Available online at www.sciencedirect.com
SCIENCE DIRECT®
Forest Ecology and Management 186 (2003) 133–145
Forest Ecology and Management
www.elsevier.com/locate/foreco

Effects of ice storm-created gaps on forest breeding bird communities in central Vermont

Steven D. Faccio*

Conservation Biology Department, Vermont Institute of Natural Science, Woodstock, VT 05091, USA

Received 18 November 2002; received in revised form 12 December 2002; accepted 12 May 2003

Abstract

A damaging ice storm struck northern New England, NY, and adjacent Canada in January 1998, affecting nearly 7 million ha of forest lands. Although relatively rare at this scale, such natural disturbances provide a unique opportunity to study short- and long-term impacts on forest ecosystems and wildlife species. I investigated the storm's short-term effects on breeding birds in a northern hardwood forest in central Vermont. Point counts ($n = 52$) at six 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 five control sites ($n = 25$) 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. Overall, species richness and diversity increased only at ice storm sites, whereas total abundance increased at controls. Three forest-interior species declined in abundance ($P \leq 0.046$) following the storm, two canopy-foragers (Red-eyed Vireo and Blackburnian Warbler), and a ground-forager/nester normally associated with closed-canopy woodlands (Ovenbird). Another ground-forager/nester, Dark-eyed Junco, was the only species to increase in abundance ($P = 0.046$) after the storm, although Winter Wren showed a marginal increase ($P = 0.075$). Among habitat/foraging guilds, two forest-interior groups (canopy-foragers and ground/shrub foragers) declined significantly ($P \leq 0.034$), whereas open-edge ground/shrub feeders increased marginally ($P = 0.069$). Results from this study are consistent with investigations of bird responses to selective forest management, particularly "group selection" and "single-tree selection", suggesting that these management strategies may effectively emulate natural disturbance events such as ice storms.

Keywords: Ice storm; Breeding birds; Forest canopy gaps; Northern hardwoods; Vermont

1. Introduction

In January 1998, a destructive ice storm hit northern New England, NY, and adjacent Canada, causing widespread damage to trees. Over 6,800,000 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). Ice events at this scale are relatively rare, occurring in this region just once or twice a century (Irland, 2000; Smith, 2000). Therefore, the 1998 ice storm provided a unique opportunity to study the short- and long-term impacts of ice damage on forest ecosystems and wildlife populations.

*Tel.: +1-802-457-2779x123; fax: +1-802-457-1053.
E-mail address: sfaccio@vinsweb.org (S.D. Faccio).

0378-1127/$ – see front matter © 2003 Elsevier B.V. All rights reserved.
doi:10.1016/S0378-1127(03)00232-9

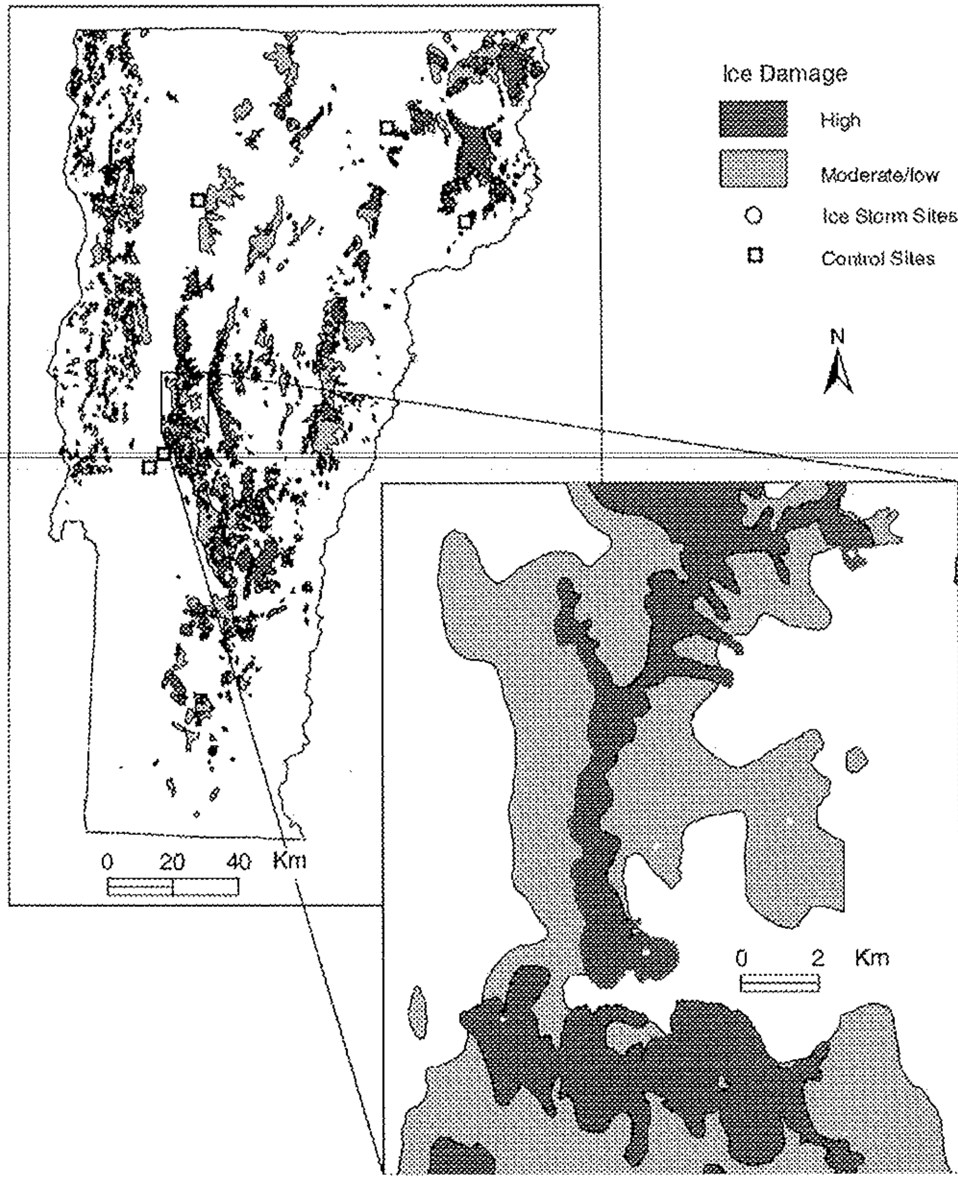

Fig. 1. Forest damage resulting from 1998 ice storm, and location of control and ice storm study sites in Vermont.

In the northeast alone, numerous recent studies have documented the effects of timber harvesting on forest bird communities (Thompson and Capen, 1988; Derleth et al., 1989; Rudnicky and Hunter, 1993; Welsh and Healy, 1993; Lent and Capen, 1995; Hagan et al., 1996; King et al., 1996, 1997; Germaine et al., 1997). 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-dependent 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 the southern Appalachians, Greenberg and Lanham (2001) investigated breeding bird assemblages in hurricane-created gaps. In addition, several researchers have studied the impacts of hurricanes on resident and migratory birds in tropical forests (Thurber, 1980; Wauer and Wunderle, 1992; Wunderle, 1995; Wunderle et al., 1992).

There appear to be 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; Seymour et al., 2002). However, unlike selective harvests, ice damage from the 1998 storm resulted in the retention of basal area and an accumulation of large quantities of downed woody material on the forest floor.

The impacts of selective logging on forest birds have been well documented, and Robinson and Robinson (1995) recently reviewed the literature. They reported that many of the trends in bird populations following selective harvests were 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 ground-foraging species (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). However, it is not known whether birds respond similarly to a natural disturbance that creates forest openings without decreasing basal area. 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. Results provide evidence for the efficacy of selective harvests to mimic such natural disturbances.

2. Methods

2.1. 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, six 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 overlaid on the ice damage GIS layer in ArcView 3.2 (ESRI, Redlands, CA), resulting in 52 point count stations falling within mapped areas of ice damage (6–10 point counts/site). Using a global positioning system (GPS), I located each of these 52 points during May 1999. 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. Forest stands consisted primarily of northern hardwoods dominated by American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula lutea*), with lesser amounts of paper birch (*B. papyifera*) and red spruce (*Picea rubens*) at higher elevations.

Five control sites from the Vermont Forest Bird Monitoring Program (FBMP) were selected based on habitat type, elevation, and biophysical region. A long-term monitoring project of the Vermont Institute of Natural Science, 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 five 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 two controls were located in northeastern Vermont (Fig. 1). Elevations ranged from 365 to 700 m. 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.

2.2. Vegetation measurements

Pre- and post-storm habitat measurements were made at each of the 52 ice-damaged point count stations. Canopy cover was estimated using a sighting tube at 40 equally spaced points along two 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. commun.), while post-storm metrics were collected in July 1999. In addition, during June 1999, the amount and type of ice damage was visually assessed at each point count station. In a 50 m radius plot (0.79 ha) centered on the point count station, each ice-damaged tree was identified to species, type of damage classified as either broken branch(es), 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%.

2.3. Bird surveys

At each census point, 10 min point counts were conducted twice annually during June. Observers, all experts in visual and aural bird identification, recorded all individuals detected within two distance classes—within and beyond a 50 m radius. To avoid observer bias in estimating distance, data from both distance classes were included in analyses, although birds flying above the canopy and obviously not using the stand being sampled were excluded. Surveys began by 06:00, concluded by 10:00, and were not conducted on days with rain or high winds.

2.3.1. Ice-damaged sites

Pre-storm surveys were conducted by two observers, each visiting all points once, and data were collected at three sites in 1993 and at three sites in 1994 (total of two visits per point). Although post-storm surveys were conducted by a total of six observers, most surveys (80%) were conducted by three of these observers. Data were collected at all six sites during 1999–2001 (total of six visits per point).

2.3.2. Control sites

Surveys were conducted by four 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 (four visits per point). However, to balance the study design between control and ice-damaged sites, I randomly selected one visit/site from each of the 2 years (1993 and 1994) for a total of two pre-storm visits per point. Post-storm surveys were conducted during 1999–2001 (six visits per point).

2.4. Data analysis

2.4.1. 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 per year. 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, which accounts for species richness, abundance, and evenness, to calculate species diversity (Zar, 1996).

I defined eight groups of birds based on foraging guild and breeding habitat association. Species were assigned to these groups based on similar classifications by Sabo and Holmes (1983), and Greenberg and Lanham (2001). Foraging guilds included canopy gleaners, ground and/or shrub gleaners, flycatchers, bark gleaners, and bark probers. Canopy and ground/shrub gleaners were subdivided into forest-interior, forest-edge, and open-edge groups based on habitat association. An additional group consisted of three species of Corvid nest predators.

Two-way ANOVA was used to test for differences among treatment, years, and treatment × year interactions on bird abundance (individual species, total, and within foraging guilds), species richness, and Shannon's diversity index. In every case, effects of year and treatment × year were not significant ($P > 0.05$). Therefore, within ice-storm and control sites, I averaged abundance and diversity data across pre- and post-storm years to compare changes. I used the nonparametric Wilcoxon Signed Rank test to compare changes in the abundance of foraging guilds, all species encountered, and for the 14 most common species (defined as those with a maximum count of ≥20 individuals at all sites combined in at least 1 year) since data failed to normalize after transformations. Paired t-tests were used to compare pre- and post-storm changes in the mean totals for species richness, species diversity, and number of individuals per point count, and compare pre- and post-storm changes in habitat variables at ice-damaged sites.

All analyses were performed in SYSTAT (1998) and results are presented as mean (±S.E.). Significance is reported at the $P < 0.05$ level.

3. Results

3.1. Vegetation

Ice damage from the 1998 storm varied from point to point depending on elevation, aspect, and tree species composition. Thirty-two points (61.5%) showed moderate to high amounts of damage, with the majority of these located at higher elevations and on east-facing slopes, while the remaining 20 points showed little or no visible effects from the storm. Comparison of pre-storm habitat measurements collected in 1993 and 1994 with those taken 1 year after the storm revealed a significant increase in basal area and dbh, while mean canopy cover and sapling density were unaffected (Table 1). However, comparison of pre- and post-storm metrics from the 32 points within canopy gaps revealed a significant change only in canopy cover from 80.77% (±1.59) to 73.03% (±3.33) ($t = 2.173, P = 0.038$). I expected a greater increase in sapling density within gaps 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.

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 >50% of their crowns, while just over one-third (33.9%) lost 76–100% of their canopy foliage (Fig. 2).

Table 1
Mean (±S.E.) values for vegetation variables, and results of pre- and post-storm pairwise comparisons (paired t-test) in 52 ice-affected plots in central Vermont

Variable	Pre-storm	Post-storm	t	P
Basal area (m^2/ha)	22.50 (0.81)	27.81 (1.09)	−4.250	0.0001
dbh (cm)	327.50 (18.93)	376.71 (23.23)	−2.598	0.012
Canopy cover (%)	79.29 (1.29)	77.05 (2.67)	0.726	0.471
Sapling density (stems/0.25 ha)	745.59 (74.50)	813.73 (68.31)	−0.674	0.504

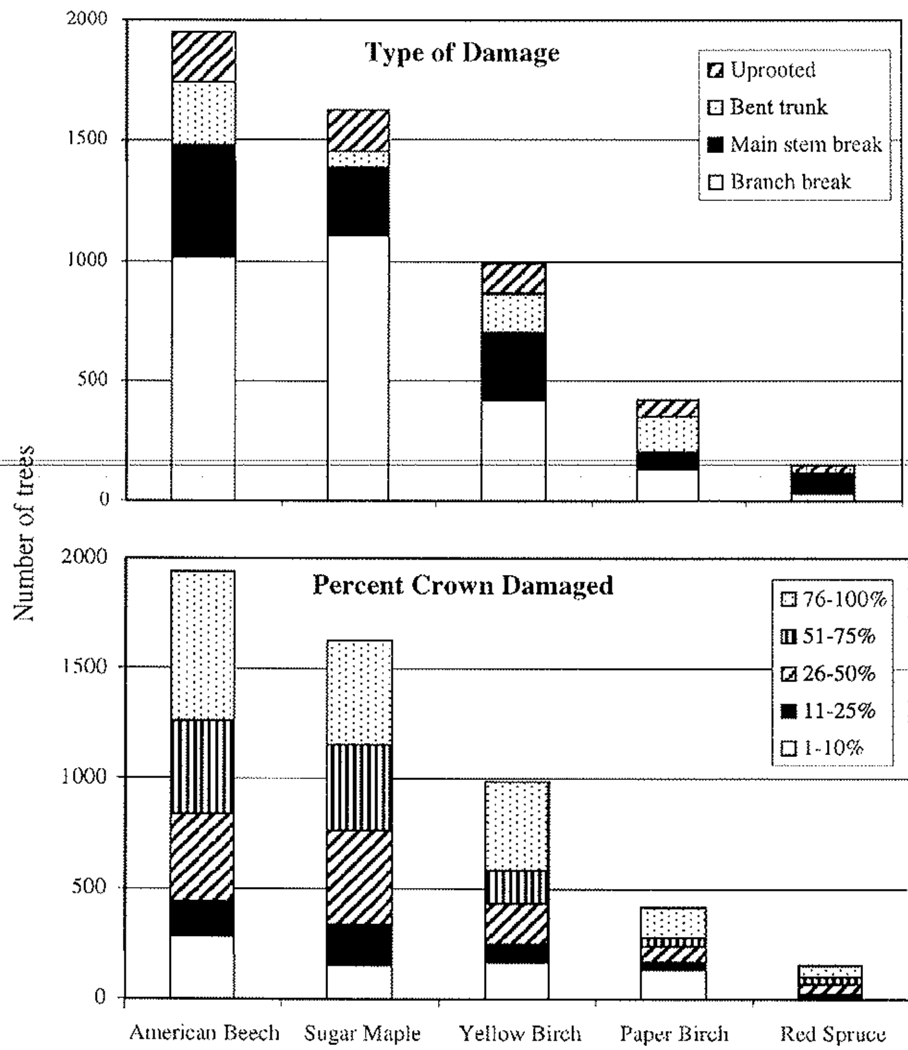

Fig. 2. Type of damage and percent crown damaged by 1998 ice storm at 52 plots in central Vermont.

3.2. Changes to the breeding bird community

3.2.1. Species abundance, richness, diversity, and turnover

At ice-affected stands, a total of 37 species were detected prior to the storm and 42 species afterwards, compared to control sites where species richness increased from 35 species before the storm to 39 afterwards. Five species at ice-damaged sites were only observed after the storm, whereas none were observed before the storm (Table 2). Among those detected after the storm, all occurred on the study area in low numbers, and were difficult to survey effectively with point counts (e.g. Common Raven, Pileated Woodpecker), therefore their recorded presence after the storm may not have been influenced by habitat change alone (see Table 2 for scientific names of species). Olive-sided Flycatcher, however, was more likely to have been positively affected by the change in forest structure, as this species typically moves into young clearcuts and forest openings created by natural disturbances such as fire or windstorm (Peterson and Fichtel, 1992).

Within study sites, species richness, and species diversity increased significantly post-storm at ice-damaged sites, while abundance increased significantly at control sites (Table 3).

Table 2
Mean number of individuals detected per point count before (1993–1994) and after (1999–2001) the 1998 ice storm at ice-damaged sites ($n = 6$, 52 points) and controls ($n = 5$, 25 points) in Vermont[a]

Group (species)	Ice storm sites					Control sites				
	Pre-storm		Post-storm		P[b]	Pre-storm		Post-storm		P[b]
	X	S.E.	X	S.E.		X	S.E.	X	S.E.	
Open-edge ground/shrub gleaners	0.18	0.04	0.27	0.06	0.069	0.16	0.03	0.17	0.03	0.374
Nashville Warbler (*Vermivora ruficapilla*)	0.17	0.17	0.04	0.04	na[c]	0	0	0	0	na
Chestnut-sided Warbler (*Dendroica pensylvanica*)	0.09	0.07	0.25	0.17	na	0	0	0.09	0.08	na
Magnolia Warbler (*Dendroica magnolia*)	0.17	0.10	0.07	0.01	na	0	0	0	0	na
Mourning Warbler (*Oporornis philadelphia*)	0.05	0.05	0.10	0.04	na	0	0	0.04	0.04	na
Common Yellowthroat (*Geothlypis trichas*)	0.18	0.13	0.17	0.05	na	0.08	0.04	0.04	0.03	na
White-throated Sparrow (*Zonotrichia albicollis*)	0.08	0.04	0.18	0.09	na	0.04	0.06	0.07	0.05	na
Dark-eyed Junco (*Junco hyemalis*)	**0.46**	**0.13**	**0.76**	**0.15**	**0.046**	0.12	0.07	0.15	0.08	0.749
Forest-interior ground/shrub gleaners	**0.93**	**0.14**	**0.77**	**0.12**	**0.034**	1.12	0.15	0.97	0.10	0.393
Veery (*Catharus fuscescens*)	0.20	0.14	0.14	0.05	na	0.52	0.17	0.19	0.11	na
Swainson's Thrush (*Catharus ustulatus*)	0.24	0.07	0.16	0.05	na	0.36	0.17	0.31	0.21	na
Hermit Thrush (*Catharus guttatus*)	0.74	0.16	0.73	0.07	0.917	0.74	0.13	0.60	0.08	0.249
Black-throated Blue Warbler (*Dendroica caerulescens*)	1.68	0.20	1.57	0.09	0.686	1.32	0.15	1.03	0.17	0.344
Ovenbird (*Seiurus aurocapillus*)	**1.79**	**0.18**	**1.30**	**0.19**	**0.028**	2.04	0.15	2.31	0.36	0.530
Forest-interior canopy gleaners	**0.81**	**0.12**	**0.52**	**0.08**	**0.006**	0.64	0.10	0.83	0.09	0.382
Blue-headed Vireo (*Vireo solitarius*)	0.34	0.16	0.16	0.04	na	0.20	0.06	0.35	0.13	na
Red-eyed Vireo (*Vireo olivaceus*)	**2.10**	**0.19**	**1.46**	**0.14**	**0.046**	1.76	0.30	2.11	0.25	0.075
Golden-crowned Kinglet (*Regulus satrapa*)	0.40	0.31	0.05	0.01	na	0.04	0.02	0.03	0.03	na
Black-throated Green Warbler (*Dendroica virens*)	1.31	0.25	1.16	0.06	0.917	0.92	0.96	1.51	0.34	0.074
Blackburnian Warbler (*Dendroica fusca*)	**1.24**	**0.26**	**0.37**	**0.07**	**0.028**	0.28	0.19	0.20	0.12	0.180
American Redstart (*Setophaga ruticilla*)	0.48	0.24	0.20	0.04	na	0.44	0.32	0.69	0.38	na
Scarlet Tanager (*Piranga olivacea*)	0.07	0.06	0.12	0.02	na	0.44	0.11	0.39	0.15	na
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	0.33	0.13	0.38	0.10	0.463	0.32	0.15	0.16	0.10	0.287
Forest-edge ground/shrub gleaners	0.26	0.09	0.30	0.05	0.109	0.35	0.05	0.34	0.05	0.978
Ruffed Grouse (*Bonasa umbellus*)	0.03	0.03	0.10	0.03	na	0	0	0.01	0.01	na
Winter Wren (*Troglodytes troglodytes*)	0.30	0.06	0.53	0.12	0.075	0.36	0.11	0.47	0.14	0.243
American Robin (*Turdus migratorius*)	0.47	0.38	0.33	0.11	0.500	0.12	0.05	0.27	0.08	na
Wood Thrush (*Hylocichla mustelina*)	0.14	0.07	0.19	0.12	na	0.24	0.16	0.19	0.12	na
Canada Warbler (*Wilsonia canadensis*)	0.24	0.10	0.24	0.07	na	0.28	0.19	0.15	0.09	0.374
Forest-edge canopy gleaners	0.29	0.06	0.33	0.06	0.426	0.40	0.20	0.25	0.05	0.315
Black-capped Chickadee (*Parus atricapillus*)	0.29	0.09	0.46	0.10	0.225	0	0	0.28	0.07	0.089
Yellow-rumped Warbler (*Dendroica coronata*)	0.35	0.07	0.39	0.04	0.893	0.20	0.11	0.23	0.08	0.481
Bark Probers	0.26	0.07	0.28	0.06	0.322	0.30	0.09	0.29	0.05	0.919
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	0.82	0.14	0.73	0.13	0.249	0.68	0.15	0.74	0.13	0.251
Downy Woodpecker (*Picoides pubescens*)	0	0	0.11	0.02	na	0.04	0.02	0.15	0.05	na
Hairy Woodpecker (*Picoides villosus*)	0.10	0.05	0.14	0.06	na	0.16	0.09	0.07	0.03	na
Pileated Woodpecker (*Dryocopus pileatus*)	0	0	0.09	0.02	na	0.08	0.05	0.10	0.03	na
Bark gleaners	0.20	0.07	0.13	0.02	0.809	0.16	0.06	0.12	0.03	0.913
Red-breasted Nuthatch (*Sitta canadensis*)	0.32	0.16	0.05	0.01	na	0.04	0.02	0.04	0.03	na
White-breasted Nuthatch (*Sitta carolinensis*)	0.09	0.06	0.16	0.03	na	0.04	0.05	0.09	0.03	na
Brown Creeper (*Certhia americana*)	0.28	0.28	0.11	0.03	na	0.04	0.04	0.07	0.03	na
Black-and-White Warbler (*Mniotilta varia*)	0.16	0.08	0.16	0.05	na	0.16	0.08	0.15	0.10	na
Flycatchers	0.12	0.07	0.11	0.03	0.310	0.18	0.05	0.14	0.05	0.244
Olive-sided Flycatcher (*Contopus borealis*)	0	0	0.03	0.03	na	0	0	0	0	na
Eastern Wood Pewee (*Contopus virens*)	0.02	0.02	0.10	0.02	na	0.12	0.11	0.19	0.17	na

Table 2 (*Continued*)

Group (species)	Ice storm sites					Control sites				
	Pre-storm		Post-storm		P^b	Pre-storm		Post-storm		P^b
	X	S.E.	X	S.E.		X	S.E.	X	S.E.	
Least Flycatcher (*Empidonax minimus*)	0.03	0.03	0.13	0.07	na	0.08	0.04	0.03	0.02	na
Great Crested Flycatcher (*Myiarchus crinitus*)	0.13	0.08	0.04	0.01	na	0.04	0.02	0.07	0.03	na
Corvid nest predators	0.14	0.07	0.23	0.07	0.239	0.28	0.07	0.31	0.06	0.841
American Crow (*Corvus brachyrhynchos*)	0	0	0.04	0.01	na	0.16	0.10	0.28	0.19	na
Common Raven (*Corvus corax*)	0	0	0.05	0.01	na	0.16	0.08	0.04	0.03	na
Blue Jay (*Cyanocitta cristata*)	0.28	0.11	0.42	0.07	0.346	0.24	0.09	0.24	0.07	0.696

[a] Boldface type indicates significant change ($P \leq 0.05$).
[b] Wilcoxon Signed Ranks test.
[c] Species not abundant enough for meaningful statistical analysis.

3.2.2. Species response

Prior to the ice storm, the five most abundant species at 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 three of these species (Red-eyed Vireo, Blackburnian Warbler, and Ovenbird) declined significantly (Table 2, Fig. 3). Despite these negative effects, all but Blackburnian Warbler remained among the five most abundant species in post-storm surveys along with Dark-eyed Junco, which increased significantly (Table 2, Fig. 3). In addition, Winter Wren showed a marginal increase ($P = 0.075$) in ice-damaged sites but not in controls

Table 3
Changes in mean number of individuals per point count, species richness, and Shannon diversity index at control sites ($n = 5$, 25 points) and ice-damaged sites ($n = 6$, 52 points) in central Vermont before and after 1998 ice storm (paired t-test used to compare changes in mean totals)

Study site	Individuals per point count, mean (S.E.)		Species richness		Shannon diversity index	
	Pre-storm	Post-storm	Pre-storm	Post-storm	Pre-storm	Post-storm
Controls						
Concord woods	10.40 (0.70)	16.27 (0.74)	17	18	2.36	2.66
May pond	9.60 (0.91)	15.40 (1.15)	16	17	2.26	2.36
Sugar hollow	10.20 (0.58)	14.40 (0.43)	18	23	2.59	2.95
The cape	9.10 (0.56)	12.67 (0.54)	20	19	2.60	2.73
Underhill State Park	7.80 (0.68)	12.67 (0.70)	18	17	2.44	2.56
Mean total	12.16	14.21[a]	17.80	18.60	2.50	2.64
S.E.	0.58	0.70	0.66	1.21	0.07	0.11
Ice storm sites						
Tunnel brook	23.11 (0.65)	16.74 (0.29)	31	32	3.04	3.04
Long trail	9.90 (0.59)	11.13 (0.46)	22	26	2.72	2.81
Hancock branch	15.00 (1.27)	14.03 (0.76)	23	27	2.73	2.98
George brook	13.33 (1.49)	10.37 (0.73)	20	20	2.70	2.68
Deer hollow	17.86 (0.85)	16.00 (0.43)	21	32	2.73	3.00
Childs Mt.	16.25 (0.73)	16.33 (0.38)	23	27	2.83	3.18
Mean total	15.91	14.10	23.33	27.33[b]	2.79	2.95[b]
S.E.	1.82	1.13	1.61	1.82	0.05	0.07

[a] $P = 0.025$.
[b] $P < 0.056$.

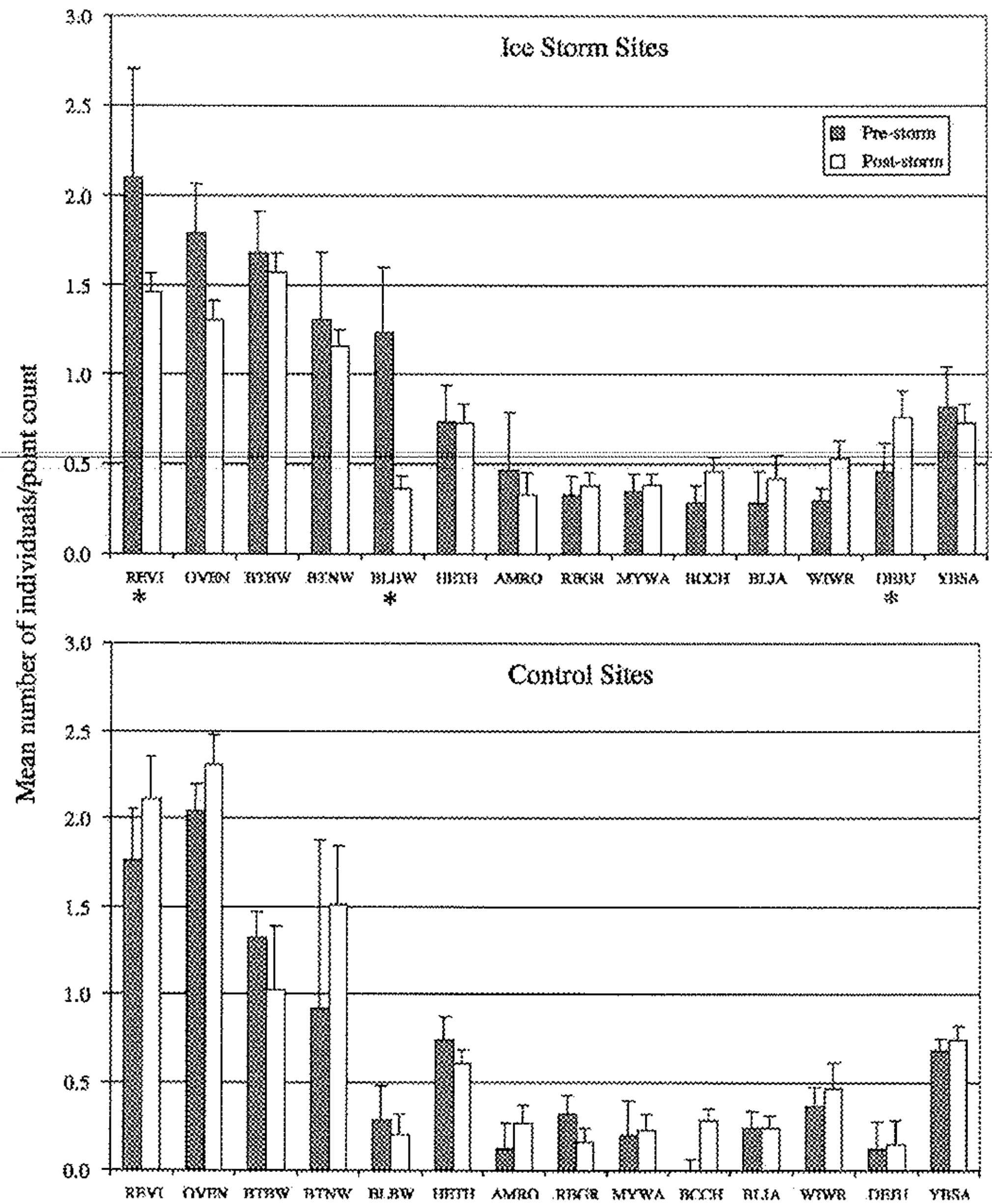

Fig. 3. Mean (±S.E.) number of individuals per point count for 14 most common species before and after 1998 ice storm at ice-affected sites and control sites in central Vermont. Species marked with * indicates significant ($P < 0.05$) change in abundance. Species codes are: REVI, Red-eyed Vireo; OVEN, Ovenbird; BTBW, Black-throated Blue Warbler; BTNW, Black-throated Green Warbler; BLBW, Blackburnian Warbler; HETH, Hermit Thrush; AMRO, American Robin; RBGR, Rose-breasted Grosbeak; MYWA, Yellow-rumped Warbler; BCCH, Black-capped Chickadee; BLJA, Blue Jay; WIWR, Winter Wren; DEJU, Dark-eyed Junco; YBSA, Yellow-bellied Sapsucker.

(Table 2, Fig. 3). Among the 32 points located within canopy gaps, Canada Warbler showed a weak increase from 0.13 (±0.10) individuals per point to 0.28 (±0.06) ($P = 0.117$).

Among control sites, four of the five most abundant species in both pre- and post-storm surveys were Ovenbird, Red-eyed Vireo, and Black-throated Green and Black-throated Blue Warblers (Table 2). 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, three species showed marginally significant increases; Black-capped Chickadee ($P = 0.089$), Black-throated Green Warbler ($P = 0.074$), and Red-eyed Vireo ($P = 0.075$) (Table 2, Fig. 3).

Among foraging/habitat guilds, the abundance of two forest-interior groups decreased significantly at ice-damaged stands but not among controls. As a group, five species of ground and/or shrub gleaners that utilize forest-interior habitats decreased in abundance ($T = -2.13, P = 0.034$). Similarly, eight species of forest-interior canopy gleaners also decreased as a group ($T = -2.74, P = 0.006$) (Table 2). In addition, the open-edge ground/shrub group showed a marginal increase among the ice-damaged sites ($P = 0.069$). Among these three groups, however, abundance data for only eight species (40%) were sufficient for statistical analysis at the species level. None of the other foraging groups showed a significant change in abundance.

4. Discussion

The presence of small forest openings created by a widespread ice storm affected the breeding bird community in several ways. Overall, species richness and diversity increased. Three forest-interior species declined significantly; two of these were canopy-foragers (Red-eyed Vireo and Blackburnian Warbler), and one a ground/shrub forager (Ovenbird). Another ground/shrub forager, Dark-eyed Junco, was the only species to increase significantly after the storm, although Winter Wren showed a marginal increase in abundance.

Red-eyed Vireo and Blackburnian Warbler both specialize in feeding on insects gleaned from canopy foliage (Sabo and Holmes, 1983), and both species have been shown to decline following canopy loss in other studies. Germaine et al. (1997) and Robinson and Robinson (1999) documented substantial declines in Red-eyed Vireo abundance in selectively harvested sites in Vermont and southern Illinois, respectively. As in this study, they did not completely disappear from treatment sites. In a Minnesota study, Apfelbaum and Haney (1981) found that the abundance of both species was negatively affected by fire which removed a large percentage of forest canopy. However, Annand and Thompson (1997) and Greenberg and Lanham (2001) reported no between-treatment differences in the abundance of Red-eyed Vireo following canopy loss.

The decline in Ovenbird abundance 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 quantities of downed limbs, tops, and uprooted trees 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.), supporting the findings of Robinson and Robinson (1999), who detected a 2–3 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 77%, it ranged widely (25–98%) and 12 of the 52 points (23%) had canopy closures ≤60%. Prior to the storm, only one point had a canopy closure below 60%. In another Vermont study, Germaine et al. (1997) detected significantly fewer Ovenbirds in 0.4 ha patch-cuts, and found that the effect extended up to 50 m into the surrounding forest. In the southern Appalachians, Greenberg and Lanham (2001) reported that Ovenbirds were the only forest-interior species that were less abundant in gaps than in controls, and Welsh and Healy (1993) showed that local Ovenbird densities in New Hampshire declined as a result of interior forest edges created by clearcut patches <20 ha in size. While the areas of heavy ice damage on sites in this study were patchy and relatively small in size (ca. 0.01–0.20 ha), the resulting increase in the amount of edge habitat may have affected Ovenbird abundance.

Among forest-interior guilds, both canopy and ground/shrub foragers declined significantly following the 1998 ice storm, suggesting that forest-interior species show an aversion to even small forest gaps. This supports the results of Germaine et al. (1997), who found that forest-interior species were significantly more abundant 200 m from small patch cuts than they were 50 m away from the cuts. However, in the southern Appalachians, Greenberg and Lanham (2001) suggested that forest-interior species were indifferent to small forest gaps that retain a partial canopy.

Species associated with forest edges and openings showed a mixed response to the ice storm. Open-edge ground/shrub foragers increased marginally following the storm, while the forest-edge canopy and ground/shrub groups showed no response. Among the species in these guilds, two ground-foragers increased in abundance: Dark-eyed Junco, and Winter Wren (although the increase of Winter Wren was marginal). In addition, Canada Warbler abundance increased marginally, but only among points located in gaps and not within the forest as a whole. All three 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. Other studies 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). On a landscape scale, the ice storm may have substantially increased the amount of edge habitat and forest gaps, benefiting several disturbance specialists, including Canada Warbler, a species of regional conservation concern (Therres, 1999; Rosenberg and Hodgman, 2000).

The increases in species richness and diversity observed in post-storm surveys at ice-damaged sites was likely due to 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; Germaine et al., 1997). It is possible that these increases could have arisen from an unbalanced sampling design (e.g. two visits to each pre-storm point vs. six visits to each post-storm point), despite efforts to minimize bias by including only those species detected in at least 2 post-storm years. I do not believe this to be the case, since an increase in richness and diversity was not detected among control sites. 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 ice-damaged patches. In Maine, Hagan et al. (1997) showed that Mourning Warbler and Olive-sided Flycatcher both had positive relationships with clearcut size.

5. Conclusions

Although forest damage from the 1998 ice storm was widespread, its severity was highly variable. At my study sites it resulted in small-scale forest gaps, rather than large-scale, stand-replacing disturbances. These small gaps provided some habitat for edge species, but were apparently too small to accommodate species that require large patches of early successional habitat, or to eliminate forest-interior species. Negative effects typically associated with forest fragmentation, such as an increase in the abundance of nest predators or brood parasites, were not detected. The abundance of a few forest-interior species declined in small forest gaps, suggesting that these species may be limited more by the presence of edges than by forest fragment size. I surmise that both positive and negative effects on the bird community will be short-lived (<10 years) as canopy cover regenerates. These results support the idea that some types of forest management, particularly selective, uneven-aged logging practices such as "group selection" and "single-tree selection" may effectively emulate natural disturbance events such as ice storms.

Acknowledgements

I gratefully acknowledge the hard work and dedication of field assistants S. Schulte, C. Reiser, and C. Rabatin. Many thanks also to T. Gaine and A. Strong who helped conduct bird surveys for the injured C. Reiser, and to E.T. McLane for assisting with vegetation measurements at ice-damaged sites. I respectfully acknowledge the cooperation of Ernie Buford and

Dave Capen of the 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. Constructive comments on an earlier version of this manuscript were provided by D. Lambert, K. McFarland, R. Renfrew, C. Rimmer, and two anonymous reviewers. 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. Additional financial support was provided by the members and trustees of the Vermont Institute of Natural Science.

References

Annand, E.M., Thompson, F.R., 1997. Forest bird response to regeneration practices in central hardwood forests. J. Wildlife Manage. 61, 159–171.

Apfelbaum, S., Haney, A., 1981. Bird populations before and after wildfire in a Great Lakes pine forest. Condor 83, 347–354.

Buford, E.W., Capen, D.E., 1999. Abundance and productivity of forest songbirds in a managed, unfragmented landscape in Vermont. J. Wildlife Manage. 63, 180–188.

Burke, D.M., Nol, E., 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. Auk 115, 96–104.

Canterbury, G.E., Blockstein, D.E., 1997. Local changes in a breeding bird community following forest disturbance. J. Field Ornithol. 68, 537–546.

Conway, C.J., 1999. Canada Warbler. In: Poole, A., Gill, F. (Eds.), The Birds of North America, No. 421. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists Union, Washington, DC.

Crawford, H.S., Hooper, R.G., Titterington, R.W., 1981. Songbird population response to silvicultural practices in central Appalachian hardwoods. J. Wildlife Manage. 45, 680–692.

Derleth, E.L., McAuley, D.G., Dwyer, T.J., 1989. Avian community response to small-scale habitat disturbance in Maine. Can. J. Zool. 67, 385–390.

Faccio, S.D., Rimmer, C.C., McFarland, K.P., 1998. Results of the Vermont Forest Bird Monitoring Program, 1989–1996. Northeastern Naturalist 5, 293–312.

Franzreb, K.E., Ohmart, R.D., 1978. The effects of timber harvesting on breeding birds in a mixed-coniferous forest. Condor 80, 431–441.

Germaine, S.S., Vessey, S.H., Capen, D.E., 1997. Effects of small forest openings on the breeding bird community in a Vermont hardwood forest. Condor 99, 708–718.

Greenberg, C.H., Lanham, J.D., 2001. Breeding bird assemblages of hurricane-created gaps and adjacent closed canopy forest in the southern Appalachians. For. Ecol. Manage. 154, 251–260.

Hagan, J.M., Vander Haegen, W.M., McKinley, P.S., 1996. The early development of forest fragmentation effects on birds. Conserv. Biol. 10, 188–202.

Hunter, M.L., 1990. Wildlife, Forests, and Forestry: Principles of Managing Forests for Biological Diversity. Prentice-Hall, New Jersey, 370 pp.

Irland, L.C., 2000. Ice storms and forest impacts. The Sci. Total Environ. 262, 231–242.

Kelley, R., 2001. The 1998 ice storm: Vermont assessment and response. In: Allen, D.C. (Compiler), Proceedings of the New York Society of American Foresters Ice Storm Symposium. USDA Forest Service Report NA-TP-03-01, pp. 91–96.

Kendeigh, S.C., 1947. Bird population studies in the coniferous forest biome during a spruce budworm outbreak. Ontario Dept. Lands For., Biol. Bull. 1.

King, D.I., Griffin, C.R., Degraaf, R.M., 1996. Effects of clearcutting on habitat use and reproductive success of the ovenbird in forested landscapes. Conserv. Biol. 10, 1380–1386.

King, D.I., Griffin, C.R., DeGraaf, R.M., 1997. Effect of clearcut borders on distribution and abundance of forest birds in northern New Hampshire. Wilson Bull. 109, 239–245.

Laughlin, S.B., Kibbe, D.P., 1985. The Atlas of Breeding Birds of Vermont. University Press of New England, Hanover, NH.

Medin, D.E., 1985. Breeding bird responses to diameter-cut logging in west-central Idaho. US Forest Service Research Paper INT-355, 12 pp.

Miller-Weeks, M., Eagar, C., 1999. The Northeastern Ice Storm 1998: A Forest Damage Assessment. North East State Foresters Association, USDA Forest Service, Durham, NH, 32 pp.

Morse, D.H., 1978. Populations of Bay-breasted and Cape May Warblers during an outbreak of the Spruce Budworm. Wilson Bull. 90, 404–413.

Peterson, J.M.C., Fichtel, C., 1992. Olive-sided Flycatcher. In: Schneider, K.J., Pence, D.M. (Eds.), Migratory Nongame Birds of Management Concern in the Northeast. US Department of Interior Fish and Wildlife Service, Hadley, MA, pp. 353–368.

Robinson, S.K., Robinson, W.D., 1995. Selective logging and forest bird communities: a review of current knowledge. Unpublished Report to the National Fish and Wildlife Foundation, Washington, DC.

Robinson, W.D., Robinson, S.K., 1999. Effects of selective logging on forest bird populations in a fragmented landscape. Conserv. Biol. 13, 58–66.

Rosenberg, K.V., Hodgman, T.P., 2000. Partners in Flight Landbird Conservation Plan: Physiographic Area 28: Eastern Spruce-Hardwood Forest, Draft 1.0. American Bird Conservancy, Washington, DC.

Rudnicky, T.C., Hunter Jr., M.L., 1993. Reversing the fragmentation perspective: effects of clearcut size on bird species richness in Maine. Ecol. Appl. 3, 357–366.

Sabo, S.R., Holmes, R.T., 1983. Foraging niches and the structure of forest bird communities in contrasting montane habitats. Condor 85, 121–138.

Schieck, J., Nietfeld, M., 1995. Bird species richness and abundance in relation to stand age and structure in aspen mixedwood forests in Alberta. In: Stelfox, J.B. (Ed.), Relationships Between Stand Age, Stand Structure and Biodiversity in

Aspen Mixedwood Forests in Alberta. Canadian Forest Service, Edmonton, Alta., pp. 115–157.

Seymour, R.S., White, A.S., deMaynadier, P.G., 2002. Natural disturbance regimes in northeastern North America—evaluating silvicultural systems using natural scales and frequencies. For. Ecol. Manage. 155, 357–367.

Smith, W.H., 2000. Ice and forest health. Northern J. Appl. For. 17, 16–19.

SYSTAT, 1998. SYSTAT 8.0 Statistics. SPSS Inc., Chicago, IL.

Therres, G.D., 1999. Wildlife species of conservation concern in the northeastern United States. Northeast Wildlife 54, 93–100.

Thompson III, F.R., Capen, D.E., 1988. Avian assemblages in seral stages of a Vermont forest. J. Wildlife Manage. 52, 771–777.

Thurber, W.A., 1980. Hurricane Fifi and the 1974 autumn migration in El Salvador. Condor 82, 212–218.

Van Horn, M.A., 1990. The relationship between edge and the pairing success of the Ovenbird. M.A. Thesis. University of Missouri, Columbia.

Van Horn, M.A., Donovan, T., 1994. Ovenbird. In: Poole, A., Gill, F. (Eds.), The Birds of North America, No. 88. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists Union, Washington, DC.

Wauer, R.H., Wunderle Jr., J.M., 1992. The effect of Hurricane Hugo on bird populations on St. Croix, US Virgin Islands. Wilson Bull. 104, 656–673.

Webb, W.L., Behrend, D.F., Saisorn, B., 1977. Effect of logging on songbird populations in a northern hardwood forest. Wildlife Monogr. 55, 1–35.

Welsh, C.J.E., Healy, W.M., 1993. Effect of even-aged timber management on bird species diversity and composition in northern hardwoods of New Hampshire. Wildlife Soc. Bull. 21, 143–154.

Wenny, D.G., Clawson, R.L., Faaborg, J., Sheriff, S.L., 1993. Populations density, habitat selection, and minimum area requirements of three forest-interior Warblers in central Missouri. Condor 95, 968–979.

Wunderle Jr., J.M., 1995. Responses of bird populations in a Puerto Rican forest to Hurricane Hugo: the first 18 months. Condor 97, 879–896.

Wunderle Jr., J.M., Lodge, D.J., Waide, R.B., 1992. Short-term effects of Hurricane Gilbert on terrestrial bird populations on Jamaica. Auk 109, 148–166.

Zach, R., Falls, J., 1975. Responses of the Ovenbird to an outbreak of the spruce budworm. Can. J. Zool. 53, 1669–1672.

Zar, J.H., 1996. Biostatistical Analysis, 3rd ed. Prentice-Hall, Upper Saddle River, NJ.