Effects of the 1998 Ice Storm on Forest Bird Populations in Central Vermont

FINAL REPORT

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Steven D. Faccio
Conservation Biology Department
Vermont Institute of Natural Science
27023 Church Hill Rd.
Woodstock, Vermont

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Steven D. Faccio
Conservation Biology Department
Vermont Institute of Natural Science
Woodstock, VT 05091
sfaccio@vinsweb.org

Abstract: A damaging ice storm struck northern New England, New York, and adjacent Canada in January 1998, affecting nearly 7 million hectares of forest lands. Although relatively rare at this scale, such natural disturbances provide a unique opportunity to study the short- and long-term impacts on forest ecosystems and wildlife species. I investigated the storm's effects on breeding birds in a northern hardwood forest in central Vermont. Point counts at 6 ice-damaged study sites in the Green Mountain National Forest were used to compare post-storm bird abundance with pre-storm samples collected at the same points in 1993 or 1994, and at 5 control sites that were unaffected by the storm. In general, damage to canopy trees consisted of broken limbs and main stems, with lesser amounts of uprooted trees. This resulted in perforations, or small forest gaps, in a forested landscape, significantly reducing % canopy cover (P=0.038), while basal area and dbh remained unchanged. Overall, mean bird abundance declined at ice-damaged sites while increasing at controls ($P \leq 0.07$). Species richness increased at both treatments (P<0.05), while species diversity increased only at ice storm sites (P<0.0005). Three forest interior species declined in abundance ($P \leq 0.038$) following the storm, two of which were canopy-foragers (Red-eyed Vireo and Blackburnian Warbler), and one a ground-forager/nester (Ovenbird). Another ground-forager/nester, Dark-eyed Junco, was the only species to increase in abundance (P=0.021) after the storm, although Canada Warbler and Winter Wren showed increasing trends ($P \leq 0.141$). These results are consistent with studies investigating bird responses to selective forest management, particularly "group selection" and "single tree selection," suggesting that these management strategies may effectively mimic some types of natural disturbance events such as ice storms.

Introduction

In January 1998, a destructive ice storm hit northern New England, New York, and adjacent Canada, causing widespread damage to trees and extended power outages. Over 6,800,000 hectares (ha) of forests were damaged across Maine, New Hampshire, Vermont, and New York (Miller-Weeks and Eagar 1999). Aerial surveys conducted in Vermont mapped damage to 260,000 ha of forest lands, roughly 20% of the state's forested area (Kelley 2001) (Fig. 1). The Champlain Valley received a high proportion of damage, while ice damage in other regions of the state was more limited to higher elevations (generally above 550 m), particularly on east-facing slopes. This widespread natural disturbance provided a unique opportunity to study the short- and long-term impacts on trees, forest stands, and wildlife communities, as well as the effects on forest resources and landowners. A Federal Emergency Appropriation to aid with forest recovery efforts included funds to investigate these types of effects. As a result, a wide variety of studies were initiated. This report details the results of one such study – an investigation of the ice storm's effect on the relative abundance, diversity, and composition of forest-breeding birds in Vermont.

Background and Purpose

In the Northeast alone, numerous recent studies have documented the effects of timber harvesting on forest bird communities (Henke 1987, Thompson and Capen 1988, Derleth et al. 1989, DeGraaf et al. 1993, Rudnicky and Hunter 1993, Welsh and Healy 1993, Lent & Capen 1995, Hagan et al. 1996, King et al. 1996, 1997, Germaine et al. 1997, Canterbury and Blockstein 1997, Ortega and Capen 1999). Large-scale natural disturbances however (e.g. fires, wind storms, ice storms, insect outbreaks, etc.), are relatively rare, and their effects on breeding bird populations have been little studied in the region. Several researchers have investigated the effects of spruce budworm outbreaks on breeding birds, including Kendeigh (1947), and Zach and Falls (1975) in Ontario, and Morse (1978) in Maine. Elsewhere, Canterbury and Blockstein (1997) studied population sizes and species composition of breeding birds following local disturbances from Dutch elm disease, drought, and wind storms in a mixed deciduous forest in northern Minnesota. In that study, natural disturbances over a 10-year period converted a closed-canopy elm-birch-ash (*Ulmus-Betula-Fraxinus*) forest to a more open habitat dominated by basswoods (*Tilia* spp.), ashes, and standing snags with large areas of dense fern cover. The resulting changes in the bird community included declines in some forest-dependant species and increases in some early successional species. Apfelbaum and Haney (1981) studied bird populations the year before and the year after a forest fire damaged a 6.25 ha plot in a jack pine-black spruce (*Pinus banksiana-Picea mariana*) forest in northern Minnesota. In addition to these studies in temperate forests, several researchers have studied the impacts of hurricanes on resident and migratory birds in tropical forests (Thurber 1980, Askins & Ewert 1991, Lynch 1991, Wauer and Wunderle 1992, Wunderle 1995, Wunderle et al. 1992).

However, I could find no published studies detailing the response of bird populations to the effects of a damaging ice storm, such as the storm that occurred in the Northeast in 1998. This storm resulted in forest canopy gaps of various sizes, primarily due to crown loss from broken branches and main stems, and, to a lesser degree, uprooted and bent trees. These impacts were similar to uneven-aged forest management, such as "group selection" or "single-tree selection," which in general more closely mimics natural disturbance regimes than large-scale harvest techniques such as clearcutting (Hunter 1990). However, unlike selective harvests, ice damage from the 1998 storm resulted in the retention of basal area and an accumulation of large amounts of downed woody material on the forest floor.

The impacts of selective logging on forest birds has been well-documented, and Robinson and Robinson (1995) recently reviewed the literature. They report that many of the trends in bird populations following selective harvests can be correlated with changes in the volume of foliage in particular forest strata. For example, following selective logging, canopy-foraging species often decline due to a concomitant decrease in canopy volume (Crawford et al. 1981). Similarly, species occupying the shrub and understory layers may increase in abundance (Franzreb and Ohmart 1978) as increased light penetration promotes understory growth. Mechanical damage from the harvesting process often increases the amount of bare ground within a forest stand, resulting in an increase of bird species that forage on the ground (Franzreb and Ohmart 1978). In addition, species richness typically increases on logged sites due to more heterogeneous vegetation structure (Welsh and Healy 1993), while forest interior species often decline (Medin 1985, Burke and Nol 1998). Whether or not birds respond similarly to a natural disturbance which creates similar forest structure without decreasing basal area, is not known. This study took advantage of existing pre-storm surveys of breeding birds and vegetation to investigate the response of the avian community to the 1998 ice storm, and provides evidence for the efficacy of selective harvests to mimic such natural disturbances.

Methods

Study Area

Field work on ice-affected stands was conducted on the Rochester and Middlebury ranger districts of the Green Mountain National Forest (GMNF) in the towns of Hancock and Granville in central Vermont (Fig. 1). Using a GIS coverage of forest area damaged by the 1998 ice storm, 6 study sites were selected that were originally established in 1993 to study songbird abundance and productivity (Buford and Capen 1999). Within each study site, Buford and Capen (1999) established bird and vegetation survey points at the intersections of 200-m, spatially referenced grids. E. Buford provided these point count coordinates, which were then overlayed on the ice damage GIS layer in ArcView, resulting in 53 point count stations falling within mapped areas of ice damage. Using GPS, I located each of these 53 points during May 1999, and marked them with aluminum tree tags and flagging tape to facilitate their relocation during post-storm bird and vegetation surveys. Five of the study sites were located on the east side of the central ridge of the Green Mountains, which drops steeply into the White River Valley, and one study site was on the more gradually sloping west side. Elevations ranged from 490 to 810 m (1,600 to 2,650 ft). Forest stands consisted primarily of northern hardwoods dominated by American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*B. lutea*), with lesser amounts of paper birch (*B. papyifera*) and red spruce (*Picea rubens*) at higher elevations.

Five study sites from the Vermont Forest Bird Monitoring Program (FBMP) were selected as controls. A long-term monitoring project of the Vermont Institute of Natural Science (VINS), the FBMP utilizes point count surveys at mature, interior forest sites throughout the state to collect habitat-specific baseline data on species composition and relative abundance (see Faccio et al. 1998). Each control site consisted of 5 point count stations (25 total) spaced at least 200 m apart. Three of the control sites were located in the northern Green Mountains, the same biophysical region as the ice-affected sites, while the other 2 controls were located in the Northeast Kingdom (Fig. 1). Elevations ranged from 365 to 700 m (1,200 to 2,300 ft). All sites consisted of mature northern hardwoods dominated by beech, maples, and birches, with some red spruce at higher elevations. No visible ice damage from the 1998 storm was evident at the control sites.

Vegetation Measurements

Pre- and post-storm habitat measurements were made at each of the 53 ice-damaged point count stations. Canopy cover was estimated using a sighting tube at 40 equally spaced points along four 22.6-m transects oriented to the cardinal directions and crossing at plot center. An index of shrub density was measured along the transects by counting the number of stems (>1 m tall, <5 cm dbh) within 1 m of the transect. Basal area (m^2/ha) was estimated using a 10-factor prism, and all trees included in the assessment were identified and their dbh (cm) measured. Pre-storm measurements were made in July and August during 1993 and 1994 (E. Buford, pers. comm.), while post-storm metrics were collected in July 1999. In addition, during June 1999, the amount and type of ice damage was assessed at each point count station. In a 0.18 ha plot (50 m radius) centered on the point count station, each ice-damaged tree was identified to species, type of damage classified as either broken branch(s), broken main stem, bent tree, or uprooted tree, and the percent of crown loss was visually estimated and placed into one of the following categories; 1-10%, 11-25%, 26-50%, 51-75%, or 76-100%.

Bird Surveys

At each census point, 10-minute point counts were conducted twice annually during June. Observers, all experts in visual and aural bird identification, recorded all species detected within two distance classes – within and beyond 50 m. Surveys began by 0600, concluded by 1000, and were not conducted on days with rain or high winds.

Ice-damaged Sites – Pre-storm surveys were conducted by 2 observers, each visiting all points once, and data were collected at 3 sites in 1993 and at 3 sites in 1994 (total of 2 visits per point). Although post-storm surveys were conducted by a total of 6 observers, most surveys (80%) were

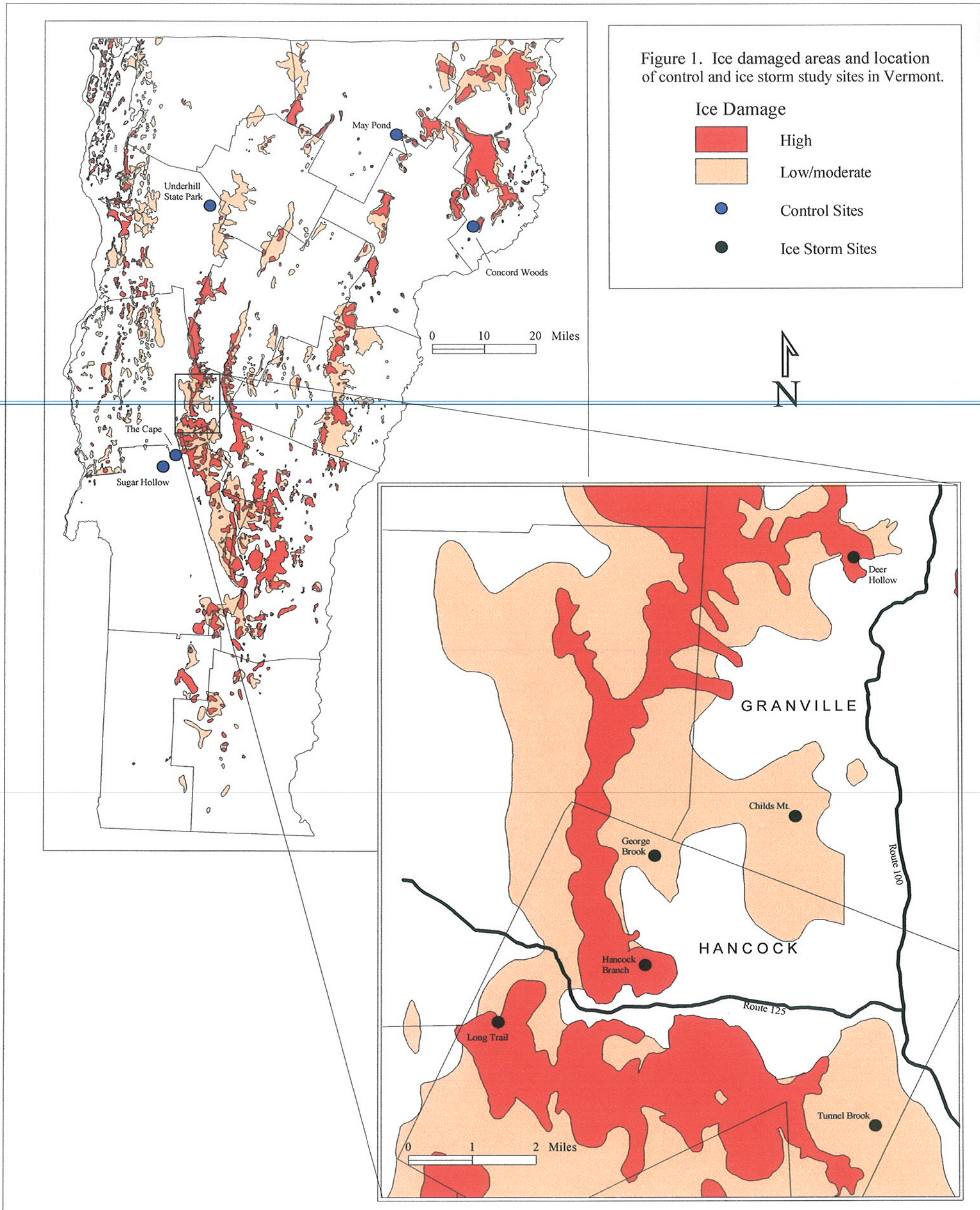

Figure 1. Ice damaged areas and location of control and ice storm study sites in Vermont.

conducted by 3 of these observers. Data were collected at all 6 sites during 1999, 2000, and 2001 (total of 6 visits per point).

Control Sites – Surveys were conducted by 4 observers, each of whom completed both pre- and post-storm counts at their respective study site(s). Two of these observers also conducted surveys at ice-damaged sites. Pre-storm data were collected during 1993 and 1994 (4 visits per point), and post-storm surveys were conducted during 1999, 2000, and 2001 (6 visits per point).

Data Analysis

During bird and vegetation surveys, it became clear that ice damage could vary dramatically from point to point, even within study sites. Therefore, data from points that sustained little to no damage were excluded from analyses, reducing the number of point counts at ice-damaged sites from 53 to 32.

Species Abundance, Richness, and Diversity – I calculated species abundances as the maximum number of detections per site (all stations combined) per year. I divided this total by the number of point counts to give a mean abundance per point. I determined pre-storm species richness on each study site by counting the total number of species detected during all surveys. However, since post-storm surveys occurred across 3 years, only those species that were detected in at least 2 years were included. I used the Shannon diversity index (H), which accounts for species richness, abundance, and evenness. In the formula below, *s* represents richness and *p* is the proportionate representation of species *i* among the total number of individuals.

$$H = -\sum_{i=1}^{s} (p_i)(\ln p_i)$$

Within treatments, I compared pre- and post-storm changes in the abundance of the 14 most common species (defined as those with a maximum count of $\geq$10 individuals at all sites combined in at least one year) using Mann-Whitney U-tests with P-value adjustments for the number of tests performed. I used a paired t-test to examine the change in the total abundance of these common species before and after the storm within treatments. Paired t-tests were also used to compare pre- and post-storm changes in the mean number of individuals per point, species richness, species diversity, and species turnover within controls and ice storm sites, and to compare before and after changes in habitat variables at ice-damaged sites. All analyses were performed in SYSTAT 8.0. To reduce the chance of committing a Type II error, significance was determined with an α level of 0.10 or less.

Results

Damage to Vegetation

Among the treatment sites, ice damage from the 1998 storm varied from point to point depending on elevation, aspect, and tree species composition. Points with the greatest amount of damage were those at higher elevations, and on east-facing slopes. Among the dominant canopy species (American beech, sugar maple, and yellow birch), branch and main stem breakage accounted for 78.3% of the damage (Fig. 2). Damage to paper birch, and pole-size American beech and yellow birch was primarily due to bent trunks, which were often completely bent over with their crowns touching the ground. More than half of the damaged trees (54.2%) lost more than half of their crowns, while just over one-third (33.9%) lost 76-100% of their canopy foliage (Fig. 2).

Comparison of pre-storm habitat measurements collected in 1993 and 1994, with those taken one year after the storm, revealed a significant change only in mean canopy cover, from 80.77% ±1.59 to 73.03% ±3.33 ($t = 2.173$, $P = 0.038$) (Table 1). Basal area, dbh, and sapling density all increased negligibly. The small increase noted in basal area and dbh was not surprising since trees had 5-6 growing seasons between measurements and the majority of damage to large trees was due to broken branches.

However, I expected a greater increase in sapling density following the storm due to increased light penetration. Although this was not detected, the number of stems appeared to increase dramatically during the second and third years of this study (pers. obs.), so that if stem density had been measured in 2001 rather than 1999, it is likely that an increase would have been noted at least at some points.

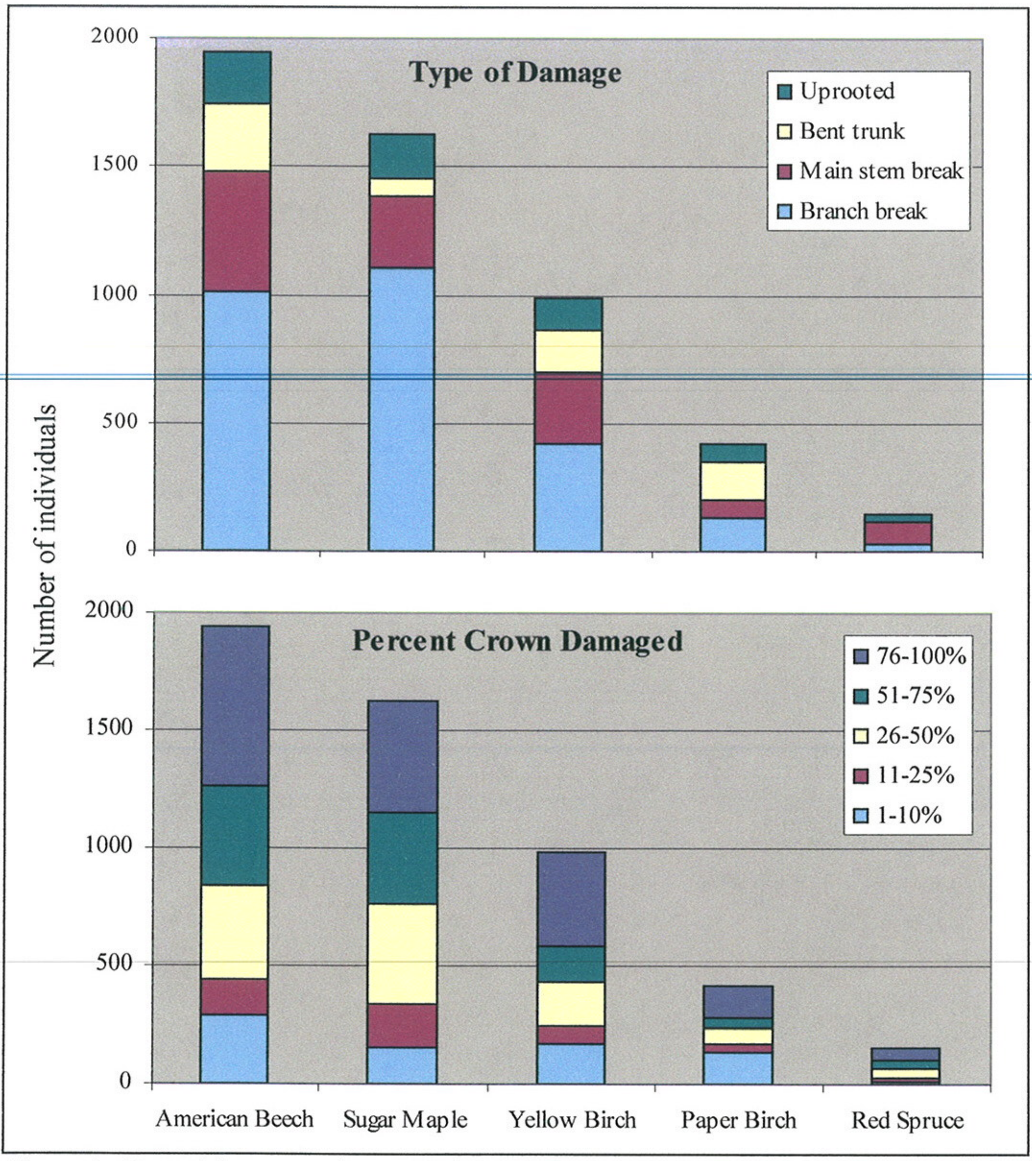

Figure 2. Type of damage and percent of crown damaged by 1998 ice storm at 32 plots in central Vermont.

Table 1. Mean (± SE) values for vegetation variables, and results of pre- and post-storm pairwise comparisons (paired *t*-test) in 32 ice-affected plots in central Vermont.

Variable	Pre-storm	Post-storm	*t*	*P*
Basal area (m^2/ha)	23.44 (1.14)	25.52 (1.13)	-1.515	0.140
DBH (cm)	317.99 (23.19)	336.73 (19.86)	-0.949	0.350
Canopy cover (%)	80.77 (1.59)	73.03 (3.33)	2.173	0.038
Sapling density (stems/ha)	827.42 (101.89)	840.63 (81.36)	-0.418	0.679

Changes to the Breeding Bird Community

Species Abundance, Richness, Diversity, and Turnover – The storm had a noticeable effect on the breeding bird community. Relative abundance, species richness, species diversity, and species turnover changed significantly at ice-damaged sites, while only abundance and species richness changed at control sites (Table 2). Following the storm, mean abundance of all species decreased at ice-damaged sites from 16.01 ±2.12 individuals/point count to 14.03 ±1.54, while it increased at control sites (12.70 ±0.64 to 14.22 ±0.70). Both control and treatment groups showed an increase in species richness. At ice-affected sites, an average of 16.5 species were detected before the storm and 22.0 species after the storm. Among controls, a mean of 18.8 species were found before the storm and 20.4 after (Table 2). Species diversity however, measured by the Shannon index, increased significantly only at ice storm sites.

Likewise, species turnover was only affected at ice storm sites, where a total of 36 species were detected prior to the storm. Following the storm, a total of 52 species were encountered, although the maximum number of species in any one post-storm survey year was 42. Of these 52 species, 35 were detected before and after, leaving a turnover of just 1 species (Blackpoll Warbler) observed only before and 16 species observed only after the storm (see Table 4 for scientific names of all species). Among those detected only after the storm, most occurred on the study area in low numbers (e.g. Chimney Swift, Wood Thrush, etc.), were difficult to detect or survey effectively with point counts (e.g. Brown Creeper, American Crow, Common Raven, etc.), or were irruptive species (e.g. Pine Siskin, Evening Grosbeak) and, therefore, their presence after the storm may not have been influenced by habitat change alone. Three of these species however, (Olive-sided Flycatcher, and Nashville and Mourning warblers) were more likely to have been positively affected by the change in forest structure. Although they occurred at low densities, all occupy early successional habitats and typically move into young clearcuts and forest openings created by natural disturbances such as fire or windstorm (Peterson and Fichtel 1992, Dunn and Garrett 1997). The mean detections per point count for all species are summarized in Table 4.

Table 2. Changes in mean number of individuals per point count, species richness, Shannon diversity index, and species turnover at control sites (n=5, 25 points) and ice-damaged sites (n=6, 32 points) in central Vermont before and after 1998 ice storm. Paired *t*-test used to compare changes in mean totals.

	Individuals/point count Mean (SE)		Species richness		Shannon diversity index		Species turnover	
Study Site	Pre-storm	Post-storm	Pre-storm	Post-storm	Pre-storm	Post-storm	Pre-storm only	Post-storm only
Controls								
Concord Woods	13.40 (0.70)	16.27 (0.74)	20	22	2.71	2.82	2	5
May Pond	13.10 (0.91)	15.07 (1.15)	16	16	2.52	2.45	4	2
Sugar Hollow	14.30 (0.58)	14.40 (0.43)	22	24	2.87	3.09	5	3
The Cape	12.20 (0.56)	12.67 (0.54)	20	21	2.82	2.88	3	1
Underhill State Park	10.50 (0.68)	12.67 (0.70)	16	19	2.58	2.70	3	2
Mean Total	12.70	14.22[b]	18.80	20.40[b]	2.70	2.79	3.40	2.60
SE	0.64	0.70	1.20	1.37	0.07	0.11	0.51	0.68
Ice Storm Sites								
Tunnel Brook	22.50 (0.65)	20.00 (0.29)	13	18	2.41	3.03	1	5
Long Trail	8.40 (0.59)	10.07 (0.46)	13	20	2.37	2.88	0	8
Hancock Branch	14.89 (1.27)	13.85 (0.76)	20	28	2.67	3.09	1	9
George Brook	12.14 (1.49)	9.95 (0.73)	14	18	2.28	2.77	2	7
Deer Hollow	19.50 (0.85)	14.83 (0.43)	17	21	2.58	3.01	2	7
Childs Mt.	18.60 (0.73)	15.47 (0.38)	22	27	2.79	3.31	2	10
Mean Total	16.01	14.03[c]	16.50	22.00[a]	2.52	3.02[a]	1.33	7.67[a]
SE	2.12	1.54	1.57	1.81	0.08	0.08	0.33	0.72

[a] $P < 0.0005$, [b] $P < 0.05$, [c] $P = 0.07$

Species Response – Prior to the ice storm, the 5 most abundant species among ice-damaged sites were Red-eyed Vireo, Black-throated Blue Warbler, Ovenbird, Black-throated Green Warbler, and Blackburnian Warbler. Following the storm, the abundance of 3 of these species (Red-eyed Vireo, Blackburnian Warbler, and Ovenbird) declined significantly (Table 3, Fig. 3). Despite these negative effects, all but Blackburnian Warbler remained among the 5 most abundant species in post-storm surveys along with Dark-eyed Junco which increased significantly (Table 3, Fig. 3). In addition, both Winter Wren and Canada Warbler showed increasing trends ($P = 0.141$, $P = 0.117$ respectively) in ice-damaged sites but not in control sites (Table 3, Fig. 3).

Among control sites, 4 of the 5 most abundant species in pre- and post-storm surveys were Ovenbird, Red-eyed Vireo, and Black-throated Green and Black-throated Blue warblers (Table 3). Hermit Thrush and Yellow-bellied Sapsucker were the fifth most abundant species in pre- and post-storm surveys respectively. In comparisons of pre- and post-storm abundance at control sites, Black-capped Chickadee increased, while Black-throated Blue Warbler declined (Table 3, Fig. 3). Among the 14 most common species analyzed, total abundance declined among ice storm sites from a mean of 13.22 ±1.75 to 10.91 ±0.92 ($t = 2.174$, $P = 0.082$) while remaining stable at control sites (Table 3).

Ignoring statistical significance and looking only at abundances, several early successional species increased in post-storm counts among ice-damaged sites including White-throated Sparrow, and Mourning, Nashville, and Chestnut-sided warblers (Table 4). These same species showed variable trends at control sites. In addition, woodpeckers, including Yellow-bellied Sapsucker, and Downy, Hairy, and Pileated woodpeckers, also increased in abundance following the storm at ice-damaged sites, while their trends at control sites varied (Table 4).

Table 3. Changes in the mean number of individuals per point count of the 14 most common species before and after the 1998 ice storm at ice-damaged sites (n=6, 32 points) and control sites (n=5, 25 points) in central Vermont.

	Individuals per point count (mean ±SE)									
	Ice Storm Sites					Control Sites				
Species	Pre-storm		Post-storm		P^a	Pre-storm		Post-storm		P^a
Yellow-bellied Sapsucker	0.71	0.16	0.85	0.15	0.814	0.56	0.15	0.74	0.13	0.600
Red-eyed Vireo	**2.27**	**0.60**	**1.34**	**0.10**	**0.038**	1.68	0.30	2.11	0.25	0.346
Blue Jay	0.34	0.18	0.44	0.13	0.502	0.24	0.09	0.24	0.07	0.917
Black-capped Chickadee	0.26	0.09	0.38	0.08	0.358	**0.08**	**0.06**	**0.28**	**0.07**	**0.044**
Winter Wren	0.26	0.07	0.56	0.10	0.141	0.34	0.11	0.47	0.14	0.527
Hermit Thrush	0.90	0.20	0.77	0.11	0.385	0.74	0.13	0.60	0.08	0.249
Black-throated Blue Warbler	1.94	0.28	1.88	0.12	0.688	**1.44**	**0.15**	**1.03**	**0.17**	**0.047**
Yellow-rumped Warbler	0.45	0.11	0.46	0.07	0.893	0.20	0.11	0.23	0.08	0.751
Black-throated Green Warbler	1.63	0.37	1.08	0.09	0.348	1.50	0.96	1.51	0.34	0.175
Blackburnian Warbler	**1.44**	**0.36**	**0.29**	**0.06**	**0.011**	0.24	0.19	0.20	0.12	0.738
Ovenbird	**1.82**	**0.23**	**1.12**	**0.11**	**0.008**	2.12	0.15	2.31	0.36	0.530
Canada Warbler	0.13	0.10	0.28	0.06	0.117	0.24	0.19	0.15	0.09	0.823
Dark-eyed Junco	**0.54**	**0.22**	**0.95**	**0.11**	**0.021**	0.24	0.07	0.19	0.08	0.749
Rose-breasted Grosbeak	0.53	0.32	0.51	0.12	0.590	0.34	0.15	0.16	0.10	0.287
Total Abundance	**13.22**	**1.75**	**10.91**	**0.92**	**0.082**[b]	9.42	0.38	10.19	1.00	0.357[b]

[a] Mann-Whitney *U*-test
[b] Paired *t*-test
NOTE: species selected had maximum counts ≥10 at all sites combined in at least 1 year
boldface type indicates significant change ($P < 0.05$)

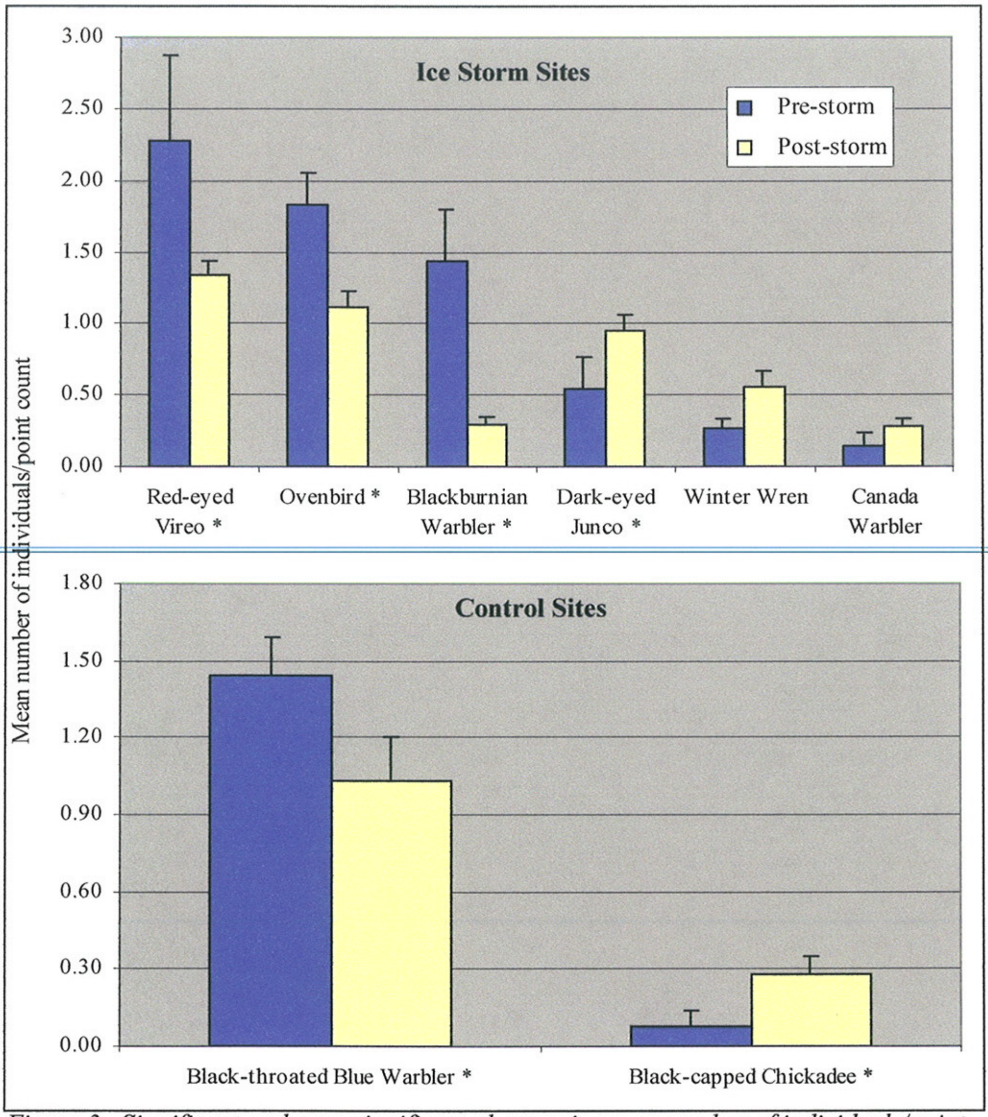

*Figure 3. Significant and near-significant changes in mean number of individuals/point count before and after 1998 ice storm at ice-affected sites and control sites in Vermont. Species with significant trends (P < 0.05) are marked with *; those with near-significant trends (P < 0.15) are unmarked.*

Table 4. Number of individuals detected per point count before and after the 1998 ice storm at ice-damaged sites (n=6, 32 points) and controls (n=5, 25 points) in Vermont.

	Ice Storm Sites				Control Sites			
	Pre-storm		Post-storm		Pre-storm		Post-storm	
Species	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
Red-shouldered Hawk (*Buteo lineatus*)	0	0	0	0	0.01	0.01	0	0
Red-tailed Hawk (*Buteo jamaicensis*)	0	0	0.05	0.05	0	0	0	0
Ruffed Grouse (*Bonasa umbellus*)	0.03	0.03	0.06	0.03	0	0	0.01	0.01
Mourning Dove (*Zenaida macroura*)	0	0	0.03	0.02	0.02	0.02	0.05	0.04
Chimney Swift (*Chaetura pelagica*)	0	0	0.02	0.02	0	0	0.03	0.03
Ruby-throated Hummingbird (*Archilochus colubris*)	0	0	0	0	0.02	0.02	0.01	0.01
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	0.71	0.16	0.85	0.15	0.56	0.15	0.74	0.13
Downy Woodpecker (*Picoides pubescens*)	0	0	0.19	0.07	0.04	0.02	0.15	0.05
Hairy Woodpecker (*Picoides villosus*)	0.09	0.07	0.18	0.06	0.16	0.09	0.07	0.03
Northern Flicker (*Colaptes auratus*)	0.03	0.03	0.01	0.01	0.02	0.02	0.07	0.07
Pileated Woodpecker (*Dryocopus pileatus*)	0	0	0.12	0.06	0.12	0.05	0.10	0.03
Olive-sided Flycatcher (*Contopus borealis*)	0	0	0.06	0.05	0	0	0	0
Eastern Wood Pewee (*Contopus virens*)	0	0	0.09	0.04	0.20	0.11	0.19	0.17
Least Flycatcher (*Empidonax minimus*)	0.03	0.03	0.08	0.03	0.06	0.04	0.03	0.02
Eastern Phoebe (*Sayornis phoebe*)	0	0	0	0	0	0	0.01	0.01
Great Crested Flycatcher (*Myiarchus crinitus*)	0.08	0.08	0.01	0.01	0.04	0.02	0.07	0.03
Blue-headed Vireo (*Vireo solitarius*)	0.15	0.11	0.11	0.04	0.16	0.06	0.35	0.13
Red-eyed Vireo (*Vireo olivaceus*)	2.27	0.60	1.34	0.10	1.68	0.30	2.11	0.25
Blue Jay (*Cyanocitta cristata*)	0.34	0.18	0.44	0.13	0.24	0.09	0.24	0.07
American Crow (*Corvus brachyrhynchos*)	0	0	0.04	0.04	0.12	0.10	0.28	0.19
Common Raven (*Corvus corax*)	0	0	0.06	0.03	0.08	0.08	0.04	0.03
Eastern Tufted Titmouse (*Parus bicolor*)	0	0	0	0	0	0	0.03	0.03
Black-capped Chickadee (*Parus atricapillus*)	0.26	0.09	0.38	0.08	0.08	0.06	0.28	0.07
Red-breasted Nuthatch (*Sitta canadensis*)	0.03	0.03	0.06	0.03	0.02	0.02	0.04	0.03
White-breasted Nuthatch (*Sitta carolinensis*)	0.24	0.17	0.24	0.06	0.14	0.05	0.09	0.03
Brown Creeper (*Certhia americana*)	0	0	0.03	0.03	0.08	0.04	0.07	0.03
Winter Wren (*Troglodytes troglodytes*)	0.26	0.07	0.56	0.10	0.34	0.11	0.47	0.14
Golden-crowned Kinglet (*Regulus satrapa*)	0.04	0.04	0.01	0.01	0.02	0.02	0.03	0.03
Veery (*Catharus fuscescens*)	0.17	0.17	0.11	0.05	0.30	0.17	0.20	0.11
Swainson's Thrush (*Catharus ustulatus*)	0.19	0.09	0.11	0.03	0.22	0.17	0.32	0.21
Hermit Thrush (*Catharus guttatus*)	0.90	0.20	0.77	0.11	0.74	0.13	0.60	0.08
Wood Thrush (*Hylocichla mustelina*)	0	0	0.05	0.05	0.22	0.16	0.19	0.12
American Robin (*Turdus migratorius*)	0.37	0.33	0.19	0.05	0.08	0.05	0.27	0.08
Cedar Waxwing (*Bombycilla cedrorum*)	0.27	0.20	0.15	0.08	0	0	0.03	0.02
Nashville Warbler (*Vermivora ruficapilla*)	0	0	0.03	0.03	0	0	0	0
Chestnut-sided Warbler (*Dendroica pensylvanica*)	0.08	0.08	0.17	0.07	0.02	0.02	0.09	0.08
Magnolia Warbler (*Dendroica magnolia*)	0.06	0.06	0.03	0.02	0	0	0	0
Black-throated Blue Warbler (*Dendroica caerulescens*)	1.94	0.28	1.88	0.12	1.44	0.15	1.03	0.17
Yellow-rumped Warbler (*Dendroica coronata*)	0.45	0.11	0.46	0.07	0.20	0.11	0.23	0.08
Black-throated Green Warbler (*Dendroica virens*)	1.63	0.37	1.08	0.09	1.50	0.96	1.51	0.34
Blackburnian Warbler (*Dendroica fusca*)	1.44	0.36	0.29	0.06	0.24	0.19	0.20	0.12
Blackpoll Warbler (*Dendroica striata*)	0.02	0.02	0	0	0	0	0	0
Black-and-White Warbler (*Mniotilta varia*)	0.09	0.06	0.14	0.04	0.16	0.08	0.15	0.10
American Redstart (*Setophaga ruticilla*)	0.28	0.21	0.22	0.06	0.32	0.23	0.41	0.25
Ovenbird (*Seiurus aurocapillus*)	1.82	0.23	1.12	0.11	2.12	0.15	2.31	0.36
Mourning Warbler (*Oporornis philadelphia*)	0	0	0.08	0.04	0	0	0.04	0.04
Common Yellowthroat (*Geothlypis trichas*)	0.13	0.13	0.06	0.06	0.04	0.04	0.03	0.03
Canada Warbler (*Wilsonia canadensis*)	0.13	0.10	0.28	0.06	0.24	0.19	0.15	0.09
Scarlet Tanager (*Piranga olivacea*)	0	0	0.13	0.06	0.38	0.11	0.39	0.15
White-throated Sparrow (*Zonotrichia albicollis*)	0.04	0.04	0.17	0.06	0.10	0.06	0.07	0.05
Dark-eyed Junco (*Junco hyemalis*)	0.54	0.22	0.95	0.11	0.24	0.07	0.19	0.08
Northern Cardinal (*Cardinalis cardinalis*)	0	0	0	0	0	0	0.01	0.01
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	0.53	0.32	0.51	0.12	0.34	0.15	0.16	0.10
Purple Finch (*Carpodacus purpureus*)	0.13	0.13	0.03	0.03	0.02	0.02	0.03	0.02
Pine Siskin (*Carduelis pinus*)	0	0	0.03	0.03	0	0	0.01	0.01
American Goldfinch (*Carduelis tristis*)	0	0	0	0	0	0	0.01	0.01
Evening Grosbeak (*Coccothraustes vespertinus*)	0	0	0.13	0.04	0.04	0.04	0	0

Discussion

Although total abundance of breeding birds decreased following the ice storm, species richness and diversity increased. Only Blackpoll Warbler was unique to the ice storm sites prior to the storm, while 16 species were unique afterwards. Three forest interior species declined in abundance following the storm, two of which were canopy-foragers (Red-eyed Vireo and Blackburnian Warbler), and 1 a ground-forager/nester (Ovenbird). Another ground-forager/nester, Dark-eyed Junco, was the only species to increase substantially after the storm, although Canada Warbler and Winter Wren showed increasing trends.

Since Red-eyed Vireo and Blackburnian Warbler both specialize in feeding on insects gleaned from canopy foliage, primarily lepidopteran larvae, their response to the loss of canopy cover in ice-damaged forests was not surprising. Both species have been shown to be affected by loss of canopy foliage in other studies. Robinson and Robinson (1999) documented a substantial decline in Red-eyed Vireo abundance in selectively harvested sites in southern Illinois, although like this study, they were not completely absent from treatment sites. In a Minnesota study, Apfelbaum and Haney (1981) found that the abundance of both these species was negatively affected by fire which removed a large percentage of forest canopy. Response to ice damage among other canopy species, Eastern Wood-pewee, Great Crested Flycatcher, and Scarlet Tanager, was inconsistent, suggesting that as a group, canopy species responded unpredictably to the storm's effects.

Species that nest and forage primarily on the ground showed a mixed response. The Ovenbird decline may have been due to several factors, including the large amount of downed woody material left on the ground following the storm, the decrease in forest canopy cover, the increase in forest edge, or a combination of these effects. Ovenbirds prefer open understories for both foraging and nesting (Wenny et al. 1993), and are typically least abundant where shrub and sapling density is high (Van Horn and Donovan 1994, Schieck and Nietfeld 1995). Although I did not document an increase in sapling density in the first year after the storm, large amounts of downed limbs, tops, and uprooted trees made it difficult to move through some ice-damaged areas on foot, and may have contributed to the reduced abundance of Ovenbirds. Anecdotally, sapling density appeared to increase substantially during the second and third years following the storm (pers. obs.). This is supported by Robinson and Robinson (1999) who detected a 2 to 3 year lag between selective timber cuts and growth of herbaceous plants and shrubs in Missouri. Another parameter documented as important for Ovenbirds is canopy closure between 60% and 90% (Thompson and Capen 1988, Van Horn 1990). Although the average canopy closure at ice-damaged points was 73%, it ranged widely (32% to 95%) and 9 of the 32 points (28%) had canopy closures ≤60%. Prior to the storm, only 3 points had canopy closures below 70% and the lowest was 66%. Additionally, Ovenbirds are known to be "area sensitive," requiring large tracts of contiguous forest for successful breeding (Robbins et al. 1989). In a New Hampshire study, Welsh and Healy (1993) showed that local Ovenbird densities declined as a result of interior forest edges created by clearcutting. While the areas of heavy ice damage were patchy and relatively small in size, the resulting increase in the amount of edge habitat may have impacted Ovenbird abundance.

Three other ground nesters/foragers increased in abundance – Dark-eyed Junco, Canada Warbler, and Winter Wren. All 3 of these species are positively associated with dense groundcover, often nesting among stumps, up-turned rootballs, and downed limbs or logs (Laughlin and Kibbe 1985, Conway 1999), and are less affected by loss of canopy cover. Several others have reported similar responses by Dark-eyed Junco and Canada Warbler to forest gaps created through natural disturbances or timber harvests (Apfelbaum and Haney 1981, Hagan et al. 1997, Conway 1999).

The increase in species richness and diversity observed in post-storm surveys was undoubtedly due to the increased heterogeneity in vegetation structure, a response frequently reported in studies of managed forest landscapes (Webb et al. 1977, Welsh and Healy 1993, Hagan et al. 1997). All the species that appeared only in post-storm surveys were detected in low numbers. For some, particularly early-successional specialists (Mourning Warbler, Nashville Warbler, and Olive-sided Flycatcher), low abundance probably reflected the small size of the ice-damaged patches. In Maine, Hagan et. al. (1997)

showed that Mourning Warbler and Olive-sided Flycatcher both had positive relationships with clearcut size. Although Chestnut-sided Warbler abundance increased slightly following the storm, prior to the storm they were only found at points within forest-disturbance openings >0.5 ha in size (Buford and Capen 1999).

Abundance of birds at ice-damaged sites was lower than before the storm. This held true for abundance of all species detected, as well as among just the 14 most common species. Total bird abundance frequently increases or remains unchanged in response to some types of forest management since declines in forest interior species are offset or exceeded by increases of edge species (Scott and Gottfried 1983, Annand and Thompson 1997). While there was an increase in edge species among ice-damaged sites, their abundance did not offset the declines of the 3 forest interior species (Red-eyed Vireo, Blackburnian Warbler and Ovenbird). This may have been due to the small size of the forest gaps created by the ice storm in relation to the surrounding forested landscape, or due to the retention of basal area.

These results suggest that some types of forest management, particularly selective, uneven-aged logging practices such as "group selection" and "single tree selection," may effectively mimic some types of natural disturbance events such as ice storms. How basal area retention among forest gaps affects breeding birds is unclear, but it may influence the abundance of some species. Regardless, the effects from the 1998 ice storm on the avian community within the GMNF are likely to be relatively short-term.

Acknowledgements

I gratefully acknowledge the hard work and dedication of my 3 sleep-deprived field assistants, Shiloh Schulte, Craig "Gimpy" Reiser, and Charlie Rabatin. Many thanks also to Ted Gaine and Allan Strong, who, on short notice, helped me conduct bird surveys for the injured C. Reiser. I thank Tii McLane for assisting with vegetation measurements at ice-damaged sites. In addition, birds were censused at FBMP control sites by Ted Gaine, Chris Rimmer, Chip Darmstadt, and myself. I respectfully acknowledge the cooperation of Ernie Buford and Dave Capen of School of Natural Resources at the University of Vermont for generously sharing bird and vegetation data collected prior to the ice storm and for providing point count coordinates. This study was made possible by a cooperative grant agreement with the Vermont Department of Forests, Parks, and Recreation, with funding made available through the USDA Forest Service. Logistical support was provided by the Green Mountain National Forest, and the members and trustees of the Vermont Institute of Natural Science.

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