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# Dynamic Old-Growth Forests? A Case Study of Boreal Black Spruce Forest Bryophytes

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Old-growth forests have sparked significant interest over the last twenty years and definitions have evolved from structure based to process based, acknowledging the diversity of forests that could be considered old growth. However studies frequently group all forests over a certain age into a single type, negating the dynamic processes that create old growth. In this study we examine a 2350-year chronosequence in boreal black spruce forests in northwestern Quebec to determine whether continued community change can be observed in the bryophyte layer. Bryophytes dominate the understory of boreal forests and influence ecosystem functioning, particularly in paludified forests where production exceeds decomposition in the organic layer. Community composition and richness changed throughout the chronosequence with no evidence of a steady state associated with an old-growth phase. In contrast the bryophyte community continued to evolve with multiple phases being evident. These results suggest that old-growth forests on the Clay Belt of northwestern Quebec and northeastern Ontario, Canada, should be regarded as part of the continuous gradient in forest development rather than a single state. This complicates conservation of these forests as multiple phases should be considered when planning forest reserves.

**Keywords** old-growth forest, succession, disturbances, boreal, bryophytes, climax, gap dynamics
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# 1 Introduction

Globally, interest in old-growth forests has sparked a variety of reviews, conferences and books in the last decade (e.g. Kneeshaw and Gauthier 2003, Moessler et al. 2003, Helms 2004, Spies 2004, With et al. 2009a.). Most of these texts have emphasized the dynamic nature of temperate and boreal forest development, and definitions of old growth based on processes or succession (Wirth et al. 2009b, Kneeshaw and Gauthier 2003, Spies 2004).

These process based definitions contrast with older structural definitions that were initially developed for the northwestern coast of North America where large long-lived tree species dominate, resulting in impressive old forests made up of very large individual trees, large downed wood and a multi-layer tree canopy (Spies et al. 1988, Wells et al. 1998, Kimmins 2003). While very applicable in the forest types for which they were initially developed, these structural definitions do not describe the vast diversity of old forest types observed globally. Furthermore structural definitions of old growth imply that forest structure remains static after a certain age, and does not represent the dynamic reality present within most forests as they age.

As many authors have suggested (Wells et al. 1998, Kneeshaw and Gauthier 2003, Helms 2004, Spies 2004) a single specific definition of old growth in which ages, structural attributes and biogeochemical processes are defined for all forests is probably impossible. However, as suggested by Moessler et al. (2003) and generalized by Wirth et al. (2009b) a process based definition that applies to nearly all forests could be defined by focussing on relative age and the presence of gap dynamics. This general definition is applied in this study.

While definitions that are based on gap dynamics inherently imply that on some scale the forest continues to change and therefore all old-growth stands will not be identical, field studies tend to imply that once the old-growth stage is reached there is no further change within the forest as they lump all forests over a threshold age into a single group (e.g. O'Hara et al. 2010, Plue et al. 2010, Stenbacka et al. 2010). The danger of ignoring this dynamic and lumping together all forests over a threshold age or demonstrating gap dynamics is that the presence of different types of communities may be obscured. Consequently forest management and conservation planning (e.g. strategies to maintain old growth; Belisle et al. this volume) may not focus on the diversity of stages present within "old growth" and species associated with the different types of habitat or processes present may not be adequately protected.

In North America, boreal old-growth forests have fairly recently been shown to be more common than previously believed (Bergeron and Harper 2009) and while they fit the generalized definition listed above they have historically been difficult to define as they are quite variable and generally do not fit structural definitions of old-growth forest. Furthermore there is frequently no species replacement, making successional definitions based entirely on the replacement of pioneer species by shade tolerant species problematic (Harper et al. 2005, Gauthier et al. 2010). Black spruce (*Picea mariana* Mill. (BSP)) is one of the most common species in boreal North America and it frequently establishes after fire and can remain as a dominant for centuries, or even millennia (Pollock and Payette 2010). In this study, black spruce forests were considered to fit into the generalized category of old growth after the age of 100 years post catastrophic fire. This age, suggested by Bergeron and Harper (2009), fits the general definition offered above as pioneer jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.) within black spruce stands start to die out resulting in canopy breakup and the beginning of gap dynamics (St-Denis et al. 2010). This is also a pragmatic age, as the forest harvest rotation time is generally considered to be 100 years, resulting in increasing rarity of forests over this age on the landscape. These forests are therefore of highest priority for conservation.

The understory of boreal forests plays important roles in ecosystem functions including nutrient cycling, water cycling, and overstory succession (for a review see Hart and Chen 2008). Bryophytes are an appropriate group with which to examine the changes in coniferous boreal forests as they dominate the forest floor (Frego 1996), and independently from vascular plants have a significant impact on ecosystem processes such as nutrient and water cycling (Gower et al. 1997, Price et al. 1997, DeLuca et al. 2002), and are indicators of ecosystem change (Fenton and Bergeron 2006).

In this context, in this article we build on our previous work in these old boreal black spruce forests (Fenton and Bergeron 2006, 2008). While these earlier analyses detailed changes in species abundance and richness along a chronosequence, the objective of this study was to determine whether multiple phases of old-growth can be identified in the bryophyte species composition of boreal old-growth black spruce forests. We will subsequently discuss the implications of the results on research focussing on old-growth forests, and on conservation strategies. Our hypothesis is that distinct phases with different relative abundances of bryophyte species groups after the forests have reached the old-growth phase will be evident.

# 2 Methods

## 2.1 Study Area

The glacial lakes Barlow and Ojibway covered a significant portion of central North America during the last glacial period, the Wisconsinan glaciation that ended approximately 10 000 years ago in the study area (Vincent and Hardy 1977). As they were present on the landscape for 2500 years, a thick layer (10–60 m) of clay accumulated at the deeper portions of the lake bottom. These glaciolacustrine deposits remain today and form the Clay Belt of north-eastern Ontario and north-western Québec (Fig. 1) Vegetation in this region can be divided into two groups, black spruce (*Picea mariana* Mill.)-feather moss (*Pleurozium schreberi* (Brid.) Mitt.) forests in the north and balsam fir (*Abies balsamea* (L.) Mill.), white birch (*Betula papyrifera* Marsh.) mixed boreal forest in the south (Grondin 1996). The

**Fig. 1.** Map of the Clay Belt of north-western Québec and north-eastern Ontario. Site locations are indicated by white circles. The location of the larger map in North America is indicated by the white box on the inset map.

entire region, and particularly the northern black spruce forests are prone to paludification between fires due to its poorly drained clay dominated soil, low topographic relief, and moderately humid and cold climate [annual precipitation 629 mm as rain and 262 mm as snow on average; coldest month (January) mean temperature –19 °C, warmest month (July) 16.5 °C (Environment Canada 2010)]. Infrequent, large stand replacing fires are the dominant disturbance type. The fire cycle has changed throughout the Holocene in response to changes in regional climate; between 1850 and 1920 it was ca 135 years, and it has since increased to ca 398 years (Bergeron et al. 2004). Consequently forests over 100 years currently dominate the landscape and likely have for much of the Holocene (Cyr et al. 2009), and as a result the average age of forests is in excess of 100 years. The Clay Belt lies just south of the Hudson Bay-James Bay Lowlands, the second largest peatland complex on the globe.

### 2.2 Field Sampling

A chronosequence (space for time) of black spruce stands initiated after severe stand replacing fire 50 to 2350 years before present has been established on the Clay Belt of western Québec. The use of chronosequences is based on the assumption that not only were the initial conditions similar among sites, but also that subsequent changes in community properties and secondary disturbances were similar for each site (Johnson and Miyanishi 2008, Walker et al. 2010). However, as suggested by Johnson and Miyanishi (2008), the patterns observed in this chronosequence have been verified by both paleoecological methods (Lecomte et al. 2005 and Lecomte et al. 2006a) and stand reconstruction (Lecomte et al. 2006b). Furthermore, the results discussed here are based on a very long time frame (>2000 years) and deal with vegetation structure changes and organic matter accumulation, all factors that Walker et al. (2010) suggest lead to improved credibility of chronosequences. While stands dominated by jack pine (*Pinus banksiana* Lamb.), and black spruce and established after both high and low severity fires were included in the chronosequence initially established by Lecomte et al. (2005), only data from stands dominated by black spruce, established after high severity fire and of sufficient size were included in this study. High severity fires were defined as fires where less than five centimetres of organic material remained after fire, which created abundant suitable tree germination microsites allowing for dense tree regeneration (Lecomte et al. 2006b, Greene et al. 2004, Johnstone and Chapin 2006). Stand age was determined by verification of stand initiation maps by dating basal cross-sections of a few dominant trees. In the oldest stands (>200 years time since fire or TSF by dendrochronology) $^{14}C$ dating of charcoal particles was also completed (See Simard et al. 2007 for details). Consequently stand ages reported here are based on dendrochronological ages for the younger stands and on $C^{14}$ dating for the older stands. In order to be certain that we were not implying greater precision in the dates than was present in the data, we created five age classes: <100 years (4 sites), 150 years (2 sites), 200–400 years (3 sites), 600–1500 years (3 sites) and 2350 (1 site) years since stand initiating fire.

The bryophyte community was studied in thirteen black spruce stands of this chronosequence initiated after high intensity fire. A variety of habitat variables were measured in each plot or quadrat, see Table 1. For details on the sampling protocol see Fenton and Bergeron (2006 and 2008). Briefly, within each site five plots of 100 $m^2$ were installed, with four nested quadrats of 25 $m^2$ for a total of 20 quadrats per site. The initial 100 $m^2$ plots were randomly placed at least 50 m from the nearest road, and subsequent plots were placed at least 10 m apart along a randomly chosen bearing. Within each 25 $m^2$ quadrat, all bryophyte species and *Cladonia rangiferina* [(L.) Weber ex F.H. Wigg] were identified and their percent cover visually estimated. *Cladonia rangiferina* is included in the analysis even though it is a lichen and not a bryophyte, as it occupies forest floor space that otherwise would be occupied by bryophytes. Samples of all non-easily identifiable species were collected for identification in the lab. Nomenclature follows Ireland (1982) for the mosses and Paton (1999) for the liverworts. A representative collection of voucher specimens are stored at the Université du Québec en Abitibi-Témiscamingue.

**Table 1.** Mean values of environmental variables for each age class. Values are means followed by standard error. Values followed by different letters are significantly different, $p<0.05$; $a<b<c$ etc.

| | Time since fire (years) | | | | |
|---|---|---|---|---|---|
| | 100 | 150 | 200–400 | 600–1500 | 2350 |
| No. of sites | 4 | 2 | 3 | 3 | 1 |
| Forest floor depth (cm) | 19.25±0.69a | 31.75±1.90b | 45.48±2.79c | 62.37±3.49d | 90.00±10.30e |
| Water table depth (cm) | 30.86±0.94a | 48.87±1.42c | 51.35±0.81c | 40.06±1.67b | 28.07±1.62a |
| Dens. open[a)] | 40.37±1.36a | 54.69±1.54b | 59.77±1.76b | 69.88±1.87c | 74.83±3.29c |
| Tot. basal area ($m^2ha^{-1}$) | 44.75±0.038d | 35.49±0.050c | 24.07±1.26b | 19.80±0.027b | 7.19±0.017a |
| Mean DBH[b)] (cm) | 14.19±0.34c | 12.59±0.26b | 13.81±0.29bc | 13.82±0.49bc | 9.49±0.27a |

[a)] Dens. open refers to the percent open canopy as measured by a densiometer.
[b)] DBH, refers to diameter at breast height.

## 2.3 Data Analysis

The analysis unit used in this study was the quadrat, which is technically pseudoreplication (Hurlbert 1984). However, boreal bryophyte communities vary at a very fine spatial scale on the forest floor (Økland 1994, Frisvoll 1997). In fact the variation between quadrats within a site and age group was analysed for this data set in our previous article (Table 2 in Fenton and Bergeron 2006) and we found as much variation within sites of a single age group as among sites of the same group. As such we feel that the use of quadrats as analysis unit is justifiable.

The presence of constant change in bryophyte community composition was verified by several methods. First nonmetric multidimensional scaling (NMDS) was used to evaluate the overall pattern of community change. NMDS was calculated in WinKyst 1.0 (Šmilauer 2002), based on an initial configuration generated by principal co-ordinate analysis. The presence of a local minimum was verified by the use of five random perturbations with an amplitude of 0.213. Bray-Curtis distances were used. A two dimensional solution was suggested by a scree plot. The plot was subsequently orientated using Principal Component Analysis (PCA) with no transformation of data or sample weights and centering by species. Similar results, obtained with detrended correspondence analysis (Hill and Gauch 1980, using Canoco ver. 4.0, ter Braak and Šmilauer 1998), were presented in Fenton and Bergeron (2006).

The differences among age classes indicated in the NMDS analysis were tested with multi-response permutation procedures (MRPP), which tests for multivariate differences among groups, in PC-Ord version 4 (McCune and Mefford 1999). This test gives both a T statistic with a probability that tests for differences among groups and an A statistic that describes the similarity of the individual members of the groups (0 = all members different, 1 = all members the same).

Species groups within this changing community were determined using cluster analysis (PC-Ord vers. 4; McCune and Mefford 1999), which is a hierarchical, agglomerative and polythetic analysis. Ward's linkage method with Euclidean distances was used. One weakness of this method is that the number of groups needs to be defined by the user. To overcome this weakness several different analyses were run with four to eight species groups. The six group analysis gave the most parsimonious interpretable results, as determined by examination of the results. Fewer groups were very heterogeneous and no interpretable pattern was present. More groups were superfluous. Indicator species analysis (in PC-Ord based on Dufrene and Legendre 1997) was then completed for the species groups determined by cluster analysis. The indicator species were verified with Monte Carlo tests with a random seed initiation.

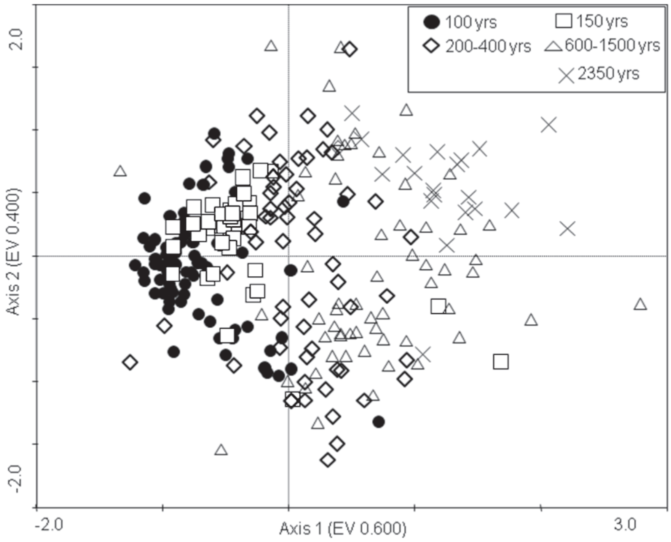

**Fig. 2.** Non-metric multidimensional scaling (NMDS) of quadrats orientated by principal components analysis (PCA). Quadrats are illustrated by age class. The eigenvalues for the two axes are indicated.

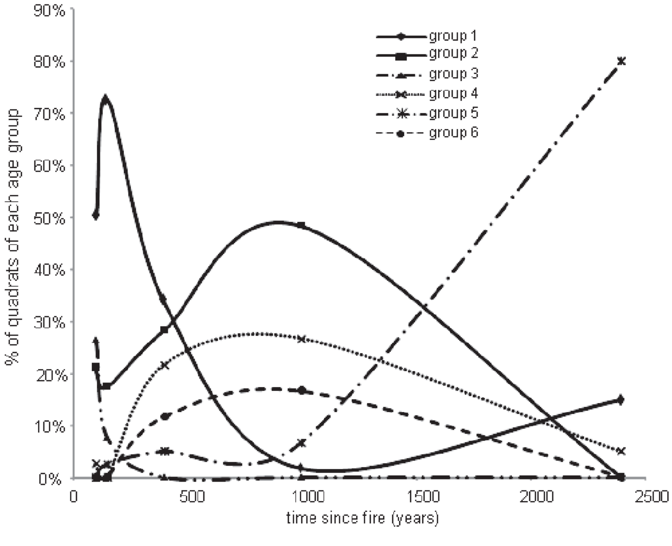

**Fig. 3.** Relative abundance of different species groups, identified via cluster analysis, through time since fire (years).

**Table 2.** Cluster analysis groups, number of plots per group and indicator species as indicated by indicator species analysis.

| Super group | Group | Number of quadrats | Indicator species |
|---|---|---|---|
| Super group 1 | Group 1 | 91 | *Pleurozium schreberi* ((Brid.) Mitt.), *Dicranum ontariense* (Peterson), *D. polysetum* (Sw. ex anon.) |
| Super group 2 | Group 2 | 69 | *Sphagnum capillifolium* (Ehrh.) Hedw., *S. girgensohnii* (Russow), *Tomentypnum nitens* (Hedw.) Loeske |
| Super group 1 | Group 3 | 23 | *Ptilium crista-castrensis* (Hedw.) De Not. |
| Super group 2 | Group 4 | 32 | *Sphagnum rubellum* (Wilson), *Tetraphis pellucida* Hedw., *Cephalozia pleniceps* (Austin) Lindb. |
|  | Group 5 | 24 | *Sphagnum fuscum* (Schimp.) H.Klinggr., *S. fallax* s.l.[a)], *Dicranum undulatum* (Scrad. ex Brid.), *Polysetum commune* Hedw., *Mylia anomola* (Hook.) Gray, *Cladonia rangiferina* (L.) Weber ex F.H. Wigg |
|  | Group 6 | 17 | *Sphagnum russowii* (Warnst.), *Barbilophozia barbata* (Schmidel. ex Schreb.) Loeske |

[a)] *S. fallax* senso lato indicates that all of the species of this difficult group are included under this name.

# 3 Results

Bryophyte community composition presents a clear shift along the first (horizontal) axis of the NMDS analysis (final stress 0.2478), with age groups clustering together along this first axis (Fig. 2). The differences between age classes suggested by the NMDS analysis were confirmed by MRPP with a T of –52.15 ($p<0.0001$) and an A value of 0.224.

Cluster analysis illustrated that quadrats fell into six species composition groups (Table 2), with two super groups. The first super group, made up of groups 1 and 3, represents 44% of all plots and 75% of quadrats from the 100 and 150 age classes, while the second super group, made up of groups 2, 4, 5 and 6, represents the remaining 56% of all quadrats and 83% of the 200–2350 age classes (data not shown). Species group membership clearly shifts between age classes (Fig. 3) with species group 1 dominant and group 3 prevalent in young stands and species group 5 dominant in the oldest stands. Species groups 2, 4, and 6 are co-dominant in the intermediate ages. Indicator species analysis of the species groups successfully identified at least one indicator species for each species group (Table 2).

# 4 Discussion

## 4.1 Multiple Old-Growth Stages

The chronosequence examined in this study showed a distinct shift not only in individual species abundance with time (Fenton and Bergeron 2006) but also a shift among species associations with time (this study). This pattern could undoubtedly be clarified with the addition of further sites to the chronosequence, particularly in the oldest age group; however we feel that the observed pattern is robust as the results are similar to those found in similar environments (Glebov and Korzukhin 1992, Klinger 1996).

Examining the changes in relative abundance of the six species groups over time, three stages within the bryophyte community in old-growth black spruce forest can be identified. These are: (1) closed canopy forests (<200TSF), (2) open paludified forest (200TSF<>1500) and (3) forested peatland (>1500). Each stage will be briefly discussed. Closed canopy forests were dominated by species groups one (*P. schreberi*) with a significant presence of groups two (*Sphagnum* spp.) and three (*Ptilium crista-castrensis* (Hedw.) De Not.). While in this study we focused on older closed canopy forests (the youngest stand in the <100 TSF age group was 50 years TSF) *P. schreberi* and *Ptilium crista-castrensis* have been found to establish underneath black spruce shortly after canopy closure (Shafi and Yarranton1973, Black and Bliss 1978, Taylor et al. 1987). The stage observed in this study can then be considered to be the end of a relatively stable bryophyte species group that exists during the closed canopy phase in black spruce forests, however the duration of this phase will depend largely on the duration of the closed canopy (see Pollock and Payette 2010). Furthermore, the bryophyte community while maintaining a constant composition at the stand scale is dynamic during this period at smaller scales (Økland and Eilertsen 1996, Frego 1996). Taylor et al. (1987), Foster (1985) and Fenton and Bergeron (2006) have all indicated that the *Sphagnum* spp. colonies, noted in this study, begin to establish relatively late in this phase, around 90 years after fire.

The transition towards open paludified forest begins with the establishment of the sphagna in the previously feathermoss dominated understory. As discussed in Fenton and Bergeron (2006) the establishment of shade and desiccation tolerant sphagna facilitates the establishment of other sphagna species by contributing to a rapidly accumulating organic layer (see Table 1). Subsequently the canopy opens (Table 1, St-Denis et al. 2010) and the water table rises to the interface between the mineral and organic soil layers; as a result the environment is variable and light and nutrient rich. The results of this study clearly indicated that several groups of species thrive during this phase (groups two, four and six) and that each group consists of sphagna and associated moss and liverwort species. The heterogeneity of this phase may be a reflection of the long time period included (1200 years), which may be hiding other sub-phases. Alternatively it may be a reflection of the accumulated effects of many small stochastic events (tree tip ups, establishment of *Larix larcinia* (Du Roi) K. Koch and deciduous shrubs (*Alnus incana ssp. rugosa* (Du Roi) Clausen and *Salix bebbiana* Sarg.) leading to substantial differences among otherwise similar sites. Økland et al. (2003), and others (e.g. Kimmerer and Driscoll 2000, Berglund et al. 2009) have observed similar heterogeneity in the understory plant composition among relatively stable forests in the tree canopy.

Forested peatlands develop when a forest is not burned over millennia. These stands have accumulated very thick organic layers where the water table is close to the surface and very far from the mineral soil and little tree canopy remains (Table 1). Fewer species can survive in this environment and species common in relatively dry environments (Kuhry 1994, Camill 1999, Benscoter and Vitt 2008), such as ombrotrophic bogs and permafrost complexes, are abundant (species groups five and one).

### 4.2 Dynamism of the Bryophyte Community

The composition of the bryophyte community in black spruce forests continued to change over time even once the forest had attained the old-growth phase. These results coupled with the continued change in the forest structure illustrated in Lecomte et al. (2006b) establish that over significant time spans the old-growth phase is not homogeneous for black spruce forests in north-western Québec. Continuous compositional or structural changes in forests that do not experience catastrophic disturbance have been observed in both boreal forests (e.g., Park et al. 2005, Gauthier et al. 2010) and hardwood forests (e.g., Frelich and Lorimer 1991, Woods 2004, Peterken and Jones 1987, Lindbladh et al. 2007). Instead these forests show a continual change over time driven by small to medium sized disturbances (Cline and Spurr 1942, Peterken and Jones 1987, Frelich and Lorimer 1991, Ziegler 2002, Woods 2004, Gauthier et al. 2010) or autogenic successional changes (Wardle et al. 2004, Boucher et al. 2006, Lecomte et al. 2006b, and this study).

Furthermore, as Johnson and Miyanishi (2008) point out, the concept of old-growth forests as the last stage in autogenic forest development (Cline and Spurr 1942, Oliver and Larson 1991, Kimmins 2003) is essentially a climax concept. However, our results, along with those of previous studies on the Clay Belt (Lecomte et al. 2006a and 2006b), question long term fate of these old-growth forests in the absence of fire. Continued paludification could lead to their ultimate transformation into peatlands (Glebov and Korzukhin 1992, Klinger 1996) with few or no trees (e.g. Viereck 1983) as seed germination sites are limited and black spruce layering may not provide sufficient regeneration to maintain forest cover (Boucher et al. 2006, St-Denis et al. 2010). Furthermore, with the development of a very thick organic layer there is little chance that all of the organic layer would burn during an eventual fire, leaving a thick unburnt layer (Shetler et al. 2008) that would limit post-fire tree establishment (Greene et al. 2004, Lecomte et al. 2006a). These results, while supporting the concept of vegetation change over time (succession as described by Drury and Nisbet 1973 and others), do not support the concept of old-growth forests as the climax stage of succession. Similarly other studies have indicated that static concepts of ecosystems are not founded in a variety of habitats (Wardle et al. 2004).

### 4.3 Concluding Remarks

While the species group replacement sequence illustrated here with these community groups is specific to areas subject to paludification, the dynamism present within these forests can be applied more generally. The work on the Clay Belt (Lecomte et al. 2005, 2006a, 2006b, this study) and Wardle et al.'s (2004) work on long-term changes in forest ecosystem functions across the globe clearly illustrate that at long time scales, old-growth forests are not static climax communities. This has consequence for ecological theory, and forest management, including conservation planning. The forest successional sequence popularized by Bormann and Likens (1979) and Oliver and Larson (1996) clearly ends with a stable old-growth phase, although Bormann and Likens (1979) specifically mention small scale variability with stability found only at a landscape scale. Recent research indicating that forests continue to change in their composition and nutrient dynamics even once the gap phase has been reached requires these concepts to be nuanced. A more accurate description of this sequence may be described by phases that are dominated by stand versus gap dynamics, without assuming stability within the phases.

The dynamism present within old-growth forests also has consequences for forest management, including conservation planning. For example in the boreal forest in Canada, both ecosystem management planning (Gauthier et al. 2009) and the boreal standard of the Forest Stewardship Council (2004) treat old forests as static and interchangeable. If the dynamism now known to be present within old-growth forests is to be included in forest management, changes in forests past the old-growth cut off (whatever it is decided to be in a certain region) need to be taken into consideration when options to conserve old growth, such as discussed by Belisle et al. (this volume), are applied. For example different types of partial cutting could be used to emulate different types of old-growth forests.

In conclusion, old-growth forests need to be examined more carefully to determine to what degree autogenic processes and low levels of disturbance result in multiple stages or types of forest communities once gap dynamics dominate. Similarly research should continue to examine the consequences of this continued dynamism on ecosystem function. Forest management strategies although consequently somewhat more complicated, should also be applied appropriately so that all types of old growth are conserved.

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