

# Effects of small-scale habitat disturbance on the ecology of breeding birds in a Vermont (USA) hardwood forest

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We studied territory placement and foraging behavior of breeding birds in relation to juxtaposition of forest vegetation and logged patches in southern Vermont, USA. Different bird species used disturbed vegetation at differing spatial scales, depending on territory size. Four species *Dendroica pensylvanica*, *Geothlypis trichas*, *Zonotrichia albicollis*, *Oporornis phuladelphia* showed strong clumping of their small (< 0.5 ha) territories in logged patches and were absent or rare in undisturbed forest. Eleven species (e.g. *Seiurus aurocapillus*, *Vireo olivaceus*) tended to avoid logged areas, especially the centers of cut patches. An additional 17 species fell between these two extremes, using a mixture of disturbed and undisturbed forest and showing no tendency to prefer one or the other. These 17 species tended to have larger (1 to > 3 ha) territories than disturbance specialists. We used ordination and quantitative matrix comparisons to describe and test relationships among 14 of the most common bird species according to their similarities in territory habitat structure, tree species composition, and foraging behavior. These analyses did not reveal any strong associations between foraging behavior and use of cut versus uncut forest. Habitat use by birds occupying this forest mosaic, with its strong local gradient of vegetation structure, was thus not associated with concurrent variation in foraging behavior. The sizes of cut patches of forest (0.7–1.6 ha) in our study area may be close to the minimum required to attract distinct breeding assemblages of non-forest birds to otherwise undisturbed forest ecosystems. Bird species that use patches of early-successional vegetation embedded in a forested landscape may adopt a fugitive strategy as they seek nesting habitats in the spring. Careful use of forest management techniques may permit both forest-interior and early-successional bird species to coexist in the landscape.

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## Introduction

Forests are mosaics of vegetation structure, consisting of gap, building, and mature phases produced by disturbance patterns that vary over space and time (Bormann and Likens 1979, Whitmore 1989). The size, frequency, and spatial arrangement of canopy gaps, broadly defined as “a patch created by the removal of the canopy” (Connell

1989), may be the major determinant of forest structure and tree species composition (Poulson and Platt 1989). In hardwood forests of the eastern United States, small gaps (< 25 m<sup>2</sup> to c. 0.1 ha) occur with high frequency, whereas large-scale, catastrophic disturbances (e.g. fire, extensive windthrow) occur at much longer intervals that may approach 1000 yr (Bormann and Likens 1979, Lorimer 1989).

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Much recent work has examined the role of disturbance in forest vegetation dynamics (e.g. Pickett and White 1985, Platt and Strong 1989); however, relatively less research has been done on the response of forest animal populations to small-scale patchy disturbances (but see Derleth et al 1989). We know that bird species composition in particular is strongly influenced by both local vegetation structure and floristics (e.g. James and Wamer 1982, Rice et al 1984, Rotenberry 1985). As a result, distributions of forest birds may track subtle vegetation gradients (Sherry and Holmes 1985), and patchy environments can enhance local bird species diversity (Roth 1976, Wiens 1976). Foraging behavior of birds can also vary with habitat structure and tree species composition (e.g. Maurer and Whitmore 1981, Robinson and Holmes 1982). Particularly in forests that have been disturbed by logging, it is known that "the vertical distribution of the vegetation, the foliage density, and the relative frequencies of tree species are of major importance in predicting the response of birds to a logged environment" (Franzreb 1983, p. 74).

We studied habitat use and foraging ecology of breeding birds in a forest mosaic produced by small-scale logging. An important objective was to test whether overall patterns of avian habitat use in disturbed versus undisturbed forest could be attributed to how different bird species foraged in the vegetation. We describe forest vegetation patterns and examine corresponding patterns of the ecological characteristics of bird species that used the disturbed forest landscape. We also compare our observations to those made in an undisturbed control site in Vermont and the Hubbard Brook Experimental Forest, New Hampshire, and discuss how our results may elucidate some of the dynamics of breeding bird populations in patchily-disturbed forests.

## Methods

### Study area

The study was conducted in Grafton, Vermont, USA (43°10'N, 72°36'W). Topography in the area is variable, ranging from level farmland and meadows to steep slopes, elevations range from 260 to 550 m. Northern hardwoods (*Betula-Fagus-Acer*) comprise the primary forest types, but 34% of the study area was composed of coniferous or mixed forest types.

We established three gridded study plots, designated A, B, and C. These 9-ha grids ("disturbed sites") were located so that a portion of each contained a patch of disturbed vegetation. The remaining area was relatively undisturbed forest,  $\geq 20$  m in height. Grid A, logged in the winters of 1977 and 1978, contained two clearcuts with a combined area of 1.4 ha. Grid C had a 0.9-ha patch that had been clearcut in the winter of 1980. Grid B contained a 1.6-ha selection-cut performed in the winter of 1978. Because of residual trees the selection cut had

more vertical structure than the clearcuts in grids A and C. Each disturbed grid was surrounded by essentially continuous, uncut forest. In addition to the disturbed sites, an 87-ha site, described by Runde and Capen (1987), was chosen as a large control area of continuous, undisturbed forest. The only open areas in this site were two beaver (*Castor canadensis*) flowages along its southern boundary and an old field that surrounded one of the beaver ponds.

### Field methods

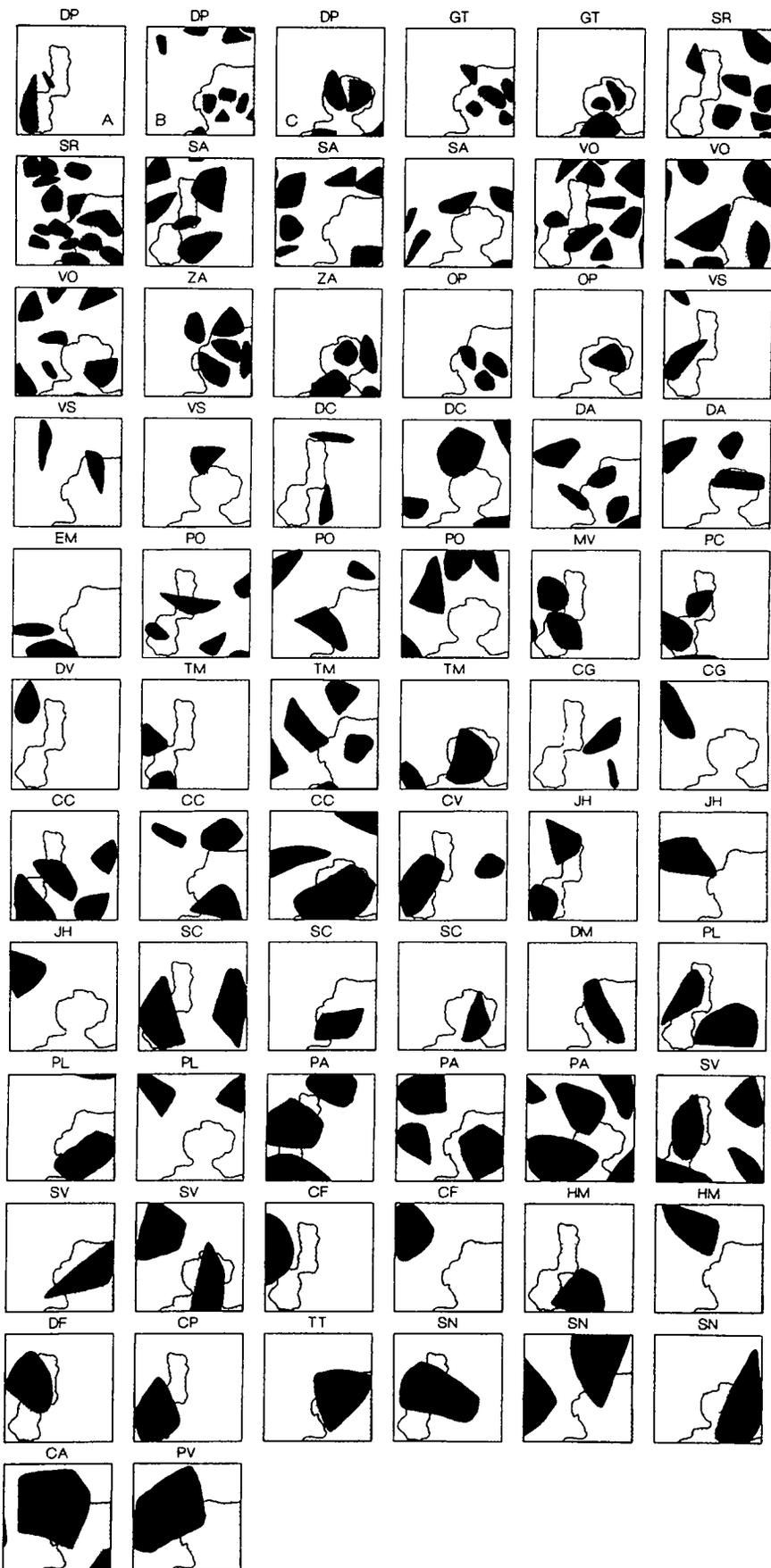
Songbird territories were mapped on the disturbed sites between 0530 and 1100 on mornings with favorable weather, following a protocol described by Robbins (1970). Twelve mapping visits were made to grids A and B from 19 May to 15 July 1981. Grid C was visited ten times from 27 May to 15 July 1982.

Birds on the control site were surveyed using a point-count technique (Ferry 1974), because the method is efficient for large areas. Forty-one points were marked in a 150-m grid pattern and censused twice during 12 visits from 21 May to 16 July 1981. Each point was visited for 15 min between 0500 and 1100 under favorable weather conditions. We recorded the number of individuals for each species detected at a point, and used the higher of the two counts of each bird species at each point in calculating a point index of abundance (Ferry 1974, Robbins 1978). Data from the control site were used to generate a list of bird species and relative abundances for comparison with that of our disturbed sites and the Hubbard Brook Forest in New Hampshire (Holmes et al 1986).

Observations of foraging birds on the disturbed sites were obtained throughout each breeding season, extending into late July. Foraging observations were not obtained in the control area. All parts of each disturbed grid were surveyed in both morning and afternoon hours. Grids A and B were surveyed in both 1981 and 1982, grid C was surveyed in 1982. Grids were systematically walked until a foraging bird was encountered. We recorded the first foraging action performed by the bird after it was identified (Altmann 1974, Wagner 1981). Only behaviors judged to be attempts to capture food were recorded. Five behaviors were defined to represent typical foraging techniques of insectivorous birds (e.g. Holmes et al 1979). These were 1) glean-taking exposed prey from a substrate while perched, 2) hover-taking prey from a substrate while actively hovering; 3) hawk-flying out from a perch to capture prey, then returning to the same or another perch; 4) hammer-pounding or chiseling with the beak at a substrate, often with twisting head movements, and 5) hang-upward probing from a small branch or twig. Foraging substrates were defined as foliage, branch ( $> 0.5$  cm in diameter), twig ( $\leq 0.5$  cm diameter), trunk, air (included as a substrate here in the

Fig 1 Territory maps of 33 bird species overlain onto vegetation maps of 300 by 300-m disturbed grids (white = forest, stippled = cutover area, black = territory) Species are arranged (left to right) in order of increasing mean territory size All grids in which a given species was territorial are shown The first 3 maps in row 1 include the grid designation, subsequent grids can be identified by the outline of the canopy gap Bird species codes in this and subsequent figures

DP, *Dendroica pensylvanica*,  
 GT, *Geothlypis trichas*,  
 SR, *Setophaga ruticilla*,  
 SA, *Seiurus aurocapillus*,  
 VO, *Vireo olivaceus*,  
 ZA, *Zonotrichia albicollis*,  
 OP, *Oporornis philadelphia*,  
 VS, *Vireo solitarius*,  
 DC, *Dendroica coronata*,  
 DA, *Dendroica caerulescens*,  
 EM, *Empidonax minimus*,  
 PO, *Piranga olivacea*,  
 MV, *Mniotilta varia*,  
 PC, *Passerina cyanea*,  
 DV, *Dendroica virens*,  
 TM, *Turdus migratorius*,  
 CG, *Catharus guttatus*,  
 CC, *Cyanocitta cristata*,  
 CV, *Contopus virens*,  
 JH, *Junco hyemalis*,  
 SC, *Sitta carolinensis*,  
 DM, *Dendroica magna*,  
 PL, *Pheucticus ludovicianus*,  
 PA, *Parus atricapillus*,  
 SV, *Sphyrapicus varius*,  
 CF, *Catharus fuscescens*,  
 HM, *Hylocichla mustelina*,  
 DF, *Dendroica fusca*,  
 CP, *Carpodacus purpureus*,  
 TT, *Troglodytes troglodytes*,  
 SN, *Sitta canadensis*,  
 CA, *Certhia americana*,  
 PV, *Picoides villosus*



sense of being the focal point of a foraging act), and ground.

Each grid point on the disturbed sites formed the center of a 0.02-ha circular vegetation plot, resulting in the sampling of 37% of the grid's area. Habitat variables related to trees, shrubs, ground and canopy cover, and vegetation height were measured following Noon's (1981) methods for forest habitats. Slash (dead woody material) and logs >0.5 cm diameter and ≤ 1 m in height were counted along two perpendicular line transects oriented along cardinal compass points and centered on the circular plot. Each intersection of slash or logs with a vertical pole passed along the transect was counted as an index of dead woody material in the plot. Understory foliage volume was measured using a density board (Noon 1981).

## Data analysis

We examined interspecific similarities in habitat use of Grafton birds by constructing two Euclidean distance matrices. One matrix contained interspecific distances computed using means of habitat variables measured in bird territories. The other matrix contained distances based on tree species composition. Means were computed across all 0.02-ha vegetation plots that fell within the territories of a given species. The habitat matrices summarized similarities among bird species according to the vegetation structure and tree species composition of their territories.

To examine interspecific similarities in foraging ecology, two additional distance matrices were constructed, based on foraging technique and foraging substrate. Here, interspecific distances were computed using the proportion of observations falling into each behavioral category.

In each of these four matrices, the smaller the Euclidean distance between species pairs, the more ecologically similar they were. Habitat and foraging similarities among species were visualized with multidimensional scaling (MDS), a robust ordination technique (Kruskal and Wish 1978, Kenkel and Orloci 1986), using program MDS in the SYSTAT statistical package (Wilkinson 1990).

The Mantel randomization test (Douglas and Endler 1982) was used to assess the level of association between avian habitat and foraging matrices (see Rotenberry 1985 for a similar approach). The Mantel test determined whether similarities among species pairs in habitat space were associated with parallel similarities in foraging space. The test employs a statistic,  $Z$ , which is tested for significance against a sampling distribution of  $Z$  obtained by random permutations of the rows and columns of one matrix. If the two matrices are correlated, the observed  $Z$  will tend to be larger than the values produced by randomization. The Pearson correlation coefficient between the elements of the two matrices was also computed. For these tests we used a Fortran program published in Manly

(1985, p. 424), modified for use on a microcomputer. Random  $Z$ -distributions were produced from 1000 matrix permutations per test. In addition to this multivariate test, we computed simple Pearson correlations between MDS axes of habitat structure and tree species composition and single foraging variables.

We compared our bird species lists to published lists from the Hubbard Brook Experimental Forest of New Hampshire. Holmes et al. (1986) published annual data on 29 bird species detected over 16 yr (1969–1984) in a 10-ha study area, representing a late-succession, unfragmented northern hardwood forest. Two of these years (1981 and 1982) overlapped with our study, and we used the average of Hubbard Brook species abundances from those years for a time-specific comparison. Fifteen of the Hubbard Brook species bred there in each of the 16 yr. Our comparisons between Grafton and Hubbard Brook were confined to these 15 species, which we consider "typical" of a mid- to late-succession northern hardwood forest.

## Results

### Spatial distribution of bird territories

We mapped territories of 33 bird species found on our disturbed sites (Fig. 1). Territory sizes ranged from 0.2 ha for *Dendroica pensylvanica* (Fig. 1, row 1, maps 1–3) to >3.0 ha for *Picoides villosus*. Four species (*Dendroica pensylvanica*, *Geothlypis trichas*, *Zonotrichia albicollis*, *Oporornis phyladelphia*) preferred disturbed vegetation and showed strong clumping of their small (<0.5 ha) territories in cut patches (Fig. 1, rows 1 and 3). *Dendroica pensylvanica* also used some small openings caused by a narrow dirt road that crossed grid B (Fig. 1, row 1, map 2). One *Dendroica magnolia* territory was present in the grid B cut (Fig. 1, row 8, map 5). Eleven species tended to avoid cuts, especially their centers: *Seiurus aurocapillus*, *Vireo olivaceus*, *Dendroica coronata*, *D. virens*, *Piranga olivacea*, *Catharus guttatus*, *Hylocichla mustelina*, *Catharus fuscescens*, *Junco hyemalis*, *Picoides villosus*, and *Empidonax minimus*. The remaining 17 species fell between these two extremes, using a mixture of cut and uncut forest vegetation and showing no tendency to prefer one or the other. Many of these species had territory sizes appreciably greater (1 to >3 ha) than the median size (0.6 ha, for *Catharus guttatus*), and their large territories often broadly overlapped both cut and uncut forest (Fig. 1, row 7 and beyond).

### Bird species composition of disturbed and undisturbed forest

A comparison of bird species detected in our disturbed sites with those detected in the undisturbed control area indicated that three disturbed-site species (*Zonotrichia*

Table 1 Territorial breeding bird species detected in three 9-ha northern hardwoods sites containing patchy disturbance, Grafton, Vermont, 1981–1982. Species are listed in order of decreasing abundance

Species	Number of territories, grnds A, B, C (total area, 27 ha)
<i>Setophaga ruticilla</i>	20.5
<i>Vireo olivaceus</i>	20
<i>Seiurus aurocapillus</i>	16
<i>Dendroica pensylvanica</i>	14.5
<i>Piranga olivacea</i>	10.5
<i>Geothlypis trichas</i>	8
<i>Cyanocitta cristata</i>	8.5
<i>Parus atricapillus</i>	8.5
<i>Zonotrichia albicollis</i>	8.5
<i>Dendroica caerulescens</i>	7.5
<i>Turdus migratorius</i>	7
<i>Sphyrapicus varius</i>	6
<i>Pheucticus ludovicianus</i>	5
<i>Dendroica coronata</i>	5
<i>Oporornis philadelphia</i>	4
<i>Junco hyemalis</i>	4
<i>Sitta carolinensis</i>	4
<i>Vireo solitarius</i>	4.5
<i>Sitta canadensis</i>	3.5
<i>Catharus guttatus</i>	3
<i>Catharus fuscescens</i>	2
<i>Mniotilta varia</i>	2
<i>Hylocichla mustelina</i>	2
<i>Contopus virens</i>	2
<i>Passerina cyanea</i>	2
<i>Empidonax minimus</i>	2
<i>Certhia americana</i>	1.5
<i>Troglodytes troglodytes</i>	1
<i>Picoides villosus</i>	1
<i>Dendroica fusca</i>	1
<i>Carpodacus purpureus</i>	1
<i>Dendroica virens</i>	1
<i>Dendroica magnolia</i>	1

*albicollis*, *Oporornis philadelphia*, *Passerina cyanea*) were absent or rare in undisturbed forest (Tables 1 and 2). *Geothlypis trichas* and *Dendroica pensylvanica*, also disturbed-site species, were detected on our control area, but at low density and only in edge habitats at boundaries of the site. Considering only "typical" northern hardwoods species found at Hubbard Brook, only one of the 15 Hubbard Brook species (*Catharus ustulatus*) was not detected in Grafton (Tables 1–3). Abundance distributions of the 15 typical species did not differ between our disturbed sites and Hubbard Brook. This was true using both the time-specific data (Table 3) to generate an expected distribution ( $G = 22.3$ ,  $d.f. = 13$ ,  $p > 0.05$ ) and the 16-yr average abundances ( $G = 20.1$ ,  $d.f. = 13$ ,  $p > 0.05$ ). Rank abundances of the 15 species also did not differ between our undisturbed site and Hubbard Brook, both for 1981–1982 averages ( $p > 0.5$ ,  $t$ -test) and 16-yr averages ( $p > 0.5$ ) of Holmes et al.'s (1986) data.

Table 2 Breeding bird species (singing males) detected by point counts in an 87-ha, undisturbed northern hardwoods forest site, Grafton, Vermont, 1981. Species are listed in order of decreasing abundance

Species	Abundance index*
<i>Vireo olivaceus</i>	1.88
<i>Seiurus aurocapillus</i>	1.27
<i>Cyanocitta cristata</i>	1.24
<i>Parus atricapillus</i>	1.24
<i>Catharus fuscescens</i>	0.80
<i>Dendroica caerulescens</i>	0.68
<i>Dendroica virens</i>	0.66
<i>Pheucticus ludovicianus</i>	0.63
<i>Mniotilta varia</i>	0.61
<i>Junco hyemalis</i>	0.61
<i>Piranga olivacea</i>	0.58
<i>Catharus guttatus</i>	0.56
<i>Sphyrapicus varius</i>	0.49
<i>Hylocichla mustelina</i>	0.44
<i>Certhia americana</i>	0.39
<i>Dendroica fusca</i>	0.37
<i>Setophaga ruticilla</i>	0.32
<i>Wilsonia canadensis</i>	0.27
<i>Sitta carolinensis</i>	0.27
<i>Sitta canadensis</i>	0.24
<i>Myiarchus crinitus</i>	0.24
<i>Contopus virens</i>	0.22
<i>Dendroica coronata</i>	0.19
<i>Picoides villosus</i>	0.19
<i>Dendroica pensylvanica</i>	0.19
<i>Colaptes auratus</i>	0.12
<i>Dryocopus pileatus</i>	0.12
<i>Icterus galbula</i>	0.12
<i>Carpodacus purpureus</i>	0.10
<i>Geothlypis trichas</i>	0.10
<i>Picoides pubescens</i>	0.10
<i>Regulus satrapa</i>	0.10
<i>Seiurus motacilla</i>	0.07
<i>Carduelis tristis</i>	0.07
<i>Seiurus noveboracensis</i>	0.05
<i>Troglodytes troglodytes</i>	0.05
<i>Quiscalus quiscula</i>	0.05
<i>Coccothraustes vespertinus</i>	0.05
<i>Dendroica magnolia</i>	0.02
<i>Archilochus colubris</i>	0.02
<i>Coccyzus erythrophthalmus</i>	0.02
<i>Turdus migratorius</i>	0.02
<i>Molothrus ater</i>	0.02
<i>Melospiza melodia</i>	0.02

\* Calculated as (maximum number of individuals)/(41 points) (Ferry 1974)

### Habitat use and foraging behavior

Fourteen bird species yielded sufficient data for a comparative analysis of habitat use and foraging ecology. Although this is only a subset of the Grafton species assemblage, the spectrum of gap versus forest usage is represented. MDS ordinated the 14 species according to successional age of the vegetation, increasing basal area of coniferous trees, and decreasing basal area of dead trees (Fig. 2A). Three disturbed-site species (*Geothlypis trichas*, *Zonotrichia albicollis*, *Dendroica pensylvanica*) were distinctly separated from the other species by hab-

Table 3 Bird census data (1981–1982) from the Hubbard Brook Experimental Forest, New Hampshire (Holmes et al 1986, p 220), adjusted to conform with data from the present study. Species are listed in order of decreasing density.

Species	Pairs/27 ha*
<i>Setophaga ruticilla</i> *	36.5
<i>Vireo olivaceus</i> *	33.1
<i>Dendroica caerulescens</i> *	17.6
<i>Seiurus aurocapillus</i> *	14.2
<i>Dendroica virens</i> *	11.8
<i>Pheucticus ludovicianus</i> *	10.2
<i>Piranga olivacea</i> *	7.5
<i>Dendroica fusca</i> *	5.4
<i>Catharus fuscescens</i> *	3.4
<i>Sitta carolinensis</i> *	3.4
<i>Picoides villosus</i> *	3.4
<i>Sphyrapicus varius</i> *	3.1
<i>Vireo philadelphicus</i> *	2.7
<i>Catharus ustulatus</i> *	2.1
<i>Hylocichla mustelina</i> *	1.7
<i>Contopus virens</i> *	1.4
<i>Cyanocitta cristata</i> *	1.4
<i>Catharus guttatus</i> *	1.4
<i>Picoides pubescens</i> *	1.0
<i>Parus atricapillus</i> *	1.0
<i>Archilochus colubris</i> *	0.7
<i>Empidonax minimus</i> *	0.7
<i>Dendroica coronata</i> *	0.7
<i>Certhia americana</i> *	0.4
<i>Troglodytes troglodytes</i> *	0.4
<i>Turdus migratorius</i> *	0
<i>Vireo solitarius</i> *	0
<i>Junco hyemalis</i> *	0
<i>Carpodacus purpureus</i> *	0

\* To adjust 1981 and 1982 data of Holmes et al (1986, p 220) for comparison with our disturbed site censuses, Holmes et al's values were expressed as pairs (by dividing their individuals/10 ha in half), averaged, then multiplied by 2.7. Values listed as "1" (trace evidence) by Holmes et al were assigned a value of 0.5 for this comparison.

\* Denotes species that bred in each of 16 yr of Holmes et al's study, and which are thus considered "typical" northern hardwoods species in our analysis.

itat structure (GT, ZA, and DP in Fig. 2A). The remaining species showed additional separation, reflecting finer-scale variation in their use of forest vegetation. Disturbed-site species were also grouped separately from forest species by low basal areas of the deciduous tree species common in undisturbed forest (*Ostrya virginiana*, *Quercus rubra*, *Acer saccharum*, *Fagus grandifolia*) and by greater basal area of *Populus* spp. and *Pinus strobus*, tree species found in regenerating logged patches (Fig. 2B). There was also considerable variation among the other bird species in the tree species composition of their territories.

Because of small sample sizes for some species, the foraging techniques of hovering and hawking were combined into a single category representing the more energetically expensive aerial techniques (Fig. 3A). Species were separated according to the relative amount of gleaning compared with that of other techniques (Fig. 4A). A core group of nine species (*Seiurus aurocapillus*, *Junco*

*hyemalis*, *Dendroica caerulescens*, *D. pensylvanica*, *Zonotrichia albicollis*, *Geothlypis trichas*, *Cyanocitta cristata*, *Pheucticus ludovicianus*, *Piranga olivacea*) used gleaning as a primary technique. Peripheral to this group were *Sphyrapicus varius* and *Sitta carolinensis*, which both gleaned and hammered. *Vireo olivaceus* and *Setophaga ruticilla* are farther away from the gleaners in Fig. 4A because they foraged aerially in addition to gleaning. *Parus atricapillus* was different from all other species because it had the highest proportion of hanging in its repertoire of foraging techniques (Figs 3A and 4A). In contrast to the habitat ordinations (Figs 2A, B), disturbed-site species are not clearly separated from the other 11 species in the foraging ordination (Fig. 4A).

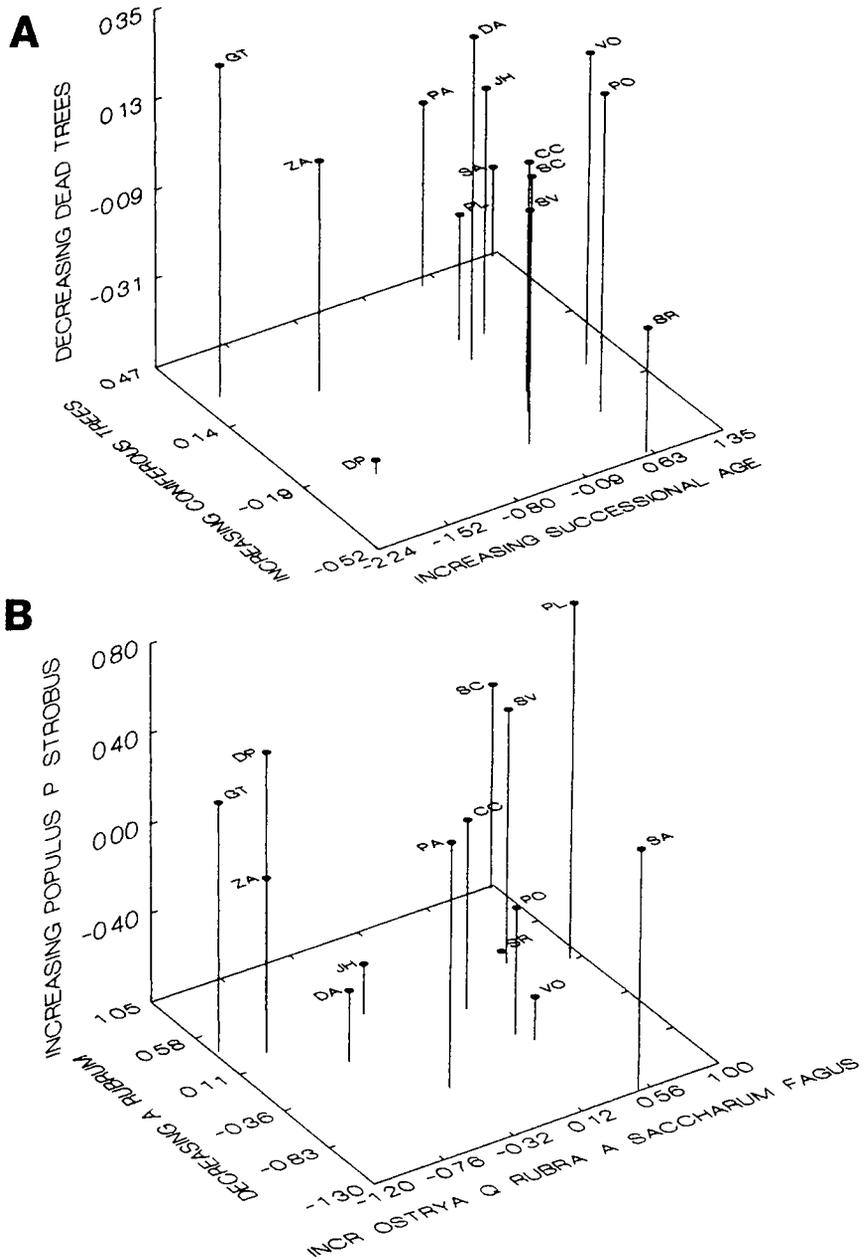
Three groups were recognized based on use of foraging substrates (Figs 3B and 4B). One group contained eight species (*Dendroica caerulescens* and *pensylvanica*, *Zonotrichia albicollis*, *Pheucticus ludovicianus*, *Piranga olivacea*, *Vireo olivaceus*, *Geothlypis trichas*, *Setophaga ruticilla*) that mainly foraged on foliage. This group included the 3 disturbed-site species. *Setophaga ruticilla* was grouped at the periphery of the foliage group because it directed its foraging toward aerial prey as well as foliage arthropods. *Sphyrapicus varius* and *Sitta carolinensis*, a second group, were the most similar species pair because their use of trunks and branches was nearly identical (Fig. 3B). The third group was intermediate (Fig. 4B), using a mixture of foraging substrates in addition to foliage, trunks, and branches.

Mantel tests showed no globally significant correlations between habitat and foraging matrices ( $r = 0.24, 0.04, -0.17, -0.09, p = 0.05, 0.4, 0.8, 0.7$ ). This result is reinforced by examining the MDS ordinations (Figs 2 and 4), which show that disturbed-site species (*Geothlypis trichas*, *Dendroica pensylvanica*, *Zonotrichia albicollis*) are distinctly separated from the other species on the basis of vegetation structure and floristics (Figs 2A, B) but not by foraging technique and substrate (Figs 4A, B). Also, none of the univariate correlations between individual foraging variables and MDS axes of habitat structure and tree species composition were significant at an experimentwise level ( $r$ 's ranging from  $-0.59$  to  $0.59$ ,  $p$ -values from  $0.025$  to  $0.99$ ).

## Discussion

An avifauna typical of a northern hardwoods forest was present on both our disturbed and undisturbed sites, and relative abundances of species in Grafton were similar to those of the long-term Hubbard Brook study. The primary difference was the absence of disturbance-associated and edge species at our control site and at Hubbard Brook. Eight species that occurred on our disturbed sites were not detected in 16 yr at Hubbard Brook: *Dendroica pensylvanica*, *Oporornis philadelphia*, *Geothlypis trichas*, *Zonotrichia albicollis*, *Passerina cyanea*, *Mniotilta*

Fig 2A. MDS ordination of 14 bird species according to similarities in territory habitat structure  
 Fig 2B MDS ordination of the same species according to similarities in territory tree species composition



*varia*, *Dendroica magnolia*, and *Sitta canadensis* (Fig 1, Table 1). Of these, the first four were primarily found in cut patches of forest in Grafton (Fig 1) The latter four are either edge species (*Passerina cyanea*) or require coniferous or mixed forest types (*Dendroica magnolia*, *Sitta canadensis*) found on the Grafton project area but absent from Hubbard Brook. We cannot account for the absence of *Mniotilta varia* at Hubbard Brook

Although the bird communities in Grafton and Hubbard Brook were similar, the forested landscape that we studied in Grafton differed in an important way from the

undisturbed Hubbard Brook forest at Grafton, very distinct patch boundaries were produced by locally intensive disturbance to the vegetation. Sharp patch boundaries are common in landscapes modified by human activity (Wiens et al 1993). In contrast, patch boundaries in an undisturbed forest tend to be less distinct than in disturbed forests, and often result from relatively subtle spatial variation in leaf type, tree species composition, and arthropod abundance (Sherry and Holmes 1985, Holmes et al. 1986). Although our evidence is indirect, we suggest that this kind of variation in landscape grain

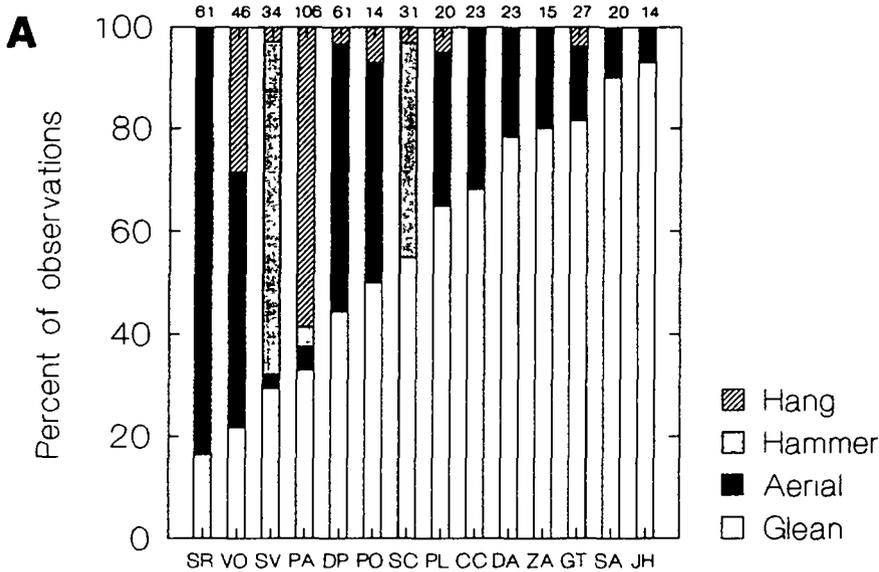
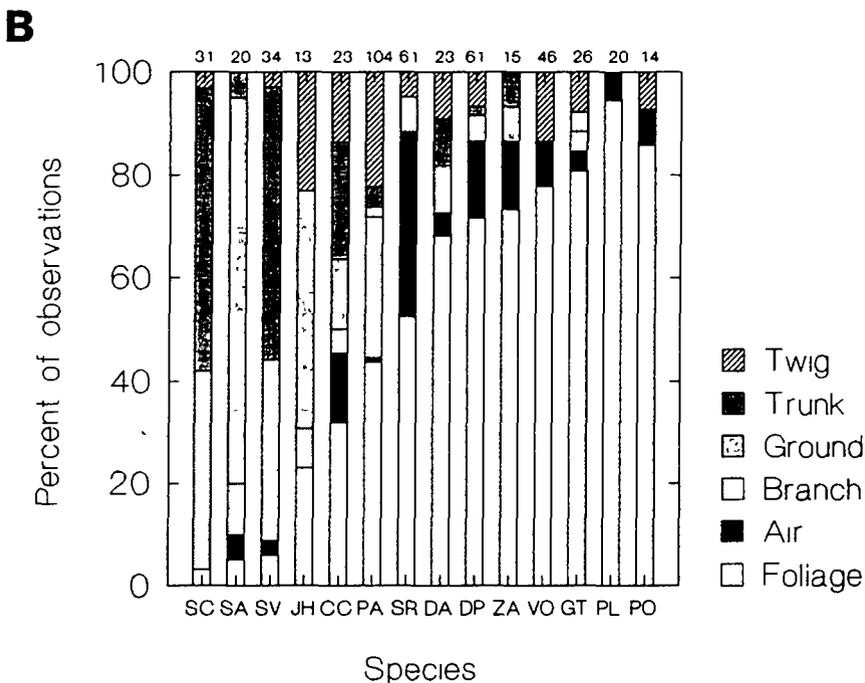


Fig 3A Foraging techniques used by 14 bird species. Species are arranged in order of increasing proportion of gleaning. Fig 3B Foraging substrates used by the same species, arranged in order of increasing foliage use. Sample sizes are shown at the top of each bar.



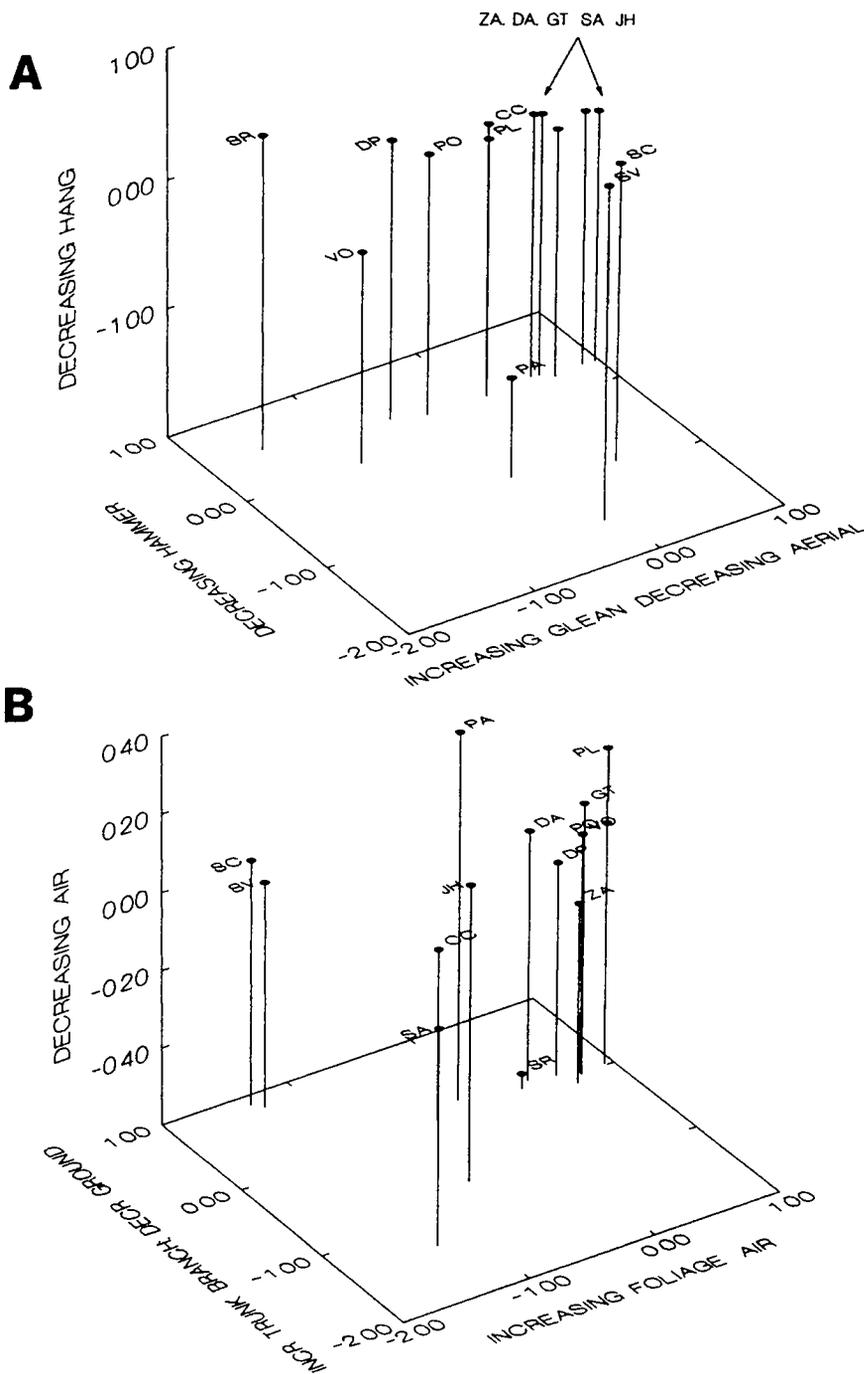
and patch boundary distinctness may influence how the various bird species in an assemblage partition habitat and food resources. In an undisturbed forest, where patches are generally small and patch boundaries indistinct, birds apparently partition habitat through interspecific differences in foraging behavior (Sherry and Holmes 1985, Holmes et al. 1986). In Grafton, boundaries between cut and uncut forest were pronounced, and differences in foraging behavior among bird species that used cut versus uncut forest were minor (Fig 4). Our results suggest that the juxtaposition of patches of cut and uncut

forest was more important in producing the observed pattern of avian distribution than were interspecific differences in foraging behavior.

Most of the bird species we studied in Grafton, as well as the majority of breeding species in the northeastern United States, are neotropical migrants (MacArthur 1959). These species seek breeding habitats across forested landscapes each spring upon their return from the wintering grounds. For migrants that prefer or require disturbed or early-successional habitats, canopy openings embedded in a matrix of forest present an ephemeral,

Fig 4A MDS ordination of 14 bird species according to similarities in foraging technique

Fig 4B MDS ordination of the same species according to similarities in foraging substrate



constantly shifting patch structure that may enable “fugitive” species to persist in forest-dominated landscapes (Hutchinson 1951, Levin and Paine 1974) In northern hardwood forests, *Dendroica pensylvanica*, *Oporornis philadelphia*, *Geothlypis trichas*, and *Zonotrichia albicollis* are among the species that may adopt a fugitive

strategy as they seek nesting habitats in this shifting mosaic of habitat patches each spring

As Hutchinson (1951) observed, a fugitive species does not have to be very different ecologically from other species in an assemblage in order to persist there This is shown by our data, where gap specialists did not differ

substantially in foraging ecology from species using adjacent forest habitat (Fig. 4). Gap-specializing birds could thus persist as metapopulations during the breeding season in forested landscapes by having relatively higher dispersal abilities than forest-interior species and a more developed perception of landscape patchiness, rather than being fundamentally different in their use of resources (Hanski and Gilpin 1991, Opdam 1991)

The relative dominance of fugitive species in a landscape also depends on the frequency and extent of disturbance and the size, arrangement, and boundary distinctness of habitat patches (Wiens 1976, Schemske and Brokaw 1981) When large areas of forest have been disturbed and habitats become extensively fragmented, forest specialists tend to disappear and fugitive bird species become ecologically dominant (Robbins 1979, Whitcomb et al 1981, Hanski 1985, Kavanagh et al 1985) In contrast, small-scale disturbances increase local bird species diversity by providing a vegetation structure not found in undisturbed forest while still allowing forest specialists to maintain high numbers (Roth 1976, Denslow 1985) When canopy openings regenerate, fugitive bird species disappear locally and forest-interior species recolonize the former openings from the surrounding undisturbed forest Fugitive species must then locate and colonize newly-opened disturbances

Blake and Hoppes (1986, p 335), who studied bird use of tree-fall gaps in Illinois, stated that it is likely that "birds are capable of recognizing and selecting tree-fall gaps as a distinct microhabitat in which to forage" (see also Schemske and Brokaw 1981, Hoppes 1987) Small canopy openings generally attract bird species of the surrounding forest that are able to forage in the modified vegetation, which often contains a greater abundance of food (Schemske and Brokaw 1981, Blake and Hoppes 1986) In contrast, the larger (0.7–1.6 ha) canopy disturbances in Grafton were of sufficient size to attract a distinct group of breeding birds that were not found in the surrounding undisturbed forest Similar results, including some of the same disturbed-site species, were found by Yahner (1984) and Derleth et al (1989), both of whom worked in forests disturbed by small-scale clearcutting

Our results have applicability both towards management of forests for early-successional bird species and in the larger ecological context of the persistence of bird populations in modern landscapes Such populations have often shifted dramatically over time with changing patterns of land use For example, in the mid- to late-1800's, lands in central New England were extensively cleared for agriculture, with the result that over 80% of the land area was open. This condition undoubtedly was beneficial to early-successional, grassland and shrubland bird species but was a detriment to forest species. Historical accounts of such species suggest that their distributions have shifted in response to changes in forest habitats With proliferation of forest clearing, habitat for edge and grassland birds greatly increased, enabling them to expand their populations and colonize new patches of dis-

turbed habitat (Brewer and Swander 1977, Litvaitis 1993) After the height of land clearing, rapid reforestation followed farm abandonment leading to the present condition where much of central New England is again covered by forest (Foster 1992) In this extensively forested landscape, creation of non-forested habitats is a key to maintaining bird species diversity (Hansen et al 1991, DeGraaf et al 1993) In such landscapes, species of open-country birds are becoming increasingly rare due to habitat loss via natural successional processes and human activities such as development of open grasslands (Askins 1993)

Careful natural resource planning, involving active habitat management, will be required to maintain populations of both forest-interior and open-country birds (Hansen et al 1991, Askins 1993) We have shown that early-successional bird species will establish territories in small clearcuts (Fig 1), so that this type of forest management may be one alternative for maintaining avian habitat diversity in northern hardwood forests Another alternative, particularly for grassland bird species with relatively large minimum area requirements, would be to segregate large clearcuts in one area of the forest, while reserving large blocks of undisturbed habitat for forest-interior species (Askins 1993) These techniques embody a recent approach to forestry ("new forestry") in which tree harvesting operations are designed to mimic natural disturbances (Hansen et al 1991) In general, forestry practices that mimic small-scale natural disturbances will have the benefit of creating habitat for early-successional birds while avoiding the high degree of forest fragmentation caused by larger-scale harvesting operations (Hansen et al 1991) Askins (1993, p 27) has noted that managed forests are one type of habitat that is an effective means for maintaining populations of early-successional bird species because "economic activity entails continual disturbance of the vegetation" For those populations to persist, small-scale disturbances must be maintained, because early-successional habitat can disappear within 10 yr (DeGraaf et al 1993) as the forest regenerates Once established by logging, disturbed patches could be maintained by mowing or burning, or allowed to regenerate if new cutover patches were continually produced

In summary, different species of forest birds respond to the size and boundary distinctness of habitat patches at varying scales (Forman and Godron 1981) Territory size in relation to landscape grain appears to be one factor in this variation (e.g. Fig. 1) Sherry and Holmes (1985) have shown how breeding birds in northern hardwood forests differ in their foraging-mediated patterns of habitat selection Such species apparently recognize subtle differences in "uniform" undisturbed forest We have described a coarser level of bird-habitat patchiness in northern hardwood forests, i.e., disturbance-mediated co-occurrence of species (Denslow 1985). Large scale forest fragmentation may lead to still more profound changes in bird species composition at the landscape level (e.g. Forman and Godron 1981, Whitcomb et al. 1981), but care-

ful habitat management may permit both forest-interior and early-successional bird species to coexist in the landscape.

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