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BIRD COMMUNITIES BEFORE AND AFTER A CATASTROPHIC BLOWDOWN IN A GREAT LAKES PINE FOREST[1]

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Abstract. We carefully inventoried the bird communities in a mature jack pine - black spruce forest (*Pinus banksiana - Picea mariana*) before (1997 - 1999) and after (2000 - 2003) a major blowdown in northern Minnesota. Because of known similarities in bird species diversity and abundance in the first year following a disturbance, bird data collected in 2000 are reported but not included in the comparisons between pre- and post-blowdown. Within our 6.25 ha study plot, a total of 19 territorial bird species were recorded before compared to 17 species after the storm. Eight species that held territories before the storm did not establish territories afterwards, in contrast to six species without territories before but having them afterwards. Magnolia Warbler (*Dendroica magnolia*), White-throated Sparrow (*Zonotrichia albicollis*), and Winter Wren (*Troglodytes troglodytes*) increased the most following the disturbance, whereas Blackburnian Warbler (*Dendroica fusca*) and Golden-crowned Kinglet (*Regulus satrapa*) did the opposite. The Bay-breasted Warbler (*Dendroica castenea*), which held territories in every year leading up to the storm, completely disappeared afterwards. Thirteen of the 18 habitat variables examined changed significantly after the disturbance. These changes reflect a 60% destruction of the overstory and a 500% increase in the shrub level of the forest, and demonstrate experimentally the importance of vegetative structure in the composition of forest bird communities.
Key words: Bird communities, blowdown, wind disturbance, Great Lakes Transition Forest, Magnolia Warbler, Winter Wren, White-throated Sparrow, Blackburnian Warbler, Golden-crowned Kinglet, Bay-breasted Warbler

COMUNIDADES DE AVES ANTES Y DESPUÉS DE UNA CATASTRÓFICA CAÍDA DE ÁRBOLES POR VIENTO EN UN BOSQUE DE PINO EN LA REGIÓN DE LOS GRANDES LAGOS DE LOS ESTADOS UNIDOS

Resumen. Realizamos un minucioso inventario de la comunidad de aves en un bosque maduro de pino-picea (Pinus banksiana – Picea mariana) antes (1997-1999) y después (2000-2003) de un gran derribo de árboles por viento en la parte norte de Minnesota. Por las similitudes conocidas en la diversidad y la abundancia de aves en el primer año después de un disturbio, los datos de aves recopilados en el año 2000 son reportados pero no incluidos en las comparaciones pre y post caída de árboles. Dentro de nuestra área de estudio de 6.25

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ha, registremos 19 especies de aves territoriales antes de la tormenta contra 17 especies después de la misma. Ocho especies que mantenían territorios antes de la tormenta no establecieron territorios después, en contraste a seis especies sin territorios antes de la tormenta que sí establecieron territorios después. Dendroica magnolia, Zonotrichia albicollis, y Troglodytes troglodytes fueron las especies que exhibieron un mayor incremento en abundancia después del disturbio, mientras que Dendroica fusca y Regulus satrapa mostraron lo contrario. Dendroica castanea, que tenía individuos con territorios en cada año previo al vendaval, desapareció por completo posteriormente. Trece de las 18 variables del hábitat medidas cambiaron significativamente después del disturbio. Estos cambios reflejan una destrucción de 60% del dosel y un aumento de 500% en la cobertura del nivel arbustivo del bosque y demuestran la importancia de la estructura de la vegetación en la composición de las comunidades de aves de bosques.

Palabras claves: Comunidades de aves, caída de árboles por viento , disturbio eólico, transición forestal de los Grandes Lagos, Dendroica magnolia, Troglodytes troglodytes, Zonotrichia albicollis, Dendroica fusca, Regulus satrapa, Dendroica castanea.

INTRODUCTION

Forest composition and structure in the Upper Great Lakes is greatly influenced by disturbances, which include primarily fire, insect outbreaks, logging, and wind (Van Wagner and Methven 1978, Bonan and Shugart 1989, Bergeron 1991, Drapeau et al. 2000; Haney et al., unpubl. data). Fire and insects affect forest structure most frequently, and are well studied, but although large-scale wind events are thought to play a significant role in canopy reduction, they occur so infrequently — at the scale of 1000 years or more — we know little about them (Frelich and Reich 1996, Larson and Waldron 2000, Frelich 2002). A number of studies have examined the effects of disturbance on avian communities in the Upper Great Lakes region (Apfelbaum and Haney 1986, Schulte and Niemi 1998, Drapeau et al. 2000), but not surprisingly few have examined the effects of wind (Smith and Dallman 1996, Dyer and Baird-Philip 1997).

On 4 July 1999 a microburst, or *derecho*, resulting in straight-line winds >145 km hr^{-1}, impacted approximately 200,000 ha of forest in northeastern Minnesota (USDA Forest Service 2002). One severely impacted stand, which we have studied >16 yr, contained one of our permanent 6.25 ha study plots. The permanent plot, first established in a mature jack pine – black spruce forest (*Pinus banksiana - Picea mariana*) in 1983, was resurveyed in each of the three years before the 1999 storm thereby providing an uncommon opportunity to compare vegetation and bird community structure pre- and post-wind disturbance.

Our objective was to compare the structure of the bird community and vegetation before and after the wind-storm reduced the canopy by approximately 60 %. Because the wind removed >50% of the tree cover, with a corresponding increase in shrub cover from fallen trees or tree-tops, we expected a shift from tree foliage-searching to ground-brush foraging species. We further anticipated an increase in woodpeckers with the increase in coarse woody debris (Lohr et al. 2002).

STUDY AREA AND METHODS

Surveys. The study was conducted in a relatively homogeneous, mature, upland jack pine – black spruce forest in northeastern Superior National Forest, MN (Fig. 1). Bird populations were estimated by plotting territories in a 250 x 250 m (6.25 ha) grid surrounded by a 25 m habitat buffering zone to reduce the effects of edge. Plots were subdivided, with flagging, into 50 x 50 m cells (Fig. 2).

Bird surveys were conducted once per day during the early morning over five days in late May through mid-June in each of the three years before (1997 – 1999) and four years after (2000 – 2003) the disturbance. Surveys were performed using a modification of Kendeigh's flush-plot technique (Kendeigh 1944, Apfelbaum and Haney 1986). Each survey consisted of one or two experienced birders plotting all birds seen or heard from grid vertices on data sheets similar to Figure 2. Surveys, which were restricted to days without significant wind or

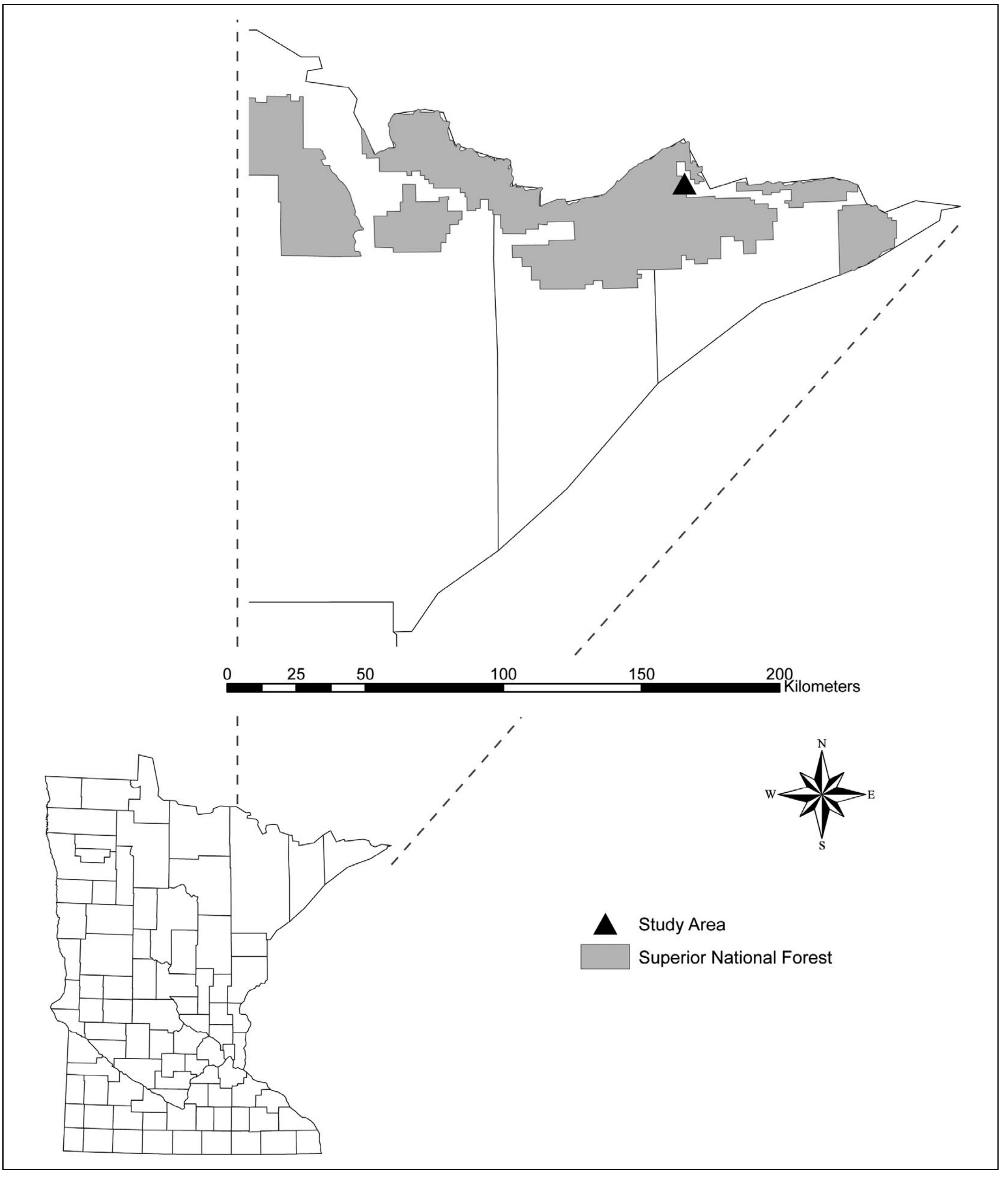

FIGURE 1. Location of study area in northeastern Superior National Forest, MN.

rain, averaged about six person-hours each with the aim of plotting every territorial male using the area.

After the completion of all five daily surveys, locations of birds on the grid and within 25 m of the grid's perimeter were compiled onto summary sheets. Territories were delineated from clusters of survey registrations and other evidence of established territories such as active nests, adults carrying food, or fecal sacs. Species were considered transient, or with territories too large to determine with our method, unless they were recorded in the same location on at least three of the five survey days. Species that were

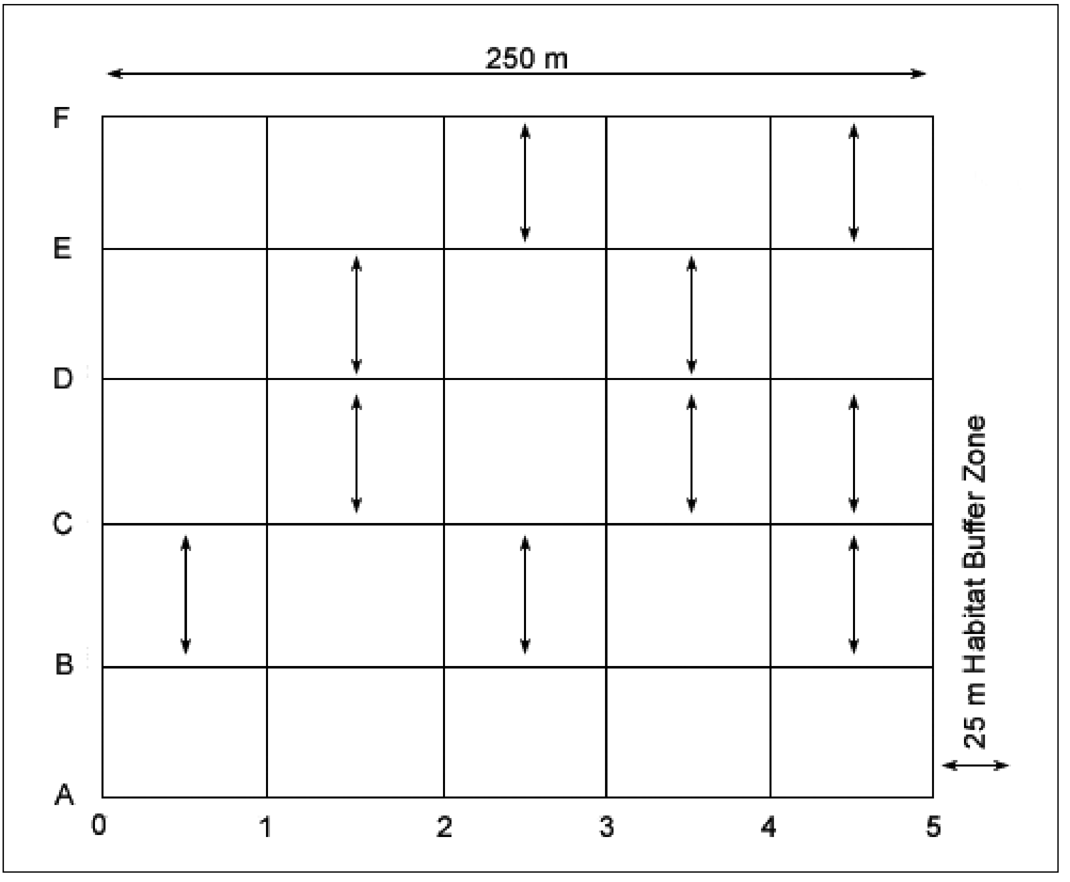

FIGURE 2. The survey grid, 250 x 250 m (6.25 ha), with each cell measuring 50 x 50 m. The total area, including a 25 m habitat buffering zone to reduce the effects of edge, is 9 ha. Ten of the 25 grid cells were randomly selected before each vegetation survey and 50 m transects (shown as arrows within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

plotted in the grid, but which did not meet the aforementioned criteria, were recorded as visitors (V). Species with territories outside the grid but in the same habitat were recorded as peripherals (P).

Four vegetation surveys, in 1997, 2000, 2001, and 2003, were conducted with each consisting of 50-m transects through 10 randomly selected grid cells (Fig. 2). Because grid cells were re-selected before each survey, some cells may have been repeatedly surveyed while others may have been surveyed only once. Cover for each vegetative species was estimated using the line intercept method. Trees were defined as stems standing more than 45° perpendicular to the ground with a d.b.h. of at least 5 cm. Shrubs were identified as all stems with a height >1 m and a d.b.h. <5 cm or as those trees that were still alive but standing <45° from vertical. Dead trees were considered coarse litter if standing <45° perpendicular and snags if standing >45°. Tree and shrub density was estimated by recording the number and diameter (rounded to the nearest 5 cm) of live and dead trees rooted within 1 m either side of the transect, as was the number of live and dead shrub stems within 1 m of the right side of the transect. Five 1 m^2 circular plots centered at 5, 15, 25, 35, and 45 m along the transect line were used to estimate percent cover of herbs (height <1 m), exposed mineral, bryophytes, coarse litter (diameter >5 cm) on the ground, and fine litter (diameter <5 cm; Fig. 3).

Data analysis. Determined for each bird species was density (the number of territories

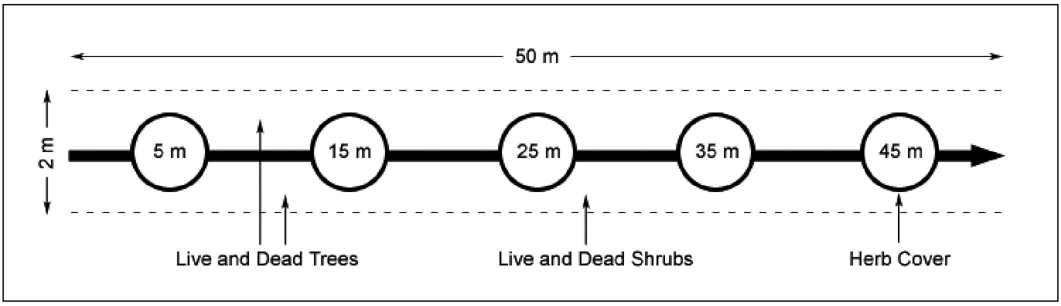

FIGURE 3. Vegetation was sampled using a 50 m transect. Tree and shrub density was estimated by recording the number and diameter of live and dead trees rooted within 1 m to either side of the transect and the number of live and dead shrub stems within 1 m to the right side of the transect. Herb cover was determined using a 1 m^2 circular plot centered at 5, 15, 25, 35, and 45 m along the transect.

within the 6.25 ha grid), territory cover (percent of grid covered), and existence energy (kcal day-1 required to maintain the observed density of birds). Existence energy was calculated using formulas that consider body mass and ambient temperatures (Kendeigh 1970, Apfelbaum and Haney 1986). Relative values for these three related variables were then combined to create an importance value index (IVI; Curtis 1959) for each species and guild. IVIs reflect relative percentages of bird number, area occupied, and required energy by species or guild and provide an abstract value ranging from 0 – 300 that indicates one species' or guild's use of resources relative to another (Apfelbaum and Haney 1981). Species were assigned to guilds following the five Bock and Lynch (1970) designations that indicate foraging behavior (e.g. timber-driller, tree foliage-searcher). An additional guild was added for raptors. To address known issues of spatial scale in regard to bird sampling (Wiens 1981, Wiens et al. 1987) and to identify trends most likely related to the disturbance, bird data for seven common species were further examined by plotting Breeding Bird Survey (BBS) trend data from Strata 28: Northern Spruce - Hardwoods (Bystrak 1981) alongside observed densities on the study site (Fig. 4).

Vegetation data were examined for normality (Q-Q plot and Shapiro-Wilk tests). When data did not meet assumptions, homogeneity of variances (Levene's test), with transformations according to Box-Cox plots (Box and Cox 1964), were tested. Rank transformation was used as a last resort when Box-Cox recommendations failed to yield a normal distribution (Conover and Iman 1981, Blake et al. 1994). For each vegetation characteristic, a one-way ANOVA was used to test for significance. Where appropriate, a comparison of means was made using Dunnett's C (does not assume equal variance) procedure.

All scientific names of bird species are included in Table 2.

RESULTS

Among the habitat variables tested, 72% (13 of 18) were found to change significantly with time (Table 1). Eleven of these 13 variables were significantly different between at least one year before and after the blowdown. Evergreen shrub cover increased 866% and the number of live shrub stems increased 981% in the first year following the storm. Notably, both decreased significantly in 2001 and again in 2003.

Despite the loss of over 60% of the tree canopy (from 64.2% in 1997 to 23.8% in 2000), the overall richness of territorial and visiting birds changed very little (Table 2). On average, 13 species in four guilds held territories in the study area before the disturbance, compared to 11 species in the same number of guilds that held territories afterwards. Before and after the storm, 20 and 24 species, respectively, were recorded only as visitors. Of the 24 species that were exclusively seen as visitors throughout the study, 13 were recorded as visitors during both periods. The Magnolia Warbler, White-throated Sparrow, and Winter Wren each averaged at least two territories more after the storm while

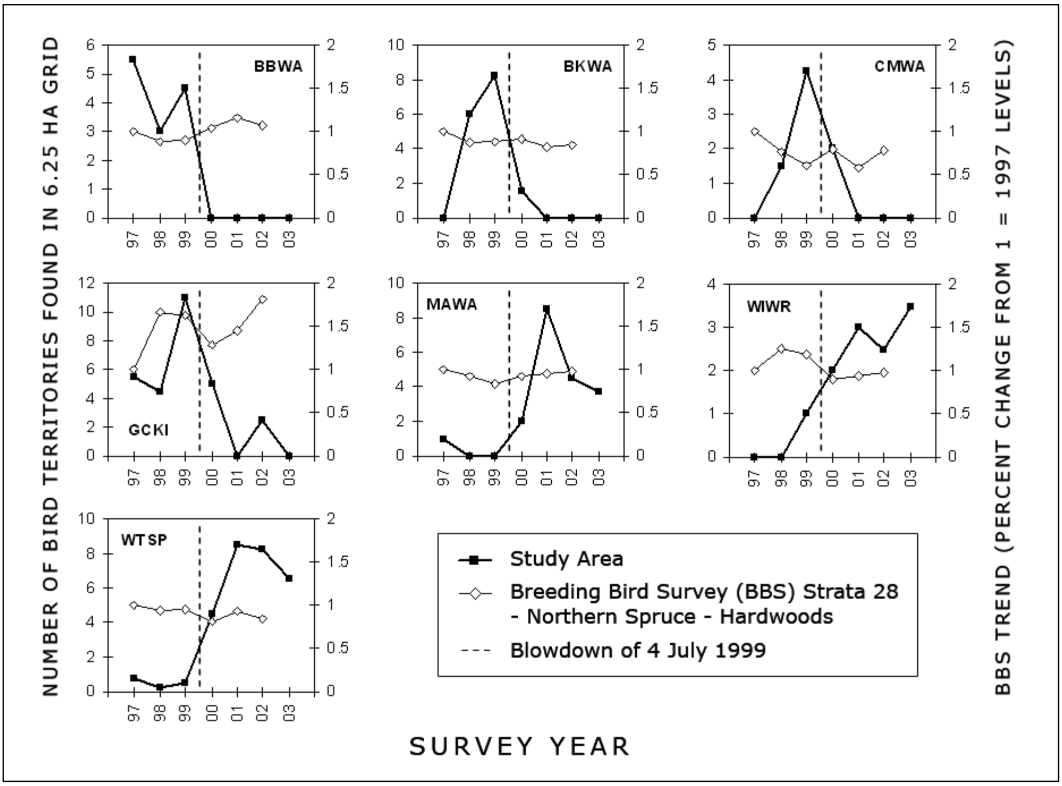

FIGURE 4. Population clines of seven common migratory birds before (1997 - 1999) and after (2000 - 2003) a major blowdown in a mature jack pine – black spruce forest, Superior National Forest, MN. BBS trend data are provided to reflect changes in bird populations occurring on a larger scale. BBWA = Bay-breasted Warbler; BKWA = Blackburnian Warbler; CMWA = Cape May Warbler; GCKI = Golden-crowned Kinglet; MAWA = Magnolia Warbler; WIWR = Winter Wren; WTSP = White-throated Sparrow.

the Blackburnian Warbler, Cape May Warbler, and Golden-crowned Kinglet each averaged at least two less. Although variability was evident in several species, it was most notable in Blackburnian Warbler and Cape May Warbler with both being conspicuously absent in 1997. The Bay-breasted Warbler, which increased slightly in the region from 1997 - 2002 (BBS data), was the only species holding territories in all three years leading up to the storm that was not recorded as either a visitor or a peripheral afterwards (Fig. 4).

By guild, tree-foliage searchers, which had the highest IVI values before the blowdown, decreased and ground-brush foragers increased in every year following the storm (Table 2). The Magnolia Warbler was the only tree-foliage searcher that notably increased following the storm. No species of ground-brush forager decreased after the storm. Changes to other guilds were minor.

DISCUSSION

The most significant effect of the storm on vegetation was a >60% decrease in canopy cover and the number of live trees and a concomitant increase in shrub cover of >500%. Jack pine and black spruce, the main overstory trees before the blowdown, were reduced from a combined 47% canopy cover in 1997 to <10% in 2000. About half of the trees that were destroyed by the wind were tipped over exposing pockets of mineral soil and reducing bryophyte cover by almost 50% between 1997 and 2000.

As with observations following fire (Emlen 1970, Apfelbaum and Haney 1981), and similar effects documented following hurricanes (Waide

TABLE 1. Mean vegetation characteristics and outcomes of one-way ANOVA on 40 (10 each year) 50 m transects surveyed before (1997) and after (2000, 2001, 2003) a blowdown in a mature jack pine – black spruce forest, Superior National Forest, MN. When ANOVA yielded a significant result, pairwise comparisons were conducted using Dunnett's C procedure; common superscripts indicate no significant difference ($P > 0.05$) between paired means.

		$\bar{X}$					
	Tr.[a]	1997	2000	2001	2003	*F*	*P*
% tree cover	ln	64.2	23.8^{b}	5.0^{b}	8.2^{b}	11.7	< 0.01
% tree cover (evergreen)	ln	52.9^{b}	21.9^{bc}	2.8^{c}	5.9^{c}	12.12	< 0.01
% tree cover (deciduous)	root	21.7	3.4^{b}	3.1^{b}	4.0^{b}	8.46	< 0.01
Live trees ha^{-1}	ln	2510	810^{a}	160^{a}	280^{a}	13.20	< 0.01
Dead trees ha^{-1}	rank	210^{ab}	40^{a}	90^{ab}	360^{b}	3.86	0.02
Live tree diameter (cm)		12.2	10.8	8.6	11.1	2.63	0.07
Dead tree diameter (cm)		8.6^{a}	17.3^{ab}	12.5^{ab}	13.5^{b}	5.43	0.01
% shrub cover	root	11.3^{a}	71.7	29.5	12.0^{a}	36.81	< 0.01
% shrub cover (evergreen)	rank	6.7^{a}	64.7	17.9	2.8^{a}	37.49	< 0.01
% shrub cover (deciduous)		4.8	13.3	12.4	9.6	1.59	0.21
Live shrub stems ha^{-1}		1080^{a}	11,680	3,740^{a}	2,220^{a}	34.88	< 0.01
Dead shrub stems ha^{-1}	rank	280^{a}	500^{a}	0^{a}	0^{a}	5.10	0.01
% shrub or tree cover		69.2^{a}	80.6^{a}	32.6	18.4	65.87	< 0.01
% herb cover		15.5	7.7	29.4	25.3	5.72	0.32
% fine litter cover		49.2	47.6	41.1	49.6	0.49	0.70
% coarse litter cover	root	18.4^{ab}	8.8^{a}	15.9^{a}	31.7^{b}	10.71	< 0.01
% mineral cover	rank	3.9	6.1	12.8	7.5	2.45	0.08
% bryophyte cover		78.3	42.3^{a}	41.0^{a}	32.5^{a}	21.1	< 0.01

[a] Transformations used include square root (root), natural log (ln), and rank (rank).

1991, Wunderle 1995), some territorial species that were negatively impacted by the storm in 1999 returned in 2000 before disappearing the following year. The typically higher-nesting (Cruickshank 1956, Morse 1994) Blackburnian Warbler, for example, which we observed nesting uncharacteristically very near the ground in 2000, held 8.25 territories in 1999, 1.5 in 2000, but no territories from 2001 – 2003. Territory numbers of the Cape May Warbler and Golden-crowned Kinglet displayed a similar trend (Fig. 4). Notably this did not hold true for the Bay-breasted Warbler, which was not even recorded as a visitor immediately after the storm despite holding multiple territories in every year leading up to it. Despite nesting in the lower one third of trees and occasionally even in shrubs (Peck and James 1987, Williams 1996), the Bay-breasted Warbler has been identified as a species sensitive to canopy loss (Morton 1992, Drolet et al. 1999).

Many species that increased as a result of the change in habitat also did not respond much the first year after the blowdown. The Magnolia Warbler, relatively uncommon before the blowdown, held two territories in 2000 then averaged nearly six from 2001 - 2003. Similarly, the White-throated Sparrow averaged 0.5 territories from 1997 - 1999, 4.5 in 2000, and then >8 from 2001 – 2003. The Yellow-bellied Flycatcher, which was not recorded before the blowdown but may have found an increase in suitable habitat in the form of roots of upturned stumps (Bent 1942, Erlich et al. 1988), established territories in 2001 and afterwards in all of the blowdown areas we studied (Haney and Thomton 2001).

Based on similar studies conducted in the wake of hurricanes (Greenberg and Lanham 2001, Tejeda-Cruz and Sutherland 2005), it was not surprising that the loss of over half the tree cover and corresponding increase in shrub cover resulted in a shift from tree-foliage-searching species to ground-brush-foraging species. Before the blowdown, tree-foliage searchers averaged

TABLE 2. Breeding bird importance values (IVI) by foraging guild before (1997 - 1999) and after (2000 - 2003) a major blowdown in a mature jack pine – black spruce forest,Superior National Forest, MN. IVI is based on relative frequency, relative territory area, and relative existence energy. Visitor (V) and peripheral (P) species are noted but not included in calculations.

Guild and Species	1997	1998	1999	2000	2001	2002	2003
FLYCATCHERS	19.1	11.4	19	25.4	14	18.1	18.5
Alder Flycatcher (*Empidonax alnorum*)	P	P	P	1.1	P	P	2.3
Common Nighthawk (*Chordeiles minor*)		P					
Least Flycatcher (*Empidonax minimus*)	19.1	11.4	19	24.3		V	12.4
Olive-sided Flycatcher (*Contopus cooperi*)					V	P	
Yellow-bellied Flycatcher (*Empidonax flaviventris*)					14	18.1	3.8
GROUND-BRUSH FORAGERS	80.2	72.3	63	168	188.2	196.4	223
American Crow (*Corvus brachyrhynchos*)		V					
American Robin (*Turdus migratorius*)			V	P	V	V	V
Blue Jay (*Cyanocitta cristata*)	V	V		V	V	V	V
Dark-eyed Junco (*Junco hyemalis*)	V			V	V	V	V
Chestnut-sided Warbler (*Dendroica pensylvanica*)	V	V			V	V	P
Chipping Sparrow (*Spizella passerina*)	19.1	14.6	7.5	31.8	28	22.8	31.4
Common Raven (*Corvus corax*)		V			V		P
Evening Grosbeak (*Coccothraustes vespertinus*)		V	V			V	
Gray Jay (*Perisoreus canadensis*)	V	P		P		V	V
Hermit Thrush (*Catharus guttatus*)	P	P	P	P	V	P	V
Lincoln's Sparrow (*Melospiza lincolnii*)	V		P				P
Mourning Warbler (*Oporornis philadelphia*)					V	V	24.6
Nashville Warbler (*Vermivora ruficapilla*)	36	36	42.3	62.6	28.9	17.1	44.2
Ovenbird (*Seiurus aurocapillus*)	V		V				P
Purple Finch (*Carpodacus purpureus*)	V		V				
Swainson's Thrush (*Catharus ustulatus*)	14.8	V			19.9	7.4	13.7
Swamp Sparrow (*Melospiza georgiana*)		15.9		P	P	P	P
White-throated Sparrow (*Zonotrichia albicollis*)	10.3	5.8	6.5	49.6	80.8	111.1	74.2
Winter Wren (*Troglodytes troglodytes*)			6.7	24	30.6	38	29.2
Veery (*Catharus fuscescens*)				P			5.7
RAPTORS							
Broad-winged Hawk (*Buteo platypterus*)			V		V		
Merlin (*Falco columbarius*)					V		
Sharp-shinned Hawk (*Accipiter striatus*)					V	V	
TIMBER-DRILLERS							
Black-backed Woodpecker (*Picoides arcticus*)				V	V	V	V
Hairy Woodpecker (*Picoides villosus*)				P			V
Northern Flicker (*Colaptes auratus*)	V	V		P		V	
TIMBER-GLEANERS		17	22.1				10.1
Black-and-white Warbler (*Mniotilta varia*)	V				P	V	10.1
Brown Creeper (*Certhia americana*)	V					V	
Red-breasted Nuthatch (*Sitta canadensis*)	V	17	22.1		V		V
TREE FOLIAGE-SEARCHERS	200.7	199.3	195.8	106.6	97.7	85.4	48.1
Bay-breasted Warbler (*Dendroica castanea*)	54.4	31.9	29.3				
Black-capped Chickadee (*Poecile atricapilla*)	6.7			V	9.2	V	V
Black-throated Green Warbler (*Dendroica virens*)			V		V		
Blackburnian Warbler (*Dendroica fusca*)	V	70.3	47.8	12.1	V		
Blue-headed Vireo (*Vireo solitarius*)	P	V				P	
Boreal Chickadee (*Poecile hudsonica*)	V	3.6			V		
Canada Warbler (*Wilsonia canadensis*)				7.1	V		
Cape May Warbler (*Dendroica tigrina*)		23.9	24.8	13.3			
Cedar Waxwing (*Bombycilla cedrorum*)		V			V		
Common Yellowthroat (*Geothlypis trichas*)		V	V	2	P	11.6	3.8

TABLE 2. Continued.

Guild and Species	1997	1998	1999	2000	2001	2002	2003
Golden-crowned Kinglet (*Regulus satrapa*)	46.7	45.6	61.2	29.4	V	25.5	
Magnolia Warbler (*Dendroica magnolia*)	10.7	P	V	23.2	60.5	48.3	30.1
Pine Siskin (*Carduelis pinus*)	16.2				V		
Red-eyed Vireo (*Vireo olivaceus*)	V	V	V	P	V	V	P
Ruby-crowned Kinglet (*Regulus calendula*)	23.8	6.4	23.2	10.5	5.9	V	P
Tennessee Warbler (*Vermivora peregrina*)	8.8	V	1.9		P		
Yellow-rumped Warbler (*Dendroica coronata*)	33.4	17.6	7.6	9	22.1	V	14.2
Total (all guilds)	300	300	299.9	300	299.9	299.9	299.7

nearly 36 more birds than ground-brush foragers with an IVI of nearly three times as much. Discounting the transition year of 2000, this proportion reversed after the blowdown with an average of 24 more ground-brush foragers than tree-foliage searchers. The Magnolia Warbler, which is associated with low conifers and mixed deciduous woods (Bent 1953, Ehrlich et al. 1988), markedly increased following the storm suggesting that it may simply prefer large amounts of structure at or near the ground. This response also suggests that, although treated as a member of the tree-foliage-searcher guild based on known foraging habits, the Magnolia Warbler could just as accurately be considered a member of the ground-brush-forager guild.

As expected, given the increase in coarse woody debris (Lohr et al. 2002) and dead and dying trees (Schreiber and DeCalesta 1992, Schulte and Niemi 1998), the number of woodpeckers using the area increased following the disturbance. However, because of the larger size of their territories, we could not estimate the actual increase in density. Black-backed and Hairy woodpeckers, which had not been recorded previously, were both recorded with Black-backed being present in all years. In 2003, a Hairy Woodpecker nest cavity was found in a snapped off hollow aspen located in the center of the study area.

The opportunity to study a large-scale wind disturbance using baseline data collected before the event provided us with a rare opportunity to examine specific changes in the structure of the vegetation and the corresponding bird community. In spite of dramatic changes in forest structure, the diversity and density of birds using the area were not greatly altered.

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