# Characterization of old "wet boreal" forests, with an example from balsam fir forests of western Newfoundland<sup>1</sup>

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Abstract: Wet boreal forests occur primarily in Atlantic Canada especially in Newfoundland, but examples are also found in Quebec and the northeastern U.S.A. These forests are dominated by balsam fir (Abies balsamea), which is susceptible to fire but flourishes in wetter environments where fire is absent. The major stand disturbances are caused by insects, primarily spruce budworm (Choristoneura fumiferana) and hemlock looper (Lambdina fiscellaria), followed by root rots and blowdown. Stands in Newfoundland were characterized by large amounts of dead standing and fallen wood, as a result of self-thinning processes and insect attacks. A comparison of 40-, 60-, and >80-year-old forests in Newfoundland indicated that the oldest stage of balsam fir forests had a distinctly different structure, including more large dead and fallen wood, a more irregular canopy including gaps, a more diverse ground flora, more moss ground cover, a more variable tree height, taller snags, fewer white birch snags, and fewer deciduous small trees. These differences were reflected in various plant and animal faunas that were distinct in the old forest including: flowering plants, beetles, Collembola, oribatid mites, mammals, and birds. Several species of plants and animals were only found in the oldest forest stands, including a high percentage among the arthropods. Suggested indicator species at the stand level include black-backed woodpeckers (Picoides arcticus) and marten (Martes americana). Logging results in a larger mean patch size than that caused by natural insect disturbances, possibly affecting dispersal by soil organisms and plants within the new landscape. A portion of the landscape, keyed to species with the largest area requirements to maintain their populations, including marten, black-backed woodpeckers, and (or) boreal owls (Aegolius funereus) could guide the amount of old forest, and individual patch sizes, required across a landscape over time.

Key words: old growth, biodiversity, species richness, forest management, balsam fir.

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Résumé : Les forêts boréales humides se trouvent principalement dans les provinces canadiennes de l'Atlantique, surtout à Terre-Neuve. Il en existe également au Québec et dans le Nord-Est des États-Unis. Dans ces forêts domine le sapin baumier (Abies balsamea), sensible au feu, qui prospère dans les milieux plus humides où le feu est absent. Les principales sources de perturbation des peuplements sont les insectes, plus particulièrement la tordeuse des bourgeons de l'épinette (Choristoneura fumiferana) et l'arpenteuse de la pruche (Lambdina fiscellaria), puis les pourridiés et les chablis. À Terre-Neuve, les peuplements se caractérisent par des quantités importantes d'arbres morts sur pied et de bois au sol résultant des processus d'éclaircie naturelle et des attaques d'insectes. Une comparaison de forêts terre-neuviennes de 40, 60 et 80+ ans a indiqué que, par rapport aux peuplements de 40 ou 60 ans, les sapinières les plus âgées présentent une structure nettement différente, se caractérisant, entre autres, par une plus grande quantité de gros bois morts, un étage supérieur plus irrégulier avec des trouées, une flore au sol plus diversifiée, une strate muscinée plus abondante, une hauteur des arbres plus variable, des chicots de plus grande hauteur, moins de chicots de bouleau à papier et moins de petits arbres feuillus. Ces différences se reflètent dans diverses composantes de la flore et de la faune qui sont distinctes dans la vieille forêt (plantes à fleurs, coléoptères, collemboles, acariens oribates, mammifères et oiseaux, entre autres). Plusieurs espèces végétales et animales, dont un pourcentage élevé d'arthropodes, n'ont été trouvées que dans les peuplements forestiers les plus âgés. Le pic à dos noir (Picoides arcticus) et la martre (Martes americana) sont suggérés en tant qu'espèces indicatrices au niveau du peuplement. La récolte forestière crée des trouées en moyenne plus grandes que celles résultant des perturbations naturelles causées par les insectes, ce qui pourrait affecter la dispersion par les organismes du sol et les plantes dans le nouveau paysage. Une portion du paysage déterminée en fonction d'espèces ayant besoin de plus d'espace pour maintenir leurs populations, incluant la nyctale boréale (Aegolius funereus), pourrait servir de guide pour établir la quantité requise de vieille forêt, et la taille appropriée des parcelles, dans un paysage en fonction du temps.

*Mots clés* : forêts anciennes, biodiversité, richesse des espèces, gestion des forêts, sapin baumier.

## Introduction

"Wet boreal" forests are conifer-dominated forests that receive sufficient moisture from precipitation and fog, especially during summer, such that fires are rare to non-existent. Rowe (1972) classified as wet boreal forests three areas of Newfoundland and southern Labrador (regions B.28b, B.29, B.30) and two areas of Acadian forests in Nova Scotia (the Cape Breton Highlands (A.6) and the east Atlantic shore (A.5b)) (Fig. 1). Other more localized wet boreal forest areas in eastern Canada include areas of the north shore of the St. Lawrence River within Rowe's Laurentide–Onatchiway region (B.1a), areas on Anticosti Island (B.28c), and locations within the Gaspé region (B.2) of Quebec. As well, some high-elevation forests of the Appalachian Mountains in the northeastern U.S.A. are also wet boreal forest types. The dominant tree species in all these forest areas is balsam fir (*Abies balsamea*), with black spruce (*Picea mariana*) occurring predominantly in wetter areas.

In most boreal forests, balsam fir is a late-successional species that can become dominant only after a period of 150–200 years of recruitment into a stand, in the absence of fire or severe insect infestation (Carleton and Maycock 1978; Cogbill 1985). However, under humid conditions, such as those provided by the maritime climate of much of Newfoundland, forest fires rarely occur, and the fire-susceptible balsam fir has become the dominant conifer. In fact, fire results in the elimination of balsam fir as a dominant species in an ecosystem (Bakuzis and Hanson 1965; Carleton and Maycock 1978). In terms of their species composition, these balsam fir ecosystems do not undergo strikingly different successional stages following logging, as do other boreal forests (Bakuzis and Hanson 1965; Carleton 2000). Stands of all ages are dominated by balsam fir at decreasing density with age, referred to as cyclic succession, ranging from >20 000 stems/ha as young trees <2 m, to older forests with tree densities of 1000–

**Fig. 1.** Location of "wet boreal" forests in eastern Canada. Areas correspond to Rowe's (1972) forest regions and sections and include two Nova Scotia Acadian sections: East Atlantic Shore (A.5b) and Cape Breton Plateau (A.6), and three Newfoundland and Labrador boreal forest sections: Corner Brook (B.28b), Northern Peninsula (B.29), and Avalon (B.30). Other smaller areas of wet boreal forest occur within other forest sections along the north shore of the St. Lawrence River, in the Gaspé, and on Anticosti Island, Quebec.



2000 stems/ha (Meades and Moores 1989; Thompson and Curran 1995). Seeds lie dormant for long periods on the forest floor, and many germinate to seedlings that may persist over decades of suppressed growth until the canopy is opened by tree mortality or logging (Bakuzis and Hanson 1965). Balsam fir trees are relatively short-lived trees once they reach canopy height, and the old-growth stage of a stand may only last 20-30 years, with trees >110 years (at breast height) being exceptionally old.

Hunter (1989) and Duchesne (1994) refer to a need for nonrestrictive definitions of old growth that are regional in nature and reflect specific ecosystem characteristics. Eastern Canadian old-growth forests have not been well quantified in terms of their characteristics or community associations (plant or animal). In western Newfoundland, the amount of natural-origin, old, balsam fir forest has been reduced mainly through logging since the 1940s, but also from a lethal outbreak of hemlock looper (*Lambdina fiscellaria* Guenée) in 1985–1988 (Newfoundland Forest Service unpubl. data; Thompson 1991) and a severe spruce budworm (*Choristoneura fumiferana* Clemens) infestation from the mid- to late-1970s (Hudak and Raske 1981). As well, the forest industry is moving towards a rotation age of about 60 years for many stands, particularly as a result of considerable pre-commercial thinning of young stands.

The purpose of this paper is to characterize wet boreal forests, especially those in Newfoundland, and to review the question of whether or not old balsam fir forests maintain communities that are distinct from those in mature balsam fir forests, and hence contribute in a particular way to regional biodiversity.

A concluding section suggests indicators for old balsam fir forests and an assessment of how closely the characteristics of these forests match published old-growth attributes in other forest systems.

### A detailed example from Newfoundland

Much of the information discussed below is from a multi-disciplinary study that was located in a large area (ca. 2500 km<sup>2</sup>) of balsam fir forest on the west coast of Newfoundland (Rowe 1972, region B.28b). In those individual studies, comparisons were made between uncut forests of  $\geq$ 80 years and older (referred to as old forest) and maturing but younger second-growth forests in the 40- and 60-year age classes. Many results from this work have been published independently (Thompson and Curran 1989, 1995; McCarthy 1996; Dwyer et al. 1997, 1998; Puvanendran et al. 1997; Thompson et al. 1999; Setterington et al. 2000; Gosse and Montevecchi 2001). Here, we synthesize the broad results from these studies to provide a more complete picture of biodiversity associated with balsam fir forests, as an example of a wet boreal forest type.

## Methods

#### Stands, plants, and animals

For the individual studies, sample sizes of stands were 10-13 stands/treatment for vegetation and birds (n = 30 to 37 stands), five stands/treatment for mammals (n = 15), and four stands/treatment (with multiple independent samples across the stand) for arthropods (n = 12). Forest stands were characterized by density and species composition of dead and live vegetation, canopy cover, standing dead trees, ground covers, and woody debris. The stands included three dominant ecosystems (Meades and Moores 1989): *Dryopteris*-balsam fir, *Dryopteris*-Hylocomium-balsam fir, and *Pleurozium*-balsam fir, with small areas of two other "richer" site types on small seepage areas (<0.5 ha) in most stands: *Rubus*-balsam fir and *Equisetum-Rubus*-balsam fir.

Communities of animal species examined for the Newfoundland study included those whose body sizes ranged from fractions of a gram to > 1000 g, because they would be expected to respond at different scales to logging of balsam fir forests (Holling 1992). Animal groups sampled included songbirds, woodpeckers, small mammals, marten (*Martes americana*), snowshoe hare (*Lepus americanus*), red squirrels (*Tamiasciurus hudsonicus*), Collembola, Coleoptera, and oribatid mites. Methods for each study are described in Thompson and Curran (1995) for mammals, Thompson et al. (1999) for birds, Setterington et al. (2000) for woodpeckers, Puvanendran et al. (1997) for Collembola, Dwyer (1995) and Dwyer et al. (1997, 1998) for oribatid mites, and McCarthy (1996) for Coleoptera. Data on the distribution of marten are also from Snyder and Hancock (1985),<sup>3</sup> Snyder (1985),<sup>4</sup> Thompson (1991), Thompson and Curran (1995), and Forsey et al. (1995). Gosse and Montevecchi (2001) reported on a study, completed later, of forest birds of prey from the same area.

Previously unpublished analyses are reported here for ground covers, species of flowering plants, and arthropods. We examined differences among the three forest age classes by discriminant function analyses (DFA) and reported the model statistics. Previously reported significant results are attributed to the authors, and only the p values are given.

<sup>&</sup>lt;sup>3</sup>Snyder, J.E., and Hancock, J. 1985. Newfoundland pine marten population estimate. Newfoundland Wildlife Division. St. John's, N.L. Unpublished Report.

<sup>&</sup>lt;sup>4</sup>Snyder, J.E. 1985. The status of pine marten in Newfoundland. Newfoundland Wildlife Division. St. John's, N.L. Unpublished Report.

## Patch sizes

We were interested in comparing the patch distributions of stands initiated following timber harvesting and natural mortality from hemlock looper. Areas of randomly chosen stands, logged between 1980 and 1986 at 2-year intervals (n = 150), and areas of forest killed by hemlock looper in the 1987–1988 outbreak (n = 150), were measured from aerial photographs to compare patch sizes from these two disturbance types.

# Characterization of Newfoundland balsam fir forests by trees, structures, and general ground covers

In Newfoundland, a minimum of 91% of the tree stems from all stands were balsam fir, and other tree species in rank order included white birch (Betula papyrifera), black spruce, trembling aspen (Populus tremuloides), and pin cherry (Prunus pensylvanica) (Thompson and Curran 1995). The oldest balsam fir stands (80+ years), and those of the two younger age classes (40 and 60 years), could be distinguished based on several stand structural and ground cover variables (Table 1) (Thompson and Curran 1995; Thompson et al. 1999). Mean height of trees (defined as >10 cm and >3 m tall) remained constant after 40 years (Fig. 2). Based on univariate statistics, old-forest stands had lower tree density, greater variance among tree heights (Fig. 2), larger diameter trees, lower small-tree density (trees <10 cm DBH (diameter at breast height)), lower density and diversity of deciduous shrubs, greater large snag density, taller snags, greater volume of logs on the ground, and a more open canopy than either younger age class (Table 1). The 40-year age class had more dead trees and small trees, and more white birch snags, but smaller mean snag DBH than did the oldest stands. The two younger age classes had a significantly greater small deciduous tree density than was found in the old-forest stands (Thompson and Curran 1995, p < 0.05). Using multivariate discriminant function analysis, the three age classes of forest could be separated based on a combination of six variables: deciduous small-tree density, volume of fallen logs, snag density, shrub diversity, coefficient of variation in tree height, and snag height (p < 0.0001) (Thompson and Curran 1995). This function correctly classified all old-forest stands, misclassified one 60-year stand as a 40-year stand, and misclassified three 40-year stands as 60-year stands (Fig. 3).

There were also differences among the stand ages in their biotic and abiotic ground covers (Table 1, Fig. 3). Area covered by small shrubs (0.1–0.5 m tall), all mosses, *Sphagnum* spp. mosses, and number and volume of fallen logs increased with age of stand, but average log diameter and area covered by total litter and conifer litter declined with stand age. Discriminant function analysis required five variables to significantly discriminate among stand age classes: percent *Sphagnum* spp., percent feather mosses, percent small shrubs, percent conifer litter, and percent low ferns (Fig. 3, Wilks'  $\lambda = 0.071$ ,  $F_{12,54} = 12.5$ , p < 0.0001). This model resulted in correct classification of all old-forest stands, nine of ten 60-year stands (one stand was misclassified as an old stand) and 11 of 12 of 40-year stands (one stand was misclassified as a 60-year stand).

## Forest stand processes in wet boreal forests

Intraspecies competition is important in wet boreal forests as shade-tolerant species dominate the tree and shrub layers. Stem density in young (<15 years) regenerating Newfoundland balsam fir stands averaged 22 400  $\pm$  7 600 stems/ha, for stands where mean height was under 3 m (Thompson and Curran 1989). By 40 years of age (age taken at 30 cm above ground), the density of live stems >3 m was 5400  $\pm$  1560 stems/ha, and at 80 years just 35% of that number remained alive (Table 1). Mean height of trees did not change significantly from 40 to  $\geq$ 80 years (to a maximum of 24 m). Bakuzis and Hanson (1965) noted that heights of 30 m are possible, but climatic limitation, such as Newfoundland's cold maritime climatic, likely reduced the maximum attainable. Average tree diameter rose significantly by 18.7% between 40 and 80 years and by 8.9% after 60 years (Table 1, p < 0.05). There was an astonishing number of dead stems in all ages of balsam fir forests, with more than 800 dead stems/ha

**Table 1.** Vegetation and forest structure measurements for 35 forest stands in three age groups (n = 12, 10, and 13, in 40-year, 60-year old post-logging, and  $\geq$ 80-year-old uncut forest, respectively), in western Newfoundland wet boreal forest (see Thompson and Curran 1995 for methods). Letters following mean values indicate significant differences across rows.

	Managed				Uncut	
	40+ years		60+ years		80+ years	
Variable <sup>a</sup>	x	SE	x	SE	x	SE
Stand variables						
Tree density (per m <sup>2</sup> )	$0.21a^b$	0.08	0.15b	0.01	0.12b	0.01
% trees deciduous	3.5	1.1	6.0	3.1	3.4	1.6
Tree height (m)	11.2	0.42	11.3	0.52	12.3	0.39
$\mathbf{C}\mathbf{V}^{c}$ tree height	0.16a	0.04	0.17a	0.06	0.27b	0.02
Tree diameter (cm)	14.4a	0.51	15.7a	0.66	17.1b	0.27
Small tree density (per m <sup>2</sup> )	0.33a	0.07	0.11b	0.02	0.07b	0.02
% small trees deciduous	18.1a	2.8	17.8a	8.4	0.6b	0.03
Small tree height (m)	6.3a	0.2	6.9a	0.4	5.5b	0.2
CV small tree height	0.33a	0.01	0.28b	0.02	0.33a	0.01
Shrub density (per m <sup>2</sup> )	0.26a	0.07	0.18b	0.06	0.23a	0.05
% shrubs deciduous	31.8a	6.5	28.4a	6.9	14.3b	5.4
Snag density (per m <sup>2</sup> )	0.16a	0.02	0.14a	0.02	0.08b	0.01
Snag density $>20$ cm DBH (per m <sup>2</sup> )	0.003a	0.002	0.004a	0.001	0.013b	0.001
White birch snag density (per $m^2$ )	0.012a	0.002	0.004b	0.002	0.006b	0.004
Mean snag DBH (cm)	5.9a	0.5	7.6b	0.5	11.9c	0.5
Mean snag height (m)	5.2a	0.2	5.9b	0.2	6.5b	0.3
Shrub diversity (H')	2.27a	0.27	2.78b	0.19	2.15c	0.14
Canopy (%)	72.7ab	1.6	74.4b	2.2b	69.0a	1.7
Ground covers						
Medium shrubs <sup>d</sup>	2.2	0.6	2.8	0.7	3.0	0.5
Low shrubs <sup>d</sup>	4.3a	0.5	6.6b	0.9	7.1b	0.5
All mosses <sup>e</sup>	36.8a	1.7	52.7b	2.1	60.8c	2.1
Sphagnum mosses	0.9a	0.2	1.8a	0.6	11.0b	1.8
Herbaceous plants	21.5	4.3	19.6	3.4	26.0	2.8
Richness of herbaceous plants (no. spp. per m <sup>2</sup> )	28.0	3.1	27.4	2.1	24.2	2.2
Small ferns <sup>f</sup>	10.0	2.2	12.9	3.4	14.4	2.8
Lichens <sup>g</sup>	0.5a	0.2	0.1b	0.1	0.03b	0.01
Total litter	45.6a	3.7	32.7b	5.9	24.9c	0.6
Conifer litter	19.3a	1.8	13.4b	1.9	11.8b	0.9
Slash	6.9	0.2	8.6	0.7	8.7	0.7
Volume logs $10 \text{cm} (\text{m}^3/\text{ha})^h$	22.2a	3.0	44.7b	4.6	55.2c	3.5
Logs > 10  cm (per 90  m)	3.3a	0.4	7.3b	0.7	14.1c	0.8
Mean log diameter (cm)	20.2a	0.7	19.4a	0.4	16.4b	0.2

<sup>*a*</sup> Standing density used plotless method of Batcheler (1975); ground covers are percent cover of  $2 \text{ m} \times 2 \text{ m}$  quadrat with four "layers" (medium shrubs; low shrubs; ferns and herbaceous plants; ground covers (moss, litter, slash)); trees >10 cm DBH, small trees >3 m tall and <10 cm DBH, shrubs <3 m, snag defined as a dead tree.

<sup>b</sup>Values followed by different letters are significantly different (p < 0.05, Thompson and Curran 1995).

 $^{c}\mathrm{CV},$  coefficient of variation.

<sup>d</sup> Predominantly balsam fir.

<sup>e</sup>Predominantly Pleurozium schreberi, Hylocomium splendens, and Sphagnum spp.

<sup>f</sup> Predominantly Onoclaea sensibilis and small Dryopteris spinulosa.

<sup>g</sup>Predominantly Cladina spp.

<sup>h</sup>Volume of logs calculated from 90 m triangular transects.

**Fig. 2.** Height distribution of balsam fir trees (>10 cm DBH) and small trees (<10 cm DBH) in western Newfoundland. Mean heights (with standard error) and coefficient of variation (CV) refer only to trees and the asterisk indicates a significant difference in the CV of trees in old forests.



even at 80 years of age. Some of this mortality, particularly in the 40-year and 60-year stands was from inter-tree competition, but much was also attributable to a spruce budworm outbreak from 1971 to 1979 that killed about 23% of the merchantable volume of trees across Newfoundland (Hudak and Raske 1981). Insects are a major cause of natural tree mortality in Newfoundland balsam fir forests (Hudak and Raske 1981) as well as in Quebec (Filion et al. 1998). Aside from spruce budworm, hemlock looper defoliated  $>73.6 \times 10^6$  ha of Newfoundland forests between 1983 and 1995, killing stands on 330 000 ha (Hudak et al. 1996).

Mortality has skewed the height distribution of Newfoundland balsam fir in the oldest stands, compared with an almost normal distribution at 60 years, as younger trees grow in gaps to replace

**Fig. 3.** Discriminant function models of vegetation variables describing 40-, 60-, and  $\geq$ 80-year-old balsam fir forests. "All vegetation" refers to all variables in Table 1 including tree, structural, and ground cover measures. "Ground vegetation" refers to only variables collected on 4-m<sup>2</sup> quadrats, also shown in Table 1. The ellipses are 95% confidence ellipses about the group centroids.



groups of trees that have died (Fig. 2). The mortality rate from 60 to 80 years in these stands averaged 15 trees ha<sup>-1</sup> year<sup>-1</sup>, although insect-caused mortality would have produced a punctuated pattern among years. Karsh (1996) estimated that, without mortality from budworm, stands of about 2500 stems/ha would have been nearer 3000 stems/ha, with about 45% greater volume. In natural old forests, mortality rate would normally be expected to increase between 80 and 100 years (Sturtevant et al. 1996), leading to an even more uneven-aged forest during very old age. Kneeshaw and Bergeron (1998) reported that about 40% of an old balsam fir stand was in gap-phase dynamics, and suggested that this process was important in structuring the stand. Gap dynamics is proximally controlled by the amount of windthrow, and Ruel (2000) reported that damage increased in old stands in Quebec, especially on shallow soils. In the Newfoundland forests, although total standing dead stems decreased with age, there was a significant increase in larger diameter dead stems, and an expected and observed increase in the total volume of fallen wood with forest age reported by Thompson and Curran (1995) and Sturtevant et al. (1996). Patch formation and distribution across a landscape can take several trajectories, depending on rate of insect infestation within and among years, as well as the age structure in the balsam fir forests at the time of an outbreak (Baskerville 1975; Ostaff and MacLean 1989; Seymour 1992; Morin 1994). Although data from Newfoundland clearly support the cyclic concept of regeneration in balsam fir, Déry et al. (2000) suggested that an infestation of spruce budworm in second-growth stands, <60 years old, could reduce balsam fir in these and in third-growth forests, in favour of deciduous species.

Height and diameter growth are known to decline in trees at old age. Hunt et al. (1999) examined possible hypotheses to explain an observed decline in productivity with age in balsam fir. They suggested that the decline of net primary productivity occurs because of an imbalance between photosynthesis and respiration that is exacerbated as a tree grows older and larger. Furthermore, balsam fir stem maintenance respiration rates are high compared with most other boreal trees (Lavigne 1997), probably

resulting in a shorter life span than other tree species. An alternative explanation for the observed decline in productivity, the hydraulic limitation hypothesis, is most likely not important to wet boreal forests because water is rarely limiting (Hunt et al. 1999).

# Characterization of plant and animal species associated with balsam fir forests

Analyses of stand structures indicated that old balsam fir forests were different from younger stands at or near rotation age. From a sustainability perspective, an important question is whether or not these structural differences translate into differences in the biodiversity associated with balsam fir forests beyond rotation age. To answer this question, the Newfoundland studies assessed taxa to determine if community structure differed among forest ages. Information was also derived from other studies in the balsam fir forests of Quebec, northeastern U.S.A., and Newfoundland.

#### Species of low shrubs, ferns, and flowering plants

Newfoundland balsam fir forests supported 85 species of shrubs and tree seedlings <1 m height, ferns, grasses, sedges, rushes, and flowering plants, among the three age classes. Species richness for these taxa did not differ by age of stand from 40 years to 80+ years ( $F_{2,27} = 0.68$ , p = 0.51). Balsam fir was the most abundant species, occurring in all stands, and was the only species to be recorded in all samples, with a range of (10 000–30 000 seedlings/ha) (see: Thompson and Curran 1989). Twelve plant species were significantly related to age of stand, ten of which were most abundant in old forests (ANOVAs, p < 0.01). Among these plants, three of the species most abundant in old-growth forests included *Epigea repens*, *Coptis groenlandicum*, and *Listera cordata*. Two species (*Streptopus roseus* and *Goodyera repens*) were primarily found in 60-year stands, and one species (*Populus tremuloides*) was most common in 40-year forests. The fern *Dryopteris noveboracensis* was the sole plant species included just four species and indicated a significant separation among the three age classes of forest (Fig. 4, Wilks'  $\lambda = 0.44$ ,  $F_{8,46} = 21.8$ , p < 0.001). Species included in the model were: *Epigea repens*, *Coptis groenlandicum*, Listera cordata, and *Streptopus roseus*. The model misclassified three of thirteen 40-year-old stands as 60 years old and correctly classified all 60- and 80-year-old stands.

Plant understory associations are known to change with age in forests, and the presence of most species depends on the physical conditions associated with the light and moisture regimes and the soil type (Carleton and Maycock 1980; Ringius and Sims 1997; Carleton 2000). In Newfoundland, although there was no net change in species richness with age, certain plant species were associated with each age class, and species may still have been accumulating into the oldest age class. The oldest stands supported the densest populations (numbers per square metre on quadrats) of 15% of the plant species, including feather mosses. Many of these plant species prefer the moderate light regimes typical of small gaps of old forests (e.g., white birch, cinnamon fern (*Osmunda cinnamomea*)), or a generally moderate light regime with limited competition (*Vaccinium* spp.); some colonize stands slowly over time under favourable conditions (feather mosses, *Gaultheria hispidula, Linnaea borealis*). The uniform and higher tree density and lack of gaps from large fallen trees in stands <80 years of age likely reduced available light and hence habitat for all of these species. Long-term recovery of herbaceous species diversity in forest habitats following logging has also been reported by MacLean and Wein (1977), Bormann and Likens (1979), Brewer (1980), and Meier et al. (1995).

## Lichens

In some forests, lichens have been identified as important components of old forests, however, the work in Newfoundland did not assess lichens. Lichens were the subject of studies in balsam fir forests in Quebec and the northeastern U.S.A. (Lang et al. 1980; Arseneau et al. 1997, 1998). Ahti (1983)



**Fig. 4.** Discriminant function model of flowering plants, ferns and small shrubs (<1 m) describing 40-, 60-, and  $\geq$ 80-year-old balsam fir forests. The ellipses are 95% confidence ellipses about the group centroids.

suggested that the nutrient-rich bark of balsam fir provided a good substrate for corticolous lichens in Newfoundland, but that insufficient illumination precluded arboreal lichen development in dense stands. Old stands of balsam fir with their relatively low tree density, numerous small gaps, and variable tree height structure would provide superior arboreal lichen habitat to that in the more shaded 40and 60-year-old forests. Further, the accumulation of fallen dead wood with age provides more habitat for lignicolous lichens, than in younger stands, including those 60 years old. Arseneau et al. (1997) showed that lichen biomass in the balsam fir forests of Quebec could be predicted by tree diameter, which had a high correlation to stand age, as also observed in our forest. In the Appalachian forests of New Hampshire, Lang et al. (1980) found increased arboreal lichen biomass with age of the balsam fir stand. This observation was also made by Selva (1994), who also concluded that undisturbed old forests contained more species of epiphytic lichens and more rare species than younger or disturbed stands in New Brunswick and the northeastern U.S.A.

#### Characterization of animal communities

## Mammals

Two species of bats occurred in western Newfoundland balsam fir forests (van Zyll de Jong 1985): little brown bats (*Myotis lucifugus*) and long-eared bats (*M. septentrionalis*). Radio-tagged bats followed by Grindal (1999) used edges between older forests and openings created by logging for feeding. Most roosts were in cavities created by woodpeckers in dead trees with a mean DBH of 29 cm and shorter (8.7 m) than average. Although shorter than the snags that we recorded (probably explained by trees with broken tops), we observed that snags >20 cm DBH were significantly more common in old-growth forests than in younger stands (Table 1, p < 0.05). Grindal (1999) expressed concern that loss of old forests would lead to a decline in important roost trees that might limit bat populations.

Three species of small mammals, snowshoe hares, and red squirrels occurred in the balsam fir forests (Thompson and Curran 1995). These few species precluded community analyses. Meadow

voles (*Microtus pennsylvanicus*) were captured only in the old forests, a result supported by Bateman (1986) and Sturtevant et al. (1996). Deer mice (*Peromyscus maniculatus*) were infrequently caught. They were found during all 4 years of the study in 40- and 60-year stands, but they were only found in two old-growth stands in 1 of 4 years. Masked shrews (*Sorex cinereus*) were found in all stand ages. Snowshoe hares were recorded in all stand ages, but they were significantly more abundant in 40-year stands than in either older age class in all years (p < 0.05). Red squirrels were found in all ages of forest, but were significantly more abundant in 40- or 60-year forests than in old forests in 3 of 4 years (p < 0.05, Thompson and Curran 1995).

Meadow voles occupy grassland habitats in general across their North American distribution (Banfield 1974), however, they have also been recorded in most eastern Canadian forests, where they showed little preference for age of stand (Morris 1955; Martell 1983; Parker 1989). Specific factors important to meadow voles in forest habitats have not been studied, although structural features are generally important to habitat use by small mammals (Dueser and Shugart 1979).

Marten are most commonly found in old balsam fir forests in western Newfoundland (Snyder and Hancock 1985; Snyder 1985; Bateman 1986; Snyder and Bissonette 1987; Bissonette et al. 1988<sup>5</sup>; Thompson 1991), and have been identified as endangered in the province. The decline in availability of suitable old forests has been suggested as the most probable cause of decline in their numbers (Forsey et al. 1995), although high mortality among juveniles incidentally caught in hare snares could also be partly responsible (Thompson and Curran 1995). An important correlate of marten abundance and habitat use is food availability within a home range (Thompson 1994). In Newfoundland, the main small mammal prey of marten is the meadow vole (Bateman 1986). Thompson and Curran (1995) suggested that certain ground covers and structures that may relate to habitat quality for meadow voles were most common in old forests, including small balsam fir seedlings, woody debris, and food plants. Further work by Sturtevant et al. (1996) and Sturtevant and Bissonette (1997) provided support for that hypothesis.

#### Birds

## Songbirds

Forty-two species of forest songbirds were found in the Newfoundland forests, of which 32 species were likely to have bred in the study area (Thompson et al. 1999). Twenty-two species were present in all three forest age classes, but the abundance of several species was significantly related to age of stand (p < 0.05) and species richness was significantly greater 40-year-old stands than in either older age class (p < 0.01, Thompson et al. 1999). Boreal chickadee (*Parus hudsonicus*), black-throated green warbler (Dendroica virens), fox sparrow (Passerella iliaca), purple finch (Carpodacus purpureus), and pine siskin (Carduelis pinus) were significantly more common in 40- and 60-year stands than in oldgrowth (80+ year) stands. Three species were equally abundant in 60-year and old-growth forests, and significantly less abundant in the 40-year stands than in old forests, including yellow-rumped warbler (Dendroica coronata), white-throated sparrow (Zonotrichia albicollis), and dark-eyed junco (Junco hyemalis). Ruby-crowned kinglet (Regulus calendula), black-backed woodpecker (Picoides arcticus), and grey-cheeked thrush (Hylocichla minima) were most abundant in old forests. Although the latter two species were uncommon, no grey-cheeked thrushes and only one black-backed woodpecker were recorded outside of 80-year forests. The bird communities separated into four distinct groups along the first two canonical correspondence analysis (CCA) axes, one of which (axis 1, Fig. 5) described a gradient based on forest age. One group described species predominantly occurring in the 40-year stands and included ovenbird (Seiurus aurocapillus) and black-throated green warbler, suggesting that the significantly greater density of small deciduous trees in the 40-year stands (Table 1) influenced

<sup>&</sup>lt;sup>5</sup>Bissonette, J.A., Frederickson, R.J., and Tucker, B.J. 1988. The effects of forest harvesting on marten and small mammals in western Newfoundland. Utah State University, Logan, Utah, U.S.A. 109 p. Unpublished report.

Fig. 5. Canonical correspondence of forest songbird communities in western Newfoundland (reprinted from Thompson et al. 1999). Axis 1 describes forest age from younger at the left to oldest at the right, axis 2 describes a gradient of soil richness. Identified groups were selected using TWINSPAN. Bird species are coded as follows (alphabetically): AMRO, American Robin; BBWA, Bay-Breasted Warbler; BBWO, Black-backed Wood-pecker; BCCH, Black-capped Chickadee; BOCH, Boreal Chickadee; BPWA, Blackpoll Warbler; BRCR, Brown Creeper; BTGW, Black-throated Green Warbler; BWWA, Black and White Warbler; DEJU, Dark-eyed Junco; DOWO, Downy Woodpecker; FOSP, Fox Sparrow; GRJA, Gray Jay; GCTH Gray-cheeked Thrush; HETH, Hermit Thrush; MAWA, Magnolia Warbler; MOWA, Mourning Warbler; NOFL, Northern Flicker; NOWA, Northern Waterthrush; OSFL, Olive-sided Flycatcher; OVEN, Ovenbird; PIGR, Pine Grosbeak; PISI, Pine Siskin; PUFI, Purple Finch; RCKI, Ruby-crowned Kinglet; WTSP, White-throated Sparrow; YBFL, Yellow-bellied Flycatcher; YRWA, Yellow-rumped Warbler.



the species in this community. The two intermediate groups included species common to 40- and 60-year-old forests and 40- and  $\geq$ 80-year-old forests (e.g., hermit thrush (*Catharus guttatus*)). An old-forest group identified by the CCA included the following eight species: brown creeper, dark-eyed junco, black-backed woodpecker, grey-cheeked thrush, olive-sided flycatcher (*Contopus borealis*), winter wren (*Troglodytes troglodytes*), mourning warbler (*Oporornis philadelphia*), and black and white warbler (*Mniotilta varia*) (Fig. 5). Regression analysis suggested that abundance of most bird species was related to various combinations of forest structures (Hogan 1996; Thompson et al. 1999).

## Woodpeckers

Downy woodpeckers (*Picoides pubescens*) were the most common woodpecker species in balsam fir forests, and they were recorded in similar numbers among the stand age classes. Hairy woodpeckers (*P. villosus*) were similarly uncommon among stand age classes. A linear regression model relating downy woodpecker abundance with stand descriptor variables, suggested that tree density and density of white birch snags were important variables influencing habitat selection (Setterington et al. 2000). Use of forest stands by hairy woodpeckers was significantly related to the density of white birch snags (p < 0.01). There were significantly more black-backed woodpeckers in  $\geq$ 80-year-old balsam fir forest stands than in either of the younger age classes (p < 0.05, Setterington et al. 2000). Other authors have

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	Only in old growth		Only or predominantly in old growth			
Taxon	Number of species	% of species	Number of species	% of species		
Plants <sup>a</sup>	1	1.2	10	11.8		
Birds <sup>b</sup>	2	4.6	3	7.1		
Mammals <sup>c</sup>	1	6.3	4	25.0		
Oribatid mites	6	7.1	21	24.7		
Coleoptera <sup>d</sup>	21	17.4	29	24.0		
Collembola	1	1.9	18	34.6		

**Table 2.** Summary of old-growth species by taxon in  $\geq$ 80-year-old balsam fir forests, in western Newfoundland.

<sup>*a*</sup>Flowering plants, sedges, rushes, and shrubs <1 m.

<sup>b</sup>Songbirds and woodpeckers.

<sup>c</sup>Based on associations from published sources.

<sup>d</sup>Ground beetles from 28 families.

also suggested that eastern old-growth forests may be important to this woodpecker species (Imbeau et al. 1999). Black-backed woodpecker occurrence was associated with two variables: density of large snags (>20 cm DBH) and negatively to the total number of dead stems. This model enabled a successful prediction of presence or absence of black-backed woodpeckers by age class of 72% (Setterington et al. 2000).

Among all birds, excluding birds of prey, only about 7% were strongly associated with old forests in Newfoundland, and most species were equally abundant in all stand ages (Table 2). Haila et al. (1994) and Imbeau et al. (1999) reported that 14 and 8% of the boreal birds in Finland and Quebec, respectively, were old-growth specialists. This suggests that many boreal birds are sufficiently generalized in their habitat requirements at the stand level, so as not to be negatively affected by forest management or other forest disturbances (Welsh 1987; Keast 1990; Drapeau et al. 2000). Black-backed woodpeckers are likely semi-obligate old-forest inhabitants, requiring large areas of forest to maintain their populations in years between hemlock looper or spruce budworm outbreaks (Setterington et al. 2000). The presence of relatively large snags (>20 cm DBH) appeared to be the essential feature important to black-backed woodpeckers in old forests, and snags of this size were absent in the 40- and 60-year-old mature stands. Imbeau et al. (1999) reached the same conclusion for the importance of old-growth black spruce forests for black-backed woodpeckers and three-toed woodpeckers (*Picoides tridactylus*) in Quebec.

#### Birds of prey

Gosse and Montevecchi (2001) reported that there was a distinct old balsam fir birds-of-prey fauna. Boreal owls (*Aegolius funereus*) and osprey (*Pandion haliaetus*) were only found in the  $\geq$ 80-year-old stands, and sharp-shinned hawks (*Accipiter striatus*) were most abundant in the same stands. Boreal owls were likely restricted to the old forests where the largest cavities were available for nesting and where the less cluttered understory with a substantive canopy facilitated hunting. Boreal owls have large area requirements (e.g., Hayward et al. 1993), and particularly with the low prey abundance in the Newfoundland forests, large expanses of uncut forest are important to this species.

## **Oribatid mites**

Certain of our results for Oribatida (Acari) were reported in Dwyer et al. (1997, 1998), and effects of forest age class were reported in Dwyer (1995). We observed 85 species or species complexes from 39 families of oribatid mites, with 84 species in soils, 42 of which were rare. Among all species, 14 genera and 36 species were new records for Newfoundland, and one genus, *Haplozetes*, was new to Canada.

A small number of common species dominated all samples, including: *Eniochthonius minutissimus* (Berlese), *Synchthonius crenulatus* (Jacot), *Steganancarus thoreaui* (Jacot), *Nanhermannia bryophila* (new record), *Tectocepheus velatus* (Michael), *Oppiella washburni* (Hammer), *Suctobella* spp., and *Parachipteria travei* (Nevin). These eight species accounted for 72–78% of all adult captures among samples and years (Dwyer 1995; Dwyer et al. 1998).

Among the sites for Oribatid mites, a significant, but complex, discriminant function model was constructed with 21 species (Wilks'  $\lambda = 0.051$ ,  $F_{42,434} = 35.5$ , p < 0.0001, Fig. 6). The model correctly classified 96% of samples from  $\geq$ 80-year stands, 98% of samples from 60-year stands, and 85% of samples from 40-year stands. Overall, 12% of the samples from 40- and  $\geq$ 80-year stands could not be distinguished from each other. Among the species selected by the model, two were common in 60-year forests (*Phthiracarus* sp., and *Ceratozetes cuspidatus* Jacot), two were least common in 60-year forests (*Parapyroppia* sp., and *Hypochthonius rufulus* C.L. Koch), and one species (*Cepheus corae* Jacot) was found predominantly in  $\geq$ 80-year-old forests.

The small number of abundant oribatid mite species that dominated community structures in Newfoundland balsam fir stands was a phenomenon also reported in other studies (Crossley and Bohnsack 1960; Behan 1972<sup>6</sup>). Negative effects of timber harvesting on the soil oribatid mite community have been documented (Mitchell and Parkinson 1976; Huhta et al. 1967; Abbott et al. 1980; Seastedt and Crossley 1981; Bird and Chatarpaul 1986) for both the short and longer term. In Newfoundland, community differences existed at 60 years after logging, compared with  $\geq$ 80-year-old stands, including the absence of several species. The accumulation of certain fungi, soil organic matter, and lichens may only occur in sufficient numbers in old forests to support some diet-specialist oribatid species. Sources for populations of the rarer species are necessary for these species to repopulate second-growth forests. Our comparison of sizes of logged vs. naturally disturbed areas suggested larger open areas were created by logging than by insect attack (see below). It is possible that large open areas may not be recolonized by microscopic animals, such as mites, because of their limited dispersal capabilities. Haila et al. (1994), Niemelä et al. (1993), and Niemelä (1999) invoked this potential problem for ground beetles, which are many times larger and more mobile than oribatid mites.

## Coleoptera

More than 120 species of beetles from 28 families of beetles were found in Newfoundland balsam fir forests (McCarthy 1996), among which three families were dominant: Staphilinidae (79.5% of all captures), Carabidae (9.0%), and Ptiliidae (7.7%). Nine species accounted for 65% of the total captures including: *Elonium diffusum* (Fauvel), *Tachinus frigidus* Erichson, *Aleocharinae* sp. #2, *Aleocharinae* sp. #5, *Acrotrichus* sp., *Proteinus limbatus* Mäklin, *Pseudopsis subulata* Herman, *Ptenidium* sp., and *Oxypoda* sp. #1. Several of these dominant species differed among age classes, and four species were common to all age classes. Among the five dominant species that differed in abundances among age classes, *Proteinus limbatus* and *Oxypoda* sp. #1 showed a significant trend of increased abundance with forest age (McCarthy 1996).

Most beetle species were rare (n = 77), and only 25 species (<21%) were sufficiently numerous for analyses. Among the many rare species, 17, 3, and 8 species were unique to  $\geq$ 80-year, 60-year, and 40-year forests, respectively. Species richness ranged from 49 to 80 species by forest age class, and 21 species, including the 17 rare ones, were unique to old forest sites (Table 2), although age did not significantly predict species richness. Four among the old forest species were abundant including *Calathus advena* (LeConte), *C. ingratus* Dejean, *Platynus decentis* (Say), and *Lesteva pallipes* LeConte. Eight other species were most abundant in old forests, and ten species were most abundant in one or both of the younger age classes compared with old forests (p < 0.05).

<sup>&</sup>lt;sup>6</sup>Behan, V.M. 1972. The effects of urea on Acarina and other arthropods in Quebec black spruce humus. M.Sc. thesis, McGill University, Montreal, Que. Unpublished



**Fig. 6.** Discriminant function models for selected arthropod communities describing 40-, 60-, and  $\geq$ 80-year-old balsam fir forests. The ellipses are 95% confidence ellipses about the group centroids.

A significant discriminant model selected seven species of beetles to significantly separate the forest age classes (Wilks'  $\lambda = 0.036$ ,  $F_{16,72} = 19.28$ , p < 0.0001) (Fig. 6). This model correctly classified all samples from old-forest stands, and 85% of the samples from all younger stands. The model included three old-forest species: *Calathus advena*, *Platynus decentis*, and *Olophrum rotundicolle* (C.R. Sahlberg); three species that were most common in 40-year forests: *Pterosticus punctatissimus* (Randall), *Acrotrichus* sp., and *Oxypoda* sp; and one species that was most abundant in 60-year forests: *Omalium* sp.

As with the other arthropod groups, common species were ubiquitous among various ages of forest, and several rare species were found in specific age classes of forests. This result was similar to those of Niemelä et al. (1993, 1988), Rykken et al. (1997), and more generally for arthropods (Weaver 1995) and other fauna (Haila et al. 1994). Niemelä et al. (1988) found only one old-growth obligate carabid beetle in Finland, and suggested that it would recover its populations by a stand age of about 50 years.

However, in western Canada, Niemelä et al. (1993) found five old-forest specialist carabid beetles and predicted that community recovery following logging would be problematic because of the lack of old-forest habitat on the landscape from which colonization would be possible. A similar situation may exist on the west coast of Newfoundland, where 21 species (17.4%) of all beetle species (i.e., not just carabids) were only found in old forests, and another eight species were most abundant in the oldest age class. Many forest arthropods, including beetles are site (or microsite) dependent, because of their obligate reliance on small-scale food resources or environmental variables such as moisture levels (Niemelä 1997). Certain structures and resources, including cavity and hollow trees, rotting large logs, dense lichens, deep litter depths, and dense mosses, develop only or predominantly in old forests and hence beetles using these habitats are most abundant there (Chandler 1987; Chandler and Peck 1992; Kremen et al. 1993; Nilsson et al. 1995; Niemelä 1997).

## Collembola

An annotated species list of Newfoundland balsam fir Collembola species was provided in Puvanendran et al. (1997). Sixty-four species from 30 genera of Collembola were found. Six species were abundant and dominated the Collembola faunas of all sites including: *Folsomia penicula* Bagnall, *Onychiurus paro* (Christiansen and Bellinger), *O. similis* Folsom, *Tulberggia granulata* Mills, *Isotomiella minor* (Schäffer), and *Isotoma notabilis* Schäffer. Among these species, only *F. penicula* was most abundant in old forests compared with both younger age classes; *O. similis* was most abundant in the 40-year stands. Species richness was similar among age classes and forest types.

The DFA model among stand ages was significant based on 19 species (Wilks'  $\lambda = 0.073$ ,  $F_{38,438} = 31.0$ , p < 0.0001) (Fig. 6). The model misclassified 4% of old-forest samples as 40-year stands, and 4.5% of the samples from 40-year stands as old forests, but overall correctly placed 91% of the samples. Among the species selected in the model, *F. penicula* was abundant in old forests, and *E. nivalis* and *N. minimus* were more abundant in both younger forest age classes than in old forests.

The highest density of Collembola was consistently in the old-forest sites, there were fewer rare species peculiar to the old forests, and only one common species was most abundant in old stands. Density of Collembola in Newfoundland balsam fir forests was similar to that reported from other forest locations (Poole 1961; Behan 1972; Peterson and Luxton 1982; Bird and Chatarpaul 1986). In Newfoundland, a distinct old-forest Collembola community existed that had not recovered 60 years after logging. The particular species diversity and increased density of Collembola in old forests can likely be attributed to the accumulation of hypogeous fungi, organic matter, and structures, such as large logs and arboreal lichens associated with old forests.

## Size distribution of stands logged or killed by hemlock looper

The distribution of stand sizes initiated by logging was significantly different than that of stands entirely killed by hemlock looper, in 1987–1988 ( $\chi^2 = 62.7$ , df = 13, p < 0.0001) (Fig. 7). The size distribution of hemlock looper-killed stands was best described by a negative power curve, while the size distribution of logged stands could be modelled by a more flattened negative exponential curve. Mean size of logged stands was 289 ha (SE = 20.2); mean size of hemlock looper-killed stands was 117 ha (SE = 13.1) (median <100 ha for looper-killed and >250 ha for logged). More than half the hemlock looper-killed stands were less than 100 ha, whereas only 23% of the logged stands were in the same size classes. Large patches were over-represented in the logging-origin stands, relative to those created by insects.

Emulating or trying to model timber harvesting on "natural" modes of forest disturbance is a common concept in current thinking about sustainable forest management (e.g., Hunter 1990; Attiwill 1994; Haila et al. 1994). The idea of emulating natural disturbance resulted from concerns over the rate at which clearcut logging was consuming old forests, the cumulative area of progressive clearcuts, the



Fig. 7. Size distribution of 150 randomly chosen forest areas killed by hemlock looper and 150 forest areas harvested over 2-year intervals using clearcut logging, in western Newfoundland.

lack of congruency between landscape patterns produced by logging and natural mortality sources especially in gap-phase temperate forests, loss of biodiversity, and the recognition that spatial and temporal change were part of the natural functioning of forest ecosystems. The idea of emulating natural forest pattern includes more than just size of patches, but also considers juxtaposition of patch sizes, spatial adjacency of age classes, amounts of forest in each age class, and sizes of residual patches within cuts. However, a comparative measure of sizes among harvested patches and naturally-created patches allows a first approximation of how similar the silvicultural system used by managers may be to natural disturbance patterns. This is especially true for a species like balsam fir, for which the preferred silvicultural treatment is clearcut logging. Patches derived from insect mortality also include patches with incomplete mortality. Therefore, in ecosystems where insect disturbances are common, consideration should be given to clearcutting a range of patch sizes consistent with natural mortality patterns, and the use of partial logging methods for at least portion of an annual cut when designing harvesting plans.

In Newfoundland, logging has resulted in fewer of the smallest patches, and a greater number of very large patches, than would have resulted from natural insect-caused mortality. Our result is consistent with anthropogenic altered landscape pattern vs. expected natural pattern reported from other boreal areas where clearcutting is employed (Wallin et al. 1996; Gluck and Rempel 1996; Perera and Baldwin 2000). How this altered forest landscape pattern may affect the specific biological diversity of Newfoundland is unknown. However, patch sizes on a landscape can affect animal dispersal, home range sizes, and capability of a given species to occupy a particular landscape (Hunter 1990; Haila et al. 1994; Niemelä 1999), and the colonization capability of small soil organisms, lichens, and some plants, as well as mammals and birds (Sutherland et al. 2000) could be affected.

## Conclusions

The inescapable conclusion from studies in balsam fir forests is that the old-forest stage, which has developed by about 80 years, provides an environment that is distinctly different from that of stands at

Proposed old-growth condition	Conformity in old-growth Newfoundland balsam fir
High density of old trees at or nearmean life expectancy	Conforming
High density of large trees	Nonconforming
Multi-layered canopy	Somewhat conforming
Multiple gaps	Conforming
Species composition dominated by late-successional species	Conforming, but only one species
Relatively large amount of large diameter fallen logs	Conforming
High density of large diameter snags	Conforming
Annual increment near zero	Conforming (Meades and Moores 1989)
Well-developed herbaceous layer	Nonconforming
Abundant arboreal lichens and fungi	Likely conforming
No human disturbances	Conforming

**Table 3.** Summary of published old-growth characteristics and conformity of Newfoundland balsam fir forests to the proposed conditions.

Note: Proposed conditions are from Thomas et al. (1988), Hunter (1989), Leverett (1996), and Kimmins (1997).

the peak of their maturity. These old stands are distinctive in their physiology, structure, and function. Furthermore, these differences support a biodiversity that can be readily distinguished at all scales, from sites to landscapes, compared to that in younger forests including mature forests. An interesting comparison that was not possible for our research, would be to compare 40- and 60-year-old forests that had originated following natural disturbance with those following logging.

Haney and Schaadt (1996) noted that the truncation of forest age rarely is discussed with respect to wildlife responses, but here that question has been addressed. A potential reduction in availability of old forests would have negative consequences for sustaining biological diversity and associated processes in balsam fir ecosystems over the long term. Species diversity differs in various ages of forests because of habitat changes associated with functional and structural changes (e.g., gaps, dead wood, lichen growth) that develop as the forest ages (Maser 1990; Franklin and Spies 1991; Noss and Cooperrider 1994). An important step in sustainable forest management is to describe forest conditions associated with old growth, and to determine measurable indicators of this condition (Noss and Cooperrider 1994). Although considerable work has been conducted in western old-growth forests (e.g., Ruggiero et al. 1991), few data are available for most eastern forest ecosystems (see Davis 1996), especially in Canada.

Age in the Newfoundland wet boreal forests was a good predictor of various structures important to animal communities. Important structural and functional changes occurred in these forests, apparently during the period between 70 and 80 years, which had implications for local and regional biological diversity. Several authors have attempted to generalize the ecological characteristics of old-growth forests to enable a broad understanding of what constitutes an old forest (Hunter 1989; Leverett 1996; Kimmins 1997) and these are summarized in Table 3. Balsam fir forests of Newfoundland conformed to eight of ten of these general characteristics, for which we had data or information. Nonconformity to two criteria was related to specific ecosystem characteristics: large trees do not exist in balsam fir forests in the oldest age class represented distinct plant and animal habitats, the characteristics of which did not develop until at least 80 years of age. Several attributes that are likely idiosyncratic to old-growth balsam fir ecosystems included a low density of small trees, a lack of small deciduous trees, a lower diversity of shrub species than is found in younger stands, and an exceptionally large number of standing dead stems.

At the broadest scale, forest management in western Newfoundland is creating a landscape pattern that differs from that produced by infestations of insects alone, based on individual patch sizes. Hansen et al. (1991) reported associations of several vertebrate species and stand sizes in the U.S. Pacific Northwest, among which the spotted owl (Strix occidentalis) is the best known. Holling (1992) suggested that large-scale change in pattern would affect animals that react to habitat at large scales. Under that hypothesis, most likely effects would be expected on species that select habitat at large landscape scales and have large home ranges such as caribou (Rangifer tarandus), moose (Alces alces), black bear (Ursus americana), marten, lynx (Felis lynx), black-backed woodpeckers, raptors, and perhaps forest bats. Analyses of species distributions in Ontario by Voigt et al. (2000) and Rempel et al. (1997) provided some evidence that broad-scale landscape pattern changes, caused by forest management, have altered populations of caribou, moose, and fisher (Martes pennanti). In Europe, Kurki et al. (1998) suggested that pattern (abundant edges) in managed forests positively affected fox populations, consequently reducing grouse numbers as a result of elevated predation (Kurki et al. 1997), and Edenius and Elmberg (1996) found that forest management produced a negative effect on avian species richness. Mönkkönen and Welsh (1994) suggested that some bird species that may appear to be generalists at a landscape scale, would be specialists at smaller scales. However, in boreal Quebec, Drapeau et al. (2000) found landscape effects on bird communities were related to landscape composition, such as the amount of old forest and increased young deciduous forest, but were not related to the landscape configuration.

For small arthropods that are not highly mobile, dispersal and recolonization of disturbed patches may not occur unless sufficient scattered undisturbed forests remains on a landscape (Haila et al. 1994; Kremen et al. 1993; Moldenke and Lattin 1990). Under a natural disturbance regime in balsam fir forests, recolonization is likely facilitated as a result of many small disturbances resulting in normally small inter-patch distances. Generally, the effects of altered landscape pattern on most forest wildlife species remain unknown and, in particular, unpredictable in the face of widespread concern that altered pattern may affect forest functioning and biodiversity.

To be an effective indicator of old-growth forest, a candidate indicator must be measurable (quantifiable in a repeatable and comparable fashion, independent of sample size), readily identifiable, and regularly found in old forests (conversely, if absent, would clearly indicate that the forest does not maintain sufficient old-growth characteristics). Furthermore, the candidate need not be a single species, particularly if a group of species (community or assemblage) can be sampled simultaneously. We suggest that the black-backed woodpecker may be a good indicator species of old-forest structures in Newfoundland, at the stand and landscape levels. Angelstam (1998) suggested three-toed woodpeckers (*Picoides tridactylus*), a holarctic species, as an indicator species in wet European boreal forests, and Mikusinski et al. (2001) suggested the same species was a good indicator because it was highly specialized. In Quebec, Imbeau et al. (1999) also believed that woodpeckers, especially three-toed and black-backed woodpeckers, would decline in managed forests.

Although not entirely certain, it appeared that the 60-year-old forests, regenerated following logging, would eventually develop the characteristics of old forest, based on the recovery of plant species, including feather mosses, and the fact that the forests will be susceptible to the insect attacks and fungi that result in dead and moribund trees. Examining these forests in another 20–25 years for the suggested indicators would confirm whether or not normal processes do indeed occur in managed forests enabling development of balsam fir to the old-growth stage. However, there are two clear answers for sustainable forestry in western Newfoundland: first, the truncation of age by working to a rotation age of 60 years may have consequences for maintaining Newfoundland biodiversity; and second, more attention needs to be given to patch size relative to natural disturbance if sustainable forestry is an objective, as well as research into the question of effects of patch distribution.

Although our work identified species and characteristics that make old balsam forests distinct from younger stands, we did not attempt to answer the question of how much old forest is needed to maintain these species and communities in space and time. We also did not attempt to understand the dynamics of

how much old forest might be expected over time in these wet boreal forests under natural disturbances alone. One way to derive a management answer to the question of how much old forest, would be to model populations of old-forest species, such as caribou, marten, and black-backed woodpeckers, to determine habitat requirements to maintain their populations over time, and to examine the populationlevel effects of altering habitat distribution on the landscape. These are important questions with respect to managing forest landscapes, and a key area for future work in Newfoundland and elsewhere.

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