

# Spatial vegetation diversity index along a postfire successional gradient in the northern boreal forest<sup>1,2</sup>

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**Abstract:** Boreal forest dynamics and biodiversity are mainly governed by natural disturbances such as fire. Because boreal forest communities are typically species-poor and composed predominantly of wide-ranging circumboreal species, all measurements of biodiversity using the most common species richness-based indices are likely to underestimate vegetation diversity at the stand level. To estimate vegetation diversity differences, we introduce a spatial diversity index (SDI), which accounts not only for species richness and species abundance, but also for the spatial occupancy of species, a neglected although important component of plant diversity. We tested the SDI along a postfire successional gradient of the lichen woodland zone in northern Québec using eleven sites with different postfire ages. The SDI allowed us to statistically differentiate three species' spatial occupancy patterns, which correspond to three successional stages (pioneer, expansion and stabilization). In our study, we were unable to discriminate between these three successional structural phases using only Simpson and Shannon diversity indices. We conclude that indices based only upon species richness and species abundance may fail to differentiate vegetation diversity between sites in the boreal forest, whereas the spatial diversity index has succeeded because it incorporates species space occupancy.

**Keywords:** boreal forest, postfire succession, lichen, moss, liverwort, patchiness, spatial occupancy, spatial diversity index.

**Résumé:** La dynamique et la biodiversité de la forêt boréale sont principalement assurées par les perturbations naturelles comme les incendies de forêts. Étant donné que les communautés forestières boréales sont des écosystèmes pauvres en terme de diversité d'espèces, toute estimation de la biodiversité, à l'aide des indices basés seulement sur le nombre et l'abondance d'espèces, est sujette à sous-évaluer la diversité végétale à l'échelle du peuplement. Afin de différencier les valeurs de diversité végétale, nous avons établi un indice de diversité spatiale (IDS) qui tient compte non seulement de la richesse spécifique et de l'abondance des espèces mais aussi de leur répartition spatiale. Nous avons testé le IDS à l'aide de données prises dans onze sites le long d'un gradient successional après feu en forêt boréale, dans le nord du Québec. Contrairement aux indices de Simpson et de Shannon, le IDS a permis, dans notre étude, de distinguer de manière significative trois patrons de répartition spatiale des espèces correspondant à autant de stades structuraux de la succession (pionnier, expansion et stabilisation). Nous en concluons que le IDS permet de mieux apprécier la diversité végétale en forêt boréale, grâce à l'ajout de la structure de la végétation.

**Mots-clés:** forêt boréale, succession après feu, lichen, mousse, hépatique, répartition spatiale, indice de diversité spatiale.

## Introduction

Fire, a natural disturbance, plays a major role in shaping boreal forest landscapes (Heinselman, 1973; Johnson, 1992; Payette, 1992). This disturbance starts a sequence of processes which favor the maintenance of biodiversity by creating a mosaic of forest stands of different ages, and by promoting the re-invasion of early successional species in burned areas. Most boreal woody species are adapted, in varying degrees, to fire events.

Boreal forest communities are usually considered species-poor because they are composed of a small number of woody species. However, they also have a relatively high number of non-vascular species, mostly lichens and mosses, (Bergerud, 1971; Maikawa & Kershaw, 1976; Black & Bliss, 1978; Johnson, 1981; Foster, 1985; Morneau & Payette, 1989; Crête *et al.*, 1995; Hanski & Hammond, 1995). Changes in fire regime due to human-caused distur-

bances such as logging and climatic changes may have important impacts on biodiversity in these ecosystems. Increases in the frequency of fire events could result in the loss of some of these plant species, which could have dramatic effects on the overall boreal forest mosaic, thus in turn threatening wildlife biodiversity (Shugart *et al.*, 1992).

To quantify the impacts of fire regime changes on boreal forest diversity, and to help forest managers identify the most diverse forests to be preserved (Haila, 1994), we need, first and foremost, to accurately estimate plant diversity. The major problem in discriminating among plant diversity values in boreal forests comes from the fact that throughout succession, there is no real record of vascular plant species replacement during the postfire recovery process. Boreal vegetation diversity measurements should therefore be based not only on woody species but also on other vascular species as well as non-vascular species, such as liverworts, mosses and lichens which are the species showing significant changes during postfire succession (Maikawa & Kershaw, 1976; Johnson, 1981; Foster, 1985; Morneau & Payette, 1989). Indeed, most species recorded in the early postfire stages are also found in late-successional stages;

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only their pattern of space occupation seems to change. Therefore, the assessment of plant diversity in such ecosystems may become problematic when it is estimated using diversity indices that rely mostly on species number and species abundance.

Shannon and Simpson indices consider only species richness and species abundance in the calculation of diversity (Peet, 1974; Magurran, 1988). Because both species richness and species abundance vary throughout succession, diversity values based only on these data are difficult to compare, and are often meaningless without a good understanding of the successional context in which the data were collected (Huston, 1994). Other biological and ecological traits pertaining to the general diversity of boreal ecosystems, such as the change in plant spatial occupation through time (Czárán, Bartha & Podani, 1993; Ricklefs & Schluter, 1993; Huston, 1994), may be more helpful in accurately evaluating boreal vegetation diversity. Furthermore, because several plant species have a clonal growth habit (Pielou, 1993), the use of species spatial occupancy, measured by their degree of patchiness, appears to be appropriate when evaluating plant species diversity at the stand level. Because plant spatial occupancy is one of the most important components allowing the discrimination of clonal and non-clonal plants through succession in open boreal forest (Morneau & Payette, 1989), it should be incorporated into vegetation diversity indices. This allows us to take into account the successional context of the species at the time of sampling, and to more adequately compare diversity values from different sites and successional stages.

The objective of this study is to illustrate how spatial structure is relevant to differentiation and comparison of vegetation diversity for stands of different ages. We propose a spatial diversity index (SDI) which allows the quantification and comparison of plant diversity based on species richness, species abundance, and species spatial structure. More specifically, we evaluated vegetation diversity using SDI in the fire-voir in the James Bay area of northern Québec (Canada).

## Material and methods

### STUDY AREA

The study area is part of the lichen woodland zone of the boreal forest (Ducruc *et al.*, 1976; Gerardin, 1980; Payette, 1992; Sirois, 1992), about 200 km east of James Bay (Figure 1). The regional forest cover consists of lichen forest stands on well-drained sites; the canopy layer is dominated by either black spruce (*Picea mariana* [Mill.] BSP.) or jack pine (*Pinus banksiana* Lamb). The ground layer is dominated by either low shrubs in early postfire stands, or lichens in late postfire stands (Gerardin, 1980; Morneau & Payette, 1989). The fire rotation period in the open boreal forest is estimated at about 100 years (Payette *et al.*, 1989).

Eleven sites surrounding the La Grande 3 (LG3) hydroelectric reservoir (Figure 1) were sampled along a postfire successional gradient to identify changes in vegetation diversity. We stratified *a priori* our sampling sites into four age-based stands of well-drained forests. Location of each site within each stratum was randomly selected among the well-drained forests accessible from the road that had com-

parable slope and orientation to minimize differences among sites not related to the postfire successional gradient. The four postfire stages of well-drained forests are stratified according to stand age (Figure 2) and dominant lichen cover (Morneau & Payette, 1989; Marineau, Fortin & Payette, 1994): three stage I sites were located in the only area burned in 1989 (each sampling site was selected randomly within this area); three stage II sites were located in three young forests originated by three different fire events (16, 24, and 28 year-old fires) and dominated by *Cladonia sp.*; three stage III sites were located in three young forests, with trees about 5 m in height, originated by two different fire events (50 and 51 year-old fires) and dominated by *Cladina mitis* and *Cladina rangiferina*; and two stage IV sites were located in two mature forests originated by two different fire events (71 and 110 year-old fires) and dominated by *Cladina stellaris*. At each site, the postfire stand age was determined by fire-scar dating of five dominant trees.

At that latitude (53°-54° N), black spruce and jack pine stands are open forests dominated by a continuous lichen cover. Tree density is therefore low and most of the species are clonal. Hence to obtain a good estimate of the relative abundance of non-vascular and vascular species, the point-sampling method was used (Mueller-Dombois & Ellenberg, 1974) whereby each species that vertically touches a dropped pin was recorded. Although this method is time consuming, it is still the most rapid method to identify the mosses, liverworts and lichens. Furthermore, this method has the advantage of providing relative abundance data for non-vascular and vascular species as well as their *x-y* coordinates, information that is needed to characterize their spatial distribution for the spatial diversity index. Given that in this open forest most of the diversity lies in the non-vascular species, a quadrat of 10 m × 20 m is sufficient to identify

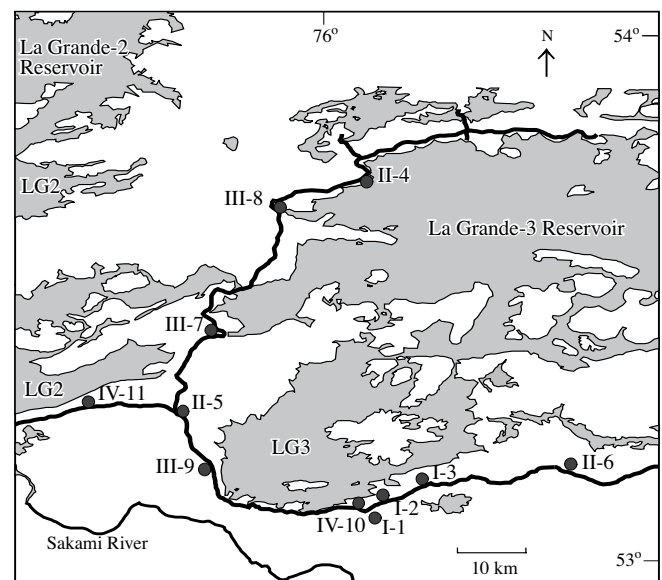


FIGURE 1. Location of the eleven sampling sites around the La Grande-3 hydroelectric reservoir. The bold solid line is the road around the reservoirs. LG2 stands for La Grande-2 reservoir and LG3 for La Grande-3 reservoir. Roman numerals indicate stand stage and Arabic numbers indicate site number.

most of the species diversity (Morneau & Payette, 1989). The quadrats were randomly located in each postfire successional stand. Each quadrat was then subdivided by a 50 cm grid corresponding to a matrix of 21 points by 41 points, for a total of 861 sampling points. At each point, plants were identified using Scoggan (1978), and Morisset, Lavoie & Payette (1987) for vascular plants, Crum & Anderson (1981) and Anderson, Crum & Buck (1990) for mosses, Stotler & Crandall-Stotler (1977) for liverworts, and Thompson (1984) and Egan (1987) for lichens.

SPATIAL DIVERSITY INDEX

There are several types of diversity indices (Magurran, 1988; Cousins, 1991; French, 1994), all seeking to provide better and different insights into species diversity. We acknowledge the fact that diversity indices must bring a significant additional understanding of community structure. Given that the most distinctive inherent property of plants is their occupation of space, we suggest incorporating this feature into the estimation of vegetation diversity. By introducing the proposed SDI, we wish to illustrate the need to consider spatial structure in order to gain a better understanding of vegetation diversity.

Recently, developments in landscape ecology have brought new indices that quantify landscape pattern and diversity (O'Neill *et al.*, 1998; McGarigal & Marks, 1995; Riitters *et al.*, 1995). Although there are several statistics that quantify vegetation pattern (Legendre & Fortin, 1989), our interests are in identifying and quantifying the diversity in small-scale (< 200 m<sup>2</sup>) patterns of species spatial occupancy. Therefore, unlike the landscape diversity indices that measure patch diversity (*i.e.*, using patches as species), we are including the within-stand vegetation spatial structure to better compare vegetation diversity values at the stand level.

Our proposed index characterizes the variability in species spatial occupation using their degree of patchiness. Given that in the present study the sample points are laid out in a regularly spaced grid pattern, species patches will be delimited by grouping neighbor sample points where the species is recorded. A patch is therefore an area where a species is present at spatially adjacent sampling points and is delineated by the absence of individuals of that species at the adjacent sampling points. We are assuming that each species present at a sample point covers potentially the same area (here 50 cm<sup>2</sup>), and that the sample point is at the center of this area. The area occupied by a species per patch is the number of sample points within the patch; the total area occupied by a species over the study site is the sum of the areas (the number of sample points) for all the patches of that species. Hence, the SDI is the summation of the ratio of the number of patches per species and the range of area occupied,

$$SDI = \sum_{i=1}^S \frac{\text{number of patches of species } i}{\text{range of area occupied by species } i} \quad [1]$$

where *S* is the number of species, the “number of patches of species *i*” is the number of patches formed by species *i*, and the “range of area occupied by species *i*” is the largest area (the largest patch in terms of sample points) minus the smallest area (the smallest patch) of species *i*. The numera-

tor has no unit while the denominator is a measure of the area occupied by a species. Here this measure is in terms of number of sampled points. When there is only one patch for a species, the range of area occupied is simply the number of sample points in the patch. Hence when there is only one sample point per patch, the range of area occupied is 1. Thus, a ratio of 1 characterizes isolated individuals of a species. The value of the ratio decreases as the patches increase in area, as normally occurs during succession.

To compare the efficiency of the SDI to detect changes in diversity along the postfire chronosequence, we also computed species richness (number of species), the Simpson diversity index which reflects species relative abundance, and the Shannon diversity index, which combines species richness and relative abundance (Magurran, 1988).

SPECIES SPATIAL OCCUPANCY IN BOREAL FOREST

Species spatial occupancy varies tremendously across ecological and successional gradients. It varies from a scattered occupancy of space by seedlings, often sprouting during the colonization phase, to the patchy occupancy of space by species filling space through vegetative growth during the expansion phase, to the final stabilization phase during late succession (Bormann & Likens, 1987).

In North American boreal forests, fire creates a colonization phase where black spruce and jack pine seeds are released from serotinous cones to germinate over the burned area, while most broad-leaved trees and shrub species sprout from surviving underground buds and suckers. Similarly, lichens, liverworts, and mosses re-invade burned sites through diaspore dispersal and sometimes sprouting (Morneau & Payette, 1989). Hence, seedlings are spread over the entire burned area, but often with a contagious pattern associated with favorable seedbeds provided by the fire-killed trees. If a particular seedling from one species is surrounded by seedlings of other species, the area occupied by this first seedling can be seen as a small isolated patch.

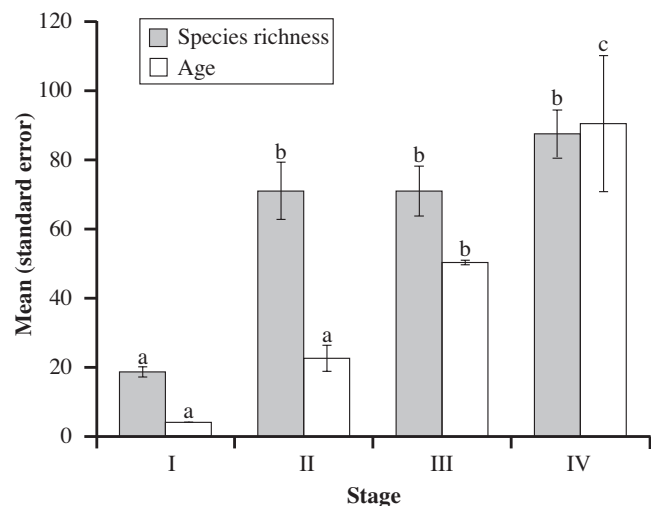


FIGURE 2. Mean and standard error of species richness and age (in years) since the last fire event of the eleven sampling sites around the La Grande-3 hydroelectric reservoir. For each variable, means with the same letter are not significantly different based on Waller-Duncan multiple comparison tests.

The colonization phase is often formed from a large number of small, intermingled patches of different species. Furthermore, since each species shows a comparable use of space (*i.e.*, a patch formed by one individual stem or clone), then it results mainly in a linear relationship between the number of patches and the area covered (Figure 3). The colonization phase is therefore characterized by a small variation in species space occupancy (*i.e.*, a low variance in patch size).

Occasionally following a fire, the majority of species composing the lichen woodland ecosystem have re-invaded the burned sites and species richness reaches its maximum about 25 years after fire (Morneau & Payette, 1989). Therefore, the main changes after 25 years are not so much linked to species richness, but rather to species abundance and distribution. Indeed, lichens, liverworts, and mosses grow vegetatively and space occupancy by individual plants increases, which implies that patch size (total area) increases due to vegetative (clonal) growth. Similarly, vascular plants expand through vegetative growth but at a slower rate. Given that each species does not have the same competitive ability, some species will eventually take over. This expansion phase is characterized by a high degree of variability in terms of species space occupancy and a high variance in patch size.

Finally, species richness drops slightly during the stabilization phase due to differential mortality rates, species' shade tolerance, and spatial expansion, resulting in variability in species' competitive ability to occupy space. This stabilization phase is therefore characterized by larger patches for few species and small isolated patches for others. Overall, however, this phase shows less variability in terms of species space occupancy than the previous expansion phase, which results in an intermediate range of variability in terms of patch size.

### Results and discussion

A total of 149 species were identified over the 11 sites: 49 vascular plants, 27 mosses, 10 liverworts, and 63 lichens (Table I). As Figure 2 illustrates, species richness increases throughout the postfire succession although the main difference in mean species richness per stage is between stage I and all the others ( $F = 24.68, p < 0.0004$ ). Although the sampled sites were randomly selected for each postfire age group among the well-drained forests having comparable slope and orientation, some sites were characterized by microtopographic heterogeneity which contributed to the presence of some mesic-site species. This heterogeneity adds some diversity while not diminishing the overall chronosequence diversity signal.

TABLE I. Abundance of species per stage (I, II, III, IV) for the 11 well-drained sites around the La Grande-3 hydroelectric reservoir. The number in parentheses is the percentage of sites where the species is present (stages I, II and III have 3 sites; stage IV has 2 sites). Abundance in italics indicates species that show a linear relationship (colonization phase), bold abundance indicates species in expansion, and normal abundance indicates not the same occupation of space in each site of a stage

Stage	I	II	III	IV
<b>MOSESSES</b>				
<i>Aulacomnium palustre</i>		21 (33)	<b>108</b> (100)	4 (33)
<i>Brachythecium oedipodium</i>			2 (33)	
<i>Buxbaumia aphylla</i>		1 (33)	1 (33)	
<i>Ceratodon purpureus</i>	2 (33)	1 (33)	1 (33)	
<i>Dicranum fuscescens</i>		5 (33)	6 (66)	14 (100)
<i>Dicranum polysetum</i>		6 (33)	23 (100)	12 (50)
<i>Dicranum scoparium</i>		7 (33)	22 (66)	4 (50)
<i>Dicranum undulatum</i>		125 (100)	252 (100)	23 (50)
<i>Drepanocladus uncinatus</i>		1 (33)	1 (33)	
<i>Isopterygiopsis pulchella</i>		1 (33)		
<i>Plagiothecium laetum</i>			1 (33)	
<i>Pleurozium schreberi</i>	10 (33)	<b>132</b> (66)	<b>1215</b> (100)	<b>681</b> (100)
<i>Pohlia nutans</i>	1 (33)	<b>514</b> (100)	175 (100)	8 (100)
<i>Polytrichum commune</i>		26 (66)	<b>170</b> (66)	3 (50)
<i>Polytrichum juniperum</i>	23 (33)	144 (100)	29 (66)	
<i>Polytrichum piliferum</i>	29 (66)	<b>706</b> (100)	10 (66)	13 (100)
<i>Polytrichum strictum</i>		<b>285</b> (66)	144 (100)	1 (100)
<i>Ptilium crista-castrensis</i>		1 (33)	37 (100)	9 (50)
<i>Racomitrium heterostichum</i>		1 (33)	24 (100)	10 (50)
<i>Sphagnum angustifolium</i>		1 (33)	4 (33)	
<i>Sphagnum fuscum</i>		26 (33)	86 (100)	1 (50)
<i>Sphagnum girgensohnii</i>			8 (33)	
<i>Sphagnum nemoreum</i>		44 (33)	<b>409</b> (100)	1 (50)
<i>Sphagnum rubellum</i>		5 (33)	9 (100)	
<i>Sphagnum russowii</i>		31 (33)	9 (100)	
<i>Sphagnum warnstorffii</i>			37 (33)	
<i>Tomenthypnum nitens</i>			38 (33)	
<b>LIVERWORTS</b>				
<i>Barbilophozia attenuata</i>				2 (50)
<i>Barbilophozia hatcheri</i>			3 (33)	1 (50)
<i>Calypogeja muelleriana</i>		7 (33)	15 (66)	
<i>Calypogeja trichomanis</i>			1 (33)	
<i>Cephalozia sp.</i>		85 (100)	7 (66)	5 (100)

TABLE I. (continued)

Stage	I	II	III	IV
<i>Lophozia bicrenata</i>		66 (100)	33 (100)	9 (100)
<i>Lophozia sp.</i>		1 (33)	1 (33)	1 (50)
<i>Mylia anomala</i>		126 (100)	97 (100)	
<i>Ptilidium ciliare</i>		3 (66)	44 (66)	<b>401</b> (100)
<i>Ptilidium pulcherrimum</i>			1 (33)	5 (100)
LICHENS				
<i>Arctoparmelia centrifuga</i>	2 (33)	1 (33)	<b>13</b> (33)	
<i>Baeomyces rufus</i>		6 (66)		
<i>Bryoria furcellata</i>		41 (33)	5 (33)	123 (100)
<i>Bryoria lanestrus</i>		2 (33)	5 (66)	195 (100)
<i>Cetraria arenaria</i>		1 (33)		
<i>Cetraria ericetorum</i>		81 (100)	18 (100)	9 (100)
<i>Cetraria hepaticum</i>			1 (33)	
<i>Cetraria islandica</i>		1 (33)	1 (50)	
<i>Cetraria pinastri</i>		115 (100)	172 (100)	82 (100)
<i>Cladina mitis</i>	1 (33)	<b>974</b> (100)	<b>1120</b> (100)	<b>530</b> (100)
<i>Cladina rangiferina</i>	1 (33)	<b>327</b> (100)	609 (100)	<b>475</b> (100)
<i>Cladina stellaris</i>		57 (100)	52 (100)	<b>1275</b> (100)
<i>Cladonia bacillaris</i>		70 (100)	9 (100)	6 (100)
<i>Cladonia botrytes</i>		74 (100)	2 (66)	2 (50)
<i>Cladonia cenotea</i>		34 (100)	8 (100)	21 (100)
<i>Cladonia coccifera</i>		60 (100)	5 (33)	10 (50)
<i>Cladonia coniocraea</i>		2 (33)	3 (66)	2 (50)
<i>Cladonia cornuta</i>		292 (100)	145 (100)	68 (100)
<i>Cladonia crispata</i>		<b>1008</b> (100)	170 (100)	66 (100)
<i>Cladonia cristatella</i>		<b>448</b> (100)	1 (33)	11 (50)
<i>Cladonia deformis</i>		<b>313</b> (100)	14 (100)	10 (100)
<i>Cladonia digitata</i>				3 (50)
<i>Cladonia fimbriata</i>			1 (33)	2 (100)
<i>Cladonia gracilis</i>		68 (100)	39 (100)	22 (100)
<i>Cladonia macrophylla</i>		<b>340</b> (100)	5 (100)	9 (50)
<i>Cladonia phyllophora</i>		10 (33)	7 (100)	8 (100)
<i>Cladonia pleurota</i>		24 (100)	1 (33)	3 (100)
<i>Cladonia rei</i>		21 (66)	10 (66)	12 (100)
<i>Cladonia squamosa</i>		5 (66)	1 (33)	2 (50)
<i>Cladonia subulata</i>		2 (66)		
<i>Cladonia sulfurina</i>		139 (100)	12 (100)	22 (100)
<i>Cladonia uncialis</i>		<b>689</b> (100)	<b>272</b> (100)	<b>211</b> (100)
<i>Cladonia verticillata</i>		1 (33)	1 (33)	1 (33)
<i>Crustose sp.</i>	1 (33)	<b>252</b> (100)	91 (100)	54 (100)
<i>Evernia mesomorpha</i>		1 (33)	3 (33)	47 (100)
<i>Hypogymnia physodes</i>		38 (100)	31 (100)	225 (100)
<i>Inshaugia aleurites</i>		6 (66)	9 (100)	181 (100)
<i>Melanelia septentrionali</i>			2 (33)	
<i>Melanelia stygia</i>		1 (33)		
<i>Mycoblastus sanguinarius</i>		1 (33)		82 (100)
<i>Nephroma arcticum</i>			1 (33)	
<i>Parmeliopsis ambigua</i>		167 (100)	160 (100)	76 (100)
<i>Parmeliopsis hyperopta</i>		178 (100)	244 (100)	95 (100)
<i>Peltigera scabrosa</i>			15 (66)	5 (100)
<i>Pertusaria geminipara</i>		2 (33)		1 (33)
<i>Placynthiella uliginosa</i>		1 (33)		
<i>Rhizocarpon eupetraeum</i>			1 (33)	
<i>Rhizocarpon geographicum</i>			1 (33)	
<i>Stereocaulon alpinum</i>			1 (33)	
<i>Stereocaulon condensatum</i>		14 (33)		1 (33)
<i>Stereocaulon grande</i>		1 (33)	1 (33)	1 (33)
<i>Stereocaulon paschale</i>	2 (33)	8 (66)	15 (66)	<b>121</b> (100)
<i>Stereocaulon saxatile</i>		5 (66)	1 (33)	3 (100)
<i>Trapeliopsis granulosa</i>		<b>719</b> (100)		
<i>Tuckermanopsis americana</i>		35 (100)	32 (100)	103 (100)
<i>Tuckermanopsis sepincola</i>		95 (100)	98 (100)	7 (100)
<i>Umbilicaria deusta</i>			4 (66)	
<i>Umbilicaria hyperborea</i>	1 (33)	1 (33)	13 (66)	
<i>Umbilicaria mammulata</i>			2 (33)	
<i>Umbilicaria muehlenbergii</i>		1 (33)		
<i>Umbilicaria torrefacta</i>		1 (33)		1 (50)
<i>Usnea cavernosa</i>				1 (50)
<i>Usnea filipendula</i>		1 (33)		2 (50)

TABLE I. (concluded)

Stage	I	II	III	IV
VASCULAR PLANTS				
<i>Abies balsamea</i>		4 (66)		
<i>Alnus crispa</i>			54 (100)	
<i>Alnus rugosa</i>		6 (33)	4 (66)	
<i>Amelanchier bartramiana</i>	1 (33)		42 (100)	2 (50)
<i>Aster sp.</i>			1 (33)	
<i>Betula glandulosa</i>	24 (100)	63 (66)	69 (66)	1 (50)
<i>Carex deflexa</i>		1 (33)		
<i>Carex sp.</i>	173 (100)	145 (66)	172 (100)	1 (50)
<i>Carex trisperma</i>	12 (33)	1 (33)	263 (100)	55 (50)
<i>Carex umbellata</i>	2 (33)			
<i>Chamaedaphne calyculata</i>	44 (66)	356 (66)	821 (100)	70 (50)
<i>Clintonia borealis</i>	5 (33)	13 (66)	76 (100)	6 (100)
Asteraceae sp.		2 (66)	1 (33)	
<i>Coptis trifolia</i>	9 (100)	56 (66)	138 (100)	7 (50)
<i>Cornus canadensis</i>	2 (33)	57 (66)	73 (100)	39 (100)
<i>Empetrum nigrum</i>	1 (33)	2 (33)	143 (66)	2 (50)
<i>Epigaea repens</i>		50 (66)	42 (66)	
<i>Epilobium angustifolium</i>	1 (33)	5 (33)	3 (66)	
<i>Equisetum sylvaticum</i>		11 (33)	24 (66)	
<i>Gaultheria hispida</i>		3 (33)	72 (100)	1 (50)
<i>Geocaulon lividum</i>	1 (33)		34 (66)	
Poaceae sp.			38 (33)	
<i>Juniperus communis</i>			1 (33)	
<i>Kalmia angustifolia</i>	222 (100)	120 (100)	48 (66)	349 (100)
<i>Kalmia polifolia</i>	6 (66)	108 (33)	313 (66)	13 (50)
<i>Larix laricina</i>		3 (66)		
<i>Ledum groenlandicum</i>	110 (100)	332 (100)	779 (100)	258 (100)
<i>Linnaea borealis</i>	4 (33)		30 (33)	
<i>Lycopodium annotinum</i>	1 (33)	13 (33)	34 (33)	4 (50)
<i>Lycopodium sabinaefolium</i>	20 (33)	10 (33)	45 (100)	3 (50)
<i>Maianthemum canadense</i>	65 (100)	5 (33)	86 (100)	9 (50)
<i>Melampyrum lineare</i>		12 (33)	35 (100)	
<i>Picea mariana</i>	3 (100)	70 (100)	575 (100)	342 (100)
<i>Pinus banksiana</i>	23 (100)	369 (100)	99 (100)	298 (100)
<i>Potentilla tridentata</i>	33 (66)	66 (66)	27 (66)	3 (50)
<i>Prunus pensylvanica</i>			1 (33)	
<i>Ribes glandulosum</i>	1 (33)			
<i>Rubus chamaemorus</i>	1 (33)	102 (33)	115 (100)	
<i>Salix humilis</i>	48 (33)			3 (100)
<i>Salix sp.</i>	64 (100)	9 (100)		9 (50)
<i>Salix uva-ursi</i>		5 (33)		
<i>Scirpus caespitosus</i>		1 (33)		
<i>Senecio pauciflorus</i>			25 (33)	
<i>Smilacina trifolia</i>			1 (33)	
<i>Trientalis borealis</i>			4 (33)	
<i>Vaccinium angustifolium</i>	580 (100)	282 (100)	966 (100)	289 (100)
<i>Vaccinium oxycoccus</i>	1 (33)	84 (66)	233 (100)	
<i>Vaccinium uliginosum</i>		1 (33)	84 (100)	
<i>Vaccinium vitis-idaea</i>	1 (33)	92 (66)	4 (33)	69 (50)
<i>Viola sp.</i>			2 (33)	

The detailed analysis of species diversity by postfire successional stage indicates that *Vaccinium angustifolium* is one of the first species to colonize burned sites (Table I). Several ericaceous plants (*Kalmia angustifolia*, *Ledum groenlandicum*, *Vaccinium angustifolium*, *V. vitis-idaea*, etc.) are present at all stages. *Ledum groenlandicum* and *Vaccinium angustifolium* are present as well as *Kalmia angustifolia* in old forest sites (stage IV; Table I). *Pinus banksiana* and *Picea mariana* are present throughout the postfire successional sequence.

Comparable patterns of species changes throughout the postfire succession sequence occurred with the non-vascular

plants. *Polytrichum piliferum* is a colonizing moss that is mainly abundant in stage II sites (27% coverage). *Pleurozium schreberi* is present in the older forest stands (stages III and IV; Table I). Given that the liverwort *Ptilidium ciliare* grows mainly within the lichen mat of *Cladina mitis* and *C. stellaris*, it is present in later successional stages, since these two species are mainly mid- and late-successional species.

Several lichens, mosses, and liverworts were present in the younger postfire sites (stage I), but they were generally difficult to identify given their very small size and early developmental stage (mainly primary thallus). The first identification of lichens was possible in stage II stands

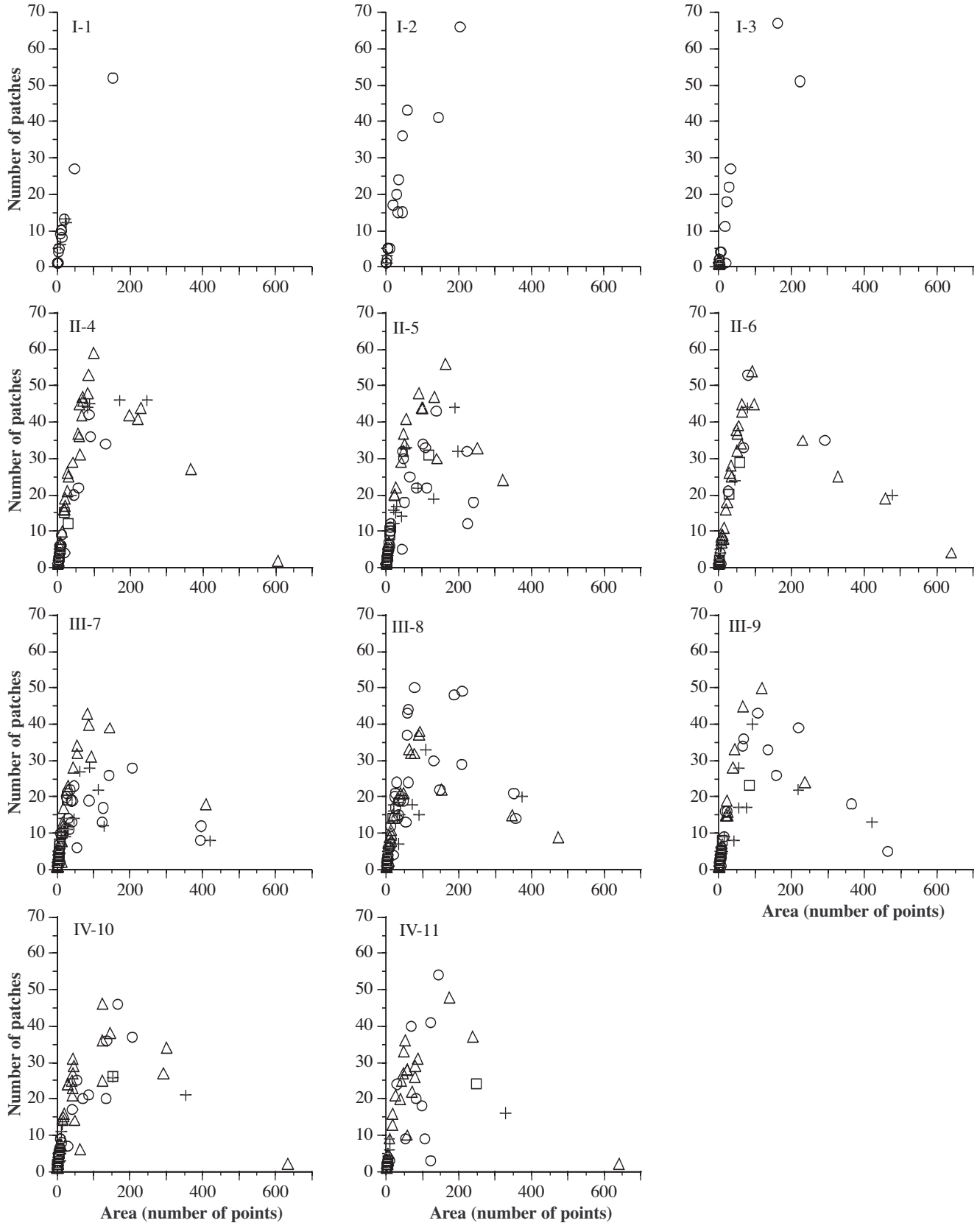


FIGURE 3. Scattergrams of species patchiness (maximum number of patches) against the range area cover (area in terms of number of sample points of 50 cm<sup>2</sup> forming a patch) per species of the eleven sampling sites, across the four postfire successional stages, around the La Grande-3 hydroelectric reservoir. Roman numbers indicate stand stage and Arabic numbers indicate site number. The plus sign indicates mosses. Square indicates liverworts. Triangle indicates lichens. Circle indicates vascular plants.



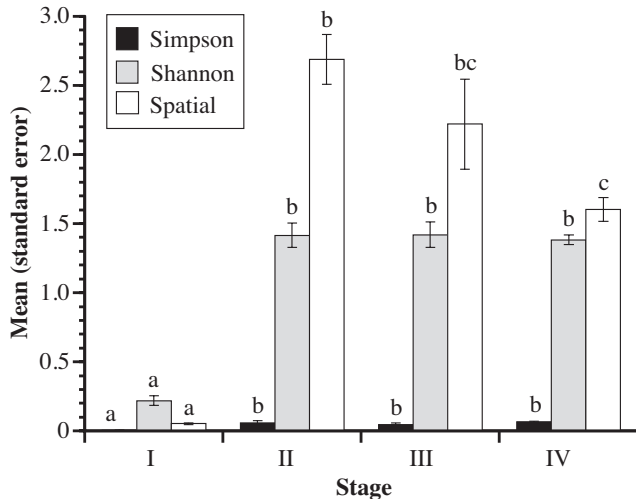


FIGURE 4. Mean and standard error of Simpson Index, Shannon Index and Spatial Diversity Index of the eleven sampling sites around the La Grande-3 hydroelectric reservoir. To be on the same scale as the other indexes, the SDI values were divided by 100. For each variable, means with the same letter are not significantly different based on Waller-Duncan multiple comparison tests.

where *Trapeliopsis granulosa* and *Cladonia sp.* were the most abundant species. *Cladina mitis* and *C. rangiferina* were the most abundant species in stage III stands. The oldest postfire stands (stage IV) were characterized by extensive carpets of *Cladina stellaris*. Overall, the postfire succession pattern found in the sampled stands is similar to that reported by Morneau & Payette (1989) at the northern limit of the lichen-spruce woodland zone, about 150 km northeast of our study area.

#### SPATIAL DIVERSITY INDEX

The relationship between species patchiness and space occupancy (*i.e.*, in terms of area covered) changes during succession, as illustrated in Figure 3 (see Table I for species names). The three stage I sites (I-1, I-2, and I-3) show the same linear relationship of one-to-one matching between the total number of patches and the total species abundance, thus total species space occupancy. During this stage, the number of patches is maximum while the area per patch is minimum (one single individual or one small clone per patch, thus a linear relationship), which corresponds to the spatial structure of a pioneer-colonization phase.

As succession progresses, the number of patches decreases because plants grow such that the total cover per species increases (expansion and stabilization phases). While the majority of species in stage II sites (II-4, II-5, and II-6) still show a linear relationship of the colonization phase (Figure 3 and Table I), some are beginning to spread and expand (see Table I for species names) to cover the entire study area (mainly in site II-6), having fewer but larger patches. Hence species start to show more variability in terms of their occupation of space.

At stage III (sites III-7, III-8, and III-9), fewer species show a linear relationship (colonization or stabilization), whereas some species have spread over the entire area of the sites (see Table I for species names). The maximum cover

per species is reached at the last stage (sites IV-10 and IV-11). The major difference between species space occupancy in stage IV and the two previous stages II and III, lies in the fact that species occupy large areas in a continuous fashion, which decreases the number of patches per species.

The SDI was then computed and its behavior compared with that of the Simpson and Shannon diversity indices (Figure 4). While the three indices were able to differentiate all of the stage I stands from the other successional stages (stages II, III and IV), only the SDI was able to discriminate between the highly-diversified stands of the mid-successional stages II and III and the lesser diversified late-successional stands (stages III and IV). Hence, the SDI was able to discriminate between the three successional phases: colonization (stage I), expansion (stages II and III), and stabilization (stages III and IV). Such differences were significant when tested by an ANOVA ( $F = 29.63$ ,  $p < 0.0002$ , Waller-Duncan multiple comparison test; Figure 4). Therefore, by adding the spatial structure of species in the computation, the SDI allows us to distinguish statistically significant differences in the plant diversity of successional stands.

In our analysis, the site showing the highest spatial diversity, site 4 (stage II), did not have the highest species richness. Indeed, the two sites having the highest values of species richness, sites 7 and 8 (stage III), show different spatial diversity behaviors (Figure 3). Furthermore, the SDI was able to indicate that site 9, although it was classified *a priori* as a stage III stand because of the age of the forest, shows a comparable spatial diversity behavior to that of the two stage IV stands (sites 10 and 11). Such insights were not detected by either the Simpson nor the Shannon diversity indices.

#### Conclusion

To measure and compare differences in plant diversity, any diversity index needs to incorporate the successional context in which plants are growing (van der Maarel, 1988). Also, in species-poor communities such as those of northern boreal forests, the combination of species richness and species abundance for assessing biodiversity may not be entirely satisfactory (Tonteri, 1994). The quantification of the spatial pattern of plant species will provide more relevant and useful vegetation diversity values. The major advantage of our index is that, even though simple, it was sensitive enough to distinguish significant differences in species diversity of space occupancy. Using real data, which incorporate a wide range of outcomes, we were able to show that the spatial index provides more information about vegetation diversity than the Simpson or Shannon indices.

The use of the SDI, as shown above, can therefore help in obtaining a better assessment of vegetation by distinguishing the structural changes occurring in plant communities, as emphasized by the abundance and spatial patterning of the constituent species. Although the SDI was developed to study boreal vegetation diversity, which is primarily composed of clonal species, it can also be used in other ecosystems and regions where clonal species dominate, such as in benthos. The SDI can also be used at the landscape scale using less intensive data sampling such as species spatial maps or species vertical structure data. Species spatial



diversity as estimated by the SDI provides a new and more accurate way to discriminate vegetation diversity, which in turn will facilitate the task of boreal forest managers of preserving stand diversity at the landscape level.

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