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Thirty Years of Post-fire Succession in a Southern Boreal Forest Bird Community

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ABSTRACT.—Birds and vegetation were surveyed in a 9 ha plot in spring 1976 in a 73 y-old jack pine (*Pinus banksiana*) – black spruce (*Picea mariana*) forest in northeastern Minnesota. A 1368 ha wildfire burned across the area that autumn. The plot was resurveyed in 1977 and periodically through 2006. Before the fire, birds with the highest importance values were Blackburnian Warbler (*Dendroica fusca*), Ovenbird (*Seiurus aurocapillus*), Red-eyed Vireo (*Vireo olivaceus*) and Bay-breasted Warbler (*D. castanea*). Within 7 y following the fire, canopy tree cover decreased to near zero as fire-damaged trees died. Afterwards, the canopy began increasing, reaching 53% cover by 30 y. Shrub cover, 8% before the fire, peaked at over 70% two decades after fire, primarily as a result of dense jack pine and black spruce regeneration, and then decreased to 58% 30 y after fire. The total number of bird species using the area doubled the first year following the fire while the number of bird species with discernable territories decreased 40%. Thereafter, territorial species began increasing and 30 y after the fire the number exceeded the pre-fire richness by 60%. Overall, density of bird territories decreased nearly three-fold the first 3 y after the fire, but by year 30, was over 56% greater than in the pre-burn mature pine forest. Loss of canopy was related to a reduction in warbler and vireo diversity while increases in woody debris and near-ground vegetation were related to an increase in ground-brush foragers such as White-throated Sparrow (*Zonotrichia albicollis*) and Chipping Sparrow (*Spizella passerina*). Brown Creeper (*Certhia americana*) populations increased briefly as trees died, and for five years following fire there was an increase in woodpeckers and secondary cavity nesting species. At 7 to 10 y after fire, White-throated Sparrow, Magnolia Warbler (*Dendroica magnolia*), Chestnut-sided Warbler (*D. pensylvanica*), Nashville Warbler (*Vermivora ruficapilla*) and Mourning Warbler (*Oporornis philadelphia*) dominated. White-throated Sparrow continued to be the most important bird species through the first two decades, followed by Magnolia Warbler and Red-eyed Vireo. Thirty years after fire, the dominant birds were Nashville Warbler and Ovenbird, followed distantly by Veery (*Catharus fuscescens*) Swainson's Thrush (*Catharus ustulatus*), Least Flycatcher (*Empidonax minimus*) and Black-and-white Warbler (*Mniotilta varia*). Overall, bird species using the area after 30 y remained over 70% higher than in the mature forest before the fire.

INTRODUCTION

In Jun. 1976, as part of a long-term study of post-fire bird community development, we established a permanent plot in a 73 y-old jack pine (*Pinus banksiana*) - black spruce (*Picea mariana*) forest in the Boundary Waters Canoe Area Wilderness (BWCAW) in northeast Minnesota. We chose this cover type and age class because it was one of the most abundant upland community types in the wilderness (Grigal and Ohmann, 1975; Heinselman, 1996) where disturbance from logging or development was absent. In late Aug. 1976, lightning ignited a wildfire that burned 1368 ha including the study area which was located along an upland ridge near the center of the burned area. The plot was reestablished and surveyed in Jun. 1977 (Apfelbaum and Haney, 1981) and again in 1979, 1983, 1995, 2001, 2002 and 2006. Historically, the primary natural disturbance of this area was fire, with return intervals

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for stand-replacing fire on uplands every 40–100 y (Telfer, 2000). Fires were typically large, averaged 4000 ha (Frelich, 2002) and commonly resulted in a stand replacement by jack pine and black spruce with various amounts of quaking aspen (*Populus tremuloides*) (Ohmann and Ream, 1971; Johnson, 1992; Heinselman, 1996).

Frequency and severity of disturbances such as fire are a major influence on floristic composition, structure, and ecological functions (Pickett and White, 1985; Frelich, 2002). Virtually all aspects of avian habitat are influenced by the type, frequency, severity and intensity of disturbance (Hutto, 1995; Brawn *et al.*, 2001). Disturbance by wildfire typically increases diversity of bird communities (Anglestam, 1998; Niemi *et al.*, 1998; Brawn *et al.*, 2001), although not necessarily by increasing alpha diversity, that is, variation within habitats (Herrando *et al.*, 2003). Landscape patchiness generally is increased because of the irregular way fire interacts with edaphic variation (Denslow, 1985). Although many studies have examined response of bird communities to fire (Bock and Lynch, 1970; Bock *et al.*, 1978; Fox, 1983; Apfelbaum and Haney, 1986; Raphael *et al.*, 1987; Hutto, 1995; Saab and Powell, 2005), few have had the opportunity to compare pre- and post-fire data or followed the same fire disturbance for more than 25 y. In this study, we examine the successional development of the bird community over the 30 y following the stand-replacing fire and compare those changes to the avian community in the mature jack pine-black spruce forest that was present on the same plot in 1976 and on an unburned replicate plot 4 km away.

METHODS

Our study was conducted in the Superior National Forest along the south-central edge of the boreal forest (Fig. 1). The stand in which our study was conducted originated from a 1903 fire. This age was determined from increment cores taken from dominant jack pines (Miron Heinselman, pers. comm.). Using hand-held compasses and tape, we established a 5 $\times$ 5 grid with each cell being 50 $\times$ 50 m. We marked each 50 m intersection with flagging (Fig. 2). Birds were surveyed from dawn to mid-morning during the last week of May through the first two weeks of Jun. with one to two experienced birders slowly walking grid lines, triangulating and recording locations of all birds seen or heard inside the grid area, as well as within 25 m of the outside of the grid. The total area covered, including the 25 m buffer, was 9 ha. Censuses ranged from 4 to 8 person-hours, averaging 6 person-hours each and were conducted only on days without significant wind and rain. An inventory involved five censuses usually spaced over 2 or more weeks. Locations for each species during the five censuses plus additional observations were compiled on summary sheets with territories being delineated from clusters of registrations, and other evidence, such as active nests, or adults carrying food or fecal sacs. Particular attention was given to locations of pair-behavior and conflicts between males. Birds were considered transient unless a species was recorded during at least three of the five surveys in the same approximate location. Transient birds, those recorded less than three times in the same location, were tallied as visitors (V) if in the plot, or peripheral (P) if outside of it.

Upon completion of the surveys, we estimated breeding density using the delineated territories and the percent area occupied by each territorial species within the plot. Numbers of territorial species were used to calculate the Shannon-Weiner index of diversity (H') for the breeding community. Using Kendeigh's (1970) energetic estimates, we also calculated the existence energy of each species in the community. Using the sum of relative cover, relative density, and relative energy consumption, we then calculated relative importance values for each territorial species, compiling the data by species and guild using Bock and Lynch's (1970) guild designations.

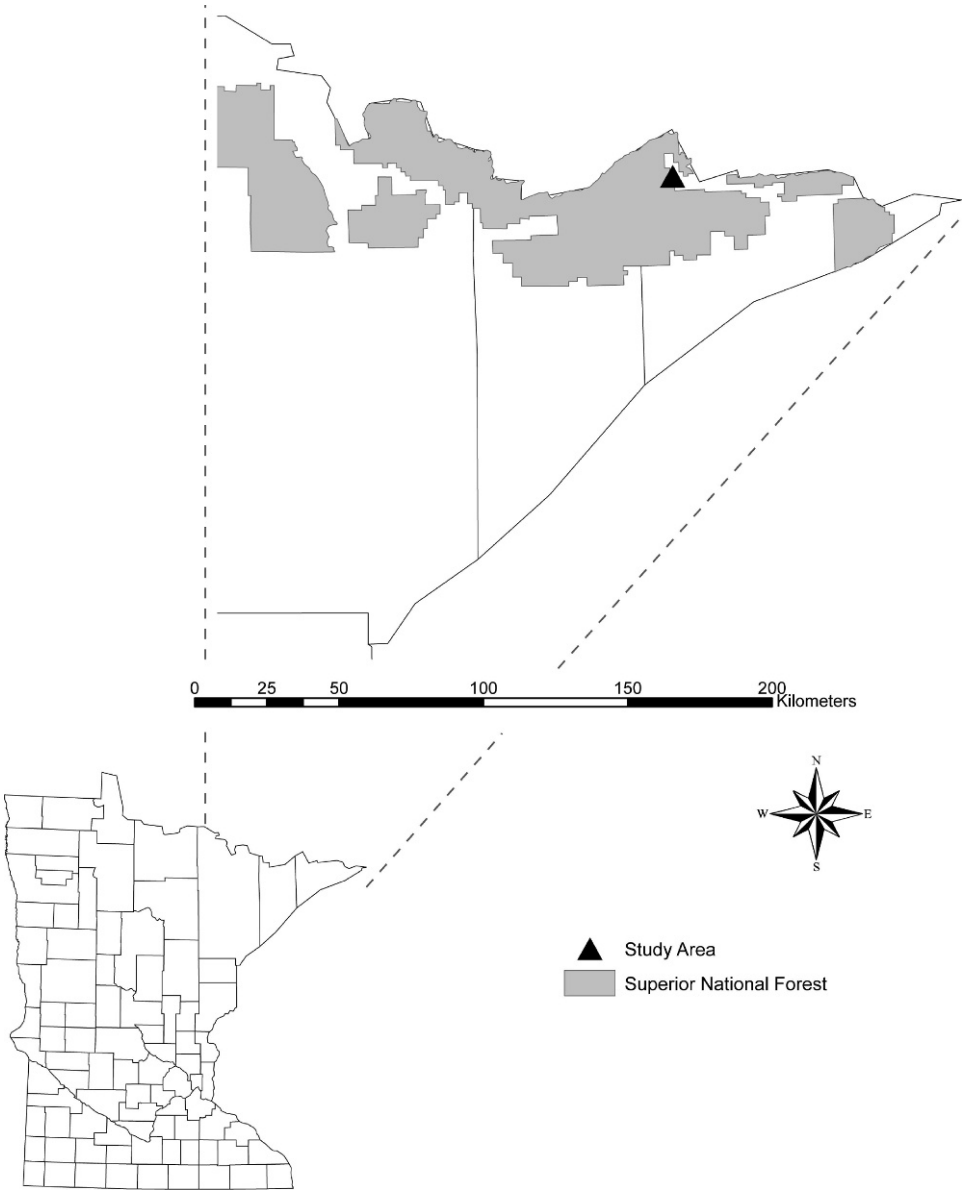

FIG. 1.—Location of study area in northeastern Minnesota's Superior National Forest

Vegetation was sampled in 8–12 randomly chosen grid cells with variation in number stemming from increased rigor in methodology. Sampling was conducted along transects that bisected selected cells. We initially used prism estimates of basal area of woody vegetation, but beginning in 1983, 50 m line intercept was used to estimate cover of trees (stems >5 cm dbh) and shrubs (stems <5 cm dbh and >1 m tall). Ground-layer cover (<1 m tall) was estimated in five 1 m^2 circular quadrats centered at 5, 15, 25, 35 and 45 m with cover for each taxa being

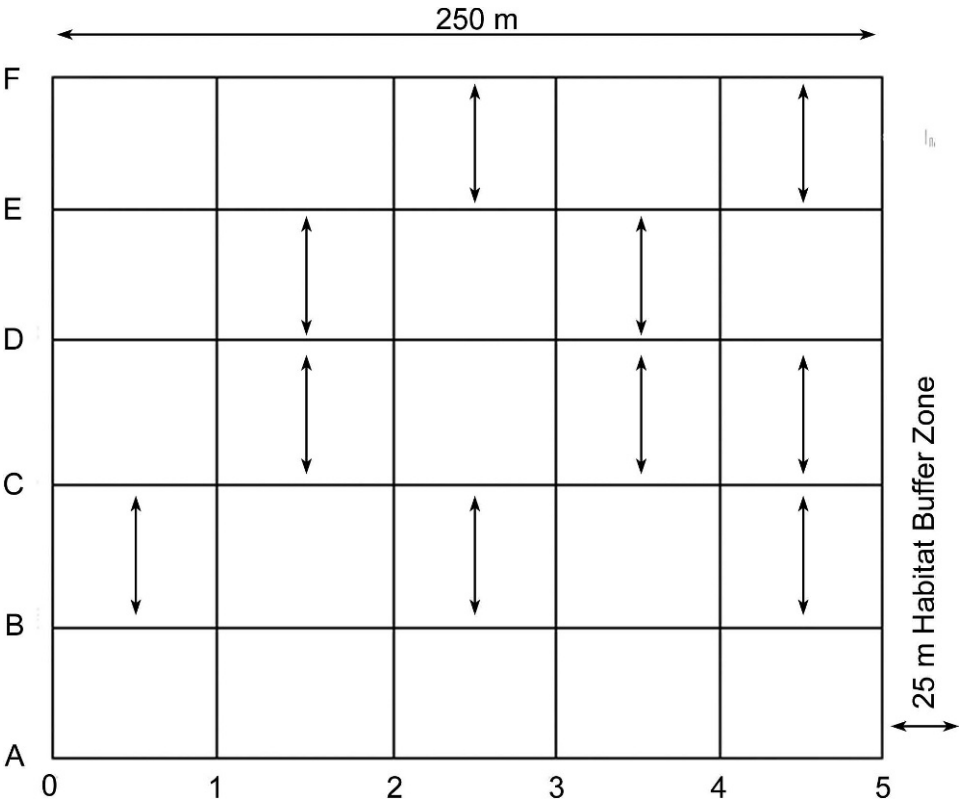

FIG. 2.—Survey Grid. The survey grid is 250 × 250 m with each grid cell measuring 50 × 50 m. The area inside the grids is 6.25 ha. The total area, including a 25 m habitat buffering zone to reduce the effects of edge, is 9 ha. Ten of the 25 grid cells are randomly selected before each vegetation survey and 50 m transects (shown as arrows within the grid cells) are used to perform the vegetation sampling

averaged across each transect. To reflect vegetation diversity related to overlap of species, we summed average cover of taxa to obtain total ground layer cover. Within each ground-layer quadrat, we also estimated percent cover of fine litter (<5 cm diam) and coarse litter (>5 cm diam), percent rock or soil and percent bryophyte and lichen cover.

To provide a comparison for evaluating stability of the bird community composition and structure in a similar forest without fire disturbance, in 1983 we established an unburned replicate plot 4 km southeast of the study site. This replicate was in the same cover type and was established following a stand-replacement fire in 1903, the same year as our study plot (pers. comm., Miron Heinselman). We resurveyed it in 1998, but its usefulness as a replicate for this study was terminated by a severe disturbance during a regional windstorm in 1999.

RESULTS

Based on air photo interpretation, the unburned forest had a total tree cover of approximately 75%, consisting of 48% evergreen trees and 28% deciduous, mostly aspen (Table 1). Aspen tended to be concentrated in draws, whereas slopes and ridges were a mix of jack pine with some black spruce. Direct estimates of shrub and small tree cover averaged

TABLE 1.—Summary of habitat variables (% cover) on the study plot over 30 y following a stand-replacing fire compared to vegetation before the fire (73 y-old forest) and on an unburned replicate plot sampled during the same period. ''ND'' indicates that no data was available for that particular year

	Age (since stand-replacing fire)								
	Post-Burn						Pre-Burn	Replicate	
Habitat variable	1	3	7	19	25	30	73	80	95
ground-layer	63	175	75	34	12	7	23	7	16
bryophyte	ND	23	22	43	55	46	61	76	78
fine litter	ND	ND	ND	34	64	37	ND	ND	49
coarse litter	ND	ND	ND	25	29	15	ND	ND	18
litter (fine and coarse litter combined)	ND	ND	40	ND	ND	ND	39	32	ND
mineral	ND	ND	8	4	2	5	3	<1	4
evergreen shrub	ND	ND	<1	63	57	52	8	12	7
deciduous shrub	ND	ND	0	22	26	11	3	12	5
shrub	ND	ND	<1	73	70	58	8	22	11
evergreen tree	ND	ND	0	4	46	36	47[a]	70	53
deciduous tree	ND	ND	0	1	13	21	28[a]	15	22
tree	48	20[a]	0	6	55	53	75[a]	77	64

[a] Values given were estimated from aerial photography

8% and consisted mostly of willow and alder in small, isolated wet pockets. The sum of the average cover for ground-layer plants was 23% while bryophytes covered 61% of the ground. Exposed rock and soil was <1%. These data compare well with the vegetation parameters from the replicate site (Table 1).

The first spring after fire, many trees still retained live foliage resulting in a canopy cover of 48%. Shrub cover was essentially eliminated whereas the combined total cover of ground layer vegetation increased to 63%. Fringed bindweed (*Polygonum cilinode*), which was not present before the fire, covered nearly 18% of the ground the first year after fire and 14% 3 y afterwards. Ground-layer vegetation continued to increase with a total of 175% 3 y after fire before declining to a low of 7% cover 30 y after fire; about the same cover as in the unburned forest (Table 1).

Shrub cover, which rapidly increased with the growth of dense jack pine and black spruce seedlings as well as aspen spouts, peaked 19 y after fire at 73%. Bryophyte cover continued to increase, approaching 50% by the 30th year. Tree cover exceeded 50% with composition approximately the same as before the fire (Table 1).

The dominant bird species before fire, based on relative importance value (Table 2) were Blackburnian Warbler (*Dendroica fusca*), Ovenbird (*Seiurus aurocapillus*), Red-eyed Vireo (*Vireo olivaceus*) and Bay-breasted Warbler (*Dendroica castanea*). Of these species, only the Blackburnian Warbler returned and retained dominance the year following fire. This species was joined the first year after fire by relatively important populations of Dark-eyed Junco (*Junco hyemalis*), Yellow-rumped Warbler (*D. coronata*) and White-throated Sparrow (*Zonotrichia albicollis*). Neither Dark-eyed Juncos nor White-throated Sparrows were recorded in or near the plot prior to fire. Ovenbirds, Red-eyed Vireos and Bay-breasted Warblers, dominant before the fire, were recorded only as visitors afterwards. Three years after fire, the only species from the mature forest that remained were Yellow-rumped Warbler and Ruby-crowned Kinglet (*Regulus calendula*), both of which increased in number. White-throated Sparrows were dominant, followed in importance by Chipping Sparrows (*Spizella passerina*), Yellow-rumped Warblers, and Dark-eyed Juncos.

TABLE 2.—Bird species importance values during 30 y of post-fire succession following a stand-replacing fire compared to birds in the unburned plot and control plot sampled during the same period. Importance value is the sum of relative numbers, relative cover, and relative existence energy (maximum value = 300). Birds plotted, but not considered territorial, were recorded as visitors (V) while birds recorded in the 25 m buffer area, but not inside the plot, were recorded as peripherals (P). Foraging guilds follow those of Bock and Lynch (1970)

		Age (since stand-replacing fire)									
		Post-Burn							Pre-Burn	Replicate	
Guild and species	Binomial	1	3	7	19	22	23	30	73	80	98
Flycatchers		0	0	17	35.4	30.7	36.2	27.4	0	12.4	11.4
Eastern wood pewee	*Contopus sordidulus*			V							
Least flycatcher	*Empidonax minimus*			V	19.1	30.7		23.3		12.4	11.4
Olive-sided flycatcher	*Contopus cooperi*	V		17			V				
Tree swallow	*Tachycineta bicolor*	V	V								
Yellow-bellied flycatcher	*Empidonax flaviventris*				16.3		36.2	4.1			
Tree-foliage searchers		161.9	97.5	22.8	91.4	100.6	111.4	84.8	212	253.6	199.2
American redstart	*Setophaga ruticilla*				5.9			V			
Bay-breasted warbler	*Dendroica castanea*	V							29.6	51	31.9
Blackburnian warbler	*Dendroica fusca*	81.9	V	V	20.3	V		P	82.8	112.7	70.3
Black-capped chickadee	*Poecile atricapilla*		17.8			V	8.6	3.3		4.6	
Black-throated blue warbler	*Dendroica caerulescens*					V					
Blue-headed vireo	*Vireo solitarius*	V						V	11.5	V	V
Boreal chickadee	*Poecile hudsonica*	17.6				V			26.3		3.6
Canada warbler	*Wilsonia canadensis*			V		15.7	3.9			3.4	
Cape may warbler	*Dendroica tigrina*										23.9
Cedar waxwing	*Bombycilla cedrorum*				V		V	V			V
Golden-crowned kinglet	*Regulus satrapa*							16.4		V	45.6
Nashville warbler	*Vermivora ruficapilla*		V	22.8	31.2	43	22.4	43.4		11.7	36
Philadelphia vireo	*Vireo philadelphicus*							2.9			
Pine siskin										19.1	
Red-eyed vireo	*Vireo olivaceus*	V		V	34	24.5	17.7	19.1	33.3	V	V
Ruby-crowned kinglet	*Regulus calendula*	5.8	25.9		V			8.6	18	34	6.4
Yellow-rumped warbler	*Dendroica coronata*	56.6	53.8	V	V	17.6	58.8	21.3	10.9	22.5	17.6
Timber gleaners		0	0	9	5.4	43.4	25.9	23.2	20.2	8.4	17
Black-and-white warbler	*Mniotilta varia*				5.4	43.4	25.9	23.2			
Brown creeper	*Certhia americana*	V		9					9.8	8.4	
Red-breasted nuthatch	*Sitta canadensis*					V		V	10.4		17
Timber drillers		0	0	0	0	0	0	0	0	0	0
Black-backed woodpecker	*Picoides arcticus*	V	V	V							
Downy woodpecker	*Picoides pubescens*						V				

TABLE 2.—Continued

Guild and species	Binomial	Age (since stand-replacing fire)									
		Post-Burn							Pre-Burn	Replicate	
		1	3	7	19	22	23	30	73	80	98
Hairy woodpecker	*Picoides villosus*							V			
Northern flicker	*Colaptes auratus*	V		V			V				V
Ground-brush foragers		138	202.5	251	167.8	125	126.5	165	67.3	25.6	72.3
American crow	*Corvus brachyrhynchos*		V		V		V				
American robin	*Turdus migratorius*	V	V		V		V				
Blue jay	*Cyanocitta cristata*	V				V	V	V		V	V
Chestnut-sided warbler	*Dendroica pensylvanica*			38.1	V						V
Chipping sparrow	*Spizella passerina*		69.9	V						13.9	14.6
Common grackle	*Quiscalus quiscula*	V	V								
Common raven	*Corvus corax*							P		V	V
Common snipe	*Gallinago gallinago*			V							
Common yellow-throat	*Geothlypis trichas*										V
Dark-eyed junco	*Junco hyemalis*	63.4	28.6								
European starling	*Sturnus vulgaris*	V									
Evening grosbeak	*Coccothraustes vespertinus*		V			V	V				V
Gray-cheeked thrush	*Catharus minimus*	V									
Gray jay	*Perisoreus canadensis*	V	V	V	V	V	V	V	V	V	
Hermit thrush	*Catharus guttatus*		V		V		V	P	V		
Magnolia warbler	*Dendroica magnolia*		V	32.4	43.1	23.7	26.6	13.2		V	
Mourning warbler	*Oporornis philadelphia*			25.8							
Ovenbird	*Seiurus aurocapillus*	V				37.8	23.1	33.5	67.3		
Purple finch	*Carpodacus purpureus*	V	V		V			V		V	
Red-winged blackbird	*Agelaius phoeniceus*		V								
Ruffed grouse	*Bonasa umbellus*		V			V					
Song sparrow	*Melospiza melodia*		V								
Spruce grouse	*Falcipennis canadensis*								V	V	
Swainson's thrush	*Catharus ustulatus*	22.2	V		30	23	15.2	25.9			V
Swamp sparrow	*Melospiza georgiana*			11.9							15.9
Tennessee warbler	*Vermivora peregrina*				4.8					6.2	V
Veery	*Catharus fuscescens*				13.2	14.3	35.1	33.6			
White-throated sparrow	*Zonotrichia albicollis*	52.4	104	133	58.3	20.5	11.4	16.2			5.8
Winter wren	*Troglodytes troglodytes*		V	9.5	18.4	5.7	V	12	V		
Yellow warbler	*Dendroica petechia*			V		V	15.1				
Raptors		0	0	0	0	0	0	0	0	0	0
Cooper's hawk	*Accipiter cooperii*		V								
Merlin	*Falco columbarius*					V					

TABLE 3.—Summary of bird community variables during 30 y of succession following a stand-replacing fire compared to the bird community before the fire (73 y-old forest) and on an unburned control plot sampled during the same period at age 80 and 95

	Age (since stand-replacing fire)									
	Post-Burn							Pre-Burn	Replicate	
Community variable	1	3	7	19	25	26	30	73	80	95
Number territorial birds	17.5	15.5	48	47	54	65	70.5	45	54	48
Total avian biomass	282.8	247.8	846.3	758	805.6	989.5	1090.7	588.6	546.6	468.0
Mean biomass/bird	16.2	16	17.6	16.1	14.9	15.2	15.5	13.1	10.1	9.75
Tot. existence energy (kcal)	243	214	704	648	713	869	930	550	568	486
Mean existence energy/bird	13.9	13.8	14.7	13.8	13.2	13.4	13.2	12.2	10.5	10.1
Years since fire	1	3	7	19	25	26	30	73	80	98
Territories/6.25 ha	8.75	7.75	24	23.5	27	32.5	35.25	22.5	27	24
Territories/10 ha	14	12.4	38.4	37.6	43.2	52	56.4	36	43.2	38.4
Territorial species (richness)	7	6	9	13	12	13	16	10	12	13
Total Cover (all species)	68	81	170	130	174	173	205	95	132	71
Total Energy	243	214	704	648	713	869	930	550	568	486
Transient species (richness)	16	19	13	9	11	12	8	4	10	12
Total species (richness)	23	25	22	22	23	25	24	14	22	25
H′	1.68	1.65	1.8	2.36	2.34	2.38	2.59	2.06	1.9	2.19
J′	0.87	0.92	0.82	0.92	0.94	0.93	0.93	0.89	0.76	0.85

Seven years after fire, White-throated Sparrows continued to dominate. Secondary dominants included Chestnut-sided Warbler (*Dendroica pensylvanica*), Magnolia Warbler (*D. magnolia*), Mourning Warbler (*Oporornis philadelphia*) and Nashville Warbler (*Vermivora ruficapilla*), all of which typically nest and forage on or near the ground. Yellow-rumped Warblers and Ruby-crowned Kinglets, present before and for several years after fire, were no longer present. Nineteen years after fire, White-throated Sparrows were still dominant, though much less so than at seven years following fire and only slightly exceeded Magnolia Warblers in importance. Secondary dominants 19 y after fire included Red-eyed Vireo, Nashville Warbler, and Swainson's Thrush (*Catharus ustulatus*). Red-eyed Vireo, Least Flycatchers (*Epidonax minimus*), Yellow-bellied Flycatchers (*Empidonax flaviventris*) and Veerys (*Catharus fuscescens*) were present for the first time since the fire. During the following 11 y, White-throated Sparrows continued to decline with concomitant increases in evenness among associated species, including Yellow-rumped Warbler, Black-and-white Warbler (*Mniotilta varia*), Veery, Yellow-bellied Flycatcher, Magnolia Warbler and Nashville Warbler.

Richness of breeding species with discernable territories dropped from ten in the unburned plot to seven the first year and six the third year before increasing to 16 by 30 y after the fire (Table 3). Species diversity (H′) exhibited the same pattern (Table 3). Visiting species, in contrast, increased from four in the unburned forest to 16 the first year after fire, peaked at 19 in the third year and then declined to eight species 30 y following fire. Total richness, the combination of territorial and transient species, remained constant during the 30 y following the fire ranging from 22 to 25. This was in sharp contrast to the combined 14 species recorded before the disturbance.

The four-fold increase in visiting species immediately after fire was mainly the result of the appearance of birds that prefer disturbed habitats such as American Crow (*Corvus brachyrhynchos*) and American Robin (*Turdus migratorius*), but it also included the arrival of

specialists such as the Black-backed Woodpecker (*Picoides arcticus*) and secondary cavity nesters such as the Tree Swallow. Moreover, several persistent species present in the mature forest such as the Yellow-rumped Warbler and Ruby-crowned Kinglet, returned during the first years after the fire. Visitors to the recently burned forest also included species present in the unburned forest that returned but did not establish territories immediately after fire, such as Ovenbirds.

Breeding bird density, based on identified territories, decreased from 22.5 territories per 6.25 ha (144 per 40 ha) in the mature forest to 8.75 (56 per 40 ha) the first year after fire and 7.75 the third year (Table 3). After the third year, there was a gradual increase in breeding bird density to over 35 territories, 30 y after fire.

Compared to the unburned forest, we found that the total existence energy of territorial species decreased to about half of pre-burn levels the first 3 y after the fire, but by 7 y was 25% higher and increased through the 30th year (Table 3). Average existence energy per bird was lowest in the mature forest and highest during the first seven years after fire, although differences were not great. These differences parallel bird weight and result from greater abundance of ground-brush foraging species that, on average, are heavier than birds foraging in the canopy.

Tree-foliage searchers, which represented over two-thirds of the total importance of birds in the unburned forest, decreased by about half the first year after fire but still remained the most important guild mainly as a result of the continuing use of surviving trees in the burned forest by Blackburnian Warblers (Table 2). The prominence of Dark-eyed Juncos, White-throated Sparrows and Swainson's Thrushes did, however, greatly increase the relative importance of ground-brush foragers. Nearly all trees on and around the plot with living foliage the first year after the fire, were dead by the third year. At that time, ground-brush foragers completely dominated, representing two-thirds the importance value of the territorial birds. By 7 y, ground-brush foragers represented over 80% of the importance and 33 of the 38 territories on the plot. Timber gleaners and flycatchers were also increasingly important after the first 3 y with the relative importance of both guilds peaking in the 19th and 23rd year communities. In contrast, we began to record timber drillers such as the Black-backed Woodpecker, less often.

DISCUSSION

The need for long-term post-disturbance studies is widely recognized (Brawn *et al.*, 2001) and are even more valuable when based on pre-disturbance data. This study resulted from a serendipitous opportunity to examine avian community development on the same plot before and after a stand-replacing fire in a mature forest. Fire is, arguably, the most important disturbance in this region and the cover type of the unburned forest was the most common upland type, having originated from a previous fire. Our plot size, 9 ha with the 25 m buffer, was very close to that used by Bock and Lynch (1970) and their successors (Bock *et al.*, 1978; Raphael *et al.*, 1987) who compared birds after fire to those in a nearby, unburned control in the Sierra Nevada. The heterogeneous diversity of landform in the area we were working necessitated keeping our plot somewhat smaller to avoid including dissimilar habitats, especially black spruce bogs or open peat bogs. Because these observations were based on a relatively small, single plot, we felt it was important to find a reference stand outside the burn for comparison and were able to find an unburned replicate in the same age class and cover type 4 km away. Although the breeding bird data were similar, there was a much higher number of non-territorial, or transient, species on the replicate plot (Table 3). One of the most striking effects of fire on the overall structure of

the bird community was the four-fold increase in non-territorial species, a response that persisted through at least the first 26 y (Table 3). The number of non-territorial species on the undisturbed replicate plot were comparable. We believe this unexpected similarity may have resulted from a nearby clear-cut, and if so, that suggests that the 25 m buffer we used was inadequate to separate very dissimilar habitats.

Like many others, (Bock and Lynch, 1970; Apfelbaum and Haney, 1986; Hutto, 1995; Helle and Neimi, 1996; Hobson and Schieck, 1999; Imbeau *et al.*, 1999; Drapeau *et al.*, 2000; Schieck and Hobson, 2000; Hannon and Drapeau, 2005), we found that tree-foliage searchers were the dominant guild in the mature forest and, following fire, these species soon are largely replaced by ground-brush foragers, woodpeckers and secondary cavity nesters with a concomitant increase in non-territorial species. Most Corvids and Picoids have territories much larger than we could detect with our 9 ha study plot. These, therefore, are recorded as non-territorial when, in fact, many may have been foraging within territories. Thus, our breeding bird density and related estimates, including diversity, are conservative.

The increase in ground-brush foragers, including transients, is consistent with the shifts in vegetation structure (Table 1). Live tree canopy cover was gone by 7 y following fire and ground cover increased by an order of magnitude. The ground layer decreased after the first decade giving way to small tree and shrub cover which increased nearly ten-fold. In addition to elimination of the canopy and increase in shrub and ground layer vegetation following the fire, there were important specific habitat changes. For example, fringed bindweed (*Polygonum cilinode*) , an annual herb that dominated the ground the first year or two after the fire, is an important food for ruffed grouse (Apfelbaum and Haney, 1984) and probably several other seed-eating species in mid- to late-summer. Ground-brush foragers reached peak dominance while tree-foliage searchers reached their lowest numbers 7 y after the fire. Tree-foliage searchers remained half as important as before the fire for three decades afterwards even when the canopy had recovered to over 50% cover.

Consistent with findings of Bock and Lynch (1970) and Fox (1982), we found that density of territorial species was only 42% the first year after fire compared to the pre-fire forest, and 34% the third year. Density then increased through 30 y. This differs from Hutto (1995), who reported similar territorial density on burned and unburned plots the first 2 y after fire in the northern Rocky Mountains. Intermediate stages of succession, 19 to 30 y in our data, had consistently higher breeding diversity than either the younger or older stands. Although the 30-y old forest had the highest territorial richness of species, density, biomass and existence energy, we expect that these parameters will soon begin a decline toward the levels in the pre-burn forest. This expectation is based both on the fact that density and richness were positively linked ($P < 0.01$) ($r^2 = .801$) as well as on our earlier findings in a wide range of post-fire habitats (Apfelbaum and Haney, 1986) which demonstrated the same.

Richness of territorial species dropped by over 30% immediately following fire and did not recover to pre-fire levels for nearly a decade. The decrease in territorial species, however, was more than offset by the increase in non-territorial species, which included generalists such as American Robin and American Crow that are more common in disturbed areas, and fire-dependent species such as the Black-backed Woodpecker (Nappi *et al.*, 2003). Bock and Lynch (1970) reported similar differences. Like Bock and Lynch (1970), we also found that the average size of birds using the plot after fire was greater. Existence energy (Kendeigh, 1970) is closely related to the size of birds, but provides another metric for comparison of bird communities. Total number of territorial birds, total biomass, and total existence energy all increased about four-fold from the first year after fire to the 30th year, which was roughly twice as high as those metrics in the avian community in the unburned forest.

The reason richness, diversity and existence energy of the territorial population reaches a peak during intermediate stages of succession likely is related to increased vertical and spatial diversity of the vegetation structure (MacArthur and MacArthur, 1961; Erdelen, 1984; Schieck *et al.*, 1995). Our observations are similar to the changes in vegetation following fire reported by Morissette *et al.* (2002). Foliage height diversity is lowest as the jack pine-black spruce forest first reaches maturity at about 60 y. After the first 20 to 30 y following fire, ground-layer vegetation and shrub layers are nearly absent on upland sites in larger burn scars until 100+ y when jack pine and aspen begin to give way to spruce and fir (Apfelbaum and Haney, 1986). The open understory and relatively dense canopy are unfavorable to most ground-nesting and foraging species. Moreover, the trees that did not survive during the self-thinning period have largely died and decayed before surviving trees reach maturity, so snags and cavities are uncommon, and remaining trees are all about the same size.

In contrast to territorial species, total richness of bird species using the habitat remained nearly constant during the 30 y after fire, and was more than 150% of the total richness of the mature forest, an observation also noted by Hutto (1995). The initial reduction in territorial species was more than offset by increased numbers of non-territorial species. These included species that had territories in the undisturbed forest and which returned after fire, but did not establish territories, a carry-over phenomenon we have observed after severe wind disturbance (Burris and Haney, 2005).

Much has been written about specialization within bird communities, but most emphasis is on diet and foraging strategies (Recher, 2004). Small passerines generally nest and forage in the same habitat and presumably habitat selection represents some optimization between reproductive success and foraging opportunities. Predictions of where species might occur depend on understanding habitat preferences (MacArthur and MacArthur, 1961). Highest overall avian diversity, in our study, was in early successional stages where generalists, or birds less particular about habitat, overlapped the specialists that are more restricted to heavier ground cover. As the forest approached maturity, generalists and ground-brush specialists decreased and canopy specialists dominated.

Results from this study clearly demonstrate the role of disturbance in maintaining ecosystem diversity especially over time. Of the 60 species recorded on our plot during this study, only 14 occurred in the mature forest before fire. The others were recorded after the fire during the first 30 y of succession. Not only did fire create opportunities for non-specialists during the first few years after the disturbance, it also provided opportunities for some specialized species. In contrast, some species that responded negatively to fire in the short term, profited by habitat conditions created during later succession. Although less direct, these late-successional species are as disturbance dependent as those that responded shortly after the fire. By taking a longer-term look, the dynamic relationship between diversity, habitat, and disturbance is better illuminated.

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LITERATURE CITED

ANGELSTAM, P. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *Journal of Vegetation Science*, **9**:593–602.

APFELBAUM, S. I. AND A. HANEY. 1981. Bird populations before and after wildfire in a Great Lakes pine forest. *The Condor*, **83**:347–354.

——— AND ———. 1984. Note on the foraging and nesting habits of Goshawks. *Loon*, **56**:132–133.

——— AND ———. 1986. Changes in bird populations during succession following fire in the Northern Great Lakes Wilderness, p. 10–16. *In:* R. C. Lucas, proceeding compiler. Proceedings – National Wilderness Research Conference: current Research. U.S.D.A. Forest Service General Technical Report INT-212.

BOCK, C. E. AND J. F. LYNCH. 1970. Breeding bird populations of burned and unburned conifer forest in the Sierra Nevada. *The Condor*, **72**:182–189.

———, M. RAPHAEL AND J. H. BOCK. 1978. Changing avian community structure during early post-fire succession in the Sierra Nevada. *The Wilson Bulletin*, **90**:119–123.

BRAWN, J. D., S. K. ROBINSON AND F. R. THOMPSON, III. 2001. The role of disturbance in the ecology and conservation of birds. *Annual Review of Ecology and Systematics*, **32**:251–276.

BURRIS, J. M. AND A. HANEY. 2005. Bird communities after blowdown in a late-successional Great Lakes spruce-fir forest. *The Wilson Bulletin*, **117**:341–352.

DENSLOW, J. S. 1985. Disturbance-mediated coexistence of species, p. 307–323. *In:* S. T. A. Pickett and P. S. White (eds.). The ecology of natural disturbances and patch dynamics. Academic Press, Orlando, Florida, USA.

DRAPEAU, P., A. LEDUC, J. F. GIROUX, J. P. L. SAVARD, Y. BERGERON AND W. L. VICKERY. 2000. Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. *Ecological Monographs*, **70**:423–444.

EHRLICH, P. R., D. S. DOBKIN AND D. WHEYE. 1988. The Birders Handbook. Simon and Schuster, Inc. 785 p.

ERDELEN, M. 1984. Bird communities and vegetation structure: I. Correlations and comparisons of simple and diversity indices. *Oecologia*, **61**:277–284.

FOX, J. F. 1983. Post-fire succession of small-mammal and bird communities, p. 155–180. *In:* R. W. Wein and D. A. McLaren (eds.). The Role of Fire in Northern Circumpolar Ecosystems. John Wiley and Sons, Toronto, Canada.

FRELICH, L. E. 2002. Forest dynamics and disturbance regimes. Cambridge University Press, Cambridge, United Kingdom. 266 p.

GRIGAL, D. F. AND L. F. OHMANN. 1975. Classification, description, and dynamics of upland plant communities within a Minnesota wilderness area. *Ecological Monographs*, **45**:389–407.

HANNON, S. J. AND P. DRAPEAU. 2005. Bird responses to burning and logging in the boreal foarest of Canada, *In:* V. A. Saab and H. D. W. Powell (eds.). Fire and avian ecology in North America. Cooper Ornithological Society, Camarillo, Ca. 193 p.

HEINSELMAN, M. 1996. The Boundary Waters wilderness ecosystem. University of Minnesota Press, Minneapolis, Mn. 334 p.

HELLE, P. AND G. J. NIEMI. 1996. Bird community dynamics in boreal forests, p. 209–234. *In:* R. M. DeGraaf and R. I. Miller (eds.). Conservation of Faunal Diversity in Forested Landscapes. Chapman and Hall, London. 633 p.

HERRANDO, S., L. BROTONS AND S. LLACERNA. 2003. Does fire increase the spatial heterogeneity of bird communities in Mediterranean landscapes? *Ibis*, **145(2)**:307–317.

HOBSON, K. A. AND J. SCHIECK. 1999. Changes in bird communities in boreal mixwood forest: harvest and wildfire effects over 30 y. *Ecological Applications*, **9**:849–863.

HUTTO, R. L. 1995. Composition of bird communities following stand-replacement fires in Northern Rocky Mountain (U.S.A.) conifer forests. *Conservation Biology*, **9**:1041–1058.

IMBEAU, L., J. P. L. SAVARD AND R. GAGNON. 1999. Comparing bird assemblages in successional black spruce stands originating from fire and logging. *Canadian Journal of Zoology*, **77(12)**:1850–1860.

JOHNSON, E. A. 1992. Fire and vegetation dynamics: studies from the North American boreal forest. Cambridge University Press, Cambridge, U.K.

KENDEIGH, S. C. 1970. Energy requirements of existence in relation to size of bird. *Condor*, **72**:60–65.

MACARTHUR, R. H. AND J. W. MACARTHUR. 1961. On bird species diversity. *Ecology*, **42**:594–598.

MORISSETTE, J. L., T. P. COBB, R. M. BRIGHAM AND P. C. JAMES. 2002. The response of boreal forest songbird communities to fire and post-fire harvesting. *Canadian Journal of Forest Research*, **32**:2169–2183.

NAPPI, A., P. DRAPEAU, J.-F. GIROUX AND J.-P. L. SAVARD. 2003. Snag use by foraging black-backed woodpeckers (*Picoides arcticus*) in recently burned eastern boreal forests. *The Auk*, **120(2)**:505–511.

NIEMI, G., J. HANOWSKI, P. HELLE, R. HOWE, M. MONKKONEN, L. VENIER AND D. WELSH [ONLINE]. 1998. Ecological sustainability of birds in boreal forests. *Conservation Ecology*, **2(2)**:17. URL: http://www.consecol.org/vol2/iss2/art17 (18 Dec. 2006).

OHMANN, L. F. AND R. REAM. 1971. Wilderness ecology: virgin plant communities of the Boundary Waters Canoe Area. USDA Forest Service, North Central Forest Experiment Station.

PICKETT, S. T. A. AND P. S. WHITE. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, San Diego, California. 472 p.

RAPHAEL, M. G., M. L. MORRISON AND M. P. YODER-WILLIAMS. 1987. Breeding bird populations during twenty-five years of post fire succession in the Sierra Nevadas. *Condor*, **89**:614–626.

RECHER, H. F. 2004. Specialist or generalist: avian response to spatial and temporal changes in resources, p. 333–336. *In:* M. L. Morrison, C. J. Ralph, J. Verner and J. R. Jehl, Jr. (eds.). Avian Foraging: theory, Methodology, and Applications. Studies in Avian Biology – Number 13. Cooper Ornithological Society

SAAB, V. A. AND H. D. W. POWELL (eds.). Fire and avian ecology in North America. Cooper Ornithological Society, Camarillo, Ca. 193 p.

SCHIECK, J. AND K. A. HOBSON. 2000. Bird communities associated with live residual tree patches within cut blocks and burned habitat in mixedwood boreal forests. *Canadian Journal of Forest Research*, **30**:1281–1295.

———, M. NIETFELD AND J. B. STELFOX. 1995. Differences in bird species richness and abundance among three successional stages of aspen-dominated boreal forests. *Canadian Journal of Zoology*, **73**:1417–1431.

TELFER, E. M. 2000. Regional variation in fire regimes, p. 9–15. *In:* J. K. Smith (ed.). Wildland fire in ecosystems, effects of fire on fauna. USDA Forest Service General Technical Report RMRS-GTR-42, Volume 1. Ogden, Utah. 83 p.

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