Avifauna response to hurricanes: regional changes in community similarity

CHADWICK D. RITTENHOUSE*, ANNA M. PIDGEON*, THOMAS P. ALBRIGHT*, PATRICK D. CULBERT*, MURRAY K. CLAYTON†, CURTIS H. FLATHER‡, CHENGQUAN HUANG§, JEFFREY G. MASEK¶ and VOLKER C. RADELOFF*

*Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA, †Department of Statistics, University of Wisconsin-Madison, 1300 University Avenue, Madison, WI 53706, USA, ‡USDA Forest Service, Rocky Mountain Research Station, 2150 Centre Avenue, Building A, Fort Collins, CO 80526-1891, USA, §Department of Geography, University of Maryland, College Park, 2181 LeFrak Hall, MD 20742, USA, ¶Biospheric Sciences, NASA Goddard Space Flight Center, Greenbelt, MD 20771, USA

Abstract

Global climate models predict increases in the frequency and intensity of extreme climatic events such as hurricanes, which may abruptly alter ecological processes in forests and thus affect avian diversity. Developing appropriate conservation measures necessitates identifying patterns of avifauna response to hurricanes. We sought to answer two questions: (1) does avian diversity, measured as community similarity, abundance, and species richness, change in areas affected by hurricane compared with unaffected areas, and (2) what factors are associated with the change(s) in avian diversity? We used North American Breeding Bird Survey data, hurricane track information, and a time series of Landsat images in a repeated measures framework to answer these questions. Our results show a decrease in community similarity in the first posthurricane breeding season for all species as a group, and for species that nest in the midstory and canopy. We also found significant effects of hurricanes on abundance for species that breed in urban and woodland habitats, but not on the richness of any guild. In total, hurricanes produced regional changes in community similarity largely without significant loss of richness or overall avian abundance. We identified several potential mechanisms for these changes in avian diversity, including hurricane-induced changes in forest habitat and the use of refugia by birds displaced from hurricane-damaged forests. The prospect of increasing frequency and intensity of hurricanes is not likely to invoke a conservation crisis for birds provided we maintain sufficient forest habitat so that avifauna can respond to hurricanes by shifting to areas of suitable habitat.

Keywords: abundance, biodiversity, birds, community similarity, hurricane, North American Breeding Bird Survey, richness, United States

Received 19 March 2009; revised version received 11 September 2009 and accepted 24 September 2009

Introduction

Studies characterizing avifaunal responses to climate change have largely focused on changes in spatial and temporal patterns of migration and nesting due to advanced phenology (Dunn & Winkler, 1999; Both & Visser, 2001; Marra *et al.*, 2005; Beaumont *et al.*, 2006; Thorup *et al.*, 2007; Monohan & Hijmans, 2008), as well as poleward shifts in breeding range (Thomas & Lennon, 1999; Brommer, 2004) or wintering range (Butler *et al.*, 2007; La Sorte & Thompson, 2007). Shifts in ranges are predicted to have dire implications for landbirds:

Correspondence: Chadwick D. Rittenhouse, tel. + 1 608 265 2228, fax + 1 608 262 9922, e-mail: cdrittenhous@wisc.edu

under a moderate scenario of warming (2.8 °C by 2100) approximately 400–550 species may go extinct within 90 years (Sekercioglu *et al.*, 2008). However, shifts in phenology and geographic range are only two potential outcomes of climate change. Recent observations and global change models suggest increases in the frequency and intensity of extreme climatic events such as hurricanes as well (Royer *et al.*, 1998; Goldenberg *et al.*, 2001; Webster *et al.*, 2005). Such disturbance events may abruptly alter ecological conditions and processes in forests and thus affect avian communities (Dale *et al.*, 2001), but our understanding of the effects of hurricanes and similar extreme events on avian communities is limited.

Hurricanes have direct effects on avian communities via mortality (Hooper *et al.*, 1990; Collazo *et al.*, 2003) and indirect effects via alteration of habitat (Wiley & Wunderle, 1993; Wunderle, 1995; Greenberg & Lanham, 2001). Hurricanes defoliate trees, break tree limbs and trunks, and uproot trees, altering forest structure and vegetation productivity in a spatially heterogeneous manner (Foster, 1988; Brokaw & Walker, 1991; Greenberg & McNab, 1998). Changes to vegetation conditions by hurricanes affect food availability (e.g., fruit, flowers, seeds, and insects), nest and roost sites, and in turn alter local avian species richness, abundance, or density (Askins & Ewert, 1991; Wauer & Wunderle, 1992; Tejeda-Cruz & Sutherland, 2005). These effects are known from site-specific studies, but it is not clear whether these changes in avian communities will manifest at larger spatial scales as well. For example, if birds are displaced from hurricane-damaged areas then local declines in richness or abundance may simply reflect a redistribution of birds to other areas and not mortality.

To determine the extent of hurricane effects on birds, it is necessary to look for changes in avian diversity in adjacent, ecologically similar areas that have not been affected by hurricanes. Identification of hurricane-disturbed and nondisturbed areas is possible with satellite and aerial imagery: forest cover change analyses can be used to map the extent of forest disturbance and normalized difference vegetation index (NDVI; Tucker, 1979; Justice *et al.*, 1985) can be used to quantify the change in vegetation productivity (Ramsey *et al.*, 1997; Kovacs *et al.*, 2001; Cooke *et al.*, 2007). Using long-term data from the North American Breeding Bird Survey (BBS) (Sauer & Fallon, 2008) and a time series of satellite imagery, we examined the effects of hurricanes on avian communities across a broad region.

In this study we sought to answer two questions: (1) does avian diversity, measured as community similarity, abundance, and richness, change in areas affected by hurricanes compared with unaffected areas, and (2) what land cover factors are associated with the change(s) in avian diversity? Our *a priori* expectation was that species with similar behavioral traits or functional roles would respond similarly to hurricanes. Therefore, we grouped species into behavioral or functional guilds according to their migratory habit (neotropical migrant, short-distance migrant, or resident), breeding habitat (e.g., grassland, shrubland, water, woodland, urban), nest location (on or near the ground, or midstory-to-canopy), and nest type (cavity, open-cup) (Rappole, 1995; Peterjohn & Sauer, 1999; Pidgeon *et al.*, 2007). We did not classify nest location and nest type for waterfowl or raptors. See supporting information Table S1 for scientific names and guild memberships. Although intermediate frequency or intensity of

disturbance may increase diversity (Connell, 1978; Huston, 1979; Kondoh, 2001), changes in structure due to habitat disturbance decrease avian species richness and abundance (Schmiegelow *et al.*, 1997; Boulinier *et al.*, 2001; Rodewald & Yahner, 2001). Therefore, we expected community similarity, abundance, and richness to decrease for most guilds due to loss of canopy cover and changes in vegetation structure caused by hurricanes. We expected greater declines for the resident guild as residents are affected by hurricanes at the time of the event and during the winter, whereas short-distance and neotropical migrant species may avoid the hurricane or the winter season effect by migrating. Similarly, we expected greater declines for woodland species than grassland or urban species due to loss of forest structure. Three exceptions to our expectations included shrubland species, ground- or low-nesting species, and cavity-nesting species. For these guilds, we expected an increase in abundance and richness following hurricanes due to increased understory vegetation structure and potential nest sites (i.e., snags for cavity-nesting species) following hurricane disturbance.

Methods

Geographic and temporal information about avian community similarity, abundance, and richness

We used North American BBS data to quantify community similarity, abundance and richness for each guild by year for the period 1984–2005 (Sauer & Fallon, 2008). The BBS is a roadside survey of >4000 routes, each 39.4 km long, in the United States and Canada. Each year volunteers record the number of individual birds, by species, seen or heard during 50 3-min point counts conducted at 0.8 km intervals along each route.

A concern with count data such as the BBS is that species may be present on a route yet not detected (Thompson, 2002). Nondetection of species that are present can introduce bias, such as underestimation of species richness and abundance in communities with many rare species, and affect variance estimates. We did not explicitly account for nondetection of species in the community similarity and abundance analyses as methods to do so are difficult to implement retroactively for the BBS (Johnson, 2008). However, we followed standard protocols for minimizing the potential for other sources of bias in BBS analyses, including inclement weather conditions during surveys, routes surveyed outside of the start and finish time standards or breeding season window for a given location (Bystrak, 1981; Robbins *et al.*, 1986), and routes surveyed by first year observers (Kendall *et al.*, 1996). We also removed routes lacking at least one survey before and after a hurricane,

routes experiencing multiple hurricanes such that we could not isolate at least five hurricane-free years preceding or following a hurricane event, and routes located outside of the five focal area boundaries (see 'Linking hurricane disturbance to bird response'). We omitted unidentified species that could not be reliably assigned to a species based on geographic location and grouped subspecies at the species level (e.g., northern flicker, yellow-rumped warbler, and dark-eyed juncos). Finally, all species with >30 route-year observations, meeting the above requirements, were included in the analysis. The resulting data consisted of counts of individuals for each species by route, grouped by guild, which we used for the community similarity, abundance, and richness analyses.

We determined community similarity by guild for each route using the formula:

$$\frac{\sum_i^n p_i q_i}{\sum_i^n (p_i - q_i)^2 + \sum_i^n p_i q_i},$$

where p_i is the proportional abundance of species i in community p, q_i is the proportional abundance of species i in community q, and n is the pooled count of species observed in communities p and q (Yue & Clayton, 2005). The Yue–Clayton index calculates similarity based on species proportions of both shared and non-shared species among two communities. In this case, p represents abundance for the community of a route in year t and q represents abundance for the community of the same route in year $t + 1$. The range of this index is 0–1, with 0 indicating completely different communities and 1 indicating identical communities with respect to species richness and species proportion. Thus, the Yue–Clayton index is sensitive to changes in three common measures of biodiversity: richness, abundance, and evenness (Buckland *et al.*, 2005). When the species proportions are uniform, the Yue–Clayton index is identical to Jaccard's index (Yue & Clayton, 2005).

We estimated route-level richness, by year and guild, from the counts of individuals for each species using the program COMDYN (Hines *et al.*, 1999). COMDYN provides an adjusted estimate of species richness to account for differences in species detection probability by treating 10-stop segments along a BBS route as replicate samples of the bird community along the route.

Linking hurricane disturbance to bird response

We selected five focal areas along the Gulf Coast and Atlantic Coast of the United States based on the intersection of hurricane tracks and a time series of annual or biennial Landsat TM/ETM + imagery (30 m pixel size) for the period 1984–2005 (Huang *et al.*, 2009a) (Fig. 1). Each focal area was approximately 185 km × 185 km. Four Category 1 or greater hurricanes on the Saffir–Simpson scale, defined as sustained winds exceeding 119 km h^{-1}, made landfall within the focal areas during the study period. Hurricane Hugo made landfall in South Carolina on September 22, 1989 as a Category 4
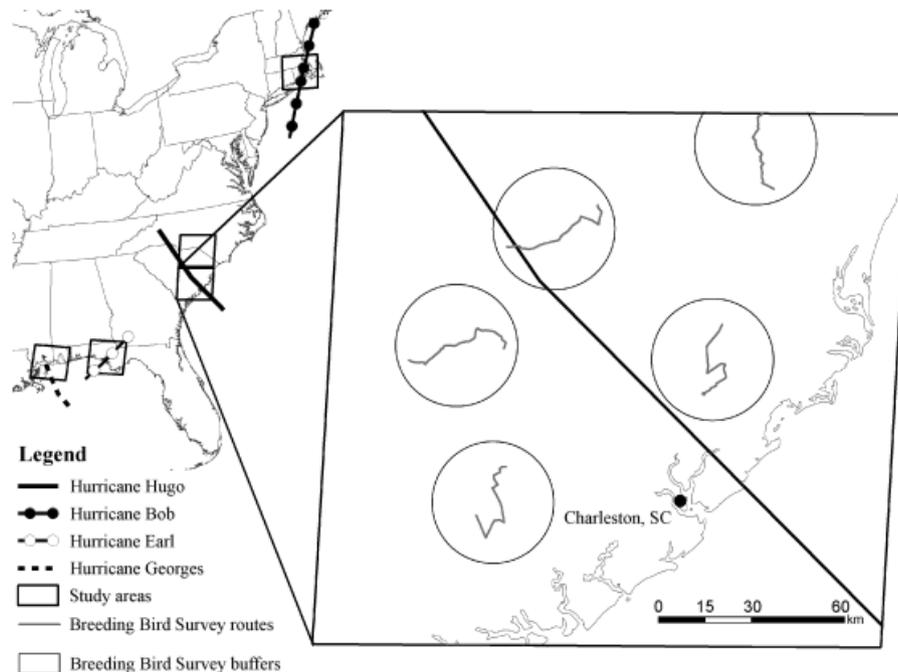
Fig. 1 Location of focal areas, hurricane tracks, and (inset) Breeding Bird Survey routes with corresponding 19.7 km buffers.

hurricane. Hugo persisted as a Category 1 hurricane through Charlotte, North Carolina, 320 km from the Atlantic Coast; therefore we included Hugo in two different focal areas. Hurricane Bob made landfall on August 19, 1991 on Rhode Island and continued through southeastern Massachusetts as a Category 2 hurricane. Hurricane Earl made landfall on September 3, 1998 as a Category 1 hurricane near Panama City, FL. Hurricane Georges made landfall on September 28, 1998 near Biloxi, Mississippi as a Category 2 hurricane.

Land cover change was assessed using the time-series satellite imagery via per-pixel time series analysis. For each image in the time series, disturbed forest was identified using an integrated forest index (IFI), a forest change detection algorithm that quantified the probability of a pixel being a forest pixel based on spectral values (Huang *et al.*, 2008). We used the IFI and a vegetation change tracker algorithm to identify six land cover change classes for each image year: persistent forest, persistent nonforest, persistent water, disturbed forest, postdisturbance forest, and postdisturbance nonforest (Huang *et al.*, in press). Disturbed forest was synonymous with forest loss relative to the previous image. Postdisturbance forest and postdisturbance nonforest represented the return to forest or retention of nonforest cover, respectively, following disturbance. The magnitude of forest disturbance was characterized as the change in several spectral indices, including an integrated Z-score index, NDVI, and normalized burn ratio index. The accuracy of the forest disturbance maps was assessed for a stratified random sample of pixels and compared on a per-pixel basis with visual assessments of disturbance history (from the Landsat imagery) and postdisturbance land cover (from high-resolution aerial photography). The overall accuracy (diagonal of the error matrix) ranged from 78% to 87%, and the accuracy increased when multiple forest disturbance events were taken into account (Huang *et al.*, 2009b, Huang *et al.*, in press).

We used distance from a hurricane track to BBS route center and distance from BBS route center to the nearest coast as proxies for the magnitude of disturbance for nonforest, water, and postdisturbance nonforest land cover classes. We classified routes within 30 km of a hurricane track as high disturbances and routes 30–185 km from a hurricane track as low disturbances. The cutoff was based on data from Hurricane Katrina indicating that the heaviest disturbance in bottomland hardwood and hardwood pine stands occurred within 30 km of a hurricane track (>67% tree blowdown; Kupfer *et al.*, 2008).

For each BBS route within the focal areas, we quantified the proportion of each land cover class and the mean and standard deviation of vegetation productivity

within a 19.7 km radius circle (1/2 of route length) centered on the centroid of a minimum bounding rectangle encompassing the route (hereafter, circular landscape; Flather & Sauer, 1996; Pidgeon *et al.*, 2007). Defining the spatial extent of the observation unit on BBS route length would be a weak design if such an observation scale was ecologically irrelevant to birds. The population process that links the circular landscape to avian ecology is dispersal. Understanding and predicting the effects of landscape alteration on the biota must account for the dispersal characteristics of the target species (Turchin, 1998; Clobert *et al.*, 2001). Among birds, the most extensive movement takes place before an individual's first reproductive event and is termed natal dispersal (Greenwood, 1980; Sutherland *et al.*, 2000). We assume that natal dispersal distance is an index of the spatial extent over which populations integrate the effects of the landscape surrounding a BBS route. Our 19.7 km buffer radius approximates the median maximum natal dispersal distance of 31.0 km for 98 forest-associated North American landbirds (C.H. Flather, unpublished results) based on allometric relationships developed by Sutherland *et al.* (2000). We included in the analysis only routes for which >80% of the area of this circular landscape was located within a focal area.

Statistical analyses

Because the BBS data and satellite imagery consisted of multiple observations for the same BBS routes over time we used a mixed-effects model for repeated measures, with year as the repeated effect and route as the subject (random effect), to examine the effects of hurricanes on avian communities for all routes located within the five focal areas. We fit separate models for each response variable: guild community similarity, guild abundance (sum of abundance for all guild members), and guild richness. We applied a logarithmic transformation to the abundance response variable to meet assumptions of normality and homogeneity of variances.

We did not have sufficient route-year observations to fit a separate model for each hurricane or for hurricanes grouped by Saffir–Simpson hurricane category. Instead, we used a hurricane-centric definition of time to increase sample size and facilitate fitting models of multiple hurricanes simultaneously. That is, we defined 10 time periods such that Periods 1–5 corresponded to the 5 years preceding a hurricane, and Periods 6–10 the 5 years after a hurricane. All hurricanes occurred between the breeding seasons of Periods 5 and 6.

To assess change in avian diversity due to hurricanes (question 1), we tested for main effects of time (Period 1–Period 10) and distance to hurricane track (DistHurr

<30 km or DistHurr 30–185 km), as well as a time × distance to hurricane interaction term. An effect of hurricanes on avian diversity may manifest as a significant main effect of time when avian diversity changes following a hurricane. However, a significant effect of time may arise from changes in avian diversity preceding the hurricane as well. In these cases, we tested significance of pair-wise comparisons of time periods (e.g., Period 1 vs. Period 2) using a Tukey–Kramer adjustment for multiple comparisons. The clearest indication of an effect of hurricanes on avian diversity would be a significant interaction term indicating a differential effect of time near the hurricane track compared with away from the hurricane track. We conducted this analysis for all routes within the focal areas that met our selection criteria. We also determined whether the effects of hurricanes identified within the five focal areas were representative of the effects of hurricanes in the eastern United States by repeating the analysis for all BBS routes located within 185 km of a hurricane track. In both the focal areas analysis, and the broad-scale analysis, we included a random effect of observer to account for differences in detection ability among observers.

For routes located within the focal areas, we carried factors forward to the second analysis if guilds exhibited significant main effects or a significant interaction term. We did not continue analyses for guilds with no significant effects of time, distance to hurricane track, or the interaction term. To identify landscape factors associated with the changes in avian diversity within the five focal areas (question 2), we included all significant effects identified in the first analysis as well as the BBS route attributes of distance to coast, ecoregion (Bailey, 1995), vegetation productivity, and land cover class.

We used Akaike's Information Criterion (AIC) to determine which covariance structure was appropriate for the main effects model in the first analysis and for the initial model in the second analysis that contained all factors (Wolfinger, 1993, 1996). In the second analysis we used a backwards step-wise procedure, forcing retention of significant main effect(s) or the interaction term identified in the first analysis, to obtain a final model for each guild that contained factors with a P-value <0.05 (from a Type 3 test of fixed effects). We conducted all analyses using the MIXED PROCEDURE of SAS version 9.1 (SAS Institute 2002, Cary, NC, USA).

Results

Our study included 31 BBS routes, 13 routes within 30 km and 18 routes >30 km from a hurricane track, totaling 139 route-year observations. The average abundance across all species and all routes was 647.00 (SE 9.67) individuals per route for the period 1967–2005 (Table 1). The mean estimated species richness for all species as a group was 53.60 (SE 0.27) per route, with a maximum of 77 species. Among the migratory habit guilds, neotropical migrants had the highest average species richness while short-distance migrants had the highest average abundance. The urban guild had the greatest average abundance and the woodland guild

Table 1 Avian abundance and species richness across all routes ($n = 31$ routes) within the focal areas for 1967–2005

Guild	Abundance			Richness		
	Average	SE	Range	Average	SE	Range
All	647.00	9.67	241–2391	53.60	0.27	26–77
Migratory habit						
Neotropical migrants	230.77	4.42	59–1113	28.36	0.21	9–45
Short-distance migrants	255.42	4.69	78–917	15.03	0.08	7–21
Permanent residents	160.80	3.72	21–737	10.21	0.08	4–16
Breeding habitat						
Grassland	22.59	0.76	1–125	2.23	0.03	1–5
Shrubland	183.87	3.92	25–743	11.43	0.08	5–18
Urban	204.70	5.24	17–885	8.99	0.07	3–12
Water	37.54	1.54	1–358	4.55	0.11	1–21
Woodland	123.50	2.40	6–427	18.02	0.18	3–29
Nest type						
Cavity	107.54	2.02	11–435	10.62	0.08	5–18
Open-cup	347.18	4.93	87–1125	27.73	0.24	13–48
Nest location						
Ground- or low-nesting	158.99	3.44	17–717	13.16	0.10	5–21
Midstory or canopy	311.20	5.32	79–1001	24.00	0.20	12–37

Values are individuals (abundance) or number of species (richness) per route.

Table 2 Effects of time and distance to hurricane track on avian community similarity, abundance, and richness

Guild	Effect	Community similarity F-value*	Pr > F	Abundance F-value	Pr > F	Richness F-value†	Pr > F
All species	Time	2.56	**0.0143**	0.64	0.7609	2.87	**0.0051**
Migratory habit							
Neotropical migrants	Time	0.99	0.4597	2.42	**0.0163**	3.69	**0.0006**
	Distance	0.01	0.9266	3.06	*0.0910*	1.45	0.2376
Short-distance migrants	Time	2.07	**0.0457**	0.31	0.9696	0.42	0.9198
	Interaction	1.95	*0.0605*	1.02	0.4317	0.75	0.6630
Breeding habitat							
Grassland	Time	0.66	0.7423	2.50	**0.0132**	1.55	0.1440
	Interaction	0.96	0.4823	1.88	*0.0643*	1.66	0.1106
Shrubland	Time	3.14	**0.0035**	1.39	0.2041	0.82	0.6004
	Interaction	1.81	*0.0836*	0.65	0.7484	1.72	*0.0948*
Urban	Interaction	1.43	0.1936	2.63	**0.0096**	0.80	0.6211
Water	Time	1.16	0.3382	1.35	0.2212	1.75	*0.0892*
	Distance	4.64	**0.0398**	0.13	0.7230	0.00	0.9539
	Interaction	0.54	0.8379	1.79	*0.0802*	1.73	*0.0928*
Woodland	Interaction	1.03	0.4232	2.04	**0.0432**	0.65	0.7511
Nest type							
Open-cup	Distance	0.04	0.8483	1.68	0.2055	3.60	*0.0679*
Nest location							
Ground- or low nesting	Time	1.57	0.1435	1.31	0.2441	3.05	**0.0032**
	Interaction	2.10	**0.0425**	0.61	0.7874	1.03	0.4212
Midstory or canopy	Time	2.33	**0.0251**	0.46	0.8965	1.55	0.1440

Significant effects in bold ($P \leq 0.05$) or italics ($P \leq 0.10$) for emphasis. Values shown for guilds with at least one significant result; nonsignificant results omitted for clarity.

*df for time and interaction terms are 9, 62; df for distance term are 1, 29 for community similarity analyses.

†df for time and interaction terms are 9, 90; df for distance term are 1, 29 for abundance and richness analyses.

had the greatest average richness among the breeding habitat guilds. The grassland guild had the lowest average abundance and richness among all breeding habitat guilds. Among the nest location guilds, the midstory and canopy nesting guild had greater abundance and richness than the ground and low-nesting guild.

Changes in avian diversity due to hurricanes

In the focal areas analysis, we found significant effects of hurricanes on avian diversity that varied by guild but were not expressed solely in the interaction term as we expected. The strongest pattern we detected was an effect of time (Table 2) and a decrease in community similarity across all focal areas in the first posthurricane breeding season (Period 6) for all species and for the midstory and canopy-nesting guild (Fig. 2a and b). For all species as a group, the immediate posthurricane change in community similarity was driven by a mean decrease in abundance of 97 individuals per route (range 2–261) on 57% of routes (12 of 21) and a mean increase in species richness of 5.1 species per route

(range 0–17) on 67% of routes (14 of 21) (supporting information Fig. S1).

When placed within a historical context, the immediate posthurricane decrease in abundance observed for all species as a group constituted 15% of the average abundance for the period 1967–2005 (Table 1, supporting information Fig. S1). Similarly, for the midstory and canopy-nesting guild, the immediate posthurricane change in community similarity was driven by a mean decrease in abundance of 57.2 individuals per route (range 6–158), and a mean increase in species richness of 2.1 species per route (range 0–7) on 62% of routes (13 of 21) (supporting information Fig. S2). After the initial posthurricane declines in community similarity for all species as a group and the midstory and canopy-nesting guild, community similarity was similar in Periods 7–10, indicating that the changes that occurred in Period 6 persisted for at least 5 years posthurricane (Fig. 2a and b). We examined whether the posthurricane community became more similar to the prehurricane community over time by creating a composite prehurricane community from the average abundance by species for Periods 1–5 combined, and then calculating community
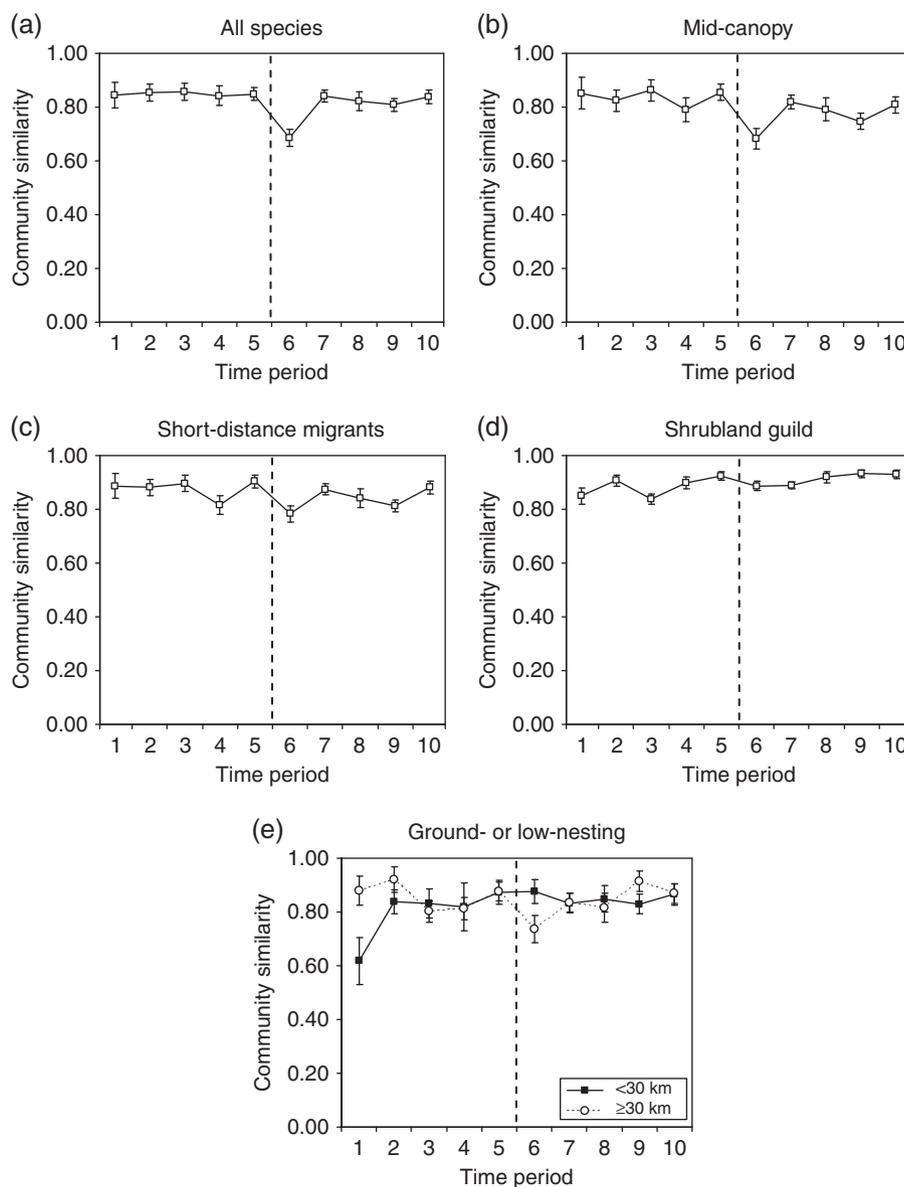
Fig. 2 Community similarity for avian guilds with a significant effect of time (a–d) or time × distance to hurricane track interaction (e). The hurricanes occurred between the breeding seasons of time periods 5 and 6, indicated by the dashed vertical line.

similarity for the composite community and each posthurricane period (6–10) individually (results not presented). Similarity to the prehurricane community for all species as a group and for the midstory and canopy-nesting guild was low for each period, confirming that the posthurricane community remained dissimilar to the prehurricane community for at least 5 years posthurricane.

Migratory habit. Contrary to our expectations, we found no significant effects of hurricanes on permanent residents. Among migratory habit guilds, the only significant effect was time (Table 2). Community

similarity for short-distance migrants declined in Period 4 (preceding the hurricane) and Period 6 (the first posthurricane breeding season; Fig. 2c). Neotropical migrant abundance and richness varied over time (Figs 3a and 4a); however, we do not attribute these changes to hurricanes as they are not confined to the posthurricane periods and are within the range of variation observed for the period 1967–2005 (Table 1).

Breeding habitat. We expected hurricanes would positively affect the shrubland guild and negatively affect the woodland guild due to hurricane-induced
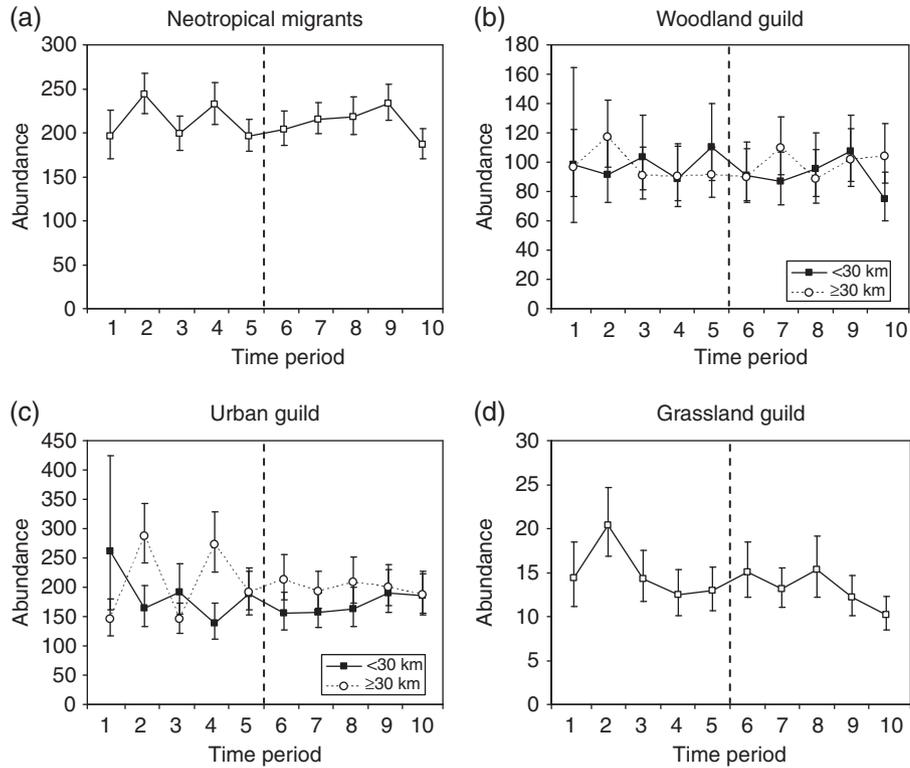
Fig. 3 Abundance for guilds with a significant effect of hurricane (a, d) or time (b, c). The hurricanes occured between the breeding seasons of years 5 and 6, indicated by the dashed vertical line.
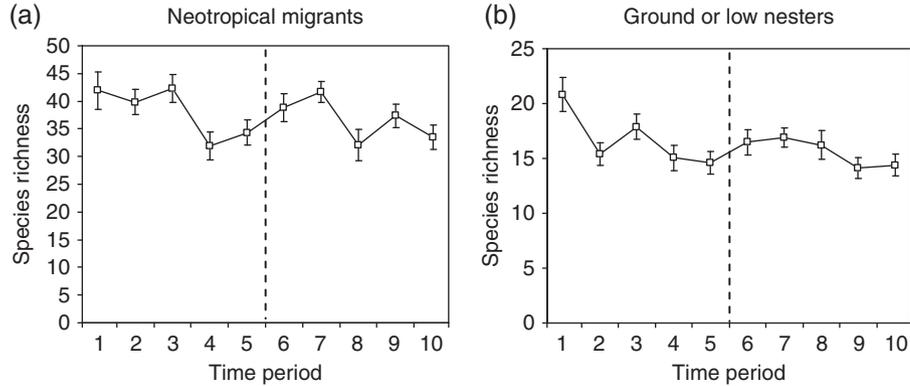
Fig. 4 Richness for guilds with significant effect of time (a, b). The hurricanes occured between the breeding seasons of years 5 and 6, indicated by the dashed vertical line.

changes in forest vegetation. Community similarity changes for the shrubland guild were statistically significant (Table 2) with a general trend of increasing similarity over time (Fig. 2d). Abundance of both woodland and urban guilds changed over time and with distance to hurricane track (i.e., a significant interaction term) (Table 2). Abundance of woodland species on routes within 30 km of the hurricane track declined by 20 individuals per route in the year

following the hurricane, but this was within the range of variation over the 10-year period we examined (Fig. 3b). Abundance of urban species varied by distance to hurricane track during the prehurricane periods yet was stable during the posthurricane periods with higher abundance on routes further from a hurricane (Fig. 3c). We found no clear effect of hurricanes on abundance of grassland species abundance despite a significant effect of time (Table 2). Grassland guild

abundance was significantly higher in Period 2 (mean abundance = 20.4, SE 4.3) than in Period 10 (mean abundance = 10.2, SE 2.1) (t-value = 3.76 on 106 df, $P = 0.0100$) and lower than the long-term average abundance for the period 1967–2005, indicative of a decline in grassland guild abundance over time for all routes (Fig. 3d, Table 1).

Nest type and nest location. We expected hurricanes would positively affect cavity-nesting species and ground- and low-nesting species, and negatively affect midstory and canopy-nesting species. We found no significant effects of hurricanes on cavity-nesting species. Community similarity for species nesting within 1 m of the ground varied over time and by distance to hurricane track (Table 2) with lower similarity in the first posthurricane breeding season on routes located farther from a hurricane track (Fig. 2e). Richness of birds that nest within 1 m of the ground decreased over time (Fig. 4b).

The broad-scale analysis included 171 routes within the eastern United States, 42 routes <30 km and 129 routes 30–185 km from a hurricane track, totaling 1236 route-year observations. We found effects of hurricanes (i.e., significant or marginally significant interaction term) on richness of all species as a group [$F(9, 988) = 2.55$, $P = 0.0068$], community similarity of grassland species [$F(9, 973) = 1.68$, $P = 0.089$], richness of urban species [$F(9, 987) = 2.04$, $P = 0.0326$], community similarity of open-cup nesting species [$F(9, 988) = 1.82$, $P = 0.0606$], and richness of species that nest on or near the ground [$F(9, 988) = 2.51$, $P = 0.0078$]. We also detected significant trends of declining abundance (i.e., significant effect of time) independent of hurricanes for grassland

species [$F(9, 973) = 10.69$, $P < 0.0001$], shrubland species [$F(9, 988) = 5.03$, $P < 0.0001$], woodland species [$F(9, 988) = 2.20$, $P = 0.0201$], open-cup nesting species [$F(9, 988) = 4.85$, $P < 0.0001$], and species that nest on or near the ground [$F(9, 988) = 9.65$, $P < 0.0001$].

Avian diversity, land cover, and vegetation productivity

Although hurricanes caused a threefold increase in the extent of disturbed forest within the focal areas (Fig. 5), this factor was associated with changes in community similarity for only three of the 13 avian groups we examined, and was not associated with patterns of avian abundance or species richness (Table 3). In fact,
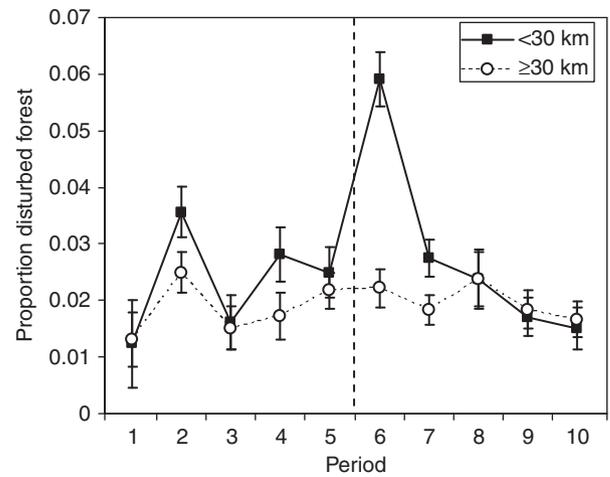
Fig. 5 Proportion of disturbed forest within a 1200 km² circular landscape surrounding Breeding Bird Survey routes, by distance to hurricane track for all focal areas. The increase in forest disturbance in Period 6 is due to hurricanes.

Table 3 Features within the 1200 km² circular landscape surrounding Breeding Bird Survey routes that affect avian guild response to hurricanes and the direction of the effect

| Effect | Community similarity | | | | | | Abundance | | | | Richness |
	All	Short distance	Shrub	Water	Ground	Canopy	Neotropical	Grass	Urban	Wood	All
Distance to hurricane <30 km					−						
Distance to coast					+					+	
Ecoregion			+		+	−			+		
Mean vegetation productivity	−	+	+	−	+			−	+		+
SD vegetation productivity	+			+		+	−	+			−
Nonforest		−		−	+	−		−	+	−	−
Forest			−					−			
Water			−					−	+		
Disturbed forest		−		+		−					
Postdisturbance forest	+		−	+							−
Postdisturbance nonforest	+		−	+							−

Only significant effects ($P < 0.05$) from the final model for each guild presented. Final models for neotropical migrant richness and ground- or low-nesting species richness not presented because time was the only significant effect.

no single factor besides time was associated with all guilds and measures of avian diversity, indicating that guild responses to hurricanes depended on local conditions. All factors were included in at least one final model, but the nature of the association, whether positive or negative, varied among guilds and among measures of diversity (Table 3; see supporting information Tables S2–S4 for estimated coefficients of all final models).

The most common factors in the final models were the proportion of nonforest and the mean vegetation productivity within route buffers (eight of 13 final models, Table 3). An increase in the proportion of nonforest within the circular landscape surrounding each route decreased avian community similarity, abundance, and richness in six of eight final models. The association of mean vegetation productivity with avian diversity was mixed; community similarity and abundance declined as productivity increased in three of eight cases and increased in five of eight cases (Table 3). In contrast, an increase in the variation of vegetation productivity increased community similarity and abundance in four of six cases. Distance to hurricane (one model), distance to coast (two models), and the proportion of forest within a route buffer (two models) were not very strongly associated with avian diversity patterns (Table 3).

Discussion

Hurricanes affected avian diversity in our analyses, but not in the manner that we expected them to. Numerous studies have documented hurricane-induced changes in avian richness and abundance at local scales (Askins & Ewert, 1991; Lynch, 1991; Waide, 1991; Wauer & Wunderle, 1992; Wunderle *et al.*, 1992; Wunderle, 1995; Tossas, 2006). Some of these studies also indicated that avian communities return to prehurricane levels of richness or abundance prior to the beginning of the next breeding season or shortly thereafter (Waide, 1991; Wauer & Wunderle, 1992). Here, we documented regional changes in avian diversity that persisted for up to 5 years after a hurricane. To our knowledge, this is the first study to quantify changes in avian diversity that extend beyond areas directly damaged by hurricanes and persist over multiple years.

The immediate posthurricane decrease in community similarity that we observed within the focal areas for all species as a group and for canopy nesters as a guild can be attributed to a decrease in abundance and an increase in richness that resulted in a shift in the proportional abundance among species (Fig. 2, supporting information Figs S1, S2). We attribute this decrease in community similarity to hurricane-induced changes in

forest habitat. Avian population sizes are reduced in areas with extensive and severe structural damage to forests (Wunderle *et al.*, 1992; Tossas, 2006). Hurricane-created gaps in closed canopy forest increase vertical structure, primary productivity, insect density, and fruit production, subsequently increasing avian richness (Greenberg & Lanham, 2001). We suggest hurricanes affect broad-scale changes in habitat, lowering carrying capacity and subsequently reducing abundance for some species, while simultaneously creating niches and opportunities for colonization by new species, thereby increasing richness. This explanation is consistent with theories of the relationships between disturbance and diversity. That is, periodic disturbance promotes diversity by decreasing population size and increasing environmental heterogeneity (Connell, 1978; Huston, 1979; Kondoh, 2001).

We expected hurricane disturbance would affect avian diversity, yet our results suggest that some avian guilds are resilient or resistant to hurricane disturbance (e.g., permanent residents, cavity nesters, and open cup nesters), whereas others are not (e.g., all species as a group, short-distance migrants, urban, woodland, species that nest in the canopy). Notably, the differences in guild response were not attributed solely to disturbed forest. The amount of nonforest, postdisturbance nonforest, and postdisturbance forest within a route buffer had significant, negative effects in more final models (10) than did disturbed forest (two final models). This suggests that hurricane-induced forest disturbance may have greater effects on avian diversity when coupled with recent, nonhurricane forest disturbance and conversion of previously disturbed forest to nonforest. A potential mechanism for these effects is the loss of refugia for birds displaced from hurricane-disturbed areas. In our focal areas, forest was the dominant land cover type. Other forest-focused studies (e.g., Flather & Sauer, 1996; Pidgeon *et al.*, 2007) found that avian abundance and richness are positively correlated with the amount of forest cover. High winds alter forest structure in a spatially heterogeneous manner with the pattern of disturbance dependent on tree position within the canopy, slope position and exposure, stand age, and tree species (Touliatos & Roth, 1971; Foster, 1988; Gresham *et al.*, 1991; Greenberg & McNab, 1998). Where persistent (undisturbed) forest exists in proximity to disturbed forest it may serve as a refugium for some species (e.g., canopy-dwelling species). However, as the proportion of forest on the landscape declines, the amount of forest that may serve as hurricane refugia declines as well. In this case, increasing the proportion of forest on landscapes may be a desirable strategy to mitigate the effects of hurricanes on avian diversity in systems where the expected natural vegetation is forest.

We also found differences in guild response to hurricanes within focal areas compared with the broad-scale analysis that included all BBS routes within 185 km of hurricane tracks. At the broad scale, hurricanes decreased community similarity of grassland birds on routes near hurricane tracks yet we were unable to detect this effect in the focal area analysis. Similarly, within the focal areas hurricanes decreased community similarity of all species as a group and midstory and canopy nesting species, yet we were unable to detect these effects in the broad-scale analysis. These differences in guild response by spatial extent of the analysis suggest that local landscape conditions, such as the area of forest or grassland, may mitigate or exacerbate the effects of hurricanes on bird communities. Unfortunately we lacked the corresponding land cover change information to fully investigate this hypothesis at the broad scale.

Studies that pair BBS data with remote sensing information offer an opportunity to investigate avian diversity, population trends, and habitat relationships at broad spatial and temporal scales (Boulinier *et al.*, 2001; Coppedge *et al.*, 2001; Donovan & Flather, 2002). Notably, there are well-known challenges and limitations to these broad scale studies. First, the effect of hurricanes on probability of detection of individuals and species are unknown. We observed effects of hurricanes on the two response variables, community similarity and abundance, that were not adjusted for detectability issues. Nondetection of species that are present can introduce bias, such as underestimation of species richness or abundance in communities with many rare species, and affect variance estimates (Thompson, 2002). Second, the number of BBS routes included in the analysis was constrained by the availability of remotely sensed information, which limits our inference of hurricane effects to those areas studied. Third, of the five hurricanes studied only one was a Category 4, all others were Category 2 or lower. We were unable to assess the effect of hurricane strength on avian communities although it may have an important effect on the magnitude and extent of avian response to hurricanes. Fourth, the forest change detection algorithm (Huang *et al.*, 2008) requires two consecutive 'nonforest' spectral values for a pixel in the time series to identify disturbance. In other words, a single season of defoliation was not classified as disturbance. The observed change in community similarity may be due to unmapped minor but widespread forest alteration due to hurricanes. Finally, the power of our analysis to detect an effect of hurricanes when an effect is present may be low due to the annual variation in avian communities over time due to nonhurricane factors (e.g., prehurricane Figs 3 and 4). Each of these issues could introduce bias or noise that obscures the signals evident in the data; however, we believe that is unlikely given that we observed a clear avifauna response across multiple hurricanes.

The posthurricane changes we observed in community similarity of all species as a group, and of midstory and canopy-nesting species, were due to subtle changes in richness and abundance. We identified several potential mechanisms for these changes in avian diversity, including hurricane-induced changes in forest habitat and the use of refugia by birds displaced from hurricane-damaged forests. Changes in community similarity persisted for up to 5 years after a hurricane. If the return interval for hurricanes reaches a frequency of 5 years or less, the shifts in community similarity that we observed may persist or community similarity may decrease further. However, our results suggest that the prospect of increasing frequency and intensity of hurricanes, while daunting for other societal reasons, are not likely to invoke a conservation crisis for birds provided we maintain sufficient mature forest habitat so that avifauna can respond to hurricanes by shifting locations to areas of suitable habitat.

References

Askins RA, Ewert DN (1991) Impact of Hurricane Hugo on bird populations on St. John, US Virgin Islands. *Biotropica*, **23**, 481–487.

Bailey RG (1995) *Description of the Ecoregions of the United States. Miscellaneous Publication Number 1391 (Revised)*. USDA Forest Service, Washington, DC.

Beaumont LJ, McAllan IAW, Hughes L (2006) A matter of timing: changes in the first date of arrival and last date of departure of Australian migratory birds. *Global Change Biology*, **12**, 1339–1354.

Both C, Visser ME (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, **411**, 296–298.

Boulinier T, Nichols JD, Hines JE, Sauer JR, Flather CH, Pollock KH (2001) Forest fragmentation and bird community dynamics: inference at regional scales. *Ecology*, **82**, 1159–1169.

Brokaw NVL, Walker LR (1991) Summary of the effects of Caribbean hurricanes on vegetation. *Biotropica*, **23**, 442–447.

Brommer JE (2004) The range margins of northern birds shift poleward. *Annales Zoologici Fennici*, **41**, 391–397.

Buckland ST, Magurran AE, Green RE, Fewster RM (2005) Monitoring change in biodiversity through composite indices. *Philosophical Transactions of the Royal Society B*, **360**, 243–254.

Butler JR, MacMynowski DP, Laurent C, Root TL (2007) Temperature-associated dynamics of songbird winter distributions and abundances. *Ambio*, **36**, 657–660.

Bystrak D (1981) The North American breeding bird survey. *Studies in Avian Biology*, **6**, 34–41.

Clobert J, Danchin E, Dhondt AA, Nichols JD, eds. (2001) *Dispersal*. Oxford University Press, Oxford, UK.

Collazo JA, White TH Jr, Vilella FJ, Guerrero SA (2003) Survival of captive-reared Hispaniolan parrots released in Parque Nacional Del Este, Dominican Republic. *Condor*, **105**, 198–207.

Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1310.

Cooke WH III, Grala K, Evans D, Collins C (2007) Assessment of pre- and post-Katrina fuel conditions as a component of fire potential modeling for southern Mississippi. *Journal of Forestry*, **105**, 389–397.

Coppedge BR, Engle DM, Masters RE, Gregory MS (2001) Avian response to landscape change in fragmented southern Great Plains grasslands. *Ecological Applications*, **11**, 47–59.

Dale VH, Joyce LA, McNulty S *et al.* (2001) Climate change and forest disturbances. *BioScience*, **51**, 723–734.

Donovan TM, Flather CH (2002) Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. *Ecological Applications*, **12**, 364–374.

Dunn PO, Winkler DW (1999) Climate change has affected the breeding date of tree swallows throughout North America. *Proceedings of the Royal Society B*, **266**, 2487–2490.

Kendall WL, Peterjohn BG, Sauer JR (1996) First-time observer effects in the North American breeding bird survey. *The Auk*, **113**, 823–829.

Flather CH, Sauer JR (1996) Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. *Ecology*, **77**, 28–35.

Foster DR (1988) Species and stand response to catastrophic wind in central New England, USA. *Journal of Ecology*, **76**, 135–151.

Goldenberg SB, Landsea CW, Mestas-Nunez AM, Gray WM (2001) The recent increase in Atlantic hurricane activity: causes and implications. *Science*, **293**, 474–479.

Greenberg CH, Lanham JD (2001) Breeding bird assemblages of hurricane-created gaps and adjacent closed canopy forest in the southern Appalachians. *Forest Ecology and Management*, **154**, 251–260.

Greenberg CH, McNab WH (1998) Forest disturbance in hurricane-related downbursts in the Appalachian mountains of North Carolina. *Forest Ecology and Management*, **104**, 179–191.

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behavior*, **28**, 1140–1162.

Gresham CA, Williams TM, Lipscomb DJ (1991) Hurricane Hugo wind damage to southeastern US coastal plain forest tree species. *Biotropica*, **23**, 420–426.

Hines JE, Boulinier T, Nichols JD, Sauer JR, Pollock KH (1999) COMDYN: software to study the dynamics of animal communities using a capture-recapture approach. *Bird Study*, **46** (Suppl.), S209–S217.

Hooper RG, Watson JC, Escano REF (1990) Hurricane Hugo's initial effects on red-cockaded woodpeckers in the Francis Marion National Forest. *Transactions of the 55th North American Wildlife and Natural Resources Conference*, **55**, 220–224.

Huang C, Goward SN, Masek JG *et al.* (2009a) Development of time series stacks of Landsat images for reconstructing forest disturbance history. *International Journal of Digital Earth*, **2**, 195–218.

Huang C, Goward SN, Schleeweis K, Thomas N, Masek JG, Zhu Z (2009b) Dynamics of National Forests assessed using the Landsat record: case studies in Eastern US. *Remote sensing of Environment*, **113**, 1430–1442.

Huang C, Song K, Kim S, Townshend JRG, Davis P, Masek JG, Goward SN (2008) Use of a dark object concept and support vector machines to automate forest cover change analysis. *Remote Sensing of Environment*, **112**, 970–985.

Huang C, Thomas N, Goward SN, Masek JG, Zhu Z, Townshend JRG, Vogelmann JE Automated masking of cloud and cloud shadow for forest change analysis. *International Journal of Remote Sensing*, in press.

Huston MA (1979) A general hypothesis of species diversity. *The American Naturalist*, **113**, 81–101.

Johnson DH (2008) In defense of indices: the case of bird surveys. *Journal of Wildlife Management*, **72**, 857–868.

Justice CO, Townshend JRG, Holben BN, Tucker CJ (1985) Analysis of the phenology of global vegetation using meteorological satellite data. *International Journal of Remote Sensing*, **6**, 1271–1318.

Kondoh M (2001) Unifying the relationships of species richness to productivity and disturbance. *Proceedings of the Royal Society B*, **268**, 269–271.

Kovacs JM, Wang J, Blanco-Correa M (2001) Mapping disturbances in a mangrove forest using multi-date Landsat TM imagery. *Environmental Management*, **27**, 763–776.

Kupfer JA, Myers AT, McLane SE, Melton GN (2008) Patterns of forest damage in a southern Mississippi landscape caused by Hurricane Katrina. *Ecosystems*, **11**, 45–60.

La Sorte FA, Thompson FR III (2007) Poleward shifts in winter ranges of North American birds. *Ecology*, **88**, 1803–1812.

Lynch JF (1991) Effects of Hurricane Gilbert on birds in a dry tropical forest in the Yucatan Peninsula. *Biotropica*, **23**, 488–496.

Marra PP, Francis CM, Mulvihill RS, Moore FR (2005) The influence of climate on the timing and rate of spring bird migration. *Oecologia*, **142**, 307–315.

Monohan WB, Hijmans RJ (2008) Ecophysiological constraints shape autumn migratory response to climate change in the North American Field Sparrow. *Biology Letters*, **4**, 595–598.

Peterjohn BG, Sauer JR (1999) Population status of North American grassland birds from the North American breeding bird survey, 1966–1996. In: *Ecology and Conservation of Grassland Birds of the Western Hemisphere* (eds Vickery PD, Herkert JR), pp. 27–44. Cooper Ornithological Society, Camarillo, CA.

Pidgeon AM, Radeloff VC, Flather CH, Lepczyk CA, Clayton MK, Hawbaker TJ, Hammer RB (2007) Associations of forest bird species richness with housing and landscape patterns across the USA. *Ecological Applications*, **17**, 1989–2010.

Ramsey EW III, Chappell DK, Baldwin DG (1997) AVHRR imagery used to identify hurricane damage in a forested wetland of Louisiana. *Photogrammetric Engineering and Remote Sensing*, **63**, 293–297.

Rappole JH (1995) *The Ecology of Migrant Birds*. Smithsonian Institute Press, Washington, DC.

Robbins CS, Bystrak D, Geissler PH (1986) *The Breeding Bird Survey: Its First Fifteen Years, 1965–1979. Resource Publication 157*. US Department of the Interior, Fish and Wildlife Service, Washington, DC.

Rodewald AD, Yahner RH (2001) Influence of landscape composition on avian community structure and associated mechanisms. *Ecology*, **82**, 3493–3504.

Royer J-F, Chauvin F, Timbal B, Araspin P, Grimal D (1998) A GCM study of the impact of greenhouse gas increase on the frequency of occurrence of tropical cyclones. *Climatic Change*, **38**, 307–343.

Sauer JR, Fallon J (2008) *The North American Breeding Bird Survey, Results and Analysis 1966–2007*. USGS Patuxent Wildlife Research Center, Laurel, MD. Available at http://www.mbr-pwrc.usgs.gov/bbs/bbs.html

Schmiegelow FKA, Machtans CS, Hannon SJ (1997) Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. *Ecology*, **78**, 1914–1932.

Sekercioglu CH, Schneider SH, Fay JP, Loarie SR (2008) Climate change, elevational range shifts, and bird extinctions. *Conservation Biology*, **22**, 140–150.

Sutherland GD, Harestad AS, Price K, Lertzman KP (2000) Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation*

Ecology, **4**. Available at http://www.ecologyandsociety.org/vol4/iss1/art16/

Tejeda-Cruz C, Sutherland WJ (2005) Cloud forest bird responses to unusually severe storm damage. *Biotropica*, **37**, 88–95.

Thomas CD, Lennon JJ (1999) Birds extend their ranges northwards. *Nature*, **399**, 213.

Thompson WL (2002) Towards reliable bird surveys: accounting for individuals present but not detected. *The Auk*, **119**, 18–25.

Thorup K, Tottrup AP, Rahbek C (2007) Patterns of phenological changes in migratory birds. *Oecologia*, **151**, 697–703.

Tossas AG (2006) Effects of Hurricane Georges on the resident avifauna of Maricao State Forest, Puerto Rico. *Caribbean Journal of Science*, **42**, 81–87.

Touliatos P, Roth E (1971) Hurricanes and trees: ten lessons from Camille. *Journal of Forestry*, **69**, 285–289.

Tucker CJ (1979) Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sensing of Environment*, **8**, 127–150.

Turchin P (1998) *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sinauer Associates, Sutherland, MA.

Waide RB (1991) The effect of Hurricane Hugo on bird populations in the Luquillo experimental forest, Puerto Rico. *Biotropica*, **23**, 475–480.

Wauer RH, Wunderle JM Jr (1992) The effect of Hurricane Hugo on bird populations on St. Croix, US Virgin Islands. *Wilson Bulletin*, **104**, 656–673.

Webster PJ, Holland GJ, Curry JA, Chang H-R (2005) Changes in tropical cyclone number, duration, and intensity in a warming environment. *Science*, **309**, 1844–1846.

Wiley JW, Wunderle JM Jr (1993) The effects of hurricanes on birds, with special reference to Caribbean islands. *Bird Conservation International*, **3**, 319–349.

Wolfinger RD (1993) Covariance structure and selection in general mixed models. *Communications in Statistics, Simulation, and Computation*, **22**, 1079–1106.

Wolfinger RD (1996) Heterogeneous variance-covariance structures for repeated measures. *Journal of Agricultural, Biological, and Environmental Statistics*, **1**, 205–230.

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

Wunderle JM Jr, Lodge DJ, Waide RB (1992) Short-term effects of Hurricane Gilbert on terrestrial bird populations on Jamaica. *The Auk*, **109**, 148–166.

Yue JC, Clayton MK (2005) A similarity measure based on species proportions. *Communications in Statistics – Theory and Methods*, **34**, 2123–2131.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Changes in richness and abundance for all species and all focal areas combined. (A) Period 5 (light gray, $n = 23$ routes), (B) Period 6 (medium gray, $n = 21$ routes), and (C) Period 7 (dark gray, $n = 24$ routes) presented. These periods correspond to the 'V' in the community similarity in Figure 2a.

Figure S2. Changes in species richness and abundance for mid-story and canopy-nesting species for all focal areas combined. (A) Period 5 (light gray, $n = 23$ routes), (B) Period 6 (medium gray, $n = 21$ routes), and (C) Period 7 (dark gray, $n = 24$ routes) presented. These periods correspond to the 'V' in the community similarity in Figure 2b.

Table S1. Classification of species by guilds. Habitat type guilds are not mutually exclusive.

Table S2. Estimated coefficients and SE for final models of richness.

Table S3. Estimated coefficients and SE for final models of abundance.

Table S4. Estimated coefficients and SE for final models of community similarity.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.