longitude and latitude on each quadrat and on the center of each plot were measured by differential GPS receivers (StarBox SSII-51CPN-19, Amtechs, Tokyo) with an antenna (GPS-701, NovAtel, Calgary). Location, aspect and slope gradient on each quadrat were measured by a laser level meter. Based on these measurements, the elevation on each quadrat was calculated. Thermometers were established from 2 cm to the surface of the permafrost; the maximum was 150 cm in three sites in August 2007 in which fire severities differed between none and completely burned. Thaw depth was inspected by temperature profiles recorded at 1-h intervals.

Data analysis

Diversity and evenness in each quadrat were calculated by Shannon-Wiener indices. Generalized linear mixed-effects models (GLMM) were used to detect significant environmental factors concerning species richness, diversity, evenness and total plant cover. Four response variables—total plant cover, species richness, diversity and evenness—were examined in the models. The distributions were assumed as Poisson for richness because of discontinuous function, gamma distribution for diversity because of continuous function without zero, and binomial for evenness and cover because of the ratio. The examined explanatory variables were burned ratio, canopy openness, elevation, slope, aspect and years after the wildfire on each plot. Plot locations, i.e., longitude and latitude, were used as random effect to reduce the effects of pseudo-replicated sampling designs.

Non-metric multidimensional scaling (NMDS) was applied to investigate relationships between environmental factors and plant cover on each species, using all taxa. NMDS is an ordination technique well suited for data that are nonnormal or occur along arbitrary or discontinuous scales, and it is considered the most effective ordination method for ecological community data (McCune and Grace 2002). NMDS does not assume a unimodal model of species responses to the environment and allows for the possibility that community variations are related to unmeasured environmental variables. Therefore, community patterns are retained regardless of which environmental variables were measured. In addition, multi-response permutation procedures (MRPP) of 999 permutations were used to examine significant differences between groups of sampling units (Reich et al. 2001).

Since the presence or absence of *Sphagnum* may greatly influence revegetation and/or the carbon cycle on and in the ground after wildfires in boreal ecosystems (Greene et al. 2004; Shetler et al. 2008; Whinam et al. 2010), two similarity analyses were compared using the Jaccard similarity index to inspect the habitat preferences, in particular of the *Sphagnum* mat, of species that showed high cover and/or frequency (hereafter, i.e., dominant species) in relation to *Sphagnum*. In the first analysis, percentage similarities between *Sphagnum fuscum* (Schimp.) Klinggr. and each dominant species or each lifeform were calculated. In the second analysis, the similarities were calculated between non-*Sphagnum* cover and the species or lifeform to investigate the preferences of species to ground surface not occupied by *Sphagnum*. On the similarity between the *Sphagnum* mat and moss lifeform, *Sphagnum* species were excluded from the lifeform. The non-*Sphagnum* surface was mostly created by burning in the first year (i.e., 2005). Therefore, non-*Sphagnum* cover was a surrogate for the burned area in 2005. All statistical analyses were conducted with the statistical program R (ver. 2.10.1) (R Development Core Team, 2010).

Results

Initial vegetation patterns and environments

There were 29 vascular plant species (27 seed plants and 2 ferns) and over 13 non-vascular plant species, i.e., mosses and lichens, recorded in the 80 quadrats. The two ferns were *Equisetum silvaticum* L. and *Lycopodium annotinum* L. Of the mosses and lichens, *S. fuscum*, occupied 29.3 % of the unburned surface in 2005. The vascular plants consisted of 13 herbs (forbs, grasses and ferns), 12 shrubs and 4 trees. Visual observation confirmed that the shrubs survived throughout the wildfire and recovered mostly by vegetative reproduction, i.e., sprouters. Of the four tree taxa, *P. mariana* was evergreen, and the others (*Betula neoalaskana* Sarg., *Populus tremuloides* Michx. and *Salix* spp.) were deciduous. *P. mariana* survived the fire when they were rooted in *Sphagnum*. Therefore, the cover was high in 2005 (0.6 %) and was derived mostly from surviving saplings. In contrast, most of all broad-leaved trees were regenerated by seedlings.

Canopy openness ranged from 57 to 94 %. The burned area averaged 66 %, ranging from 0 to 100 %. *Sphagnum* cover decreased annually, probably because of the delayed effects of burning, such as desiccation. Thaw depth increased with an increasing burned surface on the plot level from 50 to 330 cm in August 2007. The total number of species in all the quadrats ranged from 39 to 41 for 5 years and did not differ largely, indicating that the species composition was fixed soon after the wildfire. Plant cover was negatively correlated to burned area (GLMM, $P < 0.01$).

The slope gradient was negatively correlated to richness ($P < 0.01$), showing that steep slopes restricted species richness. Species diversity and evenness ranged from 1.24 to 1.61 and from 0.56 to 0.68, respectively, and were not correlated to any examined environmental variables. Canopy openness and elevation were not related to these four parameters on plant community structure ($P > 0.01$).

Temporal changes in vegetation

Total plant cover increased from 60 % ± 50 (mean with standard deviation) in 2005 to 108 % ± 38 in 2009 (GLMM, $P < 0.01$). Similarly, species richness ranging from 9.8 to 11.3 was negatively correlated to burned area ($P < 0.01$) and positively correlated to year ($P < 0.01$). A sedge, *Carex bigelowii* Torr., and a grass, *Calamagrostis canadensis* (Michx.) Beauv., gradually increased their cover from 0.9–1.7 % to 3.0–7.7 % over the 5 years. A forb, *Epilobium angustifolium* L., had peak of cover (3.0 % ± 9.0) 2 years after the wildfire and then gradually decreased to 1.9 % ± 3.4. Ferns were infrequent in the quadrats. All of the dominant shrub species gradually increased their cover from 0.3–4.3 % in 2005 to 0.9–11.3 % in 2009. Shrubs, such as *Ledum groenlandicum* L., *Vaccinium vitis-idaea* L., *Vaccinium uliginosum* L., *Betula nana* L. and *Oxycoccus microcarpus* Turcz., had high cover even soon after the wildfire.

All of the trees gradually increased in cover across time. The cover of *P. mariana* increased slowly and was 0.9 % even in 2009. In contrast, *B. neoalaskana* and *P. tremuloides* established from seeds, i.e., seeders, and thus the initial cover was low (less than 0.1 %). Increase in cover was, however, faster for the two deciduous trees than for *P. mariana*. In 2009, cover of *P. tremuloides* and *B. neoalaskana* reached 1.0 and 0.7 %, respectively. Of the mosses and lichens, *S. fuscum* was dominant but decreased in cover annually to 21.1 %. *Polytrichum commune* Hedw. and *Ceratodon purpureus* Hedw. increased in cover, annually reaching 6 and 15 %, respectively, in 2009. *Ceratodon purpureus* was established in 80 % of quadrats in 2009. These two mosses, *P. commune* and *C. purpureus*, were uncommon on unburned surfaces.

Coefficients of determination on NMDS indicated that all examined variables significantly explained the ordination patterns (test of random data permutations, $P < 0.01$). As axis I explained 52 % of variance, axis II 26 % and axis III 14 %, the first two axes were examined. The stress was 0.191. Of these, fire severity expressed by the burned surface was the prime factor determining vegetation structures (Fig. 1). Burned area and canopy openness were both negatively correlated with axis I, showing that fire severity is a strong factor in determining post-fire species composition. The other three site factors—elevation, aspect and slope gradient—were related more to axis II, showing that burn severity was not greatly related to the site characteristics. Slope gradient was related to axis II more than aspect and elevation. Year had the weakest effects of the examined variables on vegetation structures, showing that revegetation pathways were not unique. MRPP also supported these results, i.e., these examined variables were significantly different between the sampled groups, including continuous variables, at $P < 0.01$ (A ranging from 0.022 to 0.718, $\delta < 61.2$ that were less than expected, $\delta = 62.58$, and $n = 400$).

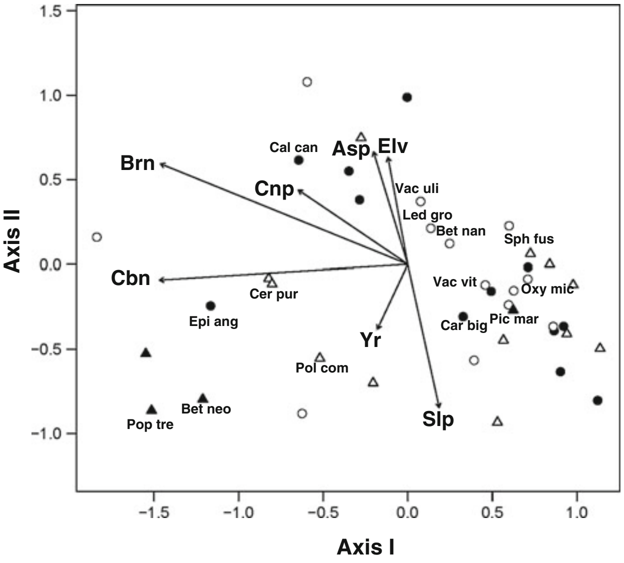

Fig. 1 NMDS ordination diagram on species scores in 400 quadrats (80 × 5 years) surveyed from 2005 to 2009 after the 2004 wildfire. Lifeforms: *closed circles* herbs and ferns (13 taxa), *open circles* shrubs (12), *closed triangles* trees (4) and *open triangles* mosses and lichens (13). Species codes explained in the text: Car big, *Carex bigelowii*; Cal can, *Calamagrostis canadensis*; Epi ang, *Epilobium angustifolium*; Led gro, *Ledum groenlandicum*; Vac vit, *Vaccinium vitis-idaea*; Vac uli, *Vaccinium uliginosum*; Bet nan, *Betula nana*; Oxy mic, *Oxycoccus microcarpus*; Pic mar, *Picea mariana*; Bet neo, *Betula neoalaskana*; Pop tre, *Populus tremuloides*; Pol for, *Polytrichum commune*; Sph fus, *Sphagnum fuscum*; Cer pur, *Ceratodon purpureus*. Environmental factors: *Yr* years after wildfire, *Brn* burned area (%), *Cbn* completely burned area (%) where the soils were exposed. *Cnp* canopy openness (%), *Elv* elevation (m), *Slp* slope gradient (°) and *Asp* aspect (°)

Species scores on NMDS showed distinct patterns among the four lifeforms—herbs, shrubs, trees and mosses (Fig. 1). Shrubs had high scores on axis I close to *Sphagnum fuscum*, while non-*Sphagnum* mosses, *P. commune* and *C. purpureus*, had low scores far from *S. fuscum* on axis I. These patterns indicated that the shrubs established less with the non-*Sphagnum* mosses. Deciduous trees scored low and clustered to each other on axis I and axis II, but *P. mariana* scored high on axis I, showing that the two deciduous trees established least with *P. mariana*. The scores of two non-*Sphagnum* mosses came close to those of deciduous trees but were slightly higher on axis I, showing that the mosses established primarily on burned surfaces but less so on the unburned surfaces. Although species richness decreased with increasing slope gradient, two deciduous trees (*P. tremuloides* and *B. neoalaskana*) and a moss (*P. commune*) established more on steep slopes, as shown by the low scores on axis II correlated to slope gradient.

High quadrat scores on axis I meant that quadrats were burned less, and vice versa (Fig. 2). The annual fluctuations of quadrat scores on NMDS became larger on more burned areas, indicating that vegetation structures changed faster on burned surfaces with increasing

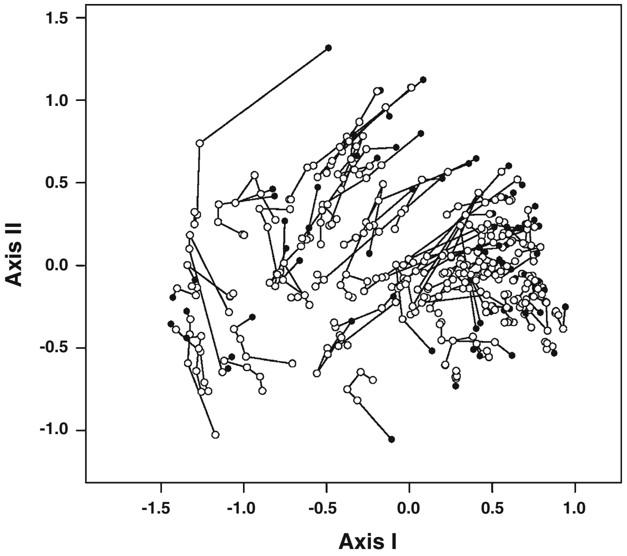

Fig. 2 NMDS ordination diagram on quadrat scores in 400 quadrats (80 × 5 years) surveyed for 5 years after the 2004 wildfire. The connected *lines* show the same quadrats surveyed from 2005 to 2009. NMDS scores at the first survey, i.e., in 2005, are shown by *solid circles* and the others by *open circles*. The *arrows* for environmental factors are not shown

fire severity. In addition, the scores on severely burned surfaces fluctuated along axis II rather than axis I, showing that the vegetation changes did not move toward less-burned vegetation. The major causes of the fluctuation patterns were derived from the colonization of two deciduous trees (*P. tremuloides* and *B. neoalaskana*, a herb, *E. angustifolium*) and two mosses (*P. commune* and *C. purpureus*), all of which established more on burned surfaces (Fig. 1).

Habitat preferences

The patterns of yearly fluctuations on the two similarities were different between burned and unburned surfaces (Fig. 3). The similarity of each lifeform was stable on unburned *Sphagnum* surfaces for the 5 years as compared with the similarity on the burned surface. These implied that the vegetation structures temporally changed more on burned surfaces than on unburned surfaces. The similarity of trees increased gradually on both unburned and burned surfaces, indicating that the trees increased their cover with time on both surfaces.

The patterns were not synchronized among the three herbs (Fig. 3). The similarity of *E. angustifolium* to *Sphagnum* cover was extremely low and to non-*Sphagnum* cover was high, showing that *E. angustifolium* established least on the unburned surface. In contrast, the similarity indicated *C. canadensis* recovered rapidly not only on *Sphagnum* surfaces but also on non-*Sphagnum* surfaces. *C. bigelowii* established on the *Sphagnum* surfaces more than on the non-*Sphagnum* surfaces, and the annual changes in the two similarities were small.

For all the dominant shrubs, the similarities to *Sphagnum* cover were high but to non-*Sphagnum* cover were low, showing that shrubs established well with *Sphagnum* as indicated by NMDS (Fig. 1).

P. mariana showed contrast patterns on the similarities on the *Sphagnum* and non-*Sphagnum* surfaces to the two deciduous species (Fig. 3). *P. mariana* showed higher similarity to the *Sphagnum* mat than any other tree species and did not show low similarity to the non-*Sphagnum* mat. Although *P. mariana* established more on unburned surfaces, this did not mean *P. mariana* did not establish on burned surfaces. In contrast, two deciduous trees established least with *Sphagnum* and

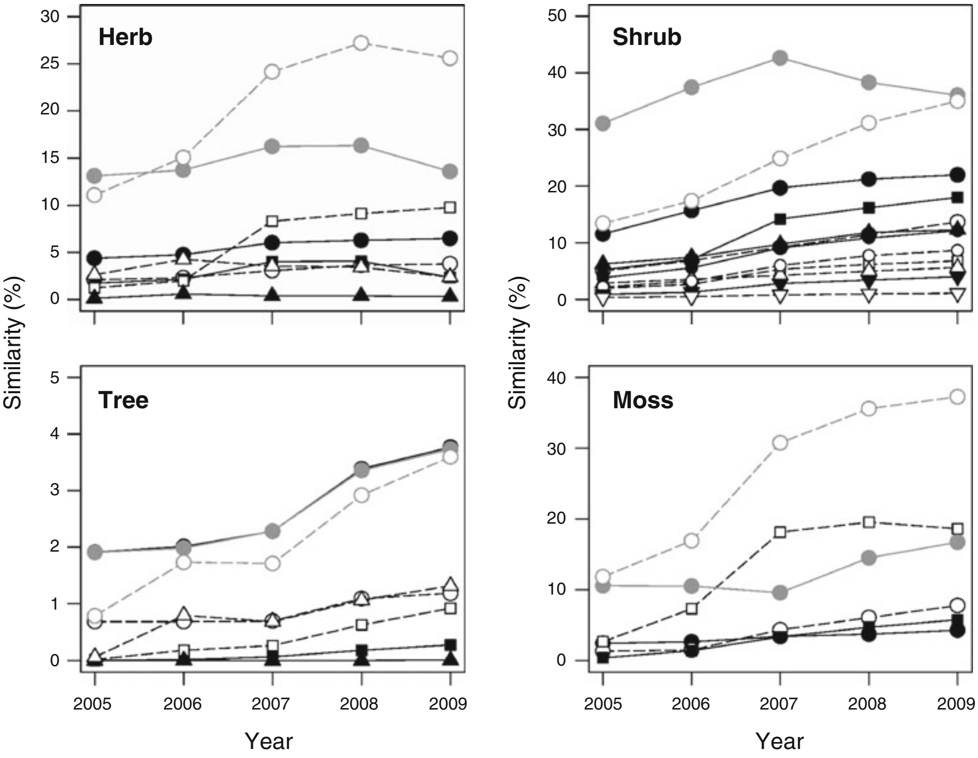

Fig. 3 Percentage similarities between *Sphagnum fuscum* surface and species or lifeform (shown by *solid lines with closed symbols*) and between non-*Sphagnum* surface and species (by *interrupted lines with open symbols*). *Gray symbols* and *lines* indicate the lifeforms. Herb: closed circles/open circles, *Carex bigelowii*; closed square/open square, *Calamagrostis canadensis*; closed triangle/open square, *Epilobium angustifolium*. Shrub: closed circles/open circles, *Ledum groenlandicum*; closed square/open square, *Vaccinium vitis-idaea*; closed triangle/open square, *Vaccinium uliginosum*; open square/open square, *Betula nana*; closed inverted triangle/open square, *Oxycoccus microcarpus*. Tree: closed circles/open circles, *Picea mariana*; closed square/open square, *Betula neoalaskana*; closed triangle/open square, *Populus tremuloides*. Moss: closed circles/open circles, *Polytrichum commune*; closed square/open square, *Ceratodon purpureus*. Note that the scales of the *y* axis are different between lifeforms and that the similarities of *P. mariana* and trees on the unburned surface overlap

increased annually the similarities to non-*Sphagnum*, showing that these species gradually increased in cover on non-*Sphagnum* surfaces.

Discussion

Vegetation patterns along gradients of fire severity

NMDS on quadrats (Fig. 1) indicated that revegetation patterns on the floor differed greatly between burned and unburned surfaces since the recovery on unburned surfaces was dependent on regeneration and that on burned surfaces on colonization. Species producing wind-dispersed seeds contribute more to revegetation after a more severe wildfire (Johnson and Miyanishi 2007). Fire severity determines community composition derived from differences in regeneration strategy and root depth among species (Hollingworth et al. 2013).

The similarities between ground-surface combustion and plants were indicated as follows (Fig. 3): *P. mariana* of the tree species produced semi-serotinous wind-dispersed seeds but established more on the unburned surface probably because of a habitat preference that is adapted to crown fire. Deciduous trees needed high severity sites where most *Sphagnum* carpets were removed for their establishment, while *P. mariana* trees colonized in both high- and low-severity sites because they were either able to survive fire on thick *Sphagnum* or germinated on burned and unburned surfaces. When post-fire residual organic matter is more than 2 cm thick, vegetation composition diverges in the *P. mariana* forest of eastern Canada (Siegwart Collier and Mallik 2010).

Species producing wind-dispersed seeds or spores established steadily when suitable habitats were provided by burning the *Sphagnum* surface, viz. all the deciduous trees produced wind-dispersed seeds, and a perennial herb, *Epilobium angustifolium*, did, too. Mosses produced spores that should be dispersed by wind. Deciduous trees do not recruit seedlings in thick organic mats but outcompete with conifers on mineral soils after wildfires (Johnstone and Chapin 2006). There should have been no safe sites for deciduous trees before the *P. mariana* forests were burned.

Vegetation patterns along gradients of topography

Species richness decreased with increasing slope gradients. In addition, NMDS on species showed that revegetation on steep slopes was altered by the establishment of deciduous trees and non-*Sphagnum* mosses (Fig. 2). Wind-dispersed seeds often accumulate in the rough microtopography provided by live plants, litter and coarse-textured soil, all of which function as seed traps (Koyama and Tsuyuzaki 2010). Deciduous trees disperse numerous seeds to treeless areas after wildfire (Landhausser and Wein 1993). The wind-dispersed seeds of broad-leaf trees should be captured by coarse and/or concave ground surfaces, even on steep slopes. Revegetation after wildfire is determined not only by fire severity, but also pre-disturbance conditions, including topography, and is not interpreted by a vegetation gradient related to time after disturbance (Rydgren et al. 2004).

Lifeforms in relation to seeders versus sprouters

All the deciduous trees were seeders at Poker Flat after the wildfire. In contrast, shrubs, most of which were sprouters, increased in cover annually, depending on the unburned surface. The clonal shrubs (e.g., *Vaccinium uliginosum* and *V. myrtilloides*) rarely produced seedlings on the *Sphagnum* mat (Eriksson 1989; Moola and Mallik 1998). Perennial grasses and sedges also reproduced vegetatively on unburned surface. Sprouters, such as perennial sedges, grasses and shrubs, are common when wildfire is not severe in a mixed-evergreen forest in Oregon (Donato et al. 2009). Revegetation progresses by species in soil bud banks (sprouters) and seed banks after weak fires that consume relatively shallow moss layers in a boreal Swedish forest, while the revegetation is conducted by seeders after deep-burning fire (Schimmel and Granstrom 1996).

Such differences in regeneration strategies between species or lifeforms determine the plant community structures and should be used for predicting successional sere with different fire severities.

Temporal changes in vegetation with reference to habitat preferences

Sphagnum cover gradually decreased for 5 years and did not re-colonize on the burned surface, probably because of post-fire stresses such as by desiccation. Albedo was reduced when the plant cover burned and did not return to the pre-fire status until plant cover became high (Tsuyuzaki et al. 2009). Low albedo leads to high ground-surface temperatures and deep thaw depths (Jorgenson et al. 2001). These changes induce drought stresses for plants, particularly *Sphagnum* mosses, which require more water than vascular plants for the short term. This is because they develop shallow belowground organs for water acquisition and have no special organs for water transportation (Schouwenaars and Gosen 2007; Thompson and Waddington 2008). *Sphagnum* is likely to recover more slowly than vascular plants, particularly when the ground surface is completely consumed by wildfire.

The increase in moss cover was mostly derived from pioneer mosses, represented by *Polytrichum strictum* and *Ceratodon purpureus*, on burned surfaces. Mineral soils exposed after disturbances, including severe wildfires, were covered with pioneer mosses, and the vegetation was totally dissimilar to the pre-fire vegetation (Bernhardt et al. 2011). The aboveground biomass and productivity of non-vascular plants are lower on drier sites after a wildfire in interior Alaska, in particular where *Ceratodon* and/or *Polytrichum* was dominant (Mack et al. 2008). Deciduous trees established with *P. commune* and *C. purpureus* on the burned surface. Since these two mosses established well on burned surfaces, they should induce the alteration of tree regeneration. The revegetation does not move directly toward *P. mariana* forest when a wildfire burns out the ground surface.

Forest revegetation seems to be delayed by severe burns (Dale et al. 2001). Furthermore, the complete removal of moss and organic matter promoted the colonization of non-*Sphagnum* mosses and deciduous trees. In conclusion, seeders represented by broad-leaved trees have a major role in revegetation after severe wildfires in *P. mariana* forests that completely burn out not only the *Sphagnum* mat but also the organic layer.

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