ELSEVIER

Forest Ecology and Management 154 (2001) 251–260

Forest Ecology and Management

www.elsevier.com/locate/foreco

Breeding bird assemblages of hurricane-created gaps and adjacent closed canopy forest in the southern Appalachians

Cathryn H. Greenberg[a,*], J. Drew Lanham[b]

[a]USDA Forest Service, Bent Creek Experimental Forest, 1577 Brevard Road, Asheville, NC 28806, USA
[b]Department of Forest Resources, Clemson University, 261 Lehotsky Hall, Clemson, SC 29634, USA

Received 14 August 2000; accepted 17 October 2000

Abstract

We studied breeding bird assemblages in forest gaps created in 1995 by Hurricane Opal at the Bent Creek Experimental Forest in Asheville, NC. We hypothesized that forest gaps and adjacent closed-canopy forest would differ in bird density, richness, diversity, and relative abundances of some species. To test this hypothesis we censused breeding bird assemblages for 2 years in 12 gaps (0.1–1.2 ha) and 12 adjacent closed canopy controls using strip transects. Gaps had more coarse woody debris, shrub cover, brushpiles, and pit and mound microtopography than controls. Canopy cover was lower in gaps than controls, but remained high (69.4 ± 2.1% versus 89.6 ± 1.7%). Bird assemblage similarity was high. Total density and species richness of birds were higher in gaps than in controls, but species diversity did not differ between treatments. Shrub (primarily Carolina Wrens) and bark-foragers, and cavity shrub and canopy-nesters were more abundant in gaps than in controls. Densities of gap-associated (Indigo Bunting, Hooded Warbler, Carolina Wren) and edge (Eastern Towhee) species were more abundant in gaps. Abundance of interior species including Red-eyed Vireo and Scarlet Tanager were about equal in gaps and controls. Only Ovenbirds were more abundant in controls than gaps. Species that require larger patches of young second-growth forest, such as Prairie Warbler, and Yellow-breasted Chat, did not occur in gaps; but neither are they abundant in the Asheville basin. No Brown-headed Cowbirds were observed in gaps or controls. Unpublished data indicate that parasitism of artificial ground nests did not occur, and predation rates did not differ between gaps and controls. Juvenile birds and other evidence of breeding were observed more often in gaps than in controls, suggesting that gaps attract bird families for foraging and provide microsites that attract breeding pairs. Gap size was positively correlated with bird density, species richness, and diversity. This study suggests that small openings and interior edge habitat created by treefall gaps within a forested matrix do not adversely affect breeding birds as measured by the abundance of individual species or community indices. We suggest that canopy gaps increase avian diversity at a landscape scale by providing habitat patches for some species that require young, second-growth forest, and serve as magnets for recruitment and foraging. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Gaps; Southern Appalachian birds; Natural disturbance and birds; Breeding bird diversity

1. Introduction

Natural disturbance that causes partial or complete death of one or many trees is an important agent for creating habitat heterogeneity in most forest types. In the southern Appalachians, gaps <400 m^2 have been

* Corresponding author. Tel.: +1-828-667-5261; fax: +1-828-667-9097.
E-mail address: kgreenberg@fs.fed.us (C.H. Greenberg).

0378-1127/01/$ – see front matter © 2001 Elsevier Science B.V. All rights reserved.
PII: S0378-1127(00)00631-9

widely cited as a dominant mechanism for tree regeneration (Runkle, 1982; Lorimer, 1989). However, natural disturbances vary in type and intensity (Pickett and White, 1985), creating a gradient in size, number of canopy trees that remain standing, and discreteness of gap boundaries (Greenberg and McNab, 1998). Prior to the landscape-scale impact of humans on habitat availability and landscape configuration, some bird species required forest openings at different scales for their persistence (Newbold and Buehler, 2000).

Forest gaps attract many bird species by providing superior foraging habitat to closed canopy forest. Increased primary productivity caused by higher light levels in gaps creates greater vegetation density and structural heterogeneity, higher density of insects, and increased fruit production (Blake and Hoppes, 1986; Martin and Karr, 1986; Noss, 1991). The relationship between food resources and bird abundance in temperate (Blake and Hoppes, 1986; Martin and Karr, 1986) and tropical (Willson et al., 1982; Levey, 1988) forest gaps has been established for spring and fall migrating birds, but few studies specifically address the influence of forest gaps on breeding bird assemblages.

Fragmentation of continuous, closed canopy forest reduces habitat patch size and increases edge habitat. This can reduce habitat suitability for forest interior species and decrease the reproductive success of some bird species in some regions due to higher levels of nest parasitism and predation (Lynch, 1987; Thompson et al., 1995). The influence of forest fragmentation on breeding success is closely linked to the landscape context (Suarez et al., 1997; Thompson et al., 1995) and edge characteristics (Suarez et al., 1997). Edge-associated nest predation and parasitism occur less frequently within a forested landscape matrix than within an agricultural context where nest predators and Brown-headed Cowbirds (*Molothrus ater*) are well established (see Thompson et al., 1995). Most studies of forest fragmentation address large-scale fragmentation, using isolated woodlots or agriculturally induced edge as study topics. "Perforation" (Forman, 1997) of continuous forest by treefall gaps creates small patches of interior edge that differ from other edge types in size and context. Yet, few studies have addressed how small forest openings, and particularly how canopy gaps created by natural disturbance affect breeding birds in temperate regions (Annand and Thompson, 1997; Kilgo et al., 1999; Robinson and Robinson, 1999).

Several species require young, second-growth forest. However, patch-size requirements vary. Indigo Buntings (*Passerina cyanea*) and Eastern Towhees (*Pipilo erythrophthalmus*) are "area generalists" that breed in young, second-growth patches as small as treefall gaps. Others, such as Hooded Warblers (*Wilsonia citrina*), are associated with large forested areas that include internal patches of early successional habitat such as occurring within treefall gaps. Yellow-breasted Chats (*Icteria virens*), Prairie Warblers (*Dendroica discolor*), and Chestnut-sided Warblers (*Dendroica pennsylvanica*) require larger openings (Thompson et al., 1995; Rudnicky and Hunter, 1993; Lanham, 1997; Lanham and Guynn, 1998; Robinson and Robinson, 1999). Hence, the size and structure of treefall gaps could affect species composition of breeding birds that use young, second-growth habitat.

The composition of breeding bird assemblages might be expected to differ between gaps and adjacent closed-canopy controls having significant differences in vegetation structure and (likely) resource abundance. However, gap size and the presence of a partial canopy within gaps could temper the contrast. We hypothesized that forest gaps and adjacent closed-canopy forest would differ in bird density, richness, and diversity. We also hypothesized that some species would differ in relative abundance between gaps and controls, and that differences would be associated with microsite availability and habitat requirements. Finally, we examine the relationship between gap size and breeding bird density, richness, and diversity.

2. Methods

This study was conducted on the Bent Creek Experimental Forest, a 2500 ha watershed in Asheville, NC. Elevation ranges from 700 to 1070 m. Annual precipitation averages 800 mm and is evenly distributed year round. Winters are short and mild, and summers are long and warm. Forests are 80–120 years old, and prior to Hurricane Opal there were no major natural gaps other than those caused by single-tree death. Common tree species on xeric sites include

scarlet oak (*Quercus coccinea*), chestnut oak (*Q. prinus*), black oak (*Q. velutina*), blackgum (*Nyssa sylvatica*), sourwood (*Oxydendrum arboreum*), and occasional pines. Tulip poplar (*Liriodendron tulipifera*) and northern red oak (*Q. rubra*) dominate on moist slopes and coves. Red maple (*Acer rubrum*), hickory (*Carya* spp.), dogwood (*Cornus florida*) and white oak (*Q. alba*) are common throughout (McNab, 1996).

We randomly selected 12 treefall gaps that were ≥0.1 ha in size and had ≥6 fallen trees. Study gaps ranged in size from 0.1 to 1.2 ha in size, and were created in October 1995 by remnant wind associated with Hurricane Opal. Each gap was paired with an adjacent (25–100 m apart), closed-canopy control site ($n = 12$). Distance between gap-control pairs ranged from 0.43 to 4.55 km. We randomly placed five 15-m line transects in each gap and control site to determine percent cover of shrubs, brushpiles (e.g., fallen tree canopies), coarse woody debris (≥12.5 cm diameter at transect), and pit and mound microtopography created by uprooted trees. Shrub height was measured at the beginning, middle, and end of each transect. Live tree and snag basal area (BA) were calculated from diameter at breast height (DBH) measurements of all trees ≥12.5-cm DBH, measured at all study sites in fixed, rectangular plots ranging from 0.96 to 0.20 ha, depending on gap size and shape. Canopy cover was estimated using a spherical densitometer at five equidistant points spaced at least 10-m apart along transects. Gap area was quantified by using a Global Positioning System to delineate boundaries. For a detailed description of five study gaps see Greenberg and McNab (1998).

We surveyed breeding birds in gaps and control sites during 1997 and 1998 using strip transects of variable area (range 0.14–0.4 ha). Transects were established along the long-axis orientation of gaps, and extended ≤100 m depending on gap length. All birds seen or heard within 20 m of the centerline (40 m width) were recorded. We censused entire gaps if they were <40 m wide. Transect dimensions were approximately equal in gaps and paired controls. We censused by walking slowly (≥10 min per site) along the centerline and recording all birds seen or heard within transect boundaries. We also recorded whether birds were seen or heard, age and sex where possible, activity (e.g., singing, foraging, carrying nest material), location (e.g., in canopy, on ground, snag), and movement (into or out of gap). Flyovers were not included. Time spent conducting transects varied among visits and sites according to the level of bird activity and difficulty of terrain. We controlled for this variation by spending equivalent time in gaps and paired controls at a given visit. Each site was visited four times during 15 May–2 July in both years, and starting times were rotated between sunrise and 09:15 h EST.

The strip transect census method has an advantage over mist netting by allowing detections of breeding birds at all forest strata (versus birds occurring 0–3 m above ground). Most censuses were conducted by the authors (a few were conducted by a third, trained observer), and the same observer censused gap-control pairs on a given day to minimize observer bias. By using a narrow strip width we minimized the likelihood of counting the same bird twice and maximized the probability of detecting all birds. Finally, the width and length of strip transects could be adjusted, allowing us to sample small gaps and gather comparative data using same-sized transects in closed-canopy controls.

For statistical analyses we averaged transect values for percent cover and shrub height within sites. We performed paired t-tests to test for differences in habitat structural features between gaps and controls. Percentage data were square-root arcsine transformed for paired t-tests. We averaged bird density over visits (4 per year) within each site and divided by the transect area of that site to calculate the mean number of birds per hectare per site ($n = 12$ sites per treatment per year). Species diversity was calculated using the Shannon–Weiner index (H') (Zar, 1984) for each site visit, and averaging index values over visits. We defined species richness as the total number of species detected within sites both years. We computed Horn's index of community similarity (Horn, 1966) to compare bird assemblages in gaps and controls.

We assigned each bird species to a nesting (ground-, shrub-, cavity-, and canopy-nesters) and foraging (aerial-, bark-, canopy-, ground-, hawking-, and shrub-foraging) guild (aerial-foragers were excluded from analyses due to low sample size) (Hamel, 1992). Two-way ANOVA was used to test for differences among treatment, years, and treatment × year

interactions on bird density (individual species, total, and within nesting or foraging guilds), species richness, and Shannon's diversity index. In every case, effects of year and treatment × year were not significant ($P > 0.10$). Therefore, we averaged density (total and within nesting and foraging guilds) and diversity data from 1997 and 1998, such that site ($n = 12$ per treatment) was the replicate unit, and tested for differences between gaps and controls using paired t-tests. We tested for treatment differences in density for species having a mean density (averaged over all visits) of ≥ 0.20 per ha in gaps or controls, using log-likelihood ratio G-tests (Zar, 1984) with a 1:1 ratio as our expected value.

We performed simple linear regression using gap size as the independent variable, and bird density, richness, and diversity as dependent variables. To ensure that these relationships were not biased by our census method (because we also tended to spend more time in gaps with higher bird activity), we compared regressions in gaps and controls using the total number of minutes spent within sites as the independent variable and bird density, richness, and diversity as dependent variables. Significance is reported at the $P < 0.10$ level.

3. Results

The density of breeding birds was higher in gaps than in adjacent controls ($t = 4.02$, d.f. $= 11$, $P = 0.0020$). Total species richness was higher ($t = 2.17$, d.f. $= 11$, $P = 0.0528$) but diversity was similar in gaps and controls ($t = 0.15$, d.f. $= 11$, $P = 0.8817$) (Fig. 1). Horn's index indicated that the similarity of breeding bird assemblages between gaps and controls was high (0.781, where 0.0 indicates no shared species, and 1.0 indicates identical assemblages).

Several "area generalist" species associated with young, second-growth forest, including Carolina Wrens, Indigo Buntings, and Eastern Towhees, and gap-associated Hooded Warblers, were more abundant in gaps than in controls (Table 1). Among forest interior species only Ovenbirds (*Seiurus aurocapillus*) were more abundant in controls. Densities of other interior species, including Red-eyed Vireos, Scarlet Tanagers, and others, were similar in both; Worm-eating Warblers were more abundant in gaps. White-breasted Nuthatches and Red-bellied Woodpeckers, both cavity-nesters and bark-foragers, were more common in gaps than in controls. Nest predators

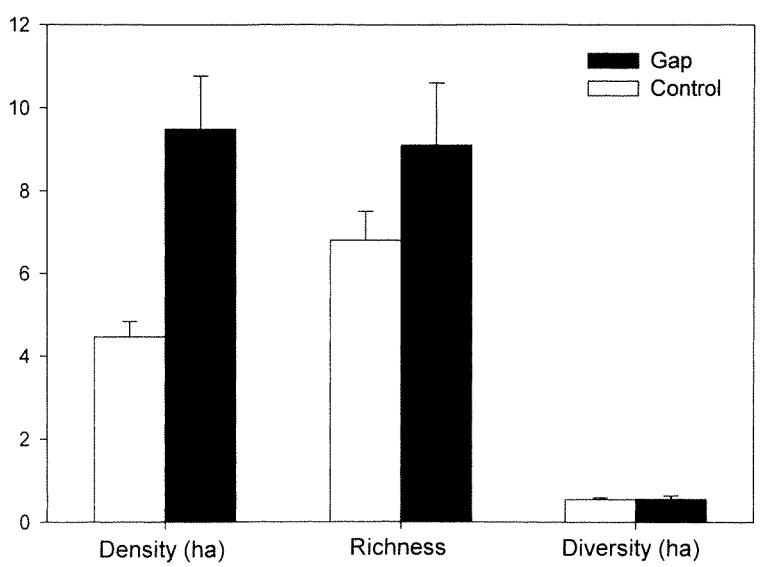

Fig. 1. Mean (±S.E.) density (per ha) (species $P = 0.0020$), richness ($P = 0.0528$) and Shannon's diversity index ($P = 0.8817$) of breeding birds in small, incomplete gaps created in 1995 by hurricane-related wind disturbance ($n = 12$) and closed canopy forest (controls) ($n = 12$) at the Bent Creek Experimental Forest, Asheville, NC.

Table 1
Frequency (presence/absence at each site, out of a total of 12 sites per treatment) and mean density (±S.E.) (averaged over all visits) of breeding birds per hectare in gaps created in 1995 by hurricane-related wind disturbance ($n = 12$) and adjacent closed canopy forest (controls) ($n = 12$) at the Bent Creek Experimental Forest, Asheville, NC

Species (code)[a]	Frequency (gap/control)	Treatment (No./ha)		G	P-value
		Gap	Control		
Ruffed Grouse (GG) *Bonasa umbellus*	1/0	0.03 ± 0.03	0.00 ± 0.00	N/A	N/A
Yellow-billed cuckoo (CT) *Coccyzus americanus*	0/1	0.00 ± 0.00	0.03 ± 0.03	N/A	N/A
Ruby-throated Hummingbird (AT) *Archilochus colubris*	5/1	0.22 ± 0.09	0.05 ± 0.05	N/A	N/A
Northern Flicker (BC) *Colaptes auratus*	1/0	0.05 ± 0.05	0.00 ± 0.00	N/A	N/A
Pileated Woodpecker *Dryocopus pileatus*	1/1	0.09 ± 0.09	0.04 ± 0.04	N/A	N/A
Red-bellied Woodpecker (BC) *Melanerpes carolinus*	5/1	0.38 ± 0.19	0.04 ± 0.04	31.18	<0.001
Downy Woodpecker (BC) *Picoides pubescens*	4/2	0.22 ± 0.11	0.06 ± 0.04	N/A	N/A
Hairy Woodpecker (BC) *Picoides villosus*	5/4	0.20 ± 0.08	0.15 ± 0.07	N/A	N/A
Eastern Wood Peewee (HT) *Contopus virens*	4/1	0.20 ± 0.10	0.03 ± 0.03	N/A	N/A
Great Crested Flycatcher (HC) *Myiarchus crinitus*	0/3	0.00 ± 0.00	0.15 ± 0.08	N/A	N/A
American Crow (GT) *Corvus brachyrhynchos*	2/1	0.37 ± 0.27	0.03 ± 0.03	N/A	N/A
Blue Jay (CT) *Cyanocitta cristata*	5/4	0.14 ± 0.07	0.18 ± 0.08	N/A	N/A
Carolina Chickadee (CC) *Poecile carolinensis*	3/2	0.19 ± 0.11	0.06 ± 0.04	N/A	N/A
Tufted Titmouse (CC) *Baeolophus bicolor*	4/3	0.49 ± 0.29	0.26 ± 0.15	7.06	<0.005
White-breasted Nuthatch (BC) *Sitta carolinensis*	5/4	0.27 ± 0.11	0.14 ± 0.06	4.13	<0.05
Carolina Wren (SC) *Thyrothorus ludovicianus*	10/2	1.94 ± 0.58	0.06 ± 0.04	222.80	<0.001
Blue-gray Gnatcatcher (CT) *Polioptila caerulea*	3/4	0.16 ± 0.09	0.23 ± 0.11	1.09	<0.50
Wood Thrush (GS) *Hylocichla mustellina*	1/1	0.10 ± 0.10	0.07 ± 0.07	N/A	N/A
Yellow-throated Vireo (CT) *Vireo flavifrons*	1/1	0.03 ± 0.03	0.03 ± 0.03	N/A	N/A
Red-eyed Vireo (CT) *Vireo olivaceus*	11/11	1.03 ± 0.18	1.10 ± 0.19	0.25	<0.75
Solitary Vireo (CT) *Vireo solitarius*	6/4	0.47 ± 0.18	0.23 ± 0.12	8.32	<0.005
Pine Warbler (CT) *Dendroica pinus*	1/2	0.05 ± 0.05	0.07 ± 0.05	N/A	N/A
Black-throated Green Warbler (CT) *D. virens*	1/1	0.03 ± 0.03	0.05 ± 0.05	N/A	N/A
Worm-eating Warbler (SG) *Helmitheros vermivora*	2/4	0.33 ± 0.26	0.19 ± 0.09	4.01	<0.05
Black-and-white Warbler (BT) *Mniotiltia varia*	4/1	0.14 ± 0.06	0.05 ± 0.05	N/A	N/A
Northern Parula Warbler *Parula americana*	1/0	0.10 ± 0.10	0.00 ± 0.00	N/A	N/A
Ovenbird (GG) *Seiurus aurocapillus*	4/9	0.28 ± 0.16	0.57 ± 0.13	10.00	<0.005
Hooded Warbler (SS) *Wilsonia citrina*	6/3	0.42 ± 0.16	0.20 ± 0.13	8.25	<0.005
Scarlet Tanager (CT) *Piranga olivacea*	5/9	0.46 ± 0.22	0.38 ± 0.07	0.82	<0.90
American Goldfinch (ST) *Carduelis tristis*	1/0	0.07 ± 0.07	0.00 ± 0.00	N/A	N/A
Slate-colored Junco (GG) *Junco hyemalis*	1/0	0.04 ± 0.04	0.00 ± 0.00	N/A	N/A
Indigo Bunting (SS) *Passerina cyanea*	5/1	0.53 ± 0.23	0.04 ± 0.04	52.08	<0.001
Eastern Towhee (GS) *Pipilo erythrophthalmus*	3/0	0.44 ± 0.34	0.00 ± 0.00	60.33	<0.001

[a] The first letter of each species code indicates foraging guild (primary foraging site) (A: aerial; B: bark; C: canopy; G: ground; H: hawking; S: shrub). The second letter indicates nesting guild (usual location of nest) (C: cavity; G: ground; S: shrub; T: tree).

(American Crows and Blue Jays (*Cyanocitta cristata*) combined) also were more abundant in gaps ($G = 13.06$, $P < 0.001$).

Eighteen juveniles of seven species including Carolina Wren (*Thyrothorus ludovicianus*), Carolina Chickadee (*Poecile carolinensis*), Tufted Titmouse (*Baeolophus bicolor*), American Crow (*Corvus brachyrhynchos*), Hooded Warbler, Eastern Towhee, and Scarlet Tanager (*Piranga olivacea*) were observed in seven gaps. In contrast, one Black-throated Green Warbler (*Dendroica virens*) juvenile was seen in one control site. Direct evidence of breeding observed in gaps (but not controls) included: a female Scarlet Tanager gathering fibrous rootlets from a tip-up mound; an aborted ground nest made of fibrous rootlet material; suspicious nest-guarding behavior by a Worm-eating Warbler (*Helmitheros vermivora*); food-carrying by a Red-bellied Woodpecker (*Melanerpes carolinus*), and mating by Indigo Buntings, Scarlet Tanagers, and Eastern Towhees.

Carolina Wrens were most frequently detected, and nearly always occurred in gaps. Of 47 recorded observations of Carolina Wren location, 30% were associated with brushpiles, 40% with open ground, 17% with the shrub layer, 11% with tip-up mounds, and 2% with snags.

Cavity-nesters ($t = 4.22$, d.f. $= 11$, $P = 0.0014$), shrub-nesters ($t = 2.00$, d.f. $= 11$, $P = 0.0713$), and canopy-nesters ($t = 1.83$, d.f. $= 11$, $P = 0.0942$) were more abundant in gaps than in controls, but the density of ground-nesters did not differ among treatments ($t = 0.23$, d.f. $= 11$, $P = 0.8212$) (Table 2). Shrub- and bark-foragers were more abundant in gaps than in controls, but the density of birds within canopy, ground, and hawking guilds did not differ between treatments (Table 2).

Breeding bird density ($F = 3.93$, d.f. $= 11$, $P = 0.0745$, $r^2 = 0.2823$) (Fig. 2a), species richness ($F = 11.55$, d.f. $= 11$, $P = 0.0068$, $r^2 = 0.5360$) (Fig. 2b), and diversity ($F = 11.64$, d.f. $= 11$, $P = 0.0006$, $r^2 = 0.5378$) (Fig. 2c) were positively correlated to gap size. The total amount of time (over

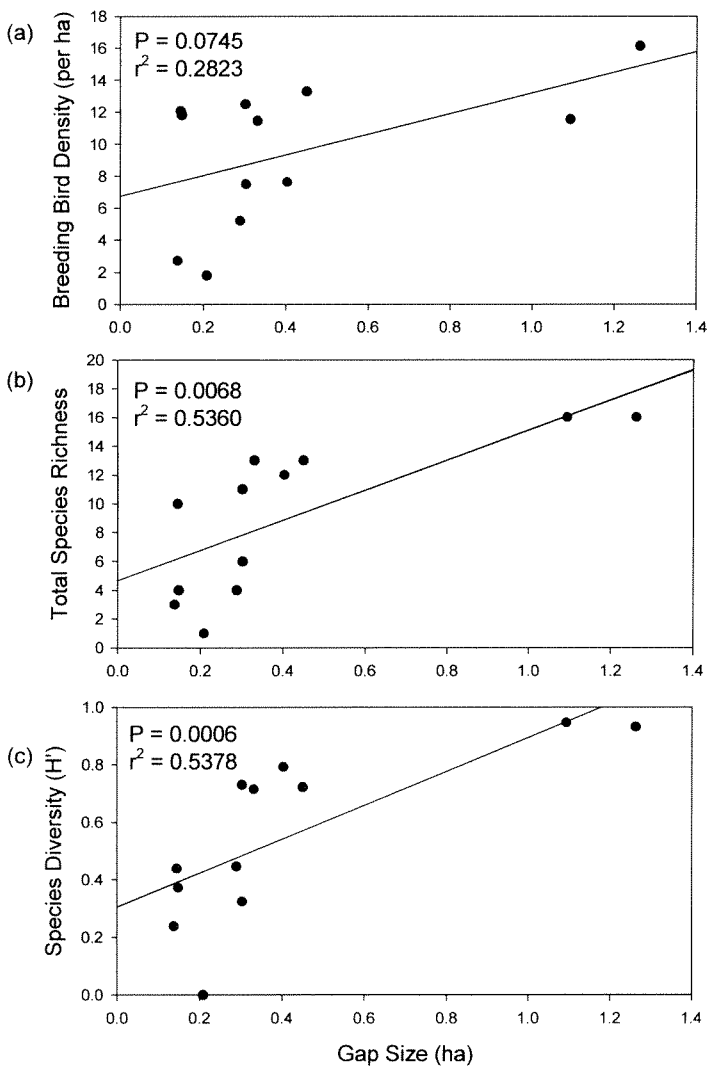

Fig. 2. Relationship between (a) density, (b) species richness, and (c) species diversity (H') of breeding birds and canopy gap size at the Bent Creek Experimental Forest, Asheville, NC.

Table 2
Mean density (±S.E.) (per ha) of breeding birds in four nesting guilds and five foraging guilds in small, incomplete gaps created in 1995 by hurricane-related wind disturbance ($n = 12$) and closed canopy forest (controls) ($n = 12$) at the Bent Creek Experimental Forest, Asheville, NC

Guild	Treatment (No./ha)		*P*-value
	Gaps	Controls	
Nesting			
Cavity	3.83 ± 0.68	0.95 ± 0.24	0.0014
Ground	0.68 ± 0.28	0.76 ± 0.16	0.8212
Shrub	1.50 ± 0.60	0.30 ± 0.14	0.0713
Tree	3.46 ± 0.49	2.45 ± 0.28	0.0942
Foraging			
Bark	1.36 ± 0.42	0.48 ± 0.15	0.0438
Canopy	3.15 ± 0.60	2.61 ± 0.30	0.4316
Ground	1.27 ± 0.50	0.66 ± 0.11	0.2888
Hawking	0.20 ± 0.10	0.17 ± 0.08	0.8705
Shrub	3.29 ± 0.68	0.48 ± 0.13	0.0015

the 2-year period) spent conducting gap transects (104.1 ± 7.8 min) did not differ significantly from time spent in control transects (96.0 ± 5.2 min) ($t = 0.86$, d.f. $= 22$, $P = 0.3978$). However, bird density, richness, and diversity were all positively correlated to time spent in gaps ($P \leq 0.0188$, d.f. $= 11$, $r^2 \geq 0.4395$) but not in controls ($P \geq 0.0130$, d.f. $= 11$, $r^2 \leq 0.2435$). This suggests that the relationship between gap size and bird density, richness, and diversity is not unduly biased by census technique.

Live tree BA and canopy cover were lower in gaps than in controls, but snag BA did not differ. Canopy cover was greater in controls than in gaps. Percent horizontal cover of shrubs was greater in gaps than in controls, but shrub height did not differ. Percent cover of brushpiles, coarse woody debris, tip-up mounds, and pits was higher in gaps than in controls (Table 3).

4. Discussion

The role that small-scale natural disturbance plays in the dynamics of southern Appalachian forests is well established (Lorimer, 1989). However, no studies have addressed the influence that canopy gaps have in the dynamics of southern Appalachian breeding bird assemblages. The dearth of information in this subject area is critical given the ecological importance of the region and concerns regarding songbird conservation. Although we found no significant difference in species diversity between gaps and adjacent, forested controls, a higher density and species richness of birds in gaps than in controls indicate that canopy gaps are "hotspots" of bird activity during the breeding season. Differences were due to the occurrence and greater abundance of species that require young, second-growth habitat, higher representation of birds within some nesting and foraging guilds, and more juvenile birds in gaps than in controls. These between-treatment differences, despite the close proximity (25–100 m apart) of gaps and paired controls, further indicate that canopy gaps serve as a magnet for recruitment and foraging.

Table 3
Structural characteristics (mean ± S.E.) of select habitat features in small, incomplete gaps created in 1995 by hurricane-related wind disturbance and closed canopy forest (controls) at the Bent Creek Experimental Forest, Asheville, NC

Structural feature	*N* (gap/control)	Treatment (No./ha)		*P*-value
		Gaps	Controls	
Live tree BA (m^2/ha)	11/12	11.7 ± 1.4	25.1 ± 1.2	0.0002
Snag BA (m^2/ha)	11/12	2.5 ± 0.5	2.1 ± 0.4	0.5102
% Canopy cover[a]	10/10	69.4 ± 2.1	89.6 ± 1.7	0.0002
% Shrub cover[a] (horizontal)	11/11	53.1 ± 5.6	24.2 ± 3.1	0.0003
Shrub height (m)	11/11	0.45 ± 0.05	0.35 ± 0.08	0.3352
% Brushpiles[a]	11/11	9.7 ± 1.6	2.1 ± 0.8	0.0037
% Coarse woody debris[a]	11/11	3.3 ± 0.5	0.4 ± 0.1	0.0001
%Tip-up mounds[a]	11/11	0.6 ± 0.2	0.0 ± 0.0	0.0180
% Pits[a]	11/11	2.1 ± 0.8	0.0 ± 0.0	0.0109

[a] Percentage data are presented as actual means but were square-root arcsine transformed for paired *t*-tests.

Several other studies (Willson et al., 1982; Blake and Hoppes, 1986; Martin and Karr, 1986; Levey, 1988; Kilgo et al., 1999) report higher densities of spring and fall migrating birds in gaps than closed-canopy forest. Higher bird abundance in gaps usually is attributed to higher productivity in these disturbed areas. Relative to undisturbed areas, forest gaps are often characterized by higher levels of primary productivity, and consequently, vegetative structural complexity, and fleshy fruit production (Blake and Hoppes, 1986; Martin and Karr, 1986; Levey, 1988). Such productive, structurally complex areas may attract breeding birds by providing better foraging and nesting habitat (Blake and Hoppes, 1986; Noss, 1991), and may be especially important for fledglings from adjacent mature-forest habitats (Anders et al., 1998; Vega Rivera et al., 1998).

Breeding birds may be attracted to different or additional gap attributes than migrating birds. In the southern Appalachians fleshy fruit is scarce during the breeding season (May and June) (Greenberg, unpublished data). Other studies suggest that arthropods, a critical source of protein for breeding and juvenile birds, are more abundant in gaps than closed canopy forest (Blake and Hoppes, 1986; Martin and Karr, 1986) due to higher levels of primary productivity and coarse woody debris. Although snag densities were virtually equal between gap and control sites, tree damage associated with the creation of gaps by wind disturbance may provide an abundance of cavities. Dramatic differences in the abundance of horizontal shrub and brushpile cover, coarse woody debris, and tip-up mounds likely are responsible for the between-treatment differences in numbers of shrub nesters such as Carolina Wrens and Indigo Buntings, because these substrates provide nesting material and microsites. Smith and Dallman (1996) suggested that gaps facilitate territorial establishment of breeding males by giving them greater visibility and song projection, as well as clear territorial boundaries. We suggest that an abundance of arthropod foods, nesting material, microsites for nesting, and vegetative structure are the primary factors that attract breeding birds to forest gaps in the southern Appalachians.

Although our study focused on differences in breeding bird assemblages between gaps and controls at a local scale, our results suggest that canopy gaps within a forested matrix increase species diversity at a landscape scale. This is because of the addition or increased abundance of some early successional species within gaps, with no apparent decrease in forest interior birds. Newbold and Buehler (2000) also reported co-occurrence of forest interior and early successional species in tornado sites with a residual overstory.

In our study, the Ovenbird was the only forest-interior species that was more abundant in controls than in gaps. This corresponds with observations of Ovenbird response to artificially created gaps (Annand and Thompson, 1997; Robinson and Robinson, 1999) and two-age timber harvest (Annand and Thompson, 1997; Baker and Lacki, 1997). Robinson and Robinson (1999) reported lower densities of Red-eyed Vireos in "perforated" forest, whereas Annand and Thompson (1997) reported no difference. We detected no between-treatment differences in the abundances of Red-eyed Vireos, Scarlet Tanagers, or other forest-interior species with the exception of Worm-eating Warblers, which were more abundant in gaps. We suggest that forest-interior species are indifferent to small gaps that retain a partial canopy.

Indigo Buntings, Eastern Towhees, Carolina Wrens, and Hooded Warblers occurred primarily or exclusively in gaps, whereas species that require large patches of young, second-growth habitat such as Prairie Warblers, Chestnut-sided Warblers, and Yellow-breasted Chats were not recorded in any of our censuses. Similar responses by these species have been observed in other studies using artificially created gaps (Annand and Thompson, 1997; Robinson and Robinson, 1999). Prairie Warblers, Chestnut-sided Warblers (common at slightly higher elevations), and Yellow-breasted Chats are uncommon in the Asheville basin (S. Thompson and W. Alexander, personal communication), so our ability to draw conclusions on this issue is limited. We suggest however that the relatively small gaps in our study may not have been large enough to elicit habitation by these species. We suggest that small natural disturbances provide habitat or microsites for "area generalist" and gap-dependent species that breed in edge habitat or young, second-growth forest, and that they increase forest diversity at a landscape scale.

Higher levels of nest parasitism near edges of gaps $\geq$0.2 ha have been reported (Brittingham and Temple, 1983). Although we did not directly examine

reproductive success, an artificial ground-nest predation study conducted in 10 of our 12 study gaps and control sites indicates that predation rates did not differ between gaps and adjacent forested controls (Greenberg, unpublished data). Hence, the higher abundance of avian nest predators (American Crows and Blue Jays) in gaps may not be biologically significant. Although Brown-headed Cowbirds are present in open and agricultural habitats within the Asheville area (including the campus area of the Bent Creek Experimental Forest), we observed no evidence of parasitism of artificial nests (Greenberg, unpublished data), nor saw cowbirds within the study sites.

We found positive species–area and density–area relationships within forest gaps. This relationship also has been reported for group-selection treatments in southern bottomland hardwood forests (Kilgo et al., 1999; Moorman, 1999) and wildlife openings in Illinois deciduous forests (Overcash and Roseberry, 1987). Higher light levels and greater surface area with high arthropod density and structural complexity in large gaps could contribute to this response. Larger gaps also are created by a greater number of fallen trees, providing microsites such as brushpiles and tip-up mounds, which clearly attract such species as the Carolina Wren. A minimum gap size may be necessary to provide young, second-growth conditions required even by area generalists.

5. Conclusions

In our forested study area that is perforated by treefall gaps, we detected none of the negative effects typically associated with forest fragmentation. We surmise that from a landscape perspective, gaps created in the Bent Creek Experimental Forest may simply act as early-successional discontinuities that provide habitat for some area generalist species, but which are too small to accommodate species that need large patches of young, second-growth forest. Likewise, although we did not compare our study area to one without treefall gaps, our data suggest that treefall gaps are too small, incomplete, and embedded too deeply within an extensive mature forest matrix to negatively affect forest-interior birds. Nonetheless, these small, regenerating patches are vital, because they do act to change the functional role of forest habitat by providing areas that are potentially more productive for some species foraging and nesting. We suggest that the size, structure, and landscape context of canopy gaps contribute to the magnitude of this function.

Acknowledgements

This work was supported by the USDA Forest Service, Southern Research Station, Bent Creek Experimental Forest. We thank Tracy Roof, Lindsay Smith, and David Johnson for field assistance. Douglas J. Levey, Scott F. Pearson, and three anonymous reviewers reviewed earlier versions of this manuscript. Paul Smith and Bernard Parresol provided useful editorial comments and statistical review.

References

Anders, A.D., Faaborg, J., Thompson III, R.R., 1998. Postfledging dispersal, habitat use, and home-range size of juvenile wood thrushes. Auk 115, 349–358.

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

Baker, M.D., Lacki, M.J., 1997. Short-term changes in bird communities in response to silvicultural prescriptions. Forest Ecol. Manage. 96, 27–36.

Blake, J.G., Hoppes, W.G., 1986. Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. Auk 103, 328–340.

Brittingham, M.C., Temple, S., 1983. Have cowbirds caused forest songbirds to decline? Bioscience 33, 31–35.

Forman, R.T.T., 1997. Land Mosaics: The Ecology of Landscapes and Regions. Cambridge University Press, Cambridge, UK

Greenberg, C.H., McNab, W.H., 1998. Forest disturbance in hurricane-related downbursts in the Appalachian mountains of North Carolina. Forest Ecol. Manage. 104, 179–191.

Hamel, P.B., 1992. The land manager's guide to birds of the south. The Nature Conservancy. Southeastern Region, Chapel Hill, NC.

Horn, H.S., 1966. Measurement of overlap in comparative ecological studies. Am. Nat. 100, 419–424.

Kilgo, J.C., Miller, K.V., Smith, W.P., 1999. Effects of group-selection timber harvest in bottomland hardwoods on fall migrant birds. J. Field Ornithol. 70, 404–413.

Lanham, J.D., 1997. Attributes of avian communities in early-successional clearcut habitats in the mountains and upper piedmont of South Carolina. Ph.D. Dissertation. Clemson University, Clemson, SC.

Lanham, J.D., Guynn Jr., D.C., 1998. Habitat–area relationships of shrub–scrub birds in South Carolina. Southeastern Assoc. Fish Wildlife Agencies Proc., 52, 222-231.

Levey, D.J., 1988. Tropical wet forest treefall gaps and distributions of understory birds and plants. Ecology 69, 1076–1089.

Lorimer, C.G., 1989. Relative effects of small and large disturbances on temperate hardwood forest structure. Ecology 70, 565–567.

Lynch, J.F., 1987. Responses of breeding bird communities to forest fragmentation. In: Saunders, D.A., Arnold, G.W., Burbidge, A.A., Hopkins, A.J.M. (Eds.), Nature Conservation: The Role of Remnants of Native Vegetation. Surrey Beatty and Sons Limited in association with CSIRO and CALM, pp. 123–140.

Martin, T.E., Karr, J.R., 1986. Patch utilization by migrating birds: resource oriented? Ornis Scand. 17, 165–174.

McNab, W.H., 1996. Classification of local- and landscape-scale ecological types in the Southern Appalachian Mountains. Environ. Monit. Assess. 39, 215–229.

Moorman, C.E., 1999. Relationships between artificially created gaps and breeding birds in a southeastern bottomland forest. Ph.D. Dissertation. Clemson University, Clemson, SC.

Newbold, C.D., Buehler, D.A., 2000. Effects of tornado and clearcut disturbances on breeding birds. J. Wildlife Manage., in press.

Noss, R.F., 1991. Effects of edge and internal patchiness on avian habitat use in an old-growth Florida hammock. Nat. Area J. 11, 34–47.

Overcash, J.L., Roseberry, J.L., 1987. Evaluation of Shawnee National Forest Wildlife Openings. Cooper. Wildlife Research Laboratory, Southern Illinois University, Carbondale.

Pickett, S.T.A., White, P.S. (Eds.), 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando, FL.

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

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.

Runkle, J.R., 1982. Patterns of disturbance in some old growth mesic forests of eastern North America. Ecology 63, 1533–1546.

Smith, R., Dallman, M., 1996. Forest gap use by breeding Black-throated Green Warblers. Wilson Bull. 108, 588–591.

Suarez, A.V., Pfennig, K.S., Robinson, S.K., 1997. Nesting success of a disturbance-dependent songbird on different kinds of edges. Conserv. Biol. 11, 928–935.

Thompson III, F.R., Probst, J.R., Raphael, M.G., 1995. Impacts of silviculture: overview and management recommendations. In: Martin, T.W., Finch, D.M. (Eds.), Ecology and Management of Neotropical Migratory Birds. Oxford University Press, New York, pp. 201–219.

Vega Rivera, J.H., Rappole, J.H., McShea, W.J., Haas, C.A., 1998. Wood thrush post-fledgling movements and habitat use in northern Virginia. Condor 100, 69–78.

Willson, M.F., Porter, E.A., Condit, R.S., 1982. Avian frugivore activity in relation to forest light gaps. Carib. J. Sci. 18, 1–4.

Zar, J.H., 1984. Biostatistical Analysis, 2nd Edition. Prentice-Hall, Englewood Cliffs, NJ.