

Article

Patterns of Early Postfire Succession of Alpine, Subalpine and Lichen-Woodland Vegetation: 21 Years of Monitoring from Permanent Plots

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Abstract: Field observations using chronosequences are helpful to study vegetation succession. This method allows to establish comparisons based on soil composition, stand structure, micro- and macrofossil remains from sites of different ages but on similar edaphic and topographic conditions. In the boreal forest, post-fire succession through time is triggered by climate, disturbance history (insect epidemics, fire and logging), latitude and altitude. The main objective of this research is to identify the main patterns of early post-fire succession, including similarities and differences in vegetation composition and attributes, of three contrasted ecosystems distributed along an altitudinal gradient. To do so, we have monitored the successional development of the alpine, subalpine and boreal lichen-woodland sites during the first 21 years (1991 to 2011) of post-fire sequence in eastern Canada 1991 to 2011. Each site was characterized by a different functional group that became established following fire. A rapid resurgence of ericaceous shrubs and lichens was observed in the lichen woodland and subalpine sites. Bryophyte and lichen species were not an important component of vegetation communities during the earlier stages of post-fire succession. For all three sites monitored, lichens were the last functional group to establish in the chronosequences. Herbs and mosses characterized the post-fire succession in alpine areas, the latter functional group established late in the chronosequence to cover >25% of the site after 15 years. Post-fire chronosequences in the three contrasted environments indicate that plant succession is a repetitive process often involving similar resilient plant assemblages.

Keywords: secondary succession; in situ monitoring; alpine and subalpine vegetation; lichen woodland; postfire succession; boreal forest; functional groups

1. Introduction

The study of vegetation succession relies predominantly on field observations from inferred chronosequences based on the comparative analysis of plant and soil structures from sites of different ages but of similar physical settings [1]. A more direct and accurate way to evaluate vegetation change over time is the long-term monitoring of postdisturbance succession from permanent lines, plots or quadrats [2]. Rephotography of the same site or area over many years and decades is also, to some extent, a reliable method to evaluate successional change [3]. Repetitive observations at specific intervals (days, months, years and even decades) provides direct evidence of in situ vegetation and ecosystem changes over time [4–8].

In North America, boreal forest stands are continuously renewed by natural and anthropogenic disturbances [9–11]. The primary disturbance agents are fire and insect epidemics, with harvesting being much important in the southern part of the boreal forest [12]. Those particular agents affect vegetation establishment and development as well as successional dynamics among competing species. Fire is the main factor responsible for initiation and termination of vegetation succession in boreal, temperate and tropical biomes as it controls the structural and functional properties of most plant communities [13,14].

Lichen woodlands are sparsely treed, open forests with a characteristic continuous lichen ground cover. They are usually located in a zonal belt between the closed boreal forest to the south, and the forest tundra to the north [15–18]. Lichen succession is mainly triggered by fire although caribou activity can alter significantly the ground layer vegetation, and interfere with the successional processes, especially during periods of demographic peaks [19]. Based on changes in the abundance of lichen and moss species recorded along postfire chronosequences in boreal ecosystems, four successional stages are generally identified [20–23]. The burned surface is colonised by crustose lichens (*Trapeliopsis granulosa*, etc.) and pioneer acrocarpous mosses (*Polytrichum piliferum*, *P. juniperinum*, etc.) a few years after the fire. With time, different horn and cup lichens (*Cladonia cristatella*, *C. deformis*, *C. crispata*, *C. sulphurina*, etc.) establish on the burned soil surface. These species will dominate the ground vegetation for about 20 years, before being progressively replaced by fruticose lichens, especially *Cladonia mitis* which will be dominant, along with *Cladonia rangiferina*, up to 60 years after the fire [21]. During that time however, the abundance of *Cladonia stellaris* increases until it eventually becomes dominant. In the absence of fire, old *Cladonia* woodlands can persist in the landscape for centuries due to reduced tree establishment [24].

The southernmost lichen woodlands in eastern Canada are located on the Charlevoix highlands (southern Quebec), in the “Parc des Grands-Jardins”, (hereafter, PGJ), more than 500 km south of their main range. These stands are believed to be regressive spruce–moss forests that developed following the combined disturbances of spruce budworm (*Choristoneura fumiferana* (Clem.) epidemics followed shortly by fire [18,25–27]. The PGJ also comprises subalpine and alpine vegetation located on high summits exposed to strong winds and low temperature. Fire occurrence on the Charlevoix highlands has been frequent, particularly during the 20th century where several fires burned more than 100 km² of the PGJ vegetation cover [25].

The most recent fires in the PGJ created several unique ecosystems protected against forest logging and soil exploitation for long-term conservation. Two 1991 fires burned small tracts of alpine, subalpine and boreal vegetation despite fire control measures. The 1991 fire event was the occasion to follow the pattern of vegetation recovery in the three ecosystems in order to test their resilience with time and evaluate the return to prefire vegetation. In this respect, the main objective of this project is to identify the yearly patterns of early postfire succession, including similarities and differences in vegetation composition and attributes of alpine, subalpine and boreal ecosystems distributed along an altitudinal gradient. To do so, we have monitored the successional development of the three ecosystem sites during the first 21 years of postfire chronosequence from 1991 to 2011. The analysis of the early postfire chronosequence of the sites also was used to compare the monitoring data to published postfire chronosequences from similar sites of the boreal biome.

2. Methods

2.1. Study Area

Monitoring of plant succession in the three sites was conducted in the PGJ located on the Charlevoix highlands, about 120 km northeast of Quebec City (Figure 1). The area is characterized by high hills with an average altitude between 700 and 900 m above sea level (a.s.l.), with several alpine and subalpine summits over 1000 m a.s.l. The average annual temperature is about 0 °C, the mean

temperature of the warmest month (July) is 15 °C, and the average frost free period of 60–70 days is among the shortest in southern Quebec [28].

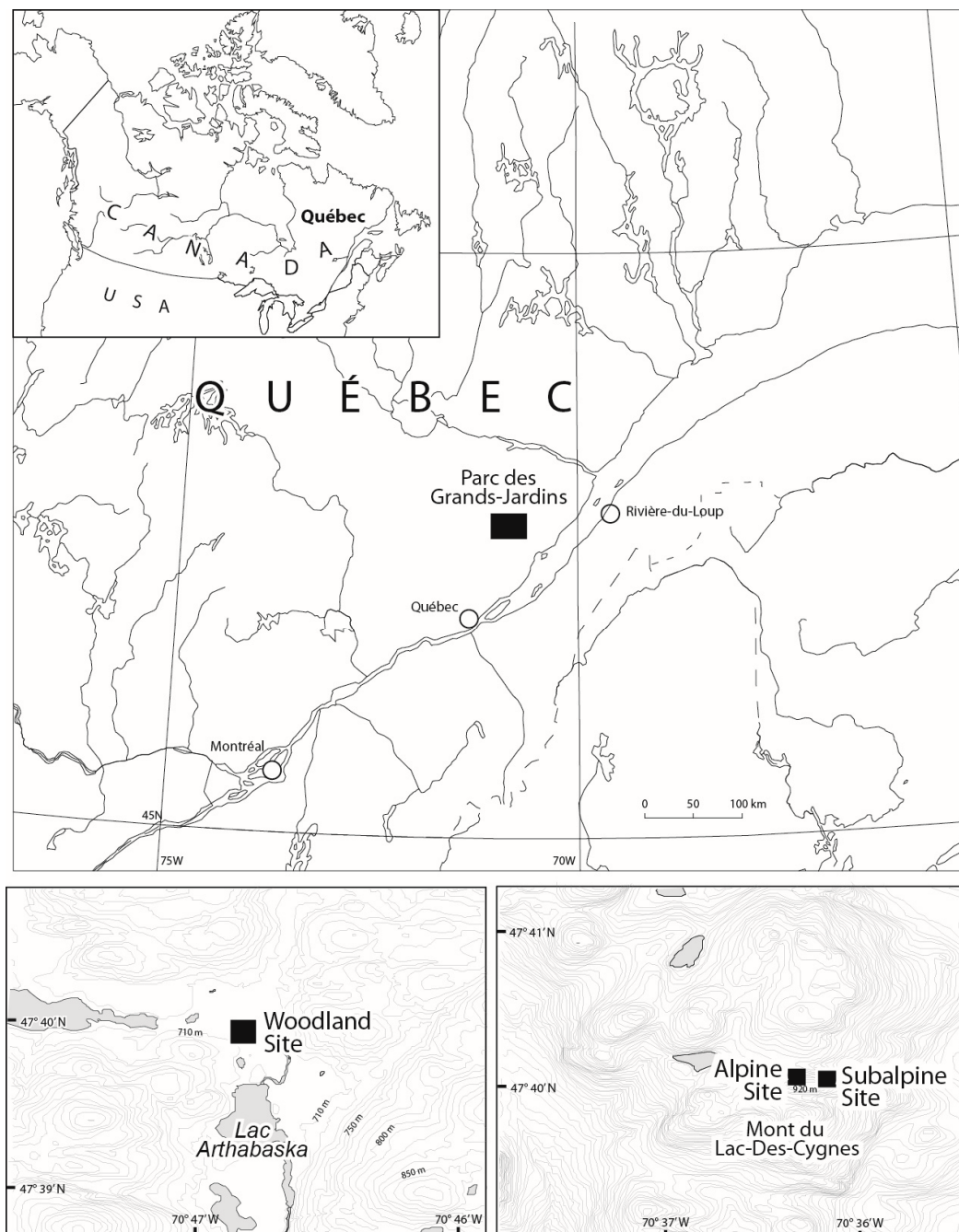


Figure 1. Location of the study area in southern Quebec, Canada.

The vegetation in the PGJ forms a mosaic of open and closed forests. Black spruce (*Picea mariana* (Mill.) B.S.P.) is the dominant tree species. Eastern larch (*Larix laricina* [Du Roi] K. Koch), balsam fir (*Abies balsamea* [L.] Mill.), and paper birch (*Betula papyrifera* [Marsh.]) are growing in protected and wet sites. Lichen woodlands make up about 10% (30 km²) of the PGJ area and are primarily found on well-drained, acidic podzol soils of the Malbaie River basin. The soils are made of fluvio-glacial sands and gravels in valleys and heterometric till on slopes. Subalpine and alpine plant communities are growing on exposed, acidic podzolic soils developed on thin coarse till deposits.

Conifer forests in the Park are subject to several disturbances, including insect outbreaks (spruce budworm, *Choristoneura fumiferana* [Clem.]) and fires. Several forest tracts were also harvested before the creation of the Park in 1981 [29]. Three recorded insect outbreaks occurred during the 20th century [30], with the last one extending from the mid-1970s to the mid-1980s [31].

2.2. Selection of Sampling Sites

The three sites selected for monitoring postfire succession were affected by fire in 1991. The alpine and the subalpine sites that burned in late May 1991 are located several tens of metres from each other on the Mont du Lac-des-Cygnés, a wind- and frost-exposed summit ranging between 950 and 1000 m a.s.l. The pre-burn vegetation at both sites developed after a large fire in 1915 [32]. The pre-burn alpine site was dominated by ericaceous shrubs, small herbs and lichens. The subalpine site was previously dominated by an open-crown balsam fir shrub community. The lichen-woodland site is part of a mosaic of postfire closed-crown and open black spruce forests distributed on the Precambrian plateau at 750–800 m a.s.l. The woodland developed after a fire in 1894, and postfire succession started immediately after a natural fire in June 1991. The three sites are representative of the main vegetation belts of the Charlevoix highlands where alpine, subalpine and boreal communities coexist along an altitudinal gradient [32,33].

2.3. Sampling

At each site, yearly postfire vegetation was monitored between 1991 and 2005 and at every 2 years between 2005 and 2011. Monitoring consisted of linear relevés [34] made of 30 permanent lines, each 1-m long and positioned according to random numbers [35], within a 200 m² quadrat. Each 1-m line was subdivided into 10-cm long segments for plant recording. The vegetation survey was conducted exactly at the same position for each of the 30 permanent lines in each site. Each line was delineated by steel stakes installed at both ends. A metric ruler was used for plant recording in the ten 10-cm long segments of each line. Species cover was evaluated at each site and along each line from 10-cm long segments using the following cover categories: <1%; 1–10%; 10–20%, . . . 90–100%. Caution was exercised to avoid trampling and compaction of the groundcover at each site. No such damage and change of the vegetation cover and soil were noticed, likely because sampling at each site was done in only one visit per year and within a rather short period of time. Absolute frequencies of each species were calculated based on presence/absence data recorded from each of the 300 segments at each site. The species' absolute frequency was calculated as the ratio of the number of 10-cm long segments where the species was present to the total number of segments. Species cover at a given site was calculated from the mean of the midpoint values of all cover categories in 300 linear segments per site. For each of the three study sites, species richness and diversity (standardized Shannon diversity index; $-\sum p_i \ln(p_i) / \ln S$, where p_i is the absolute cover of a given species and S is the species richness) were calculated for each year [36].

2.4. Statistical Analyses

For each site, a Shapiro-Wilks test was used to check normality of the dataset. Then, a General Linear Model for Repeated Measures (GLMRM) was applied using the R software [37]. The GLMRM procedure provides analysis of variance when the same measurement is made several times on each subject or case. Between-subject factors (in our case functional groups and altitude) are used to divide the dataset into groups. Using such a procedure, one can test null hypotheses about the effects of between-subjects factors (functional group, altitude) and within-subjects factors (time). Principal component analyses (PCA) [38] were conducted to evaluate changes through time in the relative abundance of the different plant functional groups (lichens, mosses, herbs, ericaceous species, dwarf birch shrub species, hereafter called the shrubs) over 21 years. PCA were conducted on the absolute cover (percentage) data of each functional group using the Vegan package in R software [38].

3. Results

3.1. Cover

The alpine, subalpine and lichen woodland sites showed major differences in their short-term response to fire disturbance (Figure 2). Only a few weeks after the fire, the plant cover in the subalpine site was greater than 30% compared to 7% and 13% in the alpine and lichen woodland sites, respectively. According to the GLMRMs, the different functional groups at each of the three study sites did not respond similarly through time during the post-fire succession (interaction between time, functional group and altitude; $p < 0.0001$).

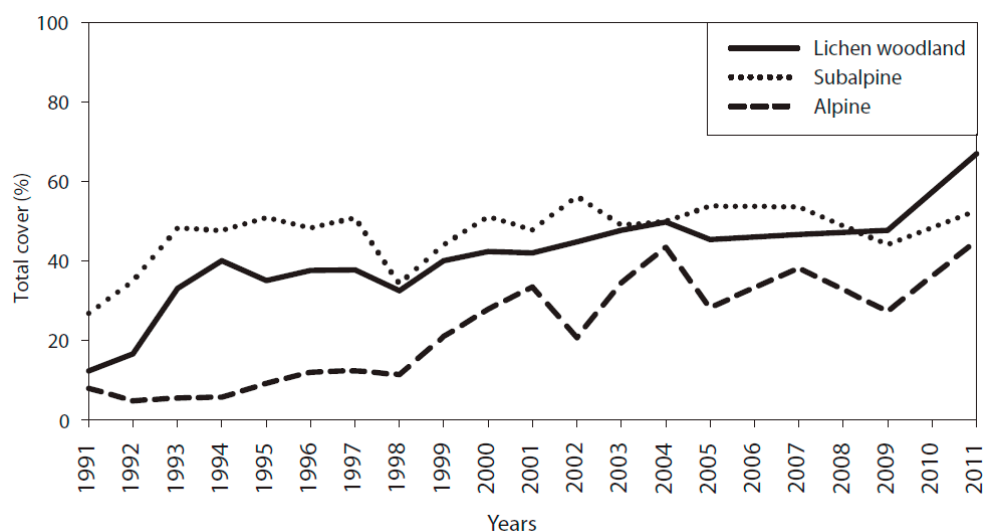


Figure 2. Vegetation cover in the lichen woodland, subalpine and alpine sites along the postfire chronosequence (extrapolated data in 2006, 2008 and 2010), Parc des Grands-Jardins, southern Quebec (Canada).

In the lichen woodland (Figure 3, black bars), plant cover slowly increased throughout the study period and showed a maximum cover of 40% in 2004. The cover of ericaceous species (mostly *Vaccinium angustifolium*) increased rapidly during the first three years of post-fire succession (from 7 to 26%) and stabilised around 18%. The shrub cover was constant throughout the study period, averaging 6% of cover. Lichens were first recorded 7 years after fire and increased to about 12% between 2002 and 2005. As shown by the high frequency, ericaceous (in 81% of the 10-cm segments) and lichen (78%) species were well distributed in the site at the end of the survey. In the subalpine site (Figure 3, light grey bars), the plant cover developed more rapidly, peaking at 74% in 2005. The plant cover is largely dominated by ericaceous species (*Vaccinium angustifolium*, *Vaccinium vitis-idaeae*, *Rhododendron groenlandicum*), which averaged 39% cover during the course of this study. Mosses (*Polytrichum* sp.) became relatively abundant a few years after the fire (average 9% of cover from 1995–2000) but decreased steadily after 2000, i.e., 10 years after the fire. Herbs (11%), lichens (8%) and shrubs (5%) appeared in 2007. Ericaceous species were well distributed in the site (recorded in 93% of the 10-cm segments) while herbs and lichens were recorded in 27% and 20% of the segments, respectively. In the alpine site (Figure 3, dark grey bars), the plant cover was comparable to the one recorded in the lichen woodland site and peaked at 42% in 2004. Mosses (*Polytrichum* sp.) were the dominant functional group, covering up to 26% of the soil surface, although they were much less abundant in dry summers of 2002 and 2005. Ericaceous species (10%) and lichens (8%) were also relatively abundant. Mosses, lichens, and ericaceous species were well distributed in the sites as shown by their recorded frequencies (67, 48 and 32%, respectively).

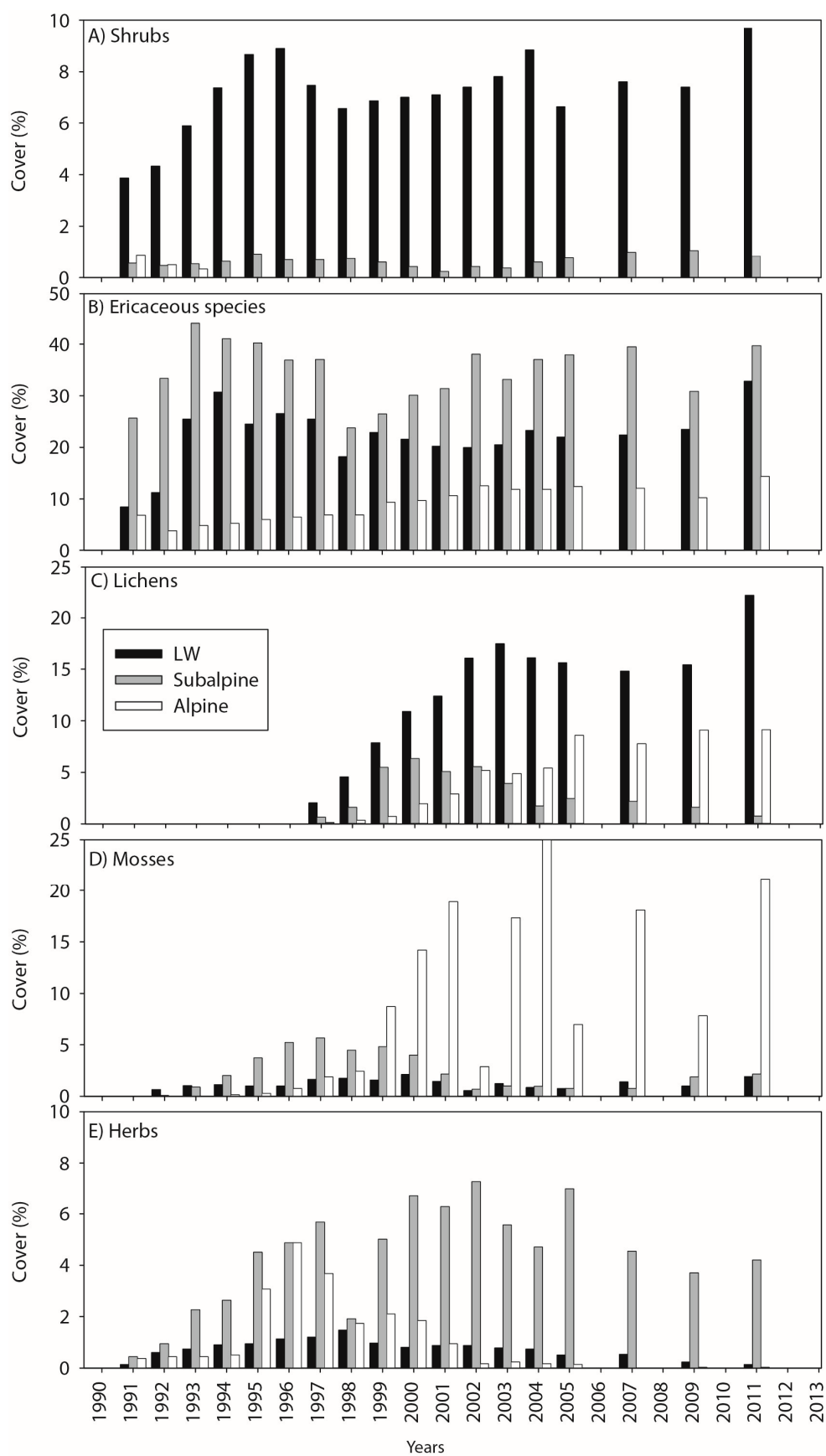


Figure 3. Total cover of shrubs (A), ericaceous species (B), lichens (C), mosses (D) and herbs (E) in lichen woodland (LW, black), subalpine (grey) and alpine (white) sites along the postfire chronosequence.

3.2. PCA Analysis

Principal component analysis was used to ordinate the composition of ground vegetation through time for each of the study sites (Figure 4). The first two PCA axes accounted for 62.5% of the variance. Axis 1 (37.84% of the variance) was positively correlated with ericaceous cover (score of 0.47) and herbs cover (0.84). On the other hand, it was negatively correlated with shrubs (−0.68), lichens (−0.70) and mosses (−0.15). Axis 2 accounted for an additional 32.89% of the variance and was positively correlated with mosses (0.72) cover and negatively correlated with shrubs (−0.65), ericaceous (−0.71), lichens (−0.36) and herbs (−0.29) cover. PCA results showed that opposed variables on axis 1 were related to fire severity. Indeed, lichens and shrubs are much more abundant where fire severity is low as in lichen woodlands. On the other hand, opposed variables on axis 2 were mainly related to altitude as mosses were the dominant species in alpine and subalpine sites.

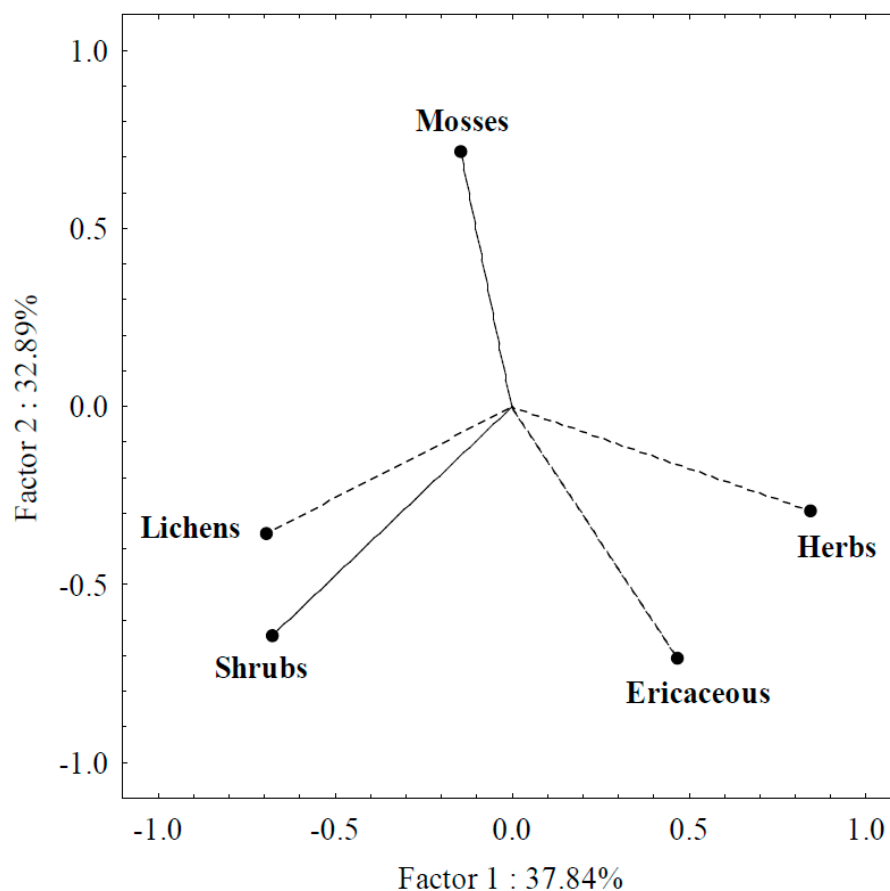


Figure 4. Principal component analysis (PCA) of the functional groups among the postfire sites. Only variables are shown to facilitate reading. Factor cases are shown at Figure 5.

Based on the total cover of the different functional groups for a given year at each site, PCA reveals different successional pathways according to the site. Ground vegetation of the lichen woodland (Figure 5A) appears to be closely associated with the abundance of lichens and shrubs. As succession proceeds, lichen cover increases and is expected to become the dominant functional group. Ground vegetation of the subalpine site (Figure 5B) can be discriminated by the very high ericaceous cover and the somewhat high herbaceous cover while the lichen cover is not sufficiently developed to be of significant importance. In the alpine site (Figure 5C), the relatively high moss cover explains most of the segregation. However, the increase in the lichen cover at the very end of the survey suggests that lichens might become more important in the following years.

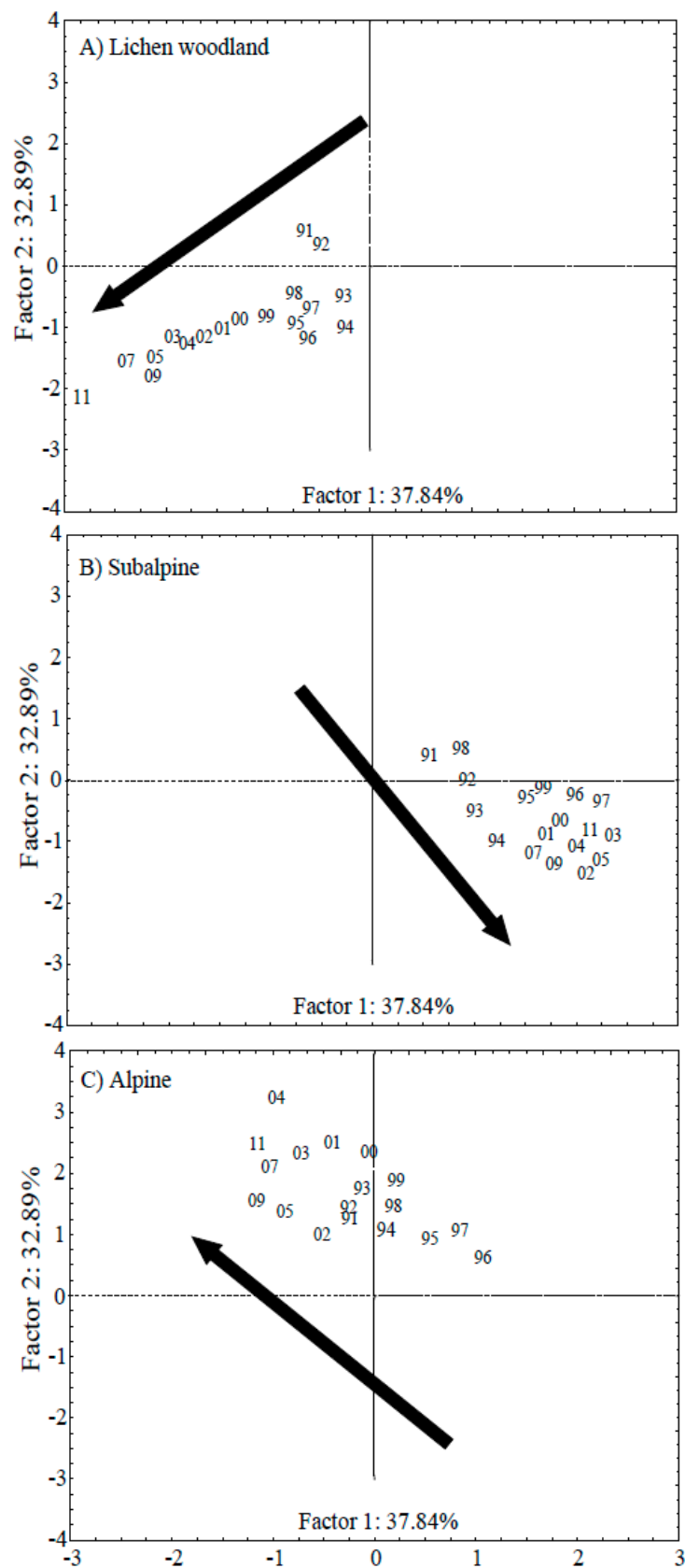


Figure 5. Principal component analysis (PCA) of the functional groups among the postfire sites. Only factor cases per experimental site are shown to facilitate reading. Variables are shown at Figure 4. The arrows represent the successional pathways for each site.

3.3. Species Richness and Shannon Diversity Index

Species richness was higher in the subalpine site than in the other 2 sites (Figure 6A). While species richness remained low in the alpine site throughout the study period, it progressively increased with time in the lichen woodland. Although initial differences between the sites could be observed, the Shannon diversity index is quite similar for the three sites by the end of the experiment despite differences in species richness (Figure 6B). While the diversity index of the lichen woodland was quite stable through 2007, the diversity of the subalpine site, which was the lowest of the three sites in 1991–1992, increased steadily up to 1999. The diversity of the alpine site decreases sharply between 1991 and 1994 but stabilised afterwards.

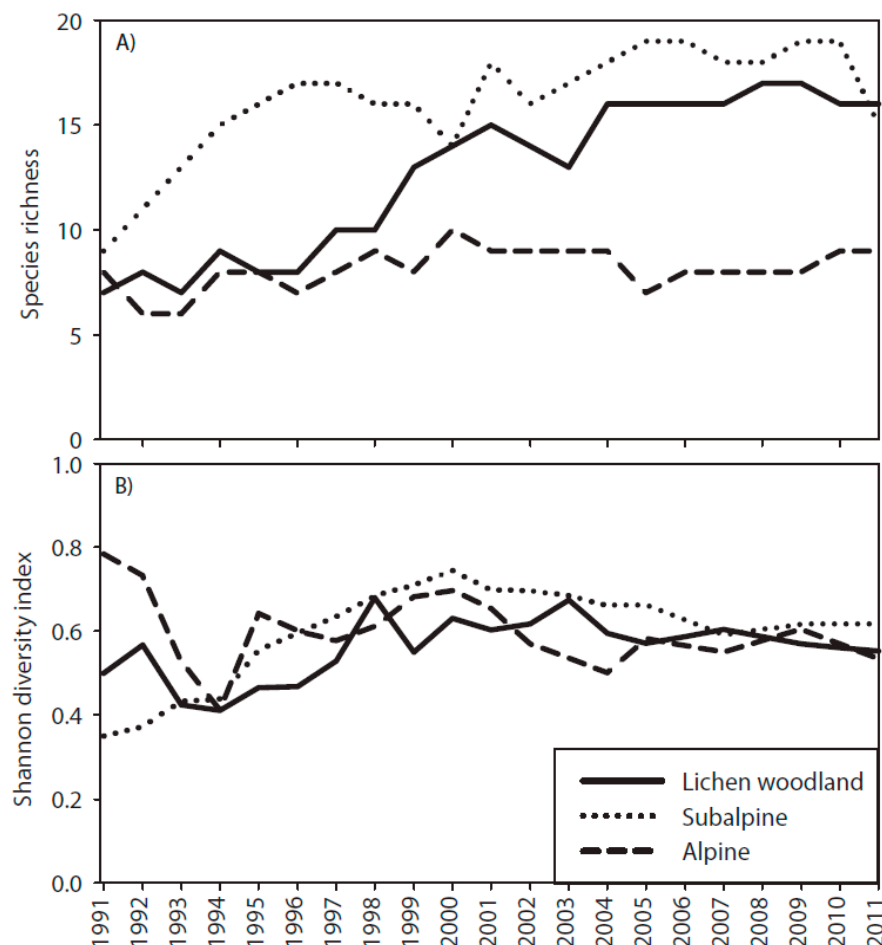


Figure 6. Species richness (A) and Shannon diversity index (B) of lichen woodland (solid line), subalpine (dotted line) and alpine (dashed line) sites.

4. Discussion

The regional mosaic of vegetation in the boreal forest comprises a mixture of successional stages and the pattern is mainly controlled by fire, soil conditions and climate [39]. Fire return intervals determine the time available for successional processes to operate, and are crucial for tree species that take many years to reach reproductive stage or to attain a size and morphology enabling them to survive a fire [40]. Maximum floristic diversity is generally attained when a large spectrum of successional communities is maintained throughout the landscape [13]. In our experimental sites, succession was triggered by interactions between climatic conditions due to elevation, fire characteristics (severity and frequency), site characteristics (moisture, drainage, texture, soil depth) and plant regeneration traits [14,41]. In the alpine site, the 1991 fire consumed most of the organic matter

down to the mineral soil. The alpine site was a convex summit, well exposed to dominant wind that favoured organic consumption. The fire caused more damages to vegetation than in the subalpine or the lichen woodland sites where vegetation survival was higher. In comparison, the lichen woodland site was protected from the wind. Field observations showed that the residual organic matter was thicker in the lichen woodland than on wind-exposed sites following the 1991 fire. As a result, plant assemblage is rather different between sites and residual organic matter proved to be a key factor explaining regeneration in experimental sites.

Shrub species play an important role in postfire regeneration. Their early and rapid reappearance after a surface fire promotes soil stability by providing a vegetative cover and acting as a sink for nutrients mobilized by fire [42]. The ericaceous shrub cover was low throughout the chronosequence in the alpine site, as *Vaccinium* establishment in 1991 was null or minor because of death of rhizomes due to fire severity. However, the rapid resurgence of ericaceous shrubs and lichens in the lichen woodland and subalpine sites due to less-severe fires suggests that local plant succession is a repetitive process involving relatively similar pre- and post-fire plant assemblages. The resistance of ericaceous rhizomes is directly related to fire severity, i.e., the amount of organic matter consumed. As rhizomes are located in the basal part of the organic matter horizon and in the upper part of mineral horizons, a light fire (low severity) will have a positive impact on the regeneration of ericaceous shrubs. Alternatively, with greater fire severity most of the organic matter is consumed and mineral soil is heated, causing local extinction or minimal regeneration [43,44]. On recently disturbed soils, rhizomes of ericaceous shrubs are stimulated by light and high soil temperatures [45], favouring extensive recovery following fire if the ericaceous species were abundant before the fire. Among ericaceous shrubs, rhizomes of *Vaccinium angustifolium* L. are the most resistant to heat [46]. In contrast to the lichen woodland and subalpine sites, fire severity exacerbated by the thin and dry soil of the alpine site was likely detrimental to survival, establishment and growth of rhizomatous ericaceous shrubs. In contrast, frost boils (barren soils) caused by frost heaving formed early after fire, in 1994 and 1995 in particular, and were favourable seedbeds for several herbs and subshrub species like *Mononeuria groenlandica* (Retzius) Dillenberger & Kadereit and *Aralia hispida* Ventenat to establish and to expand. Frost-induced root upthrusting also was a local disturbance factor causing plant death over the 21 years of the alpine chronosequence.

Bryophyte and lichen species were not an important component of the plant cover during the first years of post-fire succession. For all three sites, lichens were the last functional group to establish. It took 7 years (1997) after fire for the primary lichen thallus to establish on the blackened ground. *Cladonia cristatella* Tuck. is among the first cup lichens to colonize the lichen woodland and the subalpine sites in 2001 but later, in 2007, in the alpine site. Other cup lichens (*Cladonia crispata*, *C. deformis* and *C. gracilis*) also established 9–10 years after fire in the lichen woodland and subalpine sites. Fruticose *Cladonia* lichens colonized the lichen woodland site in 2001 (*Cladonia stellaris*) and 2005 (*Cladonia rangiferina*) and the subalpine site in 2007 (*Cladonia mitis*) and 2009 (*Cladonia stellaris*), but not the alpine site. Nonvascular species are not a large part of early post-fire plant assemblages because of their inability to grow rapidly in response to increased resources following disturbance and competition from vascular plants [47]. The cover of the different functional groups of the lichen woodland site differs with the vegetation survey realised by Morneau and Payette [48] in two subarctic sites (4 and 14 years after a fire). In the years following the fire, the ericaceous shrub cover in the lichen woodland site was 5 times greater than the one in the subarctic lichen woodland, while the shrub cover and birch was also higher in the lichen woodland site. By year 14 in the successional process, ericaceous and dwarf birch (*Betula glandulosa* Michx.) covers appeared to be similar between the two environments whereas lichen and moss covers were higher in the subarctic lichen woodland than in the lichen woodland site.

Rouse [49] studied ecological changes 1, 2, 3 and 25 years after fire in subarctic lichen spruce woodlands, similar to our survey, and compared their microclimatic regime with that of a mature lichen woodland. A sharp decrease in net radiation was observed at recently burned sites, accompanied

by a greater decrease in evaporation except at the most recently burned site. The albedo gradually increases from the youngest to the oldest fire sites, causing a corresponding decrease in the solar radiation absorbed.

Changes in herb abundance and composition are generally related to changes in the abiotic conditions (frost-induced barren soils), in the alpine site in particular. In the subalpine and alpine sites, rapid colonization of disturbed microsites by *Chamerion angustifolium* L. (commonly known as fireweed), a shade-intolerant, pioneer species, was observed early in the chronosequence (in 1992 and 1993). In contrast to the herb cover in the subalpine site ($\approx 40\%$ after five years), the herb cover was low in the lichen woodland and alpine sites with a $<5\%$ cover throughout the chronosequence. The course of succession was predictable from species life history characteristics of postfire species such as establishment ability, longevity and light tolerance [50].

Tree species have a minor influence on the early post-fire light environment and only affect the understory light environment when canopy closure occurs. Tree distribution at high elevation such as in the alpine site is limited by temperature and snowpack. In alpine areas where water loss is important due to extreme climatic conditions, seedling establishment occurs when a wet period provides adequate soil moisture and barren soil conditions for seedling growth and establishment. Several *Betula papyrifera* Marsh. seedlings became established eight years after fire, suggesting that climate was favourable for survival and growth. In contrast, in the subalpine site, only one balsam fir seedling established late after fire, in 2009, whereas three black spruce seedlings colonized the lichen woodland site several years after fire, in 2001, 2009 and 2011, respectively. Extreme soil temperatures have a negative impact on the survival of tree seedlings. Freezing soil and cold air temperatures inhibit tree establishment, and damage plant tissues directly through intercellular freezing and indirectly by dehydration resulting from extracellular freezing. Seedlings are more sensitive than mature trees to frost heaving because their shallow roots break or are exposed to desiccation as it has been the case in the alpine site during the first 10 years of the chronosequence.

5. Conclusions

Although located in a southern region, all sites investigated in this study are representative of the northern vegetation zones of the Canadian boreal forest. Combination of stand disturbance, elevation and climate trigger natural regeneration of the forest. However, in the Park area, successive stand disturbances have reduced the black spruce cover and conifer stands shifted into lichen woodlands and parklands similar to those found in the northern parts of the Canadian boreal forest (Payette & Delwaide, 2003). In this study, we have monitored the postfire succession of three contrasted environments, lichen woodland, subalpine and alpine sites. The similarity between secondary succession in the three sites is that lichens became established around the seventh year following fire. Otherwise, successional pathways were different in all three sites. In the lichen woodland site, vegetation establishment was mainly influenced by thickness of the lichen mat and the rapid resurgence of ericaceous shrubs which reduced herb and moss establishment. In the subalpine site, ericaceous shrubs emerged rapidly following fire but the low abundance of lichens allowed herbs to establish. In the alpine site, colonization of frost-disturbed soil was characterized by the rapid establishment of herbs, subshrubs and ericaceous shrubs followed by mosses a few years later. Colonization of disturbed soil was rapid in each chronosequence, with communities dominated by fast-growing vascular plants. Species richness increased rapidly on exposed mineral soil to almost continuous plant cover within five to seven years after fire. Species present following fire in all three sites were the result of local colonization from buried seeds and propagules located in the organic layer. In all sites, increased abundance of early successional vascular species, as well as bryophytes on specific microsites, increased plant diversity.

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Author Contributions: Serge Payette conceived and designed the experimental design; Serge Payette & Ann Delwaide performed the experiments; Francois Girard and Serge Payette analyzed the data and wrote the paper.

Conflicts of Interest: The authors declare no conflict of interest.

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