Natural dynamics-based silviculture for maintaining plant biodiversity in *Populus tremuloides*-dominated boreal forests of eastern Canada[1]

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Abstract: Southern boreal forests dominated by trembling aspen (*Populus tremuloides* Michx.) are notable for the biological richness of their plant communities. We used 12 plant community and plant functional group indicators to test the hypothesis that natural dynamics-based silvicultural systems better maintain biodiversity in aspen plant communities than conventional clear-cutting. Using CA ordination, box-and-whisker diagrams, and ANOVA, we compared the range of variability of our 12 bioindicators among five experimental stand types of the sylviculture et aménagement forestier écosystémiques (SAFE) project: mature (78 years) uncut; mature 1/3 partial-cut; mature 2/3 partial-cut; young (3 years) unburned clear-cut; young burned clear-cut; and three closely matched aspen stand types of northwest Quebec and northeast Ontario: old (105 years) uncut; young unburned clear-cut; young wildfire. Burned clearcuts partially emulated wildfires by reducing tall shrub abundance and regenerating post-fire specialists, but snags were lacking. The dual disturbance also retarded aspen regrowth and caused a 7-fold increase in non-native plants. Partial-cuts retained most attributes of mature uncut stands, but after 3 years showed little evidence of accelerating development of old stand characteristics. We concluded that SAFE natural dynamics-based silviculture better recreated the range of variability of naturally disturbed aspen plant communities than conventional clear-cutting. Improvements, including alternative burn prescriptions and snag or green tree retention in clearcuts, are nontheless warranted.

Key words: Populus tremuloides, forest succession, boreal mixedwood, ecosystem-based management, biodiversity indicators.

Résumé : La forêt boréale méridionale dominée par le tremble (*Populus temuloides* Michx.) comporte des communautés végétales remarquables par leur richesse biologique. En utilisant 12 indicateurs de communautés végétales et groupes fonctionnels de plantes, les auteurs testent l'hypothèse que des systèmes de sylviculture basés sur leurs dynamiques, assurent une meilleure biodiversité dans les communautés de tremble, que la coupe à blanc conventionnelle. En utilisant l'ordination CA, les diagrammes en boîtes à moustache (box-and-whisker) et le test ANOVA, les auteurs comparent l'amplitude de la variabilité des 12 bioindicateurs au sein des 5 types de parcelles expérimentales du projet sylviculture et aménagement forestier écosystémiques (SAFE) : mature (78 ans) non coupée; mature partiellement coupée au 1/3; mature partiellement coupée au 2/3; jeune (3 ans) coupée à blanc non brûlé; jeune coupée à blanc et brûlée. Ils ont inclus également 3 types de peuplement forestiers de tremble étroitement appariés, du nord-ouest du Québec et du nord-est de l'Ontario; suranné (105 ans) non coupé; jeune coupé à blanc non brûlé; jeune, incendié naturellement. Les peuplements coupés à blanc et incendiés se comparent à ceux issus de feux naturels avec une réduction de l'abondance de grands arbustes et en assurant la régénération par les espèces spécialistes d'après feu, mais les chicots font défaut. La double perturbation retarde également la régénération en tremble et multiplie par 7 l'arrivée d'espèces non indigènes. La coupe partielle retient la plupart des attributs des peuplements matures non coupés, mais montre peu de preuves d'un développement accéléré des caractéristiques des vieux peuplements, après 3 ans. Les auteurs concluent que l'approche SAFE, impliquant une sylviculture basée sur la dynamique naturelle, arrive mieux à recréer l'amplitude de variabilité des communautés de trembles naturelle-

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ment perturbées, que la coupe à blanc conventionnelle. On obtient des améliorations certaines en incluant des prescriptions de brûlage alternatives et la rétention de chicots et d'arbres verts dans les coupes à blanc.

Mots-clés : Populus tremuloides, succession forestière, forêt mixte boréale, aménagement écosystémique, indicateurs de biodiversité.

Introduction

Within the global boreal forest, ecosystems dominated by trembling aspen (*Populus tremuloides* Michx. in North America, *Populus tremula* L. in Eurasia) are notable for the biological richness of their understory and epiphytic plant communities (Kuusinen 1994; De Grandpré and Bergeron 1997; Boudreault et al. 2000; Reich et al. 2001). Conventional clear-cutting practices threaten this biodiversity principally because short-rotation, even-aged forestry eliminates large, widely spaced old trees and favours management of aspens and conifers on separate landbases (Hansen et al. 1991; Man and Lieffers 1999; Bergeron et al. 2002).

The natural disturbance paradigm suggests that forestry practices that emulate the disturbance dynamics of unmanaged forests are more likely to maintain biodiversity and ecosystem processes than conventional clear-cutting (Harris 1984; Hunter 1993; Kuuluvainen 2002). Bergeron and Harvey (1997) proposed a natural dynamics-based silviculture for boreal mixedwoods of Quebec and Ontario that uses combinations of partial cutting, clear-cutting, and prescribed fire to cycle all stands through three successional stages: a first cohort even-aged stage dominated by aspen (*P. tremuloides*); a second-cohort mixed-species stage; and a third-cohort all-aged conifer-dominated stage. This silvicultural approach is being field-tested in the Sylviculture et Aménagement Forestier Écosystémiques (SAFE) project established in 1998 at the Lac Duparquet Research and Teaching Forest in northwestern Quebec (Harvey 1999; Harvey et al. 2002). SAFE is a multiphase study that encompasses all three successional cohorts on mesic ecosystems with clay-textured soils. Our study is limited to the first phase (SAFE1), established within an area of first-cohort aspen forest that originated after a 1923 stand-destroying wildfire (Brais et al. 2004).

Our general hypothesis was that the SAFE1 silvicultural treatments would better replicate the range of variability in plant community composition, structure and diversity found in natural wildfire-origin aspen stands than current clear-cutting practices, and by extension, more effectively conserve plant biodiversity (Fig. 1). Partial-cutting treatments were intended to lessen negative effects of clear-cutting on forest-dwelling species while accelerating development of old stand attributes in mature harvest-aged stands. The purpose of prescribed burning was to emulate patterns and processes of wildfire that are absent from conventional, unburned clearcuts. A short-term evaluation of the hypothesis was carried out through a set of linked studies conducted in SAFE1 and in nearby naturally disturbed and conventionally clear-cut mesic aspen forests of northwestern Quebec and northeastern Ontario. All studies were based on a 3 year post-disturbance timeframe.

From the literature and our earlier studies, we identified a suite of five plant community and seven plant functional group indicators (Table 1) to test the following specific hypotheses: (*i*) that plant species composition, vertical and horizontal vegetation structure, alpha species richness, and beta species diversity would be intermediate in SAFE1 prescribed burn treatments between the range of variability observed in wildfires and in unburned clearcuts;

(*ii*) that plant species composition, vertical and horizontal vegetation structure, alpha species richness, and beta species diversity would be intermediate in SAFE1 partial cutting treatments between the range of variability observed in old uncut aspen forests and in mature uncut aspen forests;

(*iii*) that post-fire specialists, known to be lacking in unburned clearcuts (Song 2002; Haeussler and Kneeshaw 2003; Haeussler and Bergeron 2004), would have similar abundance in SAFE1 prescribed burn treatments to the range of variability observed in wildfires;

(*iv*) that invasive non-native plants, known to increase following machine disturbance of soils (Harvey et al. 1995; Haeussler et al. 2002), would have similar abundance in SAFE1 unburned and burned clearcuts to the range of variability observed in wildfires (Haeussler and Bergeron 2004);

(*v*) that the dominance of tall shrubs over aspen suckers, known to increase following clear-cutting (Radosevich et al. 1997; Tappeiner et al. 1997; Haeussler and Bergeron 2004), would be similar in SAFE1 prescribed burn treatments to the range of variability observed in wildfires;

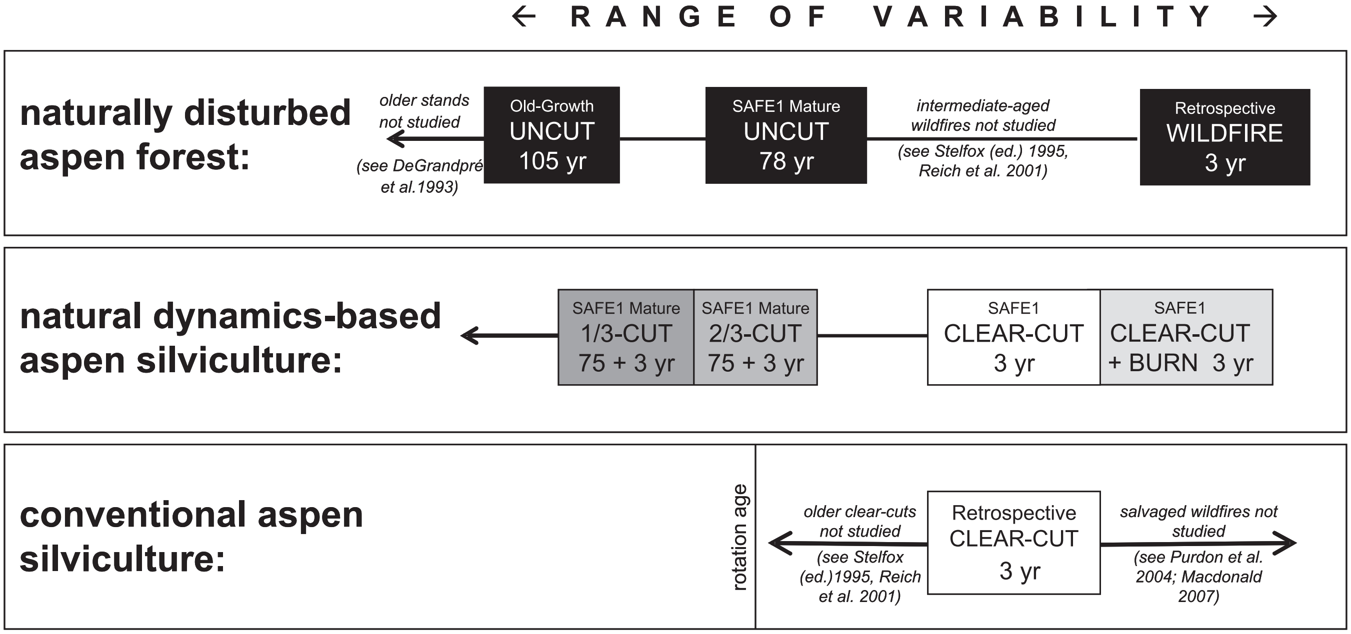
(*vi*) that the richness and frequency of old forest specialists (mycoheterotrophic herbs, aspen epiphytes, epixyles), known to increase with stand age, large old trees and logs, and to decrease with loss of tree cover and fire (Leake 1994; Boudreault et al. 2000; Thysell and Carey 2001; Haeussler et al. 2002; Haeussler and Bergeron 2004; Moola and Vasseur 2004), would exhibit a threshold effect, with SAFE1 partial-cut treatments being much more similar to mature uncut aspen stands than to clearcuts, and with unburned clearcuts having greater richness and frequency than burned clearcuts.

Methods

Study area description

The study was located in southern boreal mixedwood forests of northwestern Quebec and northeastern Ontario, Canada (48°15′N–48°48′N, 82°24′W–79°26′W; 270–355 m a.s.l.), a region of rolling, heavily glaciated terrain and cold, moist continental climate with 1 °C mean annual temperatures and 800–900 mm annual precipitation (Environment Canada 2007). Forests are mixtures of trembling aspen, balsam fir (*Abies balsamea* (L) Mill.), white spruce (*Picea glauca* (Moench.) Voss), black spruce (*Picea mariana*

Fig. 1. Predicted range of variability in plant species composition, vegetation structure, and diversity among the eight trembling aspen stand types represented in the study. Upper (black) boxes represent natural, unmanaged stand types, hypothesized to have the greatest range of variability. Lower (white) boxes represent conventional aspen silviculture, hypothesized to have the narrowest range of variability. Middle (grey) boxes represent SAFE1 natural dynamics-based partial-cut and prescribed burn treatments, hypothesized as intermediate between these extremes. SAFE1 clearcuts (white) are assumed to be comparable with industrial clearcuts from the retrospective study. Left-pointing arrows indicate successional changes as aspen stands age; right-pointing arrow indicates changes induced by more severe disturbance.



(Mill.) B.S.P.), white birch (*Betula papyrifera* Marsh.), jack pine (*Pinus banksiana* Lamb.), and Eastern white cedar (*Thuja occidentalis* L.), mainly of wildfire origin. Natural succession and disturbance dynamics in the region are well-studied (Dansereau and Bergeron 1993; Kneeshaw and Bergeron 1998; Bergeron 2000; Chen and Popadiouk 2002; Bergeron et al. 2004). On loamy to clay-textured soils with a fresh to moist (mesic) moisture regime (Brais and Camiré 1992) the first post-fire successional cohort is typically dominated by trembling aspen.

Our study integrated three aspen plant community datasets. All field sampling was done by the S. Haeussler with the intent of carefully matching site conditions to those of the SAFE1 study area. Study sites were mesic, even-aged forests with sandy loam to clay-textured Luvisols. Prior to the 1996–1999 disturbances described below, all stands were of the first post-fire cohort and had a tree canopy dominated by trembling aspen with scattered paper birch and conifers, a 2–4 m tall shrub stratum dominated by mountain maple (*Acer spicatum* Lam.) and hazel (*Corylus cornuta* Marsh.), a diverse forb layer dominated by *Aster macrophyllus* L., *Aralia nudicaulis* L., *Clintonia borealis* (Ait.) Raf., *Maianthemum canadense* Desf., *Rubus pubescens* Raf., and *Mitella nuda* L, and a discontinuous bryophyte layer, dominated by *Brachythecium* Schimp. mosses. Conifer regeneration in the understory was patchy and variable in species composition.

The first dataset was a retrospective comparison pairing mesic aspen plant communities from four 1997 wildfires with those from ten closely matched 1996–1997 industrial clearcuts near Timmins, Ontario. The study was conducted in 2000, three growing seasons after disturbance (Haeussler and Bergeron 2004).

The second dataset compared five experimental silvicultural treatments from SAFE1, 3 years after treatment. In the winter of 1998–1999 forest harvesting treatments were applied to 1–2.5 ha experimental units located in a mature, fully stocked trembling aspen stand dating from a 1923 wildfire (Brais et al. 2004; Harvey and Brais 2007). The ground was snow-covered during harvest and soil disturbance was minimal; at 3 years, ground vegetation and soils on skid trails and untracked areas were barely distinguishable. The study was a randomized block design with three replications of four harvest treatments: (*i*) uncut control; (*ii*) 1/3 partial-cut, a uniform partial harvest of mature aspen that removed 33% of merchantable basal area; (*iii*) 2/3 partial-cut, a uniform partial harvest of mature aspen that removed 61% of merchantable basal area; (*iv*) clear-cut, removal of 100% of stand basal area leaving no stems > 1 m in height. In September 1999, a low intensity broadcast burn was carried out in a randomly selected 0.3 ha subunit of each clear-cut treatment unit (Belleau et al. 2006). The mature uncut, 1/3 partial-cut, 2/3 partial-cut, and unburned clear-cut treatment (sub)units were sampled in 2001, whereas the burned clear-cut treatment subunits were sampled in 2002 (i.e., three growing seasons after treatment).

The third dataset was a sample of old growth trembling aspen stands located inside the mapped boundaries of the 1923 wildfire, approximately 5 km southwest of SAFE1, on similar slopes, soils, and aspect, and with similar floristic composition. Cores from 30 sound aspen and 5 dominant

Table 1. Plant biodiversity indicators, spatial scales of analysis, and sample sizes by aspen stand type.

		Sample size (*n*)			
				Retrospective study	
Biodiversity indicator	Scale(s) of analysis	Old uncut	All SAFE1	Clear-cut	Wildfire
Plant community indicators					
Vascular + nonvascular plant species composition	Plot	9	9	22	22
Horizontal structure of live + dead vegetation	Plot	9	9	22	22
Vertical structure of live + dead vegetation	Plot	9	9	22	22
Alpha species richness (number of vascular plant species + number of nonvascular plant species) at 4 spatial scales	Quadrat	27	27	66	66
	Plot	9	9	22	22
	Treatment unit or stand	3	3	10	14
	Study area	1	1	4	4
Beta species diversity (mean Bray-Curtis distance between 2 samples) at 3 spatial scales	Quadrats within plots	9	9	22	22
	Plots within treatment units or stands	9	9	16	12
	Treatment units within study area	3	3	4	4
Plant functional group indicators					
Post-fire specialists, includes *Ceratodon purpureus, Polytrichum juniperinum,* misc. Polytrichaceae, *Bryum caespiticium, Leptobryum pyrifolium, Pohlia* spp., *Carex houghtonii,* misc. *Carex* spp., *Geranium bicknellii, Corydalis* spp., *Luzula* spp., *Aralia hispida, Polygonum cilinode, Prunus pensylvanica, Diervilla lonicera*	Treatment unit or stand	3	3	10	14
Invasive non-native plants, includes *Artemisia vulgaris, Cerastium arvense, Hieracium pilosella, Medicago sativa, Phleum pratense, Poa pratensis, Potentilla norvegica, Ranunculus acris, Sonchus arvensis, Taraxacum officinale, Trifolium* spp.	Treatment unit or stand	3	3	10	14
Tall shrubs (>2m height at maturity), includes mainly *Acer spicatum,* some *Corylus cornuta* with minor *Alnus spp., Amelanchier alnifolia, Acer rubrum*	Treatment unit or stand	3	3	10	14
Aspen suckers ≤ 3 years old	Treatment unit or stand	3	3	10	14
Mycoheterotrophic herbs, includes *Corallorhiza maculata, Corallorhiza trifida, Goodyera repens, Platanthera orbiculata, Hypopitys monotropa, Monotropa uniflora, Moneses uniflora, Orthilia secunda, Pyrola minor*	Treatment unit or stand	0	3	0	0
Epiphytes, includes mosses, liverworts, and non-crustose macrolichens found at 0 and 1 m height on the north side of live aspen trunks	Treatment unit or stand	3	3	0	0
Epixyles, includes mosses, liverworts, and non-crustose macrolichens found on decaying logs of all species, sizes and decay classes	Treatment unit or stand	3	3	0	0

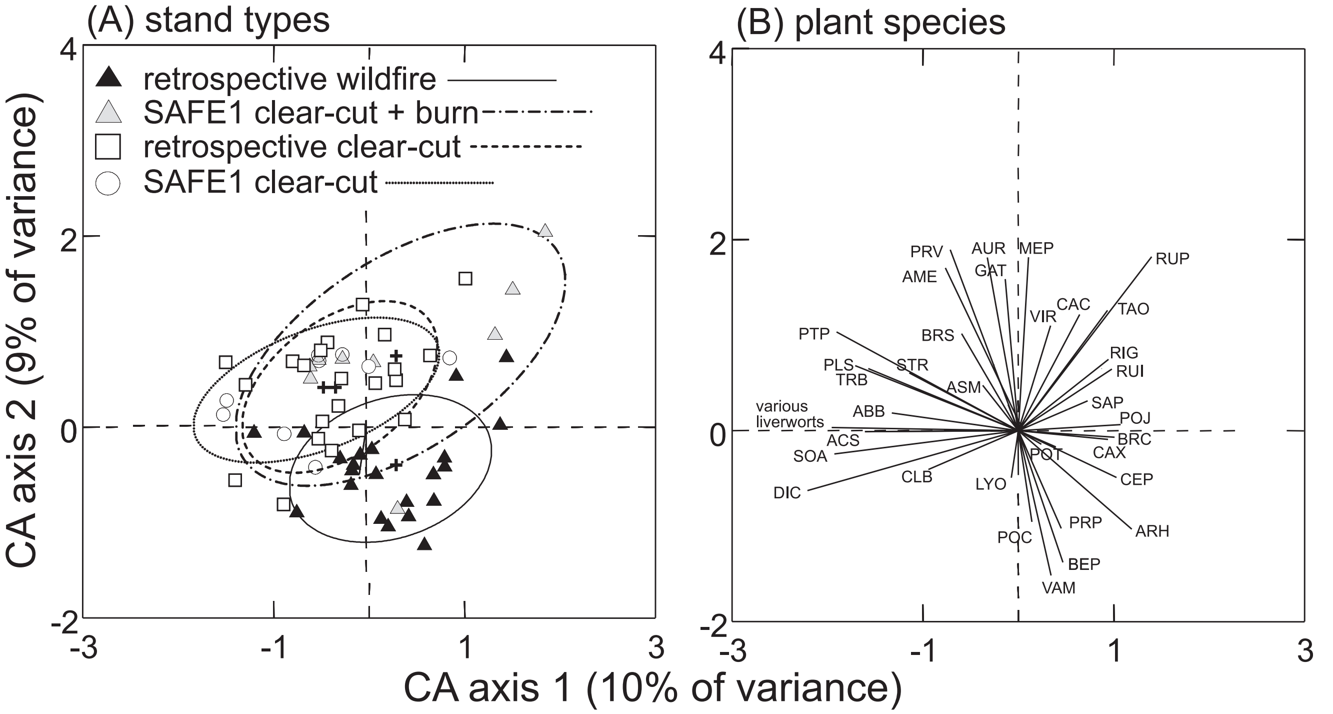
spruces indicated that this remnant forest originated from an 1896 wildfire. We located three small stands of dominantly mesic old aspen forest, also situated 0.5–2 km apart. Principal coordinates analysis of site and soil data was used to match each of the three 105-year-old stands to the most physiographically similar of the three SAFE1 experimental blocks. These stands were sampled in 2001 together with the SAFE1 treatments.

In summary, the three datasets provided information on the range of variability in composition, structure, and diversity of trembling aspen plant communities belonging to eight preliminary stand types (Fig. 1): (*i*) old (105 years) uncut; (*ii*) SAFE1 mature (78 years) uncut; (*iii*) SAFE1 mature, 1/3 cut (75 years + 3 years post-treatment); (*iv*) SAFE1 mature, 2/3 cut (75 years + 3 years post-treatment); (*v*) SAFE1 young (3 years) clear-cut; (*vi*) retrospective young (3 years) clear-cut; (*vii*) SAFE1 young (3 years) clear-cut + prescribed burn; (*viii*) retrospective young (3 years) wildfire (Fig. 1). We anticipated that the SAFE1 young clearcuts (stand type *v*) would prove not significantly different from the retrospective clearcuts (stand type *vi*), resulting in a total of seven distinct stand types: old uncut, mature uncut, 1/3 cut, 2/3 cut, unburned clear-cut, burned clear-cut, wildfire.

Data collection

Apart from the exceptions noted below, the sampling methods were identical in all stand types (details in Haeussler and Bergeron 2004). Linear transects were randomly located in uniform treatment units, subunits or stands. Plot centres were established at 50 m intervals on each transect, except for burned clearcuts where plot centres were located at the first random distance that allowed plots to be fully located within a burned patch. At plot centre we described site and soil conditions, inventoried live and dead trees, and established three 5 m linear transects. Vegetation structure and coarse woody debris were measured on 5 m transects using line intersects or cylindrical intersects 1 m in diameter (vertical structure). Plant species cover was estimated on three quadrats per plot measuring 4 m^2 for

Fig. 2. Species composition of 3-year-old wildfire, unburned clear-cut, and burned clear-cut aspen plant communities in the retrospective study (n = 22 plots) and SAFE1 study (n = 9 plots). Ordination of (A) stand types, and (B) vascular and nonvascular plant species by correspondence analysis (CA). Ellipses enclose 68.3% of the variability around the centroid (+) for each stand type (equivalent to ±1 SD). Species codes are defined in Appendix A, Table A1.



vascular plants and 1 m^2 for mosses, liverworts, and macrolichens growing below 1.3 m in height. Difficult specimens were identified in the lab.

On two plots per treatment unit in SAFE1 and old uncut stand types we collected epiphytic and epixylic bryophytes and macrolichens from 5 basal aspen trunks (10 cm × 20 cm samples) and 5 decaying logs (20 cm × circumference) for microscopic identification. In SAFE1 only, we inventoried mycoheterotrophic herbs (Orchidaceae, Monotropaceae, and all Pyrolaceae except *Pyrola asarifolia* Michx.) on 4 m-wide belt transects (1200 m^2/stand) in late June and early July of 2001 or 2002. Number of stems and total stem length was recorded for each species.

Data analysis

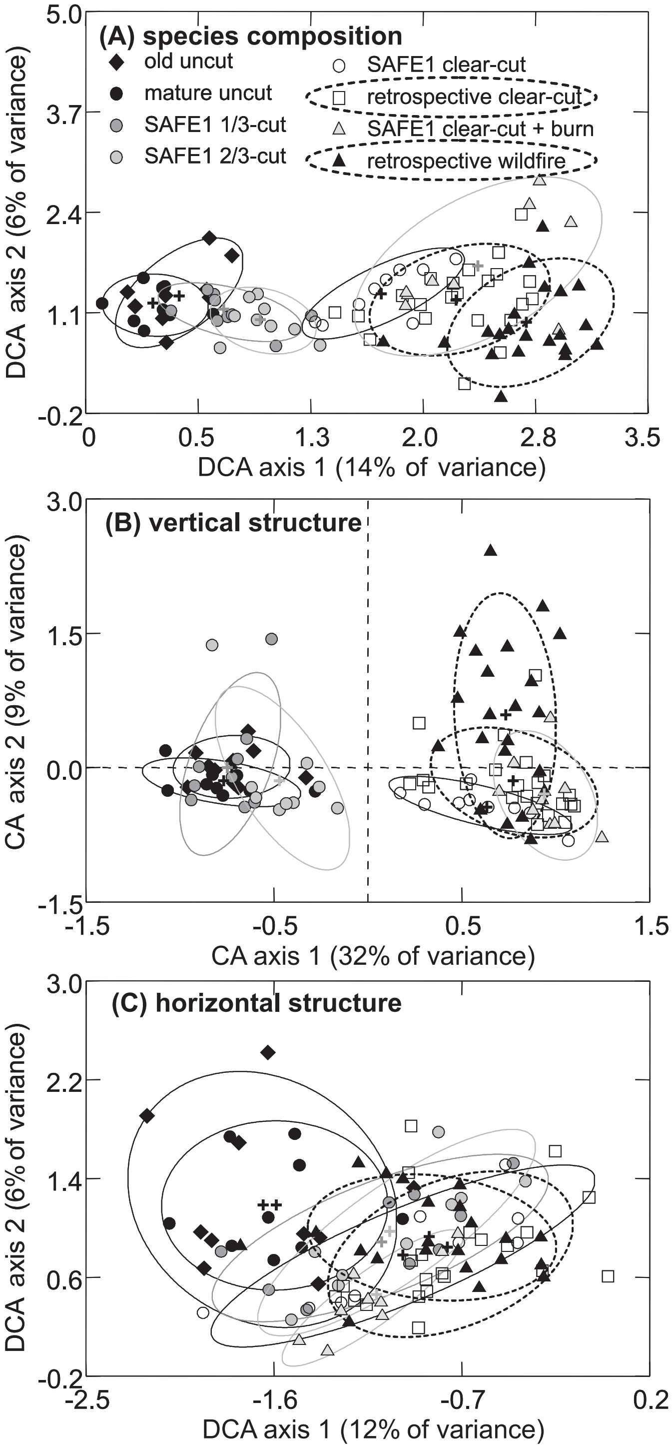
Alpha species richness was calculated at four spatial scales: (*i*) quadrat; (*ii*) pooled data from all quadrats per plot; (*iii*) pooled data from all plots per treatment (sub)unit or stand; (*iv*) pooled data from all treatment (sub)units or stands within a local study area. Beta diversity, defined as the mean Bray-Curtis distance (Legendre and Legendre 1998) between two samples, was assessed at three spatial scales: (*i*) among quadrats within a plot; (*ii*) among plots within a treatment (sub)unit or stand; (*iii*) among treatment (sub)units or stands within a local study area. All other plant community indicators were assessed at the plot scale and all plant functional group indicators were assessed at the treatment unit scale (sample sizes in Table 1). Because the retrospective study had a larger sample size and included four study areas distributed over 100 km^2, we expected a greater range of variability than for SAFE1 and old uncut stand types.

Multivariate indicators (species composition, horizontal structure, vertical structure) were assessed by correspondence analysis (CA) (ter Braak and Šmilauer 1998). CA ordinations of species composition and horizontal structure for all stand types had a strong arch effect and were detrended using DCA (Legendre and Legendre 1998). We compared the range of variability for each stand type by plotting the centroid and a 68.3% sample ellipse (equivalent to ±1 SD) on the first two ordination axes.

The first step in the data analysis was a joint CA ordination of vegetation composition of the retrospective and SAFE1 clearcut datasets. If the sample ellipse for the SAFE1 clearcuts was located within the ellipse for the retrospective clearcuts, this would confirm that the SAFE1 clearcuts were samples from the same larger population of mesic northeast Ontario – northwest Quebec trembling aspen plant communities. By extension, since all sites were carefully matched using the same site and soil criteria, differences in bioindicators among the other stand types should also reflect differences in stand disturbance history rather than inherent physiographic differences. The second stage of the analysis involved a joint ordination of all eight stand types to assess the full range of variability in composition and structure of young to old, naturally and anthropogenically disturbed aspen plant communities.

Univariate indicators available for all eight stand types (alpha richness, beta diversity, and the first four plant functional group indicators in Table 1) were compared using

Fig. 3. Range of variability in (A) plant species composition, (B) vertical vegetation structure, and (C) horizontal vegetation structure across all study plots. As in Fig. 1, black symbols represent uncut stand types, white symbols represent conventional clear-cutting and grey symbols represent SAFE1 experimental stand types. Ellipses enclose 68.3% of the variability around the centroid (+) for each stand type. Ellipses for the retrospective study are dashed lines; others are solid lines. DCA was used in (A) and (C) to remove the arch evident with CA.



box-and-whisker diagrams. Mycoheterotrophic herbs (SAFE1 dataset only) were assessed using ANOVA with three replications of five stand types followed by Fishers LSD. Epiphytic and epixylic functional group indicators (SAFE1 and old uncut stand datasets) were assessed using ANOVA and LSD with three replications of six stand types. Treatment units, subunits, and old growth stands were all treated as randomized block experimental units in the ANOVAs. To confirm threshold effects, the SAFE1 stem removal treatments were plotted on an *x* axis (0/3, 1/3, 2/3, 3/3 removal) with old uncut and burned clear-cut stand types arbitrarily positioned at –1/3 and 4/3, respectively.

Results

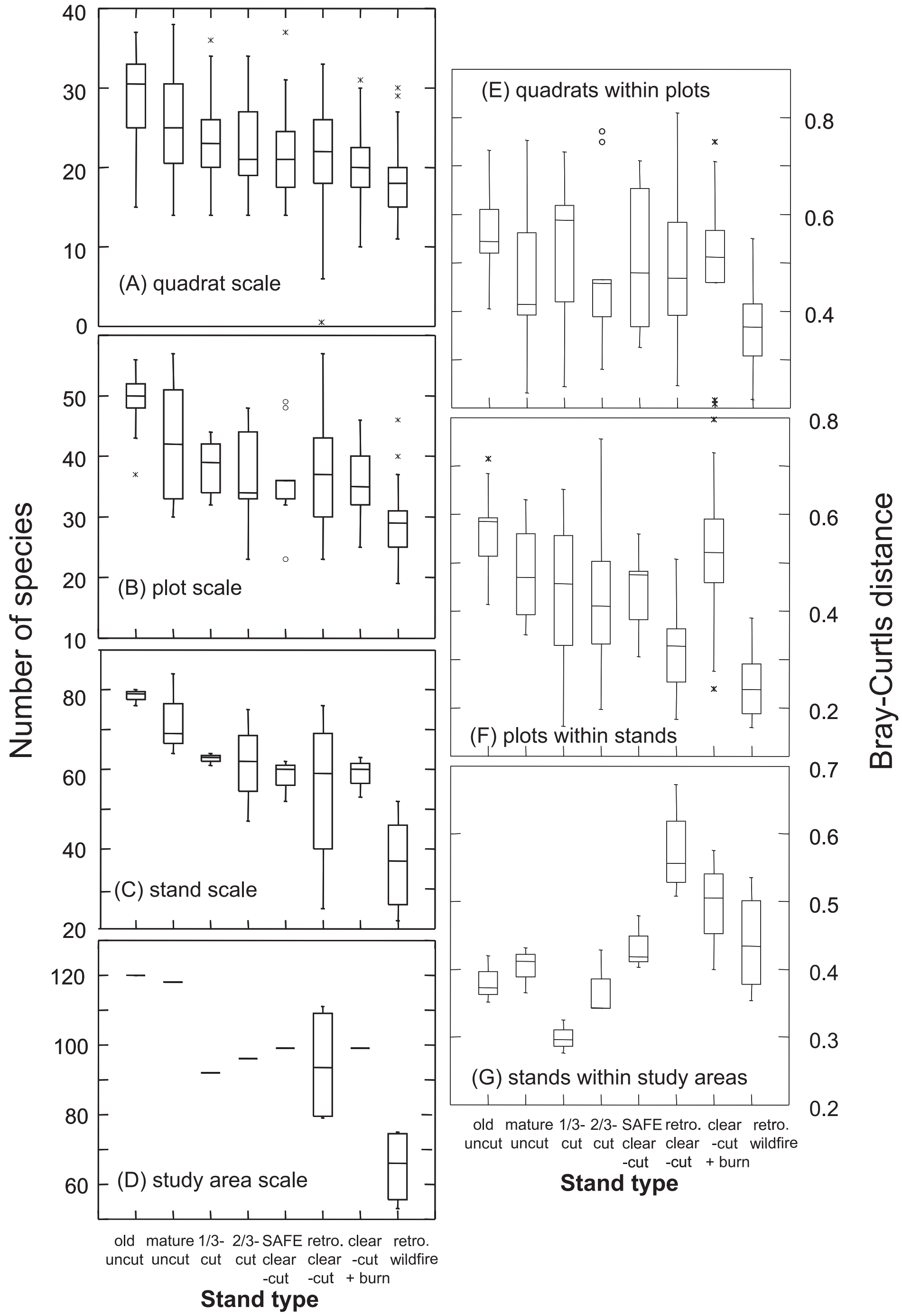
Plant species composition of SAFE1 clearcuts coincided closely with that of retrospective clearcuts (Fig. 2A), confirming that both samples were drawn from the same larger population of mesic trembling aspen plant communities. Contrary to our expectations, however, the range of variability of the 22 retrospective clear-cut plots was no greater than that of the nine SAFE1 clear-cut plots over the two dominant ordination axes.

Hypothesis 1: burning clearcuts better emulates the effects of wildfire than clear-cutting alone

Our hypothesis that the SAFE1 burned clear-cut stand type would be intermediate in species composition, vegetation structure, alpha and beta species diversity between wildfire and clear-cut stand types was only partly correct (Figs. 2–4). For these plant community indicators, the combination of clear-cutting followed by burning, while recreating some of the effects of wildfire, also created novel conditions that were outside the range of variability of either wildfire or clear-cutting.

Species composition in burned clearcuts was more variable than in either wildfires or unburned clearcuts because it included heavily burned areas dominated by post-fire specialists, lightly burned plots characterized by fire-sensitive species, and novel conditions not found in either wildfires or unburned clearcuts. While species composition was, on average, slightly more similar to unburned clearcuts than to wildfires (compare distances between centroids in Figs. 2A and 3A), both the wildfires and the burned clearcuts were shifted to the right on axis 1 relative to unburned clearcuts (Fig. 2A) owing to the presence of fire moss (*Ceratodon purpureus* (Hedw.) Brid.) and other pioneering seed- and spore-banking post-fire specialists (*Polytrichum juniperinum* Hedw., *Rubus idaeus* L., *Ribes glandulosum* Grauer, *Sambucus pubens* Michx., *Carex* L. spp., and *Aralia hispida* Vent.). Compared with unburned clearcuts, they also had lower cover of shade tolerant, fire-sensitive species such as mountain maple, *Aster macrophyllus*, *Trientalis borealis* Raf., *Clintonia borealis*, *Streptopus roseus* Michx., and bryophytes such as *Ptilidium pulcherrimum* (G. Web.) Vanio, *Pleurozium schreberi* (Brid.) B.S.G., and *Brachythecium salebrosum* (Web. & Mohr) B.S.G.). Burned clearcuts were distinct from both wildfires and unburned clearcuts on the second ordination axis because they had less aspen regeneration and higher abundance of *Rubus pubescens*, *Tar-*

Fig. 4. Range of variability by stand type in alpha species richness across four spatial scales (A–-D) and beta species diversity (Bray-Curtis distance between two samples) across three spatial scales (E–-G). The centre line represents the median, box edges indicate 1st and 3rd quartiles, and whiskers extend a farther 1.5 times the interquartile range. Asterisks represent extreme values and open circles are far outside values. Samples sizes are indicated in Table 1.

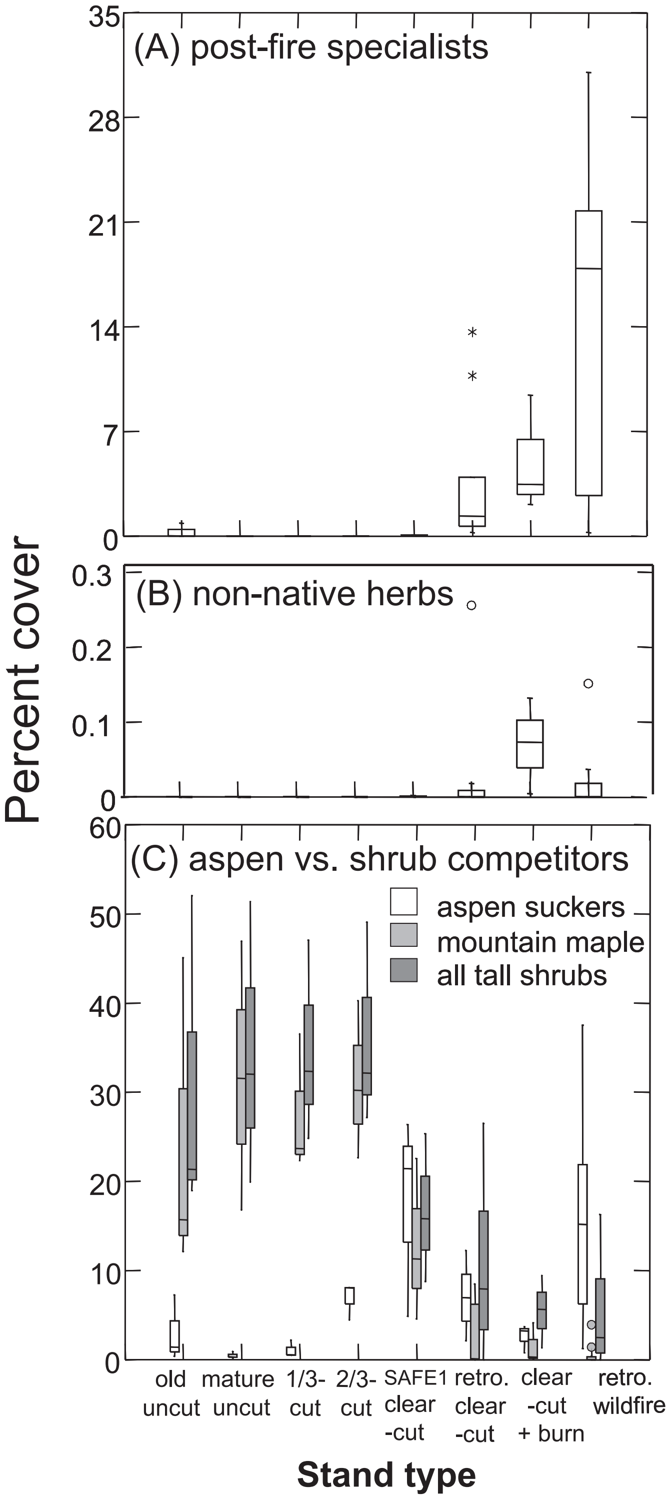


axacum officinale Weber, and *Mertensia paniculata* (Ait.) G. Don).

Vertical vegetation structure of burned clearcuts was not intermediate between that of wildfires and unburned clearcuts (Fig. 3B) for two main reasons: (*i*) standing dead trees (snags), which distinguished the wildfires on axis 2 of the ordination, were completely absent in SAFE1 clearcuts, but occasionally present (white squares) in industrial clearcuts; (*ii*) a lack of woody vegetation > 1 m tall (tall shrubs and aspen suckers), which shifted the burned clearcuts to the far right on axis 1.

Horizontal vegetation structure varied less with stand type than either species composition or vertical structure (Fig. 3C). Again, the burned clearcuts were not intermediate between wildfires and clearcuts, but occupied an outlier position on the second ordination axis because they had more bare patches and less woody vegetation than the other stand types.

Fig. 5. Range of variability by stand type in the abundance of (A) post-fire specialists; (B) invasive non-native plants; and (C) aspen suckers, mountain maple, and all tall shrub competitors. The centre line represents the median, box edges indicate 1st and 3rd quartiles and whiskers extend a farther 1.5 times the interquartile range. Asterisks represent extreme values and open circles are far-outside values. In (B), far-outside values of 4% for retrospective clearcuts and 0.7% for retrospective wildfires are not shown. Sample sizes are indicated in Table 1.



Wildfires consistently had the lowest alpha diversity (Fig. 4A–4D). Burned clearcuts, although generally intermediate, were more similar to unburned clearcuts across all spatial scales, because they retained many fire-sensitive vascular and nonvascular plant species within lightly burned patches. The beta diversity (heterogeneity) of burned clearcuts was intermediate between wildfires and unburned clearcuts at the between-stand scale, similar to clearcuts at the within-plot scale, but anomalously high and variable at the between-plot scale.

Hypothesis 2: partial-cutting accelerates the development of old aspen forest characteristics

Our hypothesis that SAFE1 1/3 and 2/3 partial-cut stand types would be intermediate in species composition, vegetation structure, and alpha and beta species diversity between mature and old uncut aspen stand types proved to be mostly incorrect at this early stage (Figs. 3–4). Three years after partial-cutting, most of these plant community indicators were shifted towards the condition of young clearcut stand types rather than towards older uncut aspen forest conditions. With a few exceptions, the 2/3-cut experienced a greater shift towards early seral conditions than the 1/3 cut.

In the species composition ordination (Fig. 3A) axis 1 represented primarily a gradient of understory light availability, and tree-sized aspen (left) versus shrub and herb dominance (right). On this axis, old uncut aspen stands were positioned between mature uncut stands and young stands (Fig. 3A), because wider tree spacing and larger canopy gaps in the old stands allowed for greater understory development than under the dense canopy of the mature stands. Thus, although the two partial-cutting treatments were not intermediate between mature and old stands, they did achieve the desired effect of being more like old uncut stands than like mature uncut stands because of their greater understory shrub and herb development.

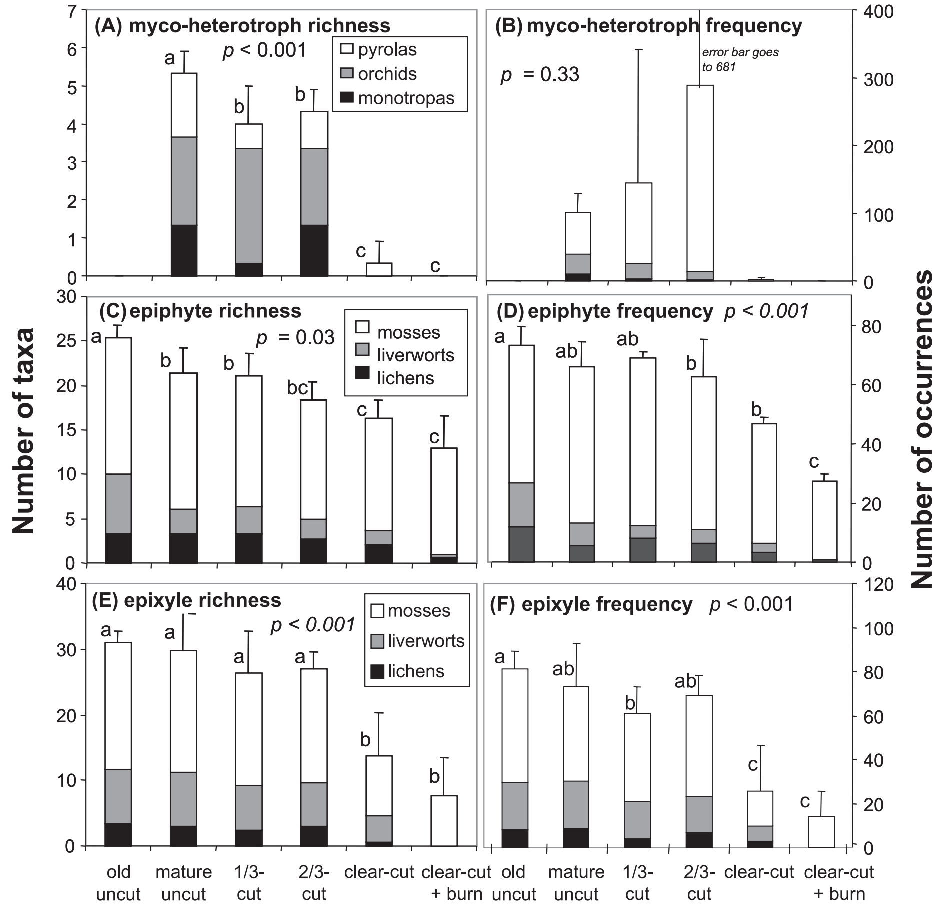
Vertical vegetation structure (Fig. 3B) differed little between mature uncut, old uncut, and 1/3-cut stand types, while the 2/3-cut stand type was somewhat more similar to young stands because of reduced overstory density and a corresponding increase in understory structure. Both partial-cut stand types had more variability in vertical structure on axis 2 than uncut stands, owing to the presence of standing dead trees and recent canopy gaps.

Old uncut aspen forests had the most variability in horizontal vegetation structure of all stand types. This structure was not well replicated in the partial-cuts, which were more similar to clearcuts than to uncut forests. Whereas old and mature stand types had continuous, well-developed herb layers, abundant mosses and tall shrubs mostly >2 m in height, partially cut understories were patchier with shrubs and aspen suckers mostly below 2 m, little moss and much more fine slash and recent woody debris.

Alpha species richness decreased from old to young stand types and with increasing disturbance severity (Figs. 4A–4D). Old uncut aspen forests consistently had the highest mean richness mainly because a great variety of bryophytes and lichens were present. Partial-cutting did not enhance species richness over the 3 year time-frame of the study.

Partial-cutting had little or no negative effect on beta diversity at within- and between-plot scales, but substantially

Fig. 6. Stand-scale richness and frequency of old forest specialists: (A and B) mycoheterotrophic herbs; (C and D) epiphytes on basal aspen trunks; and (E and F) epixyles on all types of decaying wood. Error bars are ±1 SD for all taxa combined. No comparable data are available for the retrospective study, and mycoheterotroph data are not available for old uncut forest; *p* values and lowercase letters indicating significant treatment differences (Fishers LSD) are for total richness and total frequency.



reduced beta diversity between stands. In other words, species composition of the three replicates became more homogeneous in response to uniform partial-cutting.

Hypothesis 3: post-fire specialists

Broadcast burning one growing season after clear-cutting increased the representation of post-fire specialists to within the lower end of the range observed after wildfire (Fig. 5A).

Hypothesis 4: invasive non-native plants

There was no evidence that clear-cutting, either in SAFE1 or the retrospective study, increased non-native plant invasion above levels observed on wildfires, but burned clearcuts had substantially more non-native plants than wildfires or unburned clearcuts (Fig. 6B). Non-native herbs were essentially absent on uncut and partial-cut stand types and were encountered on 14% of unburned clear-cut quadrats and 16% of wildfire quadrats. However, 47% of burned clear-cut quadrats had at least one non-native species present, and mean cover was seven times greater than on unburned clear-cuts.

Hypothesis 5: tall shrubs versus regenerating aspen suckers

Regenerating aspen suckers were dominant over mountain maple and other tall shrubs 3 years after wildfires, but were relatively less competitive after clear-cutting and were subordinate to tall shrubs at later successional stages (Fig. 6C). As we hypothesized, burning of clearcuts reduced the abundance of tall shrubs, most notably, mountain maple. This treatment did not, however, increase the abundance of aspen relative to tall shrubs, because aspen suckers were also reduced to the very low end of the range of variability observed after wildfire.

Hypothesis 6: old forest specialists

All three groups of old forest indicators (mycoheterotrophic herbs, aspen epiphytes, and epixylic bryophytes and lichens) increased in richness and frequency with stand age and decreased with disturbance severity, both among and within indicator groups, but at different rates (Fig. 6). Differences among stand types were often not statistically significant, suggesting a need for more than three replicates.

Richness of mycoheterotrophic herbs (not sampled in old uncut) showed strong evidence of a threshold effect, being highest in uncut mature forest (five to six species), slightly but significantly lower on the 1/3 and 2/3 partial cuts (four species), and substantially lower in clearcuts (one to no species) ($p < 0.001$). Although *Pyrola secunda* L. was found on unburned clearcuts (in a chlorotic state) and no mycoheterotrophs were found burned clearcuts, the difference in richness was not statistically significant. Frequencies were not significantly different across treatments owing to highly erratic numbers of *Pyrola secunda*, but seemed to echo trends in richness, especially with this species removed. Total mycoheterotrophic richness and frequency were positively associated with the presence of conifer trees and large, old conifer logs.

Aspen epiphyte richness and frequency did not exhibit a threshold effect. Instead, epiphytes declined more or less linearly from old uncut stands to burned clearcuts (Fig. 6C–6D). Old, uncut aspen stands had significantly higher epiphyte richness than all other stand types. Partially cut stands were intermediate between mature uncut stands and clearcut stands. Epiphyte frequency was significantly higher on unburned clearcuts than on burned clearcuts, but epiphyte richness was not significantly different. Liverworts were the most sensitive to stand age and disturbance, while mosses were the least sensitive. Epiphytic lichens were more tolerant of stem removal than expected (stumps in clearcuts harboured most species), but highly sensitive to burning.

Epixylic species exhibited a clear threshold effect, with partially cut stands having approximately equal richness and frequency to uncut stands and clear-cut stands having substantially fewer epixyles (Fig. 6E and 6F). There were no significant differences in the total richness and frequency of epixylic species on unburned and burned logs, although the burned logs were colonized by mosses — mostly pioneering species, with liverworts and lichens being absent. Across all stand types, large old conifer logs (mostly *Pinus* spp.) that clearly pre-dated the 1923 wildfire, supported the greatest diversity of epixylic species.

Discussion

Southern boreal aspen plant communities across North America and northern Europe share many features including well-developed multilayered understories with high vascular species diversity relative to other boreal forest types (Bartemucci et al. 2006) and rich nonvascular communities — particularly epiphytes on large, old aspen trunks (Crites and Dale 1998; Boudreault et al. 2000; Hedenås and Ericson 2003). The 12 plant community and plant functional group indicators selected for this study effectively discriminated among stand types and addressed most of the stand-level elements of plant biodiversity and ecosystem function shown by our prior studies (Bergeron et al. 2002; Haeussler et al. 2002; Haeussler and Kneeshaw 2003; Haeussler and Bergeron 2004), to be potentially threatened by short-rotation aspen silviculture. We do recommend, however, that *Pyrola secunda* and epiphytic and epixylic mosses be dropped from the list of old forest specialist indicators (Table 1).

Certain features distinguish the northwest Quebec and northeast Ontario aspen communities of this study from other trembling aspen forests. For example, in western North American boreal forests, *Calamagrostis canadensis* (Michx.) Beauv. and *Alnus crispa* (Aiton) Pursh (Lieffers et al. 1993; MacIsaac et al. 2006) replace mountain maple as the species most likely to competitively exclude other understory plants and impede tree regeneration after logging. Furthermore, because eastern Canadian boreal forests are more humid and have longer fire-free intervals than western and central forests, sequential replacement of aspen by spruce and balsam fir occurs more often (Bergeron 2000). Old forest species assemblages, particularly liverworts, are probably better developed (c.f., Crites and Dale 1998), and their ability to recolonize following disturbance is more likely to be substrate-limited and less likely to be dispersal-limited than in other regions where old forests are rare (Ojala et al. 2000; Frego 2007). With biogeographic differences such as these taken into account, we believe that the suite of plant bioindicators tested here can be adapted to evaluate the effectiveness of althernative silvicultural approaches in other boreal aspen forests.

At this early stage, SAFE1 silvicultural practices appear to have addressed several deficiencies of industrial clearcutting but fell short of emulating the range of variability found in naturally disturbed aspen plant communities. Some of the shortcomings identified in our 3 year post-treatment assessment may resolve themselves over a longer time period, while others will likely require improvements to the SAFE1 silvicultural prescriptions.

Prescribed burning one growing season after clear-cutting effectively regenerated post-fire specialist plants while reducing mountain maple and other mid- and late-seral understory dominants. But burning had several unintended negative consequences that were likely due to the dual, short-interval nature of the disturbance (Paine et al. 1998), akin to cumulative effects reported for salvage logging after wildfire (Purdon et al. 2004; Lindenmayer and Noss 2006; Macdonald 2007). Invasion by non-native plants was exacerbated by clear-cutting and burning, despite the fact that the burns were of low severity. As the burns did not expose mineral soil seedbeds (Belleau et al. 2006), we believe that the dual disturbance reduced photosynthetic reserves in resprouting native plants to the point where they were less able to compete with invasive plants for the pulse of soil and light resources made available by the fire (Davis et al. 2000). Root suckering by trembling aspen was reduced below levels considered acceptable for a fully restocked aspen stand, most likely because carbohydrate reserves were depleted at the time of the burn (Frey et al. 2003). Alternative burning scenarios that might address these shortcomings include underburning intact aspen forest immediately prior to winter logging on snow; burning immediately after winter logging and before resprouting; burning at least two growing seasons after logging when root reserves have had more time to rebuild (Smith and James 1978; Johnston and Woodard 1985; Kauffman and Martin 1990; Quintilo et al.1991). As all prescribed fire options present logistical challenges, mechanical treatments that can reduce tall shrubs, slash, and humus depths without compacting soils or encouraging non-native species invasion (Harvey et al. 1995, Haeussler and Bergeron 2004; Haeussler and Kabzems 2005) should also be tested.

The largest structural discrepancy between young SAFE1 stands and naturally disturbed wildfires was the lack of retained vertical structure in the form of snags or live trees (Fig. 3B). In this respect, SAFE1 clearcuts were more deficient than industrial clearcuts from northeastern Ontario, which retained scattered patches of damaged and dying noncommercial birches and suppressed conifers (Haeussler and Bergeron 2004). Retaining trees provide critical wildlife habitat (Bunnell et al. 2002). Although few live epiphytes are present on recently burned aspen snags (Haeussler and Bergeron 2004), snags should, over time, provide a substrate for arboreal lichen recolonization as well as large old logs for epixyles and mycoheterotrophs. Bunnell et al. (2002) recommend that a combination of dispersed trees and patches or groups be retained, with a target density of 2–3 large snags or dying trees and 10–20 smaller snags per hectare, throughout the rotation. Our data indicate that a mix of aspen and conifers retention trees will provide the greatest habitat diversity for old forest specialists.

Three years after treatment is too early to assess whether or not partial cutting successfully accelerated the development of old aspen forest characteristics in mature stands. The 1/3 and 2/3 partial-cuts retained many attributes of mature uncut stands including a majority of the mycoheterotrophic, epiphytic, and epixylic species found in mature aspen forests, but their structure and diversity and was intermediate between mature and young stands rather than, as hypothesized, between mature and old stands. We expect many of the disturbance-related attributes to diminish or disappear within a few years, as fine slash decomposes, moss layers re-establish and the tall shrub understory recovers in height. For most indicators, the 2/3 cut was only marginally different from the 1/3 cut, with the notable exception of aspen suckers (Fig. 5C), which were denser and more vigorous in the 2/3 cuts. If these aspen suckers continue to grow, two-aged aspen-dominated stands will develop over time in this treatment. Such stands, while structurally unlike the 105-year-old uncut aspen stands of this study, may ultimately resemble second cohort mixedwood stands described by Bergeron (2000) and Kneeshaw and Bergeron (1998).

In conclusion, the SAFE1 natural dynamics-based silviculture better recreated the range of variability in structure, composition, and cross-scale diversity of naturally disturbed aspen plant communities than conventional clear-cutting. The variety of experimental treatments provides a way of simultaneously addressing the conflicting requirements of old forest specialists and early, seral post-fire specialists. Our early assessment suggests that several improvements are warranted, including further experimentation with a variety of alternative prescribed fire or mechanical site preparation techniques and some live or dead tree retention in clearcuts.

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Appendix A

Table A1. Nomenclature follows Marie-Victorin (1995) and Vitt et al. (1988).

Code	Scientific name
ABB	*Abies balsamea* (L.) Mill.
ACS	*Acer spicatum* Lam.
AME	*Amelanchier* spp. Medic.
ASM	*Aster macrophyllus* L.
ARH	*Aralia hispida* Vent.
AUR	*Alnus rugosa* (DuRoi) Spreng.
BEP	*Betula papyrifera* Marsh.
BRC	*Bryum caespiticium* Hedw.
BRS	*Brachythecium salebrosum* (Web.& Mohr) B.S.G.
CAC	*Carex canescens* L.
CAX	*Carex* spp. L. (*houghtonii, aenea*, others)
CEP	*Ceratodon purpureus* (Hedw.) Brid.
CLB	*Clintonia borealis* (Ait.) Raf.
DIC	*Dicranella heteromalla* (Hedw.)Schimp.
GAT	*Galium triflorum* Michx.
LYO	*Lycopodium obscurum* L.
MEP	*Mertensia paniculata* (Ait.) Gray
PLS	*Pleurozium schreberi* (Brid.) Mitt.
POC	*Polygonum cilinode* Michx.
POJ	*Polytrichum juniperinum* Hedw.
POT	*Populus tremuloides* Michx.
PRP	*Prunus pensylvanica* L.f.
PRV	*Prunus virginiana* L.
PTP	*Ptilidium pulcherrimum* (G. Web.) Vainio
RIG	*Ribes glandulosum* Grauer
RUI	*Rubus idaeus* L.
RUP	*Rubus pubescens* Raf.
SAP	*Sambucus pubens* Michx.
SOA	*Sorbus americana* Marsh.
STR	*Streptopus roseus* Michx.
TAO	*Taraxacum officinale* Weber
TRB	*Trientalis borealis* Raf.
VAM	*Vaccinium myrtilloides* Michx.
VIR	*Viola renifolia* A. Gray