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BIRD RESPONSES TO BURNING AND LOGGING IN THE BOREAL FOREST OF CANADA

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Abstract. We compared how bird communities differed between burned and logged stands in black spruce (*Picea mariana)* forests of the boreal shield in Quebec and mixed-wood forests on the boreal plain in Alberta and Saskatchewan. Bird community composition was quite different in burns and clearcuts shortly after disturbance. In burns, cavity nesters and species that forage on beetles in dead trees predominated, whereas clearcuts were dominated by open-country species. Generally, snag-dependent species decreased and shrub-breeding species increased by 25 yr postfire. Species that forage and nest in canopy trees were more common 25 yr post-logging because of the retention of live residual trees. The bird communities tended to converge over time as the vegetation in burns and logged areas became more similar. Black-backed Woodpeckers (*Picoides arcticus*) and Three-toed Woodpeckers (*Picoides tridactylus*) exploit recently burned coniferous forest to forage on wood-boring insect larvae (Cerambycidae and Buprestidae) and bark beetle larvae (Scolytidae) for a short period after fire and then decline. Black-backs were absent from mature forests and found at low density in old-growth forest. Over the long term, burns may be temporary sources for fire specialists. The major conservation issue for fire- associated species is salvage logging, because woodpecker foraging and nesting trees are removed. Maintenance of suitable amounts of postfire forests spared from salvage logging is essential for sustainable forest management. Climate change is predicted to alter fire cycles: they will be shorter in the prairies leading to a shortage of old-growth forest and will be longer in Quebec leading to a shortage of younger forest.

Key Words: bird communities, Black-backed Woodpeckers, boreal forest, burns, clearcutting, even-age forest management, forest fire, logging, *Picoides arcticus*.

RESPUESTAS DE LAS AVES HACIA LOS INCENDIOS Y APROVECHAMIENTOS FORESTALES EN EL BOSQUE BOREAL DE CANADÁ

Resumen. Comparamos como difieren las comunidades de aves en áreas incendiadas y áreas con aprovechamientos forestales, en bosques de abeto negro (*Picea mariana*), en coberturas de bosque boreal en Québec y en bosques mixtos en tierras boreales de Alberta y Saskatchewan. La composición de las comunidades de aves era algo distinta poco después del disturbio en áreas con incendios y aprovechamientos forestales de tala-rasa. En áreas incendiadas, las especies que anidan en cavidades y las que buscan insectos para alimentarse predominan en los árboles muertos, mientras las áreas con aprovechamiento forestal a tala-rasa eran dominadas por especies de áreas abiertas. Generalmente las especies dependientes de los tocones disminuyeron, y las especies que se reproducen en arbustos aumentaron después de 25 años del incendio. Aquellas especies que se alimentan y anidan en las copas de los árboles eran más comunes, después de 25 años del aprovechamiento forestal, debido a la retención de árboles residuales vivos. A través del tiempo, las comunidades de aves tendían a converger, conforme la vegetación en incendios y aprovechamientos forestales era más similar. Los pájaros carpinteros (*Picoides arcticus*) y (*Picoides tridactylus*) aprovecharon por un período corto, después del incendio, los bosques de coníferas incendiados, para alimentarse de larvas (Cerambycidae and Buprestidae) y de larvas de escarabajo descortezador (Scolytidae), disminuyendo después de un tiempo. Los pájaros carpinteros (*Picoides arcticus*)eran ausentes en bosques maduros y se encontraron bajas densidades en bosques de viejos. En el largo plazo, los incendios probablemente serán una fuente temporal para especialistas en incendios. El aspecto de mayor relevancia para la conservación de contrariamente a los aprovechamientos forestales de salvamento , es esencial para un manejo forestal sustentable apropiado. Predicen que el cambio climático alterará los ciclos del fuego, los cuales serán menores en las praderas, provocando una deficiencia en los bosques viejos, y serán mayores en Québec, provocando deficiencia en bosques más jóvenes.

Unlike several ecosystems in North America, the boreal forest in Canada still retains a relatively intact natural fire regime. However, the increasing impact of industrial forestry and other land uses is changing this natural dynamic and its related bird communities. Hence, discovering the ecological differences between postfire and post-harvest forests is a key issue in the conservation of boreal forest birds. Although even-aged management practices, like stand-replacing fires, restart forest succession, they do not necessarily provide the same habitat conditions for birds. In this paper, we summarize results of studies conducted in the boreal plain and boreal shield regions of Canada that compared bird assemblages in logged and burned boreal forest and studies that focused on bird species associated with recently burned forest. We then evaluate how a natural-disturbance-based management approach in the boreal forest can develop strategies to maintain burn-associated species on harvested landscapes and highlight key research questions that remain to be answered.

THE BOREAL FOREST ECOSYSTEM

The boreal forest is the most extensive ecosystem in Canada encompassing >581,000,000 ha. Here we describe two major ecozones that occupy extensive areas in the boreal forest of Canada—the boreal plain ecozone and the boreal shield ecozone. Within each ecozone we describe the ecoregions where bird communities or species associated with burns have been studied. Decriptions of these zones and regions were taken from Environment Canada website (http://www.ec.gc.ca/soer-ree/English/Framework/Nardesc/default.cfm).

The Boreal Plains

The Boreal Plains ecozone extends southeast from northeastern British Columbia through north-central Alberta and Saskatchewan to southwestern Manitoba, an area of 74,000,000 ha (Fig. 1). The area is strongly influenced by continental climatic conditions: cold winters and moderately warm summers. The studies we summarize in this paper were conducted in the mid-boreal uplands and Wabasca lowland ecoregions of the boreal plain in Alberta and Saskatchewan. The boreal uplands stretch from northcentral Alberta to southwestern Manitoba. Mean summer temperature ranges from 13–5.5 C and mean winter temperature ranges from -13.5 to -16 C. A mean of 400–550 mm of precipitation falls annually and elevations range from 400–800 m above sea level (ASL). In upland mesic habitats, the dominant tree species are trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) occurring most commonly as mixed stands, but also as pure stands. Black spruce (*Picea mariana*), balsam poplar (*Populus balsamifera)*, paper birch (*Betula papyrifera*), and tamarack (*Larix laricina*) dominate wetter sites. Jack pine (*Pinus banksiana*) is found primarily in xeric sites; balsam fir (*Abies balsamea*) is relatively less common. The Wabasca lowland is a low relief area within the mid-boreal upland, where about half the area is covered with peatlands.

The Boreal Shield

At 195,000,000 ha, the boreal shield is the largest ecozone in Canada (Fig. 1). It extends from northern Saskatchewan east to Newfoundland, passing north of Lake Winnipeg, the Great Lakes, and the St. Lawrence River. Climate is strongly continental with long, cold winters and short, warm summers, but conditions are more maritime in Atlantic Canada. The studies we summarize here were conducted in the Abitibi Plains, central Laurentians and southern Laurentians ecoregions of the boreal shield in western and southern Quebec. In these ecoregions mean summer temperatures range from 12.5–14 C and mean winter temperatures from -11 to -12.5 C. Annual mean precipitation varies from 725–1600 mm. Elevation in the Abitibi Plain varies from 121–617 m ASL and in the central and southern Laurentians from 0–1100 m ASL. The southern fringe of the ecoregion is dominated by boreal mixed wood forests (white birch, trembling aspen and balsam poplar together with white (*Pinus strobus*), red (*Pinus resinosa*) and jack pine), the eastern portion by balsam fir and the central and western portions are boreal mixed woodland with an understory component of balsam fir. The northern sections of these ecoregions are dominated by pure black spruce stands with a small proportion of jack pine forests and scattered trembling aspen stands. Spruce stands (mostly black spruce) cover roughly 64% of the productive forest area, mixed stands of spruce and deciduous species 15%, aspen 11%, jack pine 4%, and balsam fir and birch 3%, whereas other species account for less than 1% (Lefort 2003). The studies reported here were conducted primarily in black spruce forest.

NATURAL DISTURBANCES

Disturbances such as fire and insect outbreaks have been major historical forces promoting the mosaic found in the boreal forest. Forest tent caterpillar (*Malacosoma disstria*) is the main herbivore of deciduous trees in western boreal, mixed woodlands, but rarely destroys entire stands (Peterson and Peterson 1992). The impact of insect herbivory on conifers in the mixed woodlands appears to be minimal compared to defoliation by spruce budworm (*Choristoneura fumiferana*) on balsam fir- and black spruce-dominated forests on the boreal shield. Here spruce budworm damage has affected far greater areas than fire or logging combined (MacLean 1980; Bergeron and Leduc 1998, Bergeron 2000). In both systems, blow downs caused by windstorms are locally important.

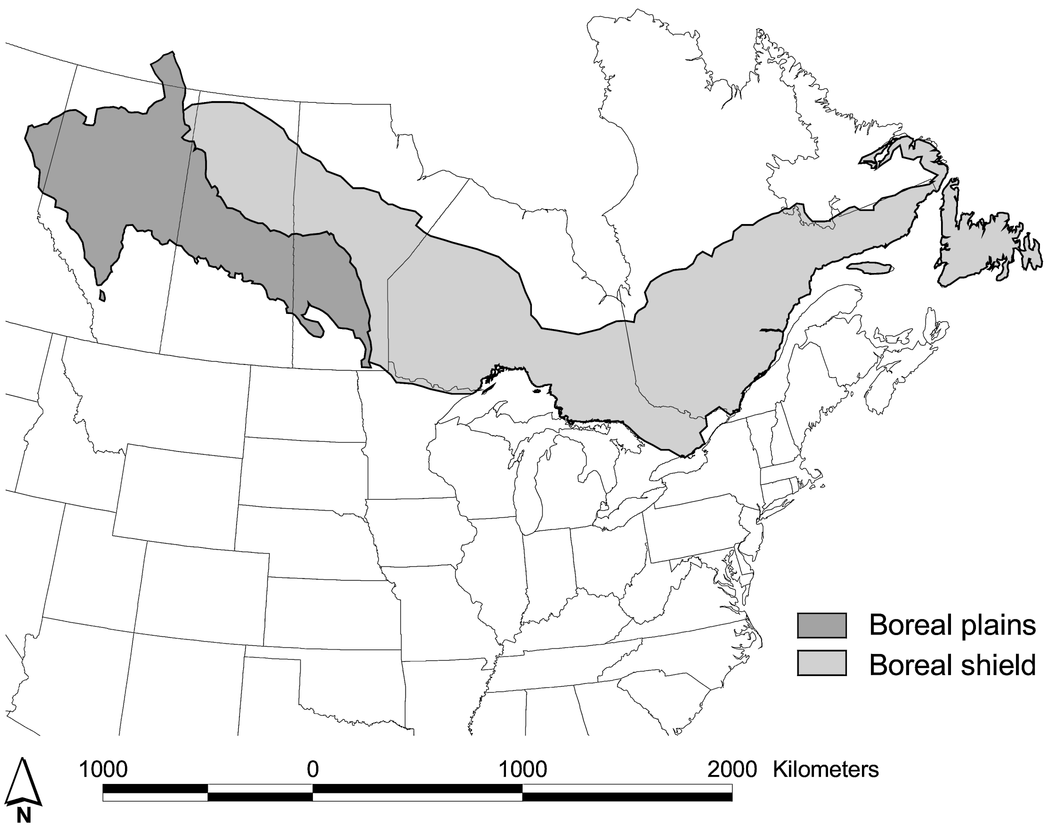

FIGURE 1. The extent of the boreal plains and the boreal shield ecozones (outlined in black) in Canada showing the ecoregions where the studies were conducted. Map taken from Environment Canada website. (http://www.ec.gc.ca/soerree/English/Framework/Nardesc/default.cfm.)

The major natural disturbance agent in the boreal, mixed-woodland forest is fire (Johnson 1992). Over centuries, fire frequencies have been dynamic and changes in frequency are related to climate changes, such as the Little Ice Age (Weir et al. 2000). The recent (past 200 yr) fire frequency in the mixed woodland forest on the boreal plain averaged 50–100 yr (Larsen 1997, Weir et al. 2000). Fire frequency showed a downturn between 1920 and1960 with a subsequent increase after 1970 (Johnson 1992), possibly related to climate cooling and then warming (Weber and Stocks 1998).

Fire-return intervals are longer in eastern boreal shield forests (Bergeron et al. 2001); in the Quebec North Shore and Labrador, fire-return intervals can reach 500 yr (Foster 1983). In a reconstruction of the past 300 yr of fire history on the boreal shield, Bergeron et al. (2001) noted a dramatic decrease in fire frequency from the mid-19th century throughout the 20th century, also corresponding to the end of the Little Ice Age. Although all areas showed a similar temporal decrease in area burned, Bergeron et al. (2001) observed that deciduous stands burn at the lowest frequency and black spruce stands burn at the highest frequency.

The distribution of fire sizes in both study regions follows a negative exponential distribution, with most fires burning <1,000 ha, accounting for less than 10% of the total area burned (Bergeron et al. 2002). Consequently, the large fires (>1,000 ha) are primarily responsible for the natural regeneration of the forest, resulting in large areas covered by a relatively uniform seral stage. Fires in the boreal forest are usually severe, killing most of the trees within their perimeter, but there is high variability in fire severity among fires related to climate conditions (Bergeron et al. 2002). Fire skips (unburned islands of trees) represent around 5% of the land base.

ANTHROPOGENIC DISTURBANCES

The forest on the boreal plain has been increasingly affected by anthropogenic disturbance, although fire is still the major disturbance factor (Lee and Bradbury 2002). Clearing for agriculture is prevalent along the southern fringe and in the Peace River area. Transportation routes, pipelines, and seismic lines have bisected many areas. Fire suppression, changes in land use practices and increases in forest fragmentation have altered the natural frequency and intensity of insect outbreaks and fire frequency (e.g., Murphy 1985, Roland 1993, Weir and Johnson 1998). Small-scale harvesting of white spruce for saw logs is common in some areas. Large-scale harvest of aspen dates back only to 1992. As recently as a decade ago, aspen was considered a weed tree by foresters and considerable effort and expense was used to eradicate it. Now, however, aspen has become economically important as a species used in the production of pulp and paper. The pure aspen and aspen-dominated mixed woodland forest are coming under increasing pressure from logging companies.

The province of Alberta has leased >75% of its mixed woodland area to forestry companies under Forestry Management Agreements. Mature (50–100 yr) and old (>100 yr) aspen forests are slated to be cut first. The rotation period will be 40–70 yr, so that few stands of aspen will reach the old-growth stage. Most stands are clear-cut in a checkerboard pattern, with an average cut-block size of 40 ha (maximum 60 ha). The intervening uncut blocks are harvested when trees on the original cut-blocks are about 3 m tall. If this harvesting pattern continues, it will result in high fragmentation of the forest, high edge/area ratios in the remaining uncut portions of the forest, and a lack of large continuous stands of older aspen and mixed woodland. Old aspen and mixed woodland forests are structurally unique compared to younger stands (Stelfox 1995).

The southern, mixed-wood, boreal forest on the boreal shield in Quebec has a longer forest management history than forests on the boreal plain. In the last 30 yr, commercial timber harvesting has moved farther north into coniferous black spruce forests. While the cutting rotation is longer (70–100 yr) in these black spruce forests than in aspen forests, so is the fire cycle. In forests of northeastern Ontario and northwestern Quebec almost 50% of the natural mosaic contains old forests (Bergeron et al. 2001). The prevalent management system is clearcutting that produces patchworks of even-aged stands. Foresters justify the use of clearcutting by the presence of frequent and severe fires that produce even-aged stands. However, even-aged forest regulation will not spare any forest that exceeds rotation age whereas fire can maintain a high proportion of the forest in older age classes (Bergeron et al. 2001). Hence, if we continue harvesting in the same way, the high proportion of mature and old forests in eastern boreal shield forests will be drastically reduced.

In Quebec's black spruce forests, regulations limit the size of clearcuts in any continuous block to <150 ha. However, while individual cut blocks are clearly smaller than the mean size of natural burns, they are harvested in a continuous progression. This clustering of cut-blocks creates thousands of square kilometers of regeneration containing fragments of mature forest in the form of cut-block separators, riparian buffer strips and unproductive or inaccessible forest. More recently, the Quebec government proposed a harvesting pattern that is similar to the one used in Alberta, where stands are harvested in two passes leaving a landscape with a checkerboard appearance of different aged stands. However, this harvesting pattern will not solve the problems linked to highly fragmented forests at large scales. While large areas of the boreal shield are still under natural disturbance regimes, forest management is progressing quickly and there is urgency for developing alternative forestry practices that are aimed at maintaining existing biodiversity.

ECOSYSTEM MANAGEMENT AND THE NATURAL DISTURBANCE PARADIGM

Increasingly the forest industry is embracing the concept of ecosystem management to ensure that harvesting is conducted in an ecologically sustainable manner. A recent focus has been to attempt to pattern forest harvesting (patch size, shape, frequency of cut, spatial pattern of cut, retention of trees in cut-blocks) to resemble that created by natural disturbance, predominantly fire (e.g., Hunter 1993). A critical prerequisite for implementing such a management scheme is a thorough understanding, at the stand and landscape scale, of the effects of natural disturbances on wildlife communities and how these compare with the effects of logging. Many recent studies in the boreal forest have focused on the loss of old forests and its potential effects on old forest dependent species. However, differences in forest conditions in early postfire and post-logged seral stages have often been neglected. These differences must be addressed if we intend to maintain biodiversity in managed forest landscapes.

BIRD ASSEMBLAGES IN BURNED AND LOGGED STANDS

We summarize four studies conducted on bird assemblages in burned and logged forest. Hobson and Schieck (1999) and Morissette et al. (2002) compared vegetation structure and composition and bird communities in burned and logged stands on the boreal plain in Alberta and Saskatchewan, respectively. Imbeau et al. (1999) and Drapeau et al. (2002) compared bird communities in logged and burned black spruce forest on the boreal shield in Quebec.

Hobson and Schieck (1999) and Lee (2002) studied aspen-spruce mixed woodland stands 1, 14, and 28 yr after either a stand-replacing fire or clear-cut logging. They found that the early post-disturbance vegetation structure of burned and logged stands differed markedly. Right after a stand-replacing fire, the stand was dominated by large burned snags and the ground cover was dominated by herbs, whereas after clear-cutting a few live residual canopy trees remained singly or in clumps and the ground cover was dominated by grasses such as *Calamagrostis canadensis* (Fig 2). The early post-disturbance bird communities were also quite different (Hobson and Schieck 1999). In burns, the community was dominated by cavity nesters and species that foraged on beetle infestations in dead trees, whereas clear-cuts were dominated by open country species (Fig 2). Over time, the vegetation structure and composition of burns and clear-cuts converged (Hobson and Schieck 1999, Lee 2002). By about 28 yr post-disturbance, many of the snags fell in burns and the shrubby understory was well developed. Conversely, on clear-cuts, some of the residual live trees died, increasing snag density to levels similar to burns and the shrub layer was more developed. Relative to immediately postfire, snag-dependent bird species decreased in 28-yr burns and shrub-breeding species increased (Fig 2). Species that foraged and nested in canopy trees were more prevalent in 28-yr-old regenerated cut-blocks than burns, because of the retention of live residuals in the cut-blocks (Fig. 2; Hobson and Schieck 1999; Schieck and Song 2002). No research in the mixed woodland system has compared burns and logging beyond 28 yr, but the assumption is that the both the vegetation structure and bird communities become more and more similar over time.

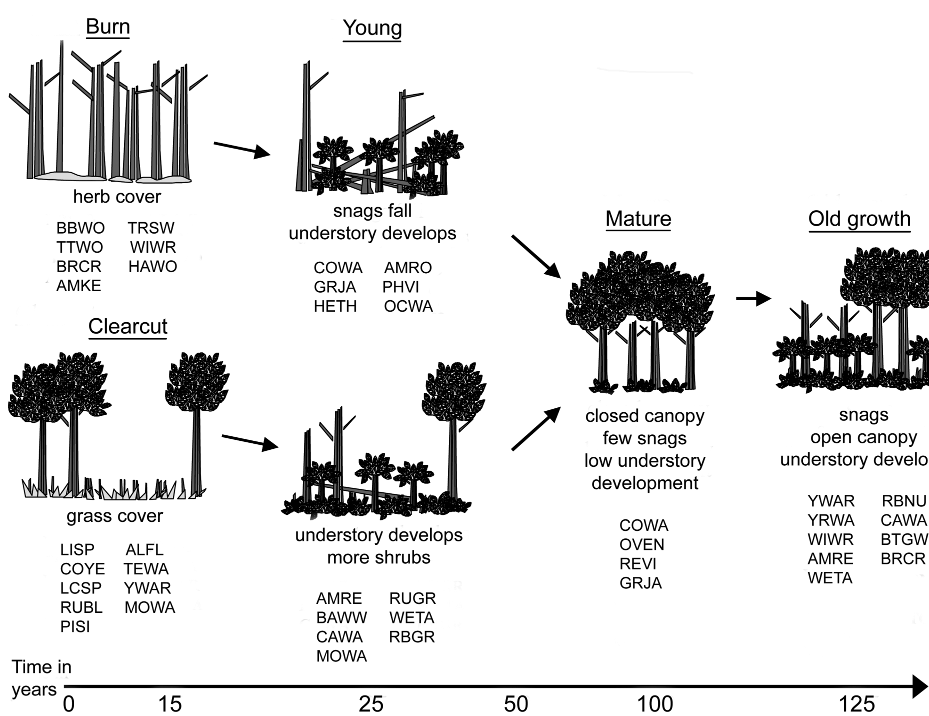

FIGURE 2. Changes in vegetation structure and bird communities after fire and logging in the boreal mixed woodland on the boreal plain of Alberta. Adapted from Hobson and Schieck (1999) and Schieck et al. (1995). Acronyms are defined in Table 1.

Morissette et al. (2002) focussed on unburned, burned and postfire salvage-logged sites three years after a stand-replacing fire in aspen-spruce mixed woodland, jack pine, and aspen stands near Meadow Lake, Saskatchewan. Burned sites had lower canopy cover, more regenerating trees, denser understory, lower litter and moss cover, higher herb and forb cover, and, in jack pine, lower lichen, and higher grass cover than unburned sites. Salvage-logged sites had no canopy cover, highest amount of grass cover and downed woody material, but were similar to burned sites in herb and litter cover and density of regenerating trees. In jack pine, salvage sites had lower moss cover than unsalvaged burns.

Bird communities reflected these differences in vegetation (Morissette et al. 2002). Most species in unburned sites were those associated with older forest: Northern Waterthrush (*Seiurus noveboracensis)* (mixed woodland), Blue-headed (*Vireo solitarius*) and Red-eyed Vireos *(V. olivaceus)* (jack pine), and Ovenbirds (*Seiurus aurocapillus)* (aspen) were most abundant in unburned stands. Burned sites were characterized by generalists, early successional species, mature forest species, and insectivores. Olive-sided Flycatcher (*Contopus cooperi)* and Western Wood-pewee (*Contopus sordidulus*) occurred most frequently in burned, un-salvaged jack pine, and aspen, and American Robin (*Turdus migratorius*) and Dark-eyed Junco (*Junco hyemalis*) were most common in jack pine burns, and Brown Creeper (*Certhia americana*) was most abundant in burned aspen. Black-backed and Three-toed woodpeckers and Black-capped Chickadees (*Poecile atricapilla*) were only encountered in burned sites. Salvage-logged sites were characterized by generalist or early successional species, cavity nesters were absent (except for House Wren (*Troglodytes aedon*), Tree Swallows (*Tachycineta bicolor*), and resident species were sparse (Boreal Chickadee [*Poecile hudsonica*], Red-breasted Nuthatch [*Sitta Canadensis*], and Brown Creeper). LeConte's Sparrow (*Ammodramus leconteii*), Song Sparrow (*Melospiza melodia*), Sharp-tailed Sparrow (*Ammodramus caudacutus*), Vesper Sparrow (*Pooecetes gramineus*), and Lincoln's Sparrow (*Melospiza lincolnii*) were only found in salvage-logged areas, and White-throated Sparrow (*Zonotrichia albicollis*), Clay-colored Sparrow (*Spizella pallida*) and Alder Flycatchers (*Empidonax alnorum*) reached their highest abundances in salvaged areas.

Imbeau et al. (1999) compared bird assemblages in black spruce forests of the boreal shield originating from fire and logging. Bird assemblages show similar responses as those on the boreal plain (Fig. 3). Bird community composition was most different between burns and logged areas immediately after fire or harvest (Imbeau et al. 1999)—species that foraged and nested in snags in recent burns were absent in harvested stands. However, these differences became less pronounced as disturbed stands reached the young forest successional stage. This emphasises the importance of standing dead wood, a key habitat feature of stand-replacement fires. Drapeau et al. (2002) studied black spruce stands after either a stand-replacing fire or logging. Comparisons in postfire and post-logged stands 20 yr after disturbance show that the mean basal area of standing snags remained significantly higher in postfire stands than in old regenerated cut-blocks, although many snags had fallen since the fire. Snag-dependent species, particularly secondary cavity nesters, also decreased in 20-yr-old burns but their abundance was significantly higher than in old cut-blocks.

FIRE ASSOCIATES

We define fire associates as species whose abundances are higher in burned stands than in older unburned stands. In Table 1 we summarized the responses of species to fire in the boreal forest in Canada. The following species appear to be associated with fire in the following stand types (i.e., they reached significantly higher abundance in burns when compared with unburned stands of the same forest type) (1) aspen-spruce mixed woodland—American Kestrel (*Falco sparverius*), Downy Woodpecker (*Picoides pubescens*), Hairy Woodpecker (*Picoides villosus*), Black-backed Woodpecker, Northern Flicker (*Colaptes auratus*), Gray Jay *(Perisoreus canadensis*), Tree Swallow, Brown Creeper, Winter Wren (*Troglodytes troglodytes*), Hermit Thrush (*Catharus guttatus*), American Robin, Connecticut Warbler (*Oporornis agilis*), and Yellow-rumped Warbler (*Dendroica coronata*); (2) aspen—White-throated Sparrow, Brown Creeper, House Wren, Chestnut-sided Warbler (*Dendroica pensylvanica*), Chipping Sparrow (*Spizella passerina*), Olive-sided Flycatcher, and Least Flycatcher (*Empidonax minimus*); (3) jack pine—Black-backed Woodpecker, Three-toed Woodpecker, Dark-eyed Junco, Olive-sided Flycatcher, American Robin, Western Wood Pewee, and Winter Wren; and (4) black spruce—Black-backed Woodpecker, American Kestrel, Tree Swallow, Eastern Bluebird (*Siala sialis*), American Robin, Hermit Thrush, and Cedar Waxwing (*Bombycilla cedrorum*). Note that these studies used point counts as survey methods

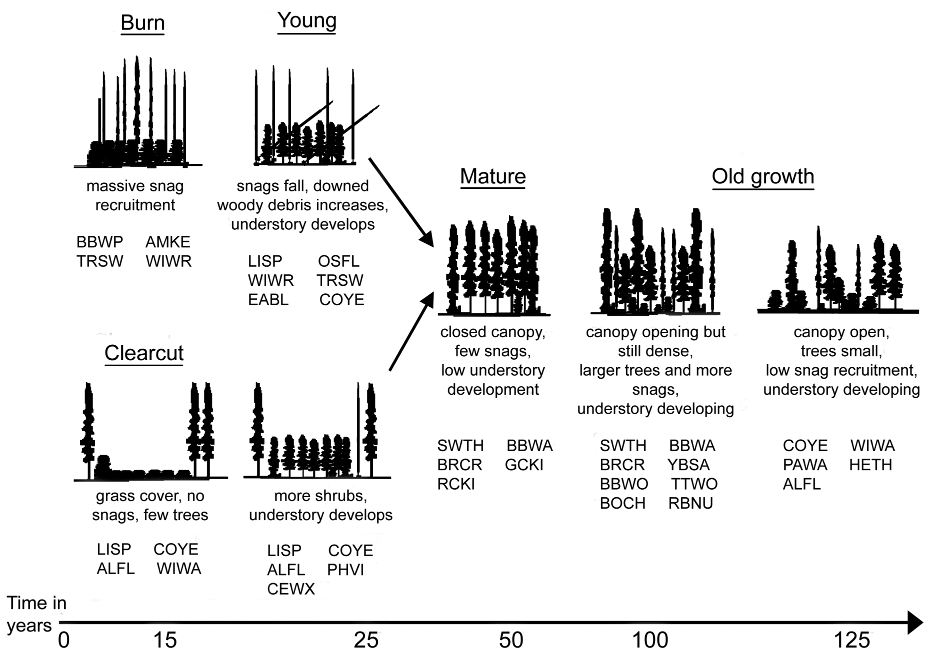

FIGURE 3. Changes in vegetation structure and bird communities after fire and logging in boreal black spruce forests on the boreal shield of Quebec. Adapted from Imbeau et al. (1999) and Drapeau et al. (2002). Acronyms are defined in Table 1, except for GCKI (Golden-crowned Kinglet, [*Regulus satrapa*]); PAWA (Palm Warbler, [*Dendroica palmarum*]); WIWA (Wilson's Warbler, [*Wilsonia Canadensis*]).

and hence did not adequately sample some taxa such as raptors, shorebirds or grouse.

Two species, Black-backed Woodpeckers and Three-toed Woodpeckers, appear to be consistent in their positive response to fire across their range, and the Black-backed Woodpecker appears to be a specialist of recently burned forests (Hutto 1995, Murphy and Lehnhausen 1998, Dixon and Saab 2000, Leonard 2001). These woodpeckers detect burns of coniferous forest and invade them rapidly after fire (Villard and Schieck 1996, Dixon and Saab 2000, Leonard 2001) to forage on insects that colonize burned trees. Black-backed Woodpeckers generally forage on moderately to heavily burned trees and excavate in the sapwood for wood-boring insect larvae (Cerambycidae and Buprestidae), whereas Three-toed Woodpeckers commonly select lightly to moderately burned trees and flake off the bark to access bark beetle larvae (Scolytidae) (Murphy and Lehnhausen 1998). The woodpeckers typically remain at high densities for 2–4 yr after fire, then decline as insect abundance declines (Niemi 1978, Murphy and Lehnhausen 1998).

On the boreal plain, Hoyt and Hannon (2002) found Three-toed Woodpeckers and Black-backed woodpeckers in burned stands of jack pine and white and black spruce (50–140 yr of age prior to burn); however, both species were absent from mature (50–100 yr) forests and were at low density in old growth (>110 yr) forest. Three-toed Woodpeckers were most abundant in sites with large diameter lightly burned spruce and persisted up to 3 yr after fire. This is probably because bark beetles were most prevalent in this type of tree (jack pine has thick bark and is more resistant to insect attack and heavily burned spruce trees are not infested at a high rate). Black-backed Woodpeckers persisted at high levels in burned stands up to 8 yr after fires, possibly because these stands contained jack pine, a species that is more fire-resistant than spruce (Hoyt and Hannon 2002). The thick bark of jack pine retards dessication, making dead and dying trees more suitable habitat for wood boring insects. Black-backed Woodpeckers in a 3-yr old patch of burned black spruce and jack pine foraged preferentially on moderately burned (100% burned, but 80–100% of the bark intact), large diameter (>15 cm diameter at breast height [dbh]) standing jack pine trees, although standing and downed spruce were also used (Hoyt 2000).

TABLE 1. SUMMARY OF AVAILABLE LITERATURE ON THE RESPONSES OF BREEDING BIRDS (CHANGE IN ABUNDANCE) TO BURNED VERSUS UNBURNED STANDS IN BOREAL FOREST HABITATS OF ALBERTA (AB), SASKATCHEWAN (SK) AND QUEBEC (QC). SPECIES CODE ACRONYMS GIVEN FOR SPECIES IN FIGS. 2 AND 3.

Species/species code	State or province	Years after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments
American Kestrel AMKE (*Falco sparverius*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	Highest in 1-yr-old burns.
American Kestrel	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. within 12-yr-burn	+	2	
Ruffed Grouse RUGR (*Bonasa umbellus*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 14, 28 yr clearcuts.
Common Snipe (*Gallinago gallinago*) (three fires)	AB	1, 14, 28	Stands 50–200 ha; fire size not given	18 (three/age class of fire, three/age class of harvest)	0	1	
Yellow-bellied Sapsucker (YBSA) (*Sphyrapicus varius*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (3 fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Downy Woodpecker DOWO (*Picoides pubescens*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	Highest in 14-yr-old burns.
Hairy Woodpecker HAWO (*Picoides villosus*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	Highest in 1-yr burns.
Three-toed Woodpecker TTWO (*Picoides tridactylus*)	AB	2–17	2-yr fire: 135,000 ha; area of older fires not given	6	+	3	Highest in 2-3-yr old burns.
Three-toed Woodpecker	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	
Three-toed Woodpecker	QC	1, 20	12,540 ha 59,720 ha (two fires)	56 stands sampled within 1-yr burn and 49 stands within 20-yr-old burn	0	5	
Three-toed Woodpecker	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. sampled within 12-yr-old burn	0	2	
Black-backed Woodpecker BBWO (*Picoides arcticus*)	AB	1	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	
Black-backed Woodpecker	AB	2–17	2-yr fire: 135,000 ha; area of older fires not given	6	+	3	Highest in 4-8-yr old burns.
Black-backed Woodpecker	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	

TABLE 1. CONTINUED.

Species/species code	State or province	Years after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments
Black-backed Woodpecker	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr old burn and 10 stands. sampled with 12-yr-old burn	+	2	
Black-backed Woodpecker	QC	1, 20	12,540 ha 59,720 ha (two fires)	56 stands sampled within 1-yr burn and 49 stands within 20-yr-old burn	+	5	
Northern Flicker (*Colaptes auratus*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	Highest in 14-yr burns.
Northern Flicker	QC	1, 20	12,540 ha, 59,720 ha (two fires)	56 stands sampled within 1-yr burn and 49 stands within 20-yr-old burn)	+	5	Highest abundance in 20-yr-old burns.
Pileated Woodpecker (*Dryocopus pileatus*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Olive-sided Flycatcher OSFL (*Contopus cooperi*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	Highest in burned jack pine and aspen.
Western Wood-Pewee (*Contopus sordidulus*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	Highest in burned jack pine and aspen.
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Alder Flycatcher ALFL (*Empidonax alnorum*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Alder Flycatcher	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in harvested stands.
Least Flycatcher (*Empidonax minimus*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Least Flycatcher	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	Highest in burned aspen.
Eastern Phoebe (*Sayornis phoebe*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Eastern Kingbird (*Tyrannus tyrannus*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Blue-headed Vireo (*Vireo solitarius*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	–	4	Highest in unburned jack pine.
Warbling Vireo (*Vireo gilvus*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Philadelphia Vireo PHVI (*Vireo philadelphicus*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	

TABLE 1. CONTINUED.

Species/species code	State or province	Years after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments
Philadelphia Vireo	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Red-eyed Vireo REVI (*Vireo olivaceus*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	–	4	Highest in unburned stands.
Red-eyed Vireo	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Gray Jay GRAJ (*Perisoreus canadensis*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Gray Jay	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	Most abundant in 14-yr burned forest.
Blue Jay (*Cyanocitta cristata*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Most abundant in 14/28 yr harvested forest.
Blue Jay	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Common Raven (*Corvus corax*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Tree Swallow TRSW (*Tachycineta bicolor*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Tree Swallow	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	
Tree Swallow	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. sampled with 12-yr-old burn	+	2	
Black-capped Chickadee (*Poecile atricapilla*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Black-capped Chickadee	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Boreal Chickadee BOCH (*Poecile hudsonica*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Boreal Chickadee	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. sampled with 12-yr-old burn	–	2	
Red-breasted Nuthatch RBNU (*Sitta canadensis*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Red-breasted Nuthatch	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	

TABLE 1. CONTINUED.

Species/species code	State or province	Years after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments
Brown Creeper BRCR (*Certhia americana*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	Highest in burned aspen.
Brown Creeper	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	Highest 1 yr after fire.
Brown Creeper	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. sampled with 12-yr-old burn	–	2	
House Wren HOWR (*Troglodytes aedon*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	Highest in burned aspen.
Winter Wren WIWR (*Troglodytes troglodytes*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	
Winter Wren	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	Highest in burned jack pine.
Winter Wren	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. sampled with 12-yr-old burn	–	2	
Ruby-crowned Kinglet RCKI (*Regulus calendula*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	Similar abundance in burned and unburned mixed woodland.
Ruby-crowned Kinglet	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. sampled with 12-yr-old burn	–	2	
Swainson's Thrush SWTH (*Catharus ustulatus*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Swainson's Thrush	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	Similar abundance in burned and unburned aspen.
Hermit Thrush HETH (*Catharus guttatus*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	Highest 14 yr after fire.
Hermit Thrush	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Hermit Thrush	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. sampled with 12-yr-old burn	+	2	
American Robin AMRO (*Turdus migratorius*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	

TABLE 1. CONTINUED.

Species/species code	State or province	Years after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments
American Robin	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	Highest in burned jack pine.
American Robin	QC	Not specified	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. sampled with 12-yr-old burn	+	2	
Eastern Bluebird EABL (*Siala sialis*)	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. sampled with 12-yr-old burn	+	2	
Cedar Waxwing CEWX (*Bombycilla cedrorum*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in harvested.
Cedar Waxwing	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. sampled with 12-yr-old burn	+	2	
Tennessee Warbler TEWA (*Vermivora peregrina*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 14-yr-old harvested.
Tennessee Warbler	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	–	4	Highest in unburned aspen.
Orange-crowned Warbler OCWA (*Vermivora celata*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Yellow Warbler YWAR (*Dendroica petechia*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in harvested.
Yellow Warbler	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Chestnut-sided Warbler (*Dendroica pensylvanica*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	Highest in burned aspen.
Magnolia Warbler (*Dendroica magnolia*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Magnolia Warbler	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Cape May Warbler (*Dendroica tigrina*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Yellow-rumped Warbler YRWA (*Dendroica coronata*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Yellow-rumped Warbler	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Black-throated Green Warbler BTGW (*Dendroica virens*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	

TABLE 1. CONTINUED.

Species/species code	State or province	Years after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments
Bay-breasted Warbler BBWA (*Dendroica castanea*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Black-and-white Warbler BAWW (*Mniotilta varia*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 28 yr harvested.
Black-and-white Warbler	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
American Redstart AMRE (*Setophaga ruticilla*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 28 yr harvested.
American Redstart	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Ovenbird OVEN (*Seiurus aurocapillus*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 28 yr harvested.
Ovenbird	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	–	4	Highest unburned aspen.
Northern Waterthrush (*Seiurus noveboracensis*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	–	4	Highest unburned mixed woodland.
Connecticut Warbler COWA (*Oporornis agilis*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	Highest in 28 yr burn.
Connecticut Warbler	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Mourning Warbler MOWA (*Oporornis philadelphia*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in harvested.
Mourning Warbler	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	–	4	Highest in salvaged mixed woodland.
Common Yellowthroat COYE (*Geothlypis trichas*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in harvested.
Common Yellowthroat	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Canada Warbler CAWA (*Wilsonia canadensis*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 28 yr harvested.
Canada Warbler	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Western Tanager WETA (*Piranga ludoviciana*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in harvested.

TABLE 1. CONTINUED.

Species/species code	State or province	Years after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments
Western Tanager	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Chipping Sparrow (*Spizella passerina*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 1 yr harvested.
Chipping Sparrow	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	Highest in burned aspen.
Clay-colored Sparrow (*Spizella pallida*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	–	4	Highest in salvaged mixed woodland, jack pine.
Vesper Sparrow (*Pooecetes gramineus*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	–	4	Highest in salvaged jack pine.
Sharp-tailed Sparrow (*Ammodramus caudacutus*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Le Conte's Sparrow LCSP (*Ammodramus leconteii*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 1 yr harvested.
Le Conte's Sparrow	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Fox Sparrow (*Passerella iliaca*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Song Sparrow (*Melospiza melodia*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	–	4	Highest in salvaged jack pine.
Lincoln's Sparrow LISP (*Melospiza lincolnii*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 1 yr harvested.
Lincoln's Sparrow	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	–	4	Highest in salvaged jack pine.
Swamp Sparrow (*Melospiza georgiana*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
White-throated Sparrow (*Zonotrichia albicollis*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	m	4	Highest in salvaged mixed woodland and jack pine, high in burned aspen.
White-throated Sparrow	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	

TABLE 1. CONTINUED.

Species/species code	State or province	Years after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments
Dark-eyed Junco (*Junco hyemalis*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	m	4	Highest in salvaged mixed woodland and burned jack pine.
Dark-eyed Junco	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Rose-breasted Grosbeak RBGR (*Pheucticus ludovicianus*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Rose-breasted Grosbeak	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 14 yr harvested.
Rusty Blackbird RUBL (*Euphagus carolinus*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 1 yr harvested.
Pine Siskin (PISI) (*Carduelis pinus*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Pine Siskin	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in harvested.

[a] Only wildland fires are reported in this table.
[b] + = increase; – = decrease; 0 = no effect or study inconclusive, m = mixed response.
[c] References: 1 = Hobson and Schieck (1999), we inferred a negative response when highest abundance was in clearcuts, no response when there was no significant difference between burns and clearcuts, and a positive response if abundance was highest in burns, no stands over 28 yr were compared; 2 = Imbeau et al. (1999); we inferred a positive or negative response for significant differences in abundance between burns and other stand types (harvested or burned) and no response when there was no significant difference; 3 = Hoyt and Hannon (2002); 4 = Morissette et al. (2002); we inferred no response if there was no significant difference among treatments. Note that some species were uncommon and hence the inference of no response could be incorrect; 5 = Nappi (2000); occurrence patterns in 1-yr- and 20-yr-old burns were compared to mature and old forests that all originate from natural disturbances.

On the boreal shield, Nappi (2000) found that the Black-backed Woodpecker reached its highest densities in early postfire black spruce forests. Its occurrence in burns was close to ten times higher than in the early stages of old forest types (>100 yr). The Three-toed Woodpecker was, however, much less abundant in burns than the Black-backed Woodpecker. Its occurrence was similar in burns and in the early stages of old growth development. Nappi et al. (2003) noted that Black-backed Woodpeckers in a 1-yr-old burned, black spruce/jack pine stand preferred to forage on large diameter pine and spruce snags that were lightly burned and still had most of their branches. They also measured the density of wood-boring beetle larvae holes on snags of different size and deterioration classes to assess the relationship between food availability and snag characteristics. Larger snags that were less deteriorated by fire contained higher prey densities (wood-boring beetle holes) than smaller and more deteriorated snags. Hence, they concluded that snag selection was not random—woodpeckers selected snags and portions of snags that contained higher densities of wood-boring insects.

Over the long-term, burns may be temporal habitat sources for fire specialists (Hutto 1995, Murphy and Lehnhausen 1998, Hoyt and Hannon 2002). Secondary cavity nesters such as Eastern Bluebird and Tree Swallow used Black-backed Woodpecker nesting cavities the second and third year following fire (Drapeau, unpubl. data). In addition, species such as Northern Hawk-Owls (*Surnia ulula*) appeared to be abundant in postfire stands (Kotliar et al. 2002). Use of burned stands by fire associates relates to a number of factors affecting insect colonization including tree species composition, age of stand prior to fire and fire severity (Hutto 1995, Murphy and Lehnhausen 1998, Morissette et al. 2002).

CRITICAL MANAGEMENT AND RESEARCH ISSUES

Fire Suppression

Provincial governments in Canada are trying to eliminate fire from boreal forest landscapes, despite the fact that several species have been lost in highly managed forests where fire has been removed (e.g., in Fennoscandia [Östlund et al. 1997, Angelstam 1998]), and that in other regions of North America fire is being reintroduced (e.g., for management of the Red-cockaded Woodpecker (*Picoides borealis*; James et al. 1997)). In Alberta, plans exist to fireproof forested landscapes by cutting fire-breaks through the forest at large scales (Cumming 2001). Another important disruptor of natural fire spread in the boreal plain is the increase in land clearing for agriculture at the fringe of the boreal forest, which might prevent the spread of large fires into forested areas (Weir and Johnson 1998).

Given the size of the boreal forest and the limited access, attempts at active fire suppression in this biome appear to have had limited effect, although this is controversial (Murphy 1985, Johnson 1992). In Québec, for example, most of the forest fires <1,000 ha (90% of the fires since 1940) are suppressed by the Fire Control Agency. Fires >1,000 ha are less likely to be controlled and these large fires are responsible for the regeneration of most of the forest cover of the boreal forest in Québec (Bergeron et al. 2002). Fire suppression has not had a real impact on these fire events. In fact, mean fire size has been greater for the period following the beginning of fire suppression activities than the previous period without intervention (Chabot et al. 1997, Johnson et al. 2001).

Salvage Logging

The most important current threat for birds associated with recently burned forests is salvage logging (e.g., Saab and Dudley 1998, Kotliar et al. 2002). Given the major contribution of recently burned forests both as a key habitat for primary cavity-nesting birds and as the main source of recruitment for dead wood, the intensification of salvage cutting in the boreal forest raises serious concerns. It may not only compromise the maintenance of viable populations for burn-dependent species such as Black-backed Woodpeckers, but it may also greatly reduce the overall availability of dead wood to wildlife across current and future landscapes. In Alberta and Québec, stands that have been recently disturbed by fire and insect outbreaks are salvage logged. All burned trees of commercial timber value are logged and the remainder are knocked down for safety reasons, although patches of live trees >4 ha are left unharvested. Harvesting is not currently conducted with guidelines that incorporate biodiversity concerns, however in both provinces new guidelines are being developed that specify retention of groups of burned trees. While large areas of forest are still inaccessible by road, timber harvesting is expanding to the north and the road network will increase considerably in next 20 yr. Burned areas will thus become increasingly accessible and salvage logging will increase and pose a problem to species that show some dependency on stand-replacement fires.

Trees that are salvaged are in the same diameter classes that woodpeckers use for foraging and nesting (i.e., >20 cm dbh) (Hoyt 2000, Nappi 2000, Nappi et al. 2003). In a study of burned, boreal mixed woodlands (*Populus* and white spruce) where the majority of trees were either harvested or knocked down (<100 standing trees/100 ha), densities of Three-toed Woodpeckers, Black-backed Woodpeckers, Downy Woodpeckers, and Hairy Woodpeckers were lower than in un-salvaged burns (Schmiegelow et al. 2001). In addition, secondary cavity nesters such as House Wrens, American Kestrels, and Brown Creepers were more abundant in un-salvaged versus salvaged-logged burns (Schmiegelow et al. 2001). Similar results were obtained in black spruce forests. Nappi et al. (2003) found that Black-backed Woodpeckers were concentrated in the un-salvaged portions of a burned forest where salvage logging covered 64% of the burned area, and where no snags were left within harvested blocks. Species vary in their responses to salvage logging; however, species tied to recently burned forests are most sensitive (Kotliar et al. 2002).

Hutto (1995) and Murphy and Lehnhausen (1998) also noted the conflict between salvage logging in recently burned or insect-infested old forest and the maintenance of suitable habitat for Black-backed Woodpeckers and other burn associates. Delaying salvage logging in burns for up to 3 yr post-harvest would allow woodpeckers to reproduce, but this conflicts with forestry management practices. Damage to trees from beetle infestations and desiccation usually restricts salvage logging operations to 2 yr postfire. While, for economic reasons, the increase in salvage logging may be unavoidable, there is a crucial need to provide science-based guidelines about how recently burned forests may be managed to provide appropriate habitat conditions to maintain biodiversity. For example, Powell (2000) found that rates of insect colonization differed considerably depending on tree species and degree of burn, hence some tree species could be salvage logged without reducing food supplies for burn-dependent birds. Maintenance of suitable amounts of postfire forests that are spared from commercial salvage logging should be considered as a prerequisite condition for sustainable forest management of early seral stages. The question, however, is how much is enough? A better understanding of the ecology of fire-dependent species in recently burned forests could help us determine the size of un-salvaged burned areas, their spatial arrangement and the quality of standing dead trees that should be left in these areas. Saab et al. (2002) provides useful guidelines for nesting Black-backed Woodpeckers in Ponderosa pine (*Pinus ponderosa*) forests of western Idaho.

Ecosystem Management: Replacing Fire with Logging

The natural disturbance paradigm suggests that the negative impacts of timber extraction on biodiversity can be mitigated by harvesting to emulate natural disturbance patterns, however it remains to be tested. Indeed, the application of ecosystem-management concepts is still not well developed (Simberloff 1998, 2001) and few studies suggest silvicultural treatments and management strategies that allow practical application of these concepts (but see Bergeron et al. 1999, 2002). A major concern for sustainable forest management has been the truncation of the age-class distribution of managed forest landscapes, with a reduction in the abundance of old forests. How forest practices should be modified to maintain structural and compositional characteristics of early postfire stages has been less of an issue. At the stand level, some forest companies have attempted to emulate fire by leaving residual patches of standing dead trees to increase the supply of snags and improve structural heterogeneity. These structured blocks have higher avian-species diversity than traditional clear-cut patches and patches of residual trees are occupied by some species usually found in older forests (Norton and Hannon 1997, Imbeau et al. 1999, Schieck and Hobson 2000, Schieck et al. 2000, Tittler et al. 2001, Schieck and Song 2002). However, they do not provide the abundance of standing dead trees that are found after natural disturbance events and that are key elements of early post-burned stands. Perhaps some form of prescribed burning after harvesting could provide the conditions for insect colonization of the burned residual trees and hence habitat for burn specialists. Wikars (2002), however, found that prescribed burning of residual trees after logging did not provide sufficient habitat for birds that require burned habitats instead of single burned trees. In addition, burn-associated species vary widely in their preferences for foraging and nesting sites (Kotliar et al. 2002). Hence, it is unlikely that modifying forest harvest practices will produce forest conditions similar to those found after natural disturbance events. Thus, a key challenge to ecosystem management is to maintain large tracts of burnt, uncut forest habitat in the landscape.

Climate Change and Habitat Supply for Burn-dependent Birds

Historical reconstruction of fire dynamics in the Canadian boreal forest has revealed that fire regimes vary regionally and temporally, and future climate change will maintain this variability (Flannigan et al. 1998). In the boreal forest of western Canada, short fire cycles (50–75 yr) (Johnson et al. 1998) could persist because the central boreal plains and western shield and taiga are predicted to have longer, warmer, drier summers, and more fires. For species associated with stand replacement fires this would mean increased habitat supply. However, a coincident increase in areas logged and burned by fire would result in a landscape dominated by young forest stands and concomitant reduction in old-growth habitat. Old-growth forests have experienced an increase in the area burned by fire since the 1970s and a coincident increase in unburned area logged, suggesting that logging is not replacing fire but is adding to it (Lee and Bradbury 2002).

In contrast, in the mixed or coniferous forest regions of northeastern Ontario and Quebec, summers are predicted to be wetter and cooler and the historical intermediate fire-return interval (around 150 yr) (Bergeron et al. 2001) should persist or lengthen. Hence, habitat supply of recent burns might decrease for fire-associated birds. Secondary disturbances such as insect outbreaks and windthrows, that occur in the absence of fire as in the Quebec North Shore or Labrador, are likely to become more important in northwestern Quebec. While these disturbances could provide some suitable habitat for Black-backed Woodpeckers (Goggans et al. 1989, Thompson et al. 1999, Setterington et al. 2000), it is not clear whether viable populations of this species could be maintained in the absence of fire.

KEY RESEARCH QUESTIONS FOR THE FUTURE

Kotliar et al. (2002) outlined a number of important research questions that address avian responses to fire. We agree with these questions and feel that for the boreal forest in Canada the most important questions are:

1. How do bird communities on burns vary with severity of the fire, season of burn, size of burn, age of burn, and stand age and composition prior to the fire? Most studies in boreal forests have focussed on comparing burns to logging and have not investigated the variation in bird responses to severity of burn, either within a single burn or across several burns. Different tree species vary in their susceptibility to fire, hold their bark, fall down, and dessicate at different rates after fires. Also many cavity nesting birds require trees of a certain diameter for nesting and foraging, hence stand composition before burns is likely to be a determinant of species composition after fire (Saab et al. 2002). In addition, some birds may be more likely to detect larger than smaller burns. Bird communities are expected to change over time after fire as bark beetles and wood boring insects decline, trees fall, and cavities are created by primary excavators.
2. How do fire-associated species find recent burns? How large should burns be to attract birds? Are isolated burns detected by fire-associates? It is unclear whether burn-associates move into burns from adjacent unburned stands or whether they can detect burns from further away. If, for example, they find burns by following smoke plumes, how far away can these be detected and how large does the fire have to be to create detectable smoke? The answers to these questions will inform decisions about which burned stands to leave unsalvaged and where one might conduct prescribed burns.
3. How can we change silvicultural prescriptions to leave habitat for burn-associated birds? If forest managers wish to leave some trees on burned stands during salvage logging, they need guidelines on how many trees to leave, their spatial arrangement, what species to leave, and the physical condition of retained trees in order to attract insects and birds. In addition, more work should be done to determine whether prescribed burning can create suitable habitat for burn-associates. Researchers should work with forest managers to set up adaptive management experiments in burned areas to test assumptions about how birds respond to burned habitats.
4. How does the spatial distribution and size of burns and old-growth forest affect the population dynamics of burn-associated birds? For fire specialists, such as the Black-backed Woodpecker, long-term population persistence may depend on a supply of burned habitat over time (Hutto 1995, Murphy and Lehnhausen 1998). In order to determine whether the population dynamics of this species is a temporal source-sink system, we need to conduct detailed demographic studies (reproductive success, survival, and dispersal) in old growth forest and recently burned forest.
5. How will the supply of burned and old-growth habitats change under various climate warming scenarios, predicted levels of forestry development,

and other land uses? Models should be developed to predict habitat supply for burn-associated birds into the future to determine whether fires will become rarer and if so, whether logging activities will further deplete the supply of burned habitats. This would allow managers to introduce prescribed burns to ensure habitat for these species.

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