

Range of variability in boreal aspen plant communities after wildfire and clear-cutting¹

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Abstract: Composition, structure, and diversity of vascular and nonvascular plant communities was compared 3 years after wildfire and clear-cutting in mesic trembling aspen (*Populus tremuloides* Michx.) forests of the southern Canadian boreal forest. We examined mean response to disturbance and variability around the mean across four to five spatial scales. Four 1997 wildfires were located near Timmins, Ontario, and ten 1996–1997 clearcuts were located adjacent to the wildfires. We randomly located plots within mesic, aspen-dominated stands selected to minimize predisturbance environmental differences. Correspondence analysis separated wildfire and clearcut samples based on community composition: wildfires had more aspen suckers, *Diervilla lonicera* Mill., and pioneering mosses; clearcuts had more understory tall shrubs, forbs, bryophytes, and lichens. Live tree basal area averaged 1.7 m²/ha in wildfires and 1.8 m²/ha in clearcuts ($p = 0.59$), and understory community structure (the horizontal and vertical distribution of live and dead plant biomass) was not markedly different. Clearcuts had higher species richness with greater variance than wildfires across all spatial scales tested, but differences in beta and structural diversity varied with spatial scale. Generally, clearcut–wildfire differences were more evident and wildfire variability greater at larger analytical scales, suggesting that plant biodiversity monitoring should emphasize cumulative effects across landscapes and regions.

Résumé : La composition, la structure et la diversité des communautés végétales, incluant les plantes vasculaires et non vasculaires, ont été comparées 3 ans après un feu ou une coupe totale dans des peuplements mésiques de peuplier faux-tremble (*Populus tremuloides* Michx.) situés dans la zone méridionale de la forêt boréale canadienne. Nous avons examiné les effets moyens, et la variation de la moyenne, des perturbations à quatre à cinq échelles spatiales différentes. Quatre feux survenus en 1997 étaient situés près de Timmins en Ontario et 10 coupes à blanc datant de 1996–1997 étaient adjacentes aux sites brûlés. Les différences environnementales entre les places-échantillons présentes avant que surviennent les perturbations ont été minimisées par une sélection aléatoire stratifiée des peuplements. L'analyse des correspondances a permis de distinguer les stations brûlées des stations coupées sur la base de la composition végétale. Les stations brûlées sont caractérisées par un plus grande abondance de drageons de tremble, de *Diervilla lonicera* Mill. et de mousses pionnières. À l'opposé, davantage d'arbustes hauts, de plantes herbacées, de bryophytes et de lichens résiduels sont présents dans les sites coupés. La surface terrière des arbres vivants atteint en moyenne 1,7 m²/ha après un feu et 1,8 m²/ha après une coupe à blanc ($p = 0,59$) et la structure des communautés végétales du sous-bois (distribution horizontale et verticale de la biomasse végétale morte et vivante) est semblable peu importe le type de perturbation. La richesse en espèce et sa variation sont plus élevées après une coupe qu'après un feu à toutes les échelles spatiales testées tandis que la diversité structurale et la diversité bêta varient selon l'échelle spatiale retenue. Généralement, les différences entre la coupe et le feu ainsi que la variabilité après un feu sont plus prononcées aux échelles du paysage et de la région, indiquant que le suivi de la biodiversité végétale à ces échelles devrait mettre l'emphase sur les effets cumulatifs.

Introduction

A consensus is emerging among scientists and resource managers that to maintain ecological integrity, forest management must retain critical types and ranges of variability

found in unmanaged or natural ecosystems (Holling and Meffe 1996; Aber et al. 2000). In response, progressive forest managers around the world have begun to incorporate a natural-disturbance-based approach to landscape planning and silvicultural management (Bergeron and Harvey 1997;

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Swanson et al. 1997; Kuuluvainen 2002; Lindenmayer and McCarthy 2002). This approach involves studying disturbance regimes and their effects on ecosystem patterns and processes and adopting management practices that reduce discrepancies between natural and anthropogenic disturbances (e.g., Bergeron et al. 2002).

Most approaches for quantifying natural variability focus on historical variation in a particular ecosystem trait or process over time (Morgan et al. 1994; Chapin et al. 1996; Landres et al. 1999). The concept applies equally well to spatial variability in ecosystem conditions at a single point in time, provided that unmanaged benchmark systems subject to minimal human impact are available. In North American boreal forests, human impacts are dispersed and large, sparsely settled tracts remain in which natural disturbance processes such as wildfires continue to dominate (Sanderson et al. 2002). Here a natural range of variability approach, which uses minimally impacted forest landscapes as benchmark systems for study, can be adopted.

A range of variability approach to the comparison of unmanaged and managed forest ecosystems considers not only the mean response of the system to the silvicultural treatment or natural disturbance event, but also explicitly examines the dispersion or variability of the response around the mean (Gould 1991; Morgan et al. 1994). It also simultaneously considers how the response of the system varies with spatial or temporal scale (Peterson and Parker 1998).

Our research program in southern boreal forests of western Quebec and eastern Ontario seeks to identify critical threats to the biodiversity and ecological integrity of plant communities on typical, upland forest ecosystems and to refine coarse-filter management strategies to reduce those threats. In this study, our objective was to identify differences in the composition, structure, and diversity of trembling aspen (*Populus tremuloides* Michx.) plant communities regenerating after wildfire and those that regenerate following conventional clear-cutting practices across a range of spatial scales. Observed differences will be used to identify bioindicators for monitoring the effectiveness of new natural-dynamics-based silvicultural approaches being tested in aspen-dominated forests at the Lac Duparquet Research and Teaching Forest, Quebec (Bergeron and Harvey 1997; Brais et al. 2004) and to develop future recommendations for changes to forest practices.

The ubiquity of fire and concerns about the effects of logging on ecosystem sustainability have sparked many fire-logging comparisons in boreal forests of North America, especially in recent years (Noble et al. 1977; Abrams and Dickman 1982; Carleton and MacLellan 1994; Johnston and Elliot 1996; Lee and Crites 1999; Nguyen-Xuan et al. 2000; McRae et al. 2001; Reich et al. 2001; Rees and Juday 2002). Research has mainly been in conifers, but recent studies in Minnesota (Reich et al. 2001), Alberta (Crites 1999) and northern Quebec (Purdon et al. In press) included trembling aspen forests. Our study complements existing research by providing a detailed, replicated comparison of the structure, composition, and diversity of one well-defined community type at a single (3-year postdisturbance) successional stage.

From these earlier comparisons and our own work (Haeussler et al. 2002; Haeussler and Kneeshaw 2003), our expectations were that (i) the structure and composition of

aspen plant communities after clear-cut logging would be outside the limits of variability observed after wildfire; (ii) differences in community structure (i.e., the horizontal and vertical distribution of live and dead plant material) between clearcuts and wildfires would be more evident and more statistically significant than differences in species composition because understory plants of aspen-dominated forests are highly resilient to a variety of disturbances; (iii) clear-cutting would reduce the abundance of indigenous, pyrophilous seed- and spore-banking species and increase the abundance of invasive, non-native species because of machine disturbance of soils during logging and site preparation; (iv) within-community (alpha) species diversity after clear-cutting would be equal to or higher than that after wildfire, but heterogeneity among communities (beta diversity) would be reduced by clear-cutting, particularly at larger spatial scales; and (v) structural diversity would be lower after clear-cutting than after wildfire as a result of lower densities of standing live trees, snags, and downed woody debris, as well as the spatially patchy nature of wildfire disturbance.

Materials and methods

Study region

The study was centred at Timmins, Ontario (48°28'N, 81°20'W) in Canada's southern boreal mixedwood forest, extending from Foleyet (48°15'N, 82°24'W) to Iroquois Falls (48°48'N, 80°42'W). In this region, mature forests are mostly of wildfire origin and composed of white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) BSP), balsam fir (*Abies balsamea* L.), jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), and balsam poplar (*Populus balsamifera* L.). Eastern white-cedar (*Thuja occidentalis* L.), red pine (*Pinus resinosa* Ait.), eastern white pine (*Pinus strobus* L.), and red maple (*Acer rubrum* L.) are occasionally present. The northeast portion of the region is a lacustrine plain derived from proglacial Lakes Ojibway and Barlow (Vincent and Hardy 1977). Elsewhere, the region has shallow glacial till over bedrock and extensive areas of sandy outwash or beach deposits with silty depressions. Ecologically, the region is classified within the Cochrane, Foleyet, and Kirkland Lake ecoregions of Hill's Ecoregion 3E (Taylor et al. 2000).

The period of 20 May – 12 June 1997 had unusually dry, warm weather during which several thunderstorms swept through the study region, igniting at least 16 fires (Canadian Geographic 1997). Four fires exceeded 100 ha and were selected for study (Table 1). These crown wildfires burned mainly through jack pine and black spruce, but extended into adjacent, partially leafed-out aspen stands.

Sampling methods

We used a stratified random approach to sample mesic, aspen-dominated plant communities that spanned the range of fire or logging disturbance severity while minimizing ecological differences prior to disturbance. On wildfires, we delineated accessible, unsalvaged, burned polygons in three categories: (i) dominated by mature (60–110 years) trembling aspen, (ii) containing a mature aspen component

Table 1. Description of study areas.

		Canadian forest fire behaviour system indices												
(a) Wildfires.		UTM		UTM	UTM	Ignition date	Fire size (ha)	FFMC	DMC	DC	ISI	BUI	FWI	ROS
Area	Geographic location	Fire name	northing	easting										
1	Mistango River – Abitibi River	Cochrane 19	5415250	538700	June 5, 1997	2514	90	44	117	12	45	24	5	
2	Baker Lake, near Timmins	Timmins 2	5362500	468500	May 29, 1997	204	91	19	45	10	19	14	5	
3	West of Watabeag Lake	Timmins 12	5344800	521000	June 7, 1997	9538	89	47	110	6	47	15	5	
4	Nat River – Groundhog River	Timmins 24	5345000	426500	June 10, 1997	3266	92	50	132	14	51	28	30	
(b) Clearcuts.														
Area	Geographic location	Cutblock (no. location)	UTM northing	UTM easting	Logging date	Silvicultural treatments after logging								
1	Mistango River – Abitibi River	2 Twin Falls	5399000	533400	Winter 1996–1997	None								
		Twin Falls	5398450	532200	Winter 1996–1997	None								
2	Baker Lake, near Timmins	2 Godfrey Creek	5365900	454700	Winter 1996–1997	None								
		Waterhen Lake	5365300	467100	Fall–Winter 1996	MSP 1997, jack pine planted 1997, glyphosate 1998 ^a								
3	West of Watabeag Lake	2 Dry Lake	5345700	528500	Winter 1996–1997	None								
		Greenock Lake	5350000	520000	Winter–Spring 1997	None								
4	Nat River – Groundhog River	4 Ivanhoe River	5370500	412000	Summer 1997	Blowdown salvaged 1999								
		Groundhog River	5380000	412000	Summer 1997	Jack pine seedlings planted 1998								
		Groundhog River	5380750	412600	Summer 1997	MSP 1998, jack pine planted 1998, glyphosate 1999 ^a								
		Six Mile Rapids	5379900	416500	Summer 1997	MSP 1998, jack pine planted 1998								

Note: Fire information supplied by Ontario Ministry of Natural Resources. UTM, Universal Transverse Mercator; FFMC, fine fuel moisture code; DMC, duff moisture code; DC, drought code; ISI, initial spread index; BUI, build-up index; ROS, rate of spread (inches per minute; 1 in. = 2.54 cm); refer to Alexander et al. (1984) for details); MSP, mechanical site preparation with disk trencher.

^aAerial application of glyphosate herbicide.

greater than 20%, (iii) dominated by near-mature trembling aspen (30–60 years). All polygons in category *i* were selected, and a random selection of category *ii* and *iii* polygons was made. In the area surrounding each wildfire, we identified clear-cut polygons logged between fall–winter 1996–1997 and fall–winter 1997–1998 containing a merchantable trembling aspen component. All clearcuts located within 10 km of a wildfire were selected, and clearcuts 10–35 km from a fire were randomly selected as needed (Table 1).

From the preselected polygons, we field-identified stands with a mostly mesic soil moisture regime (classes 3–4 in Taylor et al. 2000) dominated by mature or near-mature even-aged aspen prior to disturbance and conforming to the descriptions for ecosites ES7f, 7m, and moister 7c (ES 7f to drier ES10 in the Mistango – Abitibi River area) (Taylor et al. 2000). Sample plots (one to four per stand) were located 50 m apart on linear transects oriented to bisect the full range of live tree retention and soil disturbance visible on aerial photos or in the field. In wildfire plots, no evidence of anthropogenic disturbance was permitted. In clearcut plots, no evidence of prelogging human impact was permitted. Moisture regime classes <3 or ≥5 (Taylor et al. 2000), conifer-dominated patches, permanent roads, and gravel pits were also omitted. One to five trees per stand were aged to verify ages on forest cover maps. A running tally of environmental and predisturbance forest characteristics was maintained, and in the final days of sampling, we selectively chose stands to reduce any evident bias (i.e., because unsalvaged burned aspen tended to occur in hilly areas with sandy soils, we sought out hilly clear-cut stands with sandy soils and wildfire stands with clay soils). In total, 22 plots in four wildfires and 22 plots in 10 clear-cut blocks were sampled in July–August 2000.

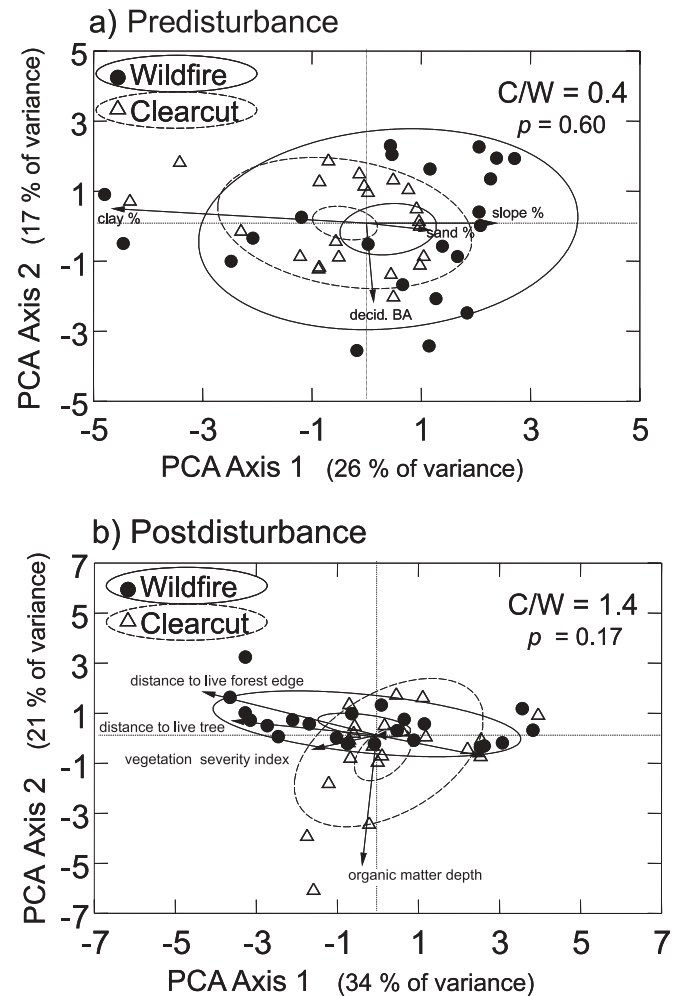
Data collection

Data on environmental characteristics, pre- and post-disturbance forest composition, and postdisturbance plant species composition and vegetation structure were collected in 0.01-ha circular sample plots. Live and dead standing trees >1.3 m tall and stumps and fallen trees >5 cm diameter at breast height (DBH) were tallied. Basal areas measured at stump height were later adjusted to breast height using allometric equations of Alemdag and Horner (1977). A nine-point modified Domin abundance scale (<0.1% to >75%; Kershaw 1973) was used for ocular estimates of substrate, vegetation structure, and plant species composition. All abundance estimates were made by the same person.

Horizontal structure was measured along three 5-m transects oriented 120° apart from plot centre. Each transect was subjectively subdivided into homogeneous sectors >50 cm in length. Sector length was recorded and abundance (% cover class) of 16 structural classes (live herbaceous, dead herbaceous, live tall shrub, dead tall shrub, live conifer, dead conifer, recent woody debris >25 cm, old woody debris >25 cm, etc.) within each sector was estimated on a vertically oriented plane to a maximum height of 1.3 m.

Vertical structure was recorded at 2.5 and 5 m on each horizontal transect. A telescopic height pole and clinometer were used to delineate 11 vertical strata (<2 cm to >20 m) and the abundance (% volume) of seven structural classes

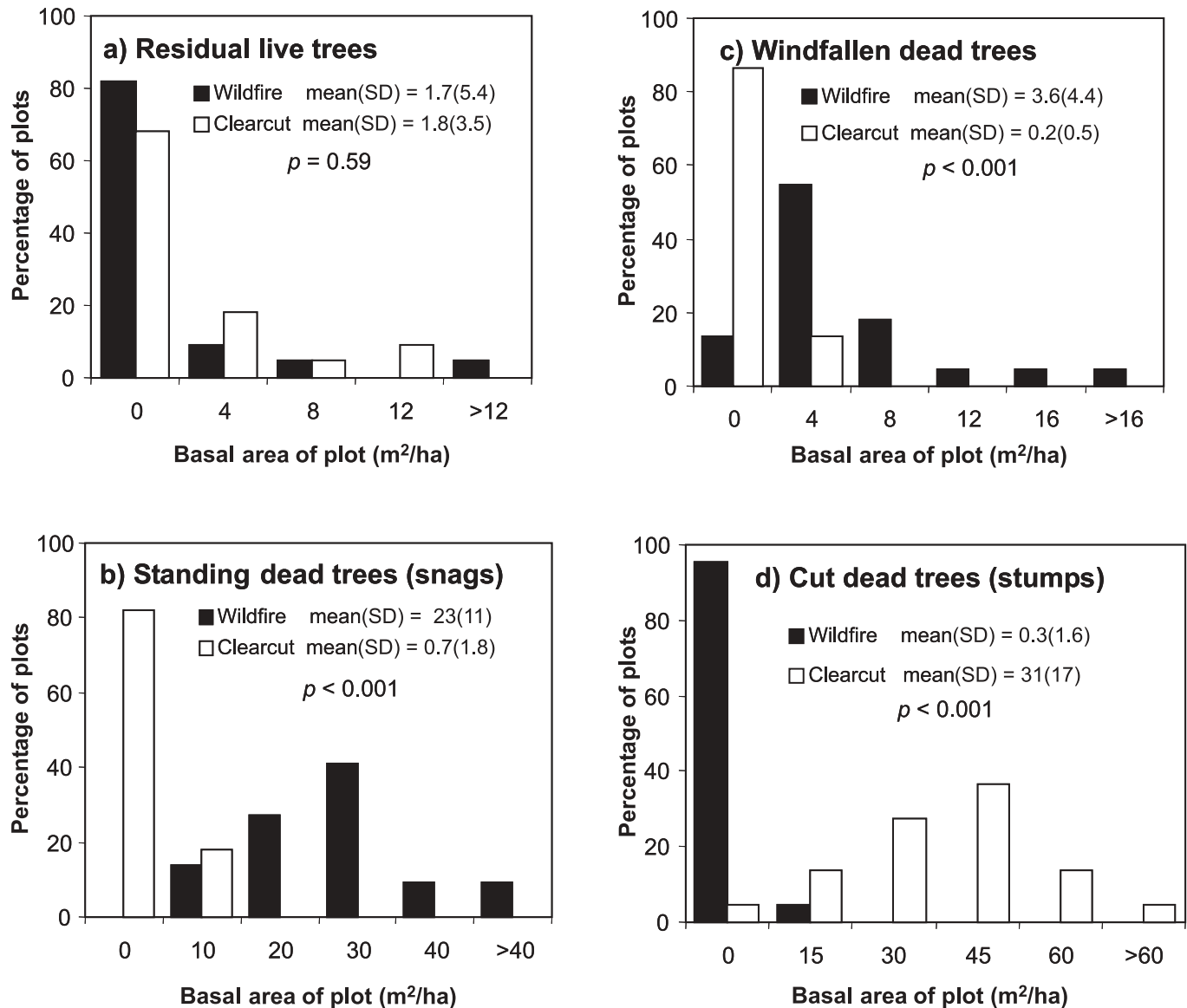
Fig. 1. Principal component analysis (PCA) of environmental and forest characteristics (a) before and (b) after wildfire and clear-cutting at the site scale. Vectors indicate descriptors with strong correlations to axes 1 and 2. The larger sample ellipses enclose 68% of the range of variability on the first two ordination axes. Axes are scaled in proportion to the percentage of variance extracted by each axis so that the clearcut:wildfire ellipse ratio (C/W) can be determined directly from the size of the two sample ellipses. The smaller centroid ellipses enclose a 95% confidence interval estimate of the mean. *p* values are for differences in mean pre- and post-disturbance conditions.



(dead conifer, live conifer, dead deciduous, live deciduous, dead herbaceous, live herbaceous, moss–lichen) in each stratum was estimated within a 50 cm radius cylinder.

Species composition and forest floor substrates were tallied in three quadrats per plot (4 m² for vascular plants and substrates, 1 m² for nonvascular plants, including epiphytes up to 1.3 m). We collected voucher specimens of all unknown species visible to the naked eye or handlens, but *Brachythecium* Schimp. species were not differentiated, and *Ceratodon purpureus* (Hedw.) Brid. and *Leptobryum pyriforme* (Hedw.) Wils. were mostly not differentiated. Depth of accumulated organic matter and slash, vegetation and soil severity indices (0 = undisturbed; 1 = lightly disturbed; 2 = moderately disturbed; 3 = highly disturbed), and the type of soil disturbance were recorded for each 4-m² quadrat.

Fig. 2. Site-scale variability in the basal area of live and dead trees 3 years after wildfire and clear-cutting. The *x* axis indicates the basal area per plot (m^2/ha); the *y* axis indicates the percentage of sample plots within each basal area class. Cut trees on wildfires in (d) are beaver trees. *p* values are for log-transformed data.



Data analysis

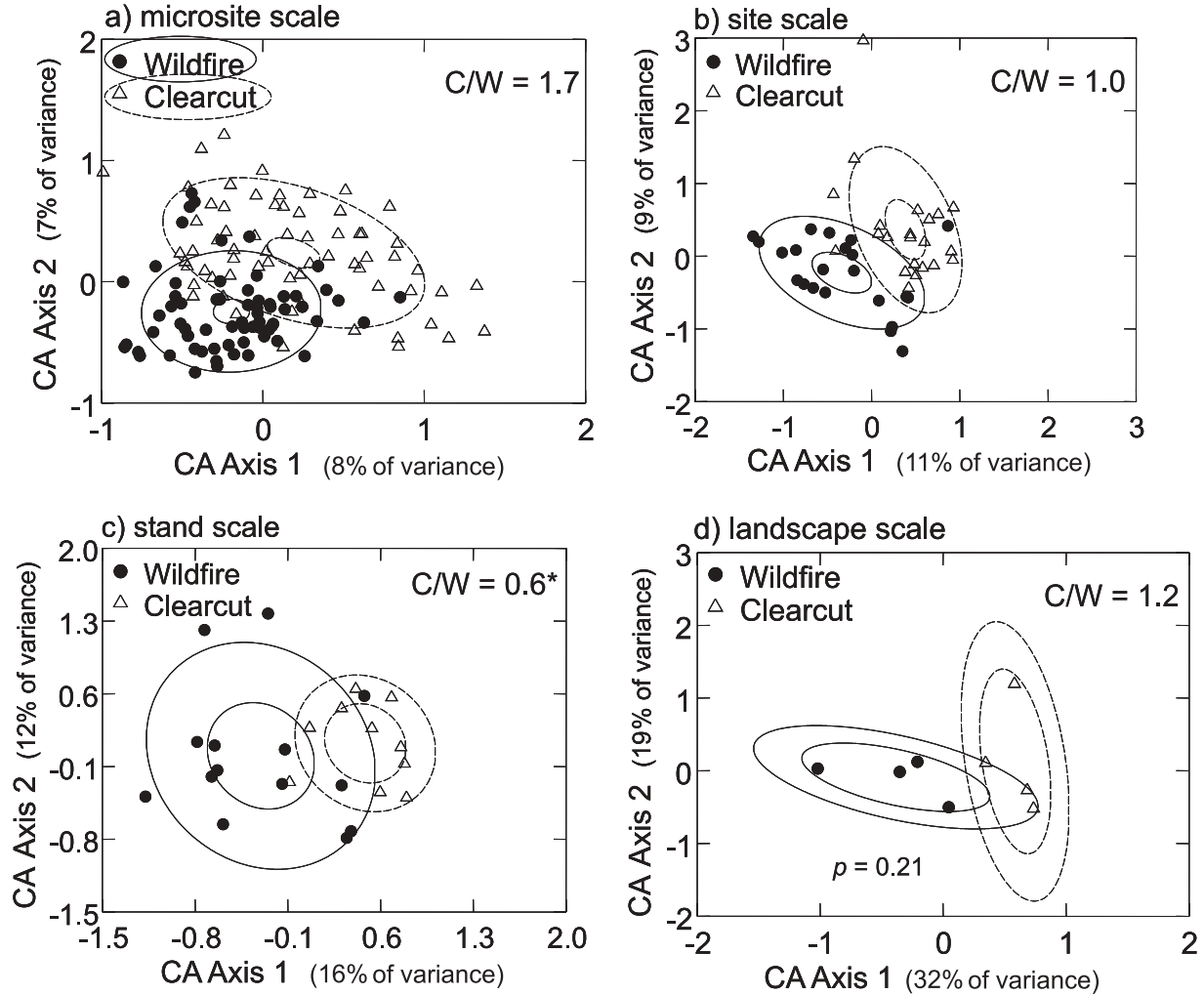
Data matrices were constructed for pre- and post-disturbance environmental and forest characteristics and postdisturbance species composition, horizontal, and vertical structure. For horizontal structure matrices, sectors within each transect were first sorted by sector length. Each structural class within a sorted transect sector was treated as a unique structural element (Class A in the longest sector became Element A1; Class A in the 2nd longest sector became A2, etc.). The abundance of each element was weighted by its sector length. The vertical structure matrix was created by crossing the seven structural classes with the 11 vertical strata and eliminating nonexistent combinations (e.g., live herbaceous >2 m) for a total of 60 possible vertical elements. Abundance values of vertical elements were relativized by the maximum value of each element.

The matrices were regrouped at up to five spatial scales prior to analysis: (i) the microsite scale used data from indi-

vidual quadrats ($n = 66$), horizontal transects ($n = 66$), or vertical cylinders ($n = 132$); (ii) the site scale pooled data from a single plot ($n = 22$); (iii) the stand scale pooled data from all plots within a stand or polygon ($n = 14$ for wildfires; $n = 10$ for clearcuts); (iv) the landscape scale pooled data from each wildfire or cluster of clearcuts surrounding a wildfire ($n = 4$); and (v) the regional scale pooled all wildfire data and all clearcut data ($n = 1$). Environmental matrices were centred and standardized at scales ii to iv, then ordinated using principal component analysis (PCA) (Legendre and Legendre 1998). Correspondence analysis with downweighting of rare species was used to ordinate the vegetation matrices at scales i to iv.

Classical experimentation in forest science has focussed on Type I statistical errors. Forest practices were adopted if they could be shown to significantly improve the variable of interest at $\alpha = 0.05$ or 0.01. However, contemporary ecosystem management is guided by the precautionary principle,

Fig. 3. Range of variability in plant species composition 3 years after wildfire and clear-cutting at four spatial scales, as indicated by correspondence analysis (CA) ordination. The larger sample ellipses enclose 68% of the range of variability in species composition on the first two ordination axes. The clearcut:wildfire ellipse ratio (C/W) indicates the relative size of the two sample ellipses (an asterisk (*) indicates adjustment for unequal sample size). The smaller centroid ellipses indicate 95% (microsite to stand scale) or 80% (landscape scale) confidence interval estimates of the mean. p values are for differences in mean species composition.



which in statistical terms seeks to avoid Type II errors. Forest practices should not be implemented unless it is shown that they do not negatively impact the variable of interest. In this study, because of our small sample size, we used the range between $\alpha = 0.05$ and $\alpha = 0.20$ as a zone of uncertainty to reduce the likelihood of Type II errors. Ideally, sample size is increased until the test has sufficient power to detect ecologically important differences.

We used Gaussian bivariate confidence ellipses to compare wildfire and clearcutting ordinations. Centroid ellipses (2-dimensional analogues of a confidence interval estimate of the mean) were used to compare mean conditions at $\alpha = 0.20$ and $\alpha = 0.05$ and to determine p values. Like standard errors, centroid ellipses are highly sensitive to sample size. Sample ellipses (2-dimensional analogues of ± 1 standard deviation of the mean) encompassed 68% of the range of variability around each centroid. With the ordination axes scaled in proportion to the percentage of variance (inertia) extracted by each axis, the ratio of clearcut sample ellipse area to wildfire sample ellipse area (C/W) was used as an index to

compare the range of variability in community characteristics after the two disturbances.

Alpha or within-sample diversity was calculated at spatial scales i through v for the vegetation data matrices using a spectrum of four diversity measures that assign increasing importance to the evenness of species abundances: richness = number of species or elements; Shannon's index; Simpson's index; evenness = Shannon's diversity index/ $\ln(\text{richness})$ (Pielou 1969; Magurran 1988). Beta (among-sample) diversity was calculated at four spatial scales (microsites within sites; sites within stands; stands within landscapes; landscapes within the region) as the mean Bray-Curtis distance (Legendre and Legendre 1998) between two samples.

Highly left-skewed distributions were normalized with logarithmic transformations. For univariate descriptors, t tests with unequal variances compared wildfire and clearcut means, and variability around the mean was evaluated by means of standard deviations and frequency distributions. PC-ORD version 4 (McCune and Mefford 1999) and

Table 2. Alpha (within-community) diversity of (i) vascular + nonvascular species, (ii) vertical structure, and (iii) horizontal structure

Diversity index	Scale					
	Microsite ($n = 66$ or 132)			Site ($n = 22$)		
	Wildfire	Clearcut	p value	Wildfire	Clearcut	p value
Vascular + nonvascular species						
Species richness	18 (4)	22 (6)	<0.0001	29 (6)	38 (9)	0.0005
Shannon's diversity index	2.65 (0.20)	2.80 (0.46)	0.015	1.84 (0.27)	2.01 (0.43)	0.12
Simpson's diversity index	0.91 (0.02)	0.91 (0.12)	0.91	0.76 (0.07)	0.77 (0.13)	0.86
Evenness	0.92 (0.02)	0.91 (0.12)	0.64	0.55 (0.08)	0.56 (0.10)	0.87
Vertical vegetation structure						
Structural richness	23 (4)	21 (5)	0.003	35 (3)	33 (6)	0.14
Shannon's diversity index	2.94 (0.17)	2.84 (0.25)	0.0001	3.22 (0.07)	3.12 (0.16)	0.015
Simpson's diversity index	0.938 (0.013)	0.929 (0.022)	<0.0001	0.951 (0.004)	0.945 (0.009)	0.007
Evenness	0.943 (0.017)	0.935 (0.022)	0.002	0.908 (0.015)	0.900 (0.026)	0.18
Horizontal vegetation structure						
Structural richness	14 (5)	15 (5)	0.10	22 (4)	24 (5)	0.17
Shannon's diversity index	1.76 (0.39)	1.72 (0.37)	0.49	2.10 (0.24)	2.10 (0.33)	0.99
Simpson's diversity index	0.75 (0.11)	0.74 (0.11)	0.73	0.81 (0.05)	0.81 (0.07)	0.83
Evenness	0.68 (0.10)	0.64 (0.10)	0.03	0.68 (0.06)	0.66 (0.08)	0.41

Note: p values are from t tests with separate variances. Values in parentheses are standard deviations.

CANOCO 4 (ter Braak and Smilauer 1998) were used for ordinations. SYSTAT 10 (SPSS Inc. 2000) was used for Gaussian ellipses and univariate statistics.

Results

Pre- and post-disturbance environmental and forest characteristics

Clearcuts and wildfires did not differ significantly in predisturbance physiographic, soil, and forest characteristics at site, stand, or landscape scales ($0.58 < p < 0.62$); thus, differences observed postdisturbance should result primarily from the disturbance itself. The range of variability in predisturbance characteristics (mainly slope, soil texture, and deciduous basal area) was more than twice as great among wildfire plots as among clearcut plots (Fig. 1a, $C/W = 0.4$). At stand and landscape scales, however, clearcuts were more variable than wildfires ($C/W = 2.8$ and 1.5 , respectively). This predisturbance variability was factored in when interpreting variability in postdisturbance plant community attributes.

After disturbance, differences in environmental characteristics of clearcuts and wildfires were evident (Fig. 1b; $0.05 < p < 0.20$). Clearcuts had somewhat greater postdisturbance variability than wildfires ($C/W = 1.4$), particularly with respect to the depth of organic matter accumulations and the amount of woody debris (strongly correlated with PCA Axis 2), while wildfire plots had more variability in vegetation and soil disturbance severity and the distance to live trees (strongly correlated with PCA Axis 1).

The depth of organic matter accumulations at the microsite scale ranged from 0.3 to 16 cm in wildfires and from 0 to 150 cm in clearcuts. Both the mean (4 cm for wildfires, 10 cm for clearcuts, $p = 0.04$) and median (4 cm for wildfires, 6 cm for clearcuts) depth were greater after clearcutting. Wildfires had a left-skewed distribution, with the majority of microsites having 1–7 cm of partially burned

forest floor. Clearcuts had a bimodal distribution, with the main peak between 5 and 9 cm (undisturbed forest floor), a secondary peak at 0 cm (forest floor completely scalped), and a long right tail (humus and slash deposited in piles).

Live tree basal area was very similar on clearcuts and wildfires (Fig. 2a, $p = 0.59$), but dead tree size distributions were very different (Figs. 2b–2d, all $p < 0.001$). The unmerchantable birch and conifers left in scattered patches on clearcuts were slightly more frequent and smaller in diameter than live trees on wildfires, which were typically large aspen or conifers situated at the fire margin. Interiors of burned aspen stands contained almost no live trees. Wildfires had 32 times more snag basal area and 18 times more windfallen tree basal area than clearcuts.

Community composition and species diversity

Because of careful site selection to limit the range of ecosystem conditions sampled, the total range of variability in species composition in this study was small (Fig. 3, $SD \leq 0.6$ for sample scores on correspondence analysis Axis 1). Wildfire and clearcut disturbances were thus the major sources of variation in plant community composition and separated out cleanly on the first ordination axis (Fig. 3; compare centroid ellipses in Fig. 3b to Fig. 1a). Mean community composition was significantly different on wildfires and clearcuts ($p < 0.05$) except at the landscape scale, where $p = 0.21$, likely because of the small sample size. At the three smaller spatial scales, 70%–82% of 3-year-old clearcut plant communities lay outside of the 68% range of variability in species composition observed after wildfire. Wildfires were associated with higher densities of aspen suckers, seedlings of paper birch and pin cherry (*Prunus pensylvanica* L.f.), bush honeysuckle (*Diervilla lonicera* Mill., a strongly rhizomatous low shrub), Houghton's sedge (*Carex houghtonii* Torr., a strongly rhizomatous seedbanker), and a carpet of pioneering fire mosses dominated by *Ceratodon purpureus*. Clearcuts had significantly more residual and re-

of aspen plant communities after wildfire and clear-cutting assessed at five spatial scales.

Stand ($n = 14$ or 10)			Landscape ($n = 4$)			Regional ($n = 1$)	
Wildfire	Clearcut	p value	Wildfire	Clearcut	p value	Wildfire	Clearcut
37 (11)	57 (17)	0.005	65 (11)	94 (17)	0.03	123	169
3.09 (0.19)	3.49 (0.32)	0.004	3.39 (0.04)	3.85 (0.21)	0.02	2.66	2.97
0.94 (0.01)	0.95 (0.01)	0.002	0.95 (0.01)	0.97 (0.01)	0.02	0.88	0.88
0.87 (0.03)	0.87 (0.02)	0.55	0.82 (0.03)	0.85 (0.02)	0.16	0.55	0.58
38 (7)	38 (8)	0.97	47 (8)	45 (5)	0.73	3.41	3.33
3.25 (0.10)	3.19 (0.18)	0.35	3.33 (0.10)	3.28 (0.08)	0.51	3.41	3.33
0.952 (0.005)	0.949 (0.008)	0.25	0.955 (0.005)	0.953 (0.004)	0.52	0.959	0.955
0.898 (0.022)	0.883 (0.023)	0.12	0.869 (0.22)	0.863 (0.003)	0.63	0.832	0.844
25 (7)	30 (8)	0.08	39 (4)	42 (7)	0.53	55	57
2.17 (0.30)	2.29 (0.39)	0.43	2.44 (0.13)	2.45 (0.22)	0.65	2.64	2.63
0.82 (0.06)	0.84 (0.07)	0.60	0.86 (0.02)	0.87 (0.03)	0.77	0.88	0.88
0.68 (0.06)	0.67 (0.07)	0.72	0.66 (0.03)	0.67 (0.03)	0.81	0.66	0.65

sprouting tall shrubs (mainly mountain maple (*Acer spicatum* Lamb.) and beaked hazel (*Corylus cornuta* Marsh.)), more residual conifers (*Abies balsamea*, *Picea* spp.), well-developed forb layers dominated by large-leaved aster (*Aster macrophyllus* L.), and a variety of forest-dwelling bryophytes and lichens (principally *Brachythecium* spp. and *Cladonia* Hill ex P. Browne spp.).

The following common species were significantly ($p < 0.05$) more abundant after fire than after clear-cutting at the site scale: *Populus tremuloides*, *Prunus pensylvanica*, wild sarsaparilla (*Aralia nudicaulis* L.), bunchberry (*Cornus canadensis* L.), and *Ceratodon purpureus*. *Aster macrophyllus*, *Abies balsamea*, and *Brachythecium* spp. were significantly ($p \leq 0.01$) more abundant after clear-cutting than after wildfire. Bracken (*Pteridium aquilinum* (L.) Kuhn), red raspberry (*Rubus idaeus* L.), and bluebead lily (*Clintonia borealis* (Ait.) Raf.) are three common species that were equally abundant after wildfires and clear-cutting ($p > 0.60$).

Known seed- or spore-banking, pyrophilous species (Rowe 1983; Haeussler and Kneeshaw 2003), such as *Ceratodon purpureus*, *Prunus pensylvanica*, Bicknell's geranium (*Geranium bicknellii* Britt.), fringed bindweed (*Polygonum cilinode* Michx.), bristly sarsaparilla (*Aralia hispida* Vent.), and *Carex houghtonii*, were present on clearcuts, but as a group were significantly more abundant on wildfires ($p < 0.05$).

Seven non-native species were encountered on study plots; three in wildfires and five in clearcuts. There was no compelling evidence that clear-cutting increased the abundance of non-native species, as there were too few after either type of disturbance for reliable statistical analysis at our low sampling intensity ($0.1 \pm 0.3\%$ cover on wildfires, $0.6 \pm 2.5\%$ cover on clearcuts; $p = 0.38$). The frequency of non-native species was higher in wildfires (16% of quadrats; 32% of plots) than in clearcuts (9% of quadrats, 23% of plots), but the only plot with $>1\%$ non-native cover was a clearcut plot located on a compacted (not artificially seeded)

skid trail dominated by alsike clover (*Trifolium hybridum* L.) and alfalfa (*Medicago sativa* L.).

Clearcuts had significantly higher vascular and non-vascular richness than wildfires at all spatial scales ($p < 0.03$), and all other species diversity indices were either equal or higher after clear-cutting than after a wildfire (Table 2). At lower spatial scales, clearcuts also displayed consistently greater variability in species diversity (compare SD in Table 2). Slash piles and some patches of compacted mineral soil on clearcuts had very few plant species, while under live birch trees, there was a profusion of pioneering and later successional species, particularly forest-dwelling mosses and lichens. On wildfires, no microsites failed to regenerate well, but neither did any have exceptional richness.

In total, 123 plant species (89 vascular and 34 non-vascular) were recorded on wildfires compared with 169 species (106 vascular and 63 nonvascular) on clearcuts. The 25 species found only on wildfires included representatives of a wide variety of plant functional types, ranging from pioneering and introduced species to peripheral temperate forest shrubs. All have been observed on unburned habitats elsewhere in the region (unpublished data). Seventy-one plant species were exclusively found on clearcuts. Again, a wide variety of functional types were represented, but forest-dwelling lichens (approx. 15 species), mosses (approx. 11 species), and liverworts (approx. 9 species) were especially prominent.

Nonvascular richness on clearcuts was strongly associated with the presence of residual live trees. On plots without live trees, wildfires had a mean of 7 ± 3 nonvascular species while clearcuts had 9 ± 4 species ($p = 0.22$). On plots with live trees, wildfires averaged 8 ± 4 nonvascular species while clearcuts had 19 ± 6 species ($p = 0.001$). High bryophyte and lichen richness in clearcuts was due not only to epiphytes, but also to forest floor and decaying wood species surviving beneath the shade of live trees.

Table 3. Beta (between-community) diversity of vascular + nonvascular species, vertical structure, and horizontal structure of aspen plant communities after wildfire and clearcutting, assessed at four spatial scales.

	Microsites within sites				Sites within stands				Stands within landscapes				Landscapes within the region			
	Wildfire	Clearcut	<i>p</i> value		Wildfire	Clearcut	<i>p</i> value		Wildfire	Clearcut	<i>p</i> value		Wildfire	Clearcut	<i>p</i> value	
Beta (between-community) diversity																
Vascular + nonvascular species	0.38 (0.08)	0.49 (0.13)	0.001		0.53 (0.14)	0.61 (0.10)	0.28		0.50 (0.17)	0.64 (0.14)	0.26		0.55 (0.11)	0.45 (0.10)	0.11	
Vertical vegetation structure	0.34 (0.05)	0.36 (0.09)	0.38		0.22 (0.06)	0.28 (0.06)	0.12		0.21 (0.04)	0.30 (0.06)	0.05		0.21 (0.06)	0.15 (0.02)	0.07	
Horizontal vegetation structure	0.57 (0.12)	0.60 (0.13)	0.45		0.54 (0.12)	0.56 (0.11)	0.69		0.43 (0.05)	0.50 (0.05)	0.1		0.37 (0.07)	0.34 (0.07)	0.48	

Note: The mean Bray–Curtis distance between two samples was used as the diversity index. *p* values are from *t* tests with separate variances. Values in parentheses are standard deviations.

Clearcuts had significantly higher species turnover (beta diversity) among microsites within sites than wildfires ($p = 0.001$) and not significantly different turnover among sites within stands and stands within landscapes ($p = 0.28$) (Table 3). The range of variability in species composition was also greater among all clearcut microsites than among all wildfire microsites (sample ellipses in Fig. 3*a*; $C/W = 1.7$) and no different among sites (Fig. 3*b*; $C/W = 1.0$). However, beta diversity results for stands within landscapes ($C = 0.64$, $W = 0.50$; $p = 0.28$) and landscapes within the study region ($C = 0.45$, $W = 0.55$; $p = 0.11$) (Table 3) conflicted somewhat with the range of variability in species composition among all stands (Fig. 3*c*; $C/W = 0.6$) and among all landscapes (Fig. 3*d*; $C/W = 1.2$).

Community structure and structural diversity

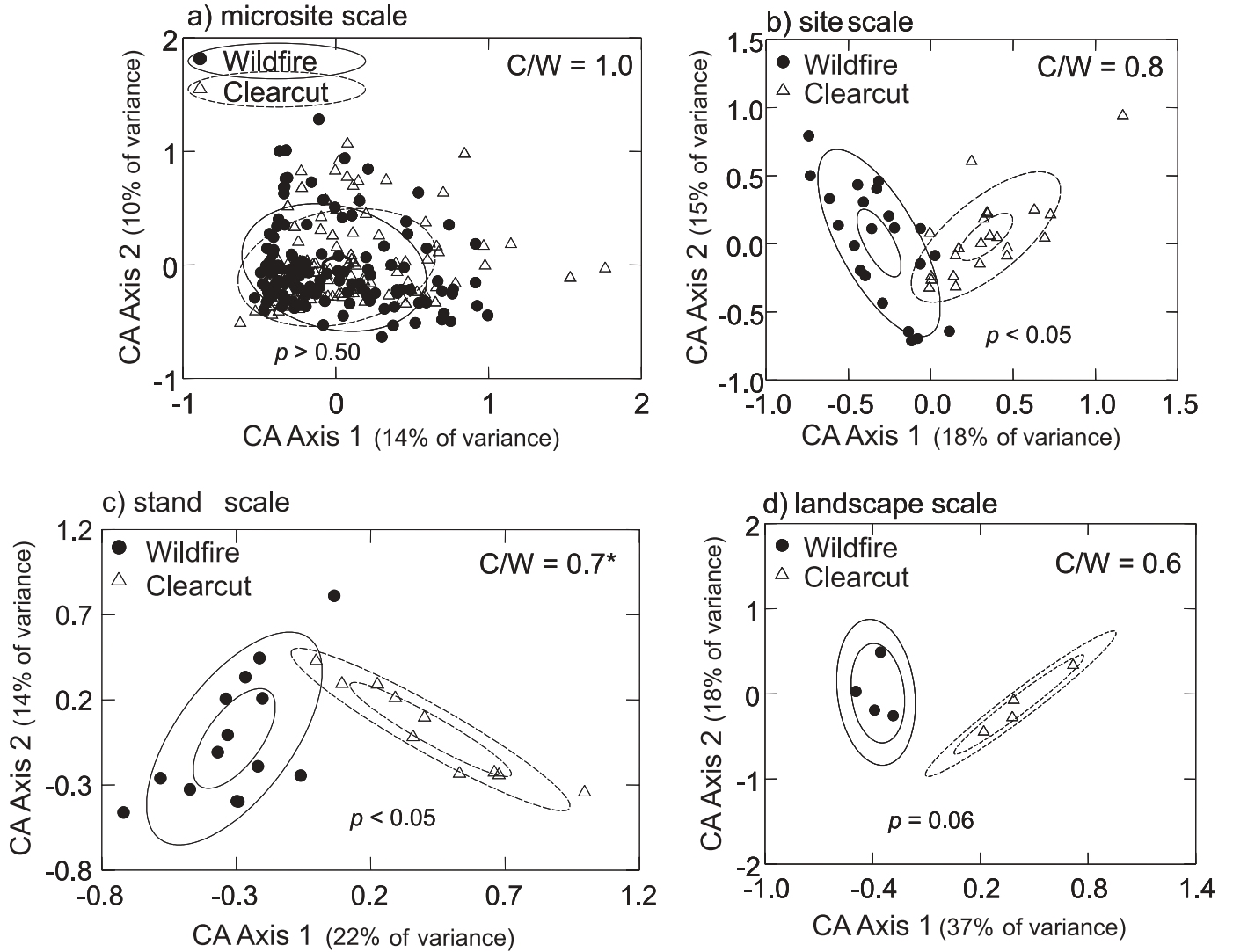
Vertical structure (Fig. 4) was remarkably similar between clearcuts and wildfires at the microsite scale ($p > 0.50$, $C/W = 1.0$), because most sample cylinders did not intersect snags. When the data were pooled at larger spatial scales, differences became very evident ($p < 0.06$) and clearcut variability declined relative to wildfire variability ($0.8 \geq C/W \geq 0.6$). All wildfires had well-spaced large aspen snags and intermittent patches of dead conifers, while clearcuts typically had dispersed patches of live conifer saplings and seedlings and scattered live or dying unmerchantable birch. The vertical distribution of moss–lichen layers also differed. In wildfires, live mosses and lichens were concentrated in dense patches on the forest floor, whereas in clearcuts they tended to grow above the forest floor on decaying wood and residual trees.

Clearcut–wildfire differences in the horizontal structure of understory layers <2 m tall were less evident than differences in species composition or vertical structure (Fig. 5). Mean horizontal structure was significantly different at the microsite scale ($p < 0.05$), but compared with vertical structure, there was little divergence as the analytical scale increased ($0.06 < p < 0.32$). Across all four scales, 59%–90% of clearcut samples lay inside the 68% wildfire sample ellipse, and clearcut variability was smaller ($0.07 < C/W < 0.7$). Clearcuts had more fine slash ($p = 0.04$) and herbaceous vegetation, while wildfires had more moss patches and dead conifers. Abundance of deciduous vegetation <2 m tall was very similar because high densities of aspen suckers on wildfires offset higher densities of tall shrubs on clearcuts. Old and recent coarse woody debris abundances were also not significantly different at this early seral stage ($p > 0.28$).

Wildfires were more diverse vertically than clearcuts at microsite and site scales (Table 2; p values mostly < 0.01), but the differences largely disappeared at stand and landscape scales (p values mostly > 0.35). For example, wildfires had a mean of 23 ± 4 vertical elements at the microsite scale compared with 21 ± 5 elements on clearcuts, a difference of 8% ($p = 0.003$). At the stand scale, the number of vertical elements differed by only 0.3% ($p = 0.97$). Beta diversity was highly sensitive to spatial scale (Table 3): clearcuts appeared to have greater variation in vertical structure among sites and among stands, but less diversity among landscapes.

Horizontal structure of clearcut understories was no less diverse than that of wildfire understories, except for slightly lower evenness at the microsite scale (Table 2; $p = 0.03$).

Fig. 4. Range of variability in vertical vegetation structure 3 years after wildfire and clear-cutting at four spatial scales, as indicated by correspondence analysis (CA) ordination. The larger sample ellipses enclose 68% of the range of variability in vertical structure on the first two ordination axes. The clearcut:wildfire ellipse ratio (C/W) indicates the relative size of the two sample ellipses (an asterisk (*) indicates adjustment for unequal sample size). The smaller centroid ellipses indicate 95% (microsite to stand scale) or 80% (landscape scale) confidence interval estimates of the mean. p values are for differences in mean vertical structure.



Standard deviations were consistently higher on clearcuts than on wildfires at site to landscape scales, but equal or lower on clearcuts at the microsite scale. Unlike sample ellipses (Fig. 5), which indicated less variability on clearcuts at all scales ($0.7 < C/W < 0.07$), the beta diversity index (Table 3) provided no indication that clearcuts were less spatially heterogeneous than wildfires.

Discussion

Clearcut-wildfire differences

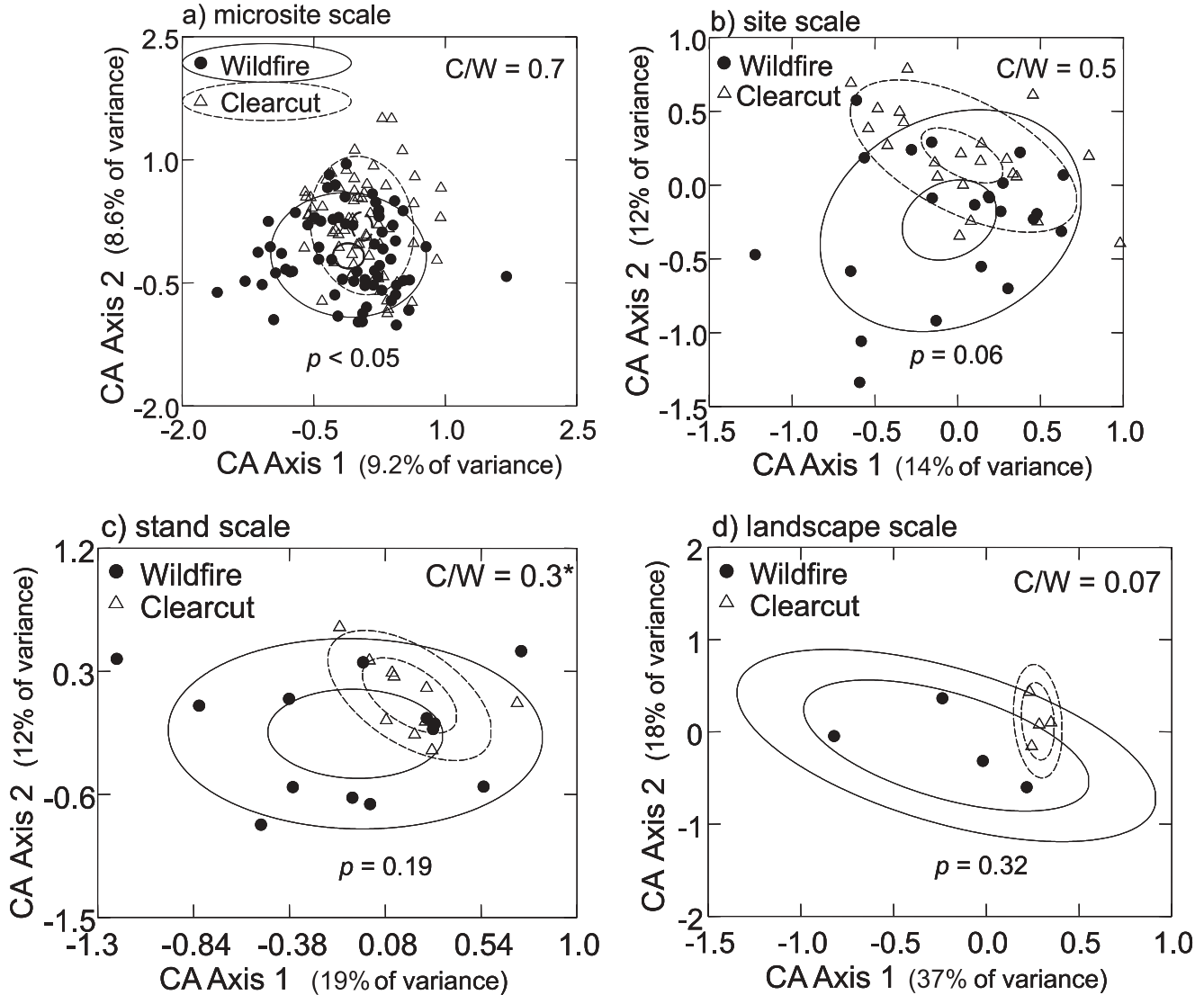
In a retrospective study of this kind, with no pre-disturbance sampling and no experimental control over disturbances, there is always a risk that observed differences are due not to the disturbance but to pre-existing differences in plant communities. We are confident that our sampling and analytical approach successfully addressed this risk. Moreover, by targeting a narrower age and species range

than previous retrospective studies (e.g., Crites 1999; Nguyen-Xuan et al. 2000; Reich et al. 2001; Rees and Juday 2002; Purdon et al. In press), and by using ecosystem classification to limit site variability, we were able to detect relatively subtle differences in plant communities despite our small sample size.

As hypothesized, clear-cutting caused substantial differences in the structure and composition of 3-year-old boreal aspen plant communities compared with wildfire, with many clearcut plant communities lying outside the limits of variability observed after wildfire, particularly when results were analysed at larger spatial scales. Contrary to our expectations, clearcut-wildfire differences in species composition were just as evident and equally or more statistically significant than differences in vegetation structure.

We thought both disturbances would leave patches of intact understory and that anthropogenic shifts in species composition would exist mainly where the mineral soil was

Fig. 5. Range of variability in horizontal vegetation structure 3 years after wildfire and clear-cutting at four spatial scales, as indicated by correspondence analysis (CA) ordination. The larger sample ellipses enclose 68% of the range of variability in horizontal structure on the first two ordination axes. The clearcut:wildfire ellipse ratio (C/W) indicates the relative size of the two sample ellipses (an asterisk (*) indicates adjustment for unequal sample size). The smaller centroid ellipses indicate 95% (microsite to stand scale) or 80% (landscape scale) confidence interval estimates of the mean. p values are for differences in mean horizontal structure.



exposed and compacted by logging machinery. Instead, the 1997 wildfires burned almost uniformly through the aspen, leaving few unburned patches and killing non-resprouting, slow-growing plants such as conifers, liverworts, and lichens. These fire-intolerant species were largely retained on clearcuts. Some understory dominants, notably trembling aspen and *Diervilla lonicera*, recovered more vigorously after wildfire than after logging, presumably because thinner organic layers, removal of overtopping foliage, and heat and nutrient pulses associated with fire stimulated sprouting of dormant, subterranean buds (Flinn and Wein 1977; Rowe 1983). Other dominants like *Acer spicatum*, *Corylus cornuta*, and *Aster macrophyllus* were set back by fire. These differences in resprouting capacity caused a clear divergence in burned and unburned plant communities. Moreover, on wildfires, fire mosses were still very dominant at 3 years.

Ruderal plants had negligible impact on the composition of aspen clearcuts. This result contrasts with a survey of conifer clearcuts in the nearby Abitibi region of Quebec (Harvey et al. 1995). We attribute the difference to three factors: less agriculture and forest fragmentation in our Ontario study area (Lefort et al. 2003); less mechanical site preparation in aspen than in conifer cutblocks; and higher resistance to invasion in herb-rich aspen understories than in sparser conifer understories (De Grandpré and Bergeron 1997).

Clearcuts were richer in species than wildfires, regardless of the scale of analysis, and there was no evidence that clear-cutting reduced community evenness. These findings are consistent with a comparison of eighty 25- to 100-year-old aspen, jack pine, and black spruce stands in northern Minnesota (Reich et al. 2001) and the aspen chronosequence comparison in Alberta (Crites 1999). They contradict

Abrams and Dickmann (1982) in Michigan and Rees and Juday (2002) in Alaska, who observed substantially higher richness after fire than after logging in coniferous and mixedwood stands because of a suite of mainly weedy forb, grass, and sedge species that occurred exclusively on burned sites. The disparate results from this group of studies suggest that species richness depends on ecosystem- and disturbance-specific circumstances rather than being inherent to wildfire or clear-cutting. In general, a disturbance that exposes substantial amounts of mineral soil will produce high vascular richness, while a disturbance that leaves behind intact organic matter, residual live trees, and shade will produce high nonvascular richness (Haeussler et al. 2002). However, if local seedbanks and seed rain are species-poor relative to the forest understory, highest richness will occur after the disturbance that leaves more understory intact (cf. Reader et al. 1991). Fires in boreal aspen forest expose little mineral soil but kill most overstory trees (Johnson 1992; Hély et al. 2003), just as we observed. Aspen stands have robust, species-rich understories (De Grandpré and Bergeron 1997; Reich et al. 2001), and their seedbanks contain few species not present prior to disturbance (Qi and Scarrat 1998; Ratel 1996). Thus, for this community type, a diverse postfire flush of short-lived species is unlikely, and there is no reason for wildfires to have more species than clearcuts.

Carleton and MacLellan (1994) drew attention to the need for multiscale analysis of diversity effects, showing that higher species diversity within clearcuts could mask a loss of beta diversity at the landscape scale. Data from Crites (1999), Nguyen-Xuan et al. (2000), and Rees and Juday (2002) also show that clearcut plant communities vary less with age or location than those of wildfire origin, while those of Reich et al. (2001) do not. In our study, we tested for a loss of beta species diversity in a single age and single community type and found that clearcuts were significantly more heterogeneous at the smallest, within-site scale and at least equally heterogeneous within stands and within landscapes. At the largest spatial scale, the pattern reversed: the four wildfires appeared to be more different from one another than the four groups of clearcuts. We do not consider this last result conclusive, given our very small sample size, a p value of 0.11, and the fact that another analytical approach (sample ellipse ratio $C/W = 1.2$) gave the opposite result. However, taking into account the findings of the researchers cited above and the fact that our clearcut stands and landscapes had more predisturbance variability than our wildfire stands and landscapes, a precautionary approach should acknowledge the potential for homogenization of aspen communities across the larger landscape. Research and operational monitoring encompassing these large spatial scales should be given priority over studies and monitoring approaches that focus exclusively at within-stand response.

It is self-evident that wildfires leave behind dead standing trees, while conventional clear-cutting does not. Aspen and conifer snags are the most important structural difference between wildfire and clear-cut aspen communities, and the functional importance of dead trees in forest ecosystems has been amply demonstrated (Harmon et al. 1986; Laudenslayer et al. 2002). Beyond the dead standing trees and dense patches of fire moss, most structural differences between

wildfire and clearcut communities were matters of absence rather than of presence. Wildfire communities had less fine debris, thinner humus layers, fewer live conifers, sparser herb layers, and less laddering of bryophytes and lichens. While all of these structural elements provide potentially valuable short-term habitat for wildlife, their presence in clearcuts could also alter long-term nutrient cycling and the direction of forest succession.

A range of variability approach

Our study looked for three types of differences between aspen plant communities after wildfire and after clear-cutting: (i) shifts in the central tendency (mean) of the plant community; (ii) novel conditions outside the range of natural variability after fire; and (iii) a narrowing of the range of variability that reduced the diversity of ecosystem conditions. We found examples of all three phenomena, for example, dominance by mid-successional rather than pioneering species, large slash piles devoid of vegetation, reduced variability in numbers of windfallen trees, and showed that focusing on mean conditions alone can obscure important differences between clear-cutting and wildfire. Although the sample size limited our ability to draw conclusions about effects at large spatial scales, we were able to demonstrate the degree to which results, especially diversity measures, can change with the scale of observation.

One approach to a range of variability study is to sample as widely as possible to capture the broad scope of an ecosystem property or properties under natural and human-altered conditions. An alternative approach, adopted here, is to strictly limit the range of conditions and, through unbiased sampling, to show how human intervention has affected the range of variability within the limits of the sample. Our study could not and did not attempt to capture the full range of wildfire conditions or silvicultural practises that might affect the ecological response of an aspen plant community. It is possible, for example, that a late summer burn or another fire year might have produced patchier wildfires with higher aspen survival and greater structural and species diversity than we observed. Again, we recommend more extensive but less intensive, large scale studies and longer-term monitoring to test the generality of our conclusions.

Implications for sustainable forestry

Our finding that aspen suckers were significantly less abundant and tall shrubs such as *Acer spicatum* and *Corylus cornuta* more abundant on 3-year-old clearcuts than on equivalent burned areas raises the question of long-term aspen productivity in the study region. Retrospective and experimental studies, coupled with simulation modelling, are needed to assess whether 3-year differences disappear through aspen self-thinning by rotation age or whether the abundance of aspen relative to tall shrubs declines further over multiple, fire-free rotations.

In terms of plant conservation, our study indicates little immediate cause for alarm. No threatened or endangered plants were found on the study sites and no obligate pyrophilous species were identified. We also recorded relatively minor non-native species invasion. In the short term and at

within-stand scales, we found that nonvascular plants were more likely to survive clear-cutting than wildfire, that few old aspen survived in burned stands, and that coarse woody debris levels in clearcuts were broadly similar to levels in 3-year-old wildfires. However, old aspen stands possess specialized epiphytic and decaying wood nonvascular floras not present on smaller trees or in younger stands (Crites and Dale 1998; Boudreault et al. 2000). Our study did not examine how unburned aspen tree patches and edges are dispersed in the landscape after multiple fires (Eberhart and Woodward 1987; DeLong and Kessler 2000) nor how woody debris levels change over time as snags fall down in wildfires (Lee and Crites 1999).

An important, unanswered question is whether shifts in community composition and loss of distinctive, postfire communities threaten long-term ecological integrity, especially when the species characterizing these communities are common plants at no risk of local or global extinction. The precautionary principle advises us to regard all such changes as potentially significant, and long-term monitoring in Fennoscandia indicates that seemingly trivial changes in the variability of plant communities today may have dramatic implications for forest composition (Reinikainen et al. 2001), biodiversity (Berg et al. 1994), and ecosystem function (Ponge et al. 1998) in 50–100 years.

We are currently testing whether prescribed burning after clear-cutting will effectively regenerate aspen and recreate distinctive postfire aspen communities. Potential treatments such as mechanical site preparation to reduce humus and slash accumulation, stimulate aspen suckers, and create artificial tip-up mounds should also be examined. In the meantime, forest managers have ample scientific evidence for leaving some mature live and dead aspen trees on all aspen clear-cut blocks.

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References

- Aber, J., Christensen, N., Fernandez, I., Franklin, J., Hidingler, L., Hunter, M., MacMahon, J., Mladenoff, D., Pastor, J., Perry, D., Slangen, R., and van Miegroet, H. 2000. Applying ecological principles to management of the U.S. National Forests. *Ecol. Soc. Am. Spec. Publ. Issues in Ecology* 6.
- Abrams, M.D., and Dickmann, D.I. 1982. Early revegetation of clear-cut and burned jack pine sites in northern lower Michigan. *Can. J. Bot.* **60**: 946–954.
- Alemdag, I.S., and Horner, T.G. 1977. Metric relationships between breast-height and stump diameters for eleven tree species from eastern and central Canada. *Can. For. Serv. For. Manage. Inst. Inf. Rep. FMR-X-49M*.
- Alexander, M.E., Lawson, B.D., Stocks, B.J., and Van Wagner, C.E. 1984. User guide to the Canadian forest fire behaviour prediction system: rate of spread relationships. Environment Canada, Canadian Forestry Service, Fire Danger Group, Ottawa, Ont.
- Berg, A., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M., and Weslien, J. 1994. Threatened plant, animal and fungus species in Swedish forests: distribution and habitat associations. *Conserv. Biol.* **8**: 718–731.
- Bergeron, Y., and Harvey, B. 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. *For. Ecol. Manage.* **92**: 235–242.
- Bergeron, Y., Leduc, A., Harvey, B.D., and Gauthier, S. 2002. Natural fire regime: a guide for sustainable management of the Canadian boreal forest. *Silva Fenn.* **36**: 81–95.
- Boudreault, C., Gauthier, S., and Bergeron, Y. 2000. Epiphytic lichens and bryophytes on *Populus tremuloides* along a chronosequence in the southwestern boreal forest of Quebec, Canada. *Bryologist*, **103**: 725–738.
- Brais, S., Harvey, B.D., Bergeron, Y., Messier, C., Greene, D., Belleau, A., and Paré D. 2004. Testing forest ecosystem management in boreal mixedwoods of northwestern Quebec: initial response of aspen stands to different levels of harvesting. *Can. J. For. Res.* **34**: 343–358.
- Canadian Geographic. 1997. Chronicle of a forest fire. Map insert. Sept.–Oct. issue, Canadian Geographic, Ottawa, Ont.
- Carleton, T.J., and MacLellan, P. 1994. Woody vegetation responses to fire versus clear-cut logging: a comparative survey in the central Canadian boreal forest. *Ecoscience*, **1**: 141–152.
- Chapin, F.S., III, Torn, M.S., and Tateno, M. 1996. Principles of ecosystem sustainability. *Am. Nat.* **148**: 1016–1037.
- Crites, S. 1999. A test case for the natural disturbance model: understory vegetation communities following fire and harvesting in aspen mixedwood stands. *In Science and Practice: Sustaining the Boreal Forest. Proceedings of the Sustainable Forest Management Network (SFMN) Conference, 14–17 February 1999, Edmonton, Alta. Edited by T.S. Veeman, D.W. Smith, B.G. Purdy, F.J. Salkie, and G.A. Larkin. University of Alberta, Edmonton. pp. 607–615.*
- Crites, S., and Dale, M.R.T. 1998. Diversity and abundance of bryophytes, lichens, and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. *Can. J. Bot.* **76**: 641–651.
- De Grandpré, L., and Bergeron, Y. 1997. Diversity and stability of understory communities following disturbance in the southern boreal forest. *J. Ecol.* **85**: 777–784.
- DeLong, S.C., and Kessler, W.B. 2000. Ecological characteristics of mature forest remnants left by wildfire. *For. Ecol. Manage.* **131**: 93–106.
- Eberhart, K.E., and Woodward, P.M. 1987. Distribution of residual vegetation associated with large fires in Alberta. *Can. J. For. Res.* **17**: 1207–1212.
- Flinn, M.A., and Wein, R.W. 1977. Depth of underground plant organs and theoretical survival during fire. *Can. J. Bot.* **55**: 2550–2554.
- Gould, S.J. 1991. Full house: the spread of excellence from Plato to Darwin. Three Rivers Press, New York.
- Haeussler, S., and Kneeshaw, D. 2003. Comparing forest management to natural processes. *In Towards sustainable management*

- of the boreal forest: emulating nature, minimizing impacts, and supporting communities. *Edited by* P.J. Burton, C. Messier, D.W. Smith, and W.L. Adamowicz. NRC Research Press, Ottawa, Ont. pp. 307–368.
- Haeussler, S., Bedford, L., Leduc, A., Bergeron, Y., and Kranabetter, J.M. 2002. Silvicultural disturbance severity and plant communities of the southern Canadian boreal forest. *Silva Fenn.* **36**: 307–327.
- Harvey, B.D., Leduc, A., and Bergeron, Y. 1995. Early postharvest succession in relation to site type in the southern boreal forest of Quebec. *Can. J. For. Res.* **25**: 1658–1672.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Jr., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* **15**: 133–302.
- Hély, C., Flannigan, M., and Bergeron, Y. 2003. Modeling tree mortality following wildfire in the southeastern Canadian mixed-wood boreal forest. *For. Sci.* **49**: 566–576.
- Holling, C.S., and Meffe, G.K. 1996. Command and control and the pathology of natural resource management. *Conserv. Biol.* **10**: 328–337.
- Johnson, E.A. 1992. Fire and vegetation dynamics. Cambridge University Press, Cambridge, U.K.
- Johnston, M.H., and Elliot, J.A. 1996. Impacts of logging and wildfire on an upland black spruce community in northwestern Ontario. *Environ. Monit. Assess.* **39**: 283–297.
- Kershaw, K.A. 1973. Quantitative and dynamic plant ecology. 2nd ed. Edward Arnold (Publishers) Ltd., London, U.K.
- Kuuluvainen, T. 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. *Silva Fenn.* **36**: 97–125.
- Landres, P.B., Morgan, P., and Swanson, F.J. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecol. Appl.* **9**: 1179–1188.
- Laudenslayer, W.F., Jr., Shea, P.J., Valentine, B.E., Weatherspoon, C.P., and Lisle, T.E. (*Technical coordinators*). 2002. Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests, 2–4, November 1999, Reno, Nev. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. PSW-GTR-181.
- Lee, P., and Crites, S. 1999. Early successional deadwood dynamics in wildfire and harvest stands. *In* Science and Practice: Sustaining the Boreal Forest. Proceedings of the Sustainable Forest Management Network (SFMN) Conference, 14–17 February 1999, Edmonton, Alta. *Edited by* T.S. Veeman, D.W. Smith, B.G. Purdy, F.J. Salkie, and G.A. Larkin. University of Alberta, Edmonton. pp. 601–606.
- Lefort, P., Gauthier, S., and Bergeron, Y. 2003. The influence of fire weather and land use on the fire activity of the Lake Abitibi area, eastern Canada. *For. Sci.* **49**: 509–521.
- Legendre, P., and Legendre, L. 1998. Numerical ecology, 2nd English ed. Developments in environmental modelling 20. Elsevier, Amsterdam.
- Lindenmayer, D., and McCarthy, M.A. 2002. Congruence between natural and human forest disturbance: a case study from Australian montane ash forests. *For. Ecol. Manage.* **155**: 319–335.
- McCune, B., and Mefford, M.J. 1999. PC-ORD. Multivariate analysis of ecological data, version 4. MjM Software Design, Gleneden Beach, Ore.
- McRae, D.J., Duchesne, L.C., Freedman, B., Lynham, T.J., and Woodley, S. 2001. Comparisons between wildfire and forest harvesting and their implications in forest management. *Environ. Rev.* **9**: 223–260.
- Magurran, A. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, N.J.
- Morgan, P., Aplet, G.H., Haufler, J.B., Humphries, H.C., Moore, M.M., and Wilson, W.D. 1994. Historical range of variability: a useful tool for evaluating ecosystem change. *J. Sust. For.* **2**: 87–109.
- Nguyen-Xuan, T., Bergeron, Y., Simard, D., Fyles, J., and Paré, D. 2000. The importance of forest floor disturbance in the early regeneration patterns of the boreal forest of western and central Quebec: a wildfire versus logging comparison. *Can. J. For. Res.* **30**: 1353–1364.
- Noble, I.R., DeBoer, L.K., Johnson, K.L., Coffin, B.A., Fellows, L.G., and Christiansen, N.A. 1977. Quantitative relationships among some *Pinus banksiana* – *Picea mariana* forests subjected to wildfire and postlogging treatments. *Can. J. For. Res.* **7**: 368–377.
- Peterson, D.L., and Parker, V.T. (*Editors*). 1998. Ecological scale: theory and applications. Columbia University Press, New York.
- Pielou, E.C. 1969. An introduction to mathematical ecology. John Wiley & Sons Inc., New York.
- Ponge, J.-F., André, J., Zackrisson, O., Bernier, N., Nilsson, M.C., and Gallet, C. 1998. The forest regeneration puzzle. *Bioscience*, **48**: 523–530.
- Purdon, M., Brais, S., and Bergeron, Y. In press. Understorey vegetation response to wildfire severity and salvage logging in Québec southern boreal forest: a comparative study. *Appl. Veg. Sci.*
- Qi, M., and Scarratt, J.B. 1998. Effect of harvesting method on seed bank dynamics in a boreal mixedwood forest in northwestern Ontario. *Can. J. Bot.* **76**: 872–883.
- Ratel, C.L. 1996. Composition de la banque de semences le long d'un gradient de succession au sud-ouest de la forêt boréale québécoise. M.Sc. thesis, Université du Québec à Montréal, Montréal, Que.
- Reader, R.J., Taylor, K.C., and Larson, D.W. 1991. Does intermediate disturbance increase species richness within deciduous forest understorey? *In* Modern ecology: basic and applied aspects. *Edited by* G. Esser and D. Overdieck. Elsevier, Amsterdam. pp. 363–373.
- Rees, D.C., and Juday, G.P. 2002. Plant species diversity on logged versus burned sites in central Alaska. *For. Ecol. Manage.* **155**: 291–302.
- Reich, P.B., Bakken, P., Carlson, D., Frelich, L.E., Friedman, S.K., and Grigal, D.F. 2001. Influence of logging, fire and forest type on biodiversity and productivity in southern boreal forests. *Ecology*, **82**: 2731–2748.
- Reinikainen, A., Mäkipää, R., Vanha-Majamaa, I., and Hotanen, J.P. 2001. Kasvit muuttuvassa metsäluonnossa. [Changes in the frequency and abundance of forest and mire plants in Finland since 1950.] *Kustannusosakayhtiö Tammi, Helsinki.* pp. 320–325.
- Rowe, J.S. 1983. Concepts of fire effects on plant individuals and species. *In* The Role of fire in northern circumpolar ecosystems. *Edited by* R.W. Wein and D.A. MacLean. John Wiley & Sons Ltd., Chichester, U.K. pp. 135–154.
- Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V., and Woome, G. 2002. The human footprint and the last of the wild. *Bioscience*, **52**: 891–904.
- SPSS Inc. 2000. SYSTAT version 10 for Windows. SPSS Inc., Chicago, Ill.
- Swanson, F.J., Jones, J.A., and Grant, G.E. 1997. The physical environment as a basis for managing ecosystems. *In* Creating a

- forestry for the 21st century. *Edited by* K.A. Kohm and J.F. Franklin. Island Press, Washington, D.C. pp. 229–238.
- Taylor, K.C., Arnup, R.W., Merchant, B.G., Parton, W.J., Niippola, J. 2000. A field guide to forest ecosystems of northeastern Ontario. 2nd ed. Northeast Science and Technology, Ontario Ministry of Natural Resources, Ont. NEST Field Guide FG-001.
- ter Braak, C.J.F., and Smilauer, P. 1998. CANOCO 4, software for canonical community ordination (version 4). Centre for Biometry Wageningen, the Netherlands.
- Vincent, J.S., and Hardy, L. 1977. L'évolution et l'extinction des lacs glaciaires Barlow et Ojibway et territoire québécois. *Géogr. Phys. Quat.* **31**: 357–372.