Comparisons between wildfire and forest harvesting and their implications in forest management

D.J. McRae, L.C. Duchesne, B. Freedman, T.J. Lynham, and S. Woodley

Abstract: Emulation silviculture is the use of silvicultural techniques that try to imitate natural disturbances such as wildfire. Emulation silviculture is becoming increasingly popular in Canada because it may help circumvent the political and environmental difficulties associated with intensive forest harvesting practices. In this review we summarize empirical evidence that illustrates disparities between forest harvesting and wildfire. As a rule, harvesting and wildfire affect biodiversity in different ways, which vary a great deal among ecosystem types, harvesting practices, and scale of disturbance. The scales of disturbance are different in that patch sizes created by logging are a small subset of the range of those of wildfire. In particular, typical forestry does not result in the large numbers of small disturbances and the small number of extremely large disturbances created by wildfires. Moreover, the frequency of timber harvesting is generally different from typical fire return intervals. The latter varies widely, with stand-replacing fires occurring in the range of 20 to 500 years in Canada. In contrast, harvest frequencies are dictated primarily by the rotational age at merchantable size, which typically ranges from 40 to 100 years. Forest harvesting does not maintain the natural stand-age distributions associated with wildfire in many regions, especially in the oldest age classes. The occurrence of fire on the landscape is largely a function of stand age and flammability, slope, aspect, valley orientation, and the location of a timely ignition event. These factors result in a complex mosaic of stand types and ages on the landscape. Timber harvesting does not generally emulate these ecological influences. The shape of cut blocks does not follow the general ellipse pattern of wind driven fires, nor do harvested stands have the ragged edges and unburned patches typically found in stand-replacing fires. Wildfire also leaves large numbers of snags and abundant coarse woody debris, while some types of harvesting typically leave few standing trees and not much large debris. Successional pathways following logging and fire often differ. Harvesting tends to favor angiosperm trees and results in less dominance by conifers. Also, understory species richness and cover do not always recover to the pre-harvest condition during the rotation periods used in typical logging, especially in eastern Canada and in old-growth forests. As well, animal species that depend on conifers or old-growth forests are affected negatively by forest harvesting in ways that may not occur after wildfire. The road networks developed for timber extraction cause erosion, reduce the areas available for reforestation, fragment the

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landscape for some species and ecological functions, and allow easier access by humans, whereas there is no such equivalency in a fire-disturbed forest.

Key words: silviculture, forest management, clearcutting, forest conservation, wildfire, biodiversity.

Résumé : La sylviculture simulée est l'utilisation de techniques sylvicoles cherchant à imiter des perturbations naturelles telles que l'incendie de forêt. La popularité de la sylviculture simulée ne cesse d'augmenter au Canada, parce qu'elle peut aider à circonscrire les difficultés politiques et environnementales associées avec les pratiques de récolte forestière intensives. Les auteurs revoient et résument les preuves empiriques qui illustrent les différences entre la récolte forestière et l'incendie de forêt. En général, la récolte et l'incendie affectent la biodiversité de différentes façons qui varient beaucoup selon les types d'écosystème, les techniques de récolte et l'échelle de perturbation. Les échelles de perturbation sont différentes, en ce que la dimension des trouées créées par la récolte constitue un petit sous-ensemble de l'échelle de celles occasionnées par l'incendie. Particulièrement, la pratique forestière typique ne conduit pas aux grands nombres de petites perturbations et aux petits nombres de grandes perturbations qui font suite à l'incendie. De plus, la fréquence des récoltes est généralement différente des intervalles de retour de l'incendie. Ces dernières varient largement, avec des intervalles de remplacement du peuplement allant de 20 à 500 ans. Au contraire, la fréquence des récoltes est définie principalement par le temps nécessaire pour atteindre des dimensions marchandes, ce qui se situe entre 40 et 100 ans. Dans plusieurs régions, la récolte forestière ne maintient pas la distribution naturelle d'âges des peuplements, notamment les classes d'âge les plus vieilles. L'incidence de l'incendie dans le paysage est largement fonction de l'âge du peuplement et de son inflammabilité, de la pente, de l'aspect, de l'orientation de la vallée, et de la localisation ainsi que du moment de la mise à feu. Ces facteurs conduisent à l'apparition d'une mosaïque complexe de types de peuplements et d'âges dans le paysage. La récolte forestière n'imite généralement pas ces influences écologiques. La forme de découpage des parcelles ne suit généralement pas le patron elliptique des incendies de forêt, et les parcelles ne montrent pas le découpage irrégulier et les îlots non-perturbés qu'on retrouve dans les peuplements venus après feu. Les incendies laissent de nombreux chicots et d'abondants macrorestes ligneux, alors que certains types de récolte laissent typiquement peu d'arbres sur pieds et peu de macrorestes ligneux. Les étapes de la succession, suite à la récolte et au feu, diffèrent fréquemment. La récolte favorise les arbres angiospermes et conduit à une moindre dominance des conifères. De plus, la richesse en espèces des sous-étages et leurs couvertures ne retournent pas toujours aux conditions précédent la récolte, au cours des intervalles de rotation typiques entre les récoltes, surtout dans l'est canadien et dans les forêts surannées. Aussi, les espèces animales qui dépendent des conifères ou des vieilles forêts sont négativement affectées par la récolte forestière de façons qui peuvent ne pas survenir après l'incendie. Les réseaux routiers développés pour la récolte causent de l'érosion, réduisent les surfaces disponibles pour le reboisement, fragmentent le paysage pour certaines espèces et fonctions écologiques, et facilitent l'accès par les humains, situations qui n'existent pas dans les forêts perturbées par l'incendie.

Mots clés : sylviculture, aménagement forestier, coupe à blanc, conservation des forêts, l'incendie forestier, biodiversité.

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Introduction

Forest management practices are the object of unprecedented debate by the scientific community and the general public. Indeed, whereas clearcutting is usually the preferred harvesting practice in Canada for economic reasons (Keenan and Kimmins 1993), many people perceive it to be ecologically unsound. The importance of this issue has grown as additional interest groups lay claim to the diverse resource values of forests. Hence, there is a clear need to develop forestry practices and integrated management plans that are accepted by all forest stakeholders.

Three basic concepts are emerging to help resolve conflicts among forest users: (1) the allocation of areas to relatively intensive timber management, thereby reducing pressures on remaining forests; (2) the development of broader, more ecological approaches to forest management; and (3) the use of emulation silviculture, based on silvicultural practices thought to emulate natural disturbances. Intensive forest management practices have been discussed by others (Duchesne 1992; Kimmins 1997; Rotherham 1999; Lautenschlager 2000) and ecological forest management is now accepted as a guiding principle for forestry operations in Canada.

A cornerstone of ecological management is the recognition that natural forests are maintained by periodic events of stand-replacing disturbance caused by fire, windstorms, irruptive insects, or pathogens. In Canada, wildfire is by far the most important stand-replacing disturbance in terms of frequency and distribution (Weber and Flannigan 1997). Because the species of Canadian forests have been interacting with fire since at least the Miocene era (about 30 million years) (Weber and Taylor 1992), their ecosystems have evolved in response to this pervasive natural disturbance (Weber and Flannigan 1997). Therefore, studies of disturbance by wildfire offer valuable insights into the ecological dynamics of Canada's forests. Indeed, before the arrival of Europeans fire was the most dominant landscape-scale stressor, with typical frequencies ranging from about 20 years in boreal Ontario to more than 500 years in humid Newfoundland and the rainforests of coastal British Columbia (Foster 1983; Van Wagner 1990; Duchesne 1994*a*, 1994*b*; Duchesne and Hawkes 2000).

Because wildfire is a natural process to which indigenous species and their ecosystems are well adapted in terms of survival, recovery, and productivity, it has been suggested that this kind of disturbance is an efficient land manager that foresters should seek to emulate (Hunter 1993), regardless of the fact that the impact of wildfire varies widely from mild to highly destructive. Moreover, the managers of national parks and other protected areas often promote the simulation of natural fire regimes for management to conserve natural values and indigenous biodiversity (Panel on the Ecological Integrity of Canada's National Parks 2000). Ecological integrity has been suggested as a management goal; an ecosystem has integrity when it is deemed characteristic of its natural region, including the composition and abundance of native species and ecological communities, rates of change, and supporting processes (Panel on the Ecological Integrity of Canada's National Parks 2000).

Here, we also advocate that indicators of ecological integrity should become criteria in forest management. In some regions, ecological integrity is being pursued through the application of "emulation silviculture", a term we have coined to describe silvicultural activities designed to mimic natural ecological processes and disturbance. Although emulation silviculture is a new term, it is based on principles espoused elsewhere. In Ontario, for example, one of the two principles of *The Crown Forest Management Act* (Bill 171; Statutes of Ontario 1994) states that forests will be managed through the emulation of natural disturbance caused by fire. In Alberta, there is a substantial, ongoing, multi-disciplinary effort known as Ecosystem Management by Emulating Natural Disturbance (EMEND) to develop forestry practices that emulate natural disturbance (Spence et al. 1999). More locally, various regional authorities and companies have been incorporating some elements of emulation silviculture into newer management plans, particularly with respect to mimicking spatial patterns caused by wildfire.

In recent decades, the forestry profession has been exposed to numerous trendy keywords and concepts, which is the case for emulation silviculture. Nevertheless, we believe that emulation silviculture is a worthwhile addition to the forestry lexicon. This novel approach offers a guiding principle to forest managers, along with an appealing tool set for dealing with ecological issues important to the domestic and international public. Because emulation silviculture is a new field, there is a need to assess the empirical evidence supporting its application. Hence the objective of this review is to provide a comparative analysis of the ecological impacts of forest harvesting — mostly clearcutting because of its widespread use — and wildfire on forests ecosystems. We will interpret the analyses in terms of the potential benefits and drawbacks of emulation silviculture. In this paper we have omitted to compare the effect of fire and forest harvesting on aquatic environments. However, this topic has been addressed by Carignan and Steedman (2000) along with numerous authors in a special issue of the *Canadian Journal of Fisheries and Aquatic Sciences*, Volume 57, Supplement S2.

Tenets of emulation silviculture

Although we advocate the use of emulation silviculture as a management tool, its promotion by the general public, environmentalist groups, and forest agencies is often based on tenets that cannot be supported by scientific scrutiny:

(1) *It is possible to tailor the ecological effects of forestry practices, particularly clearcutting, to emulate those of fire disturbance.* This assertion is based on the hypothesis that there is some overlap of beneficial ecological impacts between forest harvesting and wildfire. Furthermore, it is presumed that some of the undesirable effects of clearcutting can be avoided by the use of silvicultural methods that mimic those of wildfire. Opponents of emulation silviculture might note that fire is a chemical reaction whereas clearcutting is a mechanical disturbance; obviously, timber harvesting cannot emulate the rapid oxidative reaction occurring during combustion. However, the time necessary for the combustion of much of the biomass of an ecosystem, which is measured in minutes or hours, is much smaller than the temporal scale of post-fire succession, which is measured in decades or centuries. As such, emulation silviculture should focus on the ecological processes (chemical, physical, and biological) occurring during the post-disturbance recovery, rather than the ephemeral processes taking place during combustion.

(2) *Pre-settlement fire regimes displayed natural ecological integrity.* An underlying, yet disputable, assumption associated with emulation silviculture is that Canada's forests before the European colonization were in a condition of near-equilibrium with climate and the natural disturbance regime (especially wildfire). Although palynological studies show wide variations in species composition and abundance in pre-settlement forests, suggesting that post-glacial equilibrium landscapes had not fully developed (Campbell and McAndrews 1991, 1993), the only support to this assertion is that historical records show old-growth forests, which we define as all forests past rotation age (Duchesne 1994*b*), were more abundant in pre-Columbian times than at the present. This is especially the case of the humid west coast, and in eastern forests where species such as red spruce (*Picea rubens*) and white pine (*Pinus strobus*) were more abundant and of larger size than at present. Undeniably, anthropogenic disturbances associated with timber harvesting, agriculture, urbanization, and other activities have greatly modified Canada's forests, and the changed ecosystems may make it impossible and even undesirable to fully restore the primeval landscapes.

(3) *The ecological effects of wildfire are "natural" and therefore ecologically acceptable, whereas those of forest harvesting are less so.* Presumably, the primeval forests of Canada were maintained by natural, pre-settlement disturbance regimes, despite the growing evidence that First Nations communities tended the forests by making use of prescribed burning. Nevertheless, proponents of emulation silviculture hypothesize that wildfire had positive impacts at the broad scale of regions and landscapes and over long periods of time, but we emphasize that wildfire can have effects damaging to the environment and to human interests. Moreover, although natural aesthetics are sometimes invoked as a reason to promote natural disturbances instead of anthropogenic ones (Kimmins 1999), not all people regard the effects of wildfire to be aesthetically pleasing.

Fire ecology and emulation silviculture

A great deal of information has been developed about the ecological effects of fire in forests (reviewed by Van Wagner 1990). There are, however, several impediments that limit the application of fire ecology to emulation silviculture. First, there are few specific comparisons of the ecological effects of forest harvesting and wildfires in the same kind of forest ecosystem (Wuerthner 1995). Second, there is not yet an established link between fire behavior and the resulting ecological effects. For example, of the many studies that have examined post-fire plant communities (reviewed by Tellier et al. 1995, 1996; Whittle et al. 1997*a*), few have characterized fire behavior well enough to allow prediction of the non-tree regeneration. This is important, because fire effects must be linked to fire behavior before well-supported decisions can be made in favor of emulation silviculture. In practice, this kind of research should help us determine which kind of fire we want to emulate during forest harvesting. And third, although a large body of literature on the effects of disturbance on forests has accumulated, most of this knowledge is of a correlative nature; there has not been much experimental manipulation of conditions to examine the basic precepts of fire ecology. For example, despite the axiom that wildfire prepares germination seedbeds by exposing mineral soil, roughly half the papers reviewed by Herr et al. (1999) found that mineral substrates are not necessary for the establishment of conifer seedlings. In practice, appropriate controlled experiments have not been conducted to confirm the importance of seedbed conditions for seedling establishment, or of other environmental variables such as soil moisture, seed predation, shading, or microclimate. Likewise, a thorough comparison of clearcutting and fire is hampered by our limited knowledge of the long-term effects of timber harvesting. Aside from some extreme harvesting operations that have created obvious problems, such as the erosion of steep slopes and damage to streams from logging without riparian buffers, little research has dealt with the ecological effects of clearcut harvesting, especially the longer-term effects. On the one hand, past research often has emphasized aspects of forests that are pertinent to short-term productivity and wildlife abundance, rather than ecological processes. On the other hand, most developing commercial forests are second-growth stands and have not yet been sufficiently studied to allow statements regarding the impacts of repeated disturbances by harvesting.

Another impediment to emulation silviculture is that the dynamics of Canada's forests vary greatly among and within biophysical regions, as affected by climate, topography, species distribution, past forest use, and other factors. Research in fire ecology and silviculture has focused on specific forest regions or community types, but failed to develop an overall picture of Canadian forests. As a rule it is not appropriate to transfer generalizations regarding fire or logging disturbances across forest regions or between ecosystem types within the same forest region.

Wildfire characteristics

An average of about 10 000 wildfires burns annually in Canada, with approximately 40% ignited by lightning and the rest by humans (Stocks and Simard 1993). From 1986 to 1989, wildfires burned an average of about 2.5×10^6 ha per year, although 95% of the area burned was caused by only 1.5% of the larger fires that were greater than 1000 ha (Stocks and Simard 1993). Fire occurrence is distributed unevenly across Canada. From 1980 to 1989 British Columbia averaged 2700 fires annually, while Ontario had 1700 fires, Alberta and Québec 1000 each, Saskatchewan and Manitoba 700 each, and the other provinces and territories a total of 500 (Stocks and Simard 1993).

Wildfires can vary in size from less than 0.1 ha to a conflagration covering thousands or hundreds of thousands of hectares. Natural barriers such as rivers, wetlands, ridges, or recently burned-over areas and plant associations with low flammability can be important factors affecting fire behavior.

Frontal fire intensity (or Byram's fireline intensity) is a measurement of the quantity of energy liberated as a fireline moves through an ecosystem and is an important physical measurement related to ecological impacts (Alexander 1982). Variations of frontal fire intensity are largely caused by the rate of fire spread and fuel consumption. Values for some common forest types have been determined as parameters in the Canadian Forest Fire Behavior Prediction System (Forestry Canada Fire Danger Group 1992). The variability of fire behavior is widespread among all fuel types in Canada and has been illustrated by the studies of Stocks (1987, 1989), who conducted experimental burns in jack pine

(*Pinus banksiana*) ecosystems ignited under different weather conditions based on the Canadian Forest Fire Weather Index (FWI) System (Canadian Forest Service 1987). The range of calculated frontal fire intensity was 134 to 40 903 kW/m, equivalent to low-intensity surface burns to high-intensity fire crowning through the treetops, respectively. The depth of burn, which is an indication of forest floor removal, ranged from 1.8 to 5.5 cm.

During a wildfire, which may burn for days over the landscape, the fire behavior typically varies drastically, depending on the burning conditions. Such variability greatly affects the post-burn ecological effects through variations of depth of the remaining forest floor, seedbed preparation, vegetation changes, and other variables. Moreover, some local areas may not burn and serve as nuclei of survival and recolonization by some species.

Heinselman (1983) reviewed the tolerance of various tree species to wildfire under low to moderate fire intensities, although ultimately all species perish under high fire intensities. Because vegetation types influence fuel characteristics, loading, and availability, fire behavior prediction can be improved using the Forest Ecosystem Classification System for a particular site (McRae 1996). The ecological impact of any wildfire depends substantially on the adaptations of the dominant tree species (Rowe 1983). For example, trembling aspen (*Populus tremuloides*) is thin-barked and highly sensitive to fire, and even low-intensity burns (<500 kW/m) can lead to stand-replacing mortality (Brown and Debyle 1987). In contrast, red pine (*Pinus resinosa*) is relatively tolerant because of its thick insulating bark, and fire intensities of <600 kW/m should be harmless to most mature trees (Van Wagner and Methven 1978). Emulation silviculture must take into account the ability of key tree species to tolerate and regenerate after fire. The emulation management system must account for the natural stand-replacing and non-stand-replacing fire regime to develop suitable landscape patterns, age-class and species distributions, and ecosystem functions such as productivity and carbon storage.

Fire return intervals

The fire return interval is the average length of time between events on a given site and is an indicator of processes controlling ecosystem functioning. For example, the longer-term effects of wildfire on the forest floor are strongly dependent on the return interval. Although wildfire was the most prominent stand-replacing disturbance in the pre-settlement forests of Canada, the return intervals varied greatly among boreal and forest types, being as little as 20 years in some jack forests of Ontario and as long as 500 years in black spruce (*Picea mariana*) in Labrador (Foster 1983). Considerably longer return intervals occurred in non-boreal old-growth forests of the humid Pacific coast. In areas with a long fire return interval (such as northern black spruce, eastern tolerant hardwoods, northern aspects, and stands with low ignition potential), emulation of the natural disturbance regime would require much longer harvest rotations than are now considered economically viable by the forest industry. However, in low elevation montane forests, such as those dominated by ponderosa pine (*Pinus ponderosa*), low-intensity fires had a typical return interval of 4–25 years. In these forests, emulation silviculture may be limited to selection logging, which mimics the selective mortality caused by low-intensity surface burns and differs from the unacceptable practices of selective logging, normally characterized by exploitative high grading.

Characteristics of forest harvesting

Almost 1 million ha of forests are harvested annually in Canada, roughly 90% by clearcutting, which represents 0.4% of the total commercial forest area (Natural Resources Canada 2000); hence we emphasize the ecological impact of clearcutting in this review. Clearcutting is the harvest of all or most merchantable timber from a forest and is the preferred means of harvesting in Canada because of its short-term economic benefits. Like wildfire, clearcutting can vary a great deal in size distribution, residual vegetation, and environmental impacts. In some cases, "islands" of mature trees are left to promote natural seeding-in, while in other situations clearcuts are staged over time as multiple intervention harvests or as progressive strip-cuts. As well, clearcut harvests are also at the culmination of shelterwood systems.

Where larger block-type clearcuts are used, they are typically arranged as a mosaic on the landscape, with age-class adjacency intended to foster natural regeneration and habitat variability. The most intensive application of clearcutting typically involves subsequent site preparation and planting of desired tree species to establish a forestry plantation. However, the largest clearcuts in Canada are associated with salvage efforts following stand damage caused by wildfire or irruptive insects, such as spruce budworm (*Choristoneura fumiferana*) or bark beetles.

The upper limits of clearcut size is controlled by provincial legislation (Table 1), but in practice clearcuts vary greatly in size and shape because of stand boundaries, topography, presence of waterways, and management objectives. Within clearcuts, the distribution and abundance of large woody debris varies according to the extraction method and any subsequent site preparation. Relatively intensive harvesting may involve machinery that carries felled whole trees to landings, where they are de-limbed and de-topped and the debris windrowed or burned. Less-intensive harvesting leaves woody debris and foliage on-site, and only the merchantable stems are taken away. Clearcutting conducted in winter, when the ground may be frozen and covered with snow and (or) ice, may not result in much scarification of the forest floor but protects most of the pre-established advance regeneration of tree seedlings. In contrast, skidding cut trees during snow-free months exposes patches of mineral soil, which may promote the seeding-in of certain tree species. The greatest challenge of emulation silviculture is to discover harvesting impacts (including those of clearcutting in some forest types) that are similar to those of disturbance by wildfire and are necessary for maintaining the integrity of the ecosystem.

Comparing wildfire and clearcutting at the landscape scale

Recently, advanced forest management approaches, called natural disturbance models, have been developed to emulate timber supplies after the regional disturbance regimes associated with wildfire (Hunter 1993; Armstrong et al. 1999). From a landscape perspective, the emulation regime must consider the shapes, size, return interval, and age-class adjacency of disturbance associated with wildfire. However, we question whether all of these wildfire features are desirable within a particular management plan. These considerations with respect to clearcutting are discussed below.

Size of cut-blocks

The size of cut-blocks refers to their contiguous area, regardless of their distribution on the landscape. Appropriate sizes of cut-blocks has long been a controversial issue in the public arena. On the one hand, some argue that large cut-blocks are unacceptable from an ecological perspective. On the other hand, others argue that large cut-blocks are justified in some forest ecosystems based on observations that wildfires can be much more extensive than regulated cut-blocks sizes (Table 1). Indeed, the largest known fire in the boreal forest of Canada affected more than 1.4 million ha (Murphy and Tymstra 1986).

The size of clearcuts in Canada have varied with time, getting larger with the increasing mechanization of harvesting techniques during the 1970s and 1980s, and then being reduced in the 1990s because of public concern about ecological impacts. By the late 1990s, clearcuts were generally smaller than 100 ha across most of Canada (Table 1). At that time, Ontario had the largest cut-block sizes of all the Canadian provinces (Table 2).

Although some wildfires can cover an extremely large area, most are relatively small, partly because of fire suppression (Stocks and Simard 1993). Indeed, only 1.5% of the wildfires between 1986 and 1989 covered more than 1000 ha, and these accounted for about 95% of the area burned in Canada during that period (Stocks and Simard 1993). From 1931 to 1983 in Alberta, wildfires over 200 ha accounted

Table 1. A summary of clearcut sizes reported for provincial and territorial crown lands across Canada other than Ontario (source: Canadian Council of Forest Ministers 2000).

Jurisdiction	Average clearcut size (ha)
Newfoundland Crown Lease	Maximum 120
Nova Scotia Crown Land	Maximum 50
New Brunswick Crown Land	40–50
Prince Edward Island	3.5
Québec	Maximum 150
Ontario	See Table 2
Manitoba Crown Land	Maximum 100
Saskatchewan	30–40 for softwood / 60–70 for hardwood
Alberta	Maximum of 32 for softwood / 60 average, but individual blocks can vary up to 100
British Columbia	20–42 depending on zone
Yukon Crown Land	Maximum 40 (average 8.3)
Northwest Territories	Maximum 50

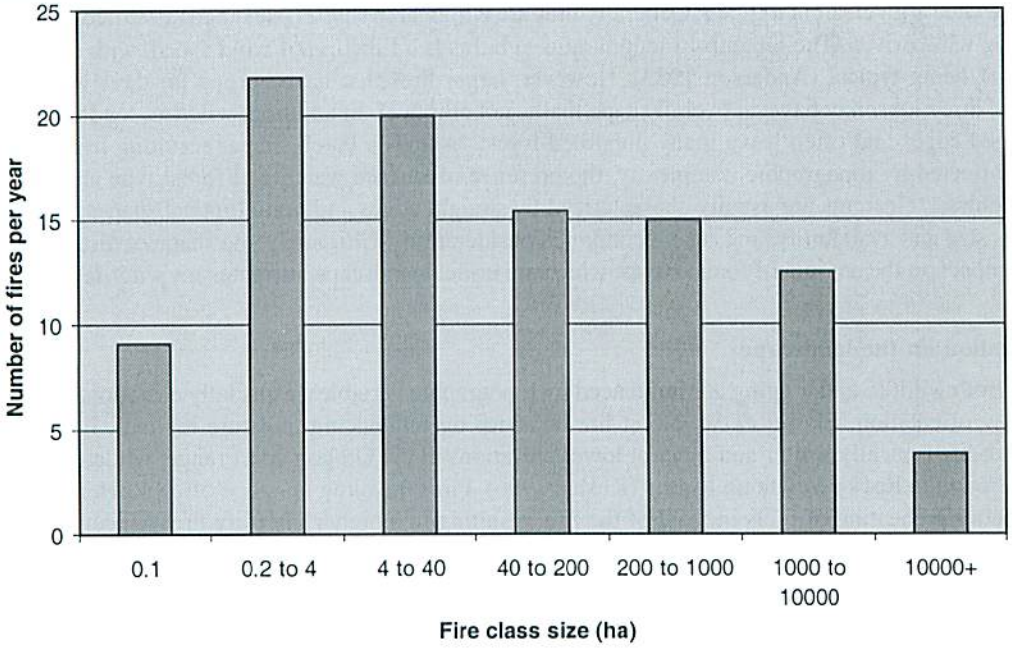
Table 2. A summary of estimated clearcut sizes reported for Ontario (source: Canadian Council of Forest Ministers 2000).

	Sample of four management units employing moose guidelines		Sample of four management units employing moose and caribou guidelines	
Clearcut size class (ha)	Percentage based on number of cuts	Percentage based on area harvested	Percentage based on number of cuts	Percentage based on area harvested
0–50	46	9	21	4
51–100	24	13	21	7
101–150	12	12	15	10
151–200	5	5	10	7
201–260	4	8	6	6
260+	9	54	27	65

for 85% of the areas burned. Morrison and Swanson (1990) found that 86% of the fires in the Cascade Mountains of Oregon affected patches less than 16 ha in area, and many of these were of low intensity and did not kill all trees within the burn area.

It is important to note that the areas annually affected by wildfires in Canada have been reduced by suppression activities, especially in more southern regions. It must be recognized that it is not considered economically desirable to eliminate fire suppression from commercial forests in favor of a let-burn policy (especially in southern regions where the great majority of fires are initiated by humans). Although it could be ecologically useful to allow wildfire to act as a "natural" management function, active suppression is needed to protect timber stocks, regularize supplies, protect human lives and property, and prevent large wildfires from devastating extensive areas. Nevertheless, the design of appropriate practices in emulation silviculture requires data on natural fire regimes unaffected by the influences of fire suppression or ignition by humans. Some relevant information can be inferred by pollen analyses of lake sediments, from historical records, and by studying regions not currently under forest management. Using data from the extensive fire management zone in northern Ontario, where wildfire is rarely suppressed, Ward and Tithecott (1993) reported a broad distribution of size classes and small frequency of large burns (Fig. 1).

Fig. 1. Average annual fire size distribution in Ontario's extensive fire management zone (where most fires are not suppressed) based on data for the period 1976–1990 (Ward and Tithecott 1993).



Thus the typical patch sizes and frequencies created by wildfire and logging are clearly dissimilar. Fires typically create both smaller and larger patches, and a forested landscape is rarely burned in a uniform fashion over a large area (Bergeron 1991; MacDonald 1993).

Age classes of stands on the landscape

Forestry operations and biological conservation have differing goals in terms of maintaining stand age-class distributions on the landscape. In a regulated forest where timber harvesting is a key activity, stand age-class distributions are different from those of a natural landscape (Heinselman 1996; Bergeron et al. 1999). In forest management, the organization of a landscape to provide a continual supply of timber is central to sustained yield (Davis and Johnson 1987) and is typically achieved by the development of a regulated forest in which the various age-classes of stands are distributed evenly. In addition, old-growth age classes showing a decline in biomass production because of the mortality of old trees may be eliminated from a "working" landscape. These old-growth age classes are replaced by younger, faster growing stands with a greater productivity. The eradication of old-growth age classes from a working landscape is a potentially devastating change for any old-growth dependent species.

The negative exponential model proposed by Van Wagner (1978, 1983) is a theoretical model commonly cited to describe the distribution of age classes in a natural forested landscape. In this model, the average stand age equals the fire return interval, about 37% of the stands are older than the average age, and many stands are burned repeatedly in younger age classes. In practice, managing forests according to the negative exponential distribution must encompass large tracts of forests that should be at least 50 times larger than the size of the largest disturbance, allowing for a shifting mosaic of stands of different ages (Shugart and West 1981). For example, in the boreal forest of Canada single fires may be larger than 1.4 Mha (1400 km^2) at the extreme (Murphy and Tymstra 1986). Hence, a single equilibrium landscape, which theoretically could fit under the negative exponential distribution, should be greater than 70 000 km^2 ($50 \times 1400\ \text{km}^2$), thus making the use of the negative exponential distribution nearly impossible to apply within the current forestry context.

Patch shape

Little research has been undertaken to compare the shape of patches created by wildfire with those associated with clearcut logging. Generally fires are elliptical in shape (Alexander 1985), resulting from being wind driven. The breadth-to-length ratio of burns is a function of wind speed, with ratios of 3:1 to 4:1 being typical (Anderson 1983). However, larger fires that have burned for days with varying wind directions may have an overall shape that is not elliptical. In addition, wildfires tend to burn with ragged edges and often leave many unburned forest "islands". Patch shapes resulting from wildfires are affected by topographic complexity, the presence of surface water, and forest type and structure. In contrast, clearcuts are usually characterized by straight edges and non-elliptical shapes, dictated by trees size and availability, and other economic considerations. Ultimately, the shape of disturbance has an impact on the amount of forest edges, which are critical landscape attributes for wildlife distribution

Location on the landscape

Both wildfire and logging are influenced by topographic variables, especially elevation, aspect, and valley orientation. Elevation can affect fire behavior by influencing moisture regimes. For example, stands are typically wetter and older at lower elevations in the Oregon coast range, while the opposite was found in Rocky Mountain forests (Kushla 1996). Fires traveling up-slope often accelerate because of better preheating of fuels in front of the fire, resulting in a higher intensity fire. Aspect also affects wildfires through differential fuel drying, with north slopes being cooler and having older forests because of fewer burning opportunities (Clark 1990). Valley orientation relative to prevailing winds in mountainous areas may also affect fire frequency, although there are conflicting studies. Johnson and Larson (1991) reported that fire frequency was not significantly different between valley orientations. In contrast, Rogeau and Pengelly[2] found that valley orientation, elevation, and to a lesser degree aspect all contributed to age-class patterns in the central Canadian Rockies.

Harvesting is also influenced by topographic variables, in that stands need to be accessible and of industrial value. Trees growing on steep slopes or wetter sites are not accessible to harvesting using conventional equipment. Likewise, harvesting to emulate wildfire would be more difficult in complex topography than in flatter terrain, since wildfire can easily occur in either situation. One effect of topographic limitations on harvesting operations is that the bulk of old, uncut stands are typically located in topographic areas that are difficult to reach, whereas the younger stands created by logging operations are relatively close to each other. In contrast, the distribution of young and old stands in fire-structured landscapes tends to be more stochastic than that of comparable landscapes under forestry management. As such, the distribution pattern of old and young stands across the landscape impacts wildlife distribution by creating favorable habitats for some species, which increase in abundance, supporting novel predators that may adversely affect old-growth species. For instance, wildlife biologists speculate that one of the reasons why woodland cariboo populations are affected by clearcutting is that increases in moose populations are followed by increased wolf population, which in turn are more effective at hunting cariboo than moose, the former being a smaller prey.

Biodiversity

Biological diversity is defined as the number, variety, and variability of living organisms on earth (World Commission on Environment and Development 1987), including the sum of diversities found at the genetic, species, ecosystem, and landscape levels (Wilson 1988). The ecological processes controlling ecosystem functioning, such as decomposition and nitrogen fixation, are considered integral

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[2] Rogeau, M.P., and Pengelly, I. 1999. The importance of topography on landscape age patterns in the central Canadian Rockies. Banff National Park, AB. Unpublished manuscript.

parts of biodiversity by some authors (Noss 1990), but others (Angermeier and Karr 1994), including ourselves, ascribe the ecological processes to ecological integrity. Kimmins (1999) added temporal diversity to the biodiversity concept to capture the fact that forest ecosystems change over time as they progress after disturbance.

Biodiversity in Canada's forests comprises

(1) genetic diversity, which includes billions of genes that control basic metabolic functions and confer the ability of all living creatures in Canada's forests to adapt to changing environmental pressures.

(2) species diversity, which comprise more than 200 000 taxa (95% of which are arthropods and microbes and have not been classified by taxonomists) (Boyle 1992; Zasada et al. 1997).

(3) structural diversity, which includes the diversity in layering of forests under the dominance of approximately 60 tree species in Canada, in association with various groups of understorey vegetation. Coarse woody debris contributes to structural diversity.

(4) landscape diversity, which comprises over 1000 ecosystem types (Rowe 1972) arranged in unique mosaics that are created by the interaction of disturbance regime, climate, topography, and the ability of species to resist disturbance and regenerate. At a larger scale, landscape diversity also comprises each ecoregion of Canada.

(5) temporal diversity, which includes the different variants of each ecosystem type during various successional paths after disturbance (Kimmins 1999).

The conservation of biodiversity has become a sensitive issue in all aspects of forestry operations, including those of changes in landscape structure, road building, harvesting and silvicultural techniques, and manufacturing. The issue is hotly debated because of ecological, legal, moral, spiritual, and utilitarian concerns (Burton et al. 1992; Freedman et al. 1994; Freedman 2000). Moreover, the federal and provincial governments of Canada have committed to conserving indigenous biodiversity (Salwasser 1990; Anonymous 1992). Moral reasons for preserving diversity include the rights of future generations to inherit an intact environment, whereas spiritual reasons are related to the religious values to forests (Higgins 1998). Utilitarian reasons emphasize the conservation of biodiversity because species and ecosystems are valuable to humans, even if their usefulness is not yet known (Burton et al. 1992; Freedman 2000). Ecological reasons emphasize that biodiversity is required for ecosystems to function properly and with resilience and resistance to environmental change (Walker 1992; Baskin 1994).

As a rule all aspects of biodiversity are affected by forest harvesting. Although there is not yet an agreed-upon indicator of the integrity of biodiversity values, it is broadly agreed that indigenous elements are of greater value than introduced ones and that endangerment and extinctions should be avoided. However, pending the development of a suitable indicator of the integrity of biodiversity, it is not possible to make quantitative statements as to the disparity between ecosystems that have been clearcut or affected by natural fire regimes. Nevertheless, it is possible to make statements about the effect of natural and anthropogenic disturbances on particular elements of biodiversity. In the following sections we treat the effect of disturbance on the critical components of biodiversity separately.

Genetic diversity

Little research has compared genetic conservation between fire and clearcutting. However, trees have co-evolved with wildfire for millions of years and so have developed adaptive strategies (Buchert 1994). Indeed, fire-dependent conifer species exhibit several survival strategies. One involves maximizing the genetic contribution of parent trees by having persistent resin-sealed (or serotinous) cones so that, when a fire kills the parent tree, the stored seed is released. That seed carries the genetic variability of the original, parent population. Jack pine, lodgepole pine, and black spruce all develop serotinous cones. Some conifer species are protected by thick insulating bark and their tall stature that places their crown well above a surface fire. This allows these parent trees to survive low-intensity fires and to produce seed crops that capture the genetic variability of the fire-tolerant population. Red pine, white pine, and Douglas-fir are examples of such species. Depending on shape and size of conflagrations, wildfires do not usually impair the exchange of parent genetic material among stands. Likewise forest harvesting, particularly large clearcuts that remove most parent trees, may limit the chances of subsequent exchanges of their genetic material depending on size and shape of cutblocks, seedbed and seed predation conditions, effect of early competition, species composition of the adjacent stands, and the tree species involved.[3]

Forest harvesting may result in erosion of genetic diversity and tree vigour if post-disturbance reforestation programs are conducted with inbred seed lots. Woods and Heaman (1989) found that inbreeding occurred in Douglas-fir seed orchards where too many related parents were used to establish the orchard. Inbreeding reduced the numbers of filled seeds in mature cones. Compared to non-related matings, half-sibs had only 64% as much filled seed, full-sibs had only 53% as much, and self-matings produced only 4%. The issue here is more about the care taken in establishing seed orchards rather than forest harvesting. But if a mistake is made in establishment of a seed orchard, the increase in inbreeding is most likely to be seen on clearcuts because that is where planting stocks are used most extensively.

Inbreeding is also implicated in other species. In an experimental self-pollination of white spruce, Fowler and Park (1982) reported a 90% frequency of unfilled seeds and 45% loss in height and 64% loss in diameter at 17 years of age. Fowler (1965) reported various problems in self-pollinated eastern white pine compared to out crossed populations. Buchert (1994) pointed out that inbreeding of white pine may result in twisted needles, lack of apical dominance, chlorotic foliage, and slow growth.

A study by Buchert et al. (1997) examined the genetic diversity of two natural stands of white pine in central Ontario. Both stands were logged to remove 75% of the pine trees, leaving the surviving trees scattered evenly. The total and mean number of alleles in the remaining trees was reduced by 25% after one harvest; however, about 40% of the low frequency alleles and 80% of the rare alleles were lost because of logging. The authors suggested that the loss of rare alleles could represent an erosion of useful variation that could increase the chances of stand adaptation or improvement as unforeseen future changes occur. The lost mutations might, for example, be adaptive in coping with future pressures such as exerted by climate change. However, this problem could be mitigated if regeneration is conducted from locally collected seed that contains the same genetic diversity.[3]

When natural populations become decimated or isolated, the probabilities of inbreeding and self-pollination increase. For example, data from Michigan and Ontario show that white pine has been reduced to a small component of its historical abundance (Fig. 2). Buchert (1994) warned about eroded gene pools of this species due to harvesting selection (i.e., genetic high grading) and a lack of guidelines for the minimum number of individuals required to maintain a genetically viable population. An important question with respect to white pine is whether there are sufficient numbers of mature individuals remaining in surrounding stands to ensure outbreeding, so as to offset the loss of genetic diversity lost during logging. Will the progeny show gene diversity similar to the original stand? Following logging operation in Ontario, sites are replanted with white pine but with no assurance that the gene diversity has been protected. There is a need for studies that compare the gene diversity of natural regeneration on harvested sites with that of planted stock. Rajora and Dancik (1994) found a 12% reduction in genetic diversity in white spruce plantations as compared with natural regeneration of that species.

Namkoong (1984) suggested that managers have created conditions that threaten the extinction of alleles and populations of "critically important crop species". Gordon (1996) uses the term "commercial extinction" to summarize the damage that past logging systems have done to certain forest trees (i.e.,

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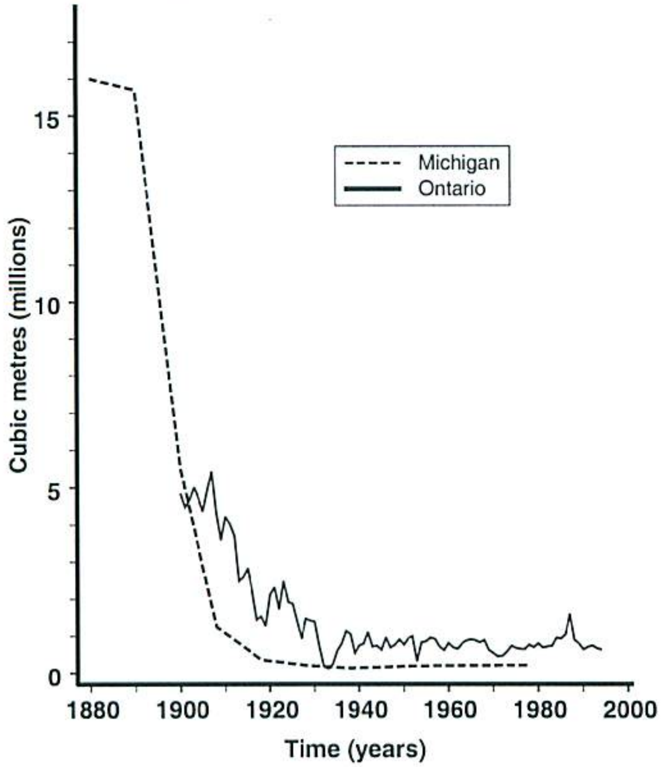
[3] J.P. Kimmins, personal communication.

Fig. 2. Annual volume of white pine used in the Upper Peninsula of Michigan from 1880 to 1978 (Whitney 1987), and annual volume of red pine and white pine harvested in Ontario from 1890 to 1994 (McKenney et al. 2001).



the rarification of a species below the point of commercial availability). White pine is essentially commercially extinct in Michigan, Wisconsin (except on the Menominee Forest), Minnesota, and on the verge of this degradation in Ontario (Fig. 2).

Red spruce was once the leading pulpwood and lumber species in the northeastern United States (Buttrick 1916; after Gordon 1996). Today, red spruce is at about one-fifth of its former abundance and is essentially commercially extinct in Ontario. Likewise, yellow birch (*Betula alleghaniensis*) is commercially extinct and hemlock (*Tsuga canadensis*) has been decimated in Ontario, Québec, the Maritime Provinces, and New England. Unsustainable harvesting has led to the loss of these and other species. White spruce, which once seemed in inexhaustible supply in boreal mixedwood forests from Ontario to Cape Breton Island, is now a relatively minor component in these forests because of excessive logging coupled with the ravages of introduced diseases and insect pests (Gordon 1996). It is important to point out that the extirpation of these species came from past logging practices that consisted mostly of selective, high-grading, logging.

Species diversity

Of Canada's 353 species at risk, 85 are forest dependant and include the woodland cariboo, wild ginseng, and several reptiles (Natural Resources Canada 2000). These observations reflect that species composition of Canada's forests has already been extensively altered by harvesting operations.

There is considerable literature showing that disturbance level and type affects almost all taxa pre-existing in the stand, but especially the forest specialists that require critical mature habitat elements such as abundant snags, coarse woody debris, and cavity trees, and also species sensitive to fragmentation

(Freedman et al. 1994). This is particularly evident in regions where fire-return intervals are long, such as coastal rainforests and other old-growth forest types.

Because species richness is generally greater in early successional stands than in older ones, the conservation of indigenous diversity is best achieved through landscape-scale management that emulates natural phenomena. For most temperate forests, species richness in younger successional communities is greater than in later stages. This occurs because recently disturbed ecosystems generally have greater quantities of available nutrients, and energy exchange, than do older ecosystems. As well, the fragmentation of old-growth landscapes by stand-replacing disturbances increases species richness at that scale (Harris and Silva-Lopez 1992). It must be noted, however, that species of patchily disturbed landscapes include many opportunistic taxa with broad distribution ranges and habitat tolerances. As such, favoring such opportunistic species is done to the detriment of taxa that are specialists of contiguous mature and old-growth forests, which could then become at risk (Harris and Silva-Lopez 1992; Monkkonen and Welsh 1994). Consequently, excessive landscape fragmentation impoverishes the abundance and diversity of native wildlife, even while overall species richness is increased. For this reason, it must be recognized that an essential component of any landscape-scale management program in forestry must include the designation of non-harvested protected areas of an appropriate size, shape, and number to sustain those elements of indigenous biodiversity whose survival is incompatible with forestry practices. This is particularly the case of species dependent on old-growth forests.

Wildlife responses to disturbance are strongly correlated with changes in ecosystem structure (Hunter 1990; Freedman et al. 1994). As described earlier, forest structure is greatly influenced by the disturbance regime and secondary succession. In general, species richness and diversity differ relatively little among variously aged stands, but the wildlife species composition is quite different. At a stand level, clearcut logging typically leaves few standing trees, snags, live cavity trees, or coarse woody debris. As was previously described, all of these habitat elements are critical to many dependent species (Harmon et al. 1986; Freedman et al. 1994, 1996). Cavities and woody debris, for example, are important as nesting and denning sites, feeding areas, and thermal and drought refuges for many species of animals.

In practice, four types of experimentation are available to compare the effects of wildfire and clearcutting on species diversity. These are (1) studies comparing the effects of disturbance on taxonomic groups of species (e.g., Tellier et al. 1996); (2) studies comparing the effects on groups of species organized as ecological guilds (e.g., Staddon et al. 1997); (3) studies comparing the effects on ecological processes controlling biodiversity (e.g., Whittle et al. 1997*b*; Staddon et al. 1998, 1999; Duchesne and Wetzel 2000); and (4) studies comparing effects on indicator species of economic or regulatory importance (such as the northern spotted owl (*Strix occidentalis caurina*), red-cockaded woodpecker (*Picoides borealis*), or woodland caribou (*Rangifer tarandus caribou*) (e.g., Pimentel et al. 1992).

The effects of wildfire on species diversity vary with the fire behaviour experienced. For example, frontal fire intensity has a large influence on the subsequent regeneration of blueberry species (*Vaccinium* spp.), bracken fern (*Pteridium aquilinum*), trembling aspen, raspberry (*Rubus* spp.), and beaked hazel (*Corylus cornuta*) (Johnston and Woodard 1985; Weber 1991; Tellier et al. 1995). Fire severity is also a key factor that can vary greatly among events. Fire severity refers to the degree of consumption of the forest floor (Alexander 1982) and can be measured by loss of biomass (kilograms per square metre), depth of burn (centimetres), or percent organic layer removal (McRae 1980). Fire severity influences the consumption or lethal heating of buried propagules, thus affecting the post-fire regeneration (Rowe 1983). Fire severity also influences microbial decomposition of organic matter, soil nutrient availability, and soil aggregation, which also affect succession. It may also prepare the organic layer, resulting in a better seedbed for some species (Ahlgren 1959), an important factor for the establishment of windblown-seed species. Studies have shown that fire severity is a critical factor on forest floor removal and subsequent regeneration by seedlings (Herr and Duchesne 1995*a*, 1995*b*).

Taxonomic groups of species have been used to compare the effects of clearcutting and wildfire using various diversity indices (Tellier et al. 1996). Such studies show that the diversity of various groups of organisms may be affected by disturbances, although effects on the species composition of communities tend to be much larger (Freedman et al. 1994). A simultaneous comparison of the responses of Carabid beetles (Coleoptera: Carabidae) (Duchesne and McAlpine 1993; Beaudry et al. 1997), vascular plants (Tellier et al. 1995, 1996), and forest floor microbes (Staddon et al. 1996, 1998) showed that these groups vary independently of each other in response to fire or logging (Duchesne 1996). However, both types of disturbance generally increased species diversity on the affected sites in the short term. However, an important corollary of these and many similar observations is that practices aimed at increasing diversity are not necessarily consistent with good conservation objectives — the actual species involved are also important, particularly if they are endangered. This latter concern is based on the global observation that the rate of extinction has been enormously increased because of anthropogenic influences and is now comparable in intensity to the mass extinctions that punctuate the geological record. This concern about endangered species is especially great in regions where indigenous biodiversity has been drastically depleted by human activities, such as much of the tropics and subtropics. Although there have been far fewer extinctions in Canada, the concern is also highly relevant here.

Structural diversity

Stand structural diversity can be measured using a range of variables, including stem density and the spatial complexity of the canopy (both vertical and horizontal). By any measure, stand structural diversity after disturbance is highly variable, depending on the particulars of the initial disturbance and the stage of succession. Table 3 summarizes changes in stand structure associated with several disturbance regimes. In this section we emphasize the effect of disturbance on stand age-class distribution as well as the presence of coarse woody debris.

In general, severe wildfires result in even-age regeneration, whereas clearcut harvesting may produce an uneven-aged stand comprised of a mixture of advanced regeneration and post-disturbance seedlings. Often, the advance regeneration is not of the same species that dominated the original overstorey. The effects of disturbances by both wildfire and logging can vary widely (Table 4). For this paper, we assume that most wildfires in Canada are stand-replacing disturbances, and most harvesting is by clearcutting.

In central Canada, balsam fir is the least commercially desirable, tree-sized conifer species. However, advanced regeneration on many logged sites favors a strong presence of balsam fir, which historically would have been reduce by wildfires. The advanced fir regeneration provides competition to more commercially desirable conifers, such as black, white, and red spruces. Balsam fir also provides a preferred source of food and habitat for spruce budworm, allowing it to maintain its endemic populations ready to start another infestation once the habitat reaches maturity. In Québec and the Maritime Provinces, pre-settlement forest contained a greater component of white spruce and red spruce than occurs now (Gordon 1996). Indeed, both of these spruce species regenerate better after fire than after logging, whereas balsam fir can sustain itself with advanced regeneration.

The presence of coarse woody debris is critical for biodiversity conservation. In a mature mixedwood forest dead trees commonly represent at least 5–10% of the standing trees. In the northwestern United States, snag densities were 3–5 times higher in non-harvested plots than in clearcuts, in a study of 220 plots in stands ranging from 40 to 200 years of age (Ohmann 1990). Data for New Brunswick were previously described (Fleming and Freedman 1998). Snags are critical wildlife habitat; for example, 85 species of North American birds use tree-cavities as nesting habitat, and more than 20 species of mammals use them for denning trees (Freedman et al. 1994, 1996). Greenberg et al. (1995) compared bird communities of mature pine forest with three disturbance treatments: (1) high-intensity wildfire, salvage logged, and naturally regenerated; (2) clearcut, roller chopped, and broadcast seeded; and (3) clearcut and seeded. Canopy- and cavity-nesters, and canopy- and bark-foraging species were virtually restricted to the mature forest habitats in that study.

As a post-wildfire stand develops, fire-created snags fall and become coarse woody debris on the ground. Forest harvesting and silvicultural management typically decreases the quantities of coarse-

Table 3. Comparisons of fire and logging as disturbances on stand structure.

Disturbance category	Timing	Frequency	Post-disturbance stand condition*	Postfire stand structure†
Fire B frequent, mild severity	Spring or fall	Short (<30 years)	Partial stand replacement, some standing dead, wounded. Large percentage of survivor trees and organic layer largely unburned	Multi-aged, open grown, low stocking density, a few very old trees
Fire B frequent, intermediate severity	Spring or summer	Short (<30 years)	Partial stand replacement, mix of survivors, many standing dead, and wounded	Multi-aged stand with some survivors from each burn
Fire B intermittent, intermediate severity	Spring or summer	Intermediate (31–60 years)	Partial stand replacement, mix of survivors, many standing dead, and wounded	Multi-aged stand with some survivors from each burn
Fire B intermittent, severe	Spring or summer	Intermediate (31–60 years)	Stand replacing, most standing trees killed. Organic layer removed	Even aged stands
Fire B infrequent, severe	Spring or summer	Long (61–100 years)	Stand replacing, most standing trees killed. Organic layer removed	Main canopy is fire origin with some other aged recruits possible
Fire B very infrequent, severe	Spring or summer	Very long (101–1000 years)	Stand replacing, most standing trees killed. Organic layer removed	Main canopy is fire origin, but other dynamics than fire tend to dominate
Clearcutting B short rotation	Year round	Short (<30 years)	Stand replacing, very few standing dead, wounded. Organic layer removed from skid trails, roads	Even aged
Clearcutting B intermediate rotation	Year round	Intermediate (31–60 years)	Stand replacing, very few standing dead, wounded. Organic layer removed from skid trails and roads	Main canopy originates after cut with some other aged recruits
Selection cutting B short rotation	Year round	Intermediate (31–60 years)	Partial stand replacement, very few standing dead, wounded? Organic layer removed from skid trails and roads	Aged classes tend to be compressed
Selection cutting B intermediate rotation	Year round	Intermediate (31–60 years)	Partial stand replacement, very few standing dead, wounded. Organic layer removed from skid trails and roads	Aged classes tend to be compressed
Selection cutting B long rotation	Year round	Long (61–100 years)	Partial stand replacement, very few standing dead, wounded. Organic layer removed from skid trails and roads	Main canopy originates after cut with some other aged recruits possible

*The idea of "variable retention" may fit well here, as a percentage of stand remaining after the disturbance: 95–100% (gap – single tree disturbance), 51–95% (patch replacement), 26–50% (partial stand replacement), 0–25% (stand replacement).
†Stand structure describes the general post disturbance horizontal and vertical elements of the forest.

Table 4. Biomass and nutrients removed by conventional (stem-only) and whole-tree clear-cuts, compared with amounts present in the forest floor and soil, for various mature stand types in Nova Scotia (Freedman et al. 1982, 1986). Harvest data are based on predictions made from species-specific equations relating biomass and nutrient content of trees to their diameter, coupled with field measurements of trees in eight plots of 20 m × 20 m per site. Forest floor data are based on 20 quadrants of 25 cm × 25 cm per site, and soil data on 20 pits to rooting depth (in parenthesis) per site.

Stand type	Sample	Biomass (t/ha)	Nutrients (kg/ha) N	P	K	Ca	Mg
Aspen	Stem only	42	66	7	53	109	15
	Whole tree	64	185	22	117	226	32
	Forest floor	20	303	31	62	48	37
	Soil (37 cm)	479	3625	914	11 900	569	11 900
Maple–birch	Stem-only	113	159	15	85	256	24
	Whole tree	155	355	38	183	448	45
	Forest floor	19	314	22	56	51	26
	Soil (39 cm)	325	4945	921	12 580	855	1139
White spruce	Stem-only	104	94	16	54	175	19
	Whole tree	143	263	37	126	340	37
	Forest floor	32	465	43	82	81	44
	Soil (48 cm)	314	5461	906	30 600	3660	18 540
Red spruce – balsam fir	Stem-only	167	192	24	93	278	28
	Whole tree	224	469	63	221	520	57
	Forest floor	94	798	81	138	165	86
	Soil (26 cm)	170	2257	551	10 800	292	3 290

woody debris in subsequent stands (Covington and Sackett 1992; Fleming and Freedman 1998). The progressive loss of woody debris under successive clearcut harvests was modelled by Spies and Cline (1988). They predicted that snag and log abundance would be 30% of the pre-harvest level at the end of the first 100-year rotation and only 6% after the second. Thus, the many wildlife species requiring these habitat elements would also be diminished.

There has been a focus in contemporary forestry on leaving standing dead and live trees, with typical management prescriptions calling for retaining 1–25 snags/ha (Freedman et al. 1994). After severe wildfires, virtually all trees are killed and converted to standing snags, with densities up to 10 000 stems/ha. In the Acadian forest of eastern Canada, snag densities ranged from 138 to 1115 stems/ha in mature non-harvested forest, but were only 0–25 stems/ha in plantations up to 25 years old (Freedman and Keith 1996). The size classes of snags are also critical for most dependent species. For example, pileated woodpeckers (*Dryocopus pileatus*) typically use nest trees greater than 64 cm in diameter (Maser et al. 1988). Criteria for the management of snags are available for some jurisdictions. In old-growth forests dominated by Douglas-fir of eastern Oregon, woodpeckers require the following snag characteristics for use as nest trees: pileated woodpecker, 0.32 snags/ha, larger than 64-cm diameter; common flicker (*Colaptes auratus*), 0.93 snags/ha, larger than 43-cm diameter; hairy woodpecker (*Picoides villosus*), 4.5 snags/ha, greater than 38-cm diameter; and black-backed three-toed woodpecker (*Picoides arcticus*), 1.5 snags/ha (Thomas et al. 1979; Maser et al. 1988). For the same region, Bull et al. (1980) recommended that at least 4 snags/ha be left on harvested sites to ensure maintenance of at least 70% of the potential woodpecker population. In the Acadian Forest of eastern Canada, recommendations are to leave at least 12–15 snags/ha (preferably >20 cm dbh) for feeding plus 10–12 live or dead, mature aspen or beech (*Fagus grandifolia*) for sustaining tree cavities (Woodley and Forbes 1996).

There are few criteria for the management of coarse woody debris, although the USDA Forest Service has suggested some for forests of the Rocky Mountains (Graham et al. 1994). Recommendations were given by habitat type and ranged form 5.6 t/ha in grand fir (*Abies grandis*)/mountain maple (*Acer spicatum*), to 74 t/ha in western hemlock (*Tsuga heterophylla*). These recommendations are based on relationships between ectomycorrhizal activity and woody debris (Harvey et al. 1981). In the Acadian Forest, it has been recommended that there should be at least 200 pieces/ha of coarse woody debris (average diameter >10 cm) and 10 m^3/ha throughout the stand rotation (Woodley and Forbes 1996). These criteria are based on average values found in mature, non-harvested forest in the region.

Depending on the frontal fire intensity and tree species, a wildfire may kill some or all of the mature trees in an affected stand (Rowe and Scotter 1973; Freedman et al. 1996; Stocks and Kauffman 1997). However, usually less than 25% of the total live biomass is consumed by fire, resulting in a large inventory of standing dead tree biomass in the aftermath stand (Auclair and Carter 1993). Eventually these snags are weakened by decay and fall down, resulting in the deposition to the ground surface of a large amount of large-dimension woody debris. In general, post-fire forest ecosystems include the presence of large numbers of snags and downed woody debris. This dead material provides important habitat elements for many species of plants and animals, while also storing a great deal of carbon (MacDonald 1993; Fleming and Freedman 1998; Freedman et al. 1996).

Clearcut harvesting of natural forests results in the removal of most of the aboveground woody biomass from the site, because trees are the commodity being harvested. However, clearcutting also results in a substantial deposition of woody debris to the ground in the form of slash, although this effect is much less in the case of whole-tree harvesting where branches and tops are removed from the site (Freedman 1995; Kimmins 1997; see also Table 4). Many clearcuts also retain substantial numbers of non-harvested trees, usually of non-economic species (for example, the conifers may be harvested and less-desired hardwoods left behind). However, these "leave trees" often die after the harvest (sometimes because of a silvicultural herbicide treatment) and eventually they become snags and then coarse woody debris. In subsequent rotations, particularly in plantations, snags and woody debris become much less abundant. This occurs because of the simplification of the plantation ecosystem in terms of species composition and size distribution (Cooper 1983; Spies and Clines 1988; Fries et al. 1997; Freedman and Keith 1996; Fleming and Freedman 1998; Freedman et al. 1996). For example, a study in southeastern New Brunswick found that snags and coarse woody debris were reduced to only 0.20 t/ha in 20-year-old spruce plantations, compared with 19.1 t/ha in natural, mature, mixedwood forests (Fleming and Freedman 1998). Because clearcut harvesting concentrates on the removal of biomass, it fails to produce large-dimension snags and coarse-woody debris in intensively managed forests, especially if plantations are established, as woody debris is often compromised during site preparation prior to planting.

Landscape diversity

Managing for high levels of diversity in stands and landscapes entails maximizing entropy within a site or ecosystem. This is a non-ecological objective because each forest region has a unique level of natural indigenous biodiversity. Within the boreal forest, biodiversity varies among ecosystems in response to natural disturbance regimes, topography, climate, and interactions among the species present. Before fire suppression in the boreal forest, burn frequencies ranged from about 20 years in northern Ontario to more than 500 years in western Newfoundland and coastal British Columbia (Foster 1983; Duchesne et al. 1994*a*). Varying fire cycles, along with other agents of disturbance, lead to unique mosaics of age-class distributions, stand sizes and shapes, and abundance of old-growth that, in turn, maintain regional forest biodiversity (Duchesne 1994*a*). Clearly, it must be recognized that all ecological regions display unique levels of indigenous biodiversity. In the forests of Canada, the natural disturbance regime, mainly associated with wildfire and irruptive insects, must be characterized, and their role in creating and maintaining local and regional biodiversity understood.

Perera and Baldwin (2000) state that differences in spatial patterns between harvesting and fire have resulted in a tremendous increase in the amount of edge created by forest harvesting compared to fire over the past 45 years in the boreal forest of Ontario. In turn, edge effects associated with road building and scattering small cut blocks across landscapes have greatly affected the distribution of wildlife in Canada. In part, this occurs because edges create novel habitats that favour opportunistic predators and parasites that take advantages of forest specialists.

Temporal diversity

In general, the advanced regeneration in the understorey is killed by wildfire. In addition, mature conifer trees are often killed, through crown consumption, crown scorching of the foliage, or by having thin-barked stems girdled. Some intolerant hardwoods, such as poplar (*Populus* spp.) and white birch (*Betula papyrifera*), are easily top-killed by fire but then regenerate well by sprouting (Rowe 1983; Bergeron et al. 1999). However, conifer-dominated boreal forests typically regenerate after fire by the prolific establishment of seedlings, which stabilizes the longer-term composition of forest types on the landscape (Heinselman 1981; Payette 1992). Most boreal conifer species, except balsam fir (*Abies balsamea*), tend to be abundant in post-fire stands (Furyaev et al. 1983; Carleton and MacLellan 1994).

Harvesting may also selectively remove longer-lived, more tolerant species such as red spruce, resulting in greater stand dominance by white spruce (*Picea glauca*) (Bergeron et al. 1999).

In fact, in some forest ecosystems wildfire is regarded as a stabilizing factor that ensures a high conifer component in post-disturbance stands, while logging may have the opposite effect (Van Wagner and Methven 1978; Payette 1992; Carleton and MacLellan 1994; MacDonald 1996). For example, abundant regeneration of mature jack pine nearly always follows wildfires but not necessarily timber harvesting, unless suitable remedial post-cut site preparation is carried out (Cayford et al. 1967). Similarly, fire-origin stands of lodgepole pine (*Pinus contorta*) in Montana were more strongly dominated with seedlings of that species than were stands of clearcut-origin.

Hardwood species often become more abundant on post-logging sites after the conifer component is removed (Davidson et al. 1988; Carleton and MacLellan 1994; Heinselman 1996). Timoney et al. (1997) concluded there was no evidence of post-logging convergence to the original conifer-dominated community and described the succession as a "long-term deciduous disclimax". This conversion can be especially prominent when mixedwood stands of spruce and poplar are logged, because the latter suckers even more densely after harvesting than after wildfire (Davidson et al. 1988; Weber 1991). Similar observations were made in Québec, where mountain maple (*Acer spicatum*) was less abundant after wildfire than after clearcutting (Archambault et al. 1997). Such conversions to intolerant hardwood species often result from their ability to sprout and seed-in after disturbance, coupled with relatively slow rates of establishment and growth of conifer seedlings. This so-called "hardwood conversion" may continue even if planting or direct seeding is practised after harvesting. The silvicultural use of herbicide is used sometimes to manage this process (Carleton and MacLellan 1994; Heinselman 1996). Adversely, the hardwood component of some boreal ecosystems, which is critical for wildlife, is maintained by fire.

The suppression of wildfire, coupled with the afforestation of abandoned agriculture land and post-harvest dominance by fir and white spruce, together with the abandonment of agricultural land, are thought to have increased the importance of certain insect pests, such as spruce budworm, red pine cone beetle (*Conophthorus resinosae*), and white pine cone beetle (*C. coniperda*) (Miller 1978; Blais 1985; Wade et al. 1989).

Depending on fire intensity, wildfire consumes some or most of the forest floor and, in the process, kills or retards the regeneration of understorey plants (Flinn and Wein 1977). The actual fire conditions experienced have varying effects on the post-fire vegetation (Rowe 1983). Because wildfires often leave islands of surviving forests, these can act as nuclei for revegetation (Carleton and MacLellan 1994).

Compared to burned-over sites, Carleton and MacLellan (1994) found post-logging black spruce sites had a higher abundance of broad-leaved shrubs. Johnston and Elliott (1996) suggest that fire mineralizes large amounts of biomass, providing available nutrients that are rapidly taken up by regenerating and colonizing vegetation. One unique effect of fire is that soil nitrogen is heat sensitive, which leads to nitrogen depletion under the upper range of the fire intensity scale. Given that most forest soils of Canada are nitrogen-limited, fire tends to reduce soil fertility. In comparison, logging results in less-rapid biomass mineralization, while nutrients, often cations, are taken from the site with logs (Freedman 1981; Freedman et al. 1986; Chrosciewicz 1990).

Although both harvesting and wildfire kills trees, only fire leaves them as dead standing biomass. Conifer snags, especially jack pine, and to a lesser degree black spruce, support a large, aerial seed bank found in the serotinous cones. Jack pine can store up to 5 million seeds/ha (Eyre 1938), which may be released from fire-killed trees for up to 3 years (Chrosciewicz 1990). In fact, the prescribed aerial seeding rate for scarified areas is only 50 000 seeds/ha of jack pine (Riley 1980). Although high seeding densities can lead to overstocking, there can be advantages in terms of form as trees may grow straighter and with less weevil (*Pissodes* spp.) damage. The fire-killed snags and woody debris cast partial shade, which ameliorates the surface microclimate and may enhance the survival of pine seedlings (Fraser and Farrar 1953; Cayford and McRae 1983; Carleton and MacLellan 1994). In addition, the growth of poplar suckers is less on sites well-shaded by fire-killed trees (Steneker 1974; Schier et al. 1985).

The greater abundance of broadleaved shrubs observed by Carleton and MacLellan (1994) on post-logging black spruce sites (compared with post-fire sites) could be due to differences in surface microclimate. Fires tend to have complex spatial patterns and often leave unburned patches that affect microclimate and also provide an important seed source. Fires also tend to reduce the forest floor biomass more than logging as they consume, depending on intensity, parts of the organic soil layers. At the extreme of difference, clearcut logging of Ontario boreal ecosystems favours the establishment of species of broad-leafed plants that are relatively efficient at dispersal and vegetative spread compared with conifers (Whittle 1997*b*). Certainly, the survival of regenerative structures after disturbance is a critical determinant of the pathway of secondary succession (Viro 1974; Kimmins 1977; Freedman 1995). Many plants are fire-adapted, having heat-resistant bark or protected buds, seeds, rhizomes, or bulbs that allow survival and rapid regrowth. Wildfire and logging can be expected to impact each of these regenerative structures differently, depending on the intensity of the disturbance, weather during the initial aftermath conditions, time of year, and other factors. Some mechanisms are favoured exclusively by fire, such as serotinous cones (Cayford and McRae 1983; Kimmins 1987). Without site preparation, these effects of wildfire on vegetation are not well emulated by clearcutting (Bergeron et al. 1999).

Some studies have suggested that the cover and richness of the understorey vegetation of a natural forest may never fully recover from clearcutting. Such conclusions have been made in chronosequence studies of intolerant hardwood forests in eastern North America (Flaccus 1959; MacLean and Wein 1977) and in Douglas-fir (*Pseudotsuga menziesii*) forests of the Pacific west (Halpern and Thomas 1995). The time since disturbance in those studies ranged from several decades to more than 430 years, but all showed incomplete recovery of the ground vegetation in post-clearcut stands compared with older, non-harvested forests. Some species of ground vegetation, especially old-growth specialists, are unable to recover following timber harvesting because of (1) longer-term recovery period than is provided by the length of the rotation, and so repeated disturbance leads to the permanent extirpation of such species, (2) changing climatic conditions that eliminate the possibility of some species to thrive, and (3) the facultative need for gap-phase disturbance conditions, which reintroduce understorey vegetation in older forests. In another study in Appalachian hardwood forest, Duffy and Meier (1992) concluded that cover and species richness did not increase with post-harvest age, at least up to 87 years following logging. Because of a dearth of studies, it is not known whether similar results apply to post-harvesting regeneration in boreal forest or even to post-fire succession. Nevertheless, this points to the issue of successional time when comparing fire and logging as disturbances. The study of Duffy and Meier (1992) was criticized because of undue focus on vernal species (Elliot and Loftus 1993; Johnson et al. 1993). The rebuttal by Bratton (1994) focussed on measuring a range of species responses, including taxa particularly sensitive to logging. The issue of post-harvest recovery of the understorey vegetation is not yet scientifically resolved, but it has clear policy implications with respect to maintaining indigenous biodiversity.

Because wildfire and harvesting are different at both local and landscape scales, these disturbances result in ecosystems that are different in both structure and function (Gluck and Remple 1996; Johnston 1996; Bergeron et al. 1999). Such factors as spatial patterns of disturbance, scarification, species composition, biomass and nutrient accumulation, and nutrient availability may be quite different on burned as compared to logged sites (Johnston and Elliott 1996).

Pests and pathogens

Wildfires reduce the presence of some hosts that assist the spread of pests and pathogens, while clearcutting may promote them. For example, balsam fir is a key food of the spruce budworm, and species of currants (*Ribes* spp.) are alternate hosts for white pine blister rust (*Cronartium ribicola*). Stands with high levels of tree mortality caused by budworm or other pathogens are predisposed to fire (Stocks 1987). For example, the largest known burns in New Brunswick (the Miramichi fire of 1825) and Ontario (the Chapleau–Mississaugi fire of 1948) were substantially fuelled by large amounts of standing budworm-killed timber. Fire temporarily eliminates balsam fir from burned areas because it is extremely vulnerable to this disturbance — even a low-intensity fire can kill this species because of its thin bark. In contrast, clearcutting in boreal mixedwood usually leaves a large amount of advanced regeneration of balsam fir, allowing the species to survive and be prominent in the succeeding stand.

Logging may also have increased the preference of cone beetles for jack pine. De Groot (1991) suggests that the jack pine cone beetle (*Conophthorus banksianae*) is actually an ecotype of the red pine cone beetle that has shifted its preference from red pine to jack pine. De Groot suggests this may have occurred because of logging practices that have reduced the abundance of red pine in Ontario, while favouring jack pine. This interesting hypothesis needs to be substantiated by comparative studies of the DNA or other biochemical attributes of these cone beetles. The case of the cone beetles illustrates the notion that pests and pathogens are themselves forest "managers", whose effects are not necessarily compatible with the economic objectives of humans (Castello et al. 1995).

Research on the white pine weevil (*Pissodes strobi*) has shown no difference in damage between planted and aerially seeded stands of jack pine (Bellocq and Smith 1994). Unfortunately, there is no similar comparison of weevil damage between planted and naturally regenerated jack pine, which often occurs in high densities following wildfire. Katovich (1992) discusses the effects of shading on weevil damage in white pine stands. He notes that shade provides a cooler microclimate that significantly reduces weevil egg-laying, larval development, and damage (see Graham 1918; Sullivan 1960). The silvicultural recommendation is to grow white pine in partial shade (about 55% of full sunlight) to promote the growth of thin leaders with a lesser chance of weevil attacks (Katovich 1992; Wetzel and Burgess 1994).

Because jack pine needs about 85% of full sunlight for optimal growth, it is not practical to grow it in shade to reduce weevil damage. For jack pine, reducing weevil damage requires the promotion of thin leaders by some means other than shading. This may be a key difference between jack pine planted after clearcutting and its natural regeneration after wildfire. In plantations, a stocking of about 1600 to 3200 seedlings/ha has been considered acceptable in Ontario (Galloway 1984). However, typical densities of regeneration after wildfires are much greater with up to 37 500 to 50 000 seedlings/ha reported (Ahlgren 1959). Jack pine open-grown in a plantation is more likely to have thicker leaders, because of less competition for light, compared with denser post-fire stands.

In British Columbia Dwarf mistletoe (*Arceuthobium* spp.) are common parasites of *P. contorta,* and *Larix occidentalis* that tend to accumulate during rotation (Parmeter and Uhrenholt 1976). The exclusion of fire from such ecosystems, along with forestry practices that leaves young infected trees in the residual stand, leads to increased abundance of this parasite. In contrast, fire eliminates Dwarf mistletoe.

Forest floor biomass

Wildfire consumes much of the biomass of the surface litter and forest floor. In practice, biomass removal by fire depends on fuel moisture at the time of the burn (Viro 1974; Freedman et al. 1996; Kimmins 1997; Stocks and Kauffman 1997). For example, a study of boreal forest in northwestern Québec found that wildfire had decreased the mass of the forest floor by about 10–22% (Brais et al. 1995), while a similar study in Finland found a decrease of about 20% (Viro 1974). However, larger reductions have been observed in other studies. Work in boreal forest has found that experimental burns decreased the thickness of the forest floor by 27–63% in Alaska (Dyrness and Norum 1983), 79–91% in northwestern Ontario (Smith 1970), and up to 100% in northeastern Ontario (Stocks 1987).

The post-fire forest floor and upper soil typically have a warmer surface temperature compared to the pre-fire conditions. This occurs because of the combined effects of a darker surface colour and a higher intensity of insolation through a thinned or destroyed overhead canopy (Viro 1974). For instance, the average mid-day summer temperature at the forest floor surface was 31°C on a burned site in Finland, compared with 18°C on an unburned spruce stand (Viro 1974). Such warming, when not associated with excessive evaporation of soil moisture, stimulates microbial activity and speeds up the decomposition of litter and organic matter of the forest floor. For example, raising the temperature of forest floor humus from 6°C to 12.5°C in a laboratory incubation resulted in a doubling in the rate of decomposition, while raising it to 20°C quadrupled the rate (Viro 1974). In addition, surface burns may kill shrubs, whose root mat helps to keep the forest floor porous; the death of these plants contributes to a compression of the forest floor in subsequent years (Viro 1974). Both of these factors (i.e., increased decomposition and compression), in combination with decreased inputs of leaf litter during the initial stages of post-fire succession, contribute to decreases in the thickness of the forest floor. Such post-fire influences on the forest floor can persist for as long as 20 years, followed by recovery as the next stand develops and matures (Viro 1974).

Clearcutting and other harvesting systems can also affect the biomass of the forest floor (Freedman et al. 1996; Kimmins 1999), but their effects depend largely on forest types, type of disturbance, aspect, slope, and other ecoclimatic factors. Decay rates are affected by disturbance by a reduction in the rate of litter deposition, coupled with an increased rate of litter decomposition. The faster decomposition is due to a higher surface temperature (because of less shading by an overhead canopy), increased moisture availability (because of less evapotranspiration), and physical mixing of the organic substrate by logging machinery. Various studies have demonstrated a higher rate of litter decomposition in clearcut stands (Covington 1981; Binkley 1984; Federer 1984; Startsev et al. 1998; Prescott 1997). For example, studies of montane conifer-dominated forest at four sites in west-central Alberta found that clearcutting significantly increased the rates of litter decomposition and soil respiration (Startsev et al. 1998). Research at three sites on Vancouver Island, ranging from low elevation to montane, found that the rate of litter decomposition on the surface was not increased on clearcuts, compared with the reference conifer forest (Binkley 1984). However, the rate of decomposition was 3–5 times faster deeper in the profile, both within the forest floor and at its interface with the upper mineral soil. This difference was presumably due to the drier conditions occurring in the surface of the forest floor of the clearcuts. Another study involving a comparison of clearcuts with old-growth, coniferous Montane forest on Vancouver Island found a higher rate of leaf-litter decomposition in the first 2 years after harvesting, because of moister, more moderate climate conditions at the ground surface (Prescott 1997). Overall, however, this study did not find a significant difference among treatments in the rate of decomposition of the forest floor itself.

Some other studies have not found that clearcutting increased the rate of decomposition of plant litter or the forest floor. Studies of a chronosequence of hardwood stands in Nova Scotia did not find a significant effect of clearcutting on the decomposition of leaf litter (Wallace and Freedman 1986). Another study of mixedwood forest in southwestern New Brunswick found no significant difference in the forest floor biomass of clearcuts and adjacent, mature forest (Fleming and Freedman 1998). A study of boreal mixedwood forest in northwestern Ontario found no difference in soil respiration between clearcut and uncut treatments (Mallik and Hu 1997). Another study of old-growth and second-growth coniferous forest on Vancouver Island found no significant difference in the rates of litter decomposition or forest floor respiration between clearcuts and the forested habitats (Keenan et al. 1994). Comparing the effect of clearcutting, scarification, and prescribed burning on leaf litter decay rates of jack pines forests of Ontario, Duchesne and Wetzel (2000) found that fire decay rates only for 2 years after disturbance. The decay rates of burned-over plots at different intensity did not differ from the decay rates of clear-cut, scarified, or control plots 3 years after disturbance (Duchesne and Wetzel 2000).

Although the effects of wildfire on the forest floor are highly dependent on fire characteristics, it appears that fire usually has a much greater effect on reducing the biomass of the forest floor than generally results from clearcutting.

Nutrient cycling

Wildfires have well-known effects on nutrient cycling (Rowe and Scotter 1973; Grier 1975; Raison 1979; MacLean et al. 1983; Kimmins 1997). Wildfires result in a relatively even deposition of inorganic nutrients across a burned area, particularly of calcium, magnesium, potassium, and phosphorus present in ash. There is also a large deposition of woody debris, whose content of organically bound nutrients is slowly released through decomposition. The deposition of base cations (i.e., calcium, potassium, and magnesium) in ash results in a decreased acidity of the forest floor and upper mineral soil, a change that can stimulate nitrate production through bacterial nitrification. However, fire also results in large losses of organically bound nitrogen from combusted biomass, mostly through the emission of nitric oxide and ammonia produced during pyrolysis. During post-fire succession there is a progressive re-acidification of the forest floor due to the uptake of base cations by aggrading vegetation, coupled with leaching from the site of potassium and other mobile cations. Post-fire succession is also characterized by a progressive re-accumulation of biomass and nutrient capital in living and dead forest biomass and by a decline in the concentrations of available nutrients in the forest floor and soil.

As was just noted, immediately after burning the deposition of base-rich ash results in an decrease in the acidity of the forest floor and upper mineral soil (i.e., pH is increased) (Viro 1974; Grier 1975; Dyrness and Norum 1983; Brais et al. 1995). For instance, studies of a post-fire chronosequence of boreal forest in northwestern Québec found that the acidity of the forest floor increased to about pH 5.5 in recently burned stands (from pH 3.65 in the unburned mature forest) (Brais et al. 1995). The same study found large post-fire increases in the concentrations of calcium, magnesium, potassium, and total exchangeable cations. Studies of burned boreal forest in Finland found that the pH of the forest floor increased to 5.9 in the first year after burning, with a progressive re-acidification to the pre-burn pH of about 4.0 after three decades of succession (Viro 1974). The amount of total calcium (i.e., acid digestible) in the forest floor increased by about 65% during the first six post-fire years, while that of total magnesium increased by about 30%. There were even larger increases in exchangeable calcium and magnesium in the forest floor (i.e., extracted using 1 N acetic acid at pH 4.7); the amount of calcium approximately tripled in the first post-burn year, while magnesium doubled. However, by the sixth post-fire year the amount of total potassium in the forest floor had decreased by about 40%, presumably because this monovalent, readily leached cation had moved downward into the mineral soil (calcium and magnesium are divalent cations and are more strongly bound to ion-exchange sites).

Phosphorus may also form leacheable, water-soluble compounds after burning, resulting in somewhat lower amounts in the forest floor for about 6 years after burning (Viro 1974).

Nitrogen cycling is also greatly affected by burning. During combustion the organic nitrogen of biomass is largely oxidized to gaseous nitric oxide (NO) and ammonia (NH_3), which are lost to the atmosphere. This can represent a substantial loss of the site capital of fixed nitrogen. Studies in boreal Finland estimated this nitrogen loss to typically be about 320 kg/ha, equivalent to about 10% of the total nitrogen on the site (Viro 1974). A study of a wildfire in conifer forests of the northwestern United States reported a nitrogen loss of 855 kg/ha (Grier 1975), while work on slash burning in coastal British Columbia reported a loss of 580 kg/ha (Kimmins and Feller 1976). This lost nitrogen capital is slowly re-accumulated during post-fire succession, mainly through the deposition of ammonium and nitrate in precipitation, and by the dry deposition of oxides of nitrogen (i.e., NO_x) and ammonia gases (Freedman 1995).

Burning also results in a short-term increase in ammonium concentration in the forest floor and upper soil, originating with the pyrolysis of organic nitrogen. The increased ammonium, warmed soil, and high pH in the forest floor and soil after burning can result in a stimulation of nitrification, which may lead to relatively high concentrations of nitrate for several years (Rowe and Scotter 1973; Viro 1974; Brais et al. 1995). This is why post-burn sites often support large populations of nitrophilous (or nitrate-loving) herbaceous plants, such as fireweed (*Epilobium angustifolium*) and red raspberry (*Rubus strigosus*). Studies of burned boreal forest in Finland found that the nitrate concentration in the forest floor increased to 32 ppm in the first 3 years after burning, then returned to background levels within 10–12 years (Viro 1974). The amount of total nitrogen, almost all of which is organic nitrogen, closely tracked the quantity of forest floor biomass. Studies of a post-fire chronosequence of boreal forest in northwestern Québec found that the nitrate concentration in the forest floor increased after burning, reaching a peak value in a 27-year-old stand (Brais et al. 1995). A prescribed burn in pine forest in Arizona resulted in large and immediate changes in the concentration of ammonium (NH_4-N) in the forest floor. Indeed, soil ammonium increased from 2.3 to 45 ppm in burned old-growth forests, from 1.3 to 27 ppm in pole-sized habitat, and from 1.3 to 8.3 ppm in sapling habitat (Covington and Sackett 1992). This effect declined rapidly with time, and after one post-burn year only the burned old-growth habitat was significantly different from unburned reference forest (i.e., 30 versus 2.6 ppm NH_4-N, respectively). There were no immediate post-burn changes in nitrate concentration, but by the first post-fire year its concentration increased because of a stimulation of nitrification. The greatest increase of nitrate occurred in old-growth habitat (19 ppm NO_3-N in the burned treatment compared with 0.03 ppm in the reference forest). After wildfire, streams draining burned watersheds may be enriched in nitrate, phosphate, and other nutrients (Tiedemann et al. 1979; Freedman 1981; Bayley et al. 1992).

Several studies have suggested that the deposition of charcoal after a fire may also have a beneficial effect on nutrient cycling and plant growth (Zackrisson et al. 1996; Wardle et al. 1998). This appears to be due to the sorption of phenolics and other secondary metabolites by charcoal; these substances are potentially toxic and can inhibit microbial processes and root health.

The harvesting of forests also has a great influence on nutrient cycling. The most immediate effect is the removal of large quantities of organically bound nutrients present in the harvested biomass, representing a large reduction of site nutrient capital (Kimmins 1977, 1997; Hornbeck 1977; Freedman 1981, 1995; Smith 1985; Mann et al. 1988). During a conventional, stem-only clearcut the nutrients contained in the tree boles (wood and bark) are removed from the site. This depletion is at least doubled if a whole-tree harvest is made, because this method also removes nutrients contained in branches and foliage (the additional harvest of biomass is typically about 30%, but the extra tissues have relatively high concentrations of nutrients). Whole-tree clearcuts may be made to gain the additional yield of biomass, which may be used as a source of combustible energy (e.g., as hog fuel in a pulp mill). Often, however, whole trees are skidded from the harvested site and then de-limbed at a landing, with the slash piled and later burned. This latter kind of whole-tree harvest is wasteful of both biomass and nutrient capital, but it has the short-term benefit of leaving little slash on the clearcut site, making it easier to replant.

Numerous studies have determined the potential removals of nutrients with conventional and whole-tree clearcuts of various forest types. In this paper, it will be sufficient to illustrate this point using data for several stand types in Nova Scotia (Table 4). The data show that clearcutting removes large amounts of biomass and nutrients from the site, and that these are equivalent to a substantial fraction of the site capital of these materials. This is especially evident for calcium, which is present in small quantities in acidic soils derived from oligotrophic tills of granite, gneiss, and other siliceous rocks. This is a common geomorphological feature of many forest regions of Canada (Weetman and Algar 1983; Dyck et al. 1986; Freedman et al. 1986; Freedman 1995; Likens et al. 1996; DeHayes et al. 1999).

During post-harvest succession the amounts of these materials increase again as the living and dead biomass in the stand regenerates; a so-called "ecological rotation" occurs if sufficient time has elapsed before the next harvest to allow a complete recovery of stand-level biomass and nutrients (Kimmins 1977). Forest harvesting can also increase the rate of mineralization of organically bound nutrients and thereby increase their concentration in the forest floor and mineral soil. For instance, studies at three sites on Vancouver Island, ranging from low elevation to montane, found that the availability of nitrogen (measured by ion-exchange resins) was 7–20 times higher in clearcuts than in the reference conifer forest (Binkley 1984). Another comparison of harvested treatments with old-growth, coniferous montane forest on Vancouver Island found a higher rate of nitrogen mineralization and soil nitrate after clearcut harvesting (Prescott 1997). However, not all studies have found that clearcutting increases the rate of mineralization of organic nitrogen. For example, studies of a chronosequence of hardwood forest in Nova Scotia did not find a significant effect of clearcutting on ammonium or nitrate concentration in the forest floor (Wallace and Freedman 1986).

During a wildfire, biomass capital of the stand is lost by combustion, as is that of nitrogen through the oxidation or organic compounds and the release of gaseous NO and NH_3. In intense wildfires, these losses of biomass and nitrogen can be comparable in magnitude to what would be removed by the clearcutting of comparable stands. Unlike wildfire, however, clearcutting also removes large amounts of phosphorus, potassium, calcium, and magnesium contained in the tree biomass; these materials are mostly conserved in situ during a wildfire.

Soil structure

Although much of the litter and forest floor may be consumed during a wildfire, the underlying soil profile remains relatively intact. Once snags start to fall over, however, there may be some mixing of the mineral soil in root-mat tip-ups. In addition, as previously noted, the deaths of trees and shrubs can result in a loss of root volume in the forest floor, eventually resulting in compaction (Viro 1974). Harvesting removes most of the larger trees that would normally be retained as snags and coarse woody debris on a burned area and then incorporated with time into the forest floor. Once this material is well rotted, it provides an excellent seedbed for the germination of seeds, while also enhancing survival because of high moisture retention.

Clearcut harvesting with heavy equipment can cause severe soil compaction along skidding lanes, and it can also disrupt soil profiles by churning (Greacen and Sands 1980; Froehlich and McNabb 1984; Waring and Schlesinger 1985; Freedman 1995; Kimmins 1997). In some cases, wetter conditions can develop because of impeded drainage or the reduction of evapotranspiration in the harvested stand. This change can restrict decomposition and nutrient cycling through the development of poorly oxygenated conditions and can impair root development because of decreased porosity and anaerobic conditions. Studies of clearcuts of montane coniferous forest at four sites in west-central Alberta found that skidder logging increased the bulk density of soil by an average factor of 12% (Startsev et al. 1998). In general, the use of lighter, large-wheeled logging machinery results in much less physical disturbance of the soil. Although wildfire results in some physical disturbance of the soil profile, the repeated passage of heavy equipment during clearcut logging can result in a much more severe effect on soil structure.

Microclimate

An obvious change in site microclimate following wildfire is the increase in light intensity because of the removal of shading vegetation. Kozlowski and Ahlgren (1974) state, "if this were the only change, however, then the post-fire vegetation would be similar to the vegetation following logging." Both disturbances also cause large changes in the temperature and moisture of the upper soil, surface atmospheric conditions, and in local precipitation. Comparison of the effects of clearcutting and wildfires on microclimate is made difficult because research simultaneously investigating the two disturbances has not yet been done. In fact, research on microclimatic changes after wildfires is very limited; most investigations have examined timber harvesting.

Effects of clearcut logging on microclimate were reviewed by Keenan and Kimmins (1993). They reported that the diurnal range of air temperatures (at 1.5 m above the ground) generally increase by about twofold on clearcuts compared to beneath a forest canopy, and that of the surface by 2.5–3.0 times. Precipitation input at the surface increase by 15–50%, resulting in more soil moisture and a rise in water tables in low-lying areas. In a study in Oregon, however, soil moisture returned to pre-harvest levels within 5 years (Adams et al. 1991). Keenan and Kimmins (1993) also reported that, on sunny days, maximum surface temperatures on clearcuts increased up to 20°C on bare soil and 30°C on litter. Either condition could result in plant mortality; photosynthesis declines markedly above about 35°C, and temperatures above 50°C are lethal to most plants.

Clear, calm nights have an important effect on microclimate because of the low temperatures that can lead to frost damage to plants. Net upward radiation was higher in open areas compared to beneath a forest canopy, while air and soil temperatures decreased by as much as 2–5°C. Such differences carry an increased risk of frost occurrence during the growing season (Keenan and Kimmins 1993). One study compared minimum daily surface air temperatures between clearcuts and adjacent uncut forests in Montana. During the growing season (about 150 days), 16–26% of the nighttime lows were below −5°C in clearcuts, compared to <1% in the forested habitat (Hungerford and Babbitt 1987; Sexton 1998). Sexton (1998) also reported that surface temperatures below −5°C during the growing season resulted in mortality of first-year seedlings of ponderosa pine. In an Alaskan study, Yarie (1993) reported that evaporation from the soil surface increased 5-fold following clearcutting, but there was little effect on air temperature. Sexton (1998) summarized the effects of overstorey removal on the microclimate as (1) increased daytime solar radiation at the surface; (2) increased heat loss at night (Hungerford 1980); (3) decreased afternoon relative humidity (Miller et al. 1983); and (4) decreased soil moisture (Fowler and Helvey 1981).

Rouse and Mills (1976) summarized 3 years of microclimate research following burning in open subarctic woodlands in the Northwest Territories. During the summertime, surface soil was 3.0 to 5.5°C warmer and 12–20% drier in the burns than in unburned woodland. Examination of older burns suggested that the drier soils was an effect that lasted for decades. They suggested that a large burn of several hundred square kilometres could influence the yield of water from watersheds and affect wildlife habitats on a large scale. Many fire-dependent plants of early seral stages benefit from increased soil temperature, which is favorable to their germination and growth (Scotter 1964). In subarctic climates, the active layer of the soil can become thicker because of increased post-fire soil temperatures (Viereck 1983). Other reports on changes in microclimate due to wildfires are scarce, hindering a more detailed comparison with clearcutting.

Road networks

Permanent roads are not generally associated with wildfire management or suppression (although temporary access routes may be constructed while fighting some wildfires). An extensive road network is, however, necessary for timber harvesting and subsequent stand management.

Roads affect biodiversity in many ways. Roads directly remove natural habitat, alter drainage and stream dynamics, cause erosion, introduce edge effects, fragment contiguous ecosystems, alter species movements, and act as corridors for the introduction of non-native species (McGurk and Fong 1995; Forman 1995; Evink et al. 1996; Haskell 2000; Jones et al. 2000). In addition, motor vehicles cause mortality through wildlife collisions, and roads increase local hunting pressures by improving accessibility. The effects of roads are largely a function of their density, level of use, and location on the landscape. Many of the effects of roads can be mitigated by planning that avoids steep or unstable slopes, by paying attention to stream crossings and surfacing materials, and by closing and reclaiming the roads after harvesting and (or) silviculture are finished.

It is important to examine road density in terms of the position of roads on the landscape. For example, in Banff National Park and its surrounding region, the overall road density is low. However, the area is mountainous and roads are concentrated in montane valley bottoms. But because these lowlands are critical wildlife habitat, roads have a major impact on the greater ecosystem.

Road density is a useful indicator of ecological threat by various land-management agencies. In Canada, the Atlantic Maritime ecozone has a moderate road density (>0.25 km/km^2), and in the Taiga Plains and Boreal Cordillera ecozones of British Columbia there are vast stretches with sparse road densities (<0.25 km/km^2) (Canadian Council of Forest Ministers 2000). Comparable figures for other areas are 0.08 km/km^2 in Alaska, 0.53 km/km^2 in Maine, 2.3 km/km^2 in the United Kingdom, and 8.8 km/km^2 in Connecticut. Road density can be used to indicate areas influenced by local human stressors, which are relatively close to roads and decline rapidly with distance. A distance of 1 km is sometimes suggested as representing a critical distance from a road for some ecological values (e.g., grizzly bear (*Ursus arctos*)). British Columbia has about 22% of its landscape within this distance of roads (Canadian Council of Forest Ministers 2000).

Criteria for risks to certain species have been developed based on road densities. For example, Mech (1988) described primary wolf (*Canis lupus*) range in Minnesota as having an average mean road density of <0.36 km/km^2 and the peripheral and disjunct parts having ≥ 0.54 km/km^2. Other studies indicate that road densities >6.2 km/km^2 reduce habitat security and increase mortality for a range of larger mammals, including elk (*Cervus elaphus*), bears, wolverines (*Gulo gulo*), and lynx (*Lynx lynx*). The Interior Columbia Basin Ecosystem Management Study classed road densities as follows: extremely high (2.90+ km/km^2), high (1.05–2.90 km/km^2), moderate (0.43–1.05 km/ km^2), low (0.06–0.43 km/km^2), and very low (0.06–0.01 km/km^2) (Quigley 2000). In the Boise National Forest, there are road density standards for each forest management area, based on a habitat effectiveness model for elk. Typical values are 1.85 km/km^2. Forman et al. (1997) suggested that a road density of 0.6 km/km^2 is a threshold value, which when exceeded would cause the loss of many large mammals. In general, however, criteria for assessing road density are not well developed and can vary by road-use type and species. Nevertheless, road density is an easily obtained indicator of a wide range of ecological integrity.

Conclusions

A large body of scientific literature shows that many of the ecological impacts of forest harvesting., particularly clearcutting, and wildfire differ in important ways and that it is erroneous to assume that forest harvesting plays the same ecological role as wildfire. Some of the most salient points of our review are the following:

(1) The scales of disturbance created by fire and contemporary forest harvesting are different. The patch sizes created by forest harvesting are only a small subset of the range created by wildfire.

Depending on the forest region and management objectives, forest harvesting may not always represent the wildfire-caused variations of patch sizes across the landscape which may include large numbers of small disturbances, or the small number of extremely large disturbances created by high-intensity wildfires.

(2) The frequency of harvesting is generally different from the natural fire-return interval. Fire- return intervals vary widely, with stand-replacing events occurring in the range of 20 to 500+ years in Canada. Harvest frequencies are dictated primarily by the rotational age at merchantable size, which typically ranges from 40 to 100 years. Moreover, because of re-burning of younger age classes, about 37% of a fire-disturbed forest is older than the fire-return interval. Contemporary forest harvesting does not maintain these distributions, especially in the older age classes.

(3) The location of fire on the landscape is a function of slope, aspect, and valley orientation, resulting in a complex mosaic of stand types of different ages. Clearcutting is not limited by the same constraints.

(4) The shape of clearcuts does not follow the general ellipse pattern of wind driven wildfires. Nor does it have the ragged edges and unburned internal "islands" typically found in stand-replacing fires.

(5) Fire leaves large amounts of snags and coarse woody debris, whereas contemporary harvesting leaves little of these critical habitat components.

(6) The road networks left by harvesting have many direct and indirect environmental impacts, including erosion, direct habitat loss, fragmentation, and increased access for hunters and other recreational users. There is no such equivalency in a fire-disturbed forest, as roads are not usually associated with wildfire.

(7) Biodiversity is affected in different ways, which depend largely on ecosystem type, by forest harvesting and wildfire.

(8) Successional pathways following forest harvesting and wildfire are not always equivalent. In those sites where forest harvesting and wildfire differ, harvesting tends to favor angiosperm species of trees and may result in decreased conifer dominance. An exception is balsam fir, which increases with fire exclusion. Also, understory species richness, cover, and composition appear to not always recover during the harvest rotation times used in contemporary logging, especially in places where older forest are being harvested.

Although our review shows that wildfire and harvesting may differ considerably in their ecological effects, we believe that it is still possible to promote emulation silviculture by tailoring forestry operations after desirable effects of fire in forest ecosystems. Given that wildfire has ecological impacts that can be either desirable or undesirable from a forest management perspective, it will be important to determine which features of wildfire can and should be emulated in forestry operations. In practice, emulation silviculture will become a compromise among what is ecologically desirable, what is economically feasible, and what is socially acceptable. Whatever emulation practices are selected, however, it will require a careful experimental approach to evaluate the effects of the complex disturbance patterns and to determine their similarity at the microsite, stand, and landscape level.

At the microsite and stand levels, Bergeron et al. (1999) suggest that, in the absence of site preparation, the effects of clearcutting only superficially resemble those of wildfire. They suggest silvicultural treatments that would better mimic fire at the site level, such as seed-tree retention, patch cuts with seeding or planting, and large clearcuts followed by seeding and planting. As well, for microsite management we do not exclude the use of prescribed burning as a means to improve the outcome of ecosystems after clearcutting, although prescribed burning is made complicated by various contingencies at the operational level.

At the landscape level, much could be done to bring harvesting to more closer approximate wildfire patterns, for example, by using a combination of many smaller patch cuts and a few extremely large clearcuts. Harvesting could also emulate the general ellipse shape of burned patches, leaving ragged edges and unburned "islands". More standing trees and snags should be left on site. Harvesting could also be planned to emulate the topographic complexity on the landscape. In addition, a broader range of older age-classes could be left on the landscape, including some extensive protected areas. While all these elements are possible, these emulation tactics might be considered "impractical" to implement (although this would largely be a reflection of conventional economic attitudes and values, rather than those of ecological economics).

Certain legal and political needs must also be addressed before emulation silviculture could be implemented and its success monitored. Legal questions arise relevant to the credibility of the "green certification" of forest products, along with provincial legislation promoting emulation silviculture. For example, in fire science, emulation covers everything related to wildfire behavior and post-burn effects, while in forest management only some fire attributes are usually considered. A frequently used attribute of fire emulation planning is that wildfire size is justified to support the clearcutting of large areas. Area perimeter is also often cited in recognition of the ragged edges that often occur on wildfires, and may be mimicked for wildlife management. Harvesting techniques may be adjusted to create this same type of ragged edge effect. In addition, some areas should be left untouched within harvested areas to mimic the unburned islands that occur during wildfire. A problem, however, is that when only a single fire attribute is targeted for mimicking during forest harvesting, it may inappropriately happen outside the larger ecological context. In many cases, the attribute to be emulated may have been selected for its ease of implementation rather than for broader ecological reasons. Such decisions ignore the complexity of post-fire effects (e.g., on nutrient cycling, snags, seed-trees, vegetation, soil fauna, animal wildlife, etc.), which are affected by the specific fire-behavior conditions (e.g., frontal fire intensity, crown scorch, fuel consumption, depth of burn, etc.) and the pre-fire stand characteristics (e.g., species composition, stand age, cone crop, etc.). The promotion of a more ecologically appropriate forest management could result in the one-attribute type of emulation silviculture. We argue, however, that this would not be comprehensive enough to meet the needs of ecologically based management objectives. Nor would it achieve the goal of sustaining ecological integrity and indigenous biodiversity, even while engaging in the extensive economic activity of timber harvesting.

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