Old-growth forests of the Acadian Forest Region

A. Mosseler, J.A. Lynds, and J.E. Major

Abstract: In the absence of sufficient data from directed studies of old-growth forests in the Acadian Forest Region (AFR), we must rely on a general knowledge of forest ecology and natural succession, population biology, disturbance dynamics, and palynological evidence to understand the probable extent of old-growth, late-successional forest types before European settlement, their role in the biological diversity of Acadian forests, and the silvicultural prescriptions required to maintain a component of such old growth (OG) on the landscape. The structural features of representative Acadian old growth can be understood from the few remaining stands of such forest in the AFR and from studies in the closely related forest types of the Great Lakes – St. Lawrence Forest Region of Canada and other eastern North American temperate-zone forests. Several hundred years of land clearing for agriculture and timber harvesting has eliminated most of the old-growth forests in the Maritime provinces of Canada. Nevertheless, our limited knowledge of OG suggests that, when the average age of the dominant and co-dominant trees of the typical late-successional species associations of the AFR has reached about 150 years, such forests generally appear to have attained most of the structural features commonly associated with old-growth forests (e.g., standing and fallen, dead and dying trees in various stages of decay, a layered, multi-age canopy structure). What little OG remains is largely restricted to small, isolated stands, often associated with steep gorges that were inaccessible to harvesting or areas that were otherwise protected or avoided being harvested. Late-successional, old-growth forest types dominated by relatively shade-tolerant, long-lived species such as sugar maple (Acer saccharum Marsh.), beech (Fagus grandifolia Ehrh.), eastern hemlock (Tsuga canadensis (L.) Carr.), and red spruce (Picea rubens Sarg.) and with a significant component of eastern white pine (Pinus strobus L.) and yellow birch (Betula alleghaniensis Britt.) often represent the final stages of forest stand development. Such forests may be considered archetypical of OG in the AFR. Forests dominated by these tree species mixtures tend to regenerate naturally in forest canopy gaps left by small-scale disturbances created by fallen individual trees or small groups of trees, rather than the catastrophic, stand-replacing disturbances normally associated with boreal forests. Our objectives were (i) to describe some of the remaining old-growth forest types and their extent in the AFR, (ii) to present some perspectives on their role in biodiversity conservation, and (iii) to present a basis for developing strategies for


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conservation, management, and restoration. Forest-resource inventories (FRI) suggest that as little as 1–5% of present forest cover across the Maritimes is in forest older than 100 years, but our preliminary ground surveys based on this database suggest far less than that is true old-growth forest. Based on expected patterns of ecological succession, disturbance dynamics, and stand development following catastrophic natural disturbance intervals of about 1000 years, and from what the geological record tells us about forest cover before European settlement, we can project that as much as 50% of Maritime forest landscape may have been dominated by late-successional old-growth forest types over the 4000–5000 years before European settlement. Recent genetic studies suggest that these old-growth forests were probably a rich source of the genetic diversity required by these tree species to adapt to the environmental (climatic) changes that have characterized the North American continent over the past 2 million years of its glacial history.

Key words: biodiversity, forest ecology, late-successional forests, natural succession, old growth, temperate zone.

Résumé: Les forêts anciennes de la région forestière acadienne (RFA) n’ayant pas été suffisamment étudiées, nous devons faire appel aux connaissances générales sur l’écologie et la succession naturelle des forêts, la biologie des populations, la dynamique des perturbations et la palynologie pour établir l’étendue probable des forêts anciennes de fin de succession avant la colonisation européenne, comprendre leur apport à la diversité biologique des forêts acadiennes et préciser les prescriptions sylvicoles requises pour conserver une composante de ces forêts anciennes dans le paysage. Pour définir les caractéristiques structurales d’une forêt ancienne typique, on peut s’appuyer sur les quelques peuplements résiduels de cette forêt dans la RFA et des études de forêts apparentées de la région forestière canadienne des Grands Lacs et du Saint-Laurent ainsi que d’autres forêts de la zone tempérée de l’Est de l’Amérique du Nord. Après plusieurs centaines d’années de coupe des forêts pour l’agriculture et la récolte du bois, presque toutes les anciennes forêts des provinces Maritimes ont été éliminées. Néanmoins, d’après notre connaissance limitée des forêts anciennes, il semble généralement que la plupart des caractéristiques structurales habituellement associées aux forêts anciennes (ex. : présence d’arbres moribonds et morts, sur pied et au sol, à divers stades de décomposition, et couvert multistrate, inéquienne) sont acquises lorsque les arbres dominants et codominants des associations d’essences typiques de fin de succession dans la RFA ont atteint en moyenne environ 150 ans. Le peu qui reste des forêts anciennes est sous la forme de petits peuplements isolés, qui se trouvent dans des gorges abruptes inaccessibles pour la récolte ou dans des sites protégés ou ayant pour une raison quelconque échappé à la récolte. Les forêts se caractérisant par la dominance d’essences à longue durée de vie, tolérant relativement bien l’ombre, comme l’érable à sucre (Acer saccharum Marsh.), le hêtre (Fagus grandifolia Ehrh.), la pruche du Canada (Tsuga canadensis (L.) Carr.) et l’épinette rouge (Picea rubens Sarg.), et par la présence d’une composante importante de pins blancs (Pinus strobus L.) et de bouleaux jaunes (Betula alleghaniensis Britt.) représentent souvent les derniers stades du développement des peuplements forestiers. De telles forêts peuvent être considérées comme l’archétype de la forêt ancienne dans la RFA. Les forêts dominées par des mélanges de ces essences ont tendance à se régénérer naturellement en profitant des trouées faites dans le couvert par des perturbations de petite échelle (chute d’un arbre ou d’un petit groupe d’arbres), plutôt qu’à la suite des perturbations catastrophiques entraînant le remplacement des peuplements, comme c’est souvent le cas dans les forêts boréales. Nos objectifs étaient les suivants : (i) décrire et délimiter certains vestiges des forêts anciennes de la RFA; (ii) offrir quelques perspectives concernant leur rôle pour la conservation de la biodiversité; (iii) fournir des données de base pour l’élaboration de stratégies de conservation, d’aménagement et de restauration. D’après les inventaires des ressources forestières, à peine 1–5 % du couvert forestier actuel des Maritimes aurait plus de 100 ans, mais le pourcentage de la véritable forêt ancienne serait bien moindre selon nos relevés préliminaires sur le terrain. En nous fondant sur les patrons attendus de la succession écologique, de la dynamique des perturbations et du développement des peuplements créés par une perturbation
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La catastrophe naturelle survenant à des intervalles d'environ 1000 ans et en nous appuyant sur les révélations des études géologiques concernant le couvert forestier avant la colonisation européenne, nous avons estimé que jusqu'à 50 % du paysage forestier maritime pouvait être dominé par des forêts anciennes, de fin de succession, pendant les 4000–5000 ans qui ont précédé la colonisation européenne. De récentes études génétiques permettent de croire que ces forêts anciennes étaient probablement riches en diversité génétique et pouvaient offrir ce dont avaient besoin les essences qui les composaient pour s'adapter aux changements environnementaux (climatiques) qu’a connu le continent nord-américain pendant les deux derniers millions d’années de son histoire glaciaire.

Mots clés : biodiversité, écologie des forêts, forêt de fin de succession, succession naturelle, forêt ancien, zone tempérée.

Introduction

The Acadian Forest Region (AFR) covers most of the Maritime provinces (Nova Scotia, New Brunswick, and Prince Edward Island) of Canada. With the exception of a small area (e.g., 956 728 ha out of a total area of 13 326 076 ha — or 7%) of boreal forest (Fig. 1), the Acadian forest cover is typical of the temperate zone. Many of the same shade-tolerant, late-successional forest types that would be expected to develop into the self-replacing, older forests of the Great Lakes – St. Lawrence Forest Region (Rowe 1972) in the absence of catastrophic or stand-replacing disturbances such as fire also characterize the AFR. We consider these late-successional forest types, dominated by long-lived, shade-tolerant tree species that regenerate naturally in the absence of large-scale, catastrophic disturbances, as the characteristic old-growth forest types of the AFR. One of the most important distinguishing features of the AFR is the high proportion of red spruce (Picea rubens Sarg.), a long-lived, shade-tolerant species adapted to high atmospheric moisture.

A 300- to 400-year history of land clearing for agriculture and timber harvesting has eliminated most older forests (consisting of stands in which the dominant trees have an average age of greater than 150 years) and the virgin (previously unharvested) forest of the AFR (Lynds 1991; Goldsmith 1980), including much of the red spruce component (Mosseler et al. 2000). Remnants of old growth (OG) now occur only in small, isolated stands, often associated with steep gorges that were either inaccessible to harvesting or protected for some other reason.

These older forests have become a focus of conservation concern because of their perceived value as wildlife habitat (Anonymous 2000). Although OG has many values other than those associated with wildlife habitat and biodiversity conservation (e.g., spiritual, emotional, psychological, commercial), we try as much as possible, given the lack of data on Acadian OG, to present a scientific perspective that emphasizes the ecological values associated with biodiversity conservation. We define forest biodiversity simply as the genetic variation within species, species richness, and the variation in forest types at a landscape level (Nilsson et al. 2001). Our objectives are (i) to characterize and describe potential old-growth forest types and their extent in the AFR; (ii) to present some perspectives on potential role of OG in biodiversity conservation; and (iii) to discuss aspects of old-growth forest management, silviculture, and restoration. All forest types can become old in the absence of catastrophic disturbances such as fire and may develop many of the features associated with OG (Davis 1996). However, it is the late-successional, OG forest types that have become particularly rare across the Maritimes and virtually nonexistent on Prince Edward Island (Anderson 1980; Bill Glen, Prince Edward Island Department of Energy and Forestry, personal communication 2001).

The Acadian Forest Region

The defining characteristic of the AFR is the red spruce component, in association with balsam fir (Abies balsamea (L.)), eastern hemlock (Tsuga canadensis (L.) Carr.), eastern white pine (Pinus
 strobus L.), yellow birch (Betula alleghaniensis Britt.) (Fig. 2), sugar maple (Acer saccharum Marsh.), and American beech (Fagus grandifolia Ehrh.), in predominantly late-successional forest types (Loucks 1962; Rowe 1972). In the moist, coastal climates of Nova Scotia and southeastern New Brunswick, red spruce also occurs in early successional species associations, together with black spruce (Picea mariana (Mill.) B.S.P.), red maple (Acer rubrum L.), trembling aspen (Populus tremuloides Michx.), and white birch (Betula papyrifera Marsh.). These Maritime forests, like those found in the adjacent New England states, may once have been dominated by red spruce (Hamburg and Cogbill 1988).

A boreal forest component is found in the northwestern portions of New Brunswick and on the Cape Breton Highlands (Fig. 1; Loucks 1962; Rowe 1972). The northwestern New Brunswick boreal forest is continental in character and contains associations of black spruce, balsam fir, trembling aspen, white birch, white spruce, tamarack (Larix laricina (Du Roi) K. Koch.), white pine, and red pine (Pinus resinosa Ait.). The highlands of Cape Breton Island experience a more maritime climate that results in moist forest types dominated almost exclusively by balsam fir, with black spruce, white birch, and red maple as minor associates. The eastern lowlands of New Brunswick have experienced large-scale fire disturbances during their post-European settlement history. This area is now dominated by early successional forest types with mixtures of black spruce, jack pine (Pinus banksiana Lamb.), red spruce, balsam fir, and tamarack (Larix laricina (Du Roi) K. Koch), although isolated remnants of late-successional forest types can still be found. This area is also the main zone of putative hybridization between red and black spruce (Manley 1972). After several hundred years of human occupation and fire disturbance, much of coastal Nova Scotia is now dominated by early successional forest types. White spruce is a dominant feature of the coastal forests of Nova Scotia, New Brunswick, and much of Prince Edward Island, where it readily establishes itself on abandoned farmland.
Fig. 2. A typical late-successional, old-growth, conifer forest type of the Maritimes at Panuke Lake, Nova Scotia, dominated by red spruce and eastern hemlock, with a minor component of eastern white pine and yellow birch, and abundant balsam fir in the understorey. The structural diversity and habitat value of such stands is evident in the dead and dying trees, and coarse woody debris in varying stages of decay.

The distribution of broad forest cover types depicted in Fig. 1 was based on the latest successional type likely to develop in the absence of edaphic limitations (sensu Nichols 1935) and combines the forest types identified by Loucks (1962). Louck’s classification is important from a forest-management perspective because it was intended to provide a basis for silviculture in the Maritimes. Although Louck’s classification was based largely on existing forest cover, it also described the dominant, late-successional forest types that would be expected to occur across the temperate-zone forests of the AFR in the absence of catastrophic fires and is therefore useful for an understanding of the successional stand development...
that produces self-sustaining, OG forests. The palynological record suggests that such late-successional forest types may have dominated the landscape over the past 5000 years (Mott 1975; Anderson 1980; Anderson et al. 1986; Green 1987; Warner et al. 1991). Temperate-zone Acadian forests are shown in light grey and cover about 85% of a total land base of about 13 326 076 ha. The boreal zone is shown in dark grey and covers about 7% of the land base, and the mid-grey area represents the unique Acadian–boreal coastal zone, covering about 1 070 149 ha or about 8% of the land base. These areas are based on digitized coverages from the map in Fig. 1. In the absence of large-scale disturbances such as fire, up to 85% of the AFR, or about 11 301 199 ha, may have been dominated by long-lived, shade-tolerant, late-successional tree species forming climatic climax forest associations. This estimate of 85% relates primarily to sites without serious limitations (e.g., poor drainage) to the growth of forests and will, therefore, represent an overestimate of the area actually capable of supporting the late-successional, shade-tolerant tree species associations typical of this climatic zone. For instance, the eastern lowlands area of New Brunswick contains large areas of wetlands, where the predominant forest types would likely develop into edaphic climax forest associations more typical of boreal forest environments (Vince Zelazny, New Brunswick Department of Natural Resources, personal communication 2001), dominated by species such as black spruce and tamarack. Nevertheless, pollen analysis from a bog near Point Escuminac, N.B., indicates that typical Acadian forest types containing Tsuga and Fagus may have been well established in this area by about 2900 years ago (Warner et al. 1991). Pollen data from lake sediments in adjacent northern Maine (Baxter State Park) (Anderson et al. 1986), Nova Scotia (Green 1987), southwestern New Brunswick (Mott 1975), and from bogs on Prince Edward Island (Anderson 1980) provide further evidence for the existence of typical Acadian forest tree species mixtures over the past several thousand years across the Canadian Maritimes and adjacent new England.

**Historical characterization of pre-European settlement forests**

Observations on the landscape and vegetation made by several early explorers travelling through the area (e.g., Denys 1908; Holland (cited in Harvey 1935)) suggest a landscape dominated by old forests composed of large trees. During a trip around the entire coast of Nova Scotia during the early to mid-1600s, Nicholas Denys commented on the very fine and good lands covered with big and beautiful trees. Unfortunately, many of these accounts were qualitative and incomplete and provide little quantitative information on the extent of old-growth forest types.

There is no strong empirical evidence to support the notion that northeastern aboriginals intentionally or systematically burned forested areas (Day 1953; Wein and Moore 1979; Cronon 1983; Russell 1983). Deliberate fires were probably confined to areas near villages or encampments. As only certain forest types in the northeast are fire prone (Wein and Moore 1977, 1979) and because many of the aboriginal tribes were fishers, concentrated along coastal and inland waters, there was probably only a slight increase in fire frequency above levels caused by lightning that can be attributed to aboriginal activities.

In addition to historical written accounts, techniques such as tree ring and pollen analysis have been used to reconstruct the composition and spatial pattern of pre-European settlement forests (Mott 1975; Anderson 1980; Anderson et al. 1986; Green 1987; Warner et al. 1991). Ecological studies throughout eastern North America suggest that catastrophic disturbances were infrequent in the pre-settlement forest landscape, resulting in great expanses of late-successional forests. It was only following European settlement that fires played a more important role, as evidenced by the relatively recent inclusion of charcoal fragments in the soils of the eastern lowlands of New Brunswick (Ponomarenko and Ponomarenko 2000a, 2000b).

Timber sales receipts provide another source of quantitative data that indirectly portray the forests at the time of European settlement and the changes that have occurred up to present-day forests. Simard and Bouchard (1996) used wood sales, recorded in notary deeds, to describe how the pre-settlement forests of the upper St. Lawrence River region of Quebec changed during the 19th century, showing how
a succession of economically important climax species were systematically depleted over the century through harvesting, eventually leading to the present forests dominated by early successional trees.

Land grant surveys during the early period of the European settlement of North America provide a source of quantitative data on the composition and distribution of forest types that made up pre-settlement vegetation (Lorimer 1977; Backman 1984; Whitney 1987; Frelich and Lorimer 1991; Keddy 1993; Frelich 1995; Lutz 1996; Abrams and McCay 1996). A summary of these land grant surveys indicates that the percentage of OG forest across the landscape in pre-European settlement forests of northeastern North America ranged from 60 to 85%, compared with recent estimates from Nova Scotia of between 1% of forested area aged greater than 100 years (Lynds and LeDuc 1995) and about 5% of the forested area (Anonymous 2002). These OG forests were dominated by regional climax tree species with less than 5% of forests composed of early successional species.

Ecological succession and disturbance

Given the current level of scientific information and our own observations, we believe that there are repeating and, therefore, somewhat predictable patterns in species composition in the vegetation of the AFR in the absence of major, stand-replacing disturbances. Successional patterns, the dominant, small-scale disturbance regime, and the pollen record (Mott 1975; Anderson 1980; Anderson et al. 1986; Green 1987; Warner et al. 1991) suggest that much of the AFR was dominated by late-successional tree species associations before European settlement (Nichols 1935).

Vegetation succession (the directional change in species composition, stand structure, and functioning of an ecosystem) generally moves from an unstable, constantly changing state composed of less shade-tolerant, shorter-lived species that are unable to perpetuate themselves because of micro-climatic changes to a more steady state or climax condition in which shade-tolerant, longer-lived species continue to occupy a site indefinitely in the absence of catastrophic, stand-replacing events. This “steady state” or climax condition is dynamic in that species composition at a given point on the ground is constantly changing but, at the broader forest level, the climax character is maintained over long periods of time. Two common successional scenarios are (1) early successional (shade-intolerant) species being replaced by late-successional, shade-tolerant species and (2) late-successional species being replaced by the same or different late-successional species. It is important to note that, in certain topographic situations, climax species cannot gain a foothold because of adverse climate and (or) edaphic (soil) factors. In these instances, early successional species may form a sub-climax forest and maintain dominance over the site so long as these adverse conditions remain. Examples of such forests in the Martimes are red maple fens and black spruce/tamarack wetlands.

Old growth is a stage of forest development that evolves in the absence of catastrophic or stand-replacing disturbances. Thus, ecological processes become part of the suite of features that define OG (Appendix A). A natural forest disturbance typically results in a succession of four stages of development (Table 1): stand initiation, stem exclusion, understory initiation, and old growth (Watt 1947; Sprugel 1976, 1984; Lorimer 1977; Bormann and Likens 1979; Reiners and Lang 1979; Oliver 1981). Old growth occurs when overstorey mortality results in recruitment of understorey individuals. Natural disturbance regimes have changed since the arrival of Europeans in North America. For example, Blais (1983) documented trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada and concluded that outbreaks of this insect have occurred more frequently and have covered a greater area in the 20th century than previously. This has been attributed to human activities such as pulpwood harvesting, fire suppression, and the application of pesticides. These management practices may have rendered the forest more prone to spruce budworm attack by increasing balsam fir, the favoured host of this insect.

The AFR has a somewhat modified mix of the classic natural disturbance regimes. The northern tolerant hardwood forests of the region are similar to those of the greater Eastern Deciduous Biome, where small-scale gap replacement is common (Seymour et al. 2002). The climax coniferous forest of
Table 1. Biodiversity potential for natural forest successional (stand development) stages.

<table>
<thead>
<tr>
<th>Stages in stand development</th>
<th>Stand initiation (0–20 years)</th>
<th>Stem exclusion (20–80 years)</th>
<th>Understorey initiation (80–150 years)</th>
<th>Steady state (150+ years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Attributes</td>
<td>Successional phase</td>
<td>Regeneration</td>
<td>Polestand</td>
<td>Mature</td>
</tr>
<tr>
<td>Stand density</td>
<td>Successional phase</td>
<td>Low to high</td>
<td>High</td>
<td>High</td>
</tr>
<tr>
<td>Vegetation height</td>
<td></td>
<td>Low</td>
<td>Medium</td>
<td>High</td>
</tr>
<tr>
<td>Structural diversity</td>
<td></td>
<td>Moderate to high</td>
<td>Low</td>
<td>Low to moderate</td>
</tr>
<tr>
<td>Plant species richness</td>
<td></td>
<td>High (generalists)</td>
<td>Low</td>
<td>Low to moderate</td>
</tr>
<tr>
<td>Animal species richness</td>
<td></td>
<td>High (generalist)</td>
<td>Low</td>
<td>Low to moderate</td>
</tr>
</tbody>
</table>

This region exhibits a variety of natural disturbance patterns, from stand-maintaining surface fires in pine-oak forests, to small-scale, individual tree or stand replacement via windthrow or insect infestations. The size and spatial patterns of forest vary widely across the landscape of Nova Scotia because of its highly variable mesotopography, the abundance of water bodies, and its maritime-modified continental climate. Catastrophic disturbances such as hurricane-force winds are rare events. Small, gap-creating disturbances (generally covering less than 1% of a given area annually) are the dominant form of disturbance affecting forest composition and spatial arrangement. However, major windfall events also occur sporadically in areas of high topographic relief and exposure.

The mixed coniferous and deciduous climax forest types of eastern and central North America are either not on major hurricane tracks or occur near the tail end of such tracks (Perry 1994). Major catastrophic windstorms that do occur along the eastern seaboard usually dissipate by the time they reach the Maritimes and generally do not cause frequent or major natural disturbances. Some notable exceptions were the Saxby Gale of 1869 and the Christmas Mountains Blowdown of 1994. Also, many of the climax forest types are relatively windfirm and not particularly prone to fire. Based on fire control records, Wein and Moore (1977, 1979) have estimated fire rotations of at least several hundred years for some of the more fire-resistant forest types found in New Brunswick and Nova Scotia during the 20th century. A significant finding from these studies was that only about 1% of fires were caused by lightning strikes, with the remainder attributed to human causes. Furthermore, the lack of evidence that Native Americans deliberately set fires in the AFR suggests that fire was not a major influence on this forest landscape before European settlement (Day 1953; Wein and Moore 1979). For the pre-European settlement landscape, fire rotations of 800–1000 years seem reasonable estimates for northeastern Maine (Lorimer 1977) and New Brunswick (Wein and Moore 1977). Such fire-cycle intervals suggest that there was enough time between disturbances to develop and maintain a substantial portion of late-successional OG forest across the AFR (Bormann and Likens 1979).

Natural fire as a result of lightning strikes is governed by factors affecting the ignitability of the biomass (e.g., dryness and amount of fuel). An important consideration in differentiating between the pre-European settlement fire regime and the present one is the actual compositional and physical structure of the forest. The pre-settlement forests of northeastern North America probably consisted of forest types that were much less prone to fire (Mott 1975; Anderson 1980; Anderson et al. 1986; Green 1987; Warner et al. 1991). Fires in these types of forests were probably restricted largely to surface fires, causing much less canopy mortality. For instance, the shade-tolerant hardwood forests characteristic of much of the Maritimes are not prone to crown fire disturbance. The present forest with its high percentage of a single conifer species is far more prone to destructive crown fires.
The huge fires that have swept across the Eastern Lowlands of New Brunswick (NB) over the past several hundred years may have had a major impact on succession to boreal species in what might otherwise be an area largely dominated by late-successional tree species associations, including the shade-tolerant hardwoods, red spruce, and eastern hemlock. The great Miramichi Fire of 1825 (the largest fire on record in North American history) burned across 1 214 000 ha of land and was then followed by a succession of other large fires during the 1800s and early 1900s (Ganong 1906). Nevertheless, the soil profile shows little evidence of a significant fire history over the several thousand years before European settlement (Ponomarenko and Ponomarenko 2000a, 2000b). Remnant populations of late-successional species associations, such as red spruce and the shade-tolerant hardwoods, are present throughout this area, and with appropriate management, these forest types could be restored in many areas of the Eastern Lowlands. Before European settlement, the vegetation changed very slowly over timespans of several centuries to millennia, subjected primarily to natural physical forces and biotic processes and not influenced to any great degree by humans. With the arrival of European settlers over the past four centuries, human activity has replaced natural disturbance regimes as the major force shaping landscapes.

The degree to which a steady-state, climax forest dominated the pre-European settlement forest of the Maritimes and the role of large-scale or catastrophic disturbances in interrupting the development of such OG forests will continue to be a matter of controversy and debate. Nevertheless, it is evident that the forest-disturbance interrelationships we see today are probably the result of the transformation of long-lived, disease-resistant, windfirm, less fire-prone pre-European settlement climax forests to shorter-lived, disease-, wind-, and fire-prone early successional forests (Frelish 1995). If we accept that natural disturbance cycles for large-scale or stand-replacement types of disturbance for much of the AFR averaged about 800 years, before European settlement, and that it may take 300–400 years to develop the old trees and structural complexities associated with OG forests in the Maritimes, then it may be reasonable to assume that 40–50% (e.g., (800–400)/800) \times 0.85 (proportion of temperate zone forest type; Fig. 1)) of the pre-European settlement forest was occupied by late-successional OG forest types, with the remainder in earlier stages of development.

Attributes of old growth

Broad definitions of OG have been recommended (Spies and Franklin 1996b), but more restrictive definitions related to specific regions or forest types may be more useful in guiding forest management and restoration activities. Rigorous scientific definitions of OG can be problematic from an ecological perspective. However, within reasonable limits, we can develop a definition of OG for the AFR that is both scientifically meaningful and relevant to policy development and forest management. Useful definitions must also account for public demand regarding OG. For instance, public perceptions of OG are dominated by forests that contain large, old trees. This simple definition also meets many of the important wildlife habitat requirements associated with OG forests of the AFR (Anonymous 2001) and all of their associated structural attributes (e.g., dead and dying trees, fallen stems in varying stages of decay).

We consider OG forests in the AFR to be forests in the ultimate or final stages of stand development, distinguished by old trees, and free of much evidence of human activity. The typical temperate-zone OG forest of the AFR has a multi-aged structure (or at least several recognizable age cohorts) and is composed of long-lived, shade-tolerant, late-successional trees. Natural regeneration of the dominant species occurs within canopy gaps resulting from small-scale stand disturbances (White et al. 1985; Seymour et al. 2002), such as older, windthrown trees rather than the large-scale or stand-replacing disturbances associated with the large fires typical of boreal forests. These stands can approach a steady-state condition in which species composition and diameter distribution remain reasonably constant (Leak 1987; Runkle 2000). Even though all forests not subject to catastrophic disturbance can become old and take on many of the structural features of OG, in the AFR, tree species composition — and
Table 2. Size and age for old-growth stands dominated by red spruce and eastern hemlock in Nova Scotia and New Brunswick.

<table>
<thead>
<tr>
<th>Location of population</th>
<th>Number of trees sampled</th>
<th>Height (m)</th>
<th>Diameter (cm)</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rossignol Lake, N.S.</td>
<td>15</td>
<td>26 (23–29)</td>
<td>46 (31–66)</td>
<td>136 (100–245)</td>
</tr>
<tr>
<td>Panuke Lake, N.S.</td>
<td>9</td>
<td>34 (32–37)</td>
<td>53 (37–79)</td>
<td>n.a (200–460)</td>
</tr>
<tr>
<td>Abraham Lake, N.S.</td>
<td>15</td>
<td>24 (20–29)</td>
<td>46 (35–79)</td>
<td>210 (70–296)</td>
</tr>
<tr>
<td>Quiddy River, N.B.</td>
<td>15</td>
<td>21 (19–23)</td>
<td>46 (37–67)</td>
<td>140 (70–177)</td>
</tr>
<tr>
<td>Hurlett Road, N.B.</td>
<td>20</td>
<td>18 (12–22)</td>
<td>36 (19–49)</td>
<td>133 (93–182)</td>
</tr>
<tr>
<td>Average</td>
<td>24</td>
<td>44</td>
<td></td>
<td>146</td>
</tr>
</tbody>
</table>

the ecophysiological attributes of those trees — is important in defining those forests that are largely self-sustaining in the absence of large-scale disturbances.

Davis (1996) defined OG in the northeast as forests that contain very little evidence of human interference, that have not experienced catastrophic natural disturbances that would reshape successional trajectories, and that possess characteristics associated with a “virgin” condition. There are few, if any, such forests left in the AFR. Most of our older forests may contain some, but not all, of the characteristics that we normally associate with OG. Most often, we find many gradations along a spectrum of the attributes outlined in Appendix A. For forest-management purposes, it may be best to define OG in terms of these gradations with a view to restoration activities. Thus, many of the OG characteristics listed in Appendix A could be used to develop simple indices of “old growthness” to characterize the degree or level of the OG features attained by a forest stand.

It may also be more helpful to emphasize the concept of “emergent” or immature OG (e.g., younger forest stands composed of shade-tolerant, late-successional species that may eventually develop some or all of the desired structural and compositional features of OG if left to evolve naturally or through directed silvicultural intervention). In defining or characterizing OG from the perspective of its role in biodiversity conservation, it may also be helpful to focus on the structural components that define its habitat value rather than the degree or type of past human intervention. Ultimately, there is no substitute for actual measures of biodiversity such as species richness. For instance, there are OG forests in New Brunswick in areas affected by atmospheric pollution that contain abundant structural diversity but lack important components of biodiversity (e.g., the lichens associated with OG forests; see Selva (2003)).

Age is one of the simplest and easiest criteria to measure when defining OG forests. Cogbill (1996) suggests that stands with average ages of about half that of the maximum longevity of the dominant tree species, and with some trees at or near that maximum age, have often attained OG status in the northeast. The average longevity of most native shade-tolerant trees in the AFR ranges between 300 and 400 years, and although eastern hemlock can grow much older, these age criteria are still appropriate for hemlock, red spruce, white pine, and the shade-tolerant hardwoods. When this age criterion was applied to some of the most representative older red spruce stands being studied (Mosseler et al. 2000), it appeared that the stands that met this age criterion were also those that best fit our definition of true OG based on all of the other criteria that we ascribe to OG (Appendix A). For instance, the average age of the dominant trees sampled by Mosseler et al. (2000) is shown in Table 2. The few remaining older stands located in Nova Scotia are probably among the last remaining remnants of true OG in the AFR and also tend to meet the age criterion outlined by Cogbill (1996).

Old-growth forests can perhaps be best defined by their structure and composition. A multi-aged or multi-cohort age structure and multi-storeyed canopy structure, old trees, a relatively undisturbed forest canopy where regeneration follows gap or small-scale, patch-like disturbances, some dead or dying trees in varying stages of decay, and coarse woody debris, including some larger, rotting logs, would all
form part of the structural components of OG (Tyrrell and Crow 1994). As these OG forests age, they are increasingly characterized by a relatively steady-state condition of ecosystem stability, in which stand composition and structure (endogenous rather than exogenous) change little over time (Lynds 1992). In terms of species composition, such forests are typified by long-lived, shade-tolerant, late-successional species such as sugar maple, yellow birch, American beech, red spruce, eastern hemlock, and eastern white pine. The oldest hemlock cored at Panuke Lake, N.S., was 460 years old. The oldest red spruce trees in these stands are approaching the maximum recorded ages for this species, and the average age of these stands is about half the maximum longevity. The use of tree ages is also in keeping with the simple, universal definition of OG used by the USDA Forest Service: “old-growth forests are ecosystems distinguished by old trees and related structural attributes” (Robertson 1989). These are also the criteria most easily understood by the public.

**Potential old-growth forest types**

The typical stages of succession to OG forests in the AFR follow a common pattern (Spies and Franklin 1996a). For instance, the establishment phase would typically follow a catastrophic disturbance, such as fire or windstorm (hurricane), albeit at very long time intervals. Upon canopy closure, the stand would enter a self-thinning phase in which most of the shade-intolerant species (e.g., aspens, birches, red maple), if present initially, would gradually be eliminated. Additional recruitment would be rare until increased light levels were able to penetrate to the forest floor through canopy gaps. These gaps would increasingly be created by loss of some of the dominant trees as they approached their maximum longevity. For instance, the long-lived eastern white pine, which might have become established at the time of the initial disturbance, would be in decline because it does not compete well with the much more shade-tolerant red spruce and eastern hemlock, except in larger canopy openings (Nichols 1935). Such decadence of eastern white pine is evident in the few remaining OG stands in Nova Scotia. The dominant shade-tolerant species, such as red spruce and eastern hemlock, are able to regenerate naturally within small, canopy gaps, creating the multi-aged or layered canopy structure typical of advanced OG in the AFR. At this point, canopy gap dynamics tend toward establishment of a relatively stable, steady-state condition in which the dominant, shade-tolerant species continue to regenerate naturally following small-scale disturbances that create canopy gaps, until such time as a stand-replacing disturbance occurs.

As a foundation for determining the proportion of remaining OG forest, we have classified the AFR into three primary landscape forest types in relation to their potential to develop late-successional or climax forests (Fig. 1). Climax vegetation reflects the forest environment as an integration of climate, topography, soil, and an array of species adaptations and biotic competitive equilibria (Pfister and Arno 1980). Climax vegetation thus reflects a level of relatively undisturbed ecological integration. Such a classification system allows us to (i) estimate the land available for the development of certain OG forest types, (ii) estimate the proportion of remaining OG according to forest type, (iii) predict general trends of forest succession in response to management interventions, and (iv) provide an ecologically based system of land classification useful for operational management of different forest types. Although more detailed descriptions of Maritime forest communities are underway (e.g., Fenton 2002), the following subsections describe the most common tree species associations that have the potential to develop into OG forest in the Maritimes, identifying the Maritime landscapes on which they are most likely to develop (Fig. 1; Table 4).

**Climatic climax species associations**

Recognition of the climatic climax forest community is essential to an ecological understanding of regional vegetation (Nichols 1935), forest biodiversity conservation, ecologically sustainable forest management, and the developmental trajectories of OG forest. The natural predominance of a small-scale disturbance regime indicates that the climatic climax tree species associations typical of the northeast (Nichols 1935) are among those most likely to develop into the self-sustaining OG forest
Table 3. Remaining old-growth conifer forest in the Acadian Forest Region.

<table>
<thead>
<tr>
<th>Province/Period</th>
<th>Total land&lt;sup&gt;a,b&lt;/sup&gt; (ha)</th>
<th>Total forest land&lt;sup&gt;c&lt;/sup&gt; (ha)</th>
<th>Estimated area of old-growth forest&lt;sup&gt;d&lt;/sup&gt; (ha)</th>
<th>Percentage of total forest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prince Edward Island</td>
<td>566</td>
<td>294</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Nova Scotia</td>
<td>5 284</td>
<td>3923</td>
<td>300</td>
<td>0.0008</td>
</tr>
<tr>
<td>New Brunswick</td>
<td>7 209</td>
<td>4904</td>
<td>n.a</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>13 059</td>
<td>9121</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup>From *Compendium of Canadian Forest Statistics*, Table 1.1 (Canadian Council of Forest Ministers 1998).

<sup>b</sup>Loucks (1962) maintains that 90% of the Maritime land base is either forested or is potential forest land (p. 94).

<sup>c</sup>From *Compendium of Canadian Forest Statistics*, Table 1.9 (Canadian Council of Forest Ministers 1998).

<sup>d</sup>Based on ground surveys of areas identified by the forest resource inventory database on forest land (e.g., area shown in second column).

Table 4. Harvesting methods used in the Maritime provinces from the *Compendium of Canadian Forest Statistics*, Tables 6.1 and 6.2 (Canadian Council of Forest Ministers 1998).

<table>
<thead>
<tr>
<th>Year</th>
<th>Harvest type</th>
<th>Prince Edward Island (&lt;i&gt;×&lt;/i&gt;10&lt;sup&gt;3&lt;/sup&gt;) (ha)</th>
<th>Nova Scotia (&lt;i&gt;×&lt;/i&gt;10&lt;sup&gt;3&lt;/sup&gt;) (ha)</th>
<th>New Brunswick (&lt;i&gt;×&lt;/i&gt;10&lt;sup&gt;3&lt;/sup&gt;) (ha)</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>1977</td>
<td>Total area harvested</td>
<td>16 000&lt;sup&gt;a&lt;/sup&gt;</td>
<td>28 335</td>
<td>86 500&lt;sup&gt;a&lt;/sup&gt;</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>Clearcut</td>
<td>16 000&lt;sup&gt;a&lt;/sup&gt;</td>
<td>28 335</td>
<td>86 500&lt;sup&gt;a&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>1987</td>
<td>Total area harvested</td>
<td>2 725</td>
<td>42 226</td>
<td>88 976</td>
<td>99.1</td>
</tr>
<tr>
<td></td>
<td>Clearcut</td>
<td>—</td>
<td>41 050</td>
<td>88 976</td>
<td></td>
</tr>
<tr>
<td>1997</td>
<td>Total area harvested</td>
<td>—</td>
<td>69 481</td>
<td>112 436&lt;sup&gt;a&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Clearcut</td>
<td>—</td>
<td>68 718</td>
<td>84 115&lt;sup&gt;a&lt;/sup&gt;</td>
<td>74.8</td>
</tr>
<tr>
<td></td>
<td>Selection harvested</td>
<td>—</td>
<td>—</td>
<td>25 639&lt;sup&gt;a&lt;/sup&gt;</td>
<td>22.8</td>
</tr>
</tbody>
</table>

<sup>a</sup>Estimates.

types of the AFR. The summary data presented in Appendix A describe stand characteristics in some of these forest types and come from a variety of sources and methodology. For example, during the early 1990s, in response to the World Wildlife Fund’s Endangered Spaces campaign, Nova Scotia undertook a province-wide search for potential natural areas to be considered for legislative protection. One of the criteria used in rating potential areas was the presence of older forests. Although not comprehensive, the exercise did locate several significantly older stands, i.e., older than those found in the more typical intensively worked landscape (Nova Scotia Department of Environment and Labour, Protected Areas Division 2000, unpublished data). However, as the fieldwork was in the nature of a reconnaissance, the type of information gathered in these forests was not complete in terms of some of the more generally accepted attributes of OG forests. For example, information collected on coarse woody debris was qualitative rather than quantitative.

Shade-tolerant coniferous complex

The red spruce – eastern hemlock – white pine complex of the AFR comprises associations and consociations (relatively pure stands of a single species) of these three major long-lived native species of eastern and central North America and is considered the coniferous climatic climax of xeric to mesic lowland and, to a lesser extent, upland areas of Nova Scotia and New Brunswick. This forest complex is described by Eyre (1980) as being a variant of the white pine – hemlock forest cover type, the local variant containing significant amounts of red spruce. This forest complex occurs on coarse- to medium-textured, dry to imperfectly drained soils of glacial origins. On drier sites, white pine tends to dominate. Red spruce may dominate on moister sites.

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Red spruce consociation

Most of the relatively pure red spruce forests of Nova Scotia are in the mature or immature OG stage of forest development (Lynds 1992). This includes the most significant red spruce site in the province, located at Abrahams Lake, Halifax County, which has tentatively been classified as immature old growth. The Abraham Lake site contains various stands ranging from 100 to 175 years of age, with some trees over 300 years old (Mosseler et al. 2000). Many of these stands contain appreciable amounts of coarse woody debris, albeit mostly in the early stages of decay. Tree diameters (dbh) of 50 cm and greater are common, the largest dbh being 93.2 cm. Tree heights of over 30 m are common.

Eastern hemlock consociation

Eastern hemlock is an important species of the hemlock – eastern white pine – northern hardwoods regional forest of northeastern and northcentral North America and the longest-lived tree species in the region. Eastern hemlock is best suited to a cool, humid climate with adequate moisture year round; it can be found on several topographic sites. In Nova Scotia, it prefers well-drained, gently sloping uplands in proximity to major water bodies and rapidly drained, steep-sided ravines (Keddy 1978). Both site types tend to exhibit coarse-textured surficial materials. Early surveys indicate that eastern hemlock was much more abundant throughout its natural range before European settlement (Lutz 1930; Bromley 1935; Braun 1950; Elliot 1953; McIntosh 1972). Based on pollen analysis, eastern hemlock was experiencing a natural decline before European settlement (Russell et al. 1993). Since European settlement, several factors have contributed to its further decline, including the use of its bark as an important component in the tanning process during the 1800s and its apparent susceptibility to fire (Fowells 1965). Repeated and widespread fires, many set intentionally by the early settlers, are thought to have played an important role in decreasing its abundance during earlier stages of European settlement. However, many of the even-aged hemlock stands in southwestern Nova Scotia may be of fire origin (Miles and Smith 1960). This seems to be contradictory in light of the apparent susceptibility of hemlock to fire damage. It seems that, in some instances, fire may destroy hemlock stands, while in other situations, allow for their increase (Brown 1960).

At present, intense deer browsing is probably the most important factor limiting natural hemlock regeneration throughout its range (Anderson and Loucks 1979; Frellich and Lorimer 1985; Lynds 1989, 1991). Historically, eastern hemlock has had few insect or disease problems that cause significant mortality (Nichols 1918). However, in recent decades, adelgids have caused widespread damage in the southern part of its range. According to its known longevity, it is possible that the existing eastern hemlock OG consociation has yet to reach its full development in the Maritimes. Most of the oldest stands of pure eastern hemlock in Nova Scotia are between 200 and 300 years of age and, in most cases, do not yet support a coarse woody debris component.

Eastern white pine consociation

To our knowledge, there has been no documentation of pure eastern white pine forests older than 100 years of age in the Maritimes, but pure stands of eastern white pine have been reported as a common feature of the forests of northeastern North America in the past (Nichols 1935). However, the ecological position of eastern white pine within the climatic climax forests of the northeast remains complex and varied (Nichols 1935). For instance, eastern white pine can be found in relatively pure stands elsewhere in the northeast but is most often observed merely as a component of late-successional, climax forest types; whether this comes as a result of natural regeneration following small-scale disturbances or merely as a relic from earlier successional stages is often unclear.

Shade-tolerant deciduous complex

Sugar maple and American beech are the most shade-tolerant, long-lived hardwoods of the Acadian forest. In the absence of catastrophic disturbances or logging, natural regeneration of this climax forest
association would perpetuate these species. Yellow birch, being somewhat less shade tolerant, would be expected to gradually decline in an essentially undisturbed forest of these three species (Leak 1975). Small-scale, patch-like disturbances such as the death of large single trees or small groups of trees might favour the maintenance of less shade-tolerant trees such as yellow birch and red maple. Increased gap size beyond that associated with small patches tends to increase woody species diversity (Runkle 1982). Further increases in gap size may compromise the climax equilibrium by enabling shade-intolerant trees and weedy ground plants to enter the forest.

**Mixed tolerant deciduous association**

The tolerant hardwood forest types of the AFR contain sugar maple, yellow birch, and American beech with several minor (<20% abundance) deciduous and coniferous associates. This is the climatic climax forest for much of the well-drained upland and rolling terrain of the Maritimes. Nichols (1918) and Clattenburg (1962) give us a glimpse into the composition and structure of the primary deciduous forests of northern Cape Breton Island, one of the last areas of more extensive OG forest in Nova Scotia and possibly in northeastern North America. This region was not settled until the early part of the 1800s, and because of its rugged landscapes it still contains many examples of virgin OG and also virgin ecosystems within relatively inaccessible tolerant-hardwood river canyons. Nichols (1918), in his monumental study of the forested and nonforested vegetation of northern Cape Breton Island, viewed much of this area as virgin forest land composed predominantly of climax, shade-tolerant hardwoods such as American beech, sugar maple, and yellow birch. Beech was the dominant deciduous species, constituting 65% of the mature trees in many of these stands. The Holocene pollen record for Prince Edward Island also suggests that beech was a dominant species in the recent past (Anderson 1980).

Both sugar maple and yellow birch were always present but in significantly lesser amounts. Red maple, often thought of as an early to mid-successional species, was consistently present and, in some stands, fairly abundant. This is also the case for the forests of much of the southern and western uplands of New Brunswick. Nichols indicated that northern red oak (*Quercus rubra* L.), white ash (*Fraxinus americana* L.), balsam poplar (*Populus balsamifera* L.), balsam fir, eastern hemlock, eastern white pine, white spruce, and black spruce (Nichols viewed red spruce as a variety of black spruce but noted it was present), although widely distributed, were minor species within this regional climax forest. In this primeval forest, Nichols found an abundance of climax tree species regenerating, but very few early successional species such as white spruce, white birch, or poplars. Young balsam fir was also abundant but rarely grew to become a sub-canopy or canopy because of its short lifespan and its susceptibility to fungal and insect pests. Unfortunately, Nichols gave no data on tree age, size, or amounts of coarse woody debris for this forest.

Clattenburg (1962) provided a detailed quantitative and qualitative description of 12 of the better-developed primary deciduous forests of Cape Breton Island. Most stands were a mix of the climax hardwoods, sugar maple and yellow birch, with some stands having beech as a co-dominant species. All other tree species were of minor importance in the structuring of the upper canopy. Although balsam fir was again common in the lower layers of the canopy, it did not reach the main canopy. He suggested that the deciduous forests of Cape Breton Island were similar to those on mainland Nova Scotia, differing only in the relative abundance of the dominant species present and in the scattered distribution of spruce, hemlock, eastern white pine, and red oak.

**Sugar maple consociation**

Pure sugar maple stands are the dominant tolerant hardwood forest type in Nova Scotia. Historically, American beech may have been the dominant hardwood in this association, but this changed with the introduction of beech bark disease in the 1890s (Knight and Heikkenen 1980; Boyce 1961). With the devastation of beech, sugar maple gained dominance in these hardwood stands. Today, the typical shade-tolerant hardwood forest is characterized by 100- to 125-year-old sugar maple, hummocky micro-
topography, and virtually no large recent coarse woody debris. Old-growth shade-tolerant hardwood stands are confined to the remote canyons of northern Cape Breton Island in a region where European settlement did not have a significant impact on the landscape until the early 1800s.

**American beech consociation**

The American beech consociation is a relatively rare forest type in Nova Scotia, associated primarily with burned and/or rocky sites. All known sites are rather young because of the effects of beech bark canker disease (*Nectria coccinea* var. *faginata*). One of the outstanding features of the pre-settlement forests mentioned in survey records was the former predominance of beech forests across many parts of the northeast (Nichols 1918; Siccama 1971; Anderson 1980).

**Yellow birch consociation**

If this consociation exists today, or existed at all in pre-European settlement forests, then it must have been extremely rare. Yellow birch is a widespread, yet minor component in terms of abundance but quite often significant in terms of basal area or biomass in the upper canopy of several climax forest communities (Nichols 1918; MacDonald 1958).

**Shade-tolerant mixedwood**

Cogbill (1996) described the OG red spruce and tolerant-hardwood mixed forests of the New England States as the archetype of OG forest in the northeastern U.S.A. Some attempts have been made to characterize some of the features of such OG stands in terms of basal area, stem diameter distributions, and tree sizes (Leak 1987). The shade-tolerant, late-successional, mixedwood forests of Maine described by Seymour (1992) are similar to the characteristic OG of the AFR. The presence of conifers such as red spruce and eastern hemlock within predominantly shade-tolerant hardwood forests results in a shade-tolerant mixedwood association. Because these conifers respond well to increased light, their regeneration would likely also be favoured, along with yellow birch, by relatively mild disturbances that removed small groups of trees. Typically, OG forest types of the northern temperate zone (including the shade-tolerant hardwood, mixedwood, and coniferous forest types of the AFR) are characterized by small-scale disturbances, rather than catastrophic ones (Dunn et al. 1983; Canham and Loucks 1984; Frelich and Lorimer 1991; Seymour 1992; Tyrrell and Crow 1994). However, even the larger-scale disturbances associated with severe windstorms tend to occur at intervals much longer than the lifespans of major tree species associated with OG forests (Canham and Loucks 1984; Lorimer 1977).

**Boreal and boreal plateau**

The boreal forests of the Cape Breton Highlands, the Mount Carleton Highlands, and the northwestern corner of New Brunswick (Fig. 1) are described by Rowe (1972). The northern New Brunswick highlands region consists of dry coniferous forests resulting from repeated fires, logging, and insect attacks. These forests are dominated by balsam fir, white birch, aspen, and white and black spruce, with minor components of red and sugar maple, yellow birch, red spruce, and eastern white pine. They are generally short-lived and unstable, susceptible to fire, windthrow, and insect infestation. Surrounded on three sides by ocean, the Cape Breton Highlands has a maritime climate and is composed of a natural forest dominated by balsam fir that is not susceptible to fire but rather to 60- to 80-year cycles of spruce budworm infestations and windthrow. Minor associates of this forest are white birch, American mountain-ash (*Sorbus americana* Marsh.), red maple, white spruce, and black spruce. Old growth in this forest consists of stand-initiating, 80-year cycles of balsam fir with 200-year-old white spruce remaining scattered throughout the forest, and a black spruce component in wet areas.
Boreal coastal

Much of the Atlantic coast of Nova Scotia is characterized by a windswept, poor quality landscape for forest development. This exposed, rugged, moist zone supports a stunted dense forest, primarily of white and black spruce and balsam fir, with minor associates of red maple and white birch. The region has been heavily affected by human activity and OG forest in this zone may be rare or nonexistent. This forest has been included with the Acadian – boreal forest type outlined in Fig. 1.

Acadian – boreal coastal

The Acadian – boreal forest type (Fig. 1) describes a completely mixedwood forest found in protected coves along the Atlantic coast of Nova Scotia, along the entire coastline of the Bay of Fundy and the Northumberland Strait, as well as a unique balsam fir – yellow birch transition forest surrounding the highlands of northern Cape Breton Island. Many ravines in the Fundy plateau and along the Bay of Fundy provide examples of this type of forest.

The development of the coastal spruce–fir forests of Maine described by Davis (1966) is reasonably similar to that of much of coastal Nova Scotia, where either white spruce or red spruce can predominate following stand clearing, depending on the proximity of seed sources or the characteristics of advanced growth in stands as they were harvested. White spruce tends to dominate after it invades abandoned farmland, whereas red spruce may dominate in stands harvested for timber that contained advanced growth of red spruce. Stands dominated by shade-intolerant hardwoods such as white birch and trembling aspen are normally taken over by these spruces and balsam fir through natural succession. If left relatively undisturbed, stands dominated by red spruce, often with a minor component of yellow birch, could be expected to develop into self-perpetuating OG forests dominated by red spruce.

In several sheltered areas along the Atlantic coast of Nova Scotia, there are zones of climax, shade-tolerant hardwood, or shade-tolerant mixedwood forest. The OG forest in these areas is similar to those found further inland.

The balsam fir – yellow birch Acadian – boreal transition forest surrounding the highlands of northern Cape Breton Island produces a distinct OG forest in which long-lived yellow birch occupies the upper canopy with an understory dominated by shade-tolerant but short-lived balsam fir. Greenidge (1987) has also described undisturbed, OG deciduous forests in this area composed of mixtures of southern elements such as American beech, northern red oak, white elm (Ulmus americana L.), and white ash.

Stable “subclimax” forests

Stable floodplain forests on seasonally flooded river fens appear to be able to maintain themselves over long periods and exemplify the stable forests often associated with riparian zones. Almost pure forests of red maple, silver maple (Acer saccharinum L.), and Fraxinus species maintain themselves in perpetuity along the lower St. John River Valley in New Brunswick. Other examples of such stable, nonclimax forests are listed by Lynds (1991; Table 4). Long-lived, early successional, fire-adapted trees such as red pine are also capable of producing self-sustaining, OG forests on dry, infertile sites. For instance, multi-cohort stands of red pine up to 400 years of age occur on dry, infertile sites in eastern North America. These stands contain many of the structural features associated with OG (e.g., multi-aged canopy, cavity trees, coarse woody debris).

Role in biodiversity conservation

Biodiversity conservation must be considered at different scales, from genes within a particular population to the interactions among populations across landscapes. For instance, conservation of genetic resources must consider molecular variation within individuals to gene flow among subpopulations of a larger metapopulation (Hanski and Gilpin 1991) across a landscape. Dispersal and gene flow are important components of population viability. At larger scales of biodiversity, we may be concerned with

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particular species as components of communities, with the variety of communities within a landscape, or with the diversity of landscapes within larger geographic areas. Although all of this variation is ultimately genetic in origin, its conservation is generally best addressed at the community and landscape levels.

Old-growth conservation relates most directly to conservation at the ecosystem or community level of biodiversity but addresses diversity at most levels and aspects of the biodiversity hierarchy. By focusing on OG forest, we also accept the larger ecosystem or forest stand as the foundation for activities aimed at biodiversity conservation. It is the OG stage of stand development that is most in decline and most at risk from harvesting activity. In many forest types not dominated by catastrophic natural disturbance regimes, the proportion of OG forest could become an important core indicator for biodiversity conservation and sustainable forest management. Such an OG indicator could also serve as a measurable, scientifically meaningful, yet management-relevant national indicator in connection with Canada’s obligations under international conventions, such as the Convention on Biological Diversity.

**Genetic diversity**

For demographic reasons, habitat destruction and alteration are usually considered the most immediate threat to species survival. However, the loss of genetic diversity can play a decisive role in species persistence over the longer term because genetic diversity allows species to adapt and persist in changing environments (Lande 1996). Fisher’s (1930) Fundamental Theorem of Natural Selection states that the potential rate of increase in fitness of any organism at any time is equal to its genetic variation. Thus, the conservation and maintenance of genetic diversity in natural populations is critical to their longer-term survival. Ecosystem sustainability and resilience to natural or human disturbances depends on maintaining genetic diversity (Kaufmann et al. 1994; DeWald and Mahalovich 1997).

Natural populations, and in particular older forests, may have an important evolutionary role in ensuring that tree populations maintain the genetic diversity required for adaptation to rapid changes in climate and landscape patterns and following the introduction of diseases and pests. Recent results on the reproductive and genetic status of red spruce have shown significant positive relationships between average stand age and genetic superiority in fitness traits related to height growth and reproductive success (Mosseler et al. 2000, 2003; Rajora et al. 2000). Older red spruce produced not only better quality seed in terms of growth performance but also fewer empty seeds. Therefore, a direct relationship may exist between age of the parent tree and reproductive, as well as genetic, fitness. In pitch pine (*Pinus rigida* Mill.), stem-diameter growth rate and heterozygosity increased with stand age (Ledig et al. 1983). These relationships are important because reproductive success and growth performance are the main components of fitness driving species survival and evolution. It has long been argued that diameter-limit harvesting (e.g., harvesting trees once they have attained a certain stem diameter) represents a dysgenic form of harvesting that may, over time, promote poorer-quality, slower-growing trees and eliminate the better-adapted, faster-growing genotypes (Zobel and Talbert 1984). Evidence provided by Mosseler et al. (2003) supports this argument.

Relationships between age and both the quality and quantity of progeny may be understood in terms of evolutionary theory. Increased genetic diversity (individual heterozygosity) may confer some inherent superiority in individual fitness and the capacity to buffer against environmental changes (Lerner 1954; Mitton and Grant 1984; Allendorf and Leary 1986). Also, the higher levels of inbreeding depression associated with younger stages of population development may have an adverse affect on the average fitness of natural populations. For instance, the mating and breeding system of trees (Sorensen 1982), and the close family structure observed in natural populations, fosters increased levels of self-fertilization and consanguineous mating (Rajora et al. 2000). Over time, many of these inbred individuals are eliminated as a result of the deleterious effects of inbreeding depression on fitness traits. Inbreeding affects all traits by increasing homozygosity within individuals. Genetic and reproductive relationships with tree age and stand age suggest that older forests may function as important reservoirs of genetic quality and diversity.
The strategy for survival in large, natural forest tree populations appears to be aimed at maintaining genetic diversity and quality to allow for natural selection for fitness. These genetic relationships provide some of the strongest scientific arguments in support of OG conservation. The role of OG forests in conserving genetic diversity may be particularly important from a climate change perspective. The high levels of genetic diversity maintained in forest trees compared with other plants (Hamrick and Godt 1990) have probably been important in maintaining their ability to adapt to environmental (e.g., climatic) changes over geological time scales. If OG populations constitute a reservoir of high levels of genetic diversity, then they may be especially important for the survival of the late-successional species and forest types that are currently in decline across the AFR (Mosseler et al. 2003). If, as expected, maintaining forest diversity becomes an important forest management objective, then attempts to restore certain OG forest types need to begin now.

Species at risk associated with old growth

Old growth is a stage of forest development that represents a unique physical environment in terms of light, moisture, nutrients, organic matter, and the temporal stability of biomass structures to which some species (e.g., lichens) have become adapted (Lesica et al. 1991; Selva 1994). Relatively few animal species are known to be absolutely dependent on, or restricted to, the relatively undisturbed OG forests of eastern North America. However, several native vertebrates prefer such an environment, or at least certain components of it, to facilitate particular aspects of their life history. Cavity-nesters, such as owls, bats, and woodpeckers, require larger, partially decayed, older trees as nesting sites (Erskine 1992). Some birds forage under the deeply furrowed or plated bark of old spruce and hemlock trees (e.g., brown creepers, *Certhia* spp.) or prefer older, closed forest cover (e.g., Swainson’s thrush, *Catharus ustulatus*). Other mammals, reptiles, and amphibians in the forests of the Northeast (Cogbill 1996; Meier et al. 1996) require fallen coarse woody debris to avoid predation. Certain species of lichens require the long temporal stability of older trees to establish themselves on bark and branches (Selva 1994). There are also herbaceous species (Whitney and Foster 1988; Meier et al. 1996) and arthropods (Chandler 1987; Chandler and Peck 1992) adapted to relatively undisturbed, older forests. In the Pacific Northwest, bats (*Myotis* spp.) and cavity-nesting birds were the vertebrate species most likely to be either closely associated with, or dependent on, OG forests (Carey 1989), but it was the canopy structures, snag densities, and levels of fallen trees, more than stand age per se, that determined habitat suitability for most species of forest-dependent plants and animals (Hansen et al. 1991).

Vertebrate species associated with certain structural features of older forests have been identified for the various forest cover types of New Brunswick (Anonymous 2001). They include such species as downy woodpecker (*Picoides pubescens*), pileated woodpecker (*Dryocopus pileatus*), eastern wood-pewee (*Contopus virens*), white-breasted nuthatch (*Sitta carolinensis*), and black-throated blue warbler (*Dendroica caerulescens*) for old, shade-tolerant hardwood forest types; American marten (*Martes americana*), black-backed woodpecker (*Picoides arcticus*), red-breasted nuthatch (*Sitta canadensis*), red crossbill (*Loxia curvirostra*), white-winged crossbill (*Loxia leucoptera*), evening grosbeak (*Coccothraustes vespertinus*), olive-sided flycatcher (*Contopus borealis*), winter wren (*Troglodytes troglodytes*), golden-crowned kinglet (*Regulus satrapa*), ruby-crowned kinglet (*R. calendula*), solitary vireo (*Vireo solitarius*), Cape May warbler (*Dendroica tigrina*), blackburnian warbler (*D. fusca*), bay-breasted warbler (*D. castanea*), and pine siskin (*Carduelis pinus*) for old spruce–fir forest types; and northern flying squirrel (*Glaucomys sabrinus*) and Swainson’s thrush (*Catharus ustulatus*), along with other species in older mixedwood forests (DeGraaf and Rudis 1986; DeGraaf et al. 1992). Average patch sizes of 20–30 ha are required for most birds and smaller mammals, with the exception of “umbrella species”, such as the American marten, that require larger patches of at least 375 ha (Anonymous 2001). In Fennoscandian boreal forests, it has been estimated that more than 400 species of wood-dwelling beetles (Jonsell et al. 1998) and over 200 species of cryptogams (Berg et al. 1995) are at risk because
large-diameter dead trees and logs are a sparse resource under modern logging regimes. Comparable studies are not available for the AFR.

There are likely to be many important species dependencies on OG that have yet to be identified. Therefore, the precautionary principle and our general knowledge of ecological and evolutionary relationships allow us to assume that, when a unique environment is available, various life forms will become adapted to it, especially if this environment once dominated a large portion of the pre-European settlement landscape. The focus on unique environments, such as OG, recognizes that biodiversity management decisions should be focused at the community and landscape levels, rather than on the monumental task of focusing on individual species.

**Tree species and ecophysiological attributes**

Responses to light, atmospheric moisture stress, and longevity represent key ecophysiological attributes that differentiate the long-lived, shade-tolerant, late-successional, gap-regenerating trees that characterize OG in temperate-zone forests such as the AFR. The ecophysiological adaptations of trees such as red spruce allow OG forest types to develop towards advanced age and to maintain themselves in an almost steady-state condition (Seymour 1992). These ecophysiological attributes allow for the development and continuation of the complex physical structures associated with OG in the Maritimes. Therefore, tree species composition is a key indicator of OG and potential (e.g., immature or emergent) OG forest. The presence of shade-tolerant or shade-adapted species such as red spruce, eastern hemlock, sugar maple, and American beech, even as regeneration or in the seedling, sapling, or polewood stages of development, is an important indicator of the potential for self-sustaining OG forest development.

**Size and area requirements for population viability**

The size of stand required to maintain a viable population of the dominant tree species becomes an important, albeit complicated, management issue for long-term genetic conservation of trees, but even this level of attention may not be adequate to maintain certain associated or forest-dependent species, depending on the environment created by this OG forest or its spatial configuration. The area required for sustaining a viable OG forest is a perennial question for forest management and conservation specialists. Population size has a bearing on persistence and resistance or resilience to changes over time (Davis 1996). There are several ways to approach questions about the size or area required to maintain population viability, depending on whether the focus of viability is a particular species or species guild or the dominant tree species composing the forest.

Genetic theory and the time frame for maintaining population viability suggest that an effective population size (Lande 1996) of several thousand reproductively mature individuals may be required to sustain the long-term viability of a gene pool (Lynch et al. 1995). Assuming a population size at maturity of about 100–200 individual trees per hectare in a stand dominated by a single tree species, then 20–30 ha might be considered a viable area for maintaining any one of our late-successional tree species. Forests composed of mixtures of two or three dominant tree species might require stand sizes of 60–90 ha from a population genetics perspective. Depending on its spatial configuration, the amount of interior forest, and the surrounding landscape (e.g., connectivity to other OG patches), such a stand would probably also meet the requirements of many of the native OG associated wildlife (e.g., lichens, birds, reptiles, amphibians, and perhaps also many small mammals), but certainly not of mammals such as the marten that require larger ranges (Anonymous 2001). The microclimate at the edges of stands can be modified for significant distances into the stand (Chen et al. 1993). These edge effects may influence the presence of certain species adapted to OG conditions that prevail only at the interior of larger stands.

To be considered genetically and reproductively viable over the longer term, an isolated patch of OG forest in a highly fragmented environment would need to be larger than a patch that was an integral part of an extended metapopulation (Hanski and Gilpin 1991) in which the constituent subpopulations
were interacting effectively through dispersal and gene flow. In a fragmented agricultural landscape, where a larger number of smaller 10-ha patches of OG forest were able to interact effectively through dispersal and gene flow, these smaller patches might be considered important components contributing to the viability of the larger metapopulation. For many of the wider-ranging, forest-dependent species, various degrees of physical connectivity might also be a critical issue. Therefore, population viability must be viewed from a landscape perspective to account for metapopulation dynamics (e.g., extinction and recolonization of subpopulations) related to dispersal, gene flow, and mating success.

**Conservation and management**

Based on our field surveys (using average stand ages of greater than 150 years for the dominant and co-dominant trees), the present extent of true OG conifer forest in Nova Scotia is about 300 ha or 0.0008% of the forested land base (Table 3). A similar survey for New Brunswick is underway but, based on our preliminary surveys, we suspect there is even less OG forest in New Brunswick. There is no OG on Prince Edward Island. Most of the forests in Prince Edward Island were cut by the 1860s, before Confederation (Bill Glen, PEI Department of Energy and Forests, personal communication 2001). Based on studies from various government, academic, and environmental agencies, Davis (1996) has estimated the amount of existing OG across the eastern U.S.A. ranges from 0 to less than 1% for most states and is usually placed at less than 0.1%.

Ensuring the existence of an appropriate amount of OG forest across forested landscapes will involve a combination of protected areas (areas of minimal human interference), ecologically sustainable and appropriate forest harvesting practices in late-successional, shade-adapted tree species associations, and attempts to restore late-successional forests. Given our poor understanding of all the links between OG forests and dependent wildlife, a network of protected areas will remain a central issue for biodiversity conservation. Within actively managed forests, attempts can be made to maintain some of the structural attributes linked to OG-associated wildlife. Managing OG as habitat depends on maintaining the protective micro-environments (e.g., light, temperature, and moisture conditions) created by a layered forest canopy consisting of biomass in varying stages of decay. The silvicultural practices required to maintain these light, temperature, moisture, and biomass conditions are reasonably well understood (Seymour 1992; Seymour et al. 2002). They depend on partial-harvesting systems aimed at various degrees of forest canopy retention. Old-growth forests can be restored by (i) maintaining the shade-tolerant tree species associated with late-successional forest types, (ii) allowing natural succession of these forest types to proceed from early successional stages of stand development, or under artificially established plantations, and (iii) identifying immature OG forest types and applying appropriate management (harvesting) regimes that will assure the increase in OG structural attributes.

**Impacts of forestry practices**

In the temperate-zone forests of North America, OG stands usually consist of long-lived, shade-tolerant, late-successional tree species. These forest types are particularly vulnerable to forestry practices, such as clearcutting, that alter the physical environment that has shaped their ecophysiological adaptations and determined their interspecific competitive abilities (Major et al. 2003). An important management question is whether we can manage potential OG forests to maintain the compositional and structural features that define late-successional OG forest while permitting timber extraction. The degree to which harvesting operations interrupt certain functional aspects of OG, such as the provision of essential habitat for wildlife, the time required for eliminating less fit tree genotypes, or adversely affecting processes such as nutrient cycling (Kimmins 1977), is poorly understood.

As timber rotations become shortened, maintaining long-lived, OG forest types may become more difficult. However, a trend in some areas of the AFR towards management for larger, higher-quality, and higher-value sawn-timber products may provide an opportunity to manage for both larger-dimension
timber products as well as maintain some of the characteristic structures and functions associated with OG forest. Forestry companies in the AFR that have begun to focus attention on these larger-dimension products may have an interest in managing naturally regenerated forests of species, such as red spruce, that are most clearly associated with OG conifer and mixedwood forests in the AFR. These species are capable of outliving their most serious competitors (e.g., balsam fir) with minimal management (Seymour 1992). Furthermore, it may be possible to manage these species within natural populations, on longer rotations, without the high costs associated with artificial establishment, site preparation, and the stand tending associated with intensively managed plantations. In recent years, the amount of forest being clearcut appears to be declining (Table 4). If shade-tolerant conifers, such as red spruce, respond well to increased light availability (Seymour 1992; Mosseler et al. 2000), they may be favoured by relatively mild disturbances, including logging based on individual, small group, or patch selection, and stripcut silvicultural systems.

**Old growth vs. overmature forests**

An appreciation of the ecological role of OG forests may be hindered by equating OG forest with the overmature stage of stand development in even-aged forests or plantations. In forestry terms, the overmature stage of stand development represents a decline in net primary production or standing biomass in even-aged forests. This is considered the senescent phase of stand development and is generally viewed by the forest industry as a decadent, disease-prone, unhealthy condition that is wasteful of fibre production. This concept of overmaturity was developed from an economic or timber-utilization perspective and relates to the observation that, at a certain stage in the development of even-aged stands, growth begins to stagnate and deteriorate as mean annual increment declines. This is often referred to as the “economic rotation age”, or the age at which an even-aged forest or plantation should be harvested to maximize fibre yield. However, in ecological terms, OG forests are perceived as providing important and unique habitat that can persist for thousands of years in the absence of catastrophic, stand-replacing disturbances such as fire or clearfelling. It is important not to confuse the concepts of “overmature” and “old-growth” forests. One is an economic concept, while the other is an ecological concept.

**Old forests as pest epicentres**

Older forests have also been viewed as epicentres for diseases and pests that could invade and damage surrounding, younger, “healthy” forests. However, there is little evidence in the scientific literature suggesting that old forests represent pest epicentres. Senescence (e.g., ageing, decaying, and dying) is a natural process that is very different from the death of young, vigorous, otherwise healthy organisms under attack by a virulent, aggressive pest or disease. Generally, the pest and disease communities of older forests tend to be opportunistic (secondary) rather than aggressive (primary) and normally do not have the ability to destroy younger, vigorous trees. Older trees of red spruce and eastern hemlock are excellent examples of long-lived species that have few major pest and disease problems in old age that could be held responsible for destroying vigorous, young trees.

Insects are an important component of biodiversity in healthy, natural, forest ecosystems and can even play an important role in maintaining the competitive ability of OG-associated species such as red spruce in relation to aggressive competitors such as balsam fir (Seymour 1992). Managed forests, especially those where natural ecosystems have been converted to simplified tree farms, tend to be breeding grounds for pests. They are more prone to insect and disease epidemics and sometimes promote larger and more frequent outbreaks. Some of the most destructive pest outbreaks over the past 100 years may have been a direct result of past and present forest practices (Hawley and Stickel 1948; Blais 1983; Wallner 1987; Seymour 1992; Clancy 1994; Perry 1994; Wilson and Tkacz 1994). These recent epidemics of native insects may be symptoms of a forest that is stressed with respect to its normal patterns of biodiversity and functional processes.
The spruce budworm (*Choristoneura fumiferana* (Clem.)) is a native endemic insect of balsam-fir-dominated coniferous forests of northeastern North America and has a long history in the AFR. Blais (1983) analysed the frequency, extent, and severity of spruce budworm infestations over the past 300 years in eastern Canada and found these factors to have been exaggerated by the continuous manipulation of the forest since the arrival of Europeans. Both Blais (1983) and Holling (1978) agree that the forest–budworm relationship has changed dramatically over the past century because of increasing commercial intervention in the forest, which has increased the abundance of balsam fir, the primary host of the insect, while decreasing forest diversity and its ability to accommodate budworm outbreaks. The advent of the pulpwod industry and the abandonment of agricultural lands may be the two principal factors that caused a dramatic increase in the abundance of pest-prone balsam fir and white spruce. Conversely, with respect to biodiversity, a study by Su et al. (1996) showed that an increase in the hardwood component of a balsam fir forest decreased budworm defoliation significantly. A similar interaction has been found with respect to the southern pine beetle *Dendroctonus frontalis* (Schowalter and Turchin 1993). In a study of 31 mixed-conifer forests of the southern Rocky Mountains with a history of western spruce budworm (*Choristoneura occidentalis*) outbreaks, Lynch and Swetnam (1992) found that outbreaks were no more frequent in older stands (with average stand ages ranging between 200 and 300 years) than in younger stands, nor did the outbreaks originate in older stands. Furthermore, the ideas that stand age is correlated with budworm survival or that particular types of stands act as epicentres for infestation have been rejected by Royama (1984, 1992; pp. 335–336).

**Management recommendations**

Given the available evidence on predominant disturbance patterns across the Maritimes, late-successional, shade-tolerant tree species mixtures probably dominated much of the AFR in pre-European settlement times (Seymour et al. 2002). Red spruce and eastern hemlock would have been the dominant species of OG conifer forests on moist sites (Seymour 1992). Being much sought after for its high-quality timber, red spruce was selectively harvested during the 1700s and 1800s and clearcut during much of the 1900s. Presently, only about 600 ha of red-spruce-dominated OG remains within a potential range of 3 million ha in the northeast U.S.A., and this, mostly within smaller stands of less than 100 ha in size (Cogbill 1996). Although New Brunswick has not yet been thoroughly surveyed for old-growth red-spruce-dominated stands, our estimates for Nova Scotia indicate that as little as 300 ha remain (Table 3). A survey of OG remaining in New Brunswick is currently underway. Forest resource inventory data suggest that between 1% (Lynds and LeDuc 1995) and 5% (Anonymous 2002, Fig. 1) of Nova Scotia, and perhaps less than 2–3% of New Brunswick, exists as forest older than 100 years. Based on the frequency of stand-replacing or catastrophic natural disturbances such as fire and wind in the AFR, the length of time required to develop OG, and the areal distribution of temperate-zone forests in the AFR capable of developing these late-successional forest types, we estimate that 40–50% of the pre-settlement forested landscape may have been occupied by OG forest. Although the question of how much area should be kept in OG forest types is largely an issue of social and economic policy, given our estimates of the extent of OG in the pre-settlement forest, it seems reasonable to suggest that at least 20–25% of our forest be maintained in these late-successional OG forest types: perhaps 10–12% within protected areas and 10–12% within the working forest. It is difficult to justify these amounts based purely on what science would prescribe as a minimum for maintaining a tree species according to population genetics theory. Our arguments for maintaining these amounts are based largely on our understanding of what might be necessary to maintain a viable metapopulation structure capable of continuous dispersal across a fragmented landscape in which the forest must adapt to anticipated rapid climatic changes. Furthermore, the OG forest structure required to maintain the population viability of forest-dependent wildlife, such as the American marten, and some of the larger mammals that are endangered or have been extirpated in the Maritimes (wolves, eastern cougar, wolverine, lynx) requires much larger areas than that prescribed by population genetics theory for the trees themselves.
The absence of OG in the AFR indicates that restoration activities will be needed to increase representation to a level that approaches probable historical levels (Seymour 1992; Salonius and Beaton 1997) and is compatible with the habitat requirements of associated wildlife (Anonymous 2000, 2001). Clearcutting is generally not an appropriate harvesting method for conserving and managing late-successional forests composed of long-lived, shade-tolerant trees adapted to high atmospheric moisture and capable of natural regeneration under relatively undisturbed conditions. Although natural regeneration of species such as red spruce and eastern hemlock is favoured by the seedbed disturbance and increased light associated with partial canopy removal through logging activities, the competitive ability of these species benefits from some canopy protection and is adversely affected by full canopy removal (Seymour 1992). Our observations within existing OG stands clearly demonstrate that these longer-lived trees will eventually overcome competition from the more invasive and aggressive, but shorter-lived, balsam fir. Silvicultural alternatives based on partial canopy retention (e.g., individual-tree, group-selection, or stripcutting systems) will best meet the competitive requirements of these long-lived species. Evidence from the Compendium of Canadian Forestry Statistics (Canadian Council of Forest Ministers 1998) suggests that Maritime industries are beginning to move away from the conventional, energy-intensive approach based on clearcutting, site preparation, and planting, towards a greater emphasis on natural regeneration. This developing trend away from clearcutting (Table 4) bodes well for the restoration of the higher-value species we associate with temperate-zone OG forests.

Protected areas

Regardless of whether OG can be managed and restored effectively, an adequate sample of OG forest will need to be allocated to a protected areas network that remains as free as possible of human interference. For science and research purposes, it is important to have a reference system for establishing benchmarks to monitor the processes associated with relatively undisturbed forest ecosystems. Allowing organisms to evolve naturally within an environment of minimal interference from human activities may be especially important from the genetic perspective of maintaining long-term evolutionary flexibility. There is also a human, social dimension to this need for maintaining the existence of a representative sample of primary forest on the landscape (Perlman 1996). Although these other values have driven a great deal of public debate and policy development, there are also good science-based reasons for protecting OG.

The protection of remaining older forests is a growing priority across the Maritimes. Only 0.08% of this older forest has been protected by legislation (Lynds and LeDuc 1995). In its efforts to establish a system of protected areas as a cornerstone of its goals for sustainable use of natural resources, the government of Nova Scotia has legislatively established 31 candidate protected areas, which encompass 19% of provincial Crown land, under the Wilderness Areas Protection Act (1998). Initial assessments suggest that 13 of these protected areas contain approximately 39,000 ha of old forest (>100 years old). Several Nature Reserves, protected under the Special Places Protection Act of Nova Scotia (1989), contain significant old forests. Also, major national parks in Nova Scotia and New Brunswick, such as Kejimkujik, Fundy, and Cape Breton Highlands, protect some older forests.

Forest resource inventory

Forest resource inventories can be an important tool in identifying the long-lived, OG indicator tree species that can develop into Acadian OG forests. By incorporating the age criterion described earlier, forest resource inventories could be improved for purposes of identifying OG stands. However, accurately measuring the ages of very large or old trees presents practical problems with tree size, available equipment, time, internal decay, etc. Our experience suggests that ages of trees older than 300 years must often be estimated based on a combination of age cores and diameter growth rate measurements. Size measurements alone (e.g., diameter at breast height and height) can be misleading.
determinants of age in old stands of shade-tolerant species such as red spruce and eastern hemlock (Davis 1996). Poor correlation between age and diameter are related to the variability in tree-ring growth profiles associated with random, small-scale stand disturbance events that result in alternating periods of suppression and release in shade-tolerant trees (Mosseler et al. 2000). In red spruce, tree height was of limited use as a surrogate for age because height growth is minimal after trees attain 25 m in height.

Current FRI databases have proven to be of limited use in identifying OG stands. Often, stands identified as potential OG sites based on attributes such as species identity, age, and developmental and successional characteristics no longer existed or had been logged to such an extent that they no longer constituted OG according to our criteria of age, structure, and species composition (Appendix A). Although an attempt is made to separate black spruce from red spruce through aerial photo interpretation and subsequent ground surveys, accurate identification of these species can present potential species identification problems. It is important that every effort be made to distinguish these spruces so that ecologically appropriate forest management and harvesting practices can be applied.

Re-establishment of old-growth forest types

Established expertise in plantation forestry presents a useful mechanism for restoration of long-lived, shade-tolerant species that can develop into OG forests. For instance, many of the red pine plantations that were established throughout central Ontario as part of an extensive land-reclamation program before and during the Great Depression era of the 1920s and 1930s are now experiencing natural succession to the original, shade-tolerant hardwood forest types that occupied these sites before their conversion to agriculture. Many of these pine plantations have been abandoned for forest timber production and are now deteriorating. In many of these older plantations, artificial thinning has promoted the process of natural succession to shade-tolerant species mixtures. This represents one of the largest and most successful examples of serendipitous forest restoration in Canada (Parker et al. 2001) and could be emulated in the AFR. Recently, such thinning of old plantations has been used to capitalize on their nurse-crop characteristics for the artificial establishment of shade-tolerant, late-successional species such as red spruce. The underplanted red spruce has responded well to the shelter provided by a red pine canopy. These results present an example of what can be done to expedite succession toward the development of natural, self-sustaining forests of shade-tolerant species capable of perpetuating themselves in the absence of stand-replacing disturbances. Residual uncut forest in stripcutting situations has also been used to provide the microclimate required for the artificial establishment of shade-tolerant, late-successional species (Salonius and Beaton 1997).

Summary

The public has a vision of OG forests as having large, old trees and a complex of associated biomass structures. In the AFR, we define OG primarily according to its structures, we value OG according to its functions and role in biodiversity conservation, and we can predict its development according to processes (e.g., successional trajectories). Structure, function, and processes are all important in understanding and defining OG and its ecological roles. Forest managers are primarily concerned with the structural and functional aspects of OG because these form the foundation of public perceptions and are, therefore, most relevant to public debate and policy development. In contrast, scientists may be more interested in defining OG according to the processes that shape and define its development. In the interests of policy development and management of OG, these differences in approach when defining OG need to be understood when managers and scientists attempt to develop an acceptable consensual definition of OG forest. To characterize OG in the AFR, it may be more useful to recognize that its attributes vary over a continuum, and it may be more realistic to characterize forest stands according to a simple point-based rating system, or index, that reflects the degree to which a forest displays OG
attributes (Appendix A). For practical purposes, it is important that OG be defined within reasonable limits that are both scientifically meaningful (e.g., reflect ecological relationships and reality), and policy relevant and yet operationally useful to forest managers who must work with any definition devised by scientists.

In the AFR, OG forests are probably best represented by late-successional forest types composed of various mixtures of long-lived, shade-adapted trees. Defining OG as such may appear somewhat arbitrary from an ecological perspective. For instance, even-aged stands of early successional tree species (e.g., white birch, aspen, tamarack, and black spruce) also become old, deteriorate, and create many of the biomass structures associated with OG habitat. However, overmature stands of early successional trees often represent only an intermediary stage of stand development that will eventually lead to forests composed of long-lived, shade-tolerant trees and a relatively stable forest type capable of perpetuating itself in the absence of catastrophic disturbance. If the objective is to manage for the conservation of OG forest, then our aim should be to restore forest types composed of species such as sugar maple, yellow birch, American beech, red spruce, eastern hemlock, and eastern white pine. Scientists and forest managers should focus on (i) the biodiversity associated with OG, (ii) understanding the ecological processes (e.g., disturbance regime and natural succession trajectories) that best ensure the development and maintenance of such forests, and (iii) developing appropriate management protocols.

The full role of OG forest in biodiversity conservation will only become clear when most of the species that depend on it for their survival have been identified. Nevertheless, the basic principles of evolutionary and population biology suggest that the existence of a unique habitat (such as the distinct physical and abiotic features that define the OG forest environment) will have resulted in the adaptation of many native species to that environment. Our knowledge of forest ecology, succession, and natural disturbance dynamics suggest that this OG forest environment may have occupied a significant portion of the pre-European settlement landscape. Although we cannot say with scientific certainty that we have many species that require OG forests for their survival, we do know that many of our native species prefer such forest habitat and that some of these species are in decline and have become endangered or extirpated along with the decline of OG forest. The precautionary principle demands that all parties responsible for the development of forest management policies should recognize that OG forests have a role in biodiversity conservation. These OG forests are important natural laboratories for species evolution and scientific study, as habitat for species adapted to OG conditions, and as reservoirs of the genetic diversity that forms the basis for species survival in changing environments.

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Appendix A. Key attributes of late-successional, temperate-zone old-growth forest types of the Acadian Forest Region (e.g., dominated by shade-tolerant, long-lived tree species)

Structural features
1. Uneven or multi-aged stand structure, or several identifiable age cohorts.
2. Average age of dominant species approaching half the maximum longevity for species (approximately 150+ years for most shade-tolerant trees).
3. Some old trees at close to their maximum longevity (ages of 300+ years).
4. Presence of standing dead and dying trees in various stages of decay.
5. Fallen, coarse woody debris.
6. Natural regeneration of dominant tree species within canopy gaps or on decaying logs.

Compositional features
7. Long-lived, shade-tolerant tree species associations (e.g., sugar maple, American beech, yellow birch, red spruce, eastern hemlock, eastern white pine).
8. Presence of old-growth-associated or dependent wildlife species (e.g., owls, bats, woodpeckers, martin, etc.).

Process features
9. Characterized by small-scale disturbances creating gaps in forest canopy.
10. A long natural rotation for catastrophic or stand-replacing disturbance (e.g., a period greater than the maximum longevity of the dominant tree species).
12. Final stages of stand development before a relatively steady state is reached.
13. Net primary productivity approaching zero (e.g., ingrowth balanced by mortality).
14. Natural regeneration of dominant tree species within canopy gaps.